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ORIGINAL PAPER

Is the interaction between rabbit hemorrhagic disease and hyperpredation by raptors a major cause of the red-legged partridge decline in Spain?

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Abstract Hyperpredation can be described as 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. It has been proposed that rabbit hemorrhagic disease (RHD), which decimated populations of European wild rabbit (*Oryctolagus cuniculus*) in Spain, led to prey switching by raptors towards red-legged partridges (*Alectoris rufa*) causing declines in their populations as a peculiar case of hyperpredation.

We have reviewed field studies that disagree with estimates (based on bag records) of recent increases of rabbit and partridge numbers in Spain. Because of an increase in releases of farm-reared animals, there is doubt about the use of bag records to accurately estimate population trends in recent decades. We also provide new data and discuss some analytical considerations related to the temporal and spatial scales that might affect the interpretation of data. Finally, we discuss why studies associated with raptor food habits, predator population dynamics and predator distribution suggest that diet data are not sufficient to link patterns and processes. Although we agree that the RHD outbreak has markedly affected rabbit populations, which has indirectly affected many other species in the Iberian Peninsula, we consider that hyperpredation mediated by raptors has not been clearly demonstrated. In contrast, 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.

Keywords *Alectoris* · Emerging disease · Hunting · Mediterranean ecosystem · *Oryctolagus* · Predator persecution · Shooting

Introduction

Over the past decades, the red-legged partridge (*Alectoris rufa*) has notably declined in the Iberian Peninsula, where the species probably originated and where its wild populations reach the highest densities within its current distribution range (Blanco-Aguiar et al. 2004). Excessive hunting pressure, changes in pesticide management and livestock densities, hybridization with *Alectoris chukar*, diseases associated to farm-reared game releases, and the intensification of agriculture have been cited as possible

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causes of partridge decline (e.g., Blanco-Aguiar 2007; Blanco-Aguiar et al. 2008; Villanúa et al. 2008; Casas and Viñuela 2010; Díaz-Sánchez et al. 2011). It has been recently proposed that hyperpredation could have been one of the main causes explaining partridge decline in the Iberian Peninsula. Hyperpredation process has been described as 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 (e.g., Smith and Quin 1996; Courchamp et al. 2000). However, according to Moleón et al. (2008), hyperpredation refers to an enhanced predation pressure on a secondary prey due to either an increase in the abundance of a predator population or a sudden drop in the abundance of the main prey. Following only the latter approach, the rabbit hemorrhagic disease (RHD) outbreak, which decimated populations of European wild rabbit (*Oryctolagus cuniculus*), forced raptors to switch from eating rabbits to eating red-legged partridges. In turn, this is hypothesized to have further declined or limited partridge populations. More recently, a postimmunization phase with a reduction in rabbit mortality due to the immunization led again to medium–high rabbit population densities, which would have led to partridge population increases as raptors would have stopped concentrating on secondary prey once their main prey was recovered.

We assessed the potential role of hyperpredation (or enhanced predation) on partridge decline. In particular: (1) whether or not rabbit and wild partridge populations have indeed increased during the last decade as suggested by Moleón et al. (2008), (2) whether the analytical approach used in Moleón et al. (2008) is adequate to support the hyperpredation hypothesis, and (3) whether the functional response of the three raptor species mentioned by Moleón et al. (2008), which generally are found at low population densities, can cause the suggested large-scale effects on the dynamics of partridge populations. Finally, we discuss the potential consequences of hyperpredation for the conflict between hunting and biodiversity.

Material and methods

To evaluate whether or not partridge and rabbit populations have recently increased, we reviewed the results of field studies on rabbit and partridge population trends in the Iberian Peninsula. Using this information, we discuss the reliability of current hunting bags as an indicator of game species abundance. We also reviewed some limitations of data and analyses used to test the hyperpredation hypothesis and incorporated new data that questioned this hypothesis. In this respect, we assessed whether or not the predator community fed differently before and after the outbreak of RHD. In addition, we discuss the potential consequences of prey populations by predators according to the functional response of raptors and the density dependence of productivity theories (Sinclair and Pech 1996; Valkama et al. 2005). Finally, Moleón et al. (2008) used information from national bag records to describe partridge population trends, whereas they used only four local raptor studies (Fig. 1 in reference Moleón et al. 2008) to infer processes causing these patterns (i.e., predation). However, the patterns that we observe in nature, and the processes that cause them, can change with the scale of our observation (Wiens 1989; Levin 1992). For this reason, we used the same hunting bags data from the Spanish Ministry of Agriculture, Fisheries and Food to evaluate whether rabbit and partridge densities follow the same trends at national scale as in the provinces where Moleón et al. (2008) analyzed raptor diet. Provincial (and national) harvest numbers are based on questionnaires that all managers of hunting lands are

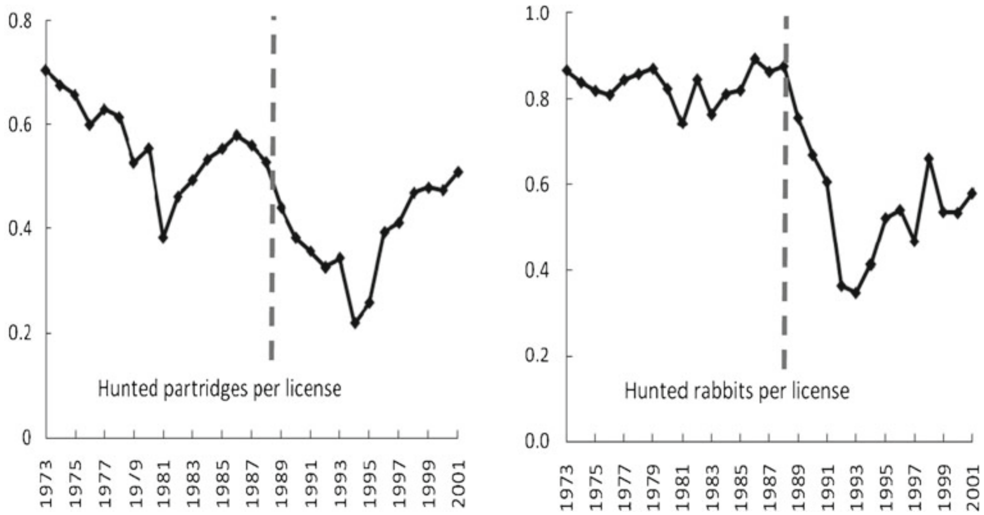

Fig. 1 Trends in numbers of red-legged partridges (*Alectoris rufa*) and rabbits (*Oryctolagus cuniculus*) hunted per licence in Spain. The *dashed line* represents the year in which rabbit hemorrhagic disease (RHD) arrived in Spain

required to complete each year and send to the Ministry of Agriculture. This agency calculates (and publishes) a summary value of the harvest in each province by summing the data from each hunting land in each province for each year. Because hunting effort can influence the number of rabbits and partridges hunted, we divided total harvest by the number of hunting licenses in each province and year to obtain a reliable estimate of population size (Cattadori et al. 2003; Virgós et al. 2007).

Results and discussion

Did rabbit and partridge populations increase during the last decade in Spain?

Monitoring programs are among the most important data sources for assessing temporal changes in biodiversity (e.g., Fewster et al. 2000; van Strien et al. 2001; Gregory et al. 2005). Most monitoring data available in the literature show that both partridges and rabbits have followed stable or even negative trends since the mid1990s, which clearly contradicts the pattern suggested by national bag records. For instance, wild partridge population trends between 1998 and 2006 estimated from the Spanish monitoring program of common breeding birds (SACRE) showed a fairly stable trend, −0.2% annual population growth rate (SEO/BIRDLIFE 2006). Also, a recent review of wild rabbit trends during the last decade in different Iberian regions showed a negative trend in five of six independent regional field studies (covering more than 300 study plots; Delibes-Mateos et al. 2009b).

The contradiction between the findings of Moleón et al. (2008) and other published studies regarding rabbit and partridge demographic trends comes apparently from the data source used by these authors to estimate population trends. They used hunting bag data from the Spanish Ministry of Agriculture, Fisheries and Food. However, bag records can be useful to estimate population trends *only* if the relationship between harvesting and population density remains unchanged throughout the time period studied. During the last decade, the Spanish Red-legged partridge bag records are likely inflated by the releases of farm-raised partridges, and the authors did not critically address this issue. There are no accurate records about releases in Spain, but Blanco-Aguiar et al. (2008) documented, using partridge-farm advertisement records in hunting journals, an exponential growth of partridge-farm facilities and releases, which started in the mid1980s but that was particularly marked from the late 1990s. It is estimated that since 2000 between 4 and 5 million farm-bred partridges have been released every year in Spain for hunting (Gortázar et al. 2000; Arroyo and Beja 2002). Unfortunately, Spanish bag records cannot discriminate between wild-born and released partridges, but it is highly probable that released partridges have been inflating bag records since the 1990s, particularly in those provinces where releases are frequent. For instance, in Navarra province, the only Spanish province where partridge releases are forbidden since 1991, field surveys of red-legged partridges have shown stable or declining trends (Gobierno de Navarra 2006). Therefore, changes in game management practices could have distorted the value of partridge hunting bags as indicators of population size since late 1990s.

Similarly, Ferreira et al. (2010) have recently observed a discrepancy between rabbit trends obtained from field data and hunting statistics in Portugal. These authors argued that hunting bags may be influenced by sporadic management operations undertaken by hunters and the lack of systematic procedures in data collection, and, therefore, hunting statistics are probably not representative of real changes in rabbit populations.

On the other hand, when national bag records per license are analyzed from 1973, it is possible to observe that rabbit populations had some fluctuations before RHD arrival (1973–1988). In contrast, partridge populations showed a marked decline in that same period (Fig. 1; see also Blanco-Aguiar 2007), and, therefore, it is not possible to discard that the same factors that were affecting partridge populations before RHD arrival were also working after RHD arrival. In fact, other possible causes of red-legged partridge decline in Spain have been suggested. These include disease, habitat loss, agricultural intensification, earlier cereal harvesting, and modification of game management (including changes in shooting intensity) (Blanco-Aguiar et al. 2004; Buenestado et al. 2008; Villanúa et al. 2008; Buenestado et al. 2009; Delibes-Mateos et al. 2009a; Casas and Viñuela 2010).

Are feeding data enough to link patterns and processes?

Assumptions associated with raptor food habits

Moleón et al. (2008) tested six alternative models to explain the temporal series of hunting bags, taking into account a climate effect, but not temporal series of predation data. This is probably due to the fact that predation data are not available at this scale. However, this is precisely the point: there are no available data to check whether predation has a role in the temporal changes of bags. Insightful papers on the theoretical dynamics of hyperpredation already exist (e.g., Courchamp et al. 2000). However, the cross-correlation (or second-order density dependent model) described between both species is not enough to link pattern and hyperpredation caused by raptors. The RHD-mediated hyperpredation hypothesis is based on the assumption that the predator community fed differently before and after the outbreak of RHD (Moleón et al. 2008). Thus, Moleón et al. (2008) maintain that they showed the existence of hyperpredation by pointing to the decline of rabbits in the local diet of three predators, which was accompanied by a relative increase in the percentage of partridge in the diet. However, this increase was statistically significant in the case of the Golden eagle (*Aquila chrysaetos*), not so in the diet of Bonelli's eagle (*Hieraaetus fasciatus*), and in only one out of two analyzed cases of the Northern goshawk (*Accipiter gentilis*). In this way, two of the four cases analyzed showed no significant increase in partridge predation and the statistical significance of the other two cases was not corrected to control for the increase in type I error due to multiple test. Thus, the evidence in favosr of the suggested mechanism is weak.

In addition, 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), rather than in a higher consumption of other prey species. This differential increase in partridge presence in the diet is certainly not occurring in the case of Bonelli's eagle (the opposite is true), is nonsignificant for the northern goshawk in heavily forested areas, and of moderate importance for the Golden eagle.

Furthermore, the revision of raptor diet studies by Moleón et al. (2008) seems to be skewed, since there are other raptor species such as the Eagle Owl (*Bubo bubo*), which have maintained a similar diet based on rabbits before and after RHD arrival (Tella and Mañosa 1993; Serrano 2000; Martínez and Zuberogoitia 2001; Martínez and Calvo 2001). The main change detected in the diet of this species after RHD arrival is an increased predation on other diurnal and nocturnal raptors, and its effect on the avian predator community may have been relevant (Tella and Mañosa 1993; Serrano 2000). Thus, increased intraguild predation by eagle owl could have even reduced overall predation pressure in the ecosystems studied.

Predator population dynamics data

Early definitions and models of hyperpredation effect (e.g., Smith and Quin 1996 and Courchamp et al. 2000) did not consider hyperpredation processes to include indirect effects mediated by predator's functional response. These studies defined hyperpredation process as the process of indirect effects mediated by the predator's numerical response. Therefore, in the strictest sense the present case should not be categorized as a hyperpredation process. In any case, even if the number of partridges consumed by the raptors had increased, it would not be possible yet with those data to prove that partridge populations are limited by raptors without knowing the functional response of raptors to partridge numbers, total predator abundance (or predator abundance change), and the density dependence of productivity (Sinclair and Pech 1996; Valkama et al. 2005). Even a high percentage of gamebirds in the diet of a predator does not necessarily mean that this predator will have a negative impact on gamebird population densities (Valkama et al. 2005). The existence of limitation due to predation would require that the per capita predation rate would overcome the per capita production rate (Newton 1998), and this point is unknown in the case of red-legged partridge and raptors. Although we do not discard this possibility, the data shown by Moleón et al. (2008) do not demonstrate limitation of partridge populations by raptors.

On the contrary, it has been clearly demonstrated in the last few decades that productivity of many raptor species in Spain may have been strongly reduced by low abundance of rabbits (e.g., Martínez and Zuberogoitia 2001; Margalida et al. 2007), even for raptor species considered generalist predators such as golden eagles or Black kites (*Milvus migrans*) (Viñuela and Veiga 1992; Fernández 1993). Thus, what may have occurred during the last decades is that raptor population parameters have been negatively affected by rabbit scarcity, and raptors have also suffered increased intraguild predation (Serrano 2000; Lourenço et al. 2011).

Predator distribution

It appears that Moleón et al. (2008) assume that the local rabbit and partridge densities follow the same trends as those observed at the national scale. These authors reviewed *H. fasciatus* and *A. gentilis* studies that had been conducted in Catalonia (Lleida, Tarragona, Barcelona, and Girona provinces) while the *A. chrysaetos* study had been conducted in Navarra province. All these provinces are located in North-eastern Spain, whereas hunting bags reflect mainly the values recorded in South-western Spain, where partridge and rabbits are hunted in higher numbers (Blanco-Aguiar et al. 2004; Virgós et al. 2007). Population patterns of both rabbits and partridges do not necessarily follow the same trends all through the Spanish territory (Blanco-Aguiar et al. 2004; Delibes-Mateos et al. 2009b), and their density show patchy patterns associated with habitat quality. In addition, molecular data show the existence in Spain of different evolutive management unit for rabbits (Carneiro et al. 2010) and red-legged partridges (Ferrero et al. 2011), thus, the assumption that both species are homogeneous throughout Spain territory might unfounded.

It is possible to compare if partridge trends in the same provinces where raptor diet was analyzed followed the

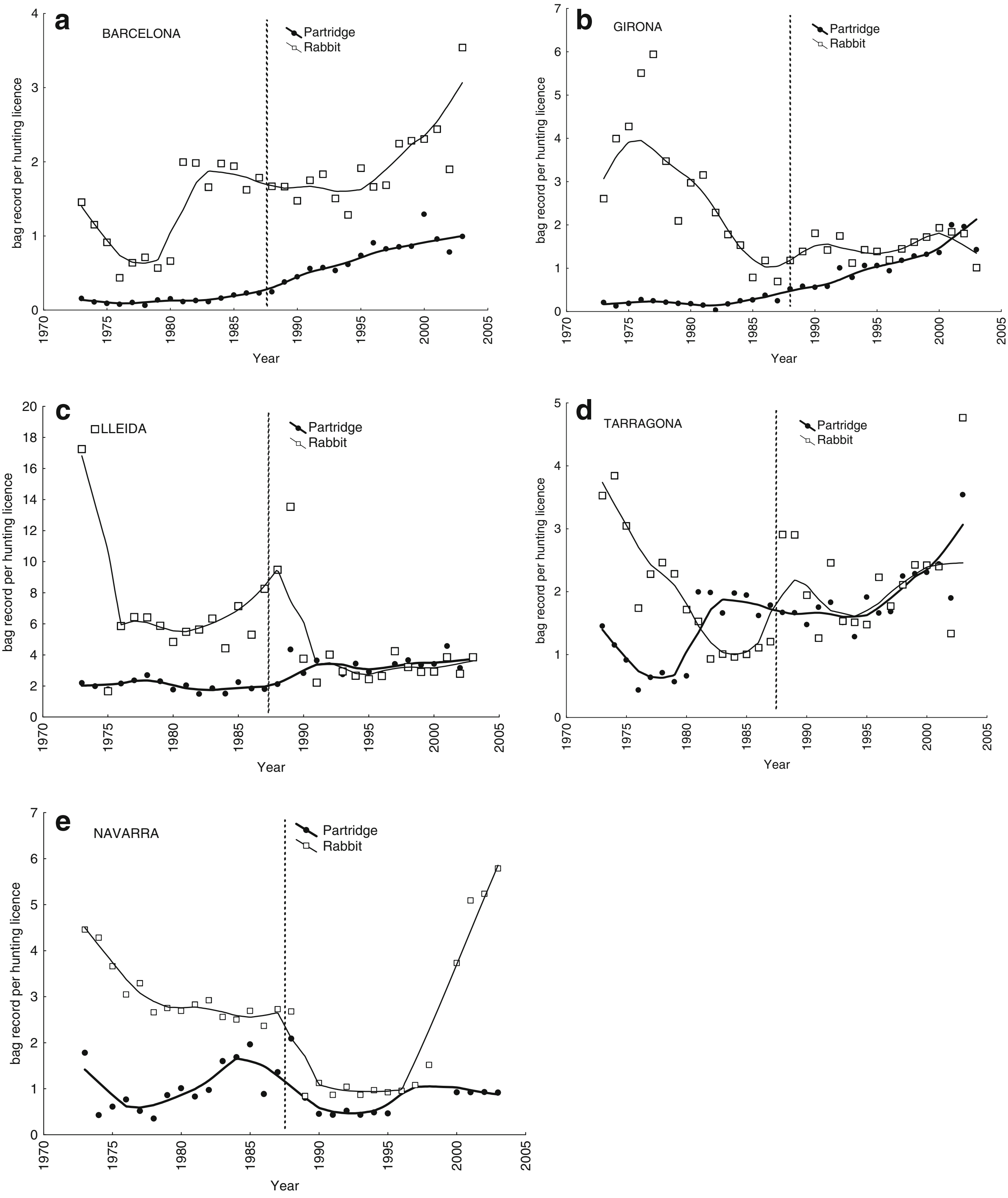

Fig. 2 Number of red-legged partridge and rabbit hunted per provincial licence and fitted (only for graphical purposes) with a robust locally weighted regression. **a** Barcelona. **b** Girona. **c** Lleida. **d** Tarragona. **e** Navarra. The *dashed line* represents the year in which rabbit hemorrhagic disease (RHD) arrived in Spain

three dynamic phases from Moleón et al. (2008) predictions. Only in Navarra province both partridge populations showed a decline after RHD outbreak (Fig. 2). However, in Catalonia, the red-legged partridge bag records showed no decline after the arrival of the RHD outbreak (Fig. 2). If we consider that bag records constitute an accurate source of population trends, then predictions of the model at a regional scale in three of the four diet studies (using the same data source) were not adjusted to the assumptions of the general model of hyperpredation hypothesis on partridges. Otherwise, if we consider that game releases have altered the records of hunting bags in these provinces, then it is possible that diet analyses might also be corrupted by these releases.

Conclusions

We agree that the RHD outbreak has markedly affected rabbit populations, which has indirectly affected many other species in the Iberian Peninsula (Delibes-Mateos et al. 2008a); this might include partridge populations (Blanco-Aguiar et al. 2004). However, caution must be taken before assuming that red-legged partridge decline was caused mainly by this factor, without taking into account other longer term factors of decline. In our view, data presented in Moleón et al. (2008) do not entirely support that hyperpredation by raptors is a main process influencing partridge population trends at a national scale. First, caution must be taken when assuming bag records in recent years are a reliable estimate of wild population size because of the effect of farm-bred bird releases. On the other hand, the relations between predation rate and partridge density are unclear. A density-dependent relationship could be due to the opportunistic nature of certain predators such as red foxes (*Vulpes vulpes*; Delibes-Mateos et al. 2008b) or to the decrease in the density and/or detectability of wild rabbits (Ontiveros et al. 2005). In any case, there are no clear data supporting a major large-scale effect of predation on red-legged partridge population dynamics.

It is always important to evaluate alternative hypotheses, but particularly so in cases when the conclusions of a study may be used to determine management criteria for the recovery of gamebirds. If hyperpredation is offered as a significant reason for partridge limitation in Spain (which we doubt), some might advocate the control raptor populations to increase partridge populations. Hunters and game managers in Spain tend to consider predator control as a valuable tool to increase game populations (Angulo 2003; Delibes-Mateos et al. 2008c); in fact, the persecution of raptors has been intensified during the last decades in Spain (Villafuerte et al. 1998). Thus, researchers must be careful before arguing that this has been a general pattern at a national scale without serious criticism of data analyzed.

We suggest that anthropogenic influence (through changes in habitat quality or game management and hunting practices, potentially due also to the decline in rabbit numbers) might explain the patterns observed in quarry populations. However, more studies and efforts are necessary to conclude which factors are working at this wide scale.

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