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Large-scale spatio-temporal shifts in the diet of a predator mediated by an emerging infectious disease of its main prey

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ABSTRACT

Aim To explore the influence of an emerging infectious disease (EID) affecting a prey species on the spatial patterns and temporal shifts in the diet of a predator over a large geographical scale. We reviewed studies on the diet of Bonelli's eagles (*Hieraaetus fasciatus*) in order to determine the repercussions of the reduction in the density of its main prey, the rabbit (*Oryctolagus cuniculus*), caused by outbreaks of rabbit haemorrhagic disease (RHD) since 1988.

Location Western continental Europe.

Methods We compiled published and unpublished information on the diet of breeding Bonelli's eagles from Portugal, Spain and France for a 39-year study period (1968–2006). Nonparametric tests were used in order to analyse temporal shifts in diet composition and trophic diversity (H') between the periods of 'high' (before outbreak of RHD) and 'low' rabbit density (after outbreak of RHD). A combination of hierarchical agglomerative clustering and non-metric multidimensional scaling (NMDS) analyses were used to test for the existence of geographical patterns in the diet of Bonelli's eagles in each period.

Results The diet of the Bonelli's eagle consisted of rabbit (28.5%), pigeons (24.0%), partridges (15.3%), 'other birds' (11.6%), 'other mammals' (7.1%), corvids (7.0%), and herptiles (6.4%). However, RHD had large consequences for its feeding ecology: the consumption of rabbits decreased by one-third after the outbreak of RHD. Conversely, trophic diversity (H') increased after outbreak of RHD. At the same time, the analyses showed clear geographical patterns in the diet of the Bonelli's eagle before, but not after, RHD outbreak.

Main conclusions Geographical patterns in the diet of the Bonelli's eagle in western Europe seem to be driven mainly by spatio-temporal variation in the abundance of rabbits and, to a lesser extent, by the local (territorial) environmental features conditioning the presence and density of alternative prey species. We show that an EID can disrupt predator–prey relationships at large spatial and temporal scales through a severe decline in the population of the main prey species. Hence we argue that strict guidelines should be drawn up to prevent human-aided dissemination of 'pathogen pollution', which can threaten wildlife not only at the population and species level but also at the community and ecosystem scale.

Keywords

Bonelli's eagle, conservation, diet, emerging infectious disease, *Hieraaetus fasciatus*, rabbit, rabbit haemorrhagic disease, spatial patterns, temporal shifts, western Europe.

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INTRODUCTION

The study of food habits may bring to light key information for understanding many of the life-history strategies of a predatory species (Newton, 1979; Partridge & Green, 1985; Dayan & Simberloff, 1996; Geffen *et al.*, 1996). Many interactions among predators and their prey can only be investigated through an in-depth exploration of the trophic spectrum. However, dietary studies are frequently performed at the local scale, which generally prevents the inference of ecologically relevant conclusions. Comprehensive knowledge of the feeding ecology of a species can therefore only be addressed when comparing its food habits at large spatial scales (Lozano *et al.*, 2006), i.e. across different geographical regions and/or habitats in the case of vertebrate predators. This type of approach may allow us to detect patterns and variations that can be related to other ecological traits (Futuyma & Moreno, 1988; Gompper & Gittleman, 1991). For instance, some conservation implications can be derived from these studies, which constitute a key factor when threatened species such as vertebrate predators are considered (Partridge & Green, 1985; Gompper & Gittleman, 1991).

Ecological processes also vary over time (Levin, 1992; Kronfeld-Schor & Dayan, 2003) and predator–prey interactions may be linked to different temporal patterns, including cycles and outbreaks in the prey populations (Ostfeld & Keesing, 2000; Hanski *et al.*, 2001; Koenig & Liebhold, 2005), leading to temporal shifts in the predator's diet at different scales. In fact, there are many ecosystems that are characterized by the temporary availability of higher or lower than normal levels of resources, or pulsed resources that may have important effects on community structure (Ostfeld & Keesing, 2000; Sánchez-Zapata *et al.*, 2007).

Temporal changes in the abundance of prey may also be related to emerging infectious diseases (EIDs) of free-living wild animals (Daszak *et al.*, 2000), currently regarded as one of the major threats to wildlife worldwide (Daszak *et al.*, 2000, 2003). This might result in diverse ecological consequences affecting population, community and ecosystem regulation. Such changes may also involve predator–prey interactions, as the optimal foraging theory predicts that a predator will show a low trophic diversity when the preferred prey is abundant, and vice versa (Stephens & Krebs, 1986; Futuyma & Moreno, 1988). Consequently, the predator might include new alternative prey sources if the preferred prey is scarce (Angelstam *et al.*, 1985), as was recently described for an Iberian broad-scale predator–prey system (Moleón *et al.*, 2008).

Here we examine a predator, the Bonelli's eagle (*Hieraaetus fasciatus* Vieillot), whose diet has been extensively studied at a continental scale in Europe, and its main prey, the rabbit (*Oryctolagus cuniculus* Linnaeus), which has suffered outbreaks of EID during the 20th century, to explore the spatial patterns and temporal shifts in the diet of the predator over a large geographical scale.

The Bonelli's eagle is a medium to large sized non-migrant raptor, irregularly distributed throughout Southeast Asia, the Indian subcontinent, the Middle East and the Mediterranean coast (Ferguson-Lees & Christie, 2001). The European population is classified as endangered due to the decline suffered from the 1970s to the early 1990s (Tucker & Heath, 1994; Real *et al.*, 1996), with the scarcity of trophic resources being a contributing factor (Real, 2004). It is well known that the most important prey for the Bonelli's eagle are lagomorphs, partridges, other similar-sized birds such as pigeons, and lizards (Ferguson-Lees & Christie, 2001). In fact, the Bonelli's eagle is one of the diurnal raptors whose diet has been most studied, so there are numerous works dealing with this aspect, mainly carried out in Europe (e.g. Jordano, 1981; Palma *et al.*, 1984, 2006; Real, 1987; Salvo, 1988; Simeon & Wilhelm, 1988; Rico *et al.*, 1990; Leiva *et al.*, 1994; Martínez *et al.*, 1994; Gil-Sánchez, 1998; Gil-Sánchez *et al.*, 2004; Iezekiel *et al.*, 2004; Ontiveros *et al.*, 2005). However, the previous studies were made at a local scale, over short time periods (but see Real, 1987; Gil-Sánchez *et al.*, 2004; Palma *et al.*, 2006) and they were largely limited merely to describing the composition of the diet (but see Gil-Sánchez, 1998; Gil-Sánchez *et al.*, 2004; Ontiveros *et al.*, 2005; Palma *et al.*, 2006). Nonetheless, these studies offer an excellent opportunity to review the feeding ecology of this species across a large geographical scale (the European continent).

One of the main prey species of the Bonelli's eagle in Europe is the rabbit (see aforementioned references), a native species in the Iberian Peninsula but currently showing a broad human-induced distribution throughout the continent (Thompson & King, 1989; Angulo & Cooke, 2002; Villafuerte, 2007). The rabbit population suffered an important reduction and fragmentation in the majority of its European range at the end of the 1980s and the beginning of the 1990s due to rabbit haemorrhagic disease (RHD) (Fa *et al.*, 1999; Fenner & Fantini, 1999; Calvete, 2006; Virgós *et al.*, 2007), an outbreak facilitated by human intervention via host (and parasite) translocations, mostly undertaken by game managers (Villafuerte *et al.*, 1995). This outbreak resulted in a loss of *c.* 50–80% of the Mediterranean population (Ceballos, 1991; Fenner & Fantini, 1999; Angulo & Cooke, 2002; Virgós *et al.*, 2007; Moleón *et al.*, 2008), which constitutes a valuable broad-scale 'natural experiment' to investigate the ecological consequences of prey crashes.

Our main aims are: (1) to describe geographical patterns in the diet of the Bonelli's eagle across western Europe, and (2) to analyse long-term trophic shifts in relation to disease mediated reductions in rabbit availability.

MATERIALS AND METHODS

Compilation and standardization of diet data

We compiled published and unpublished information on the diet of the Bonelli's eagle spanning the period 1968–2006 from Portugal, Spain and France, where 80% of the European

Figure 1 Geographical location of the studies used in this review of the Bonelli's eagle (*Hieraaetus fasciatus*) in western Europe (see Appendix S1 for definition of territory abbreviations). Black ellipses: data before the outbreak of rabbit haemorrhagic disease (RHD); white ellipses: data after the outbreak of RHD.

population of this species is present (Real, 2004; Fig. 1). The data belonged to 111 different breeding territories, well distributed across 15 geographical areas (Fig. 1; see Appendix S1 in Supporting Information for more details), and were collected during the eagle's breeding season, from February to June (Arroyo *et al.*, 1995; Gil-Sánchez, 2000), to avoid seasonal variations.

To minimize biases of sampling methods and to make the data from different sites comparable, we only used studies employing intensive direct observations, observations of prey recently deposited in nests and the results from pellet analyses, which were shown to be the best methods for assessing and comparing the diet in the Bonelli's eagle (Real, 1996), as was also the case for another similar species, the booted eagle (*Hieraaetus pennatus* Gmelin; Martínez, 2002). We discarded all territories with $n < 20$ prey items (see Ontiveros *et al.*, 2005). The between-year changes in the diet of this raptor are of small magnitude (Gil-Sánchez *et al.*, 2000, 2004; Moleón, 2007a), partially due to the absence of marked cycles in the population dynamics of the prey of the Bonelli's eagle. Consequently, as few localities had a large sample size for a single year, all the study years were pooled together for each locality (though see below). This method, broadly used in similar studies (e.g. Herrera & Hiraldo, 1976; Jaksic & Marti, 1981; Donázar *et al.*, 1989; Watson, 1997), masks short interannual oscillations in diet, which is a desirable condition for inferring geographical patterns at a continental scale (Donázar *et al.*, 1989).

However, some variations at the long-term scale have been described by Real (1987). Thus, we explore the diet of the Bonelli's eagle considering two different long time periods (about two decades each) well differentiated with regard to the abundance of the eagle's main prey – rabbits – because of the effects of RHD. Due to the potential influence of strong variations in rabbit density in the eagle's trophic pattern, we classified each sample territory as before (a period of 'high' density of rabbits) or after (a period of 'low' rabbit density) the disease (Moleón *et al.*, 2008). The date of the outbreak in each locality was taken from the hunting bag data of the Ministry of Agriculture, Fisheries and Food of Spain and by consulting the literature (Real, 1991; Fernández, 1993; Tella & Mañosa, 1993; Mañosa, 1994; Villafuerte *et al.*, 1994, 1995; Marchandeau *et al.*, 1998; Fenner & Fantini, 1999; Martínez & Calvo, 2001; Martínez & Zuberogoitia, 2001). The Algarve (southern Portugal) information was included in the after RHD data set (Palma *et al.*, 2006), despite the fact that this area did not seem to suffer from an outbreak of RHD. This resulted in a total, final sample size of 44 territories before the RHD outbreak and 81 after RHD, 14 of them having data from both before and after the disease (see Appendix S1). For both periods, we gathered data from areas with either high or low densities of rabbits (see the rabbit density distribution map in Blanco & Villafuerte, 1993; Virgós *et al.*, 2007).

Prey species were grouped into seven different categories: rabbit, 'other mammals', partridges (mainly *Alectoris rufa* L.), pigeons (*Columba* spp.), corvids, 'other birds', and herptiles (mainly *Lacerta lepida* Daudin). These groups were delimited following criteria based on taxonomic/morphological affinities among prey species and their weight in the eagle's diet, so that each one of these groups was the most frequent one in at least one territory. The data were analysed by comparing the frequency of occurrence of each group over the total of prey items, as is common in raptor diet studies (e.g. Sánchez-Zapata & Calvo, 1998; Gil-Sánchez & Pleguezuelos, 2001; Palma *et al.*, 2006). Percentage values were not transformed in order to preserve the relative importance of each dietary group.

Influence of RHD in temporal and geographical diet patterns

To explore the influence of RHD in the food spectrum of the Bonelli's eagle, we compared the 14 territories (Catalonia, north-eastern Spain: $n = 9$ territories; Navarra, northern Spain: $n = 1$ territory; Provence, southern France: $n = 4$ territories) where the diet was monitored before and after RHD. Specifically, we tested for variations in the percentage of rabbits in the diet in the two periods by means of nonparametric tests. Due to the geographical proximity of the previous subset of territories (see Fig. 1), this comparison was also undertaken taking into account all 111 territories. Nonparametric procedures were also used to look for variations in the trophic diversity between the two periods, both for these 14 territories and for the total number of territories. In order to calculate the trophic diversity, we used the Shannon–Weaver formula (ln) from the frequency of occurrence of each of the previous seven prey groups (Weaver & Shannon, 1949). Then, we explored the associations in the diet of the Bonelli's eagle between each prey group and each one of the other prey groups in the subset of 14 territories for each period (before and after RHD) by means of correlation analyses.

Because diet composition showed significant differences related to the appearance of RHD (see Results), the analyses of geographical trends in diet were also treated separately for each period. We explored the geographical taxonomic composition of the diet of the Bonelli's eagle by means of multivariate procedures using the PRIMER package (Clarke & Gorley, 2001). Firstly, we built a triangular matrix of dissimilarity in diet composition (expressed as percentage of the total diet represented by each one of the seven prey categories considered) among different territories, using the Bray–Curtis dissimilarity measure (Bray & Curtis, 1957; Mabragaña & Giberto, 2007). As mentioned above, datasets obtained in each territory were treated by separating those pertaining to periods before the RHD outbreak from those pertaining to periods after RHD.

To test geographical grouping of diet data, non-metric multidimensional scaling (NMDS) was used as the ordination method. NMDS positions samples in a two-dimensional ordination plot, so that each relative distance (d_{jk}) between the jth and kth sample points in the plot reflects their relative dissimilarity (δ_{jk}), with the most similar samples occurring closer together (Clarke & Warwick, 2001). The badness-of-fit (or *stress* value) of the nonparametric monotonic regression between the set of distances d_{jk} among sample points in the ordination diagram obtained and the corresponding dissimilarity values δ_{jk} is minimized by an iterative algorithm, so that if $d_{jk} = \hat{d}_{jk}$ (where $\hat{d}_{jk}$ is the distance predicted from the fitted regression line corresponding to dissimilarity δ_{jk}) for all $n(n-1)/2$ distances included, the stress is zero (Clarke & Warwick, 2001). Empirical evidence and simulation studies have shown that a stress value of < 0.2 gives an ordination sufficient to be interpreted in ecological terms (Clarke & Warwick, 2001). Complementarily, hierarchical agglomerative clustering was performed on the same triangular matrix of Bray–Curtis dissimilarity, using the complete linkage method. The combination of clustering and ordination analyses is a very effective way of checking the adequacy and mutual consistency of both sample representations (Clarke & Warwick, 2001). Groups obtained by clustering were then superimposed on the NMDS ordination, and the significance of the difference among groups was analysed using one-way ANOSIM (analysis of similarities) design, under the null hypothesis of no difference in diet composition among groups (Clarke & Green, 1988). In this analysis, the test statistic R measures the degree of discrimination between the groups, and a permutation procedure (based on 5000 permutations of the original dataset) is used to calculate the significance level. The overall significance level was corrected for multiple tests by means of the Bonferroni correction. Finally, Bray–Curtis dissimilarities among these groups were calculated using the SIMPER (similarity percentages) procedure (Warwick *et al.*, 1990; Clarke, 1993), so that dietary items that consistently showed a high contribution to dissimilarities between paired groups were identified; taxa were listed in decreasing order by their average contribution to the total average dissimilarity, with a cut-off at 50% of cumulative average dissimilarity.

RESULTS

Overall diet

Pooling together both periods (before and after RHD), a total of 10,203 prey items ($n = 2939$ prey before RHD and $n = 7264$ prey after RHD) were analysed. The most frequent prey for the Bonelli's eagle in western Europe over the last four decades was the rabbit (28.5% of prey items), followed by pigeons (24.0%), partridges (15.3%) and 'other birds' (11.6%). 'Other mammals' (7.1%), corvids (7.0%) and herptiles (6.4%) were less frequently consumed (see Appendix S1). Mean trophic diversity (H') was 1.43 (SD = 0.30). A minimum of 112 prey species (mostly birds) were included in the diet of the Bonelli's eagle in western Europe (see Appendix S2).

Among the peculiar prey, various species of mammalian ($n = 6$ species) and avian predators ($n = 12$ species; eight diurnal and four nocturnal) stand out, as well as other large birds, such as *Ardea cinerea*, *Phalacrocorax aristotelis*, *Podiceps cristatus*, *Larus* spp., *Tetrax tetrax*, *Phasianus colchicus* and *Corvus corax* (see Appendix S2). The big mammals, such as *Bos taurus* and *Ovis aries*, were presumably consumed as carrion, despite scavenger habits having rarely been reported for this raptor (Avella, 1978; Kumar, 1993).

Temporal patterns in diet and influence of RHD

We found a mean significant difference of about one-third fewer rabbits in the diet after RHD than before it, both for the subset of 14 territories (Wilcoxon $W = 17$; $P < 0.05$) and in the total number of territories (Mann–Whitney $U = 1126.0$; $P < 0.01$). This reduction was mainly compensated for by the increased frequency of occurrence in the diet of pigeons and

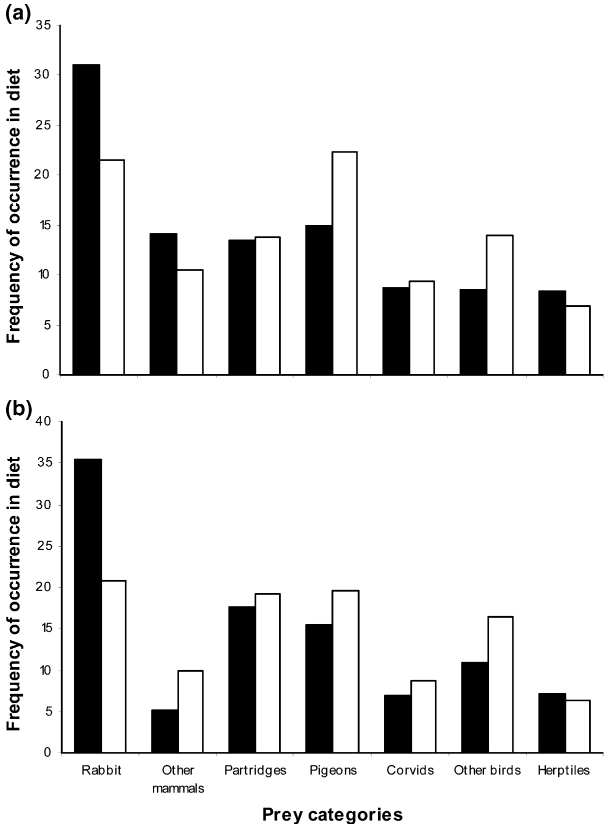

Figure 2 Average diet of the Bonelli's eagle (*Hieraaetus fasciatus*) before and after the outbreak of rabbit haemorrhagic disease (RHD), either in the subset of 14 territories having data from each period (before and after RHD outbreak; plot a) or the total number of territories (n = 111; plot b). Black bars, before RHD outbreak; white bars, after RHD outbreak.

'other birds' (Fig. 2; see also Appendix S1). Trophic diversity did not exhibit temporal differences in the set of 14 territories (Wilcoxon $W = 43$; $P > 0.05$; H' before RHD = 1.55; H' after RHD = 1.57), but important increases in H' were found after RHD (Mann–Whitney $U = 1058.5$; $P < 0.001$; see Appendix S1 for H' values) in all territories together.

The relationship between rabbits and the other prey groups in the diet of the Bonelli's eagle remained the same between the two periods (before and after RHD outbreak), so that the proportion of rabbits in the diet was inversely related to 'other mammals', pigeons, corvids and 'other birds'. However, the robustness of the previous associations was generally lower after than before RHD. Other associations among prey categories were also detected, the negative association among partridges and 'other mammals' and 'other birds', which appeared after RHD, being especially notable (Table 1).

Geographical patterns in diet and influence of RHD

NMDS performed on dietary data before the outbreak of RHD resulted in an interpretable two-dimensional ordination, as the stress value was 0.12 (Fig. 3), which consequently tolerates the superimposition of hierarchical agglomerative clustering. Clusters superimposed at the 80% dissimilarity level onto this NMDS ordination confirmed the adequacy of the NMDS representation, as it did not distort the ordination plot and showed differentiation between three groups of territories (Fig. 4): group 1 is the bigger cluster, and it is also the more heterogeneous as it is formed by a series of territories spread along the Spanish Mediterranean coast (five territories located in central-southern Murcia, 11 in Alicante, five in Catalonia, and single territories in Almería and southern France), plus distinct territories in southern Navarra, Madrid and Toledo; group 2 is a small scattered cluster of three territories in north-west Murcia and one in Alicante; group 3 mainly contains territories of Catalonia (n = 8) and southern France (n = 4), although it also includes one in northern Navarra and one in Málaga (Fig. 4). When considering a level of 60% dissimilarity, groups 1 and 3 can be subdivided into three subgroups each, while group 2 remains undivided (Fig. 4).

ANOSIM confirmed these differences to be significant (Bonferroni-corrected level) at the 80% dissimilarity level (global $R = 0.616$, $P < 0.001$); however, significance is only partial at the 60% dissimilarity level, as although within each group global R ANOSIM is significant, pairwise tests failed to find differences between subgroup 3A (formed

Table 1 Correlation matrix showing the relationships between each prey group with each one of the other prey groups in the diet of the Bonelli's eagle (*Hieraaetus fasciatus*) (relative frequency values; n = 14, i.e. there are 14 territories with data for each analysed period).

	% Rabbit	% Other mammals	% Partridges	% Pigeons	% Corvids	% Other birds	% Herptiles
% Rabbit	–	−0.258*	0.153	−0.277*	−0.480***	−0.277*	0.082
% Other mammals	−0.501***	–	−0.268*	−0.137	−0.060	−0.196	0.155
% Partridges	0.037	−0.189	–	−0.223*	−0.208	−0.336**	−0.107
% Pigeons	−0.338*	−0.121	−0.576***	–	−0.161	−0.306**	−0.210
% Corvids	−0.455***	0.361*	−0.071	−0.241	–	0.223*	−0.266*
% Other birds	−0.415**	0.173	−0.092	−0.215	0.555***	–	−0.170
% Herptiles	−0.147	0.080	−0.097	−0.222	−0.003	0.176	–

Analyses were independently performed for each period, i.e. before (lower left half) and after (top right half) the outbreak of rabbit haemorrhagic disease (RHD). Spearman rank correlation coefficients (r_s) and levels of significance for the correlation coefficients are given.

Coefficients differing between the periods before and after RHD are underlined.

$^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$; without asterisk, non-significant.

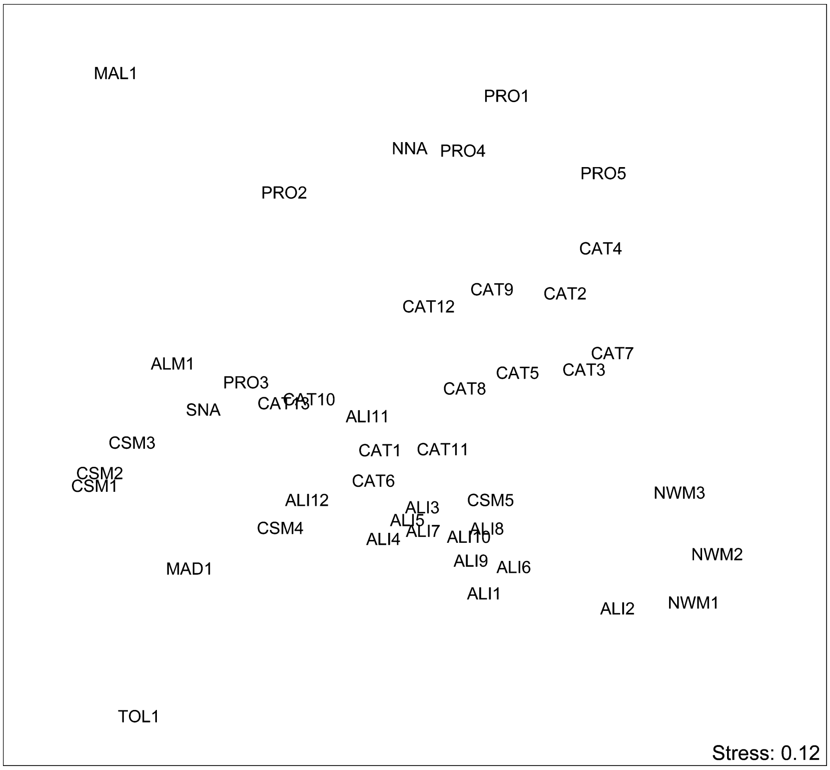

Figure 3 Non-metric multidimensional scaling (NMDS) ordination comparing the diet of Bonelli's eagle (*Hieraaetus fasciatus*) in territories before the outbreak of rabbit haemorrhagic disease (RHD) (see Appendix S1 for definition of territory abbreviations).

exclusively by one territory in Málaga) and the others within group 3 (Table 2). There were, however, only ten and five permutations available for tests of 3A vs. 3B and 3A vs. 3C, respectively.

SIMPER analysis showed the dissimilarity at the 80% level to be a result of differences in the proportion of rabbits (more frequent in group 1), pigeons (characterizing group 2) and 'other mammals' (pre-ponderant in group 3) in dietary composition (Table 2, Fig. 4). When analysing differences among subgroups (60% level of dissimilarity), SIMPER showed that dissimilarity in diet among subgroups 1A–C was due to the fact that Bonelli's eagles ate rabbits more regularly in territories clustered in subgroup 1A (Madrid and Toledo), had a diet richer in pigeons in subgroup 1B (territories in Alicante, Catalonia and central-southern Murcia), and their diet contained a greater proportion of partridges in subgroup 1C (other territories in central-southern Murcia, and several territories in Catalonia, Navarra, Almería, Alicante and southern France; Table 2, Fig. 4). The proportion of partridges, pigeons, 'other mammals' and 'other birds' in the diet were the most representative prey categories determining the differences between subgroups 3A (Málaga), 3B (southern France and Navarra) and 3C (mostly Catalonian territories; Table 2, Fig. 4). The proportions of corvids and herptiles in the diet scarcely contributed to dissimilarities among groups and subgroups.

In contrast, NMDS analyses performed on dietary data of the Bonelli's eagle after the outbreak of RHD resulted in a poor depiction of differences between territories, as the stress statistic was more than 0.2 (Fig. 5). Therefore, differences in prey composition after the disease did not render a spatially recognizable pattern.

DISCUSSION

Prey preferences and effects of RHD on temporal patterns in diet

A substantial long-term change in the composition of the diet of Bonelli's eagles in western Europe was found, related to the RHD outbreak. Overall, rabbit consumption was reduced by a third. This seemed to be in accordance with the global response of vertebrate predators in Mediterranean ecosystems after the outbreak of RHD (Real, 1991; Fernández, 1993; Tella & Mañosa, 1993; Mañosa, 1994; Villafuerte *et al.*, 1996; Martínez & Calvo, 2001; Martínez & Zuberogoitia, 2001; Moleón *et al.*, 2008). In the case of Bonelli's eagles, the reduction of rabbits in the diet (*c.* 30%) did not seem to be proportional to that experienced by the rabbit population in the wild (mean of *c.* 70%; Virgós *et al.*, 2007), thereby suggesting a preference for and a functional response of the Bonelli's eagle to this prey item in western Europe. Because sick rabbits suffering from RHD die suddenly (Marcato *et al.*, 1991), a greater availability of dying rabbits during the eagle's breeding season cannot explain this strong discrepancy, and so an increase in the foraging effort by eagles is presumed (Fernández, 1993). These circumstances could place the Bonelli's eagle in an intermediate position (Pyke *et al.*, 1977; Glasser, 1982; Stephens & Krebs, 1986) between a generalist predator and a typical rabbit specialist, like the Spanish

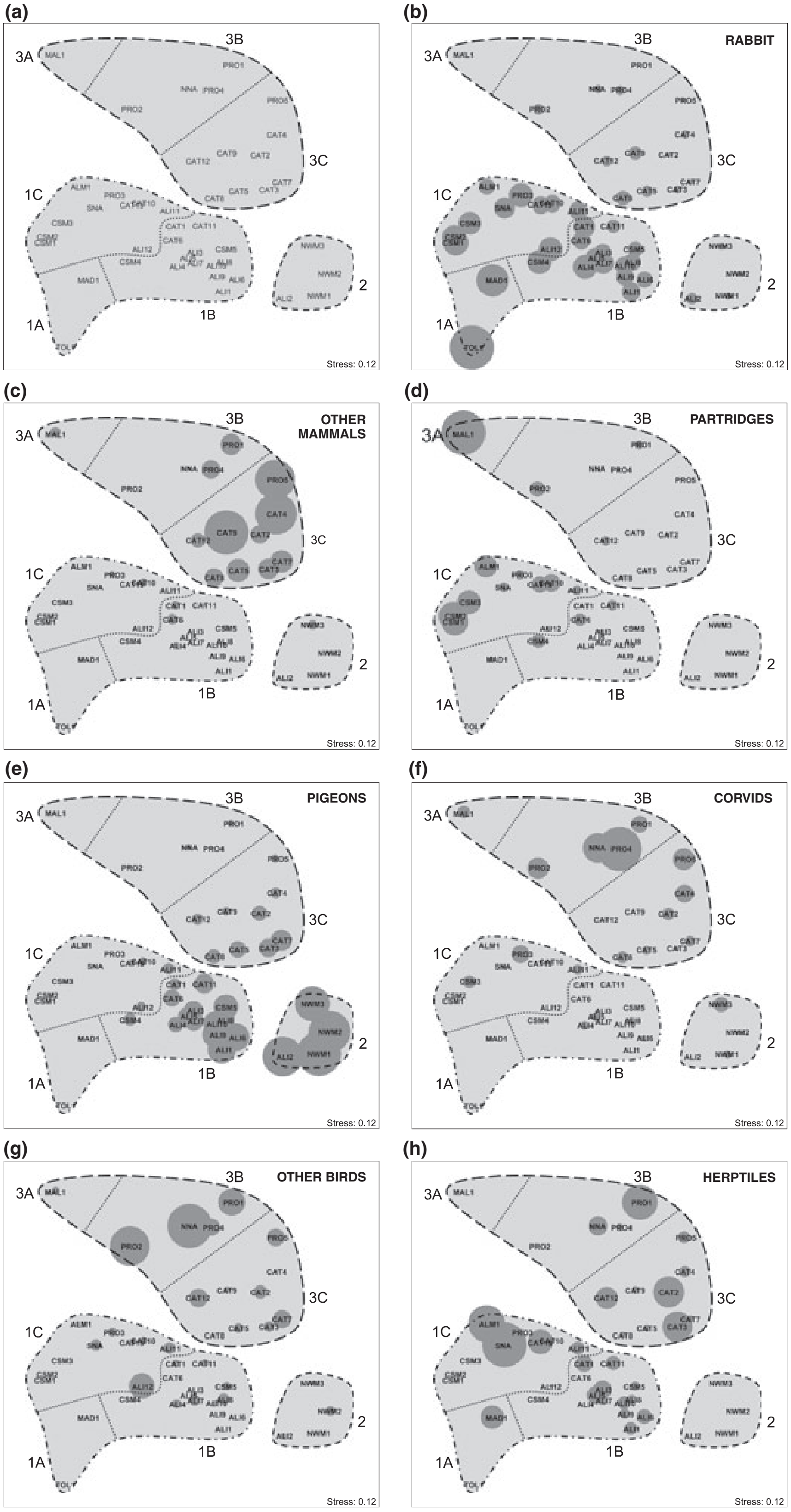

Figure 4 Non-metric multidimensional scaling (NMDS) ordination comparing the diet of Bonelli's eagle (*Hieraaetus fasciatus*) in territories before the outbreak of rabbit haemorrhagic disease (RHD), once hierarchical agglomerative clusters from the same dissimilarities were superimposed on the two-dimensional ordination diagram (see Appendix S1 for definition of territory abbreviations). In plots (b) to (h), the bubble size represents the average proportion of each prey category indicated on each diagram.

Table 2 Results of SIMPER analysis and one-way ANOSIM (*R* values and *P* significance levels) on the average proportion of prey categories of the Bonelli's eagle (*Hieraaetus fasciatus*) that showed the highest contribution (%) to average dissimilarity (AvD) among (a) groups and (b) subgroups in NMDS.

Prey category	Comparisons		
(a)	**1 vs. 2**		
	(AvD = 57.10, $P < 0.001$, $R = 0.649$)		
	Group 1	Group 2	%
Pigeons	22.1	70.9	42.96
Rabbit	47.79	16.55	27.52
	1 vs. 3		
	(AvD = 54.06, $P < 0.001$, $R = 0.589$)		
	Group 1	Group 3	%
Rabbit	47.79	18.03	27.56
Other mammals	2.2	19.71	16.51
Pigeons	22.1	17.81	16.24
	2 vs. 3		
	(AvD = 59.06, $P = 0.001$, $R = 0.655$)		
	Group 2	Group 3	%
Pigeons	70.9	17.81	45.16
Other mammals	3.03	19.71	14.6
(b)	**Within group 1**		
	($P = 0.001$, global $R = 0.757$)		
	1A vs. 1B		
	(AvD = 50.87, $P = 0.008$, $R = 0.986$)		
	Subgroup 1A	Subgroup 1B	%
Rabbit	86.45	42.82	42.96
Pigeons	0	36.24	35.68
	1A vs. 1C		
	(AvD = 44.87, $P = 0.015$, $R = 0.745$)		
	Subgroup 1A	Subgroup 1C	%
Rabbit	86.45	47.01	43.95
Partridges	4.3	27.45	25.88
	1B vs. 1C		
	(AvD = 40.16, $P = 0.01$, $R = 0.699$)		
	Subgroup 1B	Subgroup 1C	%
Pigeons	36.24	6.73	36.81
Partridges	6.53	27.45	27.42
	Within group 3		
	($P = 0.001$, global $R = 0.837$)		
	3A vs. 3B		
	(AvD = 63.21, $P = 0.2$)		
	Subgroup 3A	Subgroup 3B	%
Partridges	71.4	12.2	46.84
Other birds	4.8	22	13.61
	3A vs. 3C		
	(AvD = 69.14, $P = 0.1$)		
	Subgroup 3A	Subgroup 3C	%
Partridges	71.4	5.74	47.48
Pigeons	0	24.48	17.7
	3B vs. 3C		
	(AvD = 43.72, $P < 0.001$, $R = 0.778$)		
	Subgroup 3B	Subgroup 3C	%
Pigeons	7.25	24.48	19.71
Other mammals	10.55	24.92	17.48
Other birds	22	7.68	16.51

imperial eagle (*Aquila adalberti* Brehm: Delibes, 1978; González, 1991; Ferrer & Negro, 2004) or the Iberian lynx (*Lynx pardinus* Temminck: Delibes, 1980; Ferrer & Negro, 2004; Gil-Sánchez *et al.*, 2006).

The idea that rabbits are positively selected prey of the Bonelli's eagles in our study area is also supported by the increase in the eagles' trophic diversity after the decrease of rabbits due to RHD, as the classic predator–prey theory postulates that the prey whose frequency in a predator's diet is negatively related to the predator's trophic diversity is the preferred prey of that predator (Schoener, 1971; Pyke *et al.*, 1977; Stephens & Krebs, 1986; Futuyma & Moreno, 1988). At the local scale, however, it is possible, and predictable (Lozano *et al.*, 2006), to find slight deviations from this general pattern. Thus, in the territories of southern Portugal, where rabbits are scarce, Palma *et al.* (2006) found that pigeons also reduced the trophic diversity, just like rabbits elsewhere, but this could be interpreted as a combined effect of scarcity of rabbits and seasonal dietary changes between the early and late breeding periods (Palma *et al.*, 2006). This could also be the reason why differences in the 14 territories having data for both periods were not significant, although low statistical power could be another viable explanation for this case. In accordance with the hypothesis of the preference for rabbits at a biogeographical scale, previous studies have described a positive selection (Gil-Sánchez, 1998; Moleón, 2007a; Moleón *et al.*, in press) and a functional response (Palma *et al.*, 2006; Moleón, 2007a) of the Bonelli's eagle to this prey at a local level in western Europe. Besides, it has recently been pointed out that non-breeding birds (in the territories) and young Bonelli's eagles (in the juvenile dispersal areas), which have more possibilities to search the most profitable foraging areas, eat more rabbits than breeding territorial birds (Moleón *et al.*, 2007, in press), so confirming the rabbit as essential prey for Bonelli's eagles in continental Europe.

At a western European scale, partridges, pigeons and 'other birds' were the most important secondary prey for Bonelli's eagles before RHD. Coinciding with the irruption of RHD, the role in the eagle's diet of these prey groups – and the other prey groups – generally increased. This scenario was probably the result of two factors. Firstly, the dramatic drop in the rabbit population forced eagles to prey more than usual on alternative prey (for evidence see Moleón *et al.*, 2008). According to the 'alternative prey hypothesis' (Angelstam *et al.*, 1985), the scarcity of rabbits caused by RHD enhanced the importance of other prey for the Bonelli's eagle, which could compensate for the drop in its main prey. Secondly, certain prey, such as gulls, egrets, herons, pheasants or starlings, appeared to have increased in population level since the beginning of 1990s in many parts of the distribution range of the Bonelli's eagle (Martí & del Moral, 2003, and authors' personal observations). In contrast, the red-legged partridge (*Alectoris rufa* L.) population notably decreased after the onset of RHD (Moleón *et al.*, 2008). Subsequently, this combined situation (mainly rabbit rarity (Moleón *et al.*, 2008) and some changes in the

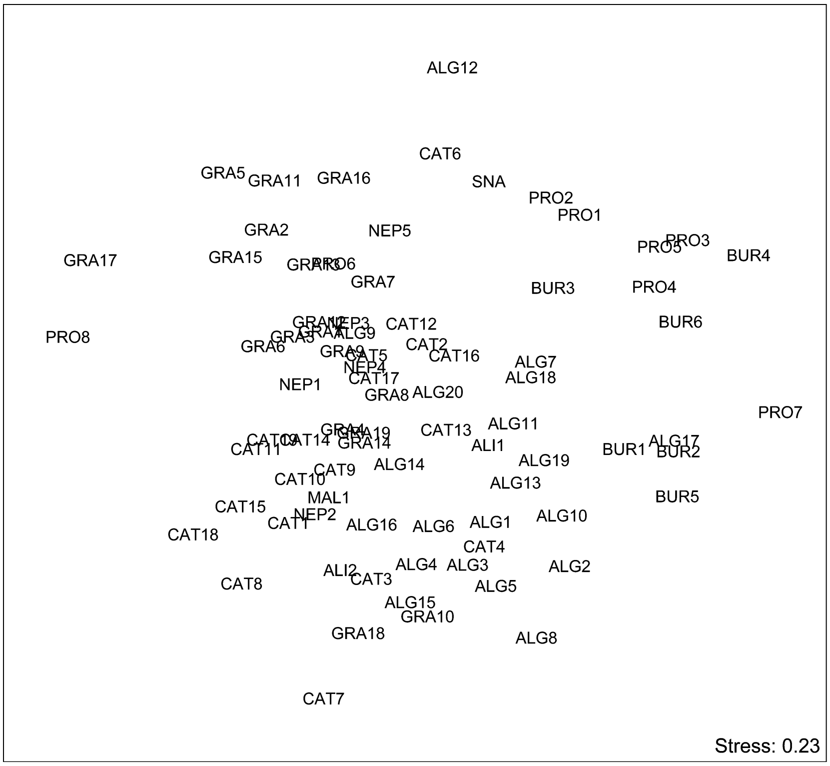

Figure 5 Non-metric multidimensional scaling (NMDS) ordination comparing the diet of Bonelli's eagle (*Hieraaetus fasciatus*) in territories after the outbreak of rabbit haemorrhagic disease (RHD) (see Appendix S1 for definition of territory abbreviations).

alternative prey community) implied new, and more complex, trophic relationships after RHD (Table 1).

Effects of RHD on geographical patterns in diet

Before RHD, we found clear geographical patterns in the diet of the Bonelli's eagle in western Europe, and the fact that rabbits were the main prey determining spatial patterns of grouping supports the idea that rabbits are the eagle's preferred prey in continental Europe (Stephens & Krebs, 1986), as mentioned above. Several spatial tendencies could be elucidated from our data. In general, eagles occupying territories in central Spain and some localities of the Spanish Mediterranean coast primarily consumed rabbits, which agrees with the well-known density distribution map of this prey before RHD (Blanco & Villafuerte, 1993; Virgós *et al.*, 2007). In relation to the substitute prey, the consumption of pigeons was clearly limited to the coastal strip of Spain and France (and southern Portugal; Palma *et al.*, 1984), and 'other mammals' and 'other birds' followed a latitudinal gradient, so that these two categories of prey were more frequently consumed in the northern localities, where the rabbit was clearly scarcer (Blanco & Villafuerte, 1993; Virgós *et al.*, 2007).

The rabbit-related biogeographical pattern in the diet of European Bonelli's eagles was broken after the irruption of RHD. Following an age-structured model (Calvete, 2006) the impact of the disease has been proposed as highly variable in medium-density rabbit populations. The rabbit populations inhabiting the breeding territories of Bonelli's eagles were mainly of low–medium density prior to RHD (Real, 1991), as they occupied habitats of low–medium carrying capacity, such as low-altitude mountains with hard soils poor for rabbits (Fa *et al.*, 1999; Calvete *et al.*, 2004). Therefore, the present distribution of rabbits within the overall breeding range of Bonelli's eagles probably shows no particular geographical tendencies (Fa *et al.*, 1999; Virgós *et al.*, 2003; Calvete *et al.*, 2004; Fernández, 2005; Calvete, 2006), as indeed the diet of our eagles indicated. The predator's spatial trophic patterns seem to be an accurate reflection of the population dynamics and densities of the preferred prey, the rabbit in our case.

In summary, the dietary geographical patterns of Bonelli's eagles in western continental Europe seem to be driven mainly by the spatio-temporal variation in abundance of rabbits and, to a lesser extent, by the local (territorial) environmental features conditioning the presence and abundance of alternative prey species, which acquired more relevance after RHD.

Four decades before RHD, rabbits suffered another strong disease outbreak due to myxomatosis, producing a *c.* 80–90% decrease in the number of rabbits present in the wild (Blanco, 1998; Fenner & Fantini, 1999). Together with RHD, the rabbit population has suffered a dramatic decrease over five or six decades, so that the current densities are about 10% of the original levels (Ceballos, 1991; Blanco, 1998; Fenner & Fantini, 1999; Angulo & Cooke, 2002), which has led to the recent inclusion of the species in the Red List of the mammals of Spain (category VU A2abde; Villafuerte & Delibes-Mateos, 2007). Given that several European predators were sensitive to the first rabbit disease (Delibes, 1978), the trophic patterns of the Bonelli's eagle and other continental predators before myxomatosis were probably even clearer than those found just before RHD. Similarly, the predatory pressure on the alternative or complementary prey should have been even less before myxomatosis.

Potential ultimate effects of RHD on rabbit predators and natural systems

Further research is required to understand the long-term consequences of RHD (and myxomatosis) outbreaks on the population dynamics of the Bonelli's eagle. RHD presumably led to a strong reduction in the energy available for eagles, and exploring the influence of rabbit scarcity on the predator's breeding success and survival may be particularly interesting. In this respect, Gil-Sánchez *et al.* (2004) found no effect of diet and prey availability on the breeding output of the Bonelli's eagle, although they studied a single population of southern Spain where the rabbit is still moderately abundant. In contrast, negative effects of rabbit scarcity have been suggested in other regions with lower rabbit densities, e.g. northern Spain (Real, 1991; Fernández *et al.*, 1998) and southern France (Cheylan, 1981). For instance, Fernández (1993) found that the number of young golden eagles (*Aquila chrysaetos* L.) that successfully fledged decreased by half after the RHD outbreak in a locality in northern Spain.

In addition to the direct effects, the drop in rabbit populations due to RHD stimulated illegal persecution of predators in Spain by small-game hunters (Villafuerte *et al.*, 1998). This probably favoured an increase in the mortality rates in the Bonelli's eagle, as shown for another European raptor, the red kite (*Milvus milvus* L., Villafuerte *et al.*, 1998), because the eagle inhabits lands typically exploited for small-game hunting, and illegal persecution by hunters is one of the two main causes of mortality in this species (Real *et al.*, 2001). Similarly, in some places the Bonelli's eagle is perceived by local people as a threat to their pigeon racing activities. Consequently, the eagle's populations on the Mediterranean coast of Spain (the Spanish region with greatest tradition of pigeon racing and where eagles captured more pigeons anyway before RHD) have suffered marked declines during the last three decades partially due to persecution by pigeon fanciers (Sánchez-Zapata *et al.*, 1995; Real *et al.*, 2001). Thus, the increase in pigeon consumption by eagles after RHD potentially further enhanced this source of conflict. On the other hand, the new relatively higher role of other game species in the diet, such as partridges or thrushes (also quarry species in Spain), could also be increasing a negative perception of eagles by hunters.

Shifts in a predator diet can arise from intrinsic (Wainwright, 1988; Walton *et al.*, 1992; Jackson *et al.*, 2004) or extrinsic factors. The latter causes can involve conservation concerns when they produce continuous and non-cyclic depletions of the predator's preferred prey, as in our case. Several proximal negative effects of disease-mediated decline of the rabbit population have been described concerning the community of Mediterranean predators (Fernández, 1993; Tella & Mañosa, 1993; Villafuerte *et al.*, 1996; Martínez & Calvo, 2001; Martínez & Zuberogoitia, 2001) highly dependent on rabbits (the rabbit comprises > 20% of the diet for 19 of the 48 Iberian predators; see updated reviews in Moleón, 2007b; Moleón *et al.*, 2008). However, the possible long-term effects related to the viability of the predator populations and other prey species, either directly or indirectly connected to the rabbit, are unknown. Extrapolating our results, the effect of RHD on the dietary patterns of the Bonelli's eagle could be an expected outcome for many Mediterranean predators, and the consequences for some of these, such as the Spanish imperial eagle and Iberian lynx, which are critically dependent on rabbits (Delibes, 1980; González, 1991; Gil-Sánchez *et al.*, 2006), may be crucial (Ferrer & Negro, 2004).

However, the consequences of RHD might not be harmful only to predators; we can also expect the new higher predation pressure to negatively affect some alternative prey species. The hyperpredation phenomenon may lead to potential reductions in the populations of a secondary prey when a different prey indirectly induces increasing predation levels in the secondary prey by means of a shared predator (Courchamp *et al.*, 2000; Roemer *et al.*, 2001; Kristan & Boarman, 2003; Whelan *et al.*, 2003; Moleón *et al.*, 2008), which seems to be the case in the natural system studied here. With respect to RHD, hyperpredation effects have already been suggested, as disease outbreaks seem to be the cause of an increase in nest predation of the Egyptian vulture (*Neophron percnopterus* L.) and northern goshawk (*Accipiter gentilis* L.) by eagle owls (*Bubo bubo* L.), whose main prey before RHD was the rabbit (Tella & Mañosa, 1993).

Particularly illustrative of the large-scale negative effects of hyperpredation mediated by RHD is a recent study which found the strong decrease in the population of red-legged partridge in Spain since 1988 (see first section of this discussion) to be the direct result of enhanced predation pressure by predators (among them, the Bonelli's eagle) when the rabbit population crashed due to RHD (Moleón *et al.*, 2008). This situation agrees with the negative association in diet between partridges and 'other mammals', pigeons and 'other birds' existing after RHD (Table 1) because the similarity in size, behaviour and habitat selection of the former in relation to rabbits (Moleón *et al.*, 2008) probably makes partridges (when available) particularly vulnerable to predation by Bonelli's eagles when the rabbits are scarce.

To conclude, we have shown that an EID is able to disrupt the whole feeding ecology of a predator at the large scale through the severe decline in the population of its principal prey species. The EID-mediated prey reduction may therefore carry negative broad-scale consequences not only for the host–prey species but for other species, such as their predators – through the reduction in the energy available – and the alternative prey species of such predators – through the hyperpredation process. Hence, strict guidelines and effective strategies must be drawn up to prevent the human-aided dissemination of 'pathogen pollution' (Daszak *et al.*, 2000), which threatens biodiversity not only at the population and species level but also at the community and ecosystem scale

(Daszak *et al.*, 2000, 2003; Williams *et al.*, 2002; Anderson *et al.*, 2004; Moleón *et al.*, 2008).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Information about the studies used in the review and diet and *H′* trophic diversity of Bonelli's eagle (*Hieraaetus fasciatus*) in western Europe.

Appendix S2 Prey species of Bonelli's eagle (*Hieraaetus fasciatus*) in western Europe inferred from the studies shown in Appendix S1.

BIOSKETCH

Marcos Moleón coordinates the conservation programme for the Bonelli's eagle in Andalucía, southern Spain (Egmasa-Consejería de Medio Ambiente, Junta de Andalucía). His main research interests are predator–prey interactions in complex ecosystems under the theoretical and applied perspectives.

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