

# Inferring ecological mechanisms from hunting bag data in wildlife management: a reply to Blanco-Aguilar et al. (2012)

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**Abstract** In a previous study, we suggested that hyperpredation by shared predators on red-legged partridges (*Alectoris rufa*), once a parasite (rabbit haemorrhagic disease, RHD) had decimated populations of rabbit (*Oryctolagus cuniculus*), the primary prey for most of the Mediterranean predators, was a major force driving partridge population dynamics in Spain years ago (Moleón et al., PLoS One 3: e2307, 2008). Recently, however, Blanco-Aguilar et al. (Eur J Wildl Res 58:433–439, 2012) have asserted that this conclusion is poorly evidence-based and can subsequently promote raptor persecution by hunters. In response to Blanco-Aguilar and colleagues, here we provide complementary insights that favour our earlier hypothesis. After explaining several key concepts of the hyperpredation process, we use additional data and analyses to show that (1) a synchronised regime shift (i.e. a step, abrupt change in population size) to significantly lower population levels in both the rabbit and partridge populations took place coinciding with the RHD outbreak; (2) rabbit and partridge population dynamics were highly synchronised after the RHD outbreak, but not before; (3) an enhanced spatial autocorrelation at all the spatial scales emerged after RHD for

partridge populations; and (4) the main shared predators' diet patterns were consistent with the hypothesis of enhanced predation pressure as a plausible mechanism behind the observed partridge dynamics. We support the idea that hunting bag data may be useful to infer realistic population dynamics and the ecological mechanisms explaining them, provided that (1) they are corrected by the number of hunting licenses; (2) appropriate statistical tools are employed; and (3) methodological constraints are adequately taken into account. Finally, we argue that the opinion of Blanco-Aguilar and colleagues that our original results can lead to raptor persecution is a misinterpretation of our study. In this sense, we make an appeal for the importance of accurately differentiating between the ultimate (e.g. infectious diseases favoured by humans) and the proximate (e.g. enhanced predation pressure) causes of the decline in prey of economic interest (e.g. game species) in order to avoid unnecessary, unfounded or presumed conflicts with lobbies of conservation concern (e.g. hunters).

**Keywords** *Alectoris rufa* · Emerging infectious disease · Hyperpredation · *Oryctolagus cuniculus* · Rabbit haemorrhagic disease · Spatial autocorrelation

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## Introduction

Unintended consequences of reporting poorly supported, controversial results on species of conservation and economic interest have been claimed by Blanco-Aguilar et al. (2012) to be either a scientific, conservation or management concern in the case of raptors (an overall threatened group of birds) and the red-legged partridge (*Alectoris rufa*; an important small-game species) in Spain. They maintain that our suggestion (see Moleón et al. 2008) that hyperpredation by shared predators (both birds of prey and mammalian carnivores) on partridges once an outbreak (rabbit haemorrhagic disease,

RHD) had decimated Spanish populations of rabbit (*Oryctolagus cuniculus*; the primary prey for most of the Mediterranean predators) was a major force driving partridge population dynamics years ago, is poorly evidence-based and can subsequently promote raptor persecution by hunters. Here, we firstly aim to highlight several key concepts of the hyperpredation process that were unclearly or wrongly presented in the paper of Blanco-Aguilar and colleagues. Secondly, we show that our previous work lacked the presumed pitfalls attributed to it by Blanco-Aguilar and colleagues, and we also use additional data and analyses that strengthen our original hypothesis. Finally, we argue that concluding that our results can lead to a conservation problem for raptors is a misinterpretation of the basic nature of our study.

### Some considerations of the hyperpredation process

Blanco-Aguilar and colleagues state that hyperpredation is ‘a restrictive case of apparent competition where an increased number of primary prey species indirectly induces the decrease of the secondary prey species through numerical response of predators to the primary prey dynamics’, citing the pioneering works of Smith and Quin (1996) and Courchamp et al. (2000). However, the mechanisms behind hyperpredation include both apparent competition (i.e. symmetric indirect interactions in the form  $-,-$ ) and apparent predation (i.e. asymmetric indirect interactions in the form  $+,-$ ; Bate and Hilker 2012). Besides, hyperpredation not only involves a numerical response of the predator to its primary prey, but also (or even only) a functional response (e.g. Norbury 2001; Bate and Hilker 2012); in the same vein, this phenomenon can be applied to not only systems in which primary prey numbers rise, but also when its population drastically lowers (e.g. Norbury 2001). All these considerations were made in our previous definition of hyperpredation (see Moleón et al. 2008).

### The case of rabbits, red-legged partridges and their shared predators in Spain

The cross-correlation between rabbit and partridge populations

In our original paper (Moleón et al. 2008), we used hunting bag data provided by the Spanish Ministry of Agriculture (and calculated on the basis of data recorded at the provincial level) to model rabbit and red-legged partridge population dynamics in continental Spain for the 1986–2003 period. In order to minimise the influence of hunting effort on population size estimates, we first divided the raw data

by the number of hunting licences per year (Cattadori et al. 2003; Virgós et al. 2007), as properly noted by Blanco-Aguilar and colleagues. After a sudden, dramatic drop in the rabbit population following the RHD outbreak (which started in 1988 and can be considered an emerging infectious disease, EID), a progressive recovery took place probably due to the natural process of immunisation against the disease (Calvete et al. 2002). The partridge population essentially mimicked this trend. However, Blanco-Aguilar and colleagues state that, since the mid-1990s, most of the Spanish wildlife monitoring programmes (although they only cite two, one on partridges and another for rabbits) show contrasting trends for both rabbit and partridge populations as compared to those patterns inferred from the national hunting bag statistics.

In particular, Blanco-Aguilar and colleagues first argue that the Spanish monitoring programme of common breeding birds (SACRE) showed a stable trend of a  $-0.2\%$  annual partridge population growth rate (SEO/BirdLife 2006), which apparently contradicts our data (which showed a clear increasing trend between 1994 and 2003) and compromises our subsequent conclusions. These authors claim that these differences can be attributed mainly to the releases of farm-raised partridges on hunting estates throughout the country, which started in the mid-1980s to become more marked and widespread as of the late 1990s. However, they do not mention that a number of the released partridges, and rabbits, rapidly die due to reasons other than hunting (starvation, diseases, predation, etc.; Calvete and Estrada 2004; Gortázar et al. 2000; Calvete et al. 2004; Pérez et al. 2004), and hence, they are not included (i.e. inflating) in the bag statistics. Yet despite its undoubted virtues, the SACRE programme has its drawbacks and cannot be conceived as the panacea, as it is performed by a highly variable effort in terms of both time and space, and by a large number of different observers (i.e. volunteers; e.g. Carrascal 2011; Murgui 2011). On the other hand, this monitoring programme started in 1998 (i.e. near the end of our study period), so a comparison with our data has little to show. All in all, but certainly most crucially, if the real trend for partridges in the last years of the studied series has not been as positive as hunting bag records show (due to the inflation effect by released partridges), the correlation between the rabbit and partridge population dynamics should be even stronger than that we found. This is a most remarkable question which was already addressed in the discussion of Moleón et al. (2008). As Blanco-Aguilar and colleagues recognise, ‘there are no accurate records about [partridge] releases in Spain’, and this is precisely why we did not explicitly introduce this factor into the models. Thus, we encourage the Spanish National Administration to urge provinces to include data about releases of partridges, rabbits and other game species into the annual hunting bag records in order to improve databases for future applications.

Secondly, Blanco-Aguilar and colleagues question the hunting bag-based national trends of rabbits based on the findings of Delibes-Mateos et al. (2009), who reviewed studies dealing with rabbit population trends since the RHD-induced crash until approximately halfway through the first decade of the twenty-first century in the Iberian Peninsula. Nevertheless, according to Delibes-Mateos et al. (2009), quantitative data for Spain were available for only four field studies, ranging from the very local to the regional scale (i.e. not six sites, and not all concerning regional scales, as asserted by Blanco-Aguilar and colleagues). Three of these studies (i.e. 75 %) found negative trends for rabbits (as opposed to the slight recovery shown by the hunting bag data), and Blanco-Aguilar and colleagues assume that the trends inferred from these local/regional studies are representative of the whole country. However, it seems too risky to extrapolate these results to the national level given the limited sample size (there are other areas where rabbits appear to have increased in recent years; Cabezas-Díaz et al., unpublished data) and the high heterogeneity of the methodologies and sampling efforts used in the reviewed studies (from interviews to transects counting rabbits or their latrines; see Delibes-Mateos et al. 2009).

Blanco-Aguilar and colleagues also question the usefulness of the Spanish hunting bag data in the light of a recent paper which compared the rabbit trends obtained from hunting statistics (number of hunted rabbits per hectare) and those from field surveys (an index based on latrine counts in transects) in Portugal (Ferreira et al. 2010) as it found a discrepancy between both data sources. However, unlike us, Ferreira et al. (2010) did not correct the number of hunted rabbits by the number of hunters, and no direct correspondence was made between the latrine abundance index and rabbit numbers, thus preventing quantitative comparisons.

Therefore, no convincing evidence has been provided against the usefulness of bag data to infer rabbit dynamics on the national scale in Spain. Indeed, these data have been used on conservation grounds by Virgós et al. (2007) to model national trends of rabbit abundance and to evaluate its status for Spain. This study was the basis of the argument of the recent re-classification of this species into the ‘Vulnerable VU A2abde’ category (Villafuerte and Delibes-Mateos 2007). Virgós et al. (2007) found the same pattern as ours for rabbit dynamics using a different analytical approach, i.e. a sudden drop after the RHD outbreak and then a slight recovery.

Anyway, the most important point here is that the populations of both prey species, i.e. rabbits and partridges, were highly cross-correlated after the arrival of RHD. As argued above, by assuming that partridge hunting bag data have been increasingly over-represented since the mid-1990s, the correlation would be even higher than that analytically found, as we already mentioned in the discussion of

Moleón et al. (2008). This important consideration reinforces our hypothesis that a common, large-scale mechanism affecting both species (e.g. hyperpredation, see below) played a major role in driving the observed rabbit and partridge population dynamics during our post-RHD study period.

Blanco-Aguilar and colleagues also state that as the Spanish partridge population had already started to decline since the 1970s, ‘it is not possible to discard that the same factors that were affecting partridge populations before RHD arrival were also working after RHD arrival’. Admittedly, several general processes other than hyperpredation (e.g. climate) could have led to the synchronised population dynamics in the rabbit–partridge example. Equally, some other causes could have forced the partridge population to decline, such as habitat destruction and deterioration, over-hunting and pesticides. Nevertheless, we already considered (either explicitly in the models or in the discussion) most of these factors and concluded that any of them can be a probable major cause of population synchrony in our study system (see Moleón et al. 2008 for complete details). Importantly, these factors may have forced both rabbit and partridge populations to decrease (and then rest regulatory plasticity), but it is highly unlikely that they were able to induce a long-term synchrony among such phylogenetically distant species with no direct interaction and in response to different external forcing mechanisms. What is more, they are unable to produce population recoveries (or stabilities or decelerated decreases) as shown by the hunting bag data given that there is no global evidence that those factors actually decreased in Spain during the study period. Blanco-Aguilar and colleagues also mention most of these potential causes of partridge decline in their paper (although they never mentioned predation, even when it explicitly appears in some of the bibliographic references they cite, i.e. Blanco-Aguilar et al. 2004), but they fail to analyse new alternative hypotheses, as they claim in their conclusions.

Using the extended data set provided by Blanco-Aguilar et al. (2012), we have re-analysed both the probability of population crashes and the cross-correlation between rabbit and partridge dynamics from 1973 to 2003 (Fig. 1). This would reveal whether rabbit and partridge populations were indeed subjected, or not, to the same common pressures before and after the RHD outbreak. We used the sequential *t* test analysis of regime shifts (STARS) developed by Rodionov (2004) to test for potential regime shifts in the rabbit and partridge time series. Interestingly, we found a synchronised shift to significantly lower population levels ( $p < 0.05$ ) in both the rabbit and partridge populations in 1988, which is concurrent with the RHD outbreak. A further step increase in the partridge population was detected in 1997, but not in the rabbit time series. At this point, it is important to note that we are dealing with step, abrupt changes in population size, and not with trends.

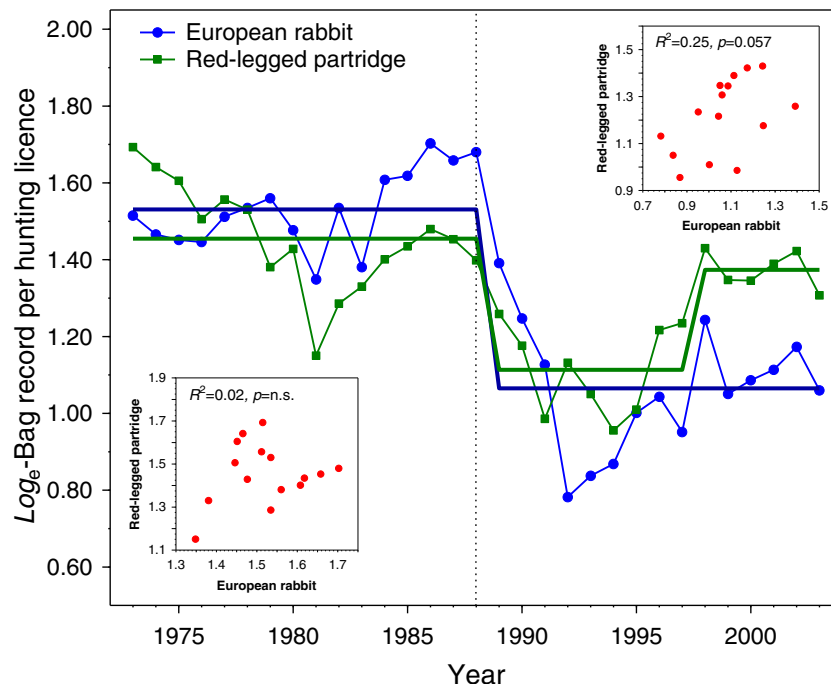
It is even more noteworthy that we found that rabbit and partridge populations were synchronised after the RHD outbreak (Pearson correlation:  $n=15$ ,  $r=0.501$ ,  $p=0.057$ ; as shown in Moleón et al. 2008), but not before (Pearson correlation:  $n=16$ ,  $r=0.136$ ,  $p=0.616$ ; Fig. 1). Consequently, it is quite likely that large-scale forces irrupted to synchronise the population dynamics of both rabbits and partridges in Spain coinciding with the RHD outbreak.

#### Correspondence between local and national scales

Hyperpredation processes would in theory lead to a population crash in hyperpredated prey species which would, in turn, synchronise the dynamics of both the main prey and the hyperpredated one (Moleón et al. 2008). However, Blanco-Aguilar and colleagues indicate a lack of correspondence within the partridge (i.e. the hyperpredated species) dynamics when comparing local (Navarre and Catalonia; Fig. 2) and large (Spain) scales after the RHD arrival. This would question the assumptions of the hyperpredation hypothesis since Navarre and Catalonia were the areas in which the predator diet data were specifically analysed in our previous paper (see below). However, here we show that the hunting bag data indeed support such a correspondence.

To test this, we firstly performed Pearson correlation analyses to explore the associations between the number of partridges hunted per hunting licence in the Navarrese or Catalanian regions and Spain for both periods (i.e. before and after RHD) using the 1973–2003 temporal series (Fig. 2). Depending on the case, we extracted the Navarrese or Catalanian data from the Spanish data set to account for data independence. While we did not find any correlation before RHD (Spain vs. Navarre:  $n=16$ ,  $r=-0.157$ ,  $p=0.561$ ; Spain vs. Catalonia:  $n=17$ ,  $r=-0.376$ ,  $p=0.137$ ), a significant association appeared after RHD in both cases (Spain vs. Navarre:  $n=15$ ,  $r=0.683$ ,  $p=0.005$ ; Spain vs. Catalonia:  $n=14$ ,  $r=0.737$ ,  $p=0.003$ ; Fig. 3). (Note that the first major RHD outbreaks in Navarre occurred in 1989—Ceballos 1991; Tella and Mañosa 1993—while RHD was present in Catalonia since 1989, but mainly since 1990—Real 1991; Mañosa 1994; thus, the calculations in this paper and in Moleón et al. 2008 refer to the 1989 and 1990 thresholds, respectively.)

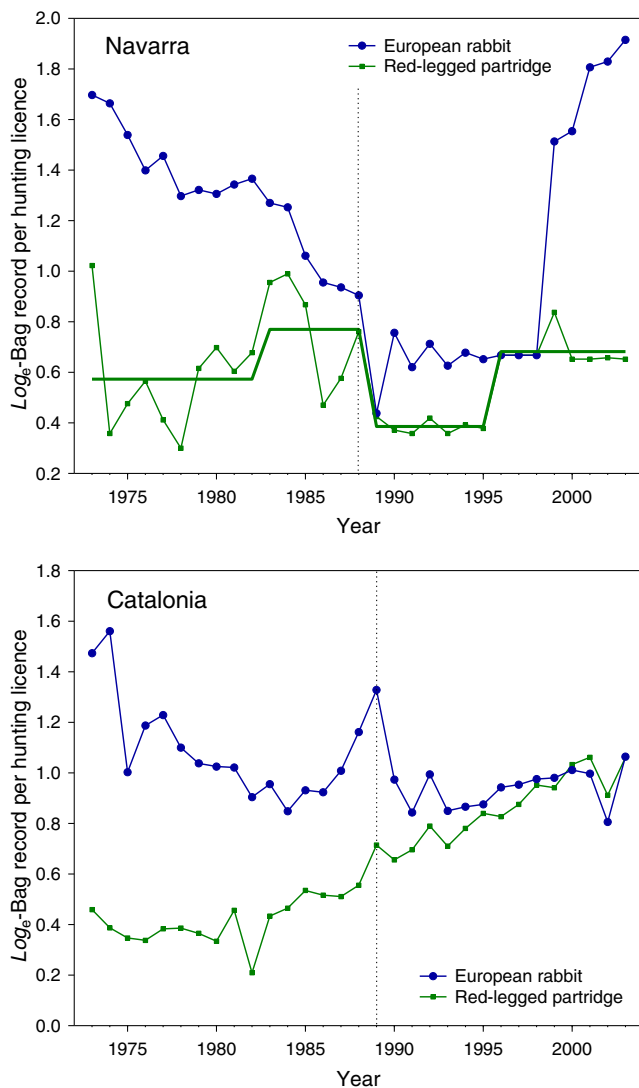
Secondly, the availability of spatially distributed hunting bag data on large spatial scales provides the opportunity to test for spatial autocorrelation in population dynamics (Liebhold et al. 2004). We focused on the dynamics of the red-legged partridge. We devised three general qualitative scenarios arising from the operation of external forcing (e.g. climate, shared predators) and internal processes (e.g.



**Fig. 1** Time series of European rabbits and red-legged partridges hunted in Spain from 1973 and 2003, standardised per yearly hunting licences. The solid, discontinuous lines within each time series depict the regime shifts detected by the STARS technique (Rodionov 2004) for both time series. Different segments represent significantly distinct sequential regimes for each time series detected at a  $p$  value of 0.05, using a cut-off

length of 6 and a Huber parameter of 1; time series were prewhitened prior to the analyses, and an OLS red noise estimation with a subsample size of 3 was used (slight changes in the input parameters yielded essentially similar results). Scatterplots within the main graph represent the cross-correlation between the rabbit and partridge time series before (lower left) and after the RHD outbreak (upper right)





**Fig. 2** Time series of European rabbits and red-legged partridges hunted in Navarra and Catalonia from 1973 and 2003, standardised per yearly hunting licences. The *solid, discontinuous lines* within the partridge time series depict the regime shifts detected by the STARS technique (Rodionov 2004). Only the regimes for the time series for which the STARS method detected significant shifts are depicted

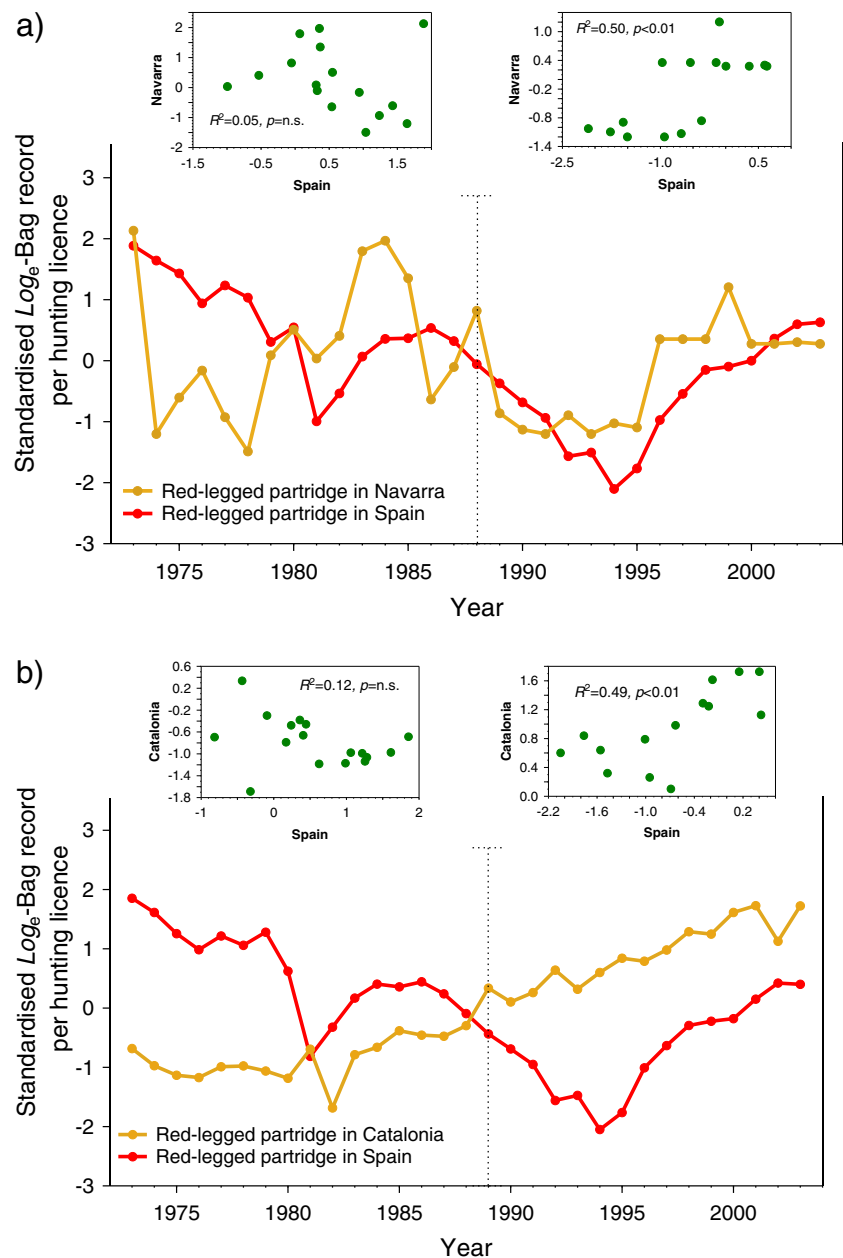
density-independent dispersal) as agents shaping the spatial autocorrelation function (Fig. 4). In the first scenario, local populations fluctuate almost independently due to the overriding effects of local processes (e.g. differing hunting pressures and/or agricultural policies among provinces), so the autocorrelation function is a flat line around 0; in the second scenario, a decreasing autocorrelation function with distance is usually regarded as the signature of short-range dispersal and/or shared predators (see Liebhold et al. 2004). Finally, a third scenario depicts a situation in which the correlation among local populations is very high and homogenous across spatial distances (Fig. 4). In these cases, large-range dispersal, strong coupling of climate or predation with demography, or even an incorrect spatial sampling of the

population well below the true spatial domain of the populations can be advocated as the mechanisms behind these patterns.

For the partridge and rabbit populations, if enhanced predation pressure on the partridge population (Moleón et al. 2008) effectively drives the joint dynamics of both game species, we expect the first scenario to be weakly supported and the second and third scenarios to be strongly supported. In particular, we expect to find a shift from the second scenario before the RHD outbreak (a decreasing autocorrelation function with distance) to the third scenario after the RHD outbreak (an enhanced spatial autocorrelation on all the spatial scales driven by enhanced predation pressure by generalist predators). Figure 4 illustrates the empirical spatial autocorrelation functions fitted to the time series of red-legged partridge for five Spanish provinces (Navarre, Lleida, Tarragona, Barcelona and Girona), estimated for the whole time series, and also both before and after the RHD outbreak. Due to the small sample size of our analysis, we did not fit a parametric spatial function; rather, we fitted a LOESS regression (Cleveland and Devlin 1988) to the set of cross-correlations between all the pairs of spatial locations, and we estimated empirical confidence intervals for the spatial functions with 10,000 bootstrapped samples. Interestingly, we find support for the expectations described above: prior to the RHD outbreak, a slightly decreasing spatial autocorrelation function suggests that spatially separated populations were less similar among them than spatially closed ones. In contrast, after the RHD outbreak, the spatial autocorrelation function became relatively constant through all the spatial dimensions and the average autocorrelation value between local populations almost doubled if compared to the period prior to the RHD outbreak, in particular for spatially separated populations. Given that we found no previous support for climate effects on the population dynamics of both game species (Moleón et al. 2008) and due to the short-range movements of the red-legged partridge (Pérez et al. 2004; Buenestado et al. 2008; Duarte et al. 2011), we interpret this pattern as the signature of an abrupt shift in the operation of large-scale predation from low to high values after the RHD outbreak. This enhanced predation pressure likely explains the enhanced autocorrelation on large spatial scales in the red-legged partridge after the RHD outbreak.

Thirdly, as Blanco-Aguar and colleagues indicate, the partridge population declined in Navarra after RHD (although there are some missing data in the Fig. 2e of their paper for hunted partridges, precisely for the years in which partridge bag records were relatively high; i.e. 1996–1999, and also for hunted rabbits in 1999), a pattern that would well fit the national one, as shown above. In contrast, the partridge trends in the other four analysed provinces (Catalonia region) after RHD did not apparently show such a decline. As these authors state, the release of partridges has been banned in Navarra since 1991, but not in Catalonia. Thus, Navarra would

**Fig. 3** Time series of red-legged partridges hunted in Navarre and Spain (a) and Catalonia and Spain (b), from 1973 and 2003, standardised per yearly hunting licences. Time series were standardised in order to visually enhance the local covariation between both series. Scatterplots within the main graphs represent the cross-correlation between the national and regional time series before (left) and after the RHD outbreak (right)



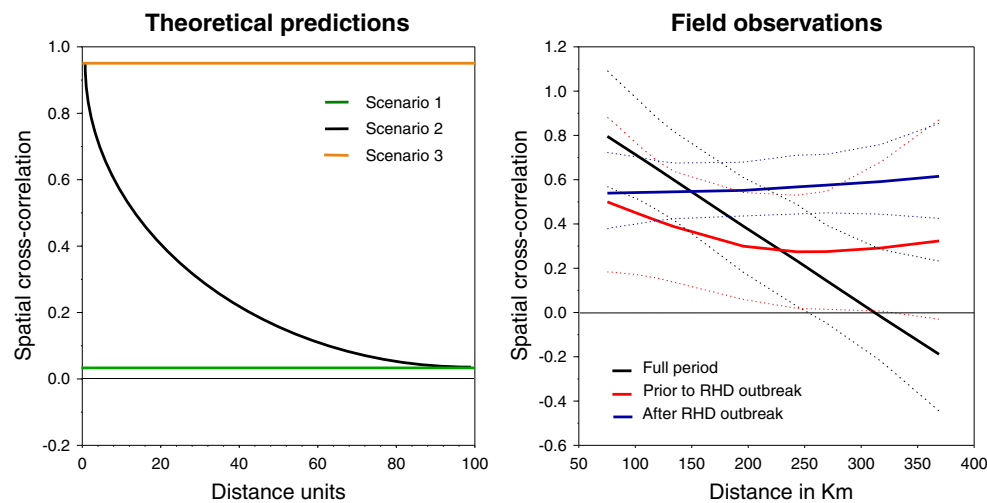
represent a valuable ‘natural experiment’ showing the effect of captive-born partridge releases on wild partridge populations, which concurs very well with our predictions. In addition, the patterns are essentially also the same when compared to areas where partridge releases were allowed. Although partridge declines in Catalonia were not so obvious (likely due, in part, precisely to the farm-reared partridge releases; in addition, relatively low hunting bags of both rabbits and partridges were recorded in Catalonia during the study period, which would reduce the reliability of the patterns found on this scale), the partridge bag data from that region also fairly well fitted those at the national level.

Fourthly, we found that rabbit and partridge populations on the infranational scale were not correlated before RHD

(Pearson correlation in Navarre:  $n=16$ ,  $r=-0.042$ ,  $p=0.877$ ; in Catalonia:  $n=17$ ,  $r=0.156$ ,  $p=0.550$ ) but clearly cross-correlated after RHD (Pearson correlation in Navarre, ln-transformed to normalise data:  $n=15$ ,  $r=0.640$ ,  $p=0.01$ ; in Catalonia:  $n=14$ ,  $r=0.593$ ,  $p=0.025$ ). Therefore, the same synchronising forces acting on the national scale after the arrival of RHD seemed to also operate on the local scale.

Enhanced predation pressure as a plausible mechanism behind the observed dynamics

In our previous paper (Moleón et al. 2008), and according to the scientific procedure standards, after analysing prey dynamics, we proceeded to find the most probable factor



**Fig. 4** Theoretical expectations for the spatial autocorrelated dynamics of the red-legged partridge according to differing ecological scenarios and the empirical results obtained with the field data. The spatial autocorrelation functions for the full time series (1973–2003) and the time series prior to (1973–1988) and after the RHD outbreak (1989–2003) were estimated non-parametrically using a LOESS function fitted to the set of all the possible cross-correlations among five

explaining the clear synchrony observed between rabbit and partridge populations after RHD. As already stated in our previous study, it is well-known that both rabbits and partridges are consumed by a plethora of Spanish predators, either birds of prey or mammalian carnivores. Strikingly, many of these predators use to capture both prey (i.e. they are ‘shared predators’ in relation to rabbits and partridges). Besides, rabbits and partridges are also similar in size and share habitat preferences and ground-related behaviour. Thus, each species (especially the partridge, because the rabbit is the staple prey for all shared predators) is expected to behave as an important alternative prey for shared predators if one becomes scarce (Moleón et al. 2008, 2009). In our case, the rabbit species directly underwent a dramatic population decline (due to RHD outbreak), so we hypothesised that partridges would subsequently experience enhanced predation, thus leaving a dynamic fingerprint on its population.

To test this possibility, we needed to provide evidence that predators increased absolute partridge consumption after the RHD irruption as compared to their ‘normal’ partridge consumption levels before RHD, and the inverse pattern with rabbit consumption. We then proceeded by four steps. Firstly, we reviewed the existing scientific information about predators’ (both raptors and carnivores) diet in Spain. This allowed us to identify the ‘shared’ predators (i.e. in terms of relative frequency, those including >5 % of both prey species in their diet). Secondly, we identified the main shared predators (i.e. those whose diet included >20 % of both rabbits and partridges), so that these were the predators which entered the next steps due to their higher prey

Spanish provinces (Navarre, Lleida, Tarragona, Barcelona and Girona). The distance between the centroid of each province was used as the measure of spatial separation. The empirical confidence intervals (dotted lines) were constructed using 10,000 bootstrapped samples of the original cross-correlations. The cross-correlation values have been omitted for clarity (see the text for further explanations)

limitation potential (as seen, the predator species selection process was not premeditatedly skewed, as suggested by Blanco-Aguilar and colleagues). Thirdly, we compiled those studies that simultaneously dealt with the diet during the period just before and after the RHD outbreak (1986–1992) and within the same area each (these two conditions were considered essential) of the main shared predators (which does not mean that similar patterns could be also found in other areas or for other, minor predators), namely the golden eagle (*Aquila chrysaetos*), Bonelli’s eagle (*Aquila fasciata*) and Eurasian goshawk (*Accipiter gentilis*; in this case, we separated the data from scarcely and heavily forested habitats). Fourthly, we effectively found significant decreases in rabbit relative consumption for all the main shared predators and in all situations; in contrast, partridge relative consumption increased in half of the cases (the increase was non-significant in the other half). What proved even more relevant is not that the partridge relative consumption generally increased, but that the partridge consumption levels did not decrease after RHD, when partridge populations notably lowered in relation to before RHD. This indeed provides strong evidence for enhanced predation pressure.

We recognise, however, that there is a potential flaw in our arguments: as properly noted by Blanco-Aguilar and colleagues, the diet data of the studied predators originated from relatively local study areas. Nevertheless, this does not imply a lack of correspondence between local and national diet patterns (as shown above for population dynamics). We employed only the local studies (golden eagle: Fernández 1993; goshawk: Mañosa 1994; Bonelli’s eagle: authors

unpublished information) in order to follow the restrictive conditions we mention above (data referring to the most critical period of the temporal series and to perfectly comparable study areas). Yet there is a number of additional bibliographic information to support the feasibility of extrapolating the findings for the major shared predators from the local to the large, national scale (and to other predators). A paradigmatic example of this is that recently provided by our team in relation to Bonelli's eagle (Moleón et al. 2009), where we show important decreases in rabbit, but not in partridge, consumption after RHD over the whole W Mediterranean continental Europe (and not only Spain), exactly what we found on the local scale.

Blanco-Aguilar and colleagues state that 'the decline of rabbit consumption due to the decrease of rabbit populations automatically entails the increase in the percentage of occurrence of the other species in the diet, even if no absolute increase in the consumption of these species occurred. Thus, to invoke the existence of hyperpredation, the authors should demonstrate that the decrease of rabbit in the diet resulted in a differential increase in partridge consumption (in relation to population densities)'. We disagree with this statement for the following main reason: Blanco-Aguilar and colleagues implicitly assume the unrealistic assumption that a predator's (or a consumer's) food requirements fluctuate exactly in the same magnitude as the oscillations in the main prey population (why should a predator's food requirement vary from, say, a daily intake of 1 kg when the main prey is abundant to a daily intake of 0.5 kg when this prey is scarce?). In other words, an absolute increase in the consumption of some alternative prey—in our case, principally the partridge—must take place for the predator to get by. In any case, by plotting the population ratio of partridges to rabbits against an averaged, weighted predation ratio of partridges to rabbits in the predators' diet for both periods (before and after RHD; see Fig. 1d in Moleón et al. 2008), we have already shown increased partridge consumption in relation to relative population densities, as outlined above.

Blanco-Aguilar and colleagues cite the example of the eagle owl (*Bubo bubo*) which, according to these authors, maintained similar rabbit consumption levels before and after RHD, but intraguild predation on other raptor species increased (which, in turn, would have diminished their numbers and 'even reduced overall predation pressure'). However, as explained above, the eagle owl has little to do with our work as it is not a main shared predator of rabbits and partridges (according to our criteria of introducing >20 % of each prey into diet). On the other hand, raptors enter eagle owls' diet at a very low rate, and the species most frequently eaten by eagle owls are raptors that do not normally consume rabbits nor partridges (i.e. these prey form <5 % of their diet). In his review study, Serrano (2000) found that eagle owls in Mediterranean Spain and France ate 14 species of diurnal and six nocturnal raptors, meaning totals of

only 1.8 and 1.7 % of the owl diet in terms of, respectively, relative and biomass frequencies. He also found that as much as 94.3 and 95.9 % of the prey items attributed to raptors corresponded to species that do not normally consume rabbits or both rabbits and partridges, respectively. In fact, he stated that 'rabbits and raptors showed significant inverse relationships, but this trend was not significant when only raptors competing for rabbits were included in the analysis'. Similar values were recently shown by Lourenço et al. (2011); these authors also found no evidence of an effect of the percentage of rabbits on the percentage of mesopredators in the diet of the eagle owl and another three large raptors in SW Europe. Thus, a very slight impact on rabbit (and even less on shared) predator numbers can be expected during our study period due to eagle owl predation. On the other hand, if rabbit consumption levels by eagle owls were similar between periods as Blanco-Aguilar and colleagues state (which is somewhat debatable, at least in some areas; see e.g. Donazar 1989; Serrano 1998), a coupled increase in intraguild predation would hardly be attributed to RHD. Whatever the case, it would undoubtedly be interesting to review the eagle owl's dietary responses to the RHD-induced rabbit population drop, from a non-biased perspective.

Blanco-Aguilar and colleagues also suggest that partridge releases could have similarly corrupted our raptor diet results as they surely altered the hunting bag records. However, our diet data refer to the late 1980s and early 1990s, i.e. well before partridge farm facilities and releases became a widespread practice in Spain (according to these authors, from the late 1990s onwards). In addition, releases usually take place out of the raptors' breeding period (Pérez et al. 2004), which means that most releases did not overlap with our predators' diet surveys.

Finally, we would like to remark that the possible reduction in the numbers or the breeding output of some Spanish predators during the prey low abundance period is not incompatible with the EID-mediated hyperpredation hypothesis: as already discussed in our original work, this non-mutually exclusive mechanism could have released both prey populations from predation and further enhanced synchrony. However, as argued in Moleón et al. (2008), there is no global evidence that the predator (usually long-living species with deferred maturity and low fecundities) populations (especially the breeding sector) in Spain responded numerically during the study period. Also, we cannot discard that human hunters behaved as hyperpredators themselves by increasingly focusing on partridges as rabbits became less abundant. In such a case, partridge real population drop after RHD might have probably been stronger than shown in hunting statistics. Anyway, either hunter activity was part or not of the hyperpredation process, the observed partridge hunting bag drop after RHD mostly reflect the contribution of factors other than hunting pressure. Approaches aimed to elucidate the separate effect of human hunters and predators on the



dynamics of game prey species would be particularly interesting from a conservation point of view.

## Conclusions

In the particular case of rabbits and red-legged partridges in Spain, unfortunately no ideal long-term data of population dynamics of the two prey species exist on the national scale. However, hunting bag data can be useful to infer realistic population dynamics and the ecological mechanisms accounting for them (interestingly, not only at the national scale, but also at lower scales, as revealed by the above-mentioned analyses), provided that (1) they are corrected by the number of hunting licenses; (2) appropriate statistical tools are employed; and (3) methodological constraints are taken into account by being either explicitly entered in models or, if detailed information on the error magnitude and trend is lacking, properly considered when discussing the results. At the same time, the best evidence available (either empirical or analytical) suggests accepting the EID-mediated hyperpredation hypothesis as the most plausible mechanism explaining rabbit and partridge dynamics and synchrony after RHD outbreak (at least until 2003, when our study period ended).

Nevertheless, the dimension of the predation impact exerted by the broad community of Spanish rabbit and partridge consumers (not only predators, but also omnivorous animals) is not a closed question. Unfortunately, the available diet (and demographic) data probably do not suffice to properly address it, especially in relation to those consumers that are able to respond numerically more rapidly and intensely than eagles and goshawks. Rabbit and partridge consumption variations by many of these consumers may have been of such a low magnitude that conventional dietary approaches could have overlooked them, but could still have contributed to limit prey populations.

Importantly, however, the more likely real underlying cause of partridge population decline in Spain two decades ago was an EID (RHD) that affected rabbits and was greatly facilitated by human action (mainly via translocations of infected individuals; Villafuerte et al. 1995). So humans were ultimately and indirectly responsible for such a drop in partridge numbers, and not predation per se. Besides, limitation of partridges by predators was probably an extreme, circumstantial situation which was possible only after the large-scale human disturbance of natural processes and by reducing the partridge- (and rabbit-) carrying capacity (through intensification of agricultural practices, over-exploitation, parasites, hybridisation with released farm-reared individuals, etc.; Blanco-Aguilar et al. 2004; Villafuerte and Delibes-Mateos 2007). Thus, the indirect effects on ecosystems caused by human-aided disruption of ecological interactions are the key point of our previous paper, as we properly remarked in the discussion (see Moleón et al. 2008).

Furthermore, there was not a single mention about the need of predator control in that paper, so we are not responsible for the misinterpretation (on either ethical or conservation grounds) of our study made by Blanco-Aguilar and colleagues that ‘endorsing the hypothesis of raptor-mediated hyperpredation without sufficient proof may have conflictive consequences if we consider the increased persecution of raptors in recent decades in Spain’ (paradoxically, note that Blanco-Aguilar and colleagues do not statistically support any of their whole chain of criticisms), or that ‘some might advocate the control raptor populations to increase game populations’. Firstly, scientists’ opinions (especially when given in a scientific arena such as a top scientific journal) is unfortunately far from influencing hunters’ behaviour in Spain, which also occurs in other parts of Europe (Thirgood and Redpath 2008). Secondly, the primary, logical management action deriving from our previous study, which is reinforced by the new insights provided in the present one, is the convenience of controlling not predator populations, but the human-aided dissemination of ‘pathogen pollution’ (as well as the other human-related factors that constrained the rabbit- and partridge-carrying capacity). The artificial spread of RHD has been proven to occur even today, more than 20 years after its first outbreak; in fact, a new variant of the virus, which has been recently detected on NE Spanish farms, should be carefully looked after, as already observed in the field (Calvete et al. 2012; Dalton et al. 2012). Finally, the hyperpredation processes that took place decades ago have limited the application to the current ecological context and related management practices, which should be revisited on the national scale. In this line, it has been suggested that the potential role of Bonelli’s eagles (one of the main shared predators) as a limiting factor of rabbits and partridges in an area of S Spain in recent times was so poor that the conflict between the predator and the hunting lobbies would be nonexistent or highly localised (probably a result that could also be extrapolated to other Spanish areas, and even to predators; Moleón et al. 2011). Besides, the relationships between the predation rate by Bonelli’s eagles and rabbit and partridge densities, as encouraged by Blanco-Aguilar and colleagues, have also been well-established on this scale; Moleón et al. 2012). New multi-scale approaches, on improved data sets, if possible, which aim to ascertain the contribution of the whole community of predators (including humans) to the rabbit and partridge dynamics in the Iberian Peninsula, would be made most welcome.

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