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Predator–prey relationships in a Mediterranean vertebrate system: Bonelli's eagles, rabbits and partridges

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Abstract How predators impact on prey population dynamics is still an unsolved issue for most wild predator–prey communities. When considering vertebrates, important concerns constrain a comprehensive understanding of the functioning of predator–prey relationships worldwide; e.g. studies simultaneously quantifying ‘functional’ and ‘numerical responses’ (i.e., the ‘total response’) are rare. The functional, the numerical, and the resulting total

response (i.e., how the predator per capita intake, the population of predators and the total of prey eaten by the total predators vary with prey densities) are fundamental as they reveal the predator's ability to regulate prey population dynamics. Here, we used a multi-spatio-temporal scale approach to simultaneously explore the functional and numerical responses of a territorial predator (Bonelli's eagle *Hieraetus fasciatus*) to its two main prey species (the rabbit *Oryctolagus cuniculus* and the red-legged partridge *Alectoris rufa*) during the breeding period in a Mediterranean system of south Spain. Bonelli's eagle responded functionally, but not numerically, to rabbit/partridge density changes. Type II, non-regulatory, functional responses (typical of specialist predators) offered the best fitting models for both prey. In the absence of a numerical response, Bonelli's eagle role as a regulating factor of rabbit and partridge populations seems to be weak in our study area. Simple (prey density-dependent) functional response models may well describe the short-term variation in a territorial predator's consumption rate in complex ecosystems.

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Keywords Functional response · Numerical response ·
Prey density-dependent model · Prey preferences ·
Total response

Introduction

A predator's ‘total response’ (i.e., the way the total prey eaten by the total predator individuals varies with changing prey densities) reveals this predator's ability to regulate its prey's population dynamics (Pech et al. 1992). This global, integrative response is derived from summing two components: the ‘functional response’, showing an individual predator's prey consumption rates (i.e., the per capita

intake); and the ‘numerical response’, which is a function of the population of (potentially) consuming predators (e.g. Erlinge et al. 1983; Krebs et al. 2001; Gilg et al. 2006). Per capita intake may be measured as either an absolute (number of prey eaten, or ‘kill rate’) or in relative way (proportion of the prey population eaten, or ‘predation rate’). According to the graphical representation shape and the effects on prey dynamics, Holling (1959) classified the kill rate-based predator functional responses into types I, II, and III; however, only the last two are realistic in a real world. Types II and III functional responses, respectively show hyperbolic (i.e., lacking positive density dependence) and sigmoid (i.e., exhibiting positive density dependence) increases of prey consumption in relation to prey density before saturation. An analogous classification can be made of the predation rate-based functional responses with curves with no positive slope (i.e., lacking positive density dependence) over any range of prey densities belonging to type II and with curves with a positive slope (i.e., showing positive density dependence) over the lower range of prey densities belonging to type III (Trexler et al. 1988; Gilg et al. 2006). Type II functional responses are typical of specialist predators, while type III responses have been frequently associated with predation switching by generalist consumers (Andersson and Erlinge 1977; Hansson and Henttonen 1985). For its part, a predator’s ability to numerically respond to prey population fluctuations depends on three major factors: mobility (emigration and immigration), death rates and reproductive rates (including predator reproductive potential, predator growth rate and predator generation time; e.g. Korpimäki and Norrdahl 1989). Both functional and numerical components need to be precisely explored to predict the effects of predation on a prey population; indeed, a positive density-dependent predation phase in the subsequent total response has been claimed as a fundamental condition to show regulation properties (Turchin 2003). Therefore, the accurate calculation of the functional, the numerical and the resulting total predator responses is essential to obtain a correct understanding of predator–prey relationships anywhere.

The functional and numerical responses are often dependent on the spatial scale on which they are measured via the mobility and patchiness of both predators and prey (Ives et al. 1999; Bergström and Englund 2004). As opposed to the functional response (an individual-based—behavioural—trait), the numerical response usually depends on demographic parameters; hence, it typically occurs on a comparatively lower time scale. Given the different demographic characteristics of both predators and prey, numerical responses tend to introduce time lags into population dynamics of predator–prey interactions (Turchin 2003), at least when resident predators are involved (Korpimäki and Norrdahl 1989). Thus, the time scale becomes an important

factor to control for the latter (O’Donoghue et al. 1997; Tornberg et al. 2005).

Due to the numerous ecological and practical implications of predation for wild, natural systems (e.g. those related to biodiversity co-evolution, biological control or game management), the scientific literature on predator responses has been prolific in the last few decades, particularly as regards theoretical models and/or laboratory approaches (see a review in Jeschke et al. 2002). Yet how predators impact their prey is still a clearly unsolved empirical issue for most wild predator–prey communities (Boutin 1995; Abrams and Ginzburg 2000; Valkama et al. 2005), particularly for examples that consider native, mainland vertebrates (Salo et al. 2007).

Among the most important concerns constraining a comprehensive understanding of vertebrate predator–prey communities functioning, the following may be highlighted. First, it is striking that very few studies have simultaneously quantified both the functional and numerical responses (see a review in Valkama et al. 2005 for raptors preying on gamebirds), which consequently limits conclusions being drawn on the whole predator population’s regulatory capacity (as reviewed by Messier 1995, and demonstrated by Joly and Patterson 2003).

Second, a strong geographical bias exists, since most previous field studies into predator–prey interactions have been done in relatively simple ecosystems where prey usually undergo cyclic dynamics, such as boreal regions (e.g. Korpimäki and Norrdahl 1989; Hanski et al. 1991; O’Donoghue et al. 1997, 1998; Nielsen 1999; Tornberg et al. 2005; Gilg et al. 2006). The traditional association of predation ecologists with higher latitudes has led to a virtual lack of knowledge on complex natural systems such as those in Mediterranean and tropical climates (Jacksić et al. 1992; Valkama et al. 2005), which contain the largest number of predators, prey—with their dynamics not following (marked) cycles—and interactions between them. This is a major concern because stability (non-cyclical behaviour) imposes obvious restrictions to the amplitude of predator responses. This not only makes the process of quantification particularly challenging, but the extrapolation of findings from simpler to more complex systems somewhat risky.

Third, the use of relative measures of prey consumption (e.g. frequency of occurrence in predator faeces) and/or predator/prey abundance (e.g. density of faeces) in a number of studies (e.g. Angerbjörn et al. 1999; Gil-Sánchez et al. 1999; Palma et al. 2006) has prevented a more reliable, realistic combination of the numerical and functional responses as an absolute total response cannot be inferred.

By studying a vertebrate one-predator–two-prey model in a warm, complex ecosystem, here we aim to simultaneously explore functional and numerical predator responses by means of a multi-spatio-temporal scale approach.

Study system and predictions

This work was conducted in a typical Mediterranean environment of south Spain to explore a predator, Bonelli's eagle *Hieraetus fasciatus*, feeding on two prey species: the European rabbit *Oryctolagus cuniculus* and the red-legged partridge *Alectoris rufa*. Bonelli's eagle is a medium- to large-sized resident, territorial, long-lived raptor, with a usual fecundity rate of 1–2 chicks per pair and year. It is irregularly distributed throughout the Mediterranean (Europe and North Africa) and Asiatic subtropical (Middle East, Indian subcontinent and Southeast Asia) biomes (del Hoyo et al. 1994). Its main prey includes medium-sized mammals and birds like rabbits and partridges (del Hoyo et al. 1994; Moleón et al. 2009). The European rabbit is a native species to the Iberian Peninsula that currently presents a broad, patchy man-induced distribution worldwide (Thompson and King 1989). In western Europe, it shares its range with the red-legged partridge (del Hoyo et al. 1994). Both species show crepuscular activity peaks, similar habitat preferences (mosaics of scrubland, pastureland and non-irrigated crops) and ground-related behaviour (del Hoyo et al. 1994; Blanco 1998). Where sympatric, rabbits are generally more abundant than partridges, although two human-facilitated emerging infectious diseases (myxomatosis and rabbit haemorrhagic disease) have decimated rabbit populations in the last five or six decades in many Mediterranean areas (Virgós et al. 2007). In the study area, both diseases are still killing rabbits, although at highly variable rates for each year.

Based on published information, we can make the following predictions about the predator's responses to its prey. Regarding the functional response, we expect to find a Holling type II, non-regulatory response by Bonelli's eagle to the rabbits in our study area as this eagle has been suggested to be a facultative specialist on this prey in western Europe. For example, rabbit is the principal prey driving the spatio-temporal patterns in the eagle's diet on a continental scale (Moleón et al. 2009). In addition, a type II functional response has already been found in an area of south Portugal, poor in wild prey (Palma et al. 2006), and the positive selection of rabbits has been described at a local level in south Spain (Gil-Sánchez 1998; see Moleón et al. 2009 for a complete list of arguments in favour of the rabbit-facultative-specialisation RFS hypothesis).

In contrast, we expect to find a Holling type III, regulatory functional response for the red-legged partridge. This partridge species seems to be a secondary prey for European Bonelli's eagles, although it is still more important than most other prey species (Moleón et al. 2009). So it is plausible that eagles respond to high relative abundance of partridges by increasing consumption of them. Predation switching from rabbits to partridges by Bonelli's eagle and

other Mediterranean predators has recently been shown in Spain on a large spatio-temporal scale; similarity in size, ecology and behaviour between both species are probably essential factors that facilitate this switch (Moleón et al. 2008, 2009). Indeed, the RFS hypothesis postulates that Bonelli's eagles prefer rabbits when they are relatively abundant, but shift to other similar prey species when rabbits become scarce (Moleón et al. 2007, 2009). Then, a regulatory consumption rate is expected for partridges.

In both cases, we assumed predation to be only a prey-dependent process, with no influence of either predator density or the prey/predator ratio. There is a good deal of theoretical discussion about the relevance of each type of predator-prey models; indeed, Abrams and Ginzburg (2000) offers a very constructive review. In our system, prey-dependent responses can be easily deduced because our predator species is highly territorial and interference and other forms of predator dependence should be of minor relevance to calculate functional responses.

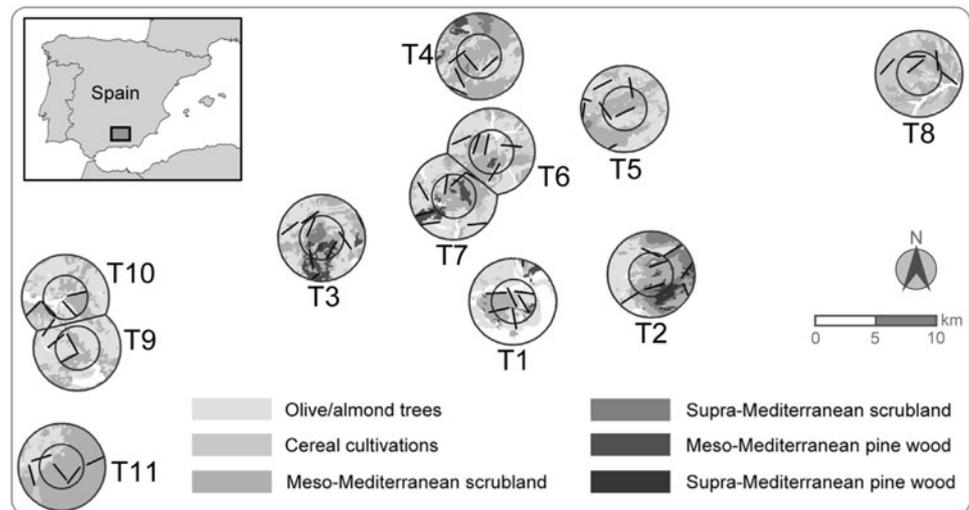
For its part, strong territoriality characterising Bonelli's eagle constrains this species' ability to numerically respond to prey density changes (especially in a stable breeding population near saturation, such as that in south Spain; Moleón 2006). Thus, the capacity to adapt the number of eagles to prey availability principally depends on the fecundity adjustment. Prey (mainly rabbit) density effects on Bonelli's eagle productivity have been found in several northern populations (Cheylan 1981; Real 1991; Fernández et al. 1998). However, in south Spain, where food supply is comparatively richer and more abundant (Moleón et al. 2009), Bonelli's eagle breeding success seems more independent on prey availability (Ontiveros and Pleguezuelos 2000; Gil-Sánchez et al. 2004). Therefore, this study is not expected to show a pronounced numerical response for Bonelli's eagle, irrespective of prey. If this assumption is confirmed, Bonelli's eagle's regulatory capacity on the rabbit and red-legged partridge populations will, therefore, be mainly conditioned by the (potential) functional response.

Materials and methods

Study area and period

The work was undertaken principally on the territorial scale; i.e., relating prey densities with prey consumption and predator numbers within territories. A total of 11 eagle territories were studied, all in the Granada province (S Spain; Fig. 1). The study area lies in meso- and, to a lesser degree, supra-Mediterranean bioclimatic zones. The habitat is characterised by a mixture of relatively natural areas (scrub and pinewoods, *Pinus halepensis*) and non-irrigated crops, mostly olive trees and cereals (Fig. 1).

Fig. 1 Study area. Territories of Bonelli's eagle *Hieraaetus fasciatus* are represented by their theoretical small (2.2 km) and large (4.4 km) radii. Territory T1 has been displaced 2 km to the NW given the presence of an unsuitable habitat in the SE area of the original theoretical territory. Straight black lines indicate prey transects. Areas in white indicate other habitat categories (irrigated crops, riverine woodland, urban areas, etc.)



All the analysed responses refer to the Bonelli's eagle breeding season (spring), from incubation to the fledging phase. This is a critical period of its life history, when its food requirements are at their highest. Likewise, rabbits and partridges in spring are, respectively, at the middle and the beginning of their breeding stages.

Predator diet, breeding success and territory

The Bonelli's eagle diet was studied during the breeding seasons of 2002–2004 by analysing the pellet samples (Real 1996) collected at perching sites on or close to breeding cliffs. Diet analyses were carried out as regards both relative frequency (%N) and relative ingested biomass (%B). Different prey types were categorised into the following seven prey groups: rabbit, other mammals, red-legged partridge, pigeons (*Columba* spp.), corvids, other birds and reptiles. The Shannon–Weaver H' (In; Weaver and Shannon 1949) index of the trophic diversity of eagle diet for each territory and year was calculated based on the relative frequency of these prey groups.

The diet data obtained were used to infer the numbers of rabbits and partridges consumed during each breeding season per breeding unit of Bonelli's eagles (adults plus chicks); i.e., the kill rate. The kill rate was calculated for a 100-day period (from mid-February to the end of May), including 40 incubation days and 60 for chicks while in their nests (Gil-Sánchez 2000; see Online Resource 1 for more details).

Breeding success was used as the principal measure for population variations to calculate the numerical response, although possible changes in territory occupation were also taken into account. All the territories were visited annually (2002–2005) to confirm occupation and to register their productivity (fledgling pair⁻¹). Fledged young were those observed to be >50 days old (Gil-Sánchez et al. 2004).

Bonelli's eagle territories were considered as circles, with a radius equal to half the minimum average distance between the pairs of the whole population in Granada (Gil-Sánchez et al. 2004). This was estimated as 4,417 m, producing a circular plot of 6,129 ha. In four cases with an overlap, the area considered was lower (5,411 ha for territories T6 and T7; 5,171 ha for territories T9 and T10; see Fig. 1), based on the assumption that eagles maintain and defend exclusive territories (Palma et al. 2006), or that neighbouring pairs equally used the overlap zones. Given the longer time spent close to nests during the breeding season (Bosch et al. 2010; personal observations), we considered another radius, which was half that of the previous one (radius = 2,209 m; area = 1,533 ha; this radius includes most of the 50% home-range probability kernel in this species and season; Bosch et al. 2010). Radiotracking three territorial eagles between 2004 and 2007 helped to corroborate the theoretical plot sizes as calculated (see Online Resource 2 for more details).

Prey densities

Rabbits and partridges were censused in all 11 territories during each consecutive breeding season (2002–2004). Linear transects of between 1 and 2 km were undertaken on foot in the early morning or late evening, with total averages of 5.7 km covered inside the smaller radius (range: 5–9 km) and 11.5 km inside the larger radius (range: 9–15 km). Transects were stratified by habitats (Tellería 1986), while paths, forest tracks, roads and level-line routes were avoided, unless a transect coincided with these by chance (Palomares et al. 2001). A total of 123 km were covered during all three census seasons (and always on the same transects). Census counts were performed halfway through the 100-day eagle breeding period, between mid-March and the end of April (see Online Resource 3 for more details).

To calculate rabbit densities, we used the method of Palomares et al. (2001), an accurate census method for low-medium rabbit density sites, this being the case of our study area. According to these authors, rabbit abundance can be estimated using the following regression line ($r^2 = 0.97$, $P < 0.0001$): “absolute rabbit density = $0.57 \times$ number of rabbits observed within 10 m of each side of the transect line per km walked”. The figure of 10 m was established to diminish the among-habitat differences in visibility (Palomares et al. 2001).

For partridges, densities were directly inferred from sightings within 10 m on either side of the transect line since we were unable to derive a partridge population estimate using census-specific software because the number of detections per territory and year was too low to obtain reliable estimates (e.g. Buckland et al. 2004). However, after reviewing previous studies done in the same study area but on a larger scale (Moleón et al. 2011), our method proved accurate, and more conservative than that employing the aforementioned software (DISTANCE 5.0 free software; Thomas et al. 2006) because the latter corrects for unobserved birds (see Online Resource 3 for more details of the rationale of this approach).

In autumn 2003 (from mid-September to the end of October), the same transects were repeated. These results were used to only explore their influence on predator productivity in the following spring (see “Numerical response”).

Prey preferences

For the purpose of obtaining additional information for further interpretations of the results, the rabbit and partridge densities obtained were used in analyses of the Bonelli's eagle trophic preferences in the study area. Specifically, these were explored using regression analyses to relate the proportion of each prey group in diet with trophic diversity since the classic predation theory predicts that the preferred prey is that which inversely relates to the predator's trophic diversity (Futuyma and Moreno 1988).

Functional response

Changes in per capita consumption in relation to prey density were calculated for both the kill and predation rates. The latter was obtained by dividing the kill rate by the prey population size (rabbit or partridge) in each territory. Analyses were done by considering prey densities for the larger (4.4 km) and smaller (2.2 km) territorial radii. All the territories and years with sufficient diet data (>20 prey; see Jovani and Tella 2006), and with positive censuses of rabbits and partridges (e.g., see Angerbjörn et al. 1999 for a similar approach), were used ($n = 18$ cases; see “Results”).

In order to distinguish between the type II and type III functional responses for the kill rate, classic functions were

used (Holling 1965; May 1973). In particular, we employed the following equations (e.g. Redpath and Thirgood 1999; Palma et al. 2006):

$$\text{type II: } y = ax/(b + x)$$

$$\text{type III: } y = ax^k/(b^k + x^k)$$

where y is the kill rate and x is prey (rabbit or partridge) density. For the predation rate, the following phenomenological equations were used:

$$\text{type II: } y = a + b/x$$

$$\text{type III: } y = a + b \ln x/x^2$$

where y is the predation rate and x is prey (rabbit or partridge) density. These equations correspond to the mathematical expressions for the curves describing typical type II and type III predation rate-based functional responses (see “Introduction”).

The maximum consumption rate a and the half-saturation constant b were numerically estimated in each case. Non-linear regression models were fitted using the NLREG software (Sherrod 1994). To evaluate the explanatory power of each tested model, the effect size was used (r value in the regression).

For further accuracy purposes, we included an additional, complementary test to discriminate between type II and III kill rate's functional responses, as weak sigmoid (type III) functional responses usually offer similar fits to the kill rate data than hyperbolic ones (type II; May 1981; Marshal and Boutin 1999). Several approaches have been proposed to discriminate between type II and III functions under these conditions. We employed an adaptation (statistically tested) of the method described by Pech et al. (1992). The general philosophy of the test is that both type II and III curves are substantially, qualitatively different when close to zero, i.e., hyperbolic and sigmoid curves are convex and concave, respectively, at a zero prey density (Joly and Patterson 2003). According to Pech et al. (1992), linear regressions were fitted to the data by successively deleting the highest x -value points until $n = 5$. The test has the following diagnostic features: for a type II functional response, the slope (parameter a in regressions) should increase and the intercept (parameter b in regressions) should decrease progressively; conversely, if the slope first increases and then decreases, and the intercept first decreases to then increase, a type III functional response is inferred (see Online Resource 4, Fig. S1, for a graphical representation of the principle).

After the above regression analyses had been applied to the kill rate data (no cases with zero prey densities were included in this test) in relation to both prey (rabbit and partridge) and spatial scales (4.4 and 2.2 km radii; Online Resource 4, Fig. S2), we checked for statistical significance in both the slope and intercept trends. For each trend, we fitted either linear (compatible with the test assumptions for a type II curve) or polynomial (compatible with the test assumptions for a type III curve) equations. Then the most explanatory model (i.e.,

with the highest effect size— r value) was selected to infer the most probable functional response type.

Numerical response

The presence of a numerical response was explored using the relationship between rabbit and partridge densities and Bonelli's eagle productivity on territorial scales (radii of 4.4 and 2.2 km). The comparisons between productivity and prey density, using each prey separately and also combined, were made with: (1) the densities found during the same breeding period (without a time delay: the densities and productivities in 2002, 2003 and 2004); (2) the densities found during the previous breeding season (with the time delay of a complete breeding cycle: the densities in 2002, 2003 and 2004 and the productivities in 2003, 2004 and 2005, respectively); and (3) the densities during the non-breeding period prior to breeding (with a time delay of months; the densities in autumn 2003 and the productivity in spring 2004). Pearson's correlations were employed in these analyses.

Variations in territorial occupation were not analysed since they were not detected throughout the study period (see “[Predator diet and breeding success: kill rate](#)”).

Results

Predator diet and breeding success: kill rate

The Bonelli's eagle diet in the study area during the breeding season was based principally on rabbits (average: 34.0% N; 55.3% B). Partridge was the second most important prey (average: 28.0% N; 22.2% B), followed closely by pigeons (average: 19.4% N; 17.1% B). The remaining groups showed a smaller presence (see Online Resources 5 and 6). The average productivity of Bonelli's eagle throughout the study period varied between 1.27 and 1.64 fledglings pair⁻¹, depending on the year. The number of chicks fledging per territory and year are shown in Online Resource 5. There were no changes in the number of eagle pairs over the study period. Based on the productivity and frequency (relative biomass) of rabbits and partridges in Bonelli's eagle diet, the average kill rate per breeding unit over the 100-day reproductive period was 48.7 rabbits (range: 20.2–67.2) and 39.9 partridges (range: 11.8–73.5; see Online Resource 6).

Prey densities, predation rate and prey preferences

The average rabbit density in the territories of the 4.4 km radius was 0.484 ind. ha⁻¹ (range: 0.029–2.052), and 0.240 ind. ha⁻¹ for partridges (range: 0.036–0.600). For the smaller radius, the average rabbit density was

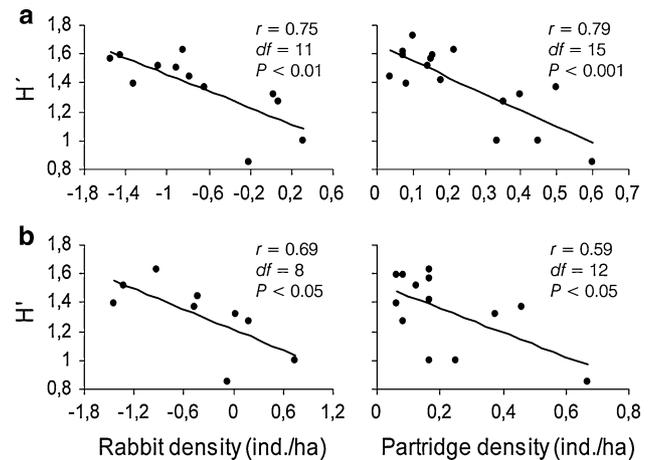


Fig. 2 Relationship between Bonelli's eagle trophic diversity (H') and the densities of European rabbit *Oryctolagus cuniculus* (log-transformed) and red-legged partridge *Alectoris rufa* (without transformation) in spring for the larger (4.4 km, **a**) and smaller eagle territory radii (2.2 km, **b**)

1.099 ind. ha⁻¹ (range: 0.036–5.558) and 0.218 ind. ha⁻¹ (range: 0.063–0.667; see Online Resource 6) for partridges. The average autumn densities for the larger radius were 0.303 rabbits ha⁻¹ (range: 0.041–1.197) and 0.366 partridges ha⁻¹ (range: 0.094–1.050), while they were 0.872 rabbits ha⁻¹ (range: 0.036–4.133) and 0.640 partridges ha⁻¹ (range: 0.188–1.750) for the smaller radius.

Given the spring rabbit and partridge densities, as well as the eagle kill rate of these prey, the average predation rate in the larger territory was 7.61% of the rabbit population (range: 0.51–33.79%) and 4.61% of the partridge population (range: 0.57–11.00%; see Online Resource 6). For the smaller radius, this rate increased to 18.54% for rabbits (range: 0.75–70.86%) and to 22.44% for partridges (range: 2.45–51.27%).

Spring rabbit and partridge densities positively correlated in the territories, but were significant only on the 4.4 km radius scale ($r = 0.56$, $P < 0.05$, $n = 18$). The proportion of rabbit in the diet positively correlated with the partridge density in the territories, but no significant relationship was found for the opposite relationship. In general, the frequencies of the remaining prey groups in the eagle diet negatively correlated with the densities of rabbit and partridge, although only three groups (pigeons, corvids and reptiles) reached minimum significance levels in some cases. The negative relationship between the proportion of pigeons in the diet and the rabbit and partridge densities in the territories for the larger radius was particularly noteworthy (Online Resource 7). Finally, the density of both rabbits and partridges in both the larger and smaller territories negatively correlated with the Bonelli's eagle trophic diversity (Fig. 2).

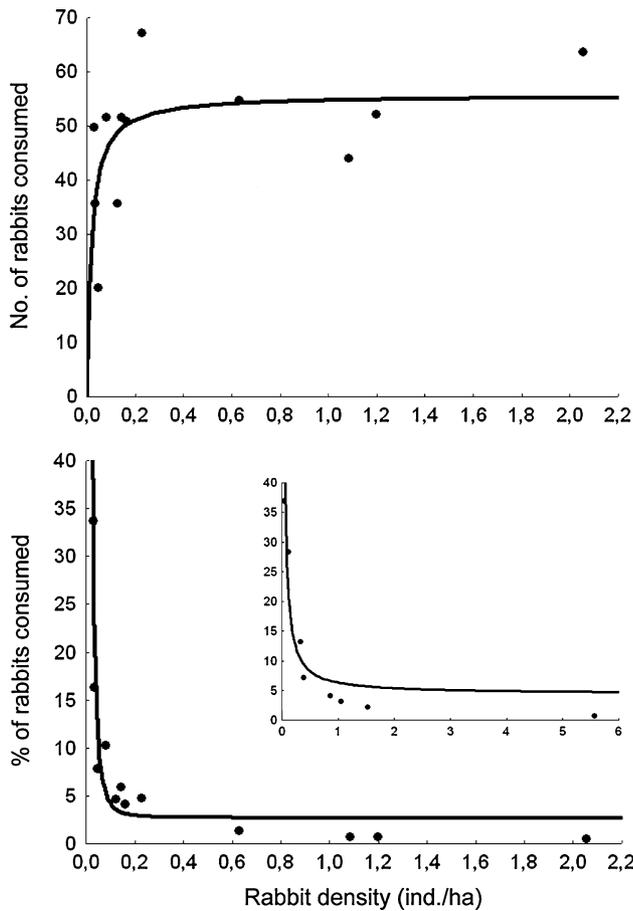


Fig. 3 Functional response (type II) of Bonelli's eagle to rabbits in spring in relation to the kill rate (4.4 km radius, $y = 55.630x / (0.017 + x)$; upper) and to the predation rate (lower). The latter is represented using the rabbit densities obtained in the territory radii of 4.4 km ($y = 0.038 + 0.704/x$; larger graph) and 2.2 km ($y = 3.534 + 2.180/x$; smaller graph)

Functional and numerical responses

At the 4.4 km radius, the eagle's best-fitting functional response to rabbit was type II for both the kill and predation rates (Fig. 3; Table 1). That said, both the type II and type

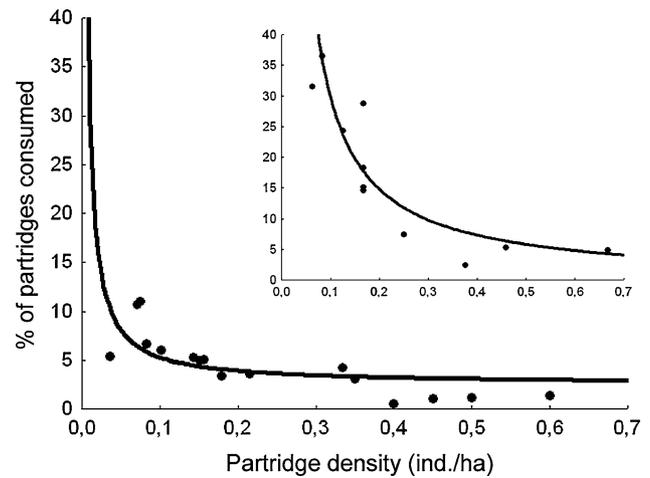


Fig. 4 Functional response (type II) of Bonelli's eagle to partridges in spring in relation to the predation rate. The larger and smaller graphs were obtained from the partridge densities in the territory radii of 4.4 km ($y = 3.802 + 0.022/x$) and 2.2 km ($y = 0.521 + 2.834/x$), respectively

III curves obtained fitted the data similarly. With partridges, type II also proved to be the best model for its predation rate (Fig. 4; Table 1), while none of the models fitted the kill rate data. In general, all the selected models explained most of the variation in prey consumption (Table 1). At the smaller radius, none of the functional response models fitted the data for the rabbit or partridge kill rates, while the model for the rabbit predation rate again corresponded most closely to a type II functional response (Fig. 3; Table 1). Both model types fitted the partridge predation rate well, but, once again, the type II response offered the best fit (Fig. 4; Table 1). The kill rate-based test offered similar results, with the type II form better characterising eagle response to both prey species on both spatial scales (except for partridges for the larger radius, where a type III response was suggested). In particular, consistent slope increasing and intercept decreasing trends were noted for rabbits, thus satisfying the assumptions for a type II functional response (although the slope

Table 1 Results of the Bonelli's eagle functional response models to rabbits and partridges

Prey	Functional response	Predation variable	Territory radius (km)	df (regression)	df (total)	F	P	r
Rabbit	Type II	Kill rate	4.4	2	12	109.00	<0.000001	0.53
Rabbit	Type II	Predation rate	4.4	2	12	93.38	<0.000001	0.96
Rabbit	Type II	Predation rate	2.2	2	9	17.34	0.001943	0.84
Rabbit	Type III	Predation rate	4.4	2	12	52.20	0.000005	0.92
Rabbit	Type III	Predation rate	2.2	2	9	8.16	0.014821	0.70
Partridge	Type II	Predation rate	4.4	2	16	31.60	0.000006	0.62
Partridge	Type II	Predation rate	2.2	2	13	72.44	<0.000001	0.89
Partridge	Type III	Predation rate	4.4	2	16	19.22	0.000097	0.31
Partridge	Type III	Predation rate	2.2	2	13	39.43	0.00001	0.80

Only the significant models are shown. The best-fitting models are depicted in bold

trend for the 4.4 km radius did not achieve the minimum statistical significance; Online Resource 4, Fig. S3a). For partridges, polynomial functions better explained both the slope and the intercept variations at the 4.4 km radius, suggesting a type III functional response on this scale. For the 2.2 km scale, the test results indicated a type II functional response (Online Resource 4, Fig. S3b).

No numerical response was found for Bonelli's eagle to rabbits, partridges, or both these prey types, on any of the analysed spatial (2.2 and 4.4 km radii) and temporal scales (without a time delay, with a 1-year delay and with a delay of several months; $r = 0.087\text{--}0.443$; $P > 0.05$ in all cases; Online Resource 8).

Discussion

Functional response and prey preferences

Our results reveal that simple (prey density-dependent) functional response models may well describe the short-term variation in a territorial predator's consumption rate in complex ecosystems. In addition, no important effects due to the spatial scale were noted. Nachman (2006) pointed out that the spatial scale is a relevant factor when calculating functional responses, especially when the predator is free to move in relation to prey distribution. However, our work is based on a highly territorial predator used as a model, and territoriality greatly constrains its ability to move in relation to its principal prey's density. Additionally, rabbits and partridges are, respectively, largely confined to the ranges of their colonies or territories in spring. Consequently, space as a factor that affects the predator's functional response in systems formed by territorial animals would lose importance, as supported by the similarity in the results obtained between our models at the two radii considered (Table 1). Furthermore, the prey densities within each eagle territory at the two radii considered in this study were correlated ($r = 0.926$, $P < 0.001$, $n = 12$ for rabbits; $r = 0.885$, $P < 0.001$, $n = 16$ for partridges); this further diminishes the importance of the spatial scale in our study.

In accordance with our first prediction, Bonelli's eagle responded functionally as a rabbit specialist. Nevertheless, the explanatory power of the type II and type III models towards rabbits was similar when considering the predation rate. A larger number of data points in the lower rabbit densities zone would probably resolve the most appropriate curve type for this predator–prey relationship (Trexler et al. 1988). However, if there were a direct density-dependent phase in Bonelli's eagle functional response to rabbits in our study area, it would be confined to rare cases of extremely low rabbit densities.

Regarding partridges, the most probable response seen in Bonelli's eagle (type II) did not coincide with that expected (type III). Nonetheless, both models once again showed similar adjustment levels, and the discriminative test was inconclusive. Even if further studies confirm one type of response or another, it seems obvious that the Bonelli's eagle in our study area exhibits a high degree of specialisation towards partridges, even with low partridge densities and irrespective of the rabbit densities. This circumstance may relate to this predator's evolutionary history. Taxonomically, Bonelli's eagle falls within a group of eagles whose diet generally includes large amounts of birds, especially galliforms (del Hoyo et al. 1994). Indeed, Bonelli's eagle itself appears to be an efficient predator of galliformes and other ground birds in ecosystems where rabbits are absent (del Hoyo et al. 1994; Iezekiel et al. 2004). This observation is in accordance with this eagle group's morphology, which is, in principle, appropriate for the capture of this avian prey type (Clouet and Goar 1984; Parellada et al. 1984). The circumstantial geographic coincidence of Bonelli's eagle with rabbits, probably much more abundant than other potential prey of similar habits and size, in the western extreme of its distribution (Iberian Peninsula, where the rabbit is native), may have locally favoured the facultative dietary specialisation in this prey, thus shifting from this raptor's possible original, bird-eating tendency (even though partridges still remain an optimal prey).

Another plausible, but not necessarily exclusive, explanation for the high degree of specialisation in partridges in our study is that the greater vulnerability of male partridges during the breeding season, due to their conspicuous behaviour (frequently singing on unprotected, highly visible perches), would make them readily visible to hunting eagles (Moleón et al. 2007). From the diet remains (tarsi, which allow partridge sexing) collected during the same study period as this research work, predation was biased towards males (Moleón et al. 2011), which supports this second hypothesis. Thus, prey behaviour would act as an important factor to modulate the predator functional response.

One interesting consideration is that the functional response was only revealed, or best explained, when considering the predation rate instead of the kill rate. Trexler et al. (1988) specifically recommended the use of the predation rate since it more rapidly, intuitively and clearly shows the density-dependence intervals (positive or negative). Our results reinforce the appropriateness of using the predation rate as a complement and support of the kill rate in those studies which aim to explore predation impact and predator–prey dynamics.

In agreement with there being a specialist functional response to both prey species is the finding that rabbit and

partridge densities strongly and negatively correlated with Bonelli's eagle trophic diversity on the territorial scale. According to the classic predation theory (Futuyma and Moreno 1988), these results suggest that the rabbits and partridges in our study area are optimal prey for Bonelli's eagle. Furthermore, this conclusion has also been suggested on a larger scale (for western continental Europe; see Moleón et al. 2009). At the same time, the negative relationship between rabbit and partridge abundance and the frequency of most of the remaining prey groups in the eagle's diet, combined with the functional responses described here, suggest that no other prey is more profitable than rabbits and partridges in this study area. One particularly notable finding was the significantly lower consumption of pigeons (the second most important prey on the continental European scale after major rabbit outbreaks; Moleón et al. 2009) while rabbit and partridge abundance in the territories increased. This coincides not only with the previously found negative selection of this prey in Granada (Gil-Sánchez 1998) but also with the ideas formulated in previous studies, which suggested the possibility of pigeons being less profitable to Bonelli's eagle than rabbits and partridges (Moleón et al. 2007, 2009). The type II functional response to pigeons found by Palma et al. (2006) in south Portugal could therefore be due to the greater relative scarcity of rabbits, and above all of partridges, whose densities were notably lower than those reported in our study area.

Absence of numerical response

The absence of a numerical response of Bonelli's eagle to both the rabbits and partridges in the study area agrees with the results reported in other studies previously undertaken in south Spain, which analysed, with less prey census effort and using a single-scale approach, the influence of the abundance of these prey on the eagle's reproductive success (Ontiveros and Pleguezuelos 2000; Gil-Sánchez et al. 2004). Although low in some territories, in general, rabbit and partridge densities are probably sufficient, at least in combination, for the Bonelli's eagle reproductive needs. This situation was not found in other areas with a lower availability of these prey, such as north Spain or south France, where a negative effect on productivity due to rabbit scarcity has in fact been indicated (Cheylan 1981; Real 1991; Fernández et al. 1998).

Gil-Sánchez (2000) pointed out a negative relationship close to statistical significance between the laying date of this raptor and the prey availability (partridge, and above all rabbit) in Granada. This implies that these prey helped improve the physiological condition of females prior to egg-laying (Newton 1998). This phenomenon may lead to increased long-term reproductive success, which may be interpreted as a numerical response. Consequently, the time

scale of our study would be insufficient to reveal a response of this type. Whatever the case, if there is such a response on our spatial scale, the effects would be so weak and dispersed over time that the contribution of this numerical response to the total response would remain very poor in comparison to the role of the functional response.

Synthesis and future research

This is the first attempt to understand the functioning of a Mediterranean (one) predator–(two) prey system in detail. In the study area, Bonelli's eagle showed a functional, but not numerical, response to rabbits and partridges. Additionally, these two prey appeared to be the most optimal for this predator on the local scale, and there is evidence available supporting this pattern in other parts of its European distribution. Given the absence of a numerical response (at least in the short term), the potential of Bonelli's eagle as a regulating factor of these prey in the study area over the study period lies completely in the functional response which, as a specialist type, confers on the eagle a weak regulatory potential. Although our findings cannot definitely rule out a weak sigmoid, generalist curve, in practice, true regulation by the predator is equally unlikely in the absence or presence of a weak density dependence, as pointed out by Joly and Patterson (2003).

Regarding future studies on predator–prey interactions, we encourage the complementary and simultaneous use of both the kill and predation rates instead of relative consumption estimates (e.g. prey frequency in diet) when investigating functional responses. If a study aims to find a global numerical response, we also suggest the use of greater spatial and temporal scales (the more stable the predator populations, the larger they should be) better than those studied here. Multi-predator studies in Mediterranean environments, which complement ours, are particularly interesting as intraguild interactions are capable of increasing or decreasing the effect of each predator (Sih et al. 1998; Griffen and Byers 2006; Schmitz 2007). These studies would determine not only the Bonelli's eagle's definitive contribution as a regulating factor on these two prey species in a broader ecological context but also how total predator pressure influences their dynamics (Moleón et al. 2008).

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