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Influence of prey densities in the distribution and breeding success of Bonelli's eagle (*Hieraaetus fasciatus*): management implications

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Abstract

Diet, prey availability, and breeding success were studied in a population of Bonelli's eagle (*Hieraaetus fasciatus*) in the province of Granada, SE Spain. The densities of the main prey species, European wild rabbit (*Oryctolagus cuniculus*), red-legged partridge (*Alectoris rufa*), wood pigeon (*Columba palumbus*), and rock dove (*Columba livia*), representing 90.2% of the biomass, were analysed in 19 territories occupied by pairs of Bonelli's eagles and 15 potential territories that were unoccupied but appropriate for nesting. We found no significant differences in prey density between the two types of territories. Contrary to other raptor species, we found no significant relationship between the density of their main prey species and the distance of the neighbouring pairs, either between that density and breeding success. These findings, together with the prior knowledge of nest-site selection of this eagle in the study area, can be used for proper planning of conservation strategies. These should avoid unnecessary effort to increase the eagle's food supply, and should promote the reintroduction of individuals to suitable sites for Bonelli's eagle.

Keywords: *Hieraaetus fasciatus*; Prey availability; Breeding density; Breeding success

1. Introduction

For most raptors, breeding density is limited by the availability of appropriate nesting sites (Newton, 1979), and food supply (Gargett, 1975; Newton et al., 1977; Donázar and Ceballos, 1989; Donázar et al., 1993). Differential reproductive success among habitats corresponding to variations in prey density has also been reported in different raptor species (Janes, 1985).

Bonelli's eagle (*Hieraaetus fasciatus*) is an endangered European raptor (Rocamora, 1994), and population declines have been confirmed in numerous European countries (Cugnase, 1984; Palma et al., 1984; Hallmann, 1985; Arroyo et al., 1995). This eagle, which has a highly disjunct global distribution (Cramp and Simmons, 1980), is a very scarce European species, and 80% of the European population is located in Spain (Real et al., 1997). In this country the nesting population has declined by 25% during the period 1980–1990 (Arroyo et al., 1995).

Reviews of dietary studies of Bonelli's eagle show a great variability in prey, depending on the habitat occupied and the available prey species (Cheylan, 1977; Simeon and Wilhelm, 1988). In the Iberian Peninsula, the European wild rabbit (*Oryctolagus cuniculus*), the red-legged partridge (*Alectoris rufa*), and pigeons (*Columba* spp.), are the main prey species (García, 1976; Jordano, 1981; Real, 1987; Gil-Sánchez et al., 1994), together representing most of the consumed biomass during the breeding season (Real, 1987). Despite agreement between studies on diet, conclusions regarding the influence of food supply in the ecology of the Bonelli's eagle are contradictory. Simeon and Wilhelm (1988) suggest that a shortage in prey does not influence reproductive success, and that food plays little part in the decline of this species. For other authors, the low productivity is related to a decrease in main prey species (Cheylan, 1981; Cugnase, 1984; Real, 1987). Although no study has examined the influence of prey abundance on the distribution and breeding success of this eagle, conflicting conservation measures have been proposed concerning the increase of prey availability in some Bonelli's eagle populations (Blanco and González, 1992; Fernández et al., 1993; Real and Mañosa, 1997).

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Here we present data on Bonelli's eagle diet, the densities of its main prey species, and breeding success in the southeastern Iberian Peninsula, in order to determine whether prey availability limits the distribution and breeding performances of the species. This information is important for the proper planning of conservation strategies.

2. Methods

2.1. Study area

A population of 19 neighbouring Bonelli's eagle pairs was studied in the province of Granada, southeastern Spain, during 1994–1998. The region is largely mountainous, with the greatest altitude range of the Iberian Peninsula (0–3482 m a.s.l.) although, in the study area, the population ranges between 570 and 1490 m a.s.l. The climate is typically Mediterranean, with mean minimum temperatures ranging from 0.5 to 6.5°C in winter (January), mean maximum temperatures from 28 to 34.5°C in summer (July), and mean annual rainfall from 375 to 850 mm (30-years standard meteorological average; Font, 1983). The vegetation consists of evergreen oak (*Quercus rotundifolia*), scrub and some pine (*Pinus* spp.) mixed with cultivated areas of cereals and trees in the foothills, plains and valleys.

2.2. Diet

The diet of seven selected pairs of eagles was analysed in the breeding season (February–May) during two consecutive years (1997–1998). For dietary analysis, some authors recommend the exclusive use of pellets rather than uneaten remains to avoid overestimating birds (Real, 1996), as the legs and feathers of bird are easier to find than the remains of mammals and reptiles. Nevertheless, other studies argue that larger prey tend to appear with greater frequency in pellets, because several pellets can contain scraps of the same individual prey (Rosenberg and Cooper, 1990). Finally, some authors recommend the combined use of both pellets and remains (Watson et al., 1992a; Oró and Tella, 1995). We followed this third option collecting under nests and perches, and estimating the biomass of each prey from published data (for birds: Cramp and Simmons, 1980; Cramp, 1985–1992; Cramp and Perrins, 1994), and original data from our study area for reptiles and mammals. For rabbits we assigned weight means according to three size categories (250, 750 and 1250 g) proposed by Donázar and Ceballos (1989), including in the middle category those remains that did not allow an estimate of individual size. Food diversity was calculated with the Shannon-Weaber (1963) index.

2.3. Prey availability and eagle territories

To determine the influence of prey availability on the distribution of the Bonelli's eagle, we studied the abundance of the main prey species (rabbits, partridges and pigeons) in up to 19 randomly selected occupied territories and 15 unoccupied territories (potential territories without previous known occupation), from a clumped population in the study area of 34 occupied territories and c. 20–30 unoccupied territories. As usual among birds of temperate areas, most raptors breed during only part of the year, when food is most readily available (Newton, 1979). Thus, densities of the main prey species of the Bonelli's eagle were studied in the breeding season in occupied and unoccupied territories of the population. This comparison has been possible because in the province of Granada the nesting cliffs do not appear to be limiting, and the population of Bonelli's eagle has remained stable since 1980 (Arroyo et al., 1995). Three apparently abandoned territories were not included in the analysis as unoccupied ones because we know that human disturbance (shooting, road construction) caused the abandonment (Ontiveros, 1997). The size of an occupied territory was taken to be a circle of radius equal to half the average distance between nests of the neighbouring pairs (Gilmer and Stewart, 1984; Rich, 1986; González et al., 1992). The size of unoccupied territories was calculated in the same way.

The unoccupied territories were located on maps 1:50000 of the Cartographic Service of the Spanish Army, using co-ordinates selected at random. In Spain, Bonelli's eagle nests most frequently in cliffs and rarely in trees (Arroyo et al., 1995). Therefore, we excluded unoccupied territories that lacked appropriate nesting cliffs. Appropriate nesting cliffs had to satisfy the following conditions: being higher than 20 m, having cavities or ledges, located below 1500 m a.s.l. (altitudinal distribution limit of the Spanish population; Arroyo et al., 1995), being >500 m from an urban centre, being separated by a minimum of 5.8 km from the closest occupied nest of Bonelli's eagle (minimum distances found in the study area), and at least 2.2 km from the closest occupied nest of the golden eagle (*Aquila chrysaetos*) to avoid the effect of possible competition (Fernández and Insausti, 1990).

Line transects were used to provide an index of prey abundance in each territory (Watson et al., 1992b). This method is effective for comparing the densities of abundant species between different zones and periods (Tellería, 1986), and to determine abundance of prey species of raptors (Fitzner et al., 1977), being less difficult to perform than absolute density methods, and equally useful (Caughley, 1977). Diurnal surveys have proved useful for censusing rabbits in Spain, where this prey species is abundant (Soriguer et al., 1997; Serrano, 1998). Although primarily nocturnal, rabbits also show

substantial diurnal activity (Soriguer, 1981, Moreno et al., 1996); thus, we deemed the diurnal rabbit census to be a more realistic estimate of prey availability for a strictly diurnal raptor such as Bonelli's eagle.

One census a year was taken along a 5-km stretch in each territory. They were taken in different zones in 1997 and 1998 to provide independent data, but possible spatial correlation was investigated in an analysis of variance model that treated year as repeated measures. As recommended by Tellería (1986), the censuses were performed by an observer on foot, between 0600 and 0930 h, on days of good visibility, walking at a speed of 1.5–2.0 km/h, during the period February–April. Censuses during May were avoided, when demographic explosions of rabbits occur in the Mediterranean area (Cheylan, 1977; Soriguer, 1981).

Habitat influences prey abundance, and the structure of the vegetation may also influence prey capture as well as prey detection (Janes, 1985); therefore, the length of the censuses was distributed proportionally over the surface area of the habitats in each territory (Caughley, 1977). Prey abundance was measured recording all main prey species in each transect as the mean for individuals per kilometre of census.

2.4. Breeding density and breeding success

We studied the relationships between breeding density and breeding performance of the Bonelli's eagle pairs with the availability of their main prey in territories. The distance from the most frequently used nest of a breeding pair to the nearest nest belonging to another pair (from a matrix of 19×19 cases), was used as inverse measure of breeding density (Donázar et al., 1993). When two nests were closer to one another than either was to a third (3 out of 19 nests) we avoided the same measure being used twice by using the second nearest nest distance. To evaluate breeding success, we used the average productivity for each pair, defined as the number of fledglings raised per number of years monitored (Donázar et al., 1993). Productivity values were available for the 19 breeding pairs of this study for five years (1994–1998). Because of the high availability of nesting cliffs in the area, and the difficulty of observations in some rugged territories, we excluded from analysis dubious cases of reproduction failure (9 out 95 cases).

3. Results

There was no difference in captured-prey frequency between the samples from 1997 and 1998 (prey items captured in only one year pooled as "other prey"; $G = 11.36$, 7 df, $p = 0.12$), and therefore, the data from both years were grouped for analysis.

Eighteen different prey species were detected in the diet of Bonelli's eagle, and diet diversity was rather low, $H = 1.83$. The European wild rabbit, the red-legged partridge, the wood pigeon, and the rock dove were the main prey, with 83.3% of the frequency and 90.2% of biomass (Table 1). Thus, we censused only these four prey species for calculating prey availability in each territory. The total number of these main prey species recorded per kilometre of census stabilised consistently after 6–8 km (Fig. 1). Therefore, we can consider the sample size sufficient to assure the precision of results in each territory (Tellería, 1986).

Table 2 shows the abundance values of the main prey species of the Bonelli's eagle for occupied and unoccupied territories. The values of the standard deviation approached or exceeded the mean values, suggesting very variable prey abundance when all 19 occupied territories were considered (Fig. 1). After Bonferroni sequential correction (Rice, 1989), no significant differences appeared for any of these prey species, although the greater abundance of partridges in the occupied territories was nearly significant. When the abundance of main prey species were pooled, we also failed to find significant differences between occupied and unoccupied territories, treating year as repeated measures (RMANOVA, $F = 3.99, p = 0.06$), or between year (RMANOVA, $F = 0.027, p = 0.87$), and no significant interaction was found between year and occupancy of territories (RMANOVA, $F = 2.38, p = 0.13$).

The breeding success for the study population during the 1994–1998 period was 1.42 ± 0.38 fledglings per year ($n = 19$). The mean distance between neighbouring pairs (inverse measure of breeding density) was 10.06 ± 3.25 km (range = 5.8–16 km; $n = 19$; Fig. 2). Neither the breeding density, nor the breeding success was related to the abundance of main prey in the territories, even when the four main prey species were pooled in the analysis (Table 3; Fig. 2).

4. Discussion

The present analysis of the Bonelli's eagle diet shows low diversity during the breeding season, when compared with the same parameter in other regions of the Western Mediterranean (southeastern France: $H = 2.06$, Clouet and Goar, 1984; northeastern Spain: $H = 2.13$, Real, 1987). This is probably due to the lower richness in prey species in the study area (only Mediterranean species) when compared with the other two northernmost regions (where Mediterranean and Eurosiberian species meet; Gasc, 1997; Hagemeijer and Blair, 1997). Although rabbits are the basic prey for other Mediterranean raptors (Delibes and Hiraldo, 1981), our results emphasise the greater importance of birds for

Bonelli's eagle, as has also been found in other studies of this species (Clouet and Goar, 1984; Real, 1987).

The breeding season of the Bonelli's eagle is the earliest among all the Mediterranean eagles, with most of the young leaving the nest in May (Arroyo et al., 1995). During the breeding season (February–May) the abundance of rabbits in the territories appears to decrease (Cramp and Simmons, 1980), but it increases sixfold from May onwards in the Mediterranean area (Cheylan, 1977; Cramp and Simmons, 1980; Soriguer, 1981). Consequently, the frequency of rabbits in the diet of this raptor is low in the breeding season (4.7%: Suetens and Groenendael, 1969; 37.2%: García, 1976; 9.6%: Clouet and Goar, 1984; 23.6%: Real, 1987; 35.9%: this study), compared with year-round data (41.4%: Jordano, 1981; 39.8%: Gil-Sánchez et al., 1994). This rabbit shortage during the breeding season is offset by a greater presence of birds in the diet (81.3%: Suetens and Groenendael, 1969; 40.1%: García, 1976; 49.5%: Real, 1987; 59.3%: this study) with respect to other large eagles.

Our results on rabbit densities are similar to those made with line transects in winter and spring in ecologically similar zones by Serrano (1998). This supports the view that rabbit abundance is low in the breeding season, and that Bonelli's eagle territories are not based on the abundance of this prey species (Table 2). Partridges are the most frequent bird in the diet and tended to be more abundant in occupied than in unoccupied eagle territories (Table 2), which suggests that, in this zone, they replace rabbits as prey during the nestling period.

The diet of the Bonelli's eagle is adapted to taking the most abundant prey available in each region (Cramp and Simmons, 1980). This eagle can even raise nestlings almost without rabbits as prey (Simeon and Wilhelm, 1988), and can radically modify the diet according to the season (Cheylan, 1977). Such adaptability is possible because of the special wing morphology of the eagle, which has a low aspect ratio compared with other large raptors (Parellada et al., 1984), making it agile and swift in flight (Janes, 1985). This also accounts for the pronounced variability in prey abundance among occupied territories (Fig. 1), and for the fact that Bonelli's eagles can maintain its breeding performance regardless of main prey availability (Table 3).

The proximity of the pairs was not determined by the abundance of their main prey species, in contrast to other raptor species that have a clear relationship between the food and breeding density (Galushin, 1971;

Table 1
Dietary composition of Bonelli's eagle in the province of Granada (SE Spain) over the breeding season

Prey	F[a]	$\%F$[b]	$\%B$[c]
Mammalia	72	37.50	53.75
Oryctolagus cuniculus	69	35.94	46.55
Lepus granatensis	3	1.56	7.20
Aves	114	59.38	45.55
Alectoris rufa	58	30.21	29.41
Columba palumbus	22	11.46	11.10
Columba livia	11	5.73	3.09
Falco tinnunculus	2	1.04	0.54
Apus apus	2	1.04	0.09
Clamator glandarius	1	0.52	0.16
Prunella modularis	1	0.52	0.02
Sturnus unicolor	1	0.52	0.09
Emberiza spp.	1	0.52	0.02
Pica pica	1	0.52	0.23
Corvus monedula	1	0.52	0.25
Corvus spp.	1	0.52	0.43
Unidentified paserines	6	3.13	0.11
Unidentified birds	6	3.13	
Reptilia	6	3.12	0.70
Lacerta lepida	4	2.08	0.45
Coluber hippocrepis	2	1.04	0.25
Total	192		

[a] F = frequency of prey.
[b] $\%F$ = percentage frequency.
[c] $\%B$ = percentage biomass.

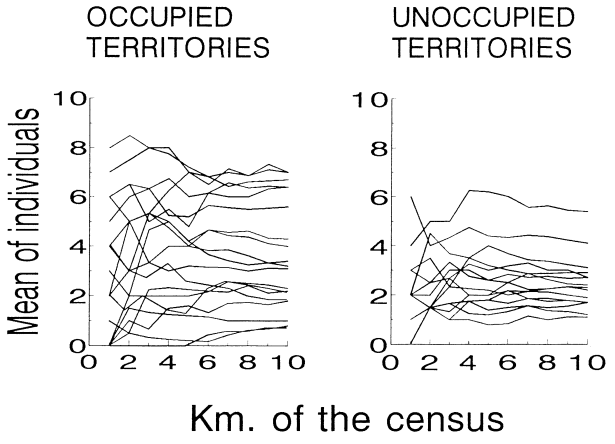

Fig. 1. Mean number of observed individuals of the prey species per unit of line transect (1 km) according to sample size.

Table 2
Comparative abundance (individuals/km) on the main prey species of the Bonelli's eagle between occupied and unoccupied (potential) territories in Granada (SE Spain)[a]

	Occupied territories ($n=19$) $\bar{x} \pm SD$	Unoccupied territories ($n=15$) $\bar{x} \pm SD$	Z	p	p^*[b]
Oryctolagus cuniculus	0.21 ± 0.29	0.26 ± 0.31	-0.88	0.37	n.s.
Alectoris rufa	2.05 ± 1.31	1.04 ± 0.75	-2.39	0.016	n.s.
Columba palumbus	0.93 ± 0.76	0.70 ± 0.57	-0.71	0.47	n.s.
Columba livia	0.54 ± 0.83	0.41 ± 0.31	-1.21	0.25	n.s

[a] The values are compared with Mann–Whitney U test.
[b] p^* = significance corrected with post-hoc Bonferroni sequential adjustments.

Gargett, 1975; Newton et al., 1977; Watson et al., 1992b). This would be also explained by their unspecialised diet, because in raptors with a wide range of prey species, habitat selection is less specifically tied to the abundance of prey (Janes, 1985).

In summary, (1) rabbits, partridges and pigeons were the main prey species in the diet of Bonelli's eagle in the study area; (2) the availability of these prey differed markedly among occupied territories; (3) occupied and unoccupied territories did not differ in the abundance of these prey; and (4) the breeding density and breeding performances were independent of the abundance of the main prey species. Thus, given the eclectic diet of this raptor, there is no reason to suspect that the abundance of the main prey limits its distribution, abundance, or productivity. The main prey are largely taken because of their greater abundance in the area. Although, therefore, the Spanish populations of golden and Spanish imperial eagles depend basically on rabbits for food, and despite periodic decreases due to myxomatosis, these raptors are now in recovery (Arroyo et al., 1990; Ferrer, 1993). However, Bonelli's eagle (a less rabbit-dependent species) is currently declining sharply in population (Rocamora, 1994; Arroyo et al., 1995; Real et al., 1997).

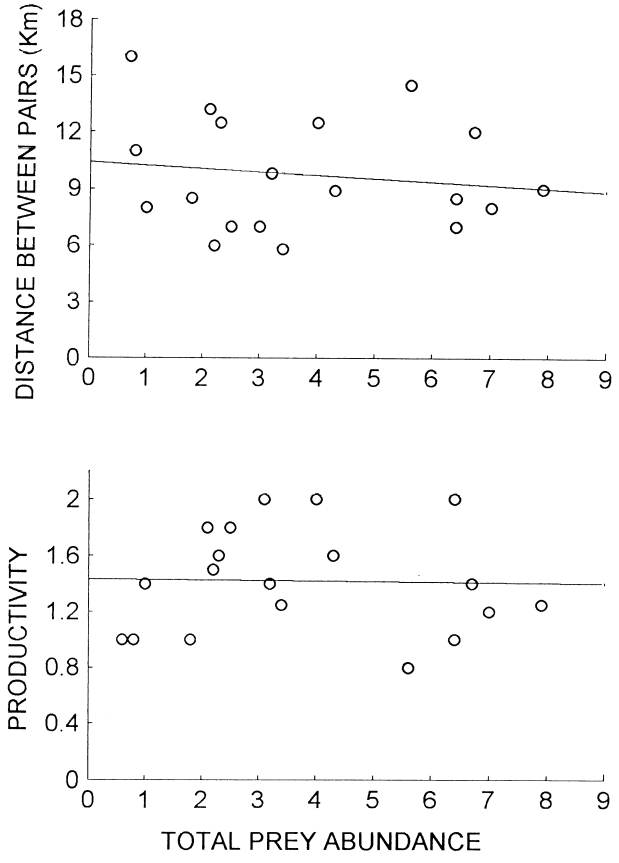

Fig. 2. Relationship between main prey abundance (kilometric index of abundance; rabbits, partridges and pigeons grouped) in territories of Bonelli's eagle, and the distance between the nearest neighbouring pairs (inverse measure of breeding density), and the productivity (average number of fledglings raised per year), in the province of Granada (SE Spain).

According to our data, factors other than prey shortage appear to be more directly related to the decrease of the populations of this raptor (see also Simeon and Wilhelm, 1988), such as human disturbance in territories. Three out of four fledglings radio-tracked in the study area during 1996 and 1997 died by shooting within 60 days (Ontiveros, unpub. data). Data from the Raptor Rehabilitation Center (RRC) "Las Mimbres" (Consejería de Medio Ambiente, Andalusia) also indicate that shooting is the main cause of mortality, with 25 injured Bonelli's eagles (8 adults and 17 juveniles) from 1985 to 1996 in the study area, and a very low survival rate in the reintroduced specimens of this eagle (F. Aranda, pers. comm.). In their review on the survival rate of different species from RRC reintroduced in the field in Spain, Asensio and Barbosa (1990) depict a hopeless panorama. A further cause of mortality is electrocution by power lines (Real and Mañosa, 1997). In our study area, nest-site availability is not a limiting factor for the species, given that we found at least 15 unoccupied territories, although we suspect that the high mortality between fledgling and adulthood precludes their occupation.

Some authors have proposed measures to increase prey availability for conservation of Bonelli's eagle (Blanco and González, 1992; Fernández et al., 1993; Real and Mañosa, 1997), but if, as our results suggest, prey availability is not the factor limiting its distribution and breeding, it would seem that the main problem is its high mortality, which has resulted in 116 abandoned territories in Spain from 1980 to 1990 (Arroyo et al., 1995). Rather, its recovery would benefit from informing the public, and especially hunters, on the conservational crisis of this eagle. Additional benefit would come from the design of an adequate programme of reintroduction to abandoned or unoccupied territories with individuals coming from RRC. This latter programme should consider (1) the importance of the availability of

Table 3
Correlation values between the abundance of main prey species in the Bonelli's eagle territories (mean numbers of individuals/km of census) and (1) the distance of the nearest pair (inverse measure of breeding density) and (2) to the average number of fledglings raised per year (productivity)

Prey abundance	Breeding density		Productivity	
	r	*p*	*r*	*p*
Oryctolagus cuniculus	−0.07[a]	0.76	−0.04[a]	0.86
Alectoris rufa	−0.22	0.35	−0.17	0.49
Columba palumbus	−0.21	0.38	−0.05	0.83
Columba livia	−0.19	0.44	−0.16	0.51
Main prey pooled	−0.26	0.28	−0.02	0.92

[a] Spearman rank correlation.

suitable nesting cliffs in territories (Ontiveros, 1999), (2) territories without dangerous power lines (Bevanger, 1994), and (3) the importance of avoiding dispersal from suitable territories (when higher mortality occurs) of released individuals. The last can be achieved by proper techniques which enable raptors to became established in a given area (Cade, 1974), or by liberating young to achieve independence on their own through "hacking back" technique (Newton, 1979), thereby minimising mortality.

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