The feeding ecology of Bonelli's eagle (*Aquila fasciata*) floaters in southern Spain: implications for conservation

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ABSTRACT

Although many studies have investigated the feeding habits of Palaearctic raptors, few have analysed non-breeding populations during dispersal. Bonelli's eagle (*Aquila fasciata*), a Threatened species in Western Europe, has a relatively long and critical dispersal period. We studied feeding habits, prey selection, and the influence of prey density on floater abundance in this species during its dispersal period in southern Spain. Differences were found between the diet of floaters and that of the closest breeding populations. Diet diversity was rather low for floaters, with European wild rabbits (*Oryctolagus cuniculus*) being the main prey and the only prey positively selected. Moreover, the number of floater Bonelli's eagles observed in the dispersal areas was positively associated with rabbit abundance. Other prey included red-legged partridges (*Alectoris rufa*) and pigeons (*Columba* sp.). We propose measures to match suitable prey availability for floater eagles in settlement areas and the use of such areas as human hunting fields.

Keywords: *Hieraaetus fasciatus*, Conservation actions, Hunting, *Oryctolagus cuniculus*, Prey selection, Settlement areas

INTRODUCTION

Dispersal is one of the most important topics in bird population biology and conservation (Gadgil 1971). For many raptor species, factors affecting survival during this stage have important consequences for the stability of populations (Morrison and Wood 2009). In raptors, the first stages of juvenile dispersal are critical for survival because, while individuals are still improving their hunting techniques, they are facing the challenge of securing food in an unknown landscape. During this period the floaters of some large eagles tend to restrict their movements to a few favourable domains in the so-called settlement areas (Morrison and Wood 2009), behaviour that has been widely studied in the Iberian Peninsula (Ferrer 1993; Mañosa et al. 1998; Balbontín 2005). Floaters stay in settlement areas for a variable period before joining breeding populations, and in the southern Iberian Peninsula these areas are used mainly by large raptor species, such as Bonelli's eagle (*Aquila fasciata*; Mañosa et al. 1998) or the Spanish imperial eagle (*Aquila adalberti*; Ferrer 1993). Settlement areas are characterized mostly by the abundance of prey and by being outside breeding territories (Ferrer and Harte 1997; Balbontín 2005, Cadahía et al. 2005, Caro et al. 2010).

The development of effective conservation programmes for Threatened species requires a clear understanding of their ecological requirements (Soulé and Wilcox 1980). The study of the diet of raptor species is a primary step in this direction (Newton 1979), since this information could help wildlife managers to take measures to preserve raptor populations (Iezekiel et al. 2004). Detailed knowledge of a species' diet and prey selection may also help the management of their main prey (Jones 2004; Piper 2006). Thus, there is an urgent need to investigate the feeding habits of such predators, as well as to propose measures to reduce conflicts between raptor conservation and game management (Thirgood and Redpath 2004). The conservation of raptor populations may

have additional problems if their prey are of economic value, because raptors are viewed by humans as competitors of shared resources, such as game (Arroyo et al. 2004).

The Bonelli's eagle is a long-lived bird of prey, which nests mainly in cliffs, having a deferred maturity (at about 3–4 years) and a modal clutch size of two eggs (Cramp and Simmons 1980). Studies on the conservation of Bonelli's eagle have focussed on the adult stage, dealing with its breeding biology, habitat selection, diet, survival, and interspecific interactions (i.e. Penteriani et al. 2003; Ontiveros et al. 2005; Carrete et al. 2006, Moreno-Rueda et al. 2009). For floaters, dispersal movements and habitat selection have also been analysed (Mañosa et al. 1998; Balbontín 2005; Cadahía et al. 2005; Caro et al. 2010).

In recent decades, Bonelli's eagle has suffered a marked population decline throughout most of its distribution area, being considered an Endangered species in Western Europe (BirdLife International/EBCC 2000; Real 2004). The decline in abundance in Spain is due to habitat change, direct persecution, electrocution by power lines (affecting mainly floaters in settlement areas), prey decrease, and disturbance around nesting areas (Ontiveros et al. 2004). The dispersal period of this eagle is relatively long and critical (Newton 1979; Mañosa et al. 1998), and the lack or reduction of appropriate settlement areas may decrease floaters' survival and seriously threaten population stability (Mañosa et al. 1998; Real 2004).

Many studies have investigated the food habits of Palaearctic raptors, though few have included non-breeding populations in the analysis (Valkama et al. 2005). The food habits of breeding populations of Bonelli's eagle have been studied in Western Europe since the 1980s, but only one local study has shown their food preferences (Moleón et al. 2009), and thus this natural-history trait cannot be adequately considered

in management strategies. This raptor exploits a wide range of prey species (mammals, birds, reptiles), some of which are valuable as game species, such as European wild rabbit (*Oryctolagus cuniculus*) or red-legged partridges (*Alectoris rufa*). The aim of this study is to establish the feeding habits (diet and prey selection) of floaters Bonelli's eagle in settlement areas of the southern Iberian Peninsula, to compare our data with information available for the closest breeding populations, to analyze the influence of prey density on floater abundance, and to assess the importance of game species in the floater's diet. The results may help management strategies for the conservation of Bonelli's eagle in the stage of its life when individuals are most prone to die (Real and Mañosa 1997).

METHODS

Study area

We selected five settlement areas occupied by Bonelli's eagle in southern Spain (from the data of the authors for the 1994–2001 period, Fig.1), where its population is mostly healthy and well known (Del Moral 2006). In the study area the climate is typically Mediterranean, with the annual temperature averaging 15.6 to 18.5ºC and contrasting mean annual rainfall, from 300 to 790 mm (CMA 1997; Carrete et al. 2002). The landscape of the settlement areas was a mosaic of orchards (including olive or citrus trees) and small patches of natural vegetation (shrubs, grasslands, and mixed forest of *Quercus ilex* and *Pinus* sp.).

Feeding habits and prey selection

Only in two dispersal areas, Valle del Genil and Sierra Escalona, did the number of pellets and prey remains high enough to provide an estimate of the feeding habits of the floaters (see Results section). Regurgitated pellets and prey remains were collected

between 2001 to 2006 on a bimonthly basis, from October to March (the main period of settlement for floaters; Mañosa et al. 1998; Caro 2010), under roosting sites and perches exclusively used by Bonelli's eagle (authors unpublished data).

Biases associated with assessing raptor diet have been analysed repeatedly (Redpath et al. 2001; Katzner et al. 2005; Margalida et al. 2007), including Bonelli's eagle (Real 1996). Combining data from pellets and prey remains should provide a more accurate picture of the eagle's diet than would data from either diet method alone (Collopy 1983, Redpath et al. 2001), as has been considered also for Bonelli's eagle (Iezekiel et al. 2004; Ontiveros et al. 2005). We identified prey items by comparison with a reference collection of potential prey from the study area, and categorized them into 9 prey types (Table 1). The minimum number of individuals in each pellet or prey remain was estimated from the number of skeletal remains, hairs and feathers of different species, in each sample (Marti 1987), and dietary composition was expressed as prey frequency. We carried out a test of independence (Chi-square) to compare the diet of floaters in settlement areas, and between the diet of floater and breeding populations in the study area. The data for the adults' diet were taken from literature, from Ontiveros and Pleguezuelos (2000) for the Valle del Genil area, and from Martínez et al. (1994) for the Sierra Escalona area.

Food diversity was calculated with the Shannon-Weaver index, which tends to emphasise rare items in the diet, as opposed to Levins' index, which tends to weight towards common items (Magurran 2003). Both are traditionally used as a measure of diet diversity in raptors (Martínez et al. 1994; García and Arroyo 2005; Margalida et al. 2009). However, we chose the Shannon-Weaver index because it was also used in the diet analysis of the closest breeding populations.

Prey availability

European wild rabbits, red-legged partridges and pigeons (*Columba palumbus* and *C. livia*) accounted for 80.67 % and 83.33 % of the diet of adults Bonelli's eagles in terms of prey frequency in the two breeding populations selected here for the diet study (Martínez et al. 1994; Ontiveros and Pleguezuelos 2000). Thus, we considered these prey types to be representative of the diet of the eagle and recorded their abundance by line transects to provide an index of prey abundance in the settlement areas. This method, which has proven effective to determine prey abundance for raptors and to compare prey densities among different zones (Fitzner et al. 1977), is less difficult to perform than absolute-density methods and is equally useful (Caughley 1977).

During the years 2005 and 2006, we performed between one and four transects in each settlement area according to its extension (see relationship raptor-prey abundance section). Surveys were of 4 km in length, stratified according to the area of the different habitats (Caughley 1977), and measured from landscape maps for the regions of Andalusia and Murcia (CMA 1999, CAAMA 2000) by using Arc View GIS 3.2. Habitat influence prey abundance and the structure of the vegetation may also influence prey detection (Janes 1985). The landscape of the five settlement areas was similar, with a predominance of the mosaic agricultural landscape (Caro et al. 2010), and thus we assumed that there were no significant differences on the detectability of the prey among the different areas (Ontiveros et al. 2005). Prey surveys were executed by an observer on foot, between 06.00 and 09.30 h., on days of good visibility, at a speed of approx. 2.0 km/h, during February and March. We made no censuses before February to avoid the hunting season, and after April because of demographic explosions of rabbits and partridges (Soriguer 1981, Casas and Viñuela 2010), such that the prey populations were estimated when they were around to their annual minimum in the settlement areas. Prey abundance was measured as the average of individuals per km

of census (Tellería 1986). We deemed the diurnal rabbit census to be a more realistic estimate of prey density than nocturnal ones for strictly diurnal predators (Palomares 2001), such as Bonelli's eagle.

Prey selection

We assessed whether prey species were depredated more or less frequently than expected according their availability through of the Savage selectivity index (Manly et al. 1993). This index is defined as $W_i = U_i/D_i$, where U_i is the percentage of prey-type i consumed by Bonelli's eagle, and D_i is the percentage of species i available in the settlement area. This selectivity index varies from zero (0) (maximum negative selection) to infinity (maximum positive selection), one (1) being the central score defining the value expected by chance. The significance of W_i values was tested with χ^2 (see Manly et al. 1993 for a description of the procedure).

Relationship raptor-prey abundance

The possible influence of prey density on raptor abundance was investigated by means of 75 raptor surveys in the five settlement areas, during the 2001-2005 period. We think that to search for eagles and for their prey in different years in some cases, would not affect our results significantly; at least in Southern Spain and for rabbits, population abundance cycle barely change between years (Cabezas and Moreno 2007). Samplings were performed in autumn and winter, seasons when maximum density was attained for floater eagles in settlement areas (Mañosa et al. 1998; Caro 2010). Eagle abundance was measured by line-transects, as straight as possible, by car, at low speed (20 km/h), on days of good visibility, in the morning, by two people, i.e. one trained observer and a driver. We recorded the number of km driven and the number of floater individuals (< 4 years), according to plumage criteria (Parellada 1986; Forsman 1999). To estimate abundance, we measured the distance between the observer and the eagle,

and the angle with respect to the line progress along the transect. The relative abundance of floater eagles in each survey was measured as the average number of eagles detected per 100 km. For a more robust estimate of the abundance, observations were truncated at 400 m, when detectability declined sharply (Buckland et al. 1993), according to the histogram for distances generated by the DISTANCE software (Laake et al. 1993). Roadside survey has repeatedly proven to be adequate for compiling information on raptor abundance (Mañosa et al. 1998; Sánchez-Zapata and Calvo 1999; Carrete et al. 2009).

To evaluate the relationship between abundances of main prey species and Bonelli's eagle, we used the Spearman's rank correlation (Quinn and Keough 2003), and we assumed that the different methods used for predator and prey censusing should not affect the results.

RESULTS

Food habits and prey selection

A total of 135 prey items were found in two settlement areas, 56 in the Valle del Genil and 79 in the Sierra Escalona, both figures being a significant number of prey items, because in this raptor the dietary proportions stabilize at around 25 prey items (Ontiveros et al. 2005). The European wild rabbit was the main prey of Bonelli's eagle, with more of 60% in terms of frequency in both settlement areas, followed by the avian prey, i.e. red-legged partridges and pigeons. Other prey such as the Iberian hare (*Lepus granatensis*), birds (unidentified passerines) or snakes, appeared occasionally. Only eight different prey species were detected in the diet of floaters Bonelli's eagle, and diet diversity was rather low (H<1.15 in both settlement areas; Table 1).

Prey frequency in the diet of floaters was marginally different between the two settlement areas (χ^2 =7.7, d.f.=3, P=0.051), and significantly different between floaters (in settlement areas) and the closest breeding populations in both study areas (χ^2=35.48, d.f.=3, P<0.0001 for Valle del Genil; χ^2=42.85, d.f.=3, P<0.0001 for Sierra Escalona), due mainly to higher rabbit and lower bird (partridges and pigeons) predation by floater eagles.

In both settlement areas floater Bonelli's eagles showed a significant positive selection only for rabbits, while birds tended to be avoided as prey. In the Valle del Genil, rabbits were more selected (greater value of Savage index) than in the Sierra Escalona (Table 2).

Relationship between abundance of floater eagles and prey

Forty-one observations of floater Bonelli's eagles in the five settlement areas, afforded an average relative density of 2.29 ± 2.27 eagles/100 km (mean ± SD) for the five settlement areas (Fig. 2). There was a positive and significant relationship between the abundance of rabbits, the main prey found in diet, and the abundance of floater Bonelli's eagles in the five settlement areas (r_s=0.9, P=0.037). The correlation between the abundance of partridges or pigeons and that of Bonelli's eagle floaters showed no significant relationship (r_s=0.10, P=0.873 and r_s=0.7, P=0.18, respectively).

DISCUSSION

Our results show that floater Bonelli's eagles had lower diet diversity in the settlement areas than in the breeding territories in the same regions, although the larger sample size for breeding populations may account for this difference to some degree. As observed in breeding populations, rabbits, partridges, and pigeons were the basic prey for floaters, although the frequency was significantly different (see data in Martínez et

al. 1994; Ontiveros and Pleguezuelos 2000). Particularly, the proportion of rabbits in the diet was much greater for floater eagles, so that rabbit abundance in settlement areas explained Bonelli's eagle floater abundance, identifying this prey species as a keystone in the ecology of Bonelli's eagle during the dispersal phase. The diet of the Bonelli's eagle is adapted to taking the most abundant prey available in each region (Cramp and Simmons 1980). In fact, in our study areas, Bonelli's eagle floaters apparently behave as a facultative predator of rabbits, with increased consumption of this prey when they are most abundant (in settlement areas). A similar pattern has also been reported in other Mediterranean predators (i.e. Revilla and Palomares 2002; Malo et al. 2004, Delibes-Mateos et al. 2008a).

Rabbits may be an ideal prey for many predators, as they can be locally abundant (Villafuerte et al. 1998), offering high energy value, low hunting costs (Revilla and Palomares 2002; Malo et al. 2004), and could become an ideal prey for inexperienced floater eagles. Consequently, floater Bonelli's eagles depend heavily on rabbits, and this would explain why in Western Europe the northernmost preadults seem to have a southern dispersal pattern (Real 2004), where the highest populations of rabbits can be found (Villafuerte 2008). Species inhabiting regions with contrasting environmental conditions could show interpopulational variation in diet composition, as a consequence of differences in prey availability (Santos et al. 2008). However, we found rather similar diet composition between the two selected settlement areas, and the only study that previously analysed the feeding habits in another settlement area also found rabbits to be the prey most consumed by preadult eagles, with a frequency similar to that of our data (Moleón et al. 2009).

A possible shortcoming of our study is that samples for analysing diet for floater and breeding populations were collected in different months of the year. Nevertheless,

despite that breeding areas were sampled when rabbits showed the highest abundance through the year (Palomares 2001), we found lower frequency of this prey for adults in breeding areas than for floaters in settlement areas, reinforcing the results. Another likely limitation of our study is that we have no synchronous information for the feeding habits of the two breeding populations used for comparative purposes. Nevertheless, this contingency is unlikely to affect our results, given that, in one of the two breeding areas, we found that diet remained constant over the years (Ontiveros et al. 2005), and Palma et al. (2006) found the same for a reproductive population of Bonelli's eagle in the southern Iberian Peninsula. Moreover, the main preys of Bonelli's eagle are subject to variations mainly in number due to epizootics, habitat degradation or inadequate game (Martínez et al. 2007). Meanwhile, in the study areas (breeding territories and settlement areas), no marked changes occurred in climatic conditions, land cover or human activities, which might have changed the abundance of the main prey (Palma et al. 2006).

In the prey-selection analysis, Bonelli's eagle floaters showed a significant positive selection only for rabbits, and a negative selection for some birds. Food availability is one 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 the predator (Widen 1994). For this raptor, food availability is constrained by land use (Palma et al. 2006), and the presence of rabbits in the diet is more related to the detectability of this prey by the eagles (measured as the percentage of open land), than with its abundance (Ontiveros et al. 2005). In this sense, in settlement areas of the southern Iberian Peninsula, where floater eagles consume more rabbits than do adult eagles, the landscape consists of a mosaic of habitats dominated by open lands with low

tree and shrub cover. By contrast, breeding territories are mountainous and mostly covered by thick, natural vegetation (i.e. maquis or forest).

In the Mediterranean Iberian ecosystems, the rabbit is a staple prey for almost 30 predators (Delibes and Hiraldo 1981; Delibes-Mateos et al. 2008b). Also in Spain rabbits are important resources for hunting (Delibes-Mateos et al. 2007). Thus, rabbit scarcity could constitute a dual problem due to its biological and economical value (Catalán et al. 2008). Certainly, among Spanish hunters, raptors have traditionally been considered as a limiting factor for game, and have been killed to protect this activity. In recent decades this prey has undergone a progressive decline in abundance due to viral diseases and loss of suitable habitat (Ratcliffe et al. 1992; Villafuerte et al. 1995). In Spain, after the outbreak of rabbit viral disease, the conflict between hunters and natural rabbit predators increased (Villafuerte et al. 1998), and the killing of raptors was commonplace, Bonelli's eagle being no exception; direct persecution is the second cause of death for Bonelli's eagle (Real et al. 2001). According to Soutullo et al. (2008), mortality of floater Bonelli's eagle plays a key role in determining the overall population trend of the species in Mediterranean Spain, so that management action for the conservation of this species should also be focused at minimizing floater mortality (Ontiveros et al. 2004; Real 2004; Soutullo et al. 2008).

Although some studies have investigated the feeding ecology of breeding populations of Bonelli's eagle in the Iberian Peninsula (Valkama et al. 2005), detailed reports during the dispersal phase are scarce, and this ecological trait during this life stage has not been considered in management strategies for this endangered raptor. Our results demonstrate that floaters of Bonelli's eagle rely on few prey for feeding, underlining the importance of a game species, the rabbit, in the eagle's diet. In the southern Iberian Peninsula, the settlement areas for Bonelli's eagle floaters lie

invariably within private hunting estates (authors unpublished data), which also provides the best feeding conditions for other threatened predators, as Iberian lynx (*Lynx pardinus*) and Spanish imperial eagle (Delibes-Mateos et al. 2009), but are always unprotected areas. Consequently, it is crucial to search for practical methods to reduce conflicts between raptor conservation and game management. Those methods may include adequate protection of settlement areas through pacts with hunters, such as economic compensation for appropriate management. The main objective of the programmes should be to maintain high-density populations of rabbits, and enhance populations where they are scarce; for instance by using habitat management, which is an effective tool for rabbit population reinforcement (Catalán et al. 2008).

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Fig. 1 Location of the settlement areas for Bonelli's eagle considered in this study: 1, Campiña de Cádiz; 2, Valle del Genil; 3, Montes Orientales; 4, Depresión de Guadix; 5, Sierra Escalona. Dietary composition was studied only in settlement areas 2 and 5 (more information in the Methods section).

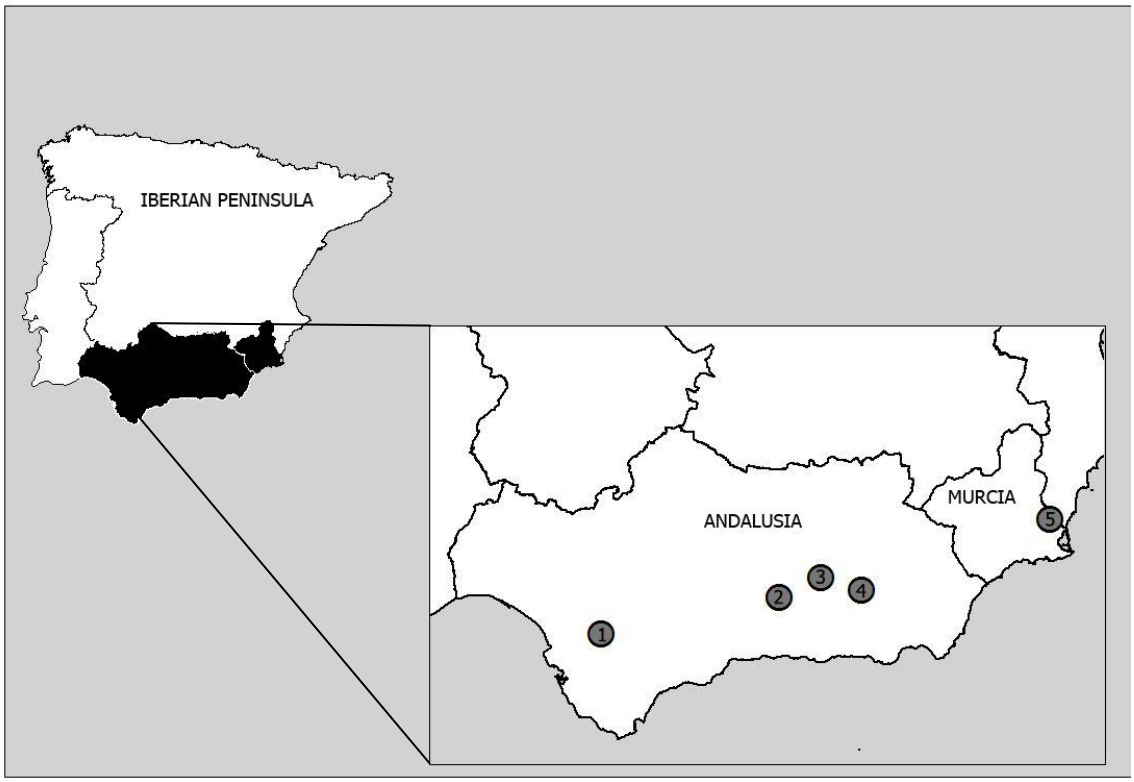

Fig. 2 Relationship between Bonelli's eagle abundance and European wild rabbit abundance in five settlement areas for floater Bonelli's eagles in southern Iberian Peninsula.

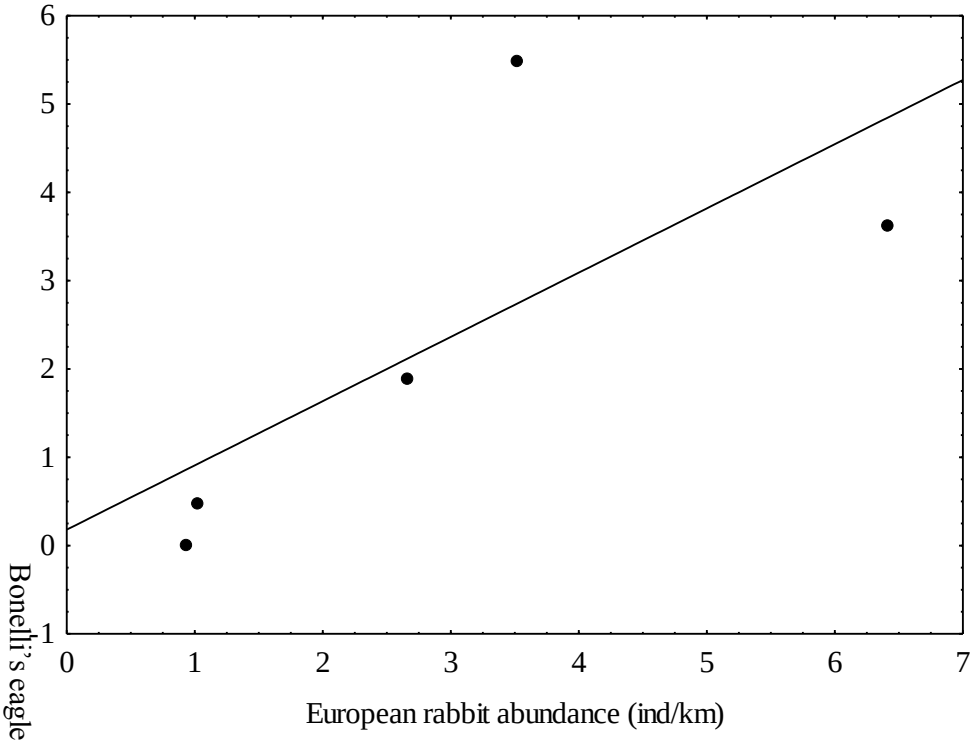

Table 1. Diet of Bonelli's eagle in two settlement areas (for floaters) in which this could be adequately studied (see Methods section), and the closest breeding populations of these settlement areas in southern Iberian Peninsula. Data for breeding populations were taken from Ontiveros and Pleguezuelos (2000) (closest breeding population of Valle del Genil) and Martínez et al. (1994) closest breeding population of Sierra Escalona). F, prey frequency.

Prey	Valle del Genil				Sierra Escalona				Total for both settlement areas	
	Settlement area		Breeding population		Settlement area		Breeding population			
	F	% F	*F*	% F	*F*	% F	*F*	% F	*F*	% F
Oryctolagus cuniculus	35	62.5	69	35.94	56	70.9	274	39.83	91	67.5
Lepus granatensis	2	3.6	3	1.57	-	-	6	0.87	2	1.5
Unidentified mammalia	-	-	-	-	1	1.3	-	-	1	0.7
Alectoris rufa	7	12.5	58	30.21	11	13.9	137	19.91	18	13.3
Columba sp.	10	17.8	33	17.18	9	11.4	144	20.93	19	14.1
Alaudidae	1	1.8	-	-	-	-	-	-	1	0.7
Unidentified passerines	-	-	6	3.13	2	2.5	4	0.58	2	1.5
Snakes	1	1.8	2	1.04	-	-	3	0.44	1	0.7
Other prey	-	-	21	10.93	-	-	120	17.44	-	-
TOTAL	56	100	192	100	79	100	688	100	135	100
Prey diversity (*H*)	1.12		1.83		0.91		2.55		1.04	

Table 2. Prey selection based on the Savage index by floater Bonelli's eagles in two settlement areas of southern Iberian Peninsula in which this could be adequately studied (see Methods section). Only the main prey types were considered. U_i is the percentage of prey-type *i* consumed for Bonelli's eagle, and D_i is the percentage of species *i* available (measured as the number of individuals per km) in the settlement area. See the Material and Methods section for more details on the procedure.

Study area	Prey type	U_i	D_i	Savage index	Statistic	*P*	Selection
Valle del Genil	*Oryctolagus cuniculus*	0.6250	0.1369	4.565	112.989	**<0.0001**	+
	Alectoris rufa	0.1250	0.2011	0.6215	2.0186	0.1553	Indifference
	Columba sp.	0.1785	0.6618	0.2697	58.480	**<0.0001**	-
Sierra Escalona	*Oryctolagus cuniculus*	0.7088	0.2371	2.9892	97.220	**<0.0001**	+
	Alectoris rufa	0.1392	0.5505	0.2528	54.036	**<0.0001**	-
	Columba sp.	0.1139	0.2123	0.5363	4.5770	**0.0324**	-