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Prey density, prey detectability and food habits: the case of Bonelli's eagle and the conservation measures

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Abstract

In the diet of raptors the presence of prey-species is influenced by their abundance and the ground-level vegetation in territories, this situation being analysed for the Bonelli's eagle (*Hieraaetus fasciatus*) in south-eastern Spain. First, the minimum number of prey-items for the reliability of results was tested, obtaining between 15 and 30 prey-items depending of pair. Second, differences in prey frequency and productivity among pairs was analysed, finding an interpair shift in both variables, but there was no relationship between the frequency of prey-species in the diet and productivity. Third, it was found that the percentage of European wild rabbit in the diet was less correlated with its abundance in territories than with the surface of open land in the same. This suggests that accessibility to rabbits would be more important for the Bonelli's eagle that the absolute abundance of this prey type. Thus, open land is the single variable selected by a multiple multiple-regression analysis explaining the frequency of rabbits in this raptor's diet. Birds as prey complemented the diet when open-land scarcity in the territories implies low rabbit detectability and consumption. Conservation measures proposed concerning the increase of prey availability in this declining population should consider both the absolute prey density and prey detectability, avoiding extensive reforestation in territories and favouring vegetation structure suitable for prey detection by eagles.

Keywords: Bonelli's eagle; Conservation measures; Prey detectability; European wild rabbit; Southern Spain

1. Introduction

One of the principal functions of territoriality in non-colonial birds, especially raptors, is to supply adequate resources, usually food and nest-site (Cody, 1985; Newton, 1997). Many studies have investigated the food habits of Palearctic raptors (Cramp and Simmons, 1980), some revealing differences among seasons (Watson et al., 1992; Mañosa, 1994), biases in methods used to study the diet (Marti, 1987; Real, 1996), and differential reproductive success among habitats corresponding to variations in prey densities (Newton, 1997; Janes, 1985). Nevertheless, few studies have included tests to evaluate biases involved in a scarce number of prey items in the analysis, or the relationships between prey density, prey detectability and food habits (but see Jaksic and Soriguer, 1981; Janes, 1985).

Food availability is one of the most important factors influencing the quality of raptor habitats, which is determined not only by prey density, but also by the accessibility to prey by predators (Widen, 1994). While absolute food abundance may certainly be of great importance, various habitat features may affect either accessibility of food or the time and energy expended in securing it. In this way, ground-level vegetation can affect the ability to detect prey and hence may influence the success of particular foraging behaviours (Bechard, 1982; Janes, 1985). This is the reason why prey accessibility has been proposed to be more important to

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reproductive success than absolute prey density (Janes, 1984). As a consequence, some authors emphasized the importance of analysis of resources of raptors (Rosenberg and Cooper, 1990), although in studies of avian foraging difficulties invariably arise in measuring resource availability (Smith and Rotenberry, 1990).

Among Mediterranean raptors, Bonelli's eagle (*Hieraaetus fasciatus*) is suffering one of the most severe population declines (Rocamora, 1994). This eagle has a highly disjointed global distribution (Cramp and Simmons, 1980), 80% of the European population being 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). In Andalusia (Southern Spain), the last stronghold of the Bonelli's eagle (Balbontín et al., 2003), we have previously found that absolute prey density in territories does not affect the distribution and breeding success of the eagle (Ontiveros and Pleguezuelos, 2000). Nevertheless there are no studies available analysing either the influence of prey detectability or diet composition in the breeding success of pairs, such information being crucial in the designing of conservation measures concerning the increase of prey densities for the Bonelli's eagle.

In this study, we analyse the minimum number of prey items per territory necessary for a reliable dietary analysis, prey density, and prey detectability (through habitat features), and their relationship to the breeding success of Bonelli's eagle.

2. Study area and methods

The study was conducted in eastern Andalusia (2°40′–4°13′ W; 36°45′–37°49′ N) a largely mountainous region, although pairs here considered are located in a rather clumped population (52 km for the most distant pairs), nesting between 800 and 1400 masl. The climate in the territories of this population is Mediterranean, with mean annual temperatures ranging between 13.3 and 16.9 °C and annual rainfall between 351 and 639 mm (30-year standard meteorological averages) and typical Mediterranean vegetation (Rivas-Martínez, 1985).

For the present analysis, we selected eight Bonelli's eagle pairs from which we obtained a high number of prey items for the dietary analysis; the difficulty of collecting many prey items in the mountainous territories of Bonelli's eagle, prevented a larger sample size for the number of pairs. The diet of the pairs was analysed in the breeding season (February–June) during the 1997–1998 period. For dietary analysis, we used pellets and remains to avoid underestimating mammals and reptiles and overestimating birds (Oró and Tella, 1995; Ontiveros and Pleguezuelos, 2000).

Line transects were used to provide an index of relative prey density in each territory. This method has proven effective to determine prey-species abundance of raptors, and to compare the densities of abundant species between different zones (Fitzner et al., 1977), being less difficult to perform than absolute-density methods, and equally useful (Caughley, 1977). Prey density was measured as the mean of individuals per km of census. Because of methodological constraints, we analysed only the abundance of the main prey species of the Bonelli's eagle in the study area (rabbits, partridges and pigeons) representing 90.2% of the diet of the eagle in terms of biomass (Ontiveros and Pleguezuelos, 2000).

One census per year was taken along a 5-km stretch each, during two consecutive years (1997 and 1998), in different zones within territories (providing the independence of the data), and grouping main prey species in a single census, which is advantageous in enabling greater precision in data over time (Watson et al., 1992; Guix et al., 1997).

The length of the censuses was distributed proportionally over the surface of the habitats in each territory (Caughley, 1977). The censuses were performed by an observer on foot, between 06.00 and 09.30 h., on days of good visibility, walking at a speed of 1.5–2.0 km/h (Bibby et al., 2000), during the period February–April. Censuses during May were avoided, when demographic explosions of rabbits occur in the Mediterranean area (Soriguer, 1981). Line transect is the most accurate method for censuring rabbits (Palomares, 2001), and diurnal censuses proved to be useful (Soriguer et al., 1997; Serrano, 1998; Palomares et al., 2001), since this prey-species, although primarily nocturnal, also shows substantial diurnal activity (Soriguer and Rogers, 1981; Moreno et al., 1996); thus, we deemed the diurnal rabbit census to be a more realistic estimate of prey density for a strictly diurnal raptor such as Bonelli's eagle.

The same territory shape and size for each pair was considered, circular and with a radius equal to half the average distance between nests of neighbouring pairs in a clumped population (5.0 ± 1.2 km; mean ± SD), according to previous data for this region (Ontiveros, 1999). In accordance with field observations of the authors, hunting areas detected for the eight pairs were included in this territory surface area. No territories overlapped in the population considered.

Different habitat features can influence the detectability of prey by raptors, such as the number and dispersion of perches, the presence of cliffs, and the ground-level vegetation (Janes, 1985). Nevertheless, the area occupied by Bonelli's eagle in the study area is largely mountainous, with a great abundance of cliffs and perches. Therefore, we tested the prey detectability through the low opportunity to conceal – that is, the amount of open lands in the territory, including grasslands, cereals crops, olive orchards, and scrublands (except dense scrubs of evergreen oak). In the semiarid study area, grasslands, low-height scrub and cereal crops, are not high and dense

enough to conceal rabbits and partridges during the census period (February–April). All forests and maquis scrub were considered closed land.

To measure ground-level vegetation we used Geographic Information System (GIS), 1:10,000 with one meter resolution (flights performed during 1998–1999), prepared by the regional government, and executed with the ARCVIEW GIS 3.1 program.

We have data on the reproduction of the pairs for the 1994–2002 period, and we used the average productivity (number of fledglings raised per number of years monitored) as a measure of breeding success during two different periods, 1997–1998 (coinciding with prey censuses and diet data collecting), and 1994–2002 (9-years). An extended study period for breeding success is the most meaningful measure of the reproductive health of a raptor population (Steenhof and Kochert, 1982). A chick was considered as fledged when it reached at least 60 days of age (Real and Mañosa, 1997).

Along an extended study period, the presence of different individuals occupying the same territory among years implies different hunting abilities (Newton, 1997), raising a possible bias for this type of analysis. Nevertheless, from a total of 72 reproduction cases considered, and according to plumage stages (Forsman, 1998), we detected only three cases of adult mortality; therefore we assumed a great stability in the mates, which also implies a presumed stability in reproductive and dietary data from the same territory and pair through the study period. In the results, means are followed by standard deviation and trophic diversity was calculated with the Shannon and Weaver (1963) index. Previous to correlations, variables were log-transformed.

3. Results

We found a total of 387 preys for the eight pairs of Bonelli's eagle analysed. According to previous data in the study area, the European wild rabbit (*Oryctolagus cuniculus*) and the red-legged partridge (*Alectoris rufa*) were the main prey of the eagle, with 29.1% and 28.8% in terms of frequency respectively; they were followed by the wood pigeon (*Columba palumbus*), and the rock pigeon (*Columba livia*), 13.3% and 8.0%, respectively. 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 d.f., $p = 0.12$).

Frequency in the diet for each prey species consistently stabilised after 15–30 prey-items, depending on the pair (Fig. 1). Therefore, we can consider the sample size large enough to assure the precision of results in each territory (mean = 48.4 ± 16.1; $n = 8$; range = 38–87). The average productivity was 1.36 ± 0.45 ($n = 72$), and was homogeneous through the two-year (Mann–Withney U test, $U = 17.50$, $p = 0.12$) and the nine-year period (Kruskal–Wallis test, $H_{8,\ 72} = 8$; $p = 0.43$). There were strong differences in the comparison among pairs, both in frequency of prey in the diet ($G = 122.7$; 28 d.f.; $p < 0.0001$) as well as in productivity (K–W: $H_{7,\ 72} = 16.8$; $p = 0.01$), but we failed to find relationships between the frequency of the main prey species in the diet and productivity, considering the 1997–1998 and 1994–2002 periods in breeding success ($r_s < 0.5$; $p > 0.14$; in all comparisons).

Data on prey density, prey percentage in diet, amount of open lands, and productivity are in Table 1. Prey frequency was correlated with prey density in territories only for rabbits (Table 2). Nevertheless, the percentage of rabbits in the diet was better correlated with the amount of open land in the territories (Table 2), and with the sequential correction of Bonferroni (Rice, 1989), significance disappeared for the prey density but not for the open-land variable. Moreover, the standard multiple-regression model included the amount of open lands in territories as the most significant predictive variable that explain the importance of rabbits in diet ($F_{2,5} = 14.64$, $R^2 = 0.85$; $P < 0.008$); the same was true for the stepwise forward ($F_{2,5} = 14.64$, $R^2 = 0.85$; $P < 0.008$) and backward ($F_{1,6} = 16.67$, $R^2 = 0.74$; $P < 0.006$) selection. These results suggest that accessibility of rabbits would be more important than absolute abundance for the Bonelli's eagle. As expected for a raptor that relies on few and prominent prey species, the presence of rabbits in the diet influenced other prey frequencies. In this way, although we failed to find relationships among the percentage of rabbits, partridges and pigeons in diet with respect to trophic diversity ($r < 0.26$; $P > 0.55$ in all comparisons), we found negative and significant relationships between the presence of rabbits with respect to red-legged partridge ($r = -0.81$; $p = 0.01$) and wood pigeons ($r = -0.89$; $p = 0.003$). Partridges and wood pigeons, prey also with high biomass, appear to complement rabbits in diet in situations of low detectability of rabbits because of the extension of closed lands in the territories (Fig. 2).

4. Discussion

As in other studies on Bonelli's eagle in southern Spain, rabbits, partridges and pigeons were found to be the main prey for this raptor in the region (Martínez et al., 1994; Gil-Sánchez et al., 2004), but in the present study, we considered the analysis of diet reliable either at population and pair levels (Fig. 1).

The diet of the Bonelli's eagle appears to be adapted to taking the most abundant prey available in each region (Cramp and Simmons, 1980). As a consequence, prey density in territories does not significantly affect

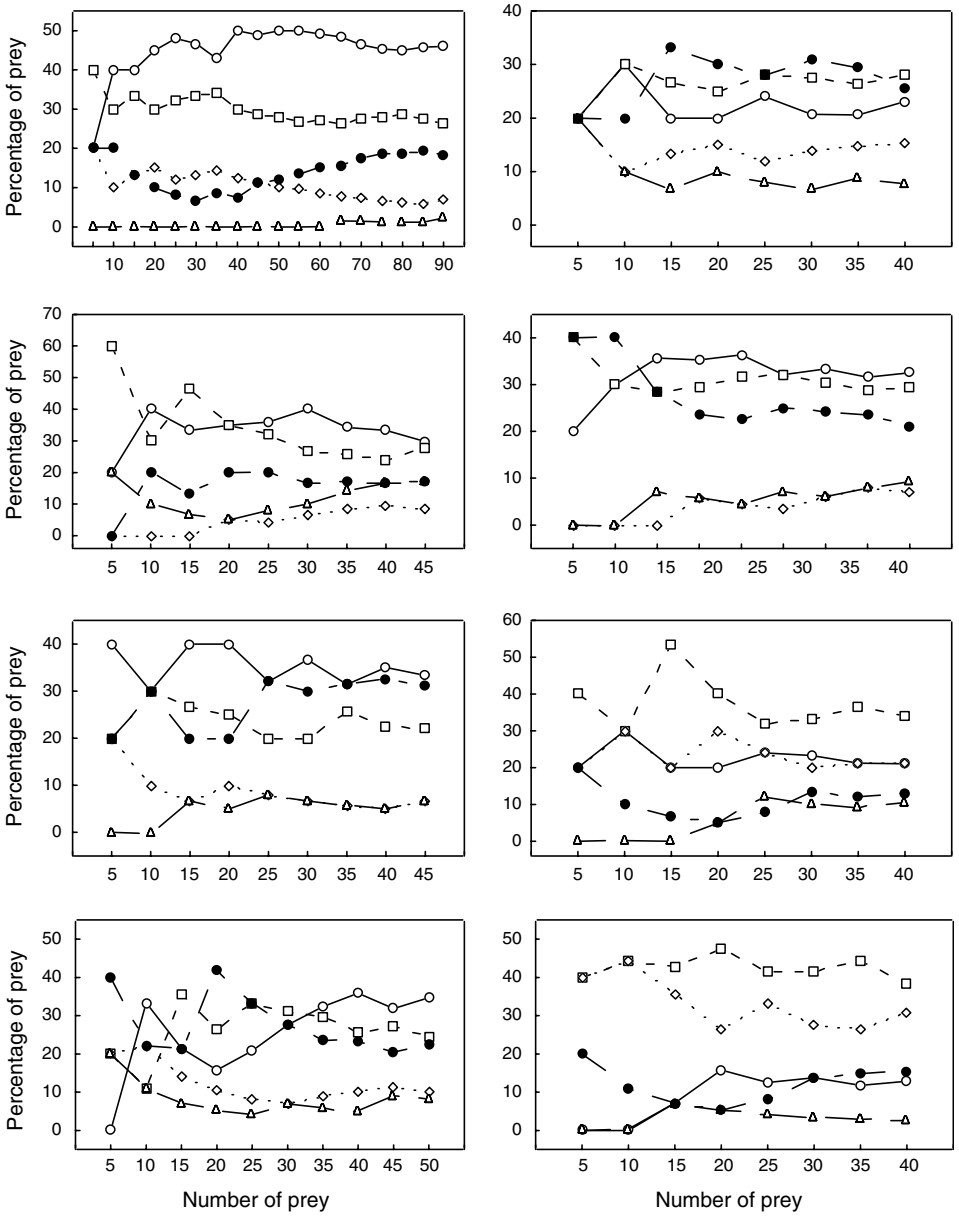

Fig. 1. Percentages of the prey species in the diet of the Bonelli's eagle according to sample size in the eight analysed territories. Symbols correspond to the following prey: European wild rabbit (○), red-legged partridge (□), wood pigeon (◇), rock pigeon (△), and other prey (●).

Table 1
Prey density, diet and percentage of open lands (1997–1998 period), and average productivity (two and nine-years periods) in the eight territories of Bonelli's eagle considered in the study (for more details to see Section 2)

Territory	Prey density (ind./km)			Diet (%)			Open lands (%)	Productivity	
	Rabbits	Partridges	Pigeons	Rabbits	Partridges	Pigeons		1997–1998	1994–2002
1	0.1	1	1.1	12.8	38.5	33.4	55	2	1.62
2	0.9	2.5	2.2	45.0	25.8	14.9	78	1	0.67
3	0.1	2.4	1.5	21.1	34.2	30.6	58	2	1.75
4	0.6	3.2	3.2	32.6	29.5	16.3	77	1.5	0.77
5	0.3	1.4	0.6	34.7	24.5	18.4	73	2	1.87
6	0.9	3.4	2.1	33.3	22.2	13.4	77	1	1.25
7	0.4	3.6	2.7	29.8	27.7	25.5	75	1.5	1.67
8	0	0.8	2.4	23.1	28.2	23.1	54	1.5	1.33

Table 2
Correlation between the percentage of main prey species in Bonelli's eagle diet, and their abundance and the amount of open lands (scrublands, grasslands and cereals crops) in territories

	Prey density		Open lands	
	r	*p*	*r*	*p*
Prey				
European wild rabbit ($N = 122$)	0.81	0.01	0.87	0.005*
Red-legged partridge ($N = 110$)	−0.39	0.34	−0.72	0.04
Wood pigeon ($N = 48$)	−0.18	0.67	−0.82	0.01
Rock pigeon ($N = 29$)	0.62	0.09	0.14	0.73

* Tests that remain significant ($p < 0.05$) after Bonferroni sequential correction (Rice, 1989).

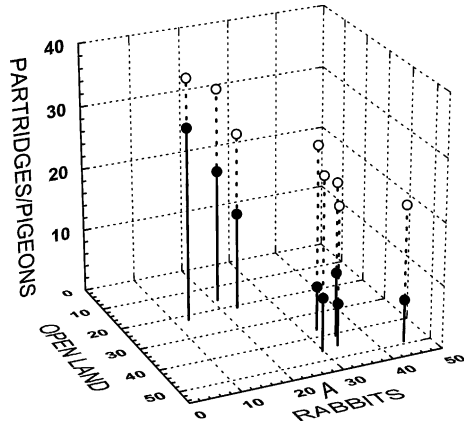

Fig. 2. Relationship between the amount of open lands in territories (scrublands, grasslands, cereals crops, and olive orchards) and the percentage of European wild rabbit, red-legged partridge (○), and wood pigeon (●) in the diet.

breeding density and breeding success of the eagle in the study area (Ontiveros and Pleguezuelos, 2000). This would also account for the results of the present analysis, in which a different percentage of taken preys are not translate as different breeding success among pairs, breeding success being controlled by other environmental factors such as cliff availability and nest orientation (Ontiveros and Pleguezuelos, 2003). In raptors, foraging success should be translated into reproductive success only where food is limiting (Janes, 1984), which does not appear to occur in Andalusia. Nevertheless, the productivity of northern populations of Bonelli's eagle would be affected by prey scarcity in these territories in recent years, and measures compensating for the decline in prey availability have been proposed (Real and Mañosa, 1997).

Some raptors utilised habitat consisting of shorter and/or sparser vegetation than expected based on the distribution of prey (Bechard, 1982; Janes, 1984) and, specifically in the case of rabbits, areas with low tree and bush canopy cover (Bautista et al., 2001), avoiding habitats where hunting for rabbits would be more difficult for raptors (Jaksic and Soriguer, 1981). In this study, we found the presence of rabbits in the diet of Bonelli's eagle to be less related to the total abundance of this prey in territories than with its detectability by the eagles (measured as percentage of open lands; Table 2). The use of protective cover by prey-species is commonly associated with high predation risk, and in this sense rabbits in southern Spain use patches of vegetation in daylight. Thus, hiding under vegetation may be adaptive for rabbits during the day, because they suffer predation by visually oriented birds of prey (Moreno et al., 1996). This would be important for the management of some Bonelli's eagle populations, since prey accessibility (depending on ground-level vegetation) is determinant for the capture of rabbits, its main prey species in Spain. Therefore, to provide an index of prey (mostly rabbits) density, line transects performed with truncated distance (which minimize differences in visibility among habitats) are adequate for mammal predators which need hiding places and hunt from short distances (Palomares et al., 2001), but less adequate for an aerial predator as Bonelli's eagle, which is affected by visibility differences (but see Gil-Sánchez et al., 2004).

We also found that the presence of alternative prey species in territories would compensate for a low supply of rabbits in diet. Thus, the scarcity of rabbits, essential prey-species for others raptors in the Mediterranean area (Cramp and Simmons, 1980), do not affect the breeding success of Bonelli's eagle in southern Spain. A low amount of open lands influence the detectability of rabbits, decreasing their presence in diet, but, in these cases, partridges and pigeons appear in higher proportion (Fig. 2) in our study area. Therefore, Bonelli's eagle shows a functional response involving a trade-off between the consumption of rabbits and other prey-species. A similar result has been found in the Mediterranean region for goshawk (*Accipiter gentilis*) and golden eagle (*Aquila chrysaetos*) with respect to rabbit consumption (Fernández, 1993; Mañosa, 1994).

Results of our study correspond to a healthy population (circumstance not common in this species), and we propose that these findings have some management implications. For southern and healthy populations, the results indicate the importance of alternative prey (red-legged partridges, pigeons) in some territories of the Bonelli's eagle (those with low open land surface); for northern and more threatened populations, indicates the importance of adequate habitat management. In this way, in Western Europe population decline of Bonelli's eagle has been reported in the northern regions of Spain and France (Real and Mañosa, 1997). The scarcity of rabbits in the northern populations has been proposed as an important cause for the decline of the Bonelli's eagle populations in these areas (Real and Mañosa, 1997).

The major landscape changes in the past century and different viral haemorrhagic-diseases of the European

rabbit are also involved in this situation (Soriguer and Rogers, 1981), given that few rabbit populations have returned to levels they held prior to the onset of these changes (Villafuerte et al., 1995). Therefore, we propose that several factors related with prey availability could be affecting northern populations of the eagle: (i) a greater rabbit scarcity in Bonelli's eagle territories (Cheylan, 1981; Real, 1991), (ii) a greater forest cover than in southern regions (Rivas-Martínez, 1985), and (iii) a lower abundance of alternative prey such as the red-legged partridge (Díaz et al., 1996).

Some researchers and management staff have proclaimed the increase of prey density in some Bonelli's eagle territories as a measure of recovery for the species (Cheylan, 1981; Real et al., 1997). After our results, we deem this measure unnecessary for the southern populations of Spain. Nevertheless, if such measures are undertaken for northern populations, they must consider this increase in two ways: the absolute prey density, and the prey detectability, by favouring vegetation structure adequate for prey detection and hunting success of the eagle. To design patches of open lands through forest management and to prevent extensive reforestation in Bonelli's eagle territories, would be the appropriate management strategy in this sense. These management measures will have applicability also in the recovery of declining populations, and in the conservation of stable populations.

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