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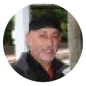

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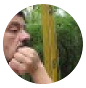

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Why do raptors take domestic prey? The case of Bonelli's eagles and pigeons

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Summary

1. Predator conservation management requires detailed understanding of the ecological circumstances associated with predation, especially that on economically valuable prey. We examined the mechanisms behind Bonelli's eagle *Hieraaetus fasciatus* predation on prey of domestic origin, using dietary data from 22 pairs breeding in south-west Portugal (1992–2001) together with information on landscape composition and prey availability.

2. Numerically, 42·7% (37·7% in biomass) of eagle prey comprised domestic species, about 70% of which were rural pigeons *Columba livia* and the remainder were racing pigeons *Columba livia* and domestic fowl *Gallus gallus*. Rabbits *Oryctolagus cuniculus*, red-legged partridges *Alectoris rufa* and jays *Garrulus glandarius* were the most frequent wild prey (43·1%; 50·8% in biomass). This dietary pattern was remarkably stable over a decade, but within each year the intake of pigeons almost halved over the course of the breeding season.

3. Landscape composition significantly affected the dietary proportion of wild and domestic prey items. This was particularly evident in territories dominated by eucalyptus *Eucalyptus globulus* plantations, where there was reduced consumption of rural pigeons and partridges, an increased intake of minor avian prey items and greater diversity in the diet overall.

4. Bonelli's eagles showed type II functional responses while preying on the most important wild (rabbit) and domestic (rural pigeon) prey, although the former was much stronger. Eagle predation on rabbits declined with increasing abundance of pigeons, and vice versa, but there was no switching in the traditional sense, as selection between these two species was inversely frequency dependent.

5. *Synthesis and applications*. Predation by Bonelli's eagle on domestic pigeons results from a combination of high vulnerability of the pigeons to eagles and a shortage of key wild prey such as rabbits and partridges, especially during the early breeding season. Given the relatively low economic value of rural pigeons and their importance in the diet of Bonelli's eagles, they could probably be used as a conservation tool to enhance food resources in breeding territories and to deflect predation from more valuable prey such as partridges and racing pigeons.

Key-words: conservation, functional response, *Hieraaetus fasciatus*, Mediterranean, partridge, pigeon, predation, rabbit, switching

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Introduction

Predators feeding on poultry, livestock and game have long been killed by humans, often resulting in population declines and even extermination (Thirgood *et al.* 2000; Treves & Karanth 2003; Graham, Beckerman & Thirgood 2005). Recently, many of these predators have recovered as a consequence of increased tolerance and protection (Treves & Karanth 2003; Valkama *et al.* 2005). However, population recovery involves major challenges when protected predators expanding into human-dominated landscapes come into contact with species that are hunted, harvested or farmed for human consumption or recreation (Meriggi & Lovari 1996; Landa *et al.* 1999; Stahl *et al.* 2001). Such food resources may actually contribute to supporting increased predator densities (Kenward, Marcström & Karlbom 1981; Selås 1997; Redpath & Thirgood 1999), thereby creating dilemmas between the protection of predators and the mitigation of predation damage (Thirgood *et al.* 2000; Woodroffe *et al.* 2005). These management conflicts need to be addressed if population recoveries of protected predators are to be sustained (Graham, Beckerman & Thirgood 2005).

Birds of prey are often perceived as damaging by hunters, gamekeepers, farmers and pigeon fanciers (Shawyer, Clarke & Dixon 2000; Thirgood *et al.* 2000; Valkama *et al.* 2005). Conflicts involving predation on economically valuable game species have been thoroughly investigated, showing that persecution remains a threat for many predatory species (Villafuerte, Viñuela & Blanco 1998; Thirgood *et al.* 2000; Carrete *et al.* 2002). Much less is known of cases involving predation on domestic prey, although they may also be a significant source of conflict (Stahl, Ruette & Gros 2002; Avery & Cummings 2004). For instance, domestic pigeons *Columba livia* L. are often consumed by recovering species such as peregrine falcons *Falco peregrinus* L., resulting in complaints that raptor attacks are becoming unacceptably high (Shawyer, Clarke & Dixon 2000; Henderson, Parrott & Moore 2004).

High predation rates on domestic prey can usually be explained by three main predatory mechanisms, each of which has different implications for the mitigation of predator damages. An alternative prey hypothesis (APH; *sensu* Angelstam, Lindström & Widén 1984) is assumed, often implicitly, when predators switch to domestic prey as wild prey becomes scarce (Meriggi & Lovari 1996). In these circumstances, the restocking of wild prey may alleviate predation on domestic species. This solution may be ineffective if predators take domestic prey primarily because of their high vulnerability, irrespective of wild prey abundance. The vulnerable prey hypothesis (VPH) calls for management strategies reducing the exposure of domestic prey, using, for instance, deterrents or fencing (Shawyer, Clarke & Dixon 2000; Kenward *et al.* 2001; Treves & Karanth 2003). Finally, the problem animal hypothesis (PAH) is proposed when predation involves a behavioural feeding specialization by a few individuals, in which case the removal of problematic animals is often advocated (Stahl *et al.* 2001; Treves & Karanth 2003).

Testing these hypotheses requires information on the responses of predators to variation in the densities and relative frequencies of wild and domestic prey. Under the APH, predation on domestic prey may be low until the abundance of wild prey declines below a minimum threshold. Switching (*sensu* Murdoch 1969) should then occur, implying a frequency-dependent response to fluctuating prey densities, with the predator eating disproportionately more of the most abundant prey item. In this case, predators are usually expected to show a Holling type III (sigmoid) functional response to fluctuations in prey density (Akre & Johnson 1979). In contrast, under the VPH the functional response to fluctuations in domestic prey density would show a type II (convex) curve, characterized by a rapid increase in the number of prey taken per predator at low prey densities, indicating the presence of highly vulnerable or rewarding prey. The PAH requires that predation on domestic prey occurs only locally and largely independently of prey abundance. In practice, these predicted responses to fluctuations in prey abundance are likely to be more complex, as predators often feed on several different wild and domestic prey types, and their abundance and profitability may change across habitats and over time. Assessing the mechanisms involved in a particular instance of predation on a domestic prey thus requires a good understanding of the predator–prey interactions and the ecological context in which they take place (Graham, Beckerman & Thirgood 2005).

Factors influencing predation on domestic prey were examined by analysing Bonelli's eagle *Hieraaetus fasciatus* Vieillot predation patterns in south-west Portugal (1992–2001). Bonelli's eagle is an endangered species showing a marked decline in Mediterranean Europe since the early 1980s (Real & Mañosa 1997). Bonelli's eagles feed on a range of vertebrates, with rabbits *Oryctolagus cuniculus* L., red-legged partridges *Alectoris rufa* L. and pigeons *Columba* spp. often being the main prey (Real 1991; Valkama *et al.* 2005). As a consequence, persecution by hunters and pigeon fanciers represents a major threat for some Bonelli's eagle populations (Real *et al.* 2001; Carrete *et al.* 2002). In the study area, rabbits and partridges are scarce, while rural pigeons are relatively abundant in small villages and isolated farmhouses. Preliminary evidence showed that eagles consume pigeons very frequently (Palma *et al.* 2005) and there was the possibility that the pigeons acted as an alternative resource to wild prey. This creates a management dilemma (Petty, Lurz & Rushton 2003) as pigeons provide an important food resource while also representing a potential cause of conflict with pigeon fanciers. A closer examination of the factors affecting predation on domestic pigeons used information on variation across breeding territories in diet composition, land uses and the abundance of wild and domestic prey. The aim was to assess: (i) the extent of predation on domestic prey; (ii) variation in diet across years and over the breeding season; (iii) the influence of habitat on predation patterns; (iv) the functional responses to variation in wild and domestic prey abundance; and (v) the eventual occurrence of switching between wild and domestic prey. This information was then used to infer the predatory mechanisms involved in this predator–prey system, and to suggest management solutions that might contribute to the conservation of these eagles while mitigating potential conflict with humans in south-west Portugal and elsewhere.

Methods

STUDY AREA

This study focused on a dense breeding nucleus of 25 Bonelli's eagle pairs occupying about 3000 km^2 in the uplands of south-west Portugal (Fig. 1). This is an area of low mountains and rolling hills mostly under 650 m a.s.l. in altitude. The climate is Mediterranean, with a dry and hot summer season with little precipitation. The land is predominantly covered by open to dense cork oak *Quercus suber* L. woodland and extensive scrubland often dominated by the gum cistus *Cistus ladanifer* L. In the western half of the area, eucalyptus *Eucalyptus globulus* Labill. plantations for paper pulp production cover up to 50% of the land. Human settlement is currently low and local; most of the former scattered dwellings are abandoned and agriculture is residual.

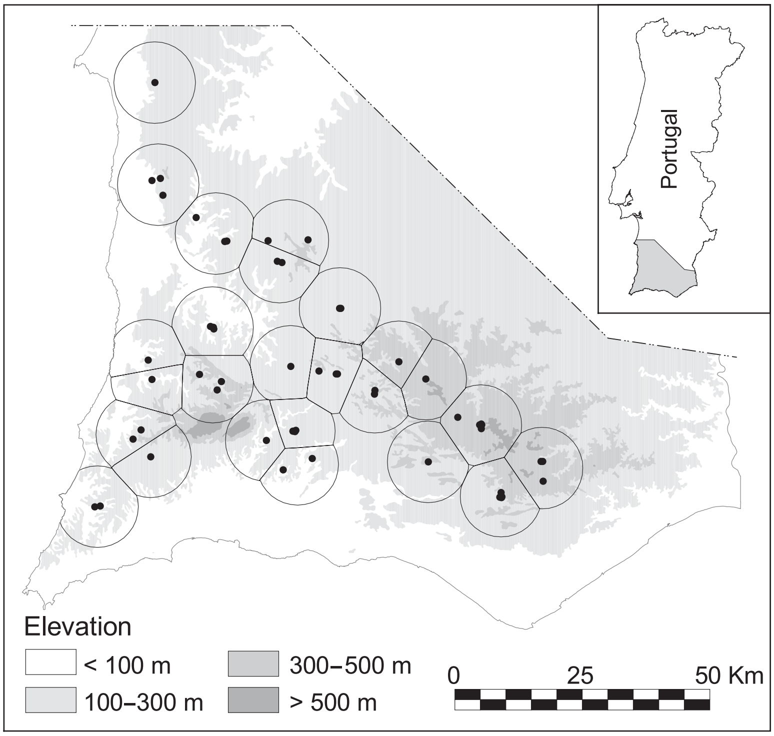

Fig. 1. Location in south-west Portugal of alternative nests of Bonelli's eagle pairs (1992–2001) and the approximate territory boundaries estimated using Dirichlet tessellation.

EAGLE DIET

The diets of 22 pairs of eagles surveyed in 1992–2001 were described from prey identified in remains ($n = 747$) and regurgitated pellets ($n = 1039$) collected during the breeding season (> 85% in March–May) at active nests and surrounding perches, together with uncollected fresh prey observed at nests ($n = 199$). Information was obtained for 9·6 ± 4·8 (2–17) pairs per year, with variation as a result of population growth, breeding failures, unknown nest locations and reduced field effort in 1992–94 and 2001. Nests were checked 5·5 ± 2·2 (1–11) times year^{-1}. The species, age and gender of each individual prey were estimated whenever possible using published identification keys and a reference collection. Metallic rings provided a minimum estimate of racing pigeons in the diet, as rural pigeons were seldom ringed within the study area.

To reduce biases normally associated with dietary studies (Real 1996; Marchesi, Pedrini & Sergio 2002) and to increase sample sizes, data from pellets, remains and direct observations were combined (Ontiveros & Pleguezuelos 2000; Penteriani, Gallardo & Roche 2002; Ontiveros, Pleguezuelos & Caro 2005). For each pair and sampling occasion, the number of individuals of a given prey species represented in the sample was taken only from the data source yielding the largest estimate, thereby avoiding duplications among data sources. In the case of two siblings, the estimated number of prey items represented in pellets was halved, to avoid duplication of the same prey in two pellets (Real 1996). The biomass of each prey species was estimated by multiplying the number of individuals by its estimated mean weight, using data from the study area, bibliographic sources (Real 1987; Cardona & Esteban 2002) and information from racing pigeon fanciers (D. Santos, personal communication). The number of individuals of each prey species taken by an average eagle pair during the breeding season was estimated following Petty, Lurz & Rushton (2003), considering one nestling per pair, an overall daily consumption of 750 g food per pair plus one nestling (Real 1987), a mean incubation period of 39 days (Arroyo, Ferreiro & Garza 1995) and a mean nestling period of 63 days (Real & Mañosa 1998).

HABITAT AND PREY AVAILABILITY

Variation in diet, landscape composition and prey availability among territories was used to estimate the factors influencing eagle predation patterns. Given the lack of detailed information on the actual breeding territories, habitat and prey data were quantified within approximate territory boundaries estimated using Dirichlet tessellation (Doncaster & Woodroffe 1993). For each pair, the mean geographical location of nests was the Dirichlet centre, and boundaries were constrained to be at a maximum of 8 km from the centre (Fig. 1). These criteria were based on home range data from other studies (Mure 2003) and on nearly 800 haphazard observations at > 500 m from active nests through the 10-year study period, suggesting that each Bonelli's eagle pair maintained an exclusive foraging territory, which only rarely extended beyond 8 km from the active nest (L. Palma, unpublished data). Although this was a relatively crude approach, each range boundary encompassed > 90% of observations of individually recognized elements of the respective breeding pair.

Landscape composition was quantified using digital land cover cartography from 1995 (www.dgrf.min-agricultura.pt/ifn/mapas.htm, accessed 1 April 2005), considering six categories: (i) native Mediterranean forests dominated by cork oaks and strawberry trees *Arbutus unedo* L., (ii) eucalyptus plantations, (iii) pine (mostly *Pinus pinaster* Ait.) plantations, (iv) scrubland, (v) farmland and (vi) urban areas (Table 1). Landscape diversity was computed using the Shannon index.

Rabbit abundance was estimated in September–October 1997 from latrine counts in 296 250-m line transects walked along dirt roads and firebreaks crossing eagle territories and neighbouring areas (Palma, Beja & Rodrigues 1999). Latrine counts were used (Iborra & Lumaret 1997; Beja, Palma & Pais 2007) as direct observation of rabbits was not feasible because of dense vegetation cover. One transect was walked per 1-km^2 grid square, with five random squares surveyed in each of 65 5-km^2 grid squares distributed in a checkerboard pattern. To increase comparability among sites, each transect was located in the most favourable shrubland habitats available within each square (Beja, Palma & Pais 2007). The mean latrine count per breeding territory was used to index relative rabbit abundance. Only 14 territories for which there were at least 10 line transects (15·2 ± 4·2, 10–23) were used in further analyses because information could not be obtained for the entire study area. A comprehensive rural pigeon survey was carried out from September 1994 to December 1995, encompassing the approximate breeding territories of 18 eagle pairs known at the time. Pigeon lofts were mapped by visiting all small villages and isolated farmhouses, where the number of pigeons was estimated for each loft either through enquiries or direct counts. Point estimates of pigeon abundance were interpolated into a 250-m raster grid using kernel density analysis with a 5-km searching radius, and these grid values were then used to estimate average rural pigeon densities within each breeding territory. The abundance of racing pigeons crossing the study area was estimated from information provided by homing pigeon fanciers on the periods and frequency of races and training flights, and the approximate numbers of pigeons involved, their origin and geographical distribution (D. Santos, personal communication).

The prey data only referred to a restricted period, whereas the dietary information spanned 10 years. This was recognized as a shortcoming in the data but was unavoidable. It was not possible to repeat the surveys and a long diet study would be needed to characterize a large number of pairs. This shortcoming was unlikely to affect the results of this study seriously as unsystematic observations suggested that regional trends in prey abundance remained essentially the same. In particular, there were no marked changes in land cover and human activities that might have changed the distribution of rabbit and pigeon abundances extensively. Also, no rabbit crashes as a result of viral haemorrhagic disease similar to that reported elsewhere (Fa, Sharples & Bell 1999) or severe myxomatosis outbreaks were observed. Moreover, surveys were carried out approximately half-way through the study period, when most dietary information was collected.

DATA ANALYSIS

Preliminary to data analysis, the angular transformation (arcsine $\sqrt{p}$) was used to reduce the influence of extreme values and to overcome problems associated with the unity sum constraint of proportional data (Zar 1996). Multicollinearity among habitat variables was investigated using principal component analysis (PCA), thereby describing the main gradients in land-use variability (Legendre & Legendre 1998). A varimax rotation was performed on the principal components with eigenvalues > 1 to enhance their interpretability (Legendre & Legendre 1998). Seasonal and annual trends in dietary proportions were examined using linear regression, including quadratic terms to check for non-linear trends (Legendre & Legendre 1998). Relationships between spatial variation in prey consumption and land-use variables were examined likewise. In temporal analyses, data from all eagle pairs were pooled per time period, whereas in spatial analyses

Table 1. Average (± SD) landscape composition and summary results of a principal component analysis with varimax rotation describing the dominant land-use gradients across Bonelli's eagle territories in south-west Portugal (1992–2001). The proportion of explained variation and the scores of each variable are provided for the first two rotated axis (PC)

Land cover types	Mean (%)	± SD	Minimum–maximum	PC1 (38·1%)	PC2 (30·1%)
Scrubland	40·1	14·2	16·8–62·5	0·84	
Mediterranean forests	26·3	12·6	6·5–46·4		–0·82
Farmland	16·7	15·7	2·7–55·6	–0·92	
Eucalyptus plantations	14·4	12·2	0·0–43·8		0·79
Pine plantations	2·1	2·7	0·0–7·5		0·63
Urban	0·4	0·4	0·0–1·4	–0·78	

data were pooled per breeding pair. Only cases for which there were at least 25 prey items were used, because dietary proportions stabilize around this threshold (Ontiveros, Pleguezuelos & Caro 2005).

Functional responses were investigated by modelling the relationships between the average number of a prey type eaten per breeding pair and the abundance of either pigeons or rabbits. In each case, functions representing linear (type I), convex (type II) and sigmoidal (type III) curves were fitted to the data (Patterson, Benjamin & Messier 1998) and the best model was selected based on second-order Aikaike information criterion (AICc) because of small sample sizes (Burnham & Anderson 1998). Type II and III responses were modelled using the generalized Michaelis–Menton function (Real 1977). The effects of pigeons and rabbits on the consumption of other prey were investigated using linear regression and partial correlation analysis (Zar 1996).

Prey switching was examined by relating the ratio of pigeons to rabbits eaten (e_1/e_2) to their availability ratio (A_1/A_2) using the equation $e_1/e_2 = (V \times A_1/A_2)^b$ (Greenwood & Elton 1979). The parameter V is a measure of frequency-independent selection, whereas b is a measure of frequency dependence: $b > 1$ provides evidence for switching, with the predator eating disproportionately more of the most abundant prey, $b < 1$ reflects disproportionate predation on the less common prey and $b = 1$ indicates frequency-independent selection. As A_1 and A_2 were expressed in distinct units and there was no absolute estimate of rabbit densities, this analysis should be regarded as approximate and the parameter V should not be interpreted. Nevertheless, the shape of the curve relating e_1/e_2 to A_1/A_2 is meaningful, providing the best approach to evaluating the presence of switching between the two prey species.

Results

HABITAT AND PREY ABUNDANCE

Bonelli's eagle territories were dominated by scrubland and oak forests, together accounting for almost 70% of landscape composition (Table 1). Eucalyptus plantations and farmland were also important, whereas land cover by pine plantations and urban areas was negligible. The PCA with varimax rotation revealed a dominant gradient largely reflecting agricultural abandonment that accounted for 38·1% of land cover variability, ranging from territories with a significant proportion of farmland and urban areas to those dominated by scrubland. The second rotated PCA axis (30·8%) represented the dominant forest types, contrasting territories dominated by Mediterranean oak forests with those that were predominantly eucalyptus plantations.

There was strong variation among territories in the abundance of rabbits and pigeons (Fig. 2). Rabbits occurred in only 27% of the 296 transects surveyed, and they tended to be fairly scarce where they occurred (4·2 latrines 250 m^{-1} (4·3, 1–24, n = 80). This resulted in a 50-fold variation in rabbit abundance among eagle territories, with densities up to 1–5 latrines 250 m^{-1} along the southern and western edges, whereas rabbits were scarce elsewhere (< 0·5 latrines 250 m^{-1}). A total of 436 pigeon lofts was identified across the region, with on average 25·5 ± 37·7 (2–550) pigeons per loft. Pigeons were more evenly distributed than rabbits, although there was about a 10-fold variation among territories, from about 0·47 to 4·71 pigeons km^{-2} (2·4 ± 1·2 pigeons km^{-2}). There was no correlation between rabbit and pigeon abundance ($r = -0·37$, $P = 0·262$)

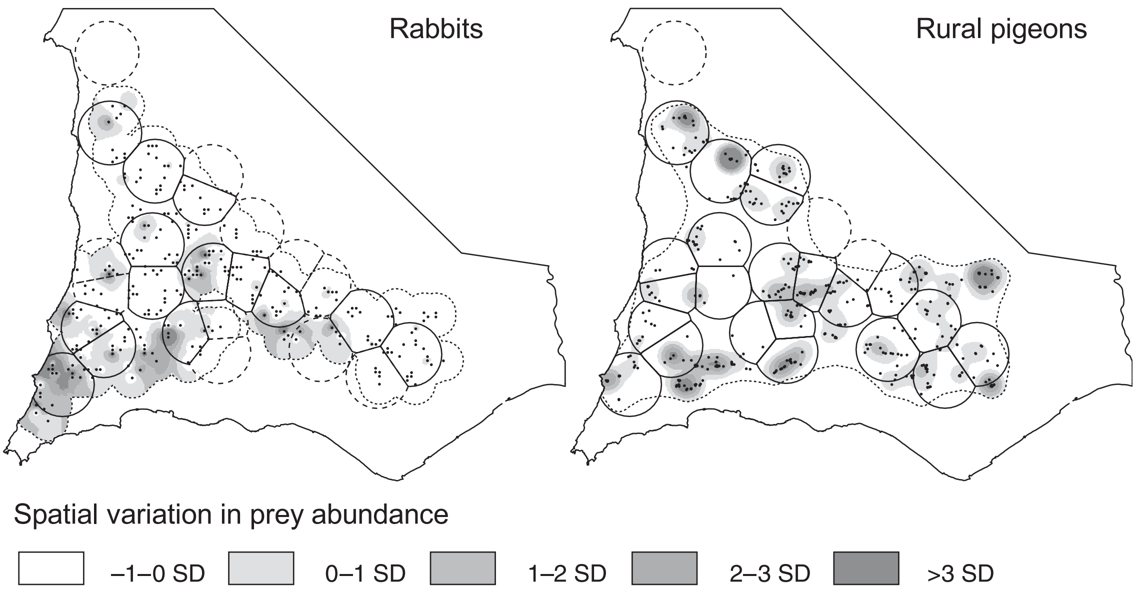

Fig. 2. Interpolated maps of spatial variation in prey abundances across Bonelli's eagles territories in south-west Portugal. Values are SD from the mean, to allow comparisons between maps. Dots are rabbit sampling sites and pigeon lofts. Dotted lines define the interpolation limits. Hatched lines indicate territories with no information on prey abundance.

across the 11 territories for which there was information on both prey.

Table 2. Diet of Bonelli's eagles and prey consumption per pair during the breeding season in south-west Portugal (1992–2001)

Prey categories	*n*	% Numbers	% Biomass	Consumption per pair, mean ± SD (minimum–maximum)
Domestic birds				
Rural pigeon	451	30·1	26·0	48·0 ± 14·6 (17–77)
Racing pigeon	136	9·1	7·2	14·7 ± 7·7 (0–37)
Domestic fowl	52	3·5	4·5	5·4 ± 8·6 (0–37)
Wild birds				
Red-legged partridge	258	17·2	14·9	28·7 ± 11·9 (6–59)
Jay	112	7·5	2·7	12·0 ± 9·2 (0–28)
Other birds	198	13·4	11·4	24·2 ± 18·3 (2–68)
Mammals				
Rabbit	276	18·4	33·2	30·4 ± 11·8 (16–58)
Hare	3	0·2	< 0·1	0·2 ± 0·6 (0–2)
Reptiles				
Ocellated lizard	11	0·7	< 0·1	1·1 ± 1·9 (0–6)

DIET COMPOSITION

Dietary analysis yielded a minimum estimate of 1497 individuals of 32 prey species (see Table S1 in the supplementary material). Numerically, prey of domestic origin comprised 42·7% of the diet (37·7% in biomass), consumed in every year and by all eagle pairs (Table 2). About 70% of these prey items were rural pigeons, but racing pigeons and domestic fowl were also consumed frequently. Considering the estimates of prey intake (Table 2), prey densities and territory sizes, the average proportion of the rural pigeons available per eagle pair that were taken through the breeding season was 17·8 ± 12·6% (5·7–57·8%). Rabbits, red-legged partridges and jays *Garrulus glandarius* L. were the most frequent wild prey, numerically representing 43·1% (50·8% biomass) of the eagle diet (Table 2).

Of the 114 racing pigeons aged through metallic rings, 31·6% were 1 year old or under, 51·8% 2–3 years old and 16·7% more than 4 years old. The remains of freshly killed domestic fowl observed at nests were all from juvenile birds ($n = 12$) whereas 86·2% of the rabbits were adults ($n = 29$). A majority of partridges killed by eagles were males (65·7%; $n = 35$).

TEMPORAL VARIATIONS IN DIET COMPOSITION

Variation in diet between years was analysed for 1993–2000, i.e. when annual samples were sufficiently large (prey per year 185·4 ± 93·1, 65–352). The relative importance of the most frequently consumed items remained largely the same over the study period (Kendall's coefficient of concordance, $W = 0{\cdot}86$, $P < 0{\cdot}001$), with no evidence for consistent trends in the consumption of any prey species (Pearson correlations $-0{\cdot}41 < r < 0{\cdot}57$, $P > 0{\cdot}14$; Fig. 3a). The numeric proportion of rural pigeons was fairly stable (23·1–33·8%), as was that of rabbits (15·4–23·1%) and racing pigeons (6·6–12·6%). The largest variation was recorded for relatively less important prey such as jays (2·0–10·8%) and domestic fowl (1·2–7·1%).

Prey were assigned to 2-week periods from 1 March to 15 June (prey per 2 weeks 210·8 ± 177·6, 44–504) to investigate variations during the breeding season (Fig. 3b). Although there was concordance in diet composition over time (Kendall's $W = 0{\cdot}73$, $P = 0{\cdot}001$), most prey species showed distinctive temporal trends. There were marked declines in the dietary importance of rural ($r = -0{\cdot}91$, $P < 0{\cdot}01$) and racing pigeons ($r = -0{\cdot}96$, $P < 0{\cdot}001$), which halved their overall numeric contribution from a maximum of about 50% in March to a minimum of 23·7% in June. This was largely compensated for by increases in jays ($r = 0{\cdot}91$, $P < 0{\cdot}05$) and a wide group of birds represented in 'other' prey ($r = 0{\cdot}92$, $P < 0{\cdot}01$), from a minimum in the second half

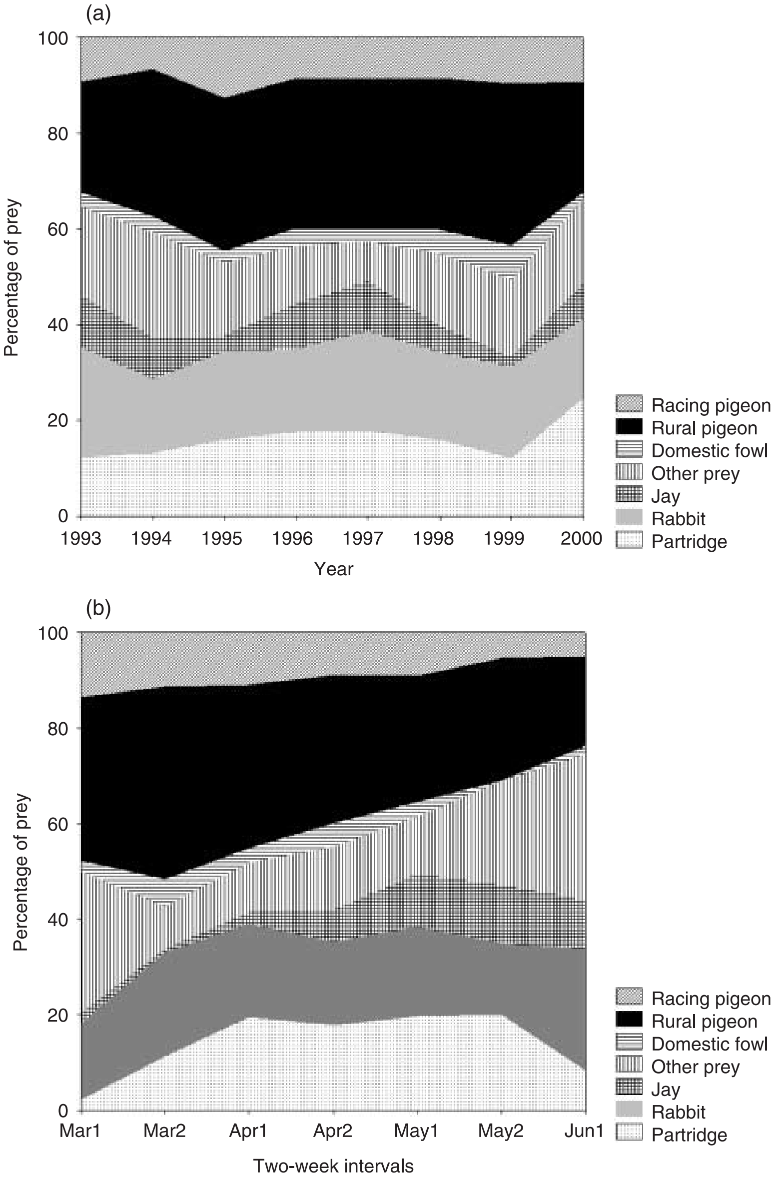

Fig. 3. Variation of Bonelli's eagle diet in south-west Portugal (a) over the years 1993–2000 and (b) across the breeding season 1 March–15 June.

Table 3. Explained variance (R^2), significance levels and directions of association (–, negative; +, positive; ∩, unimodal) for significant relationships between Bonelli's eagle diet and land uses across 20 breeding territories in south-west Portugal

Prey categories	Oak forest	Eucalyptus forest	Scrubland	Farmland	Urban
Domestic prey					
Rural pigeon		–^{a}0·40**			
Racing pigeon	∩0·41**				
Wild prey					
Rabbit					∩0·45**
Partridge	+^{a}0·38**	–^{a}0·33**	∩0·35*	–0·22*	–^{a}0·22*
Jay				∩0·45**	
Other birds		+^{a}0·61***			
Diversity		+^{a}0·33**		∩0·37*	

*$P < 0\cdot05$; **$P < 0\cdot01$; ***$P < 0\cdot001$.
a, Quadratic term.

of March (0·8% and 8·9%) up to a maximum in June (10·2% and 30·5%). Patterns for other prey species were more complex. A unimodal pattern was found for partridges (multiple $r = 0\cdot96$, $P = 0\cdot01$) that increased from about 2% in early March up to a maximum at around 20% in April–May and declined thereafter. The consumption of rabbits did not show any significant trend through the breeding season.

LANDSCAPE EFFECTS ON DIET COMPOSITION

Land use explained 22–61% of variation in the dietary proportions of both domestic and wild prey (Table 3). The consumption of rural pigeons declined steadily with increasing eucalyptus cover, while racing pigeons showed unimodal responses to Mediterranean oak forests. The intake of domestic fowl was apparently not affected by landscape composition. Partridge consumption increased with oak forests, declined with eucalyptus cover, farmland and urban areas, and responded unimodally to scrubland. The other prey category and diet diversity increased markedly with eucalyptus plantation cover. Diet diversity and the intake of jays showed unimodal responses to farmland. The unimodal response to urban areas was the only landscape effect recorded for rabbits.

FUNCTIONAL RESPONSES AND PREY SWITCHING

A type II functional curve significantly explained half the variation in rabbit consumption (Fig. 4a), while there was no support for alternative response types (ΔAICc > 2·5). The abundance of rabbits also affected the consumption of other prey, with less rural and racing pigeons eaten in territories with more rabbits (Fig. 5a). The inverse relationship between rabbit abundances and partridge consumption was marginally significant ($P < 0\cdot051$). When controlling for the effects of rural pigeon densities using partial correlations, rabbit abundances still showed significant inverse relationships with rural ($r = -0\cdot63$, $P = 0\cdot050$) and racing pigeons ($r = -0\cdot75$, $P = 0\cdot013$) and approached significance with partridges ($r = -0\cdot57$, $P = 0\cdot085$). Although the functional response curve accounted for < 25% in the consumption of rural pigeons (Fig. 4b), the type II model still performed better than the two alternative models (ΔAICc > 2·5). The number of rabbits eaten was inversely related to pigeon densities (Fig. 5b), even after controlling for rabbit abundances using partial correlations ($r = -0\cdot81$, $P = 0\cdot004$). Shannon diet diversity computed at the species level was unrelated to the abundance of both rabbits ($r = 0\cdot33$, $P = 0\cdot317$) and pigeons ($r = -0\cdot27$, $P = 0\cdot280$).

The ratio of pigeons to rabbits consumed per eagle pair increased significantly with the ratio of pigeon to rabbit abundances (Fig. 6). The frequency-dependent parameter b was significantly smaller than unity (95% confidence interval 0·09–0·42), suggesting that prey selection was inversely frequency dependent. This indicated that at low pigeon to rabbit ratios eagles captured more pigeons than might be expected, whereas more rabbits than expected were taken in breeding territories with high pigeon to rabbit ratios. There was therefore no evidence of Bonelli's eagles switching to pigeons when the abundance of rabbits declined in relation to that of pigeons. Instead, the less abundant prey always tended to be consumed more than expected.

Discussion

THE DIETARY ROLE OF DOMESTIC VS. WILD PREY

Domestic prey played a major role in the diet of Bonelli's eagles in south-west Portugal. This resulted primarily from the high consumption of rural pigeons, which was the single most important prey item, although racing pigeons and domestic fowl were also taken frequently. These were major dietary components for a very large proportion of this eagle population, and their importance was consistently high over a decade. Domestic prey was particularly important early in the breeding season when it accounted for more than half the prey eaten. Overall, however, wild prey such as rabbits, partridges and jays were a major dietary component of most eagle pairs. These species, together with several minor avian prey such as cattle egrets *Bubulcus ibis* L., thrushes *Turdus* spp. and woodpeckers *Picus viridis* L., became increasingly important later in the breeding season.

The importance of pigeons in south-west Portugal, particularly that of rural pigeons, was higher than that reported for most Bonelli's eagle populations (39·2% vs. 19·2 ± 12·8%, 1·5–39·0%, $n = 14$; Valkama *et al.* 2005). Although some studies found a relatively high consumption of woodpigeons *Columba palumbus* L. (Real 1991; Ontiveros, Pleguezuelos & Caro 2005), the overall dietary contribution of pigeons was still lower than that observed in south-west Portugal. Only in the diet of peregrine falcons and sometimes in goshawks

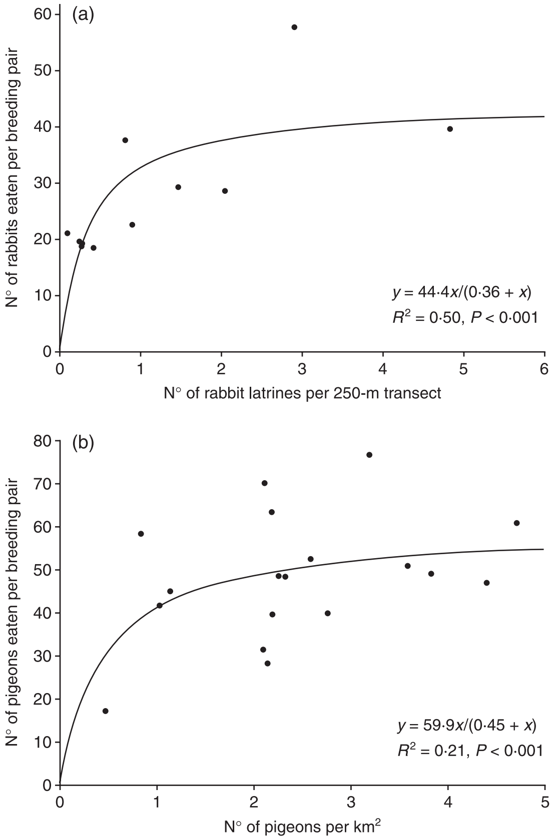

Fig. 4. Functional responses of Bonelli's eagles to variation among territories in the abundance of (a) rabbits ($n = 11$) and (b) rural domestic pigeons ($n = 18$).

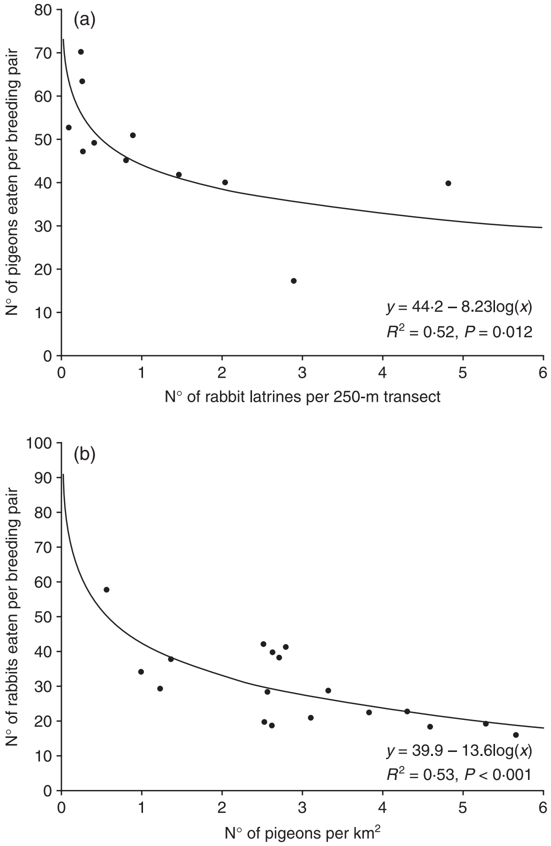

Fig. 5. Relationships between (a) rabbit abundance and rural pigeon intake, and (b) rural pigeon abundance and rabbit intake, across Bonelli's eagle territories in south-west Portugal.

Accipiter gentilis L. have similarly high frequencies of rural and racing pigeon predation been reported (Shawyer, Clarke & Dixon 2000; Henderson, Parrott & Moore 2004; Valkama *et al.* 2005). Bonelli's eagle is thus one of the raptors showing the highest potential conflict with pigeon fanciers.

When only wild prey is considered, the dietary patterns observed in south-west Portugal shared many similarities with those reported elsewhere for breeding Bonelli's eagles. These eagles frequently feed on rabbits (Real 1991; Valkama *et al.* 2005), although this prey is generally less important than in many other raptors in the Iberian Peninsula (Delibes & Hiraldo 1981). Conversely, the importance of avian prey tends to be higher than in other Mediterranean eagles, with most studies reporting that partridges, pigeons and corvids are the most frequently eaten birds (Real 1991; Ontiveros & Pleguezuelos 2000; Gil-Sánchez *et al.* 2004; Iezekiel, Bakaloudis & Vlachos 2004).

The dietary importance of wild prey increased through the breeding season, along with a decline in the intake of both rural and racing pigeons. The early peak consumption of pigeons and its subsequent replacement by other prey has been noted elsewhere (Real 1991; Iezekiel, Bakaloudis & Vlachos 2004), and it is often interpreted as resulting from temporal increases in the availability of highly profitable prey such as rabbits and juvenile birds. A similar reasoning may justify the patterns observed in south-west Portugal, where Bonelli's eagles lay their eggs in January–February (L. Palma, unpublished data), when most wild prey species normally taken by these eagles probably occur in lower numbers. These prey then become increasingly available through the breeding season, with different species peaking at different times according to their phenology and behaviour. For instance, the consumption of (mainly male) partridges peaked during the courting period in April–May, when the birds may be more vulnerable to predators. Increases in the consumption of jays and other birds through the season may reflect the progressive emergence of easily captured fledglings. The highest rabbit densities also tended to occur in late spring, but their numbers in the study area were generally low and their consumption was fairly stable through the eagle's breeding season.

WHY DO EAGLES TAKE DOMESTIC PREY?

In this study, none of the hypotheses usually invoked to explain the incidence of high predation rates on domestic prey could be fully supported. Nevertheless, the hypothesis of a feeding specialization by a few individuals (PAH) could be clearly dismissed, as predation on domestic prey was widespread and was not a feature restricted to a few eagle pairs. In contrast, the two other hypotheses gained some partial support, suggesting

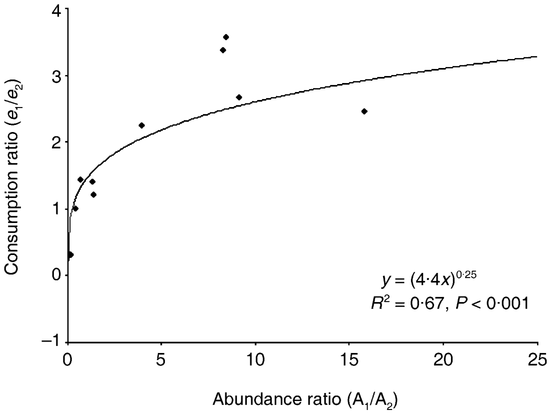

Fig. 6. Frequency-dependent selection curve for Bonelli's eagles preying on rural pigeons (1) and rabbits (2), relating the consumption (e_1/e_2) and availability (A_1/A_2) ratios.

that the heavy predation by Bonelli's eagles on domestic prey recorded in south-west Portugal might result from both a shortage of wild prey, in accordance with APH, and a positive selection of domestic prey, following the VPH.

Compared with other areas, there was a shortage in south-west Portugal of those wild prey species commonly favoured by the Bonelli's eagle, such as rabbits and partridges (Gil-Sánchez 1998). Rabbits were particularly scarce, as they were largely absent from most of the region and their abundance was reduced where they occurred (Palma, Beja & Rodrigues 1999; Beja, Palma & Pais 2007; this study). Unsystematic observations suggested that partridges also occurred at low densities across the region (L. Palma, unpublished data). In contrast, rural pigeons were very abundant through the year. Information from homing pigeon associations suggested that racing pigeons were also very abundant, with at least 10–15 thousand pigeons crossing the study area each week in January–April. Strayed or lost pigeons could thus be commonly found within the study area (L. Palma, unpublished data), presumably providing easy and rewarding prey for raptors (Shawyer, Clarke & Dixon 2000; Henderson, Parrott & Moore 2004).

Breeding territories with the lowest abundance of both wild and domestic prey were probably those with high eucalyptus cover, where there was reduced consumption of rural pigeons and partridges, along with increases in both the intake of minor prey items and diet diversity. Considering the predictions of optimal foraging theory (Stephens & Krebs 1986) and the findings of empirical studies on other birds of prey (Lindén & Wikman 1983; Marchesi, Sergio & Pedrini 2002), these dietary responses are consistent with a shift to low-ranked prey and an associated widening of niche breadth in a situation where there is reduced availability of the most profitable prey. Previous studies and personal observations suggest that both rabbits and partridges avoid eucalyptus landscapes (Palma, Beja & Rodrigues 1999; L. Palma, unpublished data), whereas rural pigeons were scarce because of the effects of marked rural depopulation. A less obvious widening of niche breadth may have occurred in territories with intermediate farmland cover, where diet diversity increased along with a high consumption of jays. This pattern might also be explained by the lower abundance of preferred wild and domestic prey. Indeed, partridges were consumed most frequently in breeding territories dominated by native oak forest and intermediate scrubland cover, where they appeared most abundant (L. Palma, unpublished data), and less with increasing cover by farmland and urban areas. In contrast, rural pigeons were presumably most abundant in farmland, although this was not evident in terms of dietary responses. Rabbits were not responsive to this gradient, probably because land-use influences were confounded by climatic gradients affecting rabbit abundances across the region (L. Palma, P. Beja & M. Pais, unpublished data).

The dietary responses of eagles to variation in the abundance of the most important prey of wild (rabbit) and domestic (rural pigeon) origin also suggested that domestic prey could compensate for the shortage of wild prey, although there was no switching in the traditional sense (Murdoch 1969). Rabbits were clearly the primary prey item, with their consumption following a pronounced type II response curve and the highest intake of both rural and racing pigeons occurring at the lowest rabbit densities. However, eagles also showed a type II functional response to rural pigeons, although much weaker than in the case of rabbits and not the type III sigmoid curve that might be expected if there was switching (Akre & Johnson 1979; Patterson, Benjamin & Messier 1998). Furthermore, there was a negative relationship between the consumption of rabbits and the abundance of rural pigeons, as well as evidence that selection between these two prey was inversely frequency dependent, with pigeons consumed more often than expected at high rabbit densities and the same occurring for rabbits at high pigeon densities. This may tentatively be related to the critical dietary role of pigeons early in the breeding season, when there seems to be low abundance of most wild prey, including rabbits. In these circumstances, many rural pigeons may be taken in areas where the abundance of rabbits will increase following their spring reproductive peak. Later in the season, rabbits may be taken more often than expected, as they could be more profitable to Bonelli's eagles than pigeons. Testing this hypothesis would require more detailed information on the seasonal variation in the abundance of wild and domestic prey and their relative profitability to the predator.

Taken together, our results suggest that rural pigeons should be regarded as complementary prey items to rabbits and partridges, rather than an alternative prey that is consumed only where there is a shortage of these primary wild prey. Conversely, racing pigeons were probably taken opportunistically because of their high vulnerability. Where the most profitable wild and domestic prey were scarce, the eagles widened their niche breadth and consumed a range of relatively minor avian prey. This is therefore a complex multispecies system that supports the view that predator conflicts cannot be addressed as a single pairwise predator–prey interaction (Graham, Beckerman & Thirgood 2005).

MANAGEMENT IMPLICATIONS

Conflicts with pigeon fanciers are considered a major threat for the conservation of some Bonelli's eagle populations (Real *et al.* 2001; Carrete *et al.* 2002). The situation is probably not yet a serious one in south-west Portugal, despite eagles generally showing high predation rates on domestic pigeons. Enquiries to rural pigeon breeders ($n = 326$) revealed that they generally attributed a low value to pigeons, regarding them simply as pets and home-grown food (93·3%), with only 6·7% of those censused making use of pigeons for trade, racing or recreational shooting (L. Palma, unpublished data). Most rural pigeon breeders disregarded eagles as a significant threat as they were generally unaware of their presence, except possibly where predation was concentrated at particular lofts. In the case of racing pigeons, Bonelli's eagles killed a very small proportion of the huge numbers released regularly, indicating that they do not represent a real threat to pigeon races. Overall, there is therefore a relatively benign situation, justifying the lack of active persecution that is apparent elsewhere (Real *et al.* 2001). However, given the dietary importance of domestic pigeons for these eagles, management options reducing the potential conflicts with pigeon breeders should not be disregarded, as it is possible that less-tolerant attitudes may develop in the near future.

Rearing pigeons in specially designed lofts might be an effective means of reducing potential conflicts with pigeon breeders while maintaining an adequate food supply for Bonelli's eagles. Lofts could be established by conservation organizations in territories with depleted food resources and in areas where persecution might be a problem. Pigeons provided at these 'conservation' lofts might act as diversionary food to reduce predatory pressure upon both game and racing pigeons (Carrete *et al.* 2002), similar to the lofts with low-value pigeons that have been used elsewhere to deflect predation by peregrine falcons (Shawyer, Clarke & Dixon 2000). In south-west Portugal, this management approach could help to offset a possible medium-term decline in traditional pigeon rearing associated with rural abandonment, with negative effects on the eagle's food resources. It might also help to reduce predation on valuable game species, such as partridges, given the development of small game hunting in this region. Providing health-screened pigeons could also reduce the infection of eagles by the protozoan *Trichomonas gallinae* Rivolta, which is a significant cause of nestling mortality in this and other Bonelli's eagle populations (Höfle *et al.* 2000; Real, Mañosa & Muñoz 2000). These applications of rural pigeons as a conservation tool require testing in south-west Portugal and elsewhere, to evaluate their potential benefit to eagle breeding success, disease prevalence and conflicts with people.

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Supplementary material

The following supplementary material is available as part of the online article (full text) from http://w.w.w.blackwell-synergy.com.

Table S1. Detailed results of Bonelli's eagle diet analysis.