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ORIGINAL PAPER

Low persistence in nature of captive reared rabbits after restocking operations

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Abstract The use of restocking of animals is common practice in the management of populations subject to hunting or recreational fishing. This practice encompasses the release of large numbers of individuals in an area where the species already exists, and thus it can have detrimental genetic impacts on the target populations, especially when captive-reared animals are involved. To better understand this practice and its conservation implications, we chose as a model the wild rabbit (*Oryctolagus cuniculus*), a species of high economic and ecological importance, and often under intense management for hunting or conservation purposes, particularly after the large decline caused by rabbit hemorrhagic disease in the 90′s. We studied the genetics of rabbit populations in an area where restocking with captive, wild–domestic hybrids was common. We collected a total of 503 samples from 15 hunting estates that had experienced differing restocking levels, as well as from five locations with no historical restocking and five game farms. All samples were analyzed to determine the mitochondrial DNA (mtDNA) lineage typical of the two European wild rabbit subspecies and domestic rabbit. Game farms and never restocked populations were very different in their haplotypic composition. In restocked areas, the proportion of the domestic lineage was higher when releases were recent and repeated, but this declined rapidly over time, in part due to selective removal by hunting. The extended use of this practice, considering the pronounced genetic and genotypic differences between domestic and wild rabbits, represents a potential danger to natural populations, especially given the marked decrease in wild rabbit numbers experienced in recent years in its original distribution range.

Keywords Captive breeding · Hunting · Hybrids · *Oryctolagus cuniculus* · Restocking · Wild rabbit

Introduction

The release of wild born or captive-bred animals is widely used to manage wildlife populations (Champagnon et al. 2012; Fischer and Lindenmayer 2000). Translocations are a controversial measure due to their generally low success (Armstrong and Seddon 2008), their high economic costs, and the genetic, ecological, and health risks linked to them (Cunningham 1996; Laikre et al. 2010; Naish et al. 2007). In particular, genetic consequences of releases such as the loss of genetic diversity, changes in population structure, and breakdown of adaptations have been well studied (Weeks et al. 2011).

There is growing awareness of the effects of animal translocations, to the point that the World Conservation Union

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(IUCN) only recommends releases when there are no alternatives for population recovery (IUCN/SSC 2013). This is the case of endangered species, where research has improved the design and implementation of conservation measures (Jule et al. 2008; Seddon et al. 2007). However, the situation is different for harvested populations, where restocking—the release of individuals in an area occupied by an existing conspecific population (Armstrong and Seddon 2008)—is frequently used with the aim of artificially sustaining higher harvest levels (Blanco-Aguiar et al. 2008; Champagnon et al. 2013). The large numbers of individuals released, and the little attention paid to their origin increases the risks of these operations.

Due to the large number of individuals demanded by hunting estates, restocking increasingly relies on captive breeding. These captive-reared animals often have lower genetic diversity and exhibit higher rates of inbreeding than wild populations as they become adapted to captive life (Williams and Hoffman 2009; Witzenberger and Hochkirch 2011). These features compromise survival and reproduction in the wild, and as a result, released individuals of captive origin have higher mortality rates than wild ones (Robert 2009). Among the reasons for this differential, mortality is a greater vulnerability to starvation, predation, or disease (Jule et al. 2008; Metcalfe et al. 2003). Also, in the case of populations restocked for hunting and sport fishing purposes, released individuals are often more easily harvested (Klefoth et al. 2013; Mezzera and Largiader 2001). All these detrimental attributes are genetically transmissible to resident populations (Lynch and O'Hely 2001; Theodorou and Couvet 2004), increasing the potential risks of restocking.

The European wild rabbit (*Oryctolagus cuniculus*) is a species that plays an important economic and ecological role in southwestern Europe (Delibes-Mateos et al. 2014), being the most important small game species and the main prey of a variety of threatened species in Mediterranean ecosystems, such as the Iberian Lynx (*Lynx pardinus*) and the Imperial Eagle (*Aquila heliaca*). Due to the decrease of rabbit abundance, mainly caused by viral diseases (myxomatosis and rabbit hemorrhagic disease, RHD) and changes in its habitat (Delibes-Mateos et al. 2009; Ferreira et al. 2010), large scale releases are carried out routinely, and as many as 500,000 rabbits are released each year in Spain and France (Calvete et al. 1997; Ward 2005). This practice, traditionally used by hunters (Delibes-Mateos et al. 2008), is now also employed by conservationists to support recovery programs for threatened species that rely on the rabbit for food (Moreno et al. 2004).

Rabbit restocking has been the subject of several studies, mainly focusing on its effectiveness in recovering wild populations (Cabezas et al. 2011; Calvete et al. 2005; Letty et al. 2003; Rouco et al. 2010). However, its potential impact on rabbit genetic diversity and structure has only recently received attention. In the Iberian Peninsula, the wild rabbit has two well-differentiated genetic lineages, A and B, which correspond to two distinct subspecies (*Oryctolagus cuniculus algirus* and *Oryctolagus cuniculus cuniculus*, respectively). Within each lineage, there is a high degree of genetic diversity, with a well-defined geographic structure (Branco et al. 2000; Carneiro et al. 2010; Carneiro et al. 2013). Domestic rabbits, however, originated entirely from lineage B and exhibit a much lower genetic diversity (Carneiro et al. 2014; Queney et al. 2002).

Previous studies, based on mitochondrial DNA (mtDNA), have suggested that frequent harvesting and translocation of wild rabbits across the distribution ranges of the two lineages might impact the genetic structure of the species (Delibes-Mateos et al. 2008). However, Carneiro et al. (2013), in a study of the patterns of allele frequency change for a larger number of markers (including mtDNA), demonstrated that introgression between the two rabbit subspecies is widespread, although its incidence is low in the case of the mtDNA. According to this study, the observed mismatched haplotypes are more compatible with natural processes associated with secondary contact after a period of isolation and subsequent gene flow. This also indicates that for a large portion of the distribution of the species, the impact of restocking on the genetic composition of wild populations may have been minimal.

However, this broad scale pattern may be characterized by frequent exceptions at a more local scale. This is so because even though rabbit restocking generally involves the release of wild-caught animals, the use of captive-bred rabbits is not uncommon (Rogers et al. 1994; Sánchez García-Abad et al. 2012) especially in the north of the Iberian Peninsula (Navarro-Gonzalez et al. 2010; Piorno 2006). In this region, because wild donor populations are often scarce, captive breeding of wild-domestic hybrids to increase productivity is frequently employed (Piorno 2007). These operations can affect not just the success of the releases but also have possible negative effects on the recipient wild populations. Unlike translocations with wild individuals, the release of captive-bred rabbits has not received enough attention.

In this paper, we evaluate, using genetic markers, the persistence of restocked rabbits with captive breeding origin in the wild. Our study area, the NW of the Iberian Peninsula, is well suited for this purpose, due to the frequent use of wild-domestic hybrid rabbits in restocking operations. Also, based on the genetic structure of the species (Carneiro et al. 2013; Queney et al. 2002), we expected to find enough differences between domestic and resident wild rabbits to measure the effect of releases. Under these premises, we sampled game farms and hunting estates that had been restocked at different intensities. Samples were obtained during the hunting season and the proportion of rabbits of captive origin monitored. We expected to observe (i) a marked genetic difference between game farms and natural sites (without restocking); (ii) a higher proportion of rabbits of captive origin in hunting estates where the intensity of restocking was higher; and (iii) a decreasing proportion of rabbits of captive origin along the hunting season, indicating their selective removal by hunting.

Methods

Study area

The study was carried out in hunting estates in Galicia (NW Iberian Peninsula, Fig. 1), during the 1999 hunting season (October–December). Restocking with captive-bred rabbits to increase huntable numbers of animals is regularly carried out in this area. Briefly, rabbits were bred in game farms using the same techniques as for meat rabbit production. Animals were reared in cages and spent a short pre-release acclimatization period in an open area. Because female wild rabbits are difficult to rear in captivity (Gonzalez-Redondo 2003), domestic females were crossed with wild males to increase productivity. The resulting offspring were backcrossed with wild males to obtain rabbits morphologically very similar to the wild ones (Piorno 2007). Rabbits were routinely vaccinated against myxomatosis and RHD before release. Rabbits are usually released in small groups (5–10 individuals) in natural refuges (abandoned warrens or areas with high vegetation cover).

Sampling design

Samples were taken in hunting estates that differed in their restocking history. Because restocking records in these estates are poorly maintained, we interviewed local hunters to ascertain whether releases had been carried out during two previous 4-year periods—hunting plans are valid for 4 years (Piorno 2006)—and during the year of sampling. With this information, we were able to establish three categories of restocked hunting estates (Table 1): (R1) estates that stopped restocking more than 4 years ago; (R2) estates that had been restocked until the last 4-year period, but not the year of sampling; and (R3) estates that had been restocked until the year of sampling. We were not able to estimate the number of released rabbits, as this information was not always available. To determine the genetic composition of the original wild populations and of the captive-bred animals, we sampled wild populations where restocking had never been reported (R0) and rabbits from captive rearing facilities that supplied the animals for restocking (CR), respectively. To take into account the possible effect of differences in rabbit abundance among hunting estates, we used an index of relative abundance. We calculated this index during the year of sampling and prior to the hunting season, by counting the number of latrines along five randomly-placed transects of 3000 m in each of the studied hunting estates (Iborra and Lumaret 1997).

Sample collection and processing

Five sites were selected at random in each of the five categories, and rabbits were sampled in each one by requesting hunters to collect tissue samples from hunted rabbits during the hunting season (October to December). A total of 503 rabbits from 25 locations were sampled. We divided the hunting season into five biweekly periods to monitor a possible change in the proportion of rabbits of captive origin occurring throughout the length of the hunting season.

From each hunted rabbit, we collected a portion of the ear and preserved it in 100 % ethanol. To distinguish between the different mtDNA haplotypes (lineages A and B), we used a previously described restriction fragment length polymorphisms (RFLPs) method (Branco et al. 2000).

Data analysis

We distinguished between captive-bred individuals and their wild counterparts by using existing information on the genetic distinctiveness of the species. We expected that lineage A would predominate in the original rabbit populations, because of the composition of the geographically closest populations (Fig. 1) and the direction of the routes of expansion of the two lineages proposed by Branco et al. (2002). Conversely, considering that domestic females are at the origin of most of the captive bred rabbits in this region, we expected that they would belong predominantly to lineage B, namely to haplotypes B1Rba and B3Rba which are highly prevalent among domestic rabbits (Branco et al. 2000; Queney et al. 2002).

We used GLMs to test for differences among restocking categories in the variables of interest (McCullagh and Nelder 1989). All statistical analysis was performed using R 2.15.1 (R Core Team 2012).

Results

Genetic characterization

Haplotypes found in each sampling site and their proportions are listed in Table 2. As expected, lineage B haplotypes predominated in the captive rearing facilities (B1Rba; 63.4 %, SE=4.8 % and B3Rba; 33.6 %, SE=4.7 %), and only one haplotype of lineage A (A2Rba) was present, although at a low percentage (3 %, SE=1.7 %). In contrast, in the R0 sites, the frequency of the two B haplotypes found in farms was very low (B1Rba; 3 %, SE=1.7 % and B3Rba; 0 %). In rabbits from these sites, the most common haplotypes were A2Rba (69.0 %, SE=4.6 %) and ARb4 (16.0 %, SE=3.6 %), which

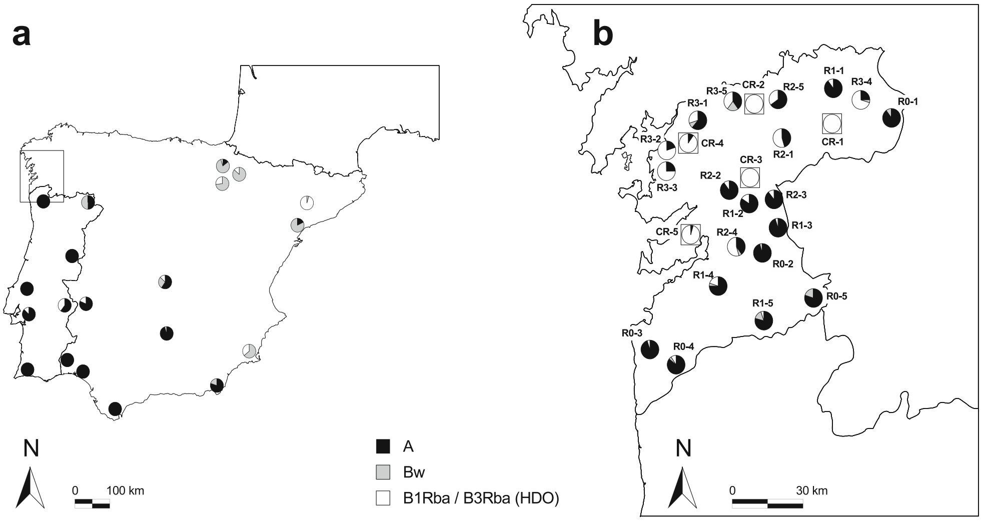

Fig. 1 Map showing: **a** the distribution in the Iberian Peninsula of the proportion of mitochondrial haplotypes of the lineage A, B1Rba and B3Rba (HDO), and the rest of the haplotypes of lineage B (Bw), according to Branco et al. (2000), and **b** the location of the sampling sites in the study area and the proportions of the studied mitochondrial haplotypes

coexisted with low proportions of other five haplotypes. The remaining wild populations (R1, R2, and R3) were dominated by the four main haplotypes found in R0 (A2Rba; ARb4) and CR (B1Rba; B3Rba) sites (Table 2).

Effect of restocking history and rabbit abundance

A GLM with a binomial error distribution and logit link was used to test the effects of restocking history and rabbit abundance on the proportion of haplotypes of potential domestic origin (HDO, B1Rba, and B3Rba) in wild populations. Only restocking history had a significant effect ($F_{3,16}$=10.716, *P*=0.001), while the effect of abundance ($F_{1,15}$=0.100, *P*=0.757) and the interaction between the two factors ($F_{3,12}$=0.541, *P*=0.664) were not significant.

Overall, the frequency of HDO is higher in sites with higher restocking levels (Fig. 2). Pooling all sampling sites in each category, the proportions of these haplotypes were 11.1 % (SE=3.2 %) in R1, 33.3 % (SE=4.7 %) in R2, and 58.3 % (SE=4.9 %) in R3. The variability of HDO proportion was also higher in the more restocked categories. In sites that were never restocked (R0), the HDO proportion was 3.0 % (SE=1.7 %), which was statistically different from R1 sites (Fisher exact test, *P*=0.027).

Table 1 Classification of sampling sites according to the occurrence of restocking during the identified periods

Restocking category	Restocking history		
	1992–1995	1996–1998	1999
R0	No	No	No
R1	Yes	No	No
R2	Yes	Yes	No
R3	Yes	Yes	Yes
CR	Captive rearing facilities		

Differences in rabbit abundance were detected among restocking history categories, revealed by means of a GLM with a Poisson error distribution and logarithmic link ($F_{3,16}$=3.392, *P*=0.041). Rabbit abundance was higher in the least intensively restocked sites (Fig. 3).

Effect of hunting date

The proportion of HDO varied along the hunting season in the more intensively restocked sites. A GLM with a binomial error distribution and logit link revealed a significant effect of the interaction between biweekly sampling period and restocking history on HDO proportion ($F_{3,58}$=3.178, *P*=0.023). There was a marked decline in the proportion of HDO from the first to the fifth biweekly period in R2 and R3 sites, but not in the R0 and R1 sites (Fig. 4).

Discussion

Differences between captive-reared and wild rabbits

Our results showed a marked difference in haplotypic composition between animals from captive breeding centers and from wild populations that were never restocked. The sites without restocking (R0) exhibited the expected genetic pattern for natural populations in this region (Branco et al. 2002), with very low proportions of B1Rba and B3Rba haplotypes, which could be explained most likely by natural levels of introgression but also by undocumented releases or dispersal from neighboring restocked areas. The crossbreeding system practiced by game farmers, using wild males and domestic females as breeders, would explain the low occurrence of wild

Table 2 Relative frequencies of mitochondrial haplotypes in each of the sampling sites and restocking categories

Code	Site name	N	Haplotypes											
			Lineage A					Lineage B						
			A2Rba	ARb4	A1Rba	ARb15	Arb17	B11Rba	B8Rba	BRb1	BRb10	BRb12	B1Rba	B3Rba
R0-1	Areosa	20	0.65	0.25				0.10						
R0-2	Traspielas	20	0.60	0.20	0.15						0.05			
R0-3	Groba	20	0.90			0.05							0.05	
R0-4	Argallo	21	0.76	0.10							0.05		0.10	
R0-5	Crecente	20	0.55	0.25					0.20					
	Subtotal	101	0.69	0.16	0.03	0.01		0.02	0.04		0.02		0.03	
R1-1	Carrio	20	0.50	0.40									0.05	0.05
R1-2	Caveiro	20	0.37	0.47									0.05	0.11
R1-3	A Laxe	20	0.60	0.35									0.05	
R1-4	Mos	20	0.55	0.05	0.15				0.05				0.10	0.10
R1-5	As Neves	19	0.32	0.47							0.16		0.05	
	Subtotal	99	0.47	0.35	0.03				0.01		0.03		0.06	0.05
R2-1	Forcarei	20	0.20	0.20	0.05								0.20	0.35
R2-2	Castelo	20	0.25	0.65									0.05	0.05
R2-3	Xesta	19	0.26	0.63										0.11
R2-4	Pazos	20	0.15	0.20			0.05				0.05		0.45	0.10
R2-5	A Rocha	20	0.40	0.25									0.20	0.15
	Subtotal	99	0.25	0.38	0.01		0.01				0.01		0.18	0.15
R3-1	Xiabre	23		0.61							0.04	0.04	0.22	0.09
R3-2	Baión	20		0.20									0.60	0.20
R3-3	Meis	20		0.25									0.55	0.20
R3-4	Alperiz	20	0.10	0.15							0.05		0.45	0.25
R3-5	Fians	20	0.20	0.20				0.10		0.10				0.40
	Subtotal	103	0.06	0.29				0.02		0.02	0.02	0.01	0.36	0.22
CR-1	Lalín	20											0.70	0.30
CR-2	Estrada	21											0.71	0.29
CR-3	Cotobade	20											0.75	0.25
CR-4	Rubiáns	20	0.10										0.15	0.75
CR-5	Castiñeira	20	0.05										0.85	0.10
	Subtotal	101	0.03										0.63	0.34

haplotypes in these centers because of maternal transmission of mtDNA. Overall, while B1Rba and B3Rba haplotypes cannot be considered diagnostic at the individual level, the unusually high frequency in some localities within our study area can be considered a reliable index of restocking intensity.

Persistence of restocked rabbits

The marked difference in genetic composition allowed us to detect the presence of captive-origin rabbits in all samples from restocked areas, suggesting an important effect of restocking on native populations in the studied region. The proportion of B1Rba and B3Rba haplotypes was in some cases very high compared to similarly managed species (Barilani et al. 2005; Blanco-Aguiar et al. 2008; Champagnon et al. 2013). This is occurring in spite of the low survival observed in releases carried out by hunters with rabbits of wild origin (Calvete et al. 1997). Moreover, we should expect a lower survival in our case, considering that captive individuals are being used, and these usually have a higher post-release mortality (Beck et al. 1994; Fischer and Lindenmayer 2000). Our results suggest that the high prevalence of domestic origin haplotypes is a consequence of intensive and repeated restocking. The highest values of B1Rba and B3Rba haplotypes are found in the intensively restocked R2 and R3 hunting states. The chosen categories of restocking indicate how much time has elapsed since the last release, but also the recurrence of this management measure. It seems reasonable

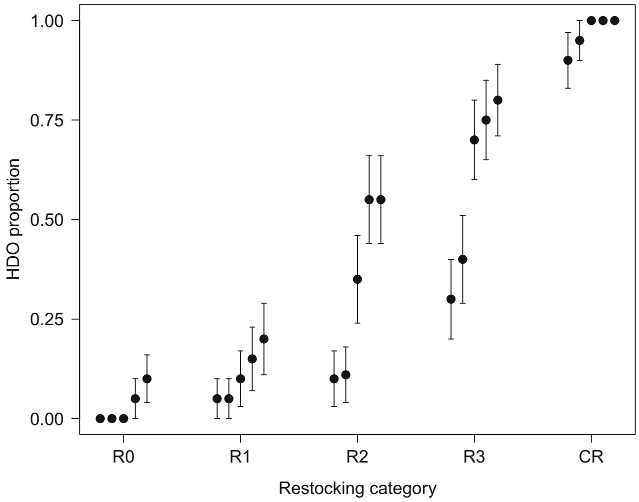

Fig. 2 Proportion of haplotypes of domestic origin (HDO) in each of the sampling sites, grouped by restocking category. *Error bars* represent one standard error

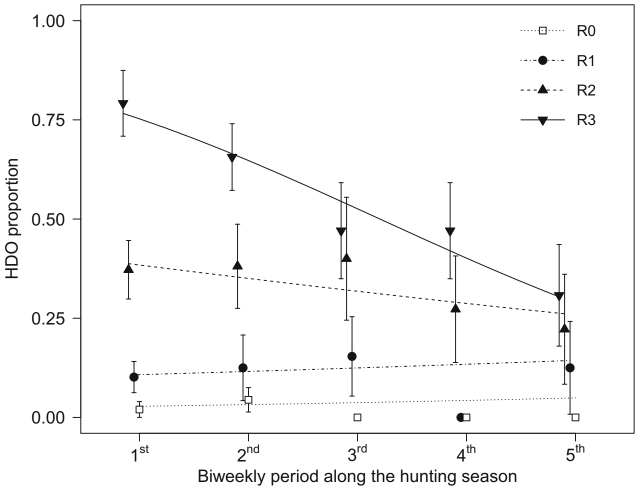

Fig. 4 Evolution of the HDO proportion along the hunting season in the different restocking categories. Each dot represents HDO proportion for a given restocking category and biweekly period. *Error bars* represent one standard error. *Trend lines* were fitted using the coefficients of the GLM

to expect that more releases will increase restocking success, as has been previously shown (Fischer and Lindenmayer 2000). But time since the last release, and its effect on survival of released rabbits, may also play a role. R2 and R3 sites, both repeatedly restocked, differ only in whether or not releases were carried out the year of sampling, and the difference in B1Rba and B3Rba haplotypes between them is very pronounced. This suggests that recent releases have a pronounced effect on the proportion of B1Rba and B3Rba haplotypes and that this effect declines rapidly if restocking efforts are not maintained.

In spite of the observed decrease over time in the proportion of released rabbits, we found that the sites that had not been restocked for at least 5 years (R1) had a higher HDO proportion from those sites that were never restocked (R0). Due to the limited diagnostic value of our markers, we cannot completely rule out natural introgression as a cause of this difference. But, this result could also indicate that the domestic lineage can persist in the long-term at low proportions, either by survival of the released rabbits—rabbit longevity in the wild may exceed 8 years (Gibb and Morgan-Williams 1994)—or by their reproduction.

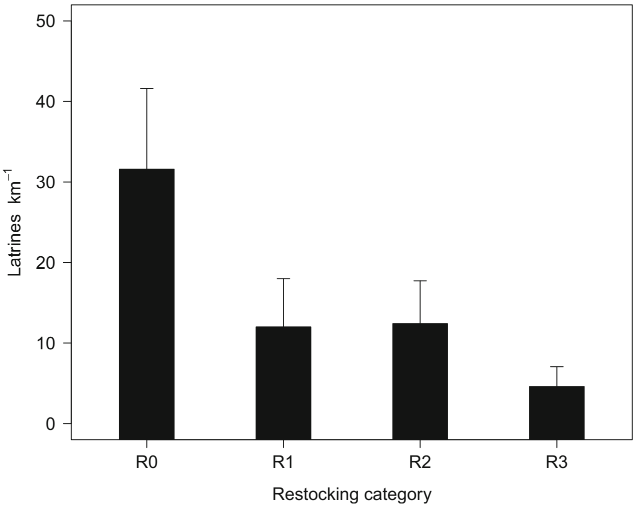

Fig. 3 Rabbit abundance for the different restocking categories. *Error bars* represent one standard error

Effect of hunting on persistence

The decreasing proportion of B1Rba and B3Rba haplotypes along the hunting season, more evident in recently restocked zones, is most likely explained by the likelihood that rabbits of putative domestic origin are more easily hunted. This effect is especially evident where rabbits have been recently released and tends to decrease over time, suggesting that surviving rabbits are less sensitive to hunting. This type of effect has been documented in other restocked species in both sport fishing (brown trout *Salmo trutta*, Mezzera and Largiader 2001; common carp *Cyprinus carpio*, Klefoth et al. 2013); and hunting (mallard *Anas platyrhynchos*, Legagneux et al. 2009). We cannot completely rule out a different mortality rate in released and resident rabbits due to natural causes, like predation or disease, but we consider it less likely. According to the available information, rabbits are released in the study area mostly in late spring and summer, several months before the onset of the hunting season. Previous studies have shown that this period is sufficient to allow acclimatization and that would equalize mortality rates between introduced and resident rabbits (Calvete and Estrada 2004; Letty et al. 2002; Rouco et al. 2008). In addition, released rabbits in our study area were vaccinated against myxomatosis and RHD, the two main causes of mortality in wild rabbits. We should expect then a lower mortality in the released hybrid individuals, since commercial vaccines are successful in protecting rabbits from these diseases in the field (Cabezas et al. 2006; Calvete et al. 2004; Ferreira et al. 2009).

While this result would suggest that hunting may be heavier upon the captive-bred rabbits, and that the observed proportions may be an overestimation of their actual abundance, it also constitutes per se an important finding. Here, we identify a potential source of mortality of restocked rabbits that has never been reported to our knowledge in a hunted mammal.

Conservation implications

As it happens with other species (Barilani et al. 2005; Blanco-Aguiar et al. 2008), the release of large numbers of captive-bred individuals with hunting purposes poses a risk for the conservation of the wild rabbit. The productive capacity of Spanish game farms has been estimated at around 225,000 rabbits per annum (Sánchez García-Abad et al. 2012). Therefore, captive rabbits represent an important proportion of the total of 500,000 rabbits released annually in Spain (Calvete et al. 1997; Ward 2005). As shown in this study and others (González-Redondo and Sánchez-Martínez 2014), many game farms pay little attention to the genetic origin of their breeding animals. The lack of attention to this issue can potentially have a major impact on the genetic composition of wild rabbit populations. Repeated releases of captive individuals will no doubt lead to genetic displacement and introgression, particularly in low density populations, where the ratio of captive-bred to resident is lower and, as shown in this study, restocking is more common. We therefore strongly advise against the release of captive hybrid rabbits, recommending the use of individuals of wild origin instead, either wild caught or from extensive breeding enclosures (Guerrero-Casado et al. 2013b).

We have also found that the more intensively restocked categories show the lowest rabbit abundances, which is coherent with the limited ability of releases to increase abundance documented for this and other species (Diaz-Fernandez et al. 2013; Moreno et al. 2004; Young 2013). In addition, hybrid rabbits between the two subspecies have lower reproductive fitness, which can further contribute to lower abundance (Carneiro et al. 2013).

Considering the apparent low contribution made by these animals to the abundance of rabbits in hunting estates, and the perception of their low efficacy by managers (Delibes-Mateos et al. 2008), it is rather paradoxical that restocking is still widely used. The finding in the present study that released rabbits are more likely to be hunted may partially explain this paradox. Thus, while hunters usually prefer wild individuals over farm-reared ones (Delibes-Mateos et al. 2014), by using releases they can artificially maintain populations which, due to the ease of capture, also provide higher hunting yields than wild populations at the same density. In situations like these, restocking cannot be regarded as a sustainable management strategy (Guerrero-Casado et al. 2013a) and should be replaced by other tools, e.g., habitat management (Ferreira and Alves 2009; Ferreira et al. 2014), in order to promote the long-term recovery of wild populations.

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Compliance with ethical standards

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Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. This article does not contain any studies with human participants performed by any of the authors.

Informed consent This article does not contain any studies with individual participants that required the obtainment of informed consent.

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