Universidade de Évora - Instituto de Investigação e Formação Avançada

Programa de Doutoramento em Biologia

Tese de Doutoramento

Strategies for enhancing management plans for the Iberian rabbit

Cláudia Sofia Marques da Encarnação

Orientador(es) | António Mira
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A eles dedico esta tese!

Strategies for enhancing management plans for the Iberian rabbit

Abstract

The European rabbit (*Oryctolagus cuniculus*), especially the subspecies Iberian rabbit (*Oryctolagus cuniculus algirus*), is a keystone species with vital ecological importance in Iberian Mediterranean ecosystems. However, its populations have experienced significant declines, leading to its classification as a threatened species. This thesis aims to evaluate the effectiveness of various management strategies employed in Iberian rabbit recovery programmes and provide recommendations to optimise their success in the Mediterranean region.

The first paper analysed the long-term sustainability of habitat management on rabbit populations. The results suggested that initial benefits from habitat management tend to diminish over time if maintenance ends, and that proximity to crops and the presence of favourable soils for digging positively influence the species' occurrence. The second paper investigated the survival and space use of Iberian rabbits after restocking in a semi-natural enclosure. Radiotelemetry monitoring revealed low survival rates in the initial weeks post-release, with predation identified as the primary cause of mortality. The study also described the movements and dispersal patterns of the restocked rabbits. The third study compared the use of four types of artificial warrens by the restocked Iberian rabbits, based on pellet counts at their entrances. Pallet warrens were shown to be significantly more used, particularly during the breeding season, and the presence of shrub vegetation near the warrens positively influenced their selection.

In conclusion, this research highlights the importance of (1) continuously managing habitat to ensure lasting results, (2) monitoring the survival and the dispersal of rabbits in restocking programmes, and (3) using cost-effective artificial warrens. Altogether, this study provides valuable tools for supporting the recovery of Iberian wild rabbit populations in Mediterranean ecosystems.

Key-words: keystone species, habitat management, Iberian rabbit, *Oryctolagus cuniculus algirus*, Mediterranean landscape, restocking, southern Portugal

Estratégias para melhorar os planos de gestão do coelho-ibérico

Resumo

O coelho-europeu (*Oryctolagus cuniculus*), em particular a subespécie coelho-ibérico (*Oryctolagus cuniculus algirus*), desempenha um papel ecológico crucial como espécie-chave nos ecossistemas mediterrânicos. Contudo, as suas populações têm sofrido declínios acentuados, levando à sua classificação como espécie em perigo. Esta tese visa avaliar a eficácia de diferentes estratégias de gestão utilizadas em programas de recuperação do coelho-ibérico, com o objetivo de fornecer recomendações para otimizar os seus resultados na região Mediterrânica.

O primeiro artigo analisou a sustentabilidade dos efeitos da gestão de habitat nas populações de coelho-ibérico. Os resultados indicaram que os benefícios iniciais da gestão de habitat tendem a diminuir ao longo do tempo se não houver manutenção contínua, e que a proximidade a áreas de pastagem e a presença de solos favoráveis à escavação influenciam positivamente a presença da espécie. O segundo artigo investigou a sobrevivência e o uso do espaço do coelho-ibérico após repovoamento num cercado seminatural. A monitorização por radiotelemetria revelou baixas taxas de sobrevivência nas primeiras semanas após a libertação, sendo a predação a principal causa de mortalidade, e descreveu os padrões de movimentação e dispersão dos coelhos libertados. O terceiro artigo comparou a utilização de quatro tipos de abrigos artificiais pelos coelhos libertados no cercado, através da contagem regular de dejetos nas entradas das tocas. Os abrigos de paletes demonstraram ser significativamente mais utilizados, especialmente durante a época de reprodução, e a presença de vegetação arbustiva perto dos abrigos influenciou positivamente a sua seleção.

Em conclusão, esta tese sublinha a importância de (1) gerir continuamente o habitat para garantir resultados duradouros, (2) monitorizar a sobrevivência e dispersão do coelho-ibérico em programas de repovoamento, e (3) usar abrigos artificiais com a melhor relação custo-benefício. Este estudo fornece assim ferramentas importantes para apoiar a recuperação das populações de coelho-ibérico nos ecossistemas mediterrânicos.

Palavras-chave: coelho-ibérico, *Oryctolagus cuniculus algirus*, espécie-chave, melhoria de habitat, repovoamento, ecossistemas mediterrânicos, sul de Portugal

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Chapter 1

General introduction

1.1. Study species

The European rabbit, *Oryctolagus cuniculus* (Linnaeus, 1758), is a member of the Lagomorpha Order and the Leporidae Family. It is the only species within the genus *Oryctolagus* (Melo-Ferreira and Alves, 2018; Delibes-Mateos et al., 2023). It exists in both wild and domestic forms.

Based on fossil records, this species originated in the Iberian Peninsula (Ferrand, 2008). By the Late Pleistocene, it was widely distributed across the Mediterranean and central Europe. However, following the last glacial maximum and into the Early Holocene, its range became restricted to the Iberian Peninsula, southern France, and perhaps northern Africa (Monnerot et al., 1994; Lopez-Martinez, 2008).

Natural European rabbit populations prevail in Portugal, Spain, southern France, and northern Africa (Villafuerte and Delibes-Mateos, 2019; Delibes-Mateos et al., 2023). However, their global distribution is more extensive, due to the successful establishment of the species following numerous human introductions after domestication. These introductions have occurred in countries across all continents, except Antarctica (Thompson and King, 1994; Ferrand, 2008; Lees and Bell, 2008), where in most places the species is considered a pest (Thompson and King, 1994). This makes the *O. cuniculus* the most successful colonising lagomorph (Hackländer et al., 2008; Delibes-Mateus et al., 2023).

In its native range, two different rabbit genetic lineages are associated with two rabbit subspecies: *Oryctolagus cuniculus algirus* and *Oryctolagus cuniculus cuniculus* (Branco et al., 2000; Carneiro et al., 2010; Delibes-Mateus et al., 2023). Both subspecies have distinct morphological, genetic, ecological, behavioural, and reproductive characteristics

(Goncalves et al., 2002; Ferreira et al., 2015; Díaz-Ruiz et al., 2023). Multiple genetic studies indicate that they evolved independently, approximately two million years ago during the Quaternary glaciations (Branco et al., 2000; Ferrand, 2008) and have different geographical ranges. The smaller subspecies, *O. c. algirus*, occurs primarily in the southwestern Iberian Peninsula, while the *cuniculus* subspecies is distributed towards the northeast (Geraldes et al., 2008; Díaz-Ruiz et al., 2023). The latter has been introduced throughout Europe and worldwide (Lees and Bell, 2008). The distribution of these two subspecies overlaps in a natural contact zone that crosses the Iberian Peninsula in a northwest-southeast direction (Branco et al., 2000; Geraldes et al., 2008; Díaz-Ruiz et al., 2023). A recent study has suggested the possible existence of a competitive exclusion zone between the rabbit subspecies in their contact area. This zone may have functioned as a biological barrier, preventing the expansion of one subspecies into the territory of the other (Díaz-Ruiz et al., 2023).

Due to genetic incompatibilities and reproductive isolation in their contact zone in central Iberia (Carneiro et al., 2010), researchers propose that these subspecies should be considered separate species (Delibes-Mateos et al., 2018b).

The Iberian rabbit, the common name of *O. c. algirus* (Mira et al., 2023), is the only subspecies found in Continental Portugal (Branco et al., 2000; Delibes-Mateos et al., 2023; Díaz-Ruiz et al., 2023). Therefore, this thesis specifically focuses on this subspecies.

1.2. Ecological and social relevance

Historically, the wild rabbit has had a complex and multifaceted relationship with humans. On the one hand, it plays a significant ecological and economic role. On the other hand, it is often considered an agricultural pest, particularly in areas where it has been introduced (Courchamp et al., 1999; Scanlan et al., 2006). The Iberian Peninsula is the only region where rabbit populations are simultaneously in sharp decline and causing crop damage (Delibes-Mateos et al., 2011; Vaquerizas et al., 2020).

The European rabbit is a keystone species in Iberian Mediterranean ecosystems and can potentially increase biodiversity at different scales (Delibes-Mateos et al., 2007).

Approximately 40 predators rely on rabbits as a food source (Delibes-Mateos et al., 2008a). These include carnivores such as the red fox (*Vulpes vulpes*) and the Egyptian mongoose (*Herpestes ichneumon*), as well as birds of prey like the eagle owl (*Bubo bubo*) and the Bonelli's Eagle (*Aquila fasciata*) (Delibes and Hiraldo, 1981; Jaksic and Soriguer, 1981; Delibes-Mateos et al., 2008a). Two highly endangered species endemic to the Iberian Mediterranean ecosystem rely on rabbits: the Iberian lynx (*Lynx pardinus*) and the Spanish Imperial eagle (*Aquila adalberti*). The diet of the Iberian lynx consists of 80-100% rabbits, while the Spanish Imperial eagle's diet includes 40-80% rabbits (Palomares et al., 2001; Ferrer et al., 2003). Consequently, the decline in rabbit populations directly impacts the reproductive success of these predators, with repercussions for the associated ecosystems (Delibes-Mateos et al., 2007).

The Iberian rabbit serves as an ecosystem engineer in Mediterranean ecosystems, providing several ecosystem services. It alters vegetation and provides resources for feeding, breeding sites, and shelter for several species (Delibes-Mateos et al., 2008a; Gálvez et al., 2008). Rabbits influence vegetation structure and plant species composition through grazing and dispersing seeds, promoting plant diversity and creating open spaces (Eldridge and Simpson, 2002; Gálvez-Bravo et al., 2009; Dellafiore et al., 2010; Bobadilha et al., 2023). Their faecal pellets enrich the soil, enhancing plant diversity and biomass and providing food sources for various invertebrate species (Willot et al., 2000). For example, Mediterranean dung beetles, such as *Onthophagus latigena* and *O. emarginatus*, are frequently collected around rabbit pellets (Sánchez-Piñero and Avila, 1991; Galante and Cartagena, 1999). Rabbit warrens serve as important refuges for various animals (Willott et al., 2000; Gálvez-Bravo et al., 2009). Amphibians, reptiles, mammals, and some bird species often benefit from these structures. For example, Blázquez and Villafuerte (1990) observed the Montpellier snake (*Malpolon monspessulanus*) nesting within rabbit warrens. Eurasian badgers (*Meles meles*) frequently expand existing rabbit warrens to create their diurnal resting dens (Revilla et al., 2001). Gálvez-Bravo and colleagues (2009) found that rabbit warrens enhance lizard density and diversity.

Additionally, the rabbit is one of the most iconic small game species in the Iberian Peninsula, where hunting plays an important socio-economic role (Angulo & Villafuerte, 2003; Paixão et al., 2009). It is a game species not only in its native range but also in countries where it has been introduced (Delibes-Mateos et al., 2023).

In Portugal, over 5,000 hunting reserves span about 76% of the country. Around 110,000 licensed hunters hunt in these areas, with rabbits among the most sought-after small game species (ICNF, 2023). In the five years preceding the detection of the new variant of the rabbit haemorrhagic disease virus in Portugal in 2012 (Abrantes et al., 2013), more than 750,000 rabbits were hunted annually (Carvalho et al., 2024). Subsequently, the number of legally harvested rabbits declined substantially, reaching approximately 100,000 during the 2020/2021 hunting season (Carvalho et al., 2024). Spain has over 32,000 hunting areas, covering 83% of its territory. In 2019, approximately 740,000 hunting licences were issued. These hunters primarily target rabbits, among other small game species. Approximately 6 million rabbits are harvested annually in Spain, underscoring the importance of this lagomorph as a game species within its native range (Ministerio de Agricultura y Medio Ambiente, 2025).

The European rabbit, particularly the subspecies *O. c. cuniculus*, has become a widespread coloniser outside its natural range, especially in human-modified landscapes, and is often regarded as a pest. In fact, rabbits are considered the most significant agricultural pests in places like Britain (Smith et al., 2007) and Australia (Williams et al., 1995). In Britain, the Centre for Agriculture and Bioscience International (CABI) estimated that 40 million rabbits contribute to over £260 million in annual losses to the economies of England, Scotland, and Wales, due to damage to infrastructure, businesses, and crops, which makes it the costliest invasive species in this country (Williams et al., 2010).

This classification as a pest arises from the rabbit's high adaptability, rapid reproduction rate, and the absence of natural predators (Thompson and King, 1994; Cooke, 2008; Lees and Bell, 2008). In these affected areas, the major impacts of rabbits include harm to native flora and fauna, competition with livestock, soil erosion caused by their burrowing activities, and damage to plant nurseries and crops, making its eradication a priority for conservation efforts (Cooke, 2008; Lees and Bell, 2008; Cooke et al., 2018).

Even within its native range in the Iberian Peninsula, where the species has sharply declined in the last decades, rabbit populations are recovering in some areas, particularly those with intensive farmland management, to the point that they are considered an emerging pest and an economic liability for farmers (Barrio et al., 2010; Ríos-Saldaña et al., 2013; Delibes-Mateos et al., 2018a). This often leads to frequent conflicts between farmers, hunters, and conservationists regarding the management of the species (Delibes-Mateos et al., 2014a; Delibes-Mateos et al., 2020).

1.3. Conservation status and threats

In 2019, the International Union for Conservation of Nature (IUCN) classified the European rabbit as Endangered (Villafuerte and Delibes-Mateos, 2019). This new classification was based on a population size reduction of 50% or more between 2009 and 2019, particularly affecting the Iberian rabbit subspecies *O. c. algirus* (Villafuerte and Delibes-Mateos, 2019). Reports indicate *O. c. algirus* is experiencing negative population trends in the Iberian Peninsula, whereas *O. c. cuniculus* has shown more stable or even positive trends (Vaquerizas et al., 2020). The species classification recently changed in Portugal from Near Threatened (Cabral et al., 2005) to Vulnerable (Mira et al., 2023). This reclassification is supported by clear evidence of a significant population decline inferred between 60% and 79% over the past three generations. Nevertheless, the breeding population remains substantial, and local population censuses, especially in well-managed areas, indicate a trend toward stabilisation (Mira et al., 2023).

Viral diseases, particularly myxomatosis and viral haemorrhagic disease, and habitat loss and fragmentation have significantly contributed to the species' decline across its native range since 1950. This decline has led to population densities that are less than 10% of those observed earlier in the 20th century (Moreno et al., 2007; Delibes-Mateos et al., 2009a; Villafuerte et al., 2017). Other factors may also play a role in the species’ decline on a smaller scale, including predation and human-induced mortality from excessive hunting or roadkill (Villafuerte and Delibes-Mateos, 2019; Mira et al., 2023).

The myxoma virus, which originates from South America and is part of the Leporipoxvirus genus within the Poxviridae family, causes myxomatosis. In the 1950s, the myxoma virus was intentionally introduced into Australia and Europe to control the overabundant rabbit populations, causing significant ecological and agricultural damage (Fenner and Ratcliffe, 1965). The virus quickly spread, resulting in mortality rates of approximately 90% (Fenner and Ratcliffe, 1965). The virus continued to affect the species in subsequent years, however, its impact was noticeably less severe (Fouchet et al., 2008) due to an increase in the population's resistance to the disease (Fenner and Ross, 1994; Kerr et al., 2012; Alves et al., 2019). Myxomatosis is currently endemic in the Iberian Peninsula and in other European countries (Villafuerte et al., 2017). Although it continues to cause direct mortality in rabbits, indirect fatalities are significantly more prevalent, as infected rabbits struggle to escape from predators or access food. Additionally, the severe immunosuppression caused by myxomatosis makes them highly susceptible to other infections, increasing the risk of secondary diseases (Marchandeau et al., 2004; Barnet et al., 2018).

Another highly infectious and often fatal viral disease that affects the European rabbit is rabbit haemorrhagic disease (RHD) (Parra and Prieto, 1990; Abrantes et al., 2012; Le Pendu et al., 2017). A calicivirus known as rabbit haemorrhagic disease virus (RHDV or GI.1) causes this disease. The first outbreak of RHD was documented in the People's Republic of China in 1984 among rabbits imported from Germany (Liu et al., 1984). The virus first appeared in Europe in 1986, with its initial documentation occurring in Italy (Cancellotti and Renzi, 1991). It subsequently spread throughout the continent, primarily due to the trade of domestic rabbits, and has become endemic in several countries (Abrantes et al., 2012). In the Iberian Peninsula, RHD was first reported in 1988 in Spain (Argüello et al., 1988; Villafuerte et al., 1995) and in 1989 in Portugal, leading to initial mortality rates of 55-75% (Villafuerte et al., 1994). RHD became enzootic and mortality rates decreased, although it continues to play a significant role in the dynamics of European rabbit populations (Calvete et al., 2006).

In 2010, a new variant of RHDV, known as RHDV2 or GI.2, was identified in France (Le Gall-Reculé et al., 2011; Le Gall-Reculé et al., 2013). This variant quickly spread across five continents and affected several lagomorph species (Asin et al., 2024), becoming endemic and replacing previously dominant strains (Calvete et al., 2014; Lopes et al., 2015). RHDV2 was first detected in Spain in 2011 (Dalton et al., 2014) and in Portugal in 2012 (Abrantes et al., 2013). The initial outbreaks resulted in a 60-80% decline in the natural rabbit population in both countries (Delibes-Mateos et al., 2014b; Monterroso et al., 2016). This new variant differs from the traditional strain because it affects younger rabbits, resulting in high mortality rates among kits under 30 days old (Dalton et al., 2012) and juveniles under 2 months old (Abrantes et al., 2013). Such high mortality rates hinder the recruitment of new individuals into the population. Furthermore, RHDV2 spreads rapidly and causes more severe outbreaks than the classic RHDV (Abrantes et al., 2013; Le Gall-Reculé et al., 2013).

Degraded and fragmented habitats in the Iberian Peninsula have also significantly contributed to the decline of rabbit populations, due to shifts in land use and agricultural practices (Virgós et al., 2003; Ward, 2005; Delibes-Mateos et al., 2010). Changes in agricultural practices have transformed traditional Mediterranean landscapes, replacing diverse mosaic habitats, particularly the interspersed pastureland and Mediterranean scrub that rabbits prefer (Moreno et al., 1996; Calvete et al., 2004), with large monocultures and dense patches of scrubland (Gonzalez-Bernaldez, 1991; Fernandez-Ales et al., 1992; Raposo et al., 2023). On the one hand, changes in the use of soil, namely agricultural intensification, extensive areas of croplands, and intensive tree plantations, such as eucalyptus (*Eucalyptus globulus* Labill.), are reducing shelter availability for rabbits (Calvete et al., 2004; Monzón et al., 2004; Ward, 2005). Intensive plantations of highly flammable eucalyptus trees have also increased the occurrence and impact of fires, resulting in the loss of large areas of favourable habitat in Spain and Portugal (Ward, 2005). On the other hand, abandoning traditional agricultural practices, such as controlled burns and scrub cleanings, has resulted in the uncontrolled growth of dense scrubland patches where food is scarce (Moreno and Villafuerte, 1995).

Although traditional hunting techniques were sustainable, recent practices may have contributed to the decline of European rabbits in the Iberian Peninsula, especially when combined with habitat loss and diseases (Angulo, 2003; Ward, 2005). Intense hunting pressure, poaching, and some hunters' lack of restrictions during rabbit shortages are threatening certain rabbit populations (Angulo, 2003). For example, Kontsiotis and colleagues (2013) found a negative correlation between rabbit population growth rates and hunting pressure on Lemnos Island, Greece. Similarly, in northeastern Spain, rabbit populations showed better recovery years after the initial outbreak of RHD in areas with low hunting pressure (Williams et al., 2007). In regions where rabbit populations are recovering, the increased availability of rabbits can surge the hunting pressure (Angulo and Villafuerte, 2003; Kontsiotis et al., 2013).

According to some authors, in a stable and abundant rabbit population, the impact of predators is reduced, and the viability of rabbit populations is unaffected (Jaksic and Soriguer, 1981; Palomares and Delibes, 1997). However, predation pressure on rabbit populations may lead to greater proportional losses when rabbit abundance is low, possibly regulating their numbers, unlike at higher densities (Delibes-Mateos et al., 2023). Predation pressure may be hindering the recovery of rabbit populations in the Iberian Peninsula, especially in areas where rabbit numbers significantly decreased following the outbreak of rabbit haemorrhagic disease (RHD) (Moreno et al., 2007). This is known as the “predator pit” theory, where rabbits, when in low density, are under a higher impact of predation and their population recovery is more difficult to achieve (Trout and Tittensor, 1989; Pech et al., 1992).

Climate change presents an additional threat to rabbit populations, introducing new challenges to their conservation and recovery. It is expected to exacerbate habitat degradation, change in composition of plant communities, and subsequently impact food availability for wild rabbit populations (Harrison, 2020). Climate change may also lead to shifts in breeding seasons, resulting in varying trends in rabbit populations throughout Europe. Tablado and Revilla (2012) predicted that, in southwestern Europe, reproductive periods will tend to decrease in magnitude and become more variable. This change could lead to population declines and an increased risk of extinction. In contrast, northern and eastern European regions may have longer and more stable breeding seasons, resulting in population increases. This dynamic might increase the likelihood of rabbit invasions into adjacent and previously unoccupied areas (Tablado and Revilla, 2012). Additionally, temperature, precipitation, and humidity fluctuations may increase the spread and incidence of infectious diseases, making outbreaks more difficult to control and posing a greater threat to population stability (Van de Vuurst and Escobar, 2023).

1.4. Management and recovery of rabbit populations

Due to the decline of rabbit populations, this species has become the focus of ongoing management programs, especially the subspecies *O. c. algirus*, the Iberian rabbit. These efforts are crucial not only due to the intrinsic value of the species but also because of the essential services it provides to ecosystems and humans.

The conservation programs encompass strategies such as monitoring population trends and disease incidence, habitat improvement, population reinforcement and/or sustainable game management.

1.4.1. Monitoring of population trends and disease incidence

Accurate assessment of wild rabbit populations and disease incidence is essential for effective conservation and management strategies. Most rabbit monitoring programs developed in Spain and Portugal are conducted locally or regionally and use different methodologies (see some examples in Delibes-Mateos et al., 2009a), which make their findings hardly comparable (Ward et al., 2005; Delibes-Mateos et al., 2023).

In this sense, it is essential to establish a long-term program for large-scale monitoring within their native range. This program should aim to determine population trends, evaluate health status, and understand the key factors influencing population dynamics (Mira et al., 2023). Monitoring population trends and disease incidence is crucial for developing effective, location-specific management strategies. Moreover, this approach supports adaptive management, allowing for strategy refinement based on the data collected through monitoring.

To achieve this goal, several stakeholders gathered in the ambit of the projects LIFE Iberconejo - "Drawing the baselines for the good management of a Mediterranean key species, the wild rabbit" (LIFE20 GIE/ES/000731) and LIFE LYNXCONNECT - "Creating a genetically and demographically functional Iberian lynx (*Lynx pardinus*) metapopulation" (LIFE19 NAT/ES/001055), both financed by the European Commission LIFE Program, to define, implement and validate standardised protocols for rabbit monitoring and/or sanitary monitoring (LIFE LYNXCONNECT, 2021; LIFE Iberconejo, 2022; LIFE Iberconejo, 2024). The LIFE Iberconejo project aims to establish a governance system for managing rabbits in the Iberian Peninsula. The main actions of this project include creating and validating population and sanitary monitoring systems. LIFE LYNXCONNECT project aims to enhance the population size and connectivity among Iberian lynx nuclei to ensure a functional, self-sustainable, and viable metapopulation. Therefore, it is essential to gather information on the rabbit population status, evolution and dynamics for effective management and conservation of the Iberian lynx.

The suggested protocols for monitoring rabbit populations include direct observations, searching for signs of their presence (such as latrines), collecting data on the hunting bag, and assessing the presence of raptors that are highly dependent on rabbit abundance (LIFE LYNXCONNECT, 2021; LIFE Iberconejo, 2024). LIFE Iberconejo uses the SMART (Spatial Management and Reporting Tool) computer platform to compile field data and analyse information from each region. Integrating technologies such as this further enhances data collection efficiency, accuracy, and dissemination (LIFE Iberconejo, 2024).

These harmonised approaches allow the collection of reliable and comparable data, providing an accurate representation of species' status across diverse habitats. The results can be used to develop management plans that can be effectively implemented across the Iberian Peninsula, ensuring the conservation of wild rabbit populations and the ecosystems they support.

1.4.2. Habitat enhancement

The rabbit prefers a mixed habitat that includes Mediterranean woodlands and shrubby vegetation for shelter, as well as open areas that provide grasses and cereals for its diet (Moreno and Villafuerte, 1995; Calvete et al., 2004; Carvalho and Gomes, 2004).

Habitat loss and fragmentation are causing declines in Iberian rabbit populations (Virgós et al., 2003; Delibes-Mateos et al., 2010). Therefore, habitat enhancement has emerged as a preferred technique for promoting population growth, as it involves lower costs and simpler implementation while minimising negative impacts on native species (Ferreira et al., 2013).

Habitat management enhances the carrying capacity of an area by increasing the availability of essential ecological resources, such as high-quality food, water, breeding sites, and cover from predators (e.g., Ferreira and Alves, 2009; Fernández-Olalla et al., 2010; Godinho et al., 2013; Armenteros et al., 2015). This approach has a positive global impact on biodiversity, benefiting the target species and several other species. Improving habitat quality may indirectly enhance rabbit disease resistance, as high-density populations respond better to disease outbreaks (Calvete, 2006; Guerrero-Casado et al., 2016).

Habitat management involves creating open areas, planting crops, and installing supplemental feeders. These efforts aim to enhance food availability and help create a habitat mosaic that integrates agricultural areas with natural vegetation, replicating traditional landscapes (Moreno and Villafuerte, 1995).

Additionally, constructing artificial warrens and maintaining shrub cover is crucial, especially in challenging habitat conditions such as open areas with no shrub protection or unfavourable soils for digging (Rouco et al., 2011). This provides breeding sites and offers refuge from predators. In restocking programs, artificial warrens are essential for helping rabbits adapt to their new environment.

Habitat management also includes establishing water points, such as drinking troughs, in dry areas, to enhance water availability.

Habitat enhancement is often not implemented long-term (except for Sarmento et al., 2012), and its effectiveness is frequently not evaluated, particularly in hunting states. However, there are documented success cases, and in general, habitat management is effective for recovering depleted rabbit populations in Mediterranean ecosystems (Moreno and Villafuerte, 1995; Catalán et al., 2008; Ferreira and Alves, 2009; Ferreira et al., 2013).

For example, Guil and colleagues (2014b) found that rabbits preferred sown areas over unsown areas, resulting in a local increase in rabbit populations. Sarmento and colleagues (2012) showed that continuous pasture creation increased rabbit occupancy and the colonisation of adjacent areas. Godinho and colleagues (2013) demonstrated the effectiveness of habitat management in helping low-density wild rabbit populations recover in southern Portugal. Their results indicated that rabbit abundance was positively correlated with proximity to artificial warrens, and rabbit presence increased as the distance to these structures and ecotones decreased. Conversely, a study by Delibes-Mateos and colleagues (2008b) investigated whether the installation of artificial warrens was associated with trends in rabbit populations and found no significant correlation. Regarding drinking trough use, a study conducted in a farmland area of northwestern Spain showed that rabbits frequently use these structures for drinking, especially during the summer months and when surrounded by shrub cover (Armenteros et al., 2015).

Habitat management is an essential response strategy to climate change, as alterations in temperature and rainfall patterns will influence water availability and vegetation growth and consequently European rabbit biology and ecology (Tablado and Revilla, 2012).

1.4.3. Population reinforcement

To combat the decline of the Iberian rabbit, conservationists and wildlife managers are implementing population reinforcements across the Iberian Peninsula. This conservation strategy aims to restore rabbit populations and improve ecosystem stability (Moreno et al., 2004; Guil et al., 2014a; Carro et al., 2019). Hunters and game managers also regularly conduct rabbit restocking programs to ensure sustainable numbers for hunting (Delibes-Mateos et al., 2008b).

Population reinforcement, also known as restocking, involves releasing individuals into an area where the species once thrived or is present in low densities (IUCN/SSC, 2013). The rabbits released in this process are either captive-bred individuals specifically raised for this purpose (Piorno et al., 2015) or rabbits translocated from healthy wild populations (Rouco et al., 2008).

Traditional restocking programs often experience high failure rates, particularly during the initial days following rabbit release, due to factors such as handling and transportation stress, as well as predation (Calvete et al., 1997; Calvete and Estrada, 2004; Tobajas et al., 2021). For instance, in a study by Calvete and colleagues (1997) on wild rabbit restocking, the observed survival rates were 1.89% for females and 3.11% for males in the first 10 days after their release. Similarly, Calvete and Estrada (2004) assessed the short-term survival and dispersal of translocated European wild rabbits, reporting a survival rate of only 9% following traditional restocking. Other researchers have indicated survival rates below 40% when rabbits are released in areas lacking any form of predator exclusion (Letty et al., 2002; Drees et al., 2009; Tobajas et al., 2021).

Given the high failure rate associated with this practice and the significant costs involved in restocking protocols (Ferreira and Delibes-Mateos, 2010), careful planning is essential to maximise success and minimise potential risks, including genetic homogenisation and the spread of disease. To ensure the effectiveness of this approach, it is crucial to implement specific evidence-based guidelines alongside habitat improvement measures and disease management strategies. For instance, restocked rabbits must be in good physical condition. Following strict veterinary protocols is essential to enhance survival rates and prevent the introduction of diseases into wild populations (Cabezas et al., 2011). The release sites should provide sufficient food, shelter, and breeding conditions (Moreno and Villafuerte, 1997; Cabezas and Moreno, 2007; Cabezas et al., 2011; Guil et al., 2014a). Habitat improvement, including the construction of artificial warrens and the planting of crops, is often necessary to facilitate the rapid adaptation of the relocated population. Restocking efforts should incorporate an acclimation period, during which the released rabbits are temporarily confined to enhance their adaptation to the new environment and reduce predation risk. This method is referred to as soft-release protocols (Rouco et al, 2010). Studies by Rouco and colleagues (2010) and Machado and colleagues (2017) indicated that longer confinement periods enhance rabbit survival rates.

Several restocking initiatives have shown promising results. For instance, Moreno and colleagues (2004) reported survival rates of nearly 80% in a study that evaluated the success of introducing rabbits for predator conservation in Spain. Also, Calvete and Estrada (2004) observed similar survival rates when rabbits were released into fenced warrens. A project conducted from 2002 to 2007 aimed at recovering rabbit populations in the compensation area of Los Melonares dam, which sought to support the breeding of Spanish Imperial Eagles in the surrounding area, noted a rabbit survival rate of 65% 100 days post-release in artificial warrens situated within fenced plots. Rabbit populations more than quadrupled over four years (Villafuerte et al., 2008).

Implementing evidence-based protocols does not always guarantee complete restocking success (e.g., Machado et al., 2017); therefore, further studies are essential to evaluate and propose measures that enhance the effectiveness of rabbit reinforcements.

1.4.4. Hunting management

The primary goal of sustainable hunting management is to balance hunters' interests and the long-term survival of rabbit populations, ensuring that hunting does not compromise the species' survival. It can involve regulating hunting pressure, monitoring rabbit population, and improving habitat (Ward, 2005).

Regulatory mechanisms of hunting pressure include limiting the number of hunters, the number of hunting days, the number of hours per hunting day, and/or the number of hunted rabbits per hunter and hunting journey (Delibes-Mateos et al., 2023; Mira et al., 2023). According to Angulo and Villafuerte (2003), hunters often make these adjustments voluntarily, resulting in positive outcomes for rabbit populations.

When aiming to minimise the negative effects of hunting on rabbit populations, it is important to acknowledge that rabbit hunting and associated habitat management can also have positive effects (Ward, 2005). Delibes-Mateos and colleagues (2009b) found that rabbit populations were more abundant in hunting estates than in protected areas in Spain. This suggests that sustainably managed hunting states, characterised, for instance, by low hunting pressure and effective habitat management, may benefit rabbit populations. In fact, in north-eastern Spain, positive rabbit population trends occurred in areas with low hunting pressure (Williams et al., 2007).

Many hunters and wildlife managers in Spain and Portugal consider predator control an essential management tool to reduce the mortality of small game species (Delibes-Mateos et al., 2008b). Delibes-Mateos and colleagues (2013) conducted interviews with game managers from small-game hunting estates in central Spain and found that 90% of these estates use predator control. This practice is regulated, allowing certain abundant opportunistic predator species control, particularly the fox (*Vulpes vulpes*) and the Egyptian mongoose (*Herpestes ichneumon*) (San Miguel, 2014). However, this regulation lacks support from local scientific studies, and there are instances where non-selective and illegal predator control methods are employed (Ward, 2005).

Hunting regulations should be flexible and responsive to changes in population trends, disease outbreaks, and habitat conditions. During years when rabbit populations are low, it is essential to reduce hunting pressure to support their recovery. Additionally, implementing management measures that enhance habitat carrying capacity can contribute to the sustainable management of rabbit populations. This approach allows for continued hunting while maintaining or even increasing rabbit population density (San Miguel, 2014).

1.5. Research goals

Due to the European rabbit *Oryctolagus cuniculus'* importance, particularly the Iberian rabbit subspecies *O. c. algirus*, as a keystone prey species, ecosystem engineer and small game species (Delibes-Mateos et al., 2008a; Gálvez et al., 2008; Paixão et al., 2009), conservationists, wildlife managers and hunters have continuously made efforts to reverse the ongoing rabbit population decline. However, these efforts, which involve significant economic costs (Ferreira and Delibes-Mateos, 2010), have often been unsuccessful (Calvete et al., 1997; Letty et al., 2002). In some cases, these have been time-limited, and their effectiveness has not been evaluated.

This thesis aims to evaluate the effectiveness of various measures commonly applied in rabbit recovery programs and provide recommendations, based on the research findings, to enhance the success and effectiveness of these recovery efforts, ultimately supporting the conservation of Iberian rabbit populations in the Mediterranean region.

Specifically, this thesis aims to reach the following specific goals:

1. Understand the effect of habitat management and its early cessation on rabbit populations (**Chapter 3, Paper I**);
2. Assess the survival and space use of a rabbit population released in a restocking park, a semi-natural enclosure (**Chapter 4, Paper II**);
3. Evaluate the efficiency of four types of artificial warrens (logs, Mayoral® – registered trademark, pallets, and tubes) as shelters for Iberian rabbits recently restocked (**Chapter 5, Paper III**).

1.6. Thesis structure

This thesis consists of six main chapters: a general introduction (**Chapter 1**), a summary description of the study area (**Chapter 2**), three papers published in peer-reviewed international journals, each one addressing one of the previous specific goals (**Chapters 3, 4, and 5**), and the general conclusions (**Chapter 6**).

Chapter 1 includes the scope and background information underlying the research goals. This chapter also presents the main objectives of the thesis and summarises the thesis' structure and contents.

Chapter 2 describes the study area and the framework of the thesis.

Chapter 3 evaluates rabbit population responses to habitat improvement in a natural landscape and analyses the consequences of prematurely stopping habitat management. This chapter compares the relative importance of managed and unmanaged habitat features on rabbit distribution before management (2007), during the implementation of measures (2008), immediately after (2009) and three years after measures ended (2012). The results of this chapter were published in the journal *Ecological Research*:

- Encarnação, C., Medinas, D., Alves, P.C., Mira, A. (2019). Does short-term habitat management for the European rabbit (*Oryctolagus cuniculus*) have lasting effects? *Ecological Research*, 34: 296-308. https://doi.org/10.1111/1440-1703.1064 (**Paper I**)

Chapter 4 analyses the effectiveness of a rabbit restocking in a semi-natural enclosure, focusing on survival and space use. The analyses are based on data collected over six months from 22 radio-collared rabbits, consisting of 11 males and 11 females, out of 75 rabbits released. The results of this chapter were published in the journal *European Journal of Wildlife Research*:

- Encarnação, C., Sabino-Marques, H., Pinheiro, P., Alves, P.C., Mira, A. (2025). Survival and space use of a restocked Iberian rabbit population in a semi-natural enclosure. *European Journal of Wildlife Research*, 71: 3. https://doi.org/10.1007/s10344-024-01881-5 (**Paper II**).

Chapter 5 compares the use of four distinct types of artificial warrens, commonly employed in Iberian rabbit recovery programmes and investigates the factors influencing warren use. In this case, the study focuses on using the artificial warrens installed inside the restocking park. The costs associated with warren installation are quantified, and the best options in terms of cost-benefit are discussed. The results of this chapter were published in the journal *World Rabbit Science*:

- Encarnação, C., Sabino-Marques, H., Pinheiro, P., Santos, S., Alves, P.C., Mira, A. (2024). Selection of artificial warrens following the restocking of an endangered keystone prey. *World Rabbit Science*, 32: 113-127. https://doi.org/10.4995/wrs.2024.20814 (**Paper III**)

Chapter 6 summarises the main findings and conclusions of the previous chapters and the overall conclusions, and, based on the results, suggests guidelines to improve rabbit restocking programs. This chapter also acknowledges the study's limitations and highlights future research issues to be addressed.

Chapter 2

Study area and framework

The study was conducted on an area of approximately 4,720 hectares (Figure 2.1a) located within Monchique Natura 2000 Special Area of Conservation (SAC) (PTCON0037) (Regulatory Decree n. º 1/2020 of 16th March) Norwest Algarve, Portugal (37° 16’ 33’’ N, 8° 29’ 27’’ W).

The SAC encompasses the Serra de Monchique, a mountain range characterised by steep slopes and valleys with significant ecological and biophysical importance. This range features the highest peak in southern Portugal, Foia, which rises to 902 meters. The unique combination of topographic, climatic, and geological features in this area supports a diverse array of habitats that are of conservation interest, many of which are protected under the EU Habitats and Birds Directives.

The study area encompasses three game estates, partners of the project: the Associative Game Estate of Esgravatadouro, Montes Velhos, and others (Process No. 3393), the Municipal Game Estate of Alferce (Process No. 4180), and the Associative Game Estate of Alferce (Process No. 3993).

The soil is generally poor and highly susceptible to rapid erosion. When erosion removes the fine-textured material, it exposes the underlying rock fragments (ICN, 2006). The most common type of soil is the incipient soil, particularly schist or greywacke lithosols of xeric-regime climates (86.4%; IHERA, 1999).

The oceanic pluvial-seasonal Mediterranean bioclimate influences the climate of the study area. The thermotype varies from thermo to mesomediterranean, and the ombrotype from sub-humid to humid (Rivas-Martínez et al., 2017).

The climate is Mediterranean (Rivas-Martínez et al., 2017) with mild and moist winters and hot and dry summers. The average minimum and maximum temperatures in winter

(January) are 5.6 °C and 11.6 ºC, and in summer (July) they are 17.3 °C and 24.0 °C. Annual rainfall averages 925.5 mm and is concentrated in October-April (Monchique, 1984 – 2022; SNIRH, 2023).

The area is situated within the Arade hydrographic bay and is characterised by two primary watercourses: "Ribeira de Monchique" and "Ribeira de Odelouca" (APA, 2018). Additionally, a network of smaller watercourses runs in the valleys. Due to the dense riparian vegetation, some areas retain water all year (António Gamito and João Dimas, personal observations). During this study, an important dam, the Odelouca Dam, was built within the study area.

Dense Mediterranean scrub (51.1%), eucalyptus (*Eucalyptus globulus*) plantations (26.1%), and cork oak (*Quercus suber*) woods (5.2%) mainly cover the hilly landscape. Agricultural activities are minimal (4.8%), and human occupation is limited to sparsely cultivated valleys and a few isolated houses (1.1%) (Figure 2.1b).

Endangered species, such as the Bonelli's eagle (*Aquila fasciata*) and the Eurasian eagle owl (*Bubo bubo*), inhabit the area (ICN, 2006). It is also located in a region where the Iberian lynx (*Lynx pardinus*) historically lived (ICN, 2006). Previous surveys have shown that wild rabbits are present in the area, but their populations are scattered and low-density.

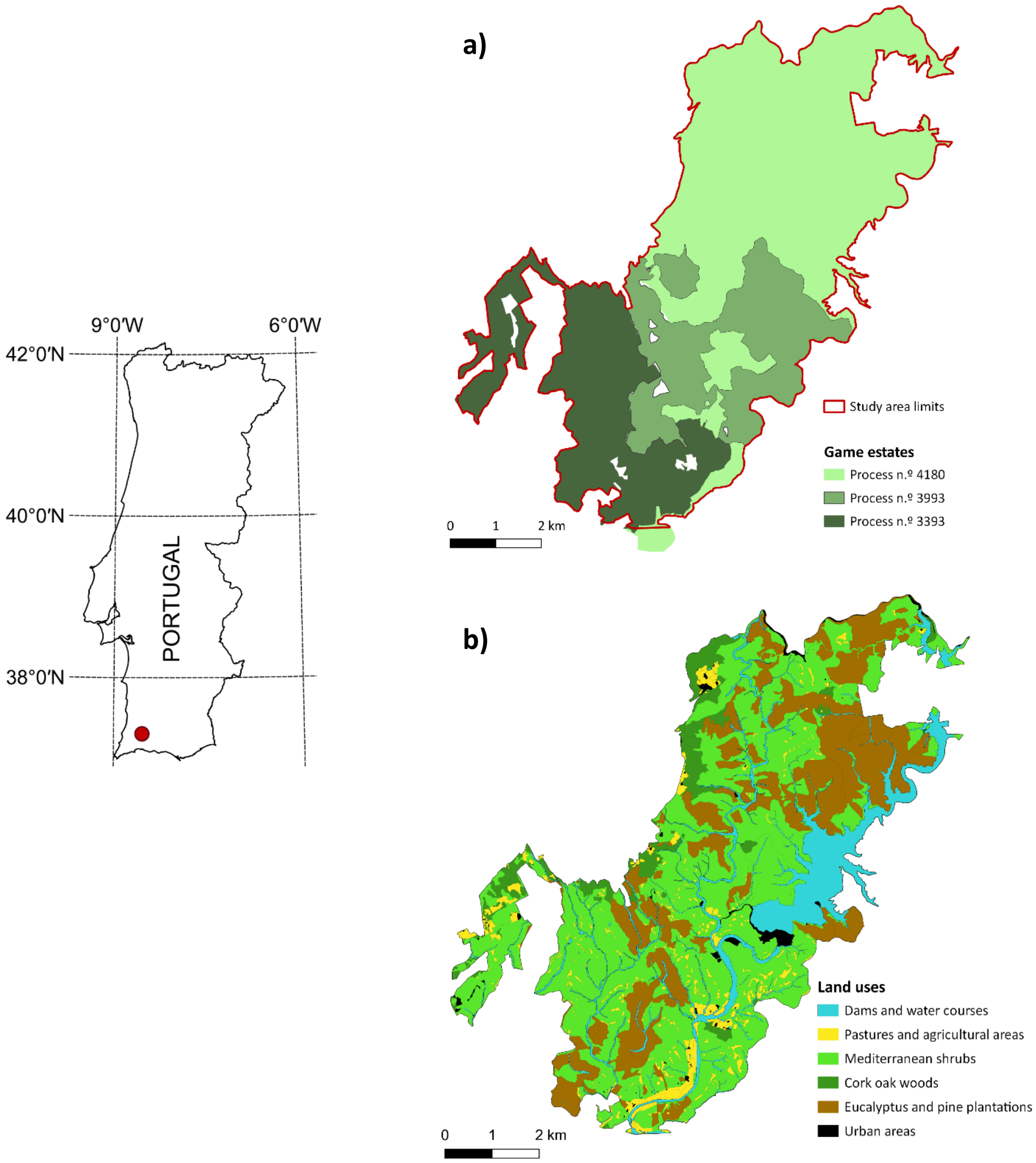

Figure 2.1 Location of the study area, limits and hunting areas within the study area (a) and main land uses (b).

The experiments and the fieldwork for this thesis were carried out in the framework of the “Compensatory measures and specific monitoring of the Odelouca’s Bonelli eagle couple, arising from the environmental impact assessment process of the Sines-Portimão high-voltage power line” project (REN et al., 2009). The research was supported by "Redes Energéticas Nacionais" (REN) and coordinated by the consortium formed by the companies “EGSP - Energia e Sistemas de Potência, Lda.” and “ECOSSISTEMA, Consultores em Engenharia do Ambiente, Lda”.

The project involved taking specific actions to support the recovery of the rabbit population, a significant food source for the Bonelli eagle (*Aquila fasciata*). The University of Évora implemented these actions from November 2006 to November 2012.

The primary objectives of these specific actions were to restore wild rabbit populations, and consequently, other species, to levels that provide sufficient food for endangered predators, especially the Bonelli's Eagle, and to establish mechanisms to maintain a high rabbit density in the long term.

Chapter 3

Does short-term habitat management for the European rabbit (*Oryctolagus cuniculus*) have lasting effects?

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Abstract

The European rabbit *Oryctolagus cuniculus*, a keystone species of Mediterranean ecosystems, is the target of several recovery and management plans throughout the Iberian Peninsula. The majority of these plans are limited in time by budget constraints and lack post-intervention monitoring of population trends. This study was conducted in southwest Portugal and aimed to understand the effect of habitat management and its early cessation on rabbit populations. We assessed rabbit presence and relative abundance before management (2007), during the implementation of measures (2008), immediately after (2009) and three years after measures ended (2012). We applied a model selection approach, using generalised linear models to determine the relative importance of MANAGED and UNMANAGED habitat features on rabbit presence in each year. We used spatial eigenvector mapping to describe the spatial autocorrelation in rabbit presence and a variation partitioning approach to quantify the relative effects of management-related variables, unmanaged environmental descriptors, and spatial characteristics on rabbit presence. Rabbit presence and abundance increased shortly after the management intervention but decreased three years after. Rabbit presence was positively related to the proximity of installed crops and the existence of favourable soils for digging. Habitat management-related variables explained most of the variation in all models. Habitat improvement actions, particularly the sowing of pastures, contributed to increased rabbit presence. We propose a continued long-term intervention and the cultivation of crops with auto-regeneration properties (e.g., subterranean clover—*Trifolium subterraneum*) to continue to increase rabbit presence and abundance in areas where rabbit populations are scarce.

Keywords: Habitat management, long-term effectiveness, Mediterranean landscape, rabbit presence, variation partitioning

3.1. Introduction

The European rabbit (*Oryctolagus cuniculus*), a species endemic to the Iberian Peninsula, is prey to a wide variety of predators in this region. It is an important source of food for various carnivores and birds of prey, such as the red fox (*Vulpes vulpes*), the Egyptian mongoose (*Herpestes ichneumon*) or the eagle owl (*Bubo bubo*), including some endangered species, such as the Iberian lynx (*Lynx pardinus*) and the imperial eagle (*Aquila adalberti*; Delibes and Hiraldo, 1981; Jaksic and Soriguer, 1981; Delibes-Mateos et al., 2008a). Within its original distribution, it also stands as one of the most harvested game species, with high socioeconomic value (Villafuerte et al., 1998; Paixão et al., 2009). In recent decades, wild rabbits have suffered a >90% population decline (Virgós et al., 2007; Ferreira et al., 2010; Cortés-Avizanda et al., 2015) with severe consequences for the specialist predator populations that depend on them. Despite preferential predation by some species (Ferreras et al., 2011; Fernandez-de-Simon, 2013) and hunting pressure (Angulo and Villafuerte, 2003; Calvete et al., 2005), the main factors contributing to this decline are the emergence of diseases, particularly myxomatosis and rabbit haemorrhagic disease (Villafuerte et al., 1995; Fa et al., 2001; Abrantes et al., 2013; Delibes-Mateos et al., 2014b) and habitat degradation (Moreno and Villafuerte, 1995; Devillard et al., 2008; Delibes-Mateos et al., 2010). Habitat changes have led to the loss of the species' preferred habitats: landscape mosaics that simultaneously provide shelter and food (Calvete et al., 2004). Conversely, in other areas, agriculture intensification leading to impoverished arable weed communities which serve rabbits as alternative food (e.g., olive groves or vineyards), has led to significant increases in rabbit numbers, causing substantial crop damage (Barrio et al., 2013; Delibes-Mateos et al., 2018a).

Hunters, conservationists, and wildlife managers have been working to reverse rabbit decline due to the species' ecological and socioeconomic importance. Several general protocols for habitat management (Delibes-Mateos et al., 2009a; Ferreira et al., 2014), hunting regulation and predator control (Delibes-Mateos et al., 2009a), semi-natural captive breeding and reintroductions (Villafuerte et al., 2008; Rouco et al., 2010) and vaccination campaigns (Ferreira et al., 2009; Rouco et al., 2016) have been implemented and, in some cases, have been successfully replicated in different regions of the Iberian Peninsula.

However, the realities differ between locations, and rabbit recovery programs should be flexible. In addition, the efficiency of rabbit management actions is often not evaluated.

Habitat improvement is the most common action currently taken to enhance rabbit populations, because it requires lower investment and produces more beneficial effects on a local scale (Ferreira et al., 2014). The main goal of habitat improvement is to promote a landscape mosaic that can guarantee the availability of key resources for this species (Moreno et al., 1996; Carvalho and Gomes, 2004). Habitat enhancement generally includes measures for increasing the availability of food, through the installation of small crops and/or supplementary artificial feeders, shelter, through scrubland management and/or construction of artificial shelters and water, through the installation of drinking troughs (e.g., Sánchez et al., 2007; Ferreira and Alves, 2009; Fernández-Olalla et al., 2010; Godinho et al., 2013).

In the Iberian Peninsula, habitat management practices generally occur in private hunting areas, and several studies have addressed the real impact of their implementation on rabbit populations (e.g., Catalán et al., 2008; Ferreira and Alves, 2009; Fernández-Olalla et al., 2010; Godinho et al., 2013). Moreover, compensatory measures from large infrastructure construction (dams, roads, power lines, etc.) aiming at predator conservation often include investments in rabbit population recovery programs (e.g. Ecosativa, 2007; REN et al., 2007; REN et al., 2009; Procesl, 2010). However, investments in rabbit habitat management are often limited in time, taking place over 2–5 years, after which no additional measures or revaluations take place. The response of the rabbit population after the cessation of these measures is thus also unknown.

We evaluated rabbit population responses to habitat improvement at the Monchique Natura 2000 site (PTCON0037; south-west Portugal) to understand the consequences of ending habitat management after a rabbit recovery program. Specifically, we intended to: (a) characterise changes in rabbit presence and abundance pre-management (2007), during management (2008), immediately after the habitat management period (2009) and three years after measures ended (2012), (b) determine which management interventions most influenced rabbit presence in each sampling period, (c) determine which ecological factors unrelated to management most influenced rabbit presence in each sampling period and (d) evaluate the real contribution of habitat management variables for increasing rabbit presence in each surveyed year.

We hypothesised that rabbit presence and abundance in 2008 and 2009 would be significantly higher than rabbit presence and abundance before habitat management (2007) and three years after habitat management abandonment (2012), because of the extremely low rabbit initial numbers and because of the shortage of resources needed for the species in 2007 and 2012. We also defined two sets of *a priori* hypotheses. The first came from the assumption that (a) management actions promote rabbit presence. Thus, we expect that rabbit presence would be increased by the proximity to crops, artificial shelters, drinking troughs and/or the perimeters of ecotones (Lombardi et al., 2007; Catalán et al., 2008; Delibes-Mateos et al., 2008b; Sarmento et al., 2012; Godinho et al., 2013). The second set of hypotheses came from the assumption that (b) other environmental variables, unrelated to management and based on species ecological requirements, also affect rabbit presence. We expect that rabbit occurrences would be favoured in non-intervention sites near agricultural or natural pastureland areas, in areas with higher shelter availability and areas with natural water availability (Trout et al., 2000; Lombardi et al., 2007; Sarmento et al., 2012). In addition, we expect that rabbit presence would be increased by soils with favourable conditions for digging (Williams et al., 2007; Serrano and Hidalgo de Trucios, 2011), smooth slopes (Calvete et al., 2004; Farfán et al., 2008; Delibes-Mateos et al., 2010) and warmer and drier terrain orientations (Delibes-Mateos et al., 2010; Godinho et al., 2013).

Finally, we also hypothesised that management-related variables should play a major role in species presence during habitat management (2008 and 2009). In contrast, other environmental variables should play a major role in species occurrence three years after ending habitat management (2012).

3.2. Materials and methods

3.2.1. Study area

The study was conducted in an area of 4,720 ha inside the Monchique Natura 2000 site (PTCON0037) in southwest Portugal (37°16’ N, 8°29’ W; Figure 3.1).

The region has a Mediterranean climate characterised by humid winters with precipitation levels above 700 mm/year and dry and hot summers, with average annual temperatures over 16ºC (Rivas-Martinez and Loidi, 1999). The area is part of the Arade hydrographic basin and is crossed by a network of smaller watercourses, which retain water in all seasons, as indicated by dense riparian vegetation. The hilly landscape (10–500 m a.s.l.; CNA, 1982) has poor soil dominated by incipient soils, particularly the schist or greywacke lithosols of xeric-regime climates (78%; IHERA, 1999) and is predominantly covered by dense Mediterranean shrubs (51.1%), eucalyptus (*Eucalyptus globulus*) plantations (26.1%) and cork oak (*Quercus suber*) woods (5.2%). Agricultural activities, excluding eucalyptus plantations, are minimal (4.8%), and human occupation is restricted to sparsely cultivated valleys and a few isolated houses (1.1%; Figure 3.1).

Between 1970 and 1990, the Monchique Natura 2000 site experienced significant changes in the habitat. There was large-scale eucalyptus forestation, replacing extensive areas originally occupied by natural vegetation (ICN, 2006). A decrease in small crop cultivation due to land abandonment (Krohmer and Deil, 2003) may also have contributed to the discontinuity of suitable habitats for the rabbit population and thus to a drastic reduction in distribution and abundance. This area was also several times devastated by wildfires, causing drastic changes in the land cover, soil characteristics and hunting pressure. In 2003, almost 80% of the whole Natura 2000 site was burned (Portaria No. 1064/2006, 2006). The wild rabbit currently has a fragmented distribution pattern in the Monchique Natura 2000 site (Ferreira et al., 2017) and hunting pressure is low and localised (Beja et al., 2007).

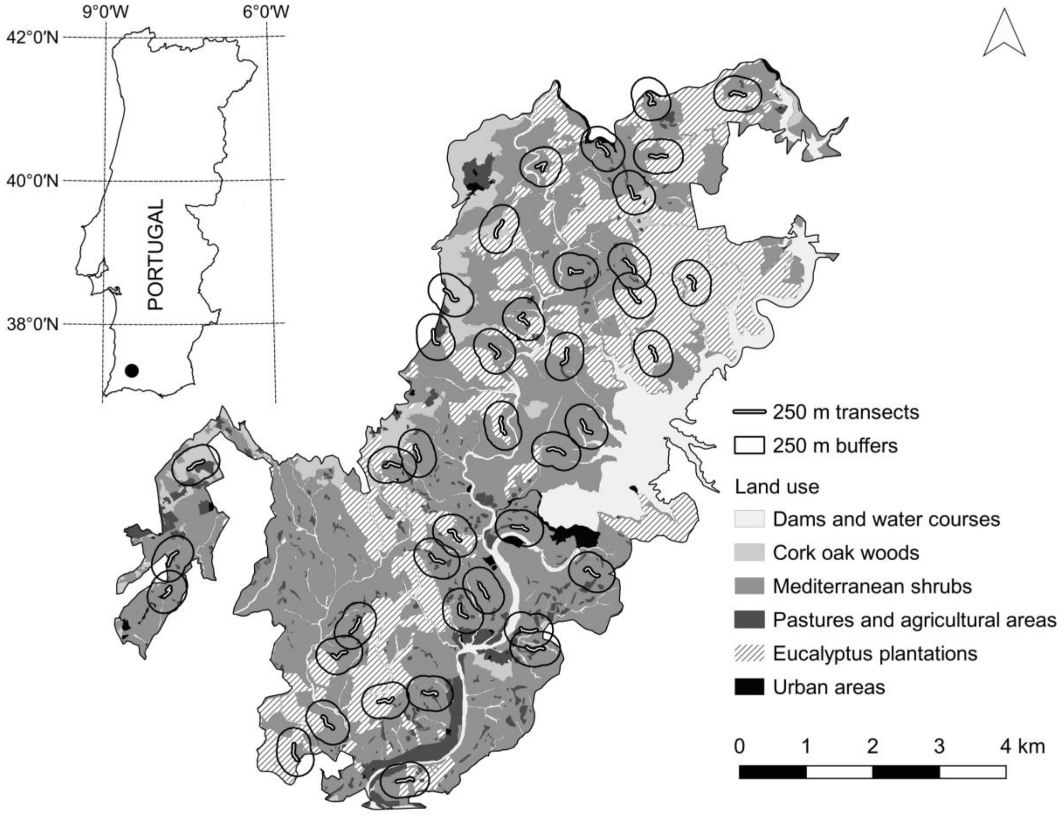

Figure 3.1 Study area location and detailed land uses. Transects for rabbit surveys (white lines) and their respective 250-m buffers (thicker black lines) are also shown.

3.2.2. Habitat management

To improve habitat quality for the wild rabbit, we implemented actions to increase the availability of food, water and shelter. These actions were taken as part of the scope of the "Compensatory measures and specific monitoring of the Odelouca's Bonelli eagle couple" project, which included specific actions aimed at supporting the recovery of the rabbit population (REN et al., 2009), a major trophic resource for Bonelli eagles (*Aquila fasciata*).

A total of 75 small patches (approximately 1 ha each) were cleared and seeded between September 2007 and January 2008 and renewed between October 2008 and January 2009, to promote food availability and create a habitat mosaic with a high edge perimeter, which is particularly suitable for rabbits (Rogers and Myers, 1979; Moreno et al., 1996; Carvalho and Gomes, 2004). All interventions started after the first autumn rains.

In May 2008, to ensure water availability in areas of water shortage, we installed 18 drinking troughs, scattered across the study region. Areas with inadequate habitat for the species (e.g., eucalyptus plantations and regions with very steep terrain) were excluded from these management actions.

Although soil conditions were unsuitable for digging burrows, a pilot study suggested that the study area had good shelter availability, due to the presence of extensive areas of dense shrub vegetation. Nevertheless, we installed 18 artificial warrens between September 2007 and January 2008 to provide additional shelter and reproduction sites.

In late 2009, at the end of the project, drinking troughs were removed, crop renewal in the ambit of our intervention stopped, and shrubs invaded the patches. During the three years after the project's conclusion, 10 artificial shelters, mostly made from wooden pallets, shrubs and dirt, collapsed and became unsuitable for rabbit use.

3.2.3. Rabbit surveys

Rabbit surveys were conducted from June to early July, at the end of each breeding season, corresponding to a population peak (Gonçalves et al., 2002), on four different occasions: pre-management (2007) as the baseline for our analysis, during the habitat management period (2008), immediately after management (2009) and three years after management ended (2012). Relative rabbit abundance was assessed in 40 randomly selected diurnal linear transects, each of approximately 250 m. One observer performed the transects in each sampling period along existing dirt roads.

Rabbit presence and abundance were determined through the detection of latrines. To ensure consistency with previous assessments of rabbit abundance in the region (e.g., Ferreira and Alves, 2005), a latrine was defined as any faecal accumulation of at least 20 pellets within an area of 200 × 300 mm^2. We applied this indirect method, which is widely used to obtain rabbit abundance indices (e.g., Virgós et al., 2003; Calvete et al., 2004;

Beja et al., 2007; Beja et al., 2009; Godinho et al., 2013), because a preliminary survey carried out in January 2007 suggested that low rabbit abundance and dense vegetation cover compromised direct counting in transects. Rabbit presence was assumed when at least one fresh latrine (with circular and aggregated pellets) was found in a sampling site.

3.2.4. Explanatory variables

We collected data on 10 environmental variables within the 40 sampling sites and grouped them into two sets of predictors: managed descriptors aiming at habitat improvement (MANAGED) and descriptors that were independent of management (UNMANAGED; Table 3.1). All descriptors, except those related to distance, were measured in a 250-m buffer around each transect. This buffer size was used because movements by rabbits in related habitats tend to be approximately equal to, or less than, this distance (e.g., Gibb, 1993; Moreno et al., 2004; Letty et al., 2005). All selected descriptors were known from previous studies to affect rabbit distribution and abundance (e.g., Trout et al., 2000; Calvete et al., 2004; Lombardi et al., 2007; Williams et al., 2007; Farfán et al., 2008; Delibes-Mateos et al., 2010; Sarmento et al., 2012; Godinho et al., 2013).

Table 3.1 Description, transformation and summary statistics of explanatory variables used to analyse European wild rabbit distribution.

Set/Variable	Variable description (Units)	Transformation	Mean ± SE	Range
MANAGED				
D_crop	Distance to the nearest installed crop (m)	Logarithmic	365.4 ± 36.5	0 – 1,749.9
D_shelter	Distance to the nearest artificial shelter (m)	Logarithmic	1,674.7 ± 94.0	9.1 – 4,230.9
D_drink	Distance to the nearest drinking trough (m)	Logarithmic	812.1 ± 50.5	2.2 – 2,087.7
Ecot	Ecotone density (m/ha)	-	30.0 ± 2.3	0 – 105.3
UNMANAGED				
Soils	Presence (1) or absence (0) of favourable soils for digging	-	-	0; 1
D_agri	Distance to the nearest agricultural patch (m)	Logarithmic	568.0 ± 40.0	0.4 – 2,301.2
D_shrub	Distance to the nearest shrub patch (m)	Logarithmic	16.2 ± 3.3	0 – 179.5
D_water	Distance to the nearest watercourse or water reservoir (m)	-	175.4 ± 9.2	33.1 – 478.0
M_slope	Mean slope (Degrees)	Logarithmic	13.8 ± 0.2	7.4 – 21.4
P_ori	Proportion of areas with favourable orientation (%)	Angular	0.6 ± 0.0	0.1 – 1.0

Note. SE: standard error.

We extracted habitat variables from land cover maps with a geographic information system (QGIS Development Team, 2014). Land cover maps were based on the photointerpretation of digital aerial photographs between 2005 and 2011 (1:5,000) and were validated and updated through field checking every year. Distance variables [distance to the nearest installed crop (D_crop), distance to the nearest artificial shelter (D_shelter), distance to the nearest drinking trough (D_drink), distance to the nearest agricultural patch (D_agri), distance to the nearest shrub patch (D_shrub) and distance to the nearest watercourse or water reservoir (D_water)], were accounted for using the function "ST_Distance" in PostGIS 2.1.6 (http://postgis.net). The shrub patches included patches with shrubs or forests with shrubs.

The ecotone corresponded to the edges between the food (crops, natural pasturelands, and agricultural areas) and shelter patches (shrubs and forest with shrubs), and the ecotone density (Ecot) was defined as the ratio between the edge length and the buffer area.

We identified the soil types from the official Portuguese soils map (1:25,000; IHERA, 1999) and categorised them as favourable or unfavourable for digging. Favourable soils are deep, soft, well-drained, and rich in carbonates and sand content (Parer and Libke, 1985; Williams et al., 2007; Serrano and Hidalgo de Trucios, 2011). We classified the humic and nonhumic litholic soils of syenite as favourable soils.

The mean slope (M_slope) and the proportions of areas with a favourable orientation (P_ori) were derived from a 25-m digital terrain model (EEA, 2013), using GRASS 6.4.4 GIS software (GRASS Development Team, 2014). We considered patches facing south and east as having more suitable orientations. These are known to be warmer and drier, due to Mediterranean winds and sun exposure, which reduce disease-vector proliferation (Osácar-Jimenez et al., 2001) and litter mortality (Rödel et al., 2009).

3.2.5. Data analyses

We estimated relative rabbit abundance at each of the 40 sampling sites and for each sampling period by calculating the total number of latrines recorded per kilometre of transect (kilometric abundance index—KAI; Wilson et al., 1996). We evaluated the differences in mean rabbit abundances between sampling periods with a nonparametric Wilcoxon signed-rank test to test our first hypothesis. The same differences but considering the proportion of rabbit presence (number of sites where at least one latrine was detected/total number of sites sampled), were evaluated using a Pearson Chi-squared test.

Before model building and when necessary, we transformed the proportions and continuous explanatory variables using angular and logarithmic transformations, respectively, to approach the normality of the residuals, homogenise variances and reduce the effect of outliers (Zuur et al., 2010). All predictors were standardised to a zero mean and unit variance to allow direct comparisons between individual regression coefficients (Schielzeth, 2010). At the data exploration stage, Spearman correlation coefficients were also computed to check for correlations between all pairs of variables. For pairs with a correlation coefficient > 0.7 (Dormann et al., 2013), we retained the variable with the lowest AICc (Akaike information criterion corrected for small samples) in the univariate model (Burnham and Anderson, 2002). In this process, we discarded D_drink, Ecot and M_slope from further modelling, because they were correlated with D_crop. D_shrub was also excluded from the analyses because, even after transformation, it presented outliers and a skewed distribution (Zuur et al., 2009; Zuur et al., 2010). Indeed, D_shrub was mostly zero or near zero (median = 0 m), showing that this is not a limiting factor for the rabbits in the study area.

To identify the factors that most influenced rabbit presence in each sampling period, we used generalised linear models (GLMs). Model selection was based on the information-theoretic approach and inferences were based on model averaging (Burnham and Anderson, 2002). Separate GLMs with binomial error distributions and a logistic link function were applied for three sampling periods: during habitat management (2008), immediately after management (2009) and three years after (2012). We decided to use rabbit presence as a response variable, due to the high number of zeros and very high overdispersion of the abundance data (Zuur et al., 2007). Despite this, the number of rabbit-presence instances in the pre-managed period (2007) was too low to produce robust GLM models.

We generated 18 candidate models with all possible combinations of the remaining variables for each hypothesis set: three models derived from two variables for the MANAGED set and 15 models derived from four variables for the UNMANAGED set (Table 3.2). We also tested the constant-only model. Models were ranked by the AICc (Burnham and Anderson, 2002) within each set of hypotheses.

Table 3.2 Models tested for determining the predictors influencing European rabbit presence for the two hypothesis sets in each sampling period.

Hypotheses sets	Models
MANAGED	D_crop
	D_shelter
	D_crop + D_shelter
UNMANAGED	Soils
	D_agri
	D_water
	P_ori
	Soils + D_agri
	Soils + D_water
	Soils + P_ori
	D_agri + D_water
	D_agri + P_ori
	D_water + P_ori
	Soils + D_agri + D_water
	Soils + D_agri + P_ori
	Soils + D_water + P_ori
	D_agri + D_water + P_ori
	Soils + D_agri + D_water + P_ori

Note. See Table 3.1 for explanatory variable descriptions.

Because no single model was convincingly the most plausible (wi ≥ 0.90; Burnham and Anderson, 2002), we performed a model averaging approach for each variable set, basing the average parameters, unconditional standard errors (SE) and 95% confidence interval (CI) inferences on the group of models with ΔAICc <2 (Burnham and Anderson, 2002). Estimates with confidence limits that included zero were viewed as having equivocal meaning (Burnham and Anderson, 2002).

Model adequacy was evaluated by plotting average model residuals and each variable presented in the final model against fitted values (Zuur et al., 2009).

Residual plots suggested the existence of spatial autocorrelation. To account for this, we used a spatial eigenvector mapping (SEVM) approach (Griffith and Peres-Neto, 2006) to select a linear combination of the most relevant eigenvector-based spatial filters (those minimising residual spatial autocorrelation; Diniz-Filho and Bini, 2005). Therefore, Spatial eigenvectors were considered the third set of explanatory variables (SPATIAL) for each year. Spatial eigenvector calculations were made using the Spatial Analysis in Macroecology software (SAM, version 4.0; Rangel et al., 2010).

As a final point, to test our last hypothesis and to assess the pure and shared effects of each of the three variable sets (MANAGED, UNMANAGED and SPATIAL) of explanatory variables on rabbit presence, we used a variation partitioning procedure (Borcard et al., 1992) and extended this method to three subsets of explanatory variables (Cushman and McGarigal, 2002; Heikkinen et al., 2004). The explained variation for the three single-set models, the three joint models (MANAGED + UNMANAGED, MANAGED + SPATIAL, UNMANAGED + SPATIAL) and the full model (MANAGED + UNMANAGED + SPATIAL), together with the unexplained variations, were estimated for each sampling period (Borcard et al., 1992). Each model contained all variables from the ΔAICc <2 subset. The explained null deviance proportion (D2) was used as a measure of the explained variance for each logistic model (Guisan and Zimmermann, 2000).

Model performance was assessed using the area under the receiver operating characteristic curve (AUC), with values between 0.5 and 0.7 indicating a low-accuracy model, values between 0.7 and 0.9 indicating good accuracy and values above 0.9 indicating excellent accuracy (Swets, 1988).

The R statistical package version 3.4.2 (R Core Team, 2017) was used for all statistical analyses. The MuMIn package (Barton, 2014) was used for model inference, and the caTools package (Tuszynski, 2014) for AUC determination.

3.3. Results

3.3.1. Rabbit distribution and abundance

We registered an increase in rabbit presence and abundance during and immediately after the application of management actions, followed by a decline three years later. Rabbits were present in 12.5% of the sites sampled in June 2007, 37.5% of the sites sampled in June 2008, 42.5% of the sites sampled in June 2009 and 27.5% of the sites sampled in June 2012 (Figure 3.2a). The species had a mean relative abundance of 4.66 latrines/km in 2007, 10.17 latrines/km in 2008, 23.80 latrines/km in 2009 and 6.40 latrines/km in 2012 (Figure 3.2b).

Rabbit presence in 2007 was significantly lower than in 2008 (χ^2 = 4.263, p = 0.039) and 2009 (χ^2 = 5.762, p = 0.016). There were no significant differences in presence proportions between 2008 and 2009 (χ^2 = 0.133, p = 0.715), 2007 and 2012 (χ^2 = 1.667, p = 0.197), 2008 and 2012 (χ^2 = 0.667, p = 0.414) and 2009 and 2012 (χ^2 = 1.385, p = 0.239).

The mean relative abundance was significantly lower during the pre-managed period than in the other three sampling periods (2008: Z = −2.313, p = 0.021; 2009: Z = −2.521, p = 0.012; 2012: Z = −2.033, p = 0.042).

Abundance was also significantly lower in 2008 and 2012, compared to the values registered in 2009 (2008: Z = −3.583, p = 0.0004; 2012: Z = −2.819, p = 0.005).

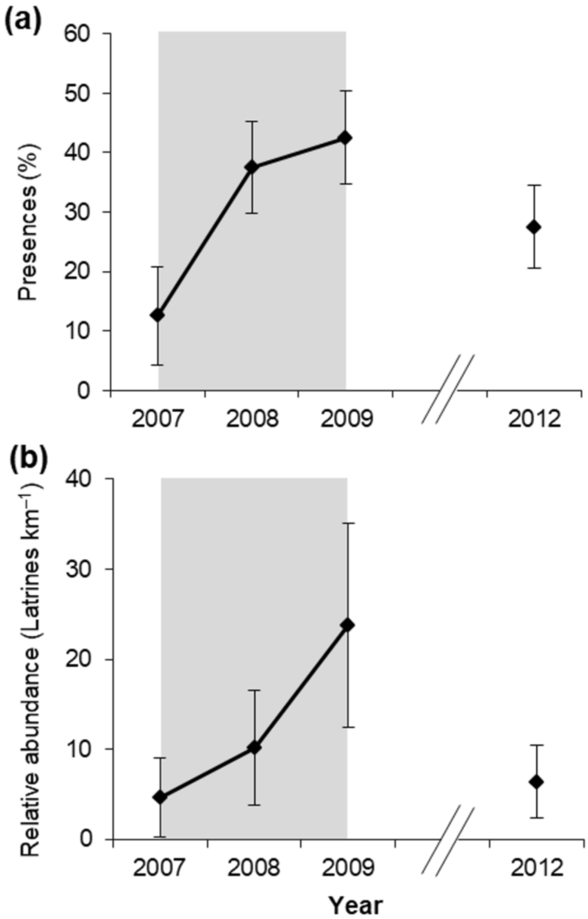

Figure 3.2 Proportion of presence (±SE) (a) and mean relative abundance (±SE) (b) of European rabbit for the four sampling periods (2007, 2008, 2009 and 2012). Grey bars indicate the duration of habitat management.

3.3.2. Rabbit presence modelling

The average models describing the estimated effects of explanatory variables on rabbit presence are presented in Table 3.3. All candidate models for each sampling year are presented in Table S3A.1 (Supplementary information 3A).

According to SEVM, two spatial eigenvectors were statistically significant. These eigenvectors were introduced into the respective models to account for autocorrelation in the data (Tables 3.3 and S3A.1).

The MANAGED set had a higher performance for all three occasions modelled (AUC = 0.869 in 2008; AUC = 0.858 in 2009; AUC = 0.824 in 2012) than the UNMANAGED set (AUC = 0.712 in 2008; AUC = 0.624 in 2009; AUC = 0.677 in 2012). The SPATIAL set had a lower accuracy in 2012 (AUC = 0.781 in 2008, AUC = 0.831 in 2009 and AUC = 0.671 in 2012).

Table 3.3 Average models describing the estimated effects of explanatory variables on European rabbit presence in the three sampling periods (2008, 2009 and 2012).

Hypotheses sets /Variables	**2008**		**2009**		**2012**	
	***β* (95% CI)**	***w+***	***β* (95% CI)**	***w+***	***β* (95% CI)**	***w+***
MANAGED						
Intercept	–0.606 (–1.492; 0.281)	–	–0.283 (–1.098; 0.536)	–	**–1.262 (–2.180; –0.344)**	–
D_crops	**–1.952 (–3.291; –0.614)**	**1.00**	**–1.622 (–2.856; –0.749)**	**1.00**	**–1.275 (–2.203; –0.346)**	**1.00**
D_shelter	0.648 (–0.428; 1.723)	0.40			–0.519 (–1.439; 0.400)	0.40
UNMANAGED						
Intercept	**–1.140 (–2.043; –0.236)**	–	–0.333 (–1.019; 0.352)	–	**–1.090 (–1.913; –0.267)**	–
D_agri			–0.519 (–1.344; 0.305)	0.45	–0.832 (–1.895; 0.231)	0.77
D_water	–0.511 (–1.285; 0.264)	0.45	–0.511 (–1.345; 0.322)	0.18	–0.702 (–1.701; 0.297)	0.25
Soils	**1.908 (0.301; 3.517)**	**1.00**	0.435 (–0.972; 1.842)	0.16	0.345 (–0.501; 1.191)	0.12
D_ori					0.555 (–1.045; 2.155)	0.11
SPATIAL						
Intercept	**–0.759 (–1.661; –0.006)**	–	–0.565 (–1.488; 0.214)	–	**–1.097 (–1.973; –0.373)**	–
Eigenvector 2	**0.945 (0.155; 1.923)**	**1.00**	**1.287 (0.467; 2.346)**	**1.00**	0.605 (–0.158; 1.491)	1.00
Eigenvector 6	**–0.972 (–2.036; –0.151)**	**1.00**	**–0.919 (–2.026; –0.073)**	**1.00**	–0.466 (–1.333; 0.299)	1.00

Note. For each variable, we show the standardised regression coefficient (β), the 95% confidence interval (95% CI) and the selection probability (w+) for the ΔAICc <2 models. Coefficient estimates whose CIs exclude zero are in bold.

In all sampling periods, rabbit presence was favoured in the proximity of installed crops (D_crop) and unmanaged water (D_water) and in areas with favourable soils for digging. D_crop was always the most important factor explaining rabbit presence, showing the highest absolute values of regression coefficient and one of the highest values of selection probability. In 2009, immediately after habitat management, rabbit presence was also negatively correlated with the distance to the agricultural patches. Distance to the nearest artificial shelter influenced rabbit presence positively in 2008 and negatively in 2012. Three years after the end of management (2012), rabbit presence was favoured by proximity to agricultural patches and in areas predominantly oriented to the west or south. Nonetheless, some predictors had an equivocal meaning in all sampling periods, since the unconditional confidence interval included zero (Table 3.3).

3.3.3. Variation partitioning

Variation partitioning analysis (Figure 3.3) showed that the 2008 full model explained 73.5% of the variance in rabbit presence, the 2009 model explained 58.9% and the 2012 model explained 41.9%. The full models obtained for 2008 and 2009 demonstrated excellent accuracy (AUC 2008 = 0.976; AUC 2009 = 0.949) and the 2012 model exhibited good accuracy (AUC 2012 = 0.893).

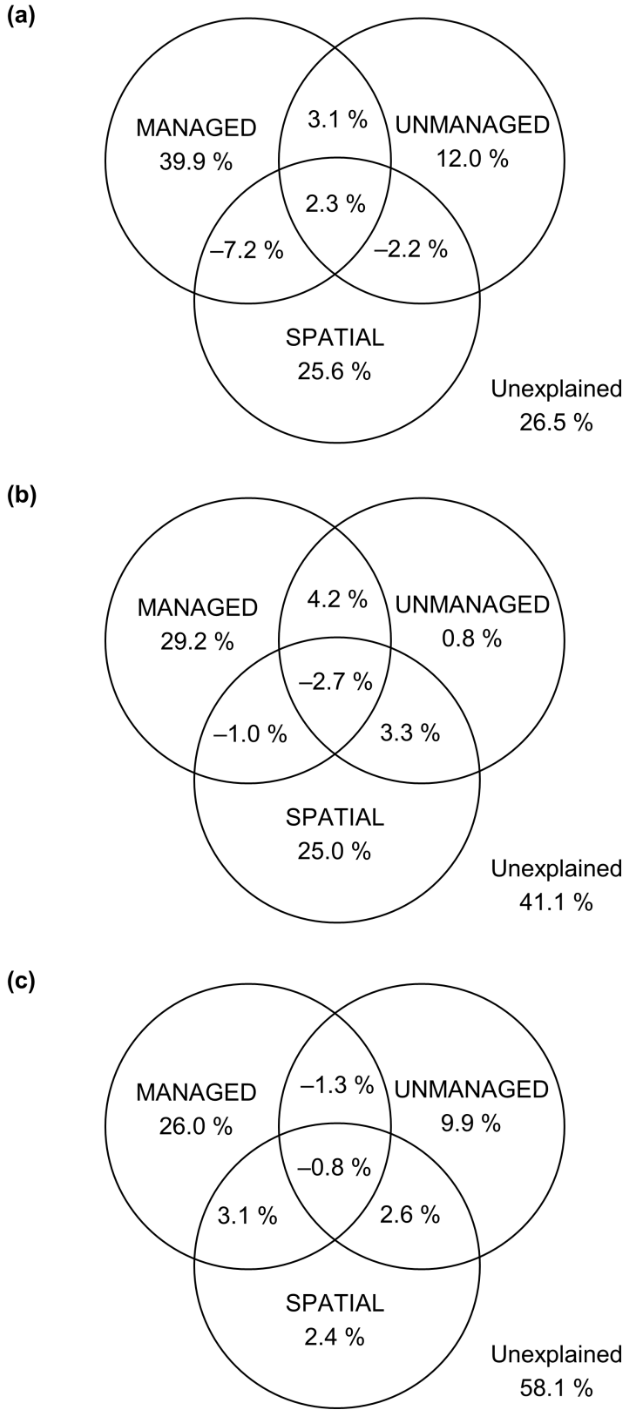

Figure 3.3 Variation partitioning results for three sampling periods: (a) 2008, (b) 2009 and (c) 2012, considering three sets of independent variables: MANAGED, UNMANAGED and SPATIAL. "Unexplained" denotes the percentage of unexplained variation.

In all sampling periods, species presence was mostly explained by MANAGED model pure effects, although with a decreasing trend over the study period (2008 = 39.9%; 2009 = 29.2%; 2012 = 26.0%). The lowest pure effects resulted from the UNMANAGED model in 2008 (12.0%) and 2009 (0.8%) and the SPATIAL model in 2012 (2.4%).

The joint fractions containing two or three sets of variables had very low values of explained variance in all sampling periods. In some cases, the explained variance was represented by a small negative value, which suggests a synergy between variable sets (Legendre and Legendre, 1998).

3.4. Discussion

We evaluated the influence of habitat management on the distribution and abundance of the European wild rabbit in a natural landscape and within its native range, and how the distribution and abundance evolved three years after management ended.

Before management (2007), rabbit distribution was narrow and localised, and abundance was very low. Our results showed an increasing trend in rabbit distribution and abundance during and in the year after habitat management actions took place, but a decrease three years after the cessation of those actions, as we initially hypothesised. Habitat improvement seems to have benefited the rabbit population, creating more suitable conditions, especially by installing new feeding areas scattered throughout a shrubby matrix. Habitat management actions improved the characteristics of the intervention area, particularly regarding food availability for the rabbits. On a broader scale, our implemented measures also contributed to creating a habitat mosaic where food and shelter were interspersed, favouring conditions highly suitable for rabbits (Moreno et al., 1996; Carvalho and Gomes, 2004). In 2012, three years after management ceased, rabbit abundance declined to pre-management levels, and the influence of MANAGED habitat descriptors on rabbit presence decreased. Rabbit presence also declined compared to 2009; however, in 2012 rabbits were still present in twice as many sites as in 2007 (before any management), so three years after management stopped, results were, in this sense, still positive.

Nevertheless, in 2012, a large proportion (58.1%) of the variance in the rabbit presence/absence pattern remained unexplained. Thus, other factors could have contributed to the low rabbit presence this year. For instance, there may have been an opportunistic intensification in hunting pressure immediately after rabbit numbers increased (Angulo and Villafuerte, 2003; Kontsiotis et al., 2013), due to higher rabbit availability. Stochastic extinction of some rabbit nuclei may also have occurred, because some sites with few or no rabbit signs were found in areas that had maintained suitability for the species and were previously occupied. Additionally, a new variant of rabbit haemorrhagic disease virus (RHDV2), resistant to vaccination, was identified in France in 2010 (Le Gall-Reculé et al., 2011; Le Gall-Reculé et al., 2013) and rapidly spread throughout the Iberian Peninsula (Abrantes et al., 2013; Dalton et al., 2014). In Spain, RHDV2 was first found in rabbit farms in 2011 (Dalton et al., 2012), but in Portugal, the first outbreaks in wild populations were not reported until November 2012 (Abrantes et al., 2013). Given the geographic proximity of the two countries, we cannot exclude the hypothesis that the virus was already present in Portugal before the 2012 sampling occasion. However, we believe an RHDV2 outbreak in the study area was very unlikely to be missed since this virus has different characteristics from the original virus: much higher mortality rates and mortality in young rabbits less than two months old (Abrantes et al., 2012; Dalton et al., 2012; Le Gall-Reculé et al., 2013). Moreover, in cooperation with hunters' associations, we found only one rabbit carcass showing myxomatosis symptoms near the study area at the end of 2008 (REN et al., 2009). Therefore, we have no evidence that suggests the occurrence of any disease outbreak during the sampling periods that could have drastically reduced rabbit numbers.

Although precipitation levels over the year could have influenced grass germination and consequently food availability for the rabbits, they are unlikely to have influenced our results, because annual precipitation patterns were very similar between years. Moreover, the beginning of the rainy season was always between August and September (APA, 2013), suggesting that the breeding season started at almost the same time every year.

The limits of the areas occupied by eucalyptus plantations are well-defined in the study area and did not differ significantly between the beginning and the end of the study period ($Z = -0.486$, $p = 0.627$). Therefore, it is unlikely that this factor could have influenced a decrease in rabbit presence and abundance in 2012.

3.4.1. Descriptors influencing distribution

As we predicted, the proximity to installed crops and the presence of favourable soils for digging significantly increased the probability of rabbit presence. Crop patches are the main food source in places where land abandonment had previously boosted dense shrub vegetation development (Palma et al., 2005; Beja et al., 2007). The creation of crop patches also improves the ecotone perimeter with shrubs and woodland, a condition considered by several authors to be the main driver of rabbit habitat quality and rabbit abundance (e.g., Rogers and Myers, 1979; Moreno et al., 1996; Lombardi et al., 2003; Carvalho and Gomes, 2004). The ecotone structure allows rabbits to optimise their spatial behaviour and easily access feeding and refuge patches (Virgós et al., 2003; Monzón et al., 2004; Lombardi et al., 2007).

The presence of favourable soils for digging warrens was a determining factor for species presence, even though above-ground refuge does not appear to be a problem due to the availability of dense shrub vegetation (Table 3.3). The species may live above ground when a dense shrub layer is present (Beja et al., 2007), but it depends on warrens for breeding and protection from predators (Parer and Libke, 1985; Kolb, 1994).

Other predictors did not seem as relevant to species presence as we hypothesised, since their unconditional confidence intervals included zero, showing an equivocal meaning and selection probabilities were low. Nonetheless, some regression coefficient estimates showed similar tendencies to those we predicted. Species presence tends to decrease with the distance to agricultural patches and with the distance to a watercourse or water reservoir, and tends to increase with the proportion of areas with favourable orientation (such as areas south and east oriented).

Our results did not support the importance of drinking troughs and proximity of artificial shelters as limiting factors for the species, as reported by other authors for the Iberian Peninsula (Carvalho and Gomes, 2004; Delibes-Mateos et al., 2010; Godinho et al., 2013). Dense Mediterranean shrub vegetation covers about 50% of the study area, and a network of small watercourses crosses it, ensuring the availability of these resources throughout the area, which may explain our results.

As hypothesised, habitat management-related variables were determinants for species presence during habitat management (2008 and 2009), as they explained most of the model's variation. On the other hand, in 2012, management-related variables still explained most instances of rabbit presence, contrary to our prediction. Although crops had not been renewed since the beginning of 2009 and were partially invaded by shrubs, some of the sown crops were still preserved and were colonised by natural herbs, providing food resources for the species. The continuation of rabbit monitoring in the following years, which was not logistically possible, could have given us the answer to whether this decreasing trend would persist.

3.4.2. Management implications

Mediterranean ecosystems have a long and intense history of human influence, resulting in landscape fragmentation and degradation (Gonzalez-Bernaldez, 1991; Myers et al., 2000), and this study area in southwest Portugal (Monchique) is no exception.

Several factors, such as changes in traditional land practices, land abandonment and proliferation of the forest industry, may have led to a decrease in rabbit abundance and to the formation of several fragmented and isolated populations in this region. This declining tendency has also been observed in other areas of the Iberian Peninsula (Moreno & Villafuerte, 1995; Calvete et al., 2006; Delibes-Mateos et al., 2010), and the results of the present study could also be useful in these areas.

In the last two decades, conservationists, hunters and other stakeholders have developed and implemented mitigation actions and have invested considerable resources in increasing rabbit populations in Iberia through active habitat management (Ferreira et al., 2014). However, most of these actions have a short timeline and their medium- and long-term effects are often neglected. In our study, despite the high rabbit recovery registered during and immediately after the cessation of the management actions, we believe that the short period for which those measures were implemented was insufficient to achieve abundant, stable, and self-sustaining rabbit populations, which are more resistant to diseases, predation, hunting pressure, and stochastic events. In a long-term study where relative rabbit abundance was assessed for 12 years, Sarmento et al. (2012) demonstrated that a steady increase in rabbit occupancy and colonisation patterns was consistently associated with continuous pasture creation.

We thus propose that habitat management should be continuous over long periods, rabbit populations should be regularly monitored (distribution, abundance, and disease incidence) throughout the intervention period, and management actions should be regularly revised based on species assessment results. This would allow two important questions to be answered: (a) can long-term habitat management lead to the presence of self-sustaining rabbit populations, and (b) if so, for how long and to what rabbit density level is habitat management needed to achieve a sustainable rabbit population. To reduce costs, we also suggest that habitat management should favour crop cultivation for rabbit food, and crop composition should aim for self-sufficiency. Crops including species with auto-regeneration properties that do not need to be replanted every year, such as subterranean clover (*Trifolium subterraneum*), yellow serradella (*Ornithopus compressus*) and the annual Wimmera ryegrass (*Lolium rigidum*), will tend to accelerate the achievement of sustainable rabbit populations. Although the eucalyptus plantations are on private properties and are an important economic resource for their owners, we also believe efforts should be made to reduce the areas occupied by them. The goal is to promote the restoration of rabbit favourable habitat and reduce the risk of wildfires.

3.5. Conclusion

Our results provide some indications that habitat management should be a continued effort to achieve its goals. We believe that our results and management suggestions provide new guidelines to improve rabbit recovery protocols, particularly in the Mediterranean region.

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Supplementary information 3A

Table S3A.1 Candidate models tested to assess factors potentially affecting rabbit presence for each variable set (MANAGED, UNMANAGED and SPATIAL) corresponding to different groups of hypotheses, in the three sampling periods (2008, 2009 and 2012). For each model, we present the Akaike Information Criterion for small samples (AICc), AICc differences (ΔAICc) and Akaike weights (w_i). Models are ranked by ΔAICc. Best-ranked models (ΔAICc < 2) are in bold. Parameters: Soils – presence of favourable soils for digging, D_crops – Distance to the nearest installed crop, D_shelter – Distance to the nearest artificial shelter, D_agri – Distance to the nearest agricultural patch, D_water – Distance to the nearest watercourse or water reservoir, P_ori – Proportion of areas with favourable orientation, Eigenvector – spatial eigenvector.

Sample	Hypotheses sets	Models	AICc	ΔAICc	w_i
2008	MANAGED	**D_crop**	**38.6**	**0.00**	**0.602**
		D_crop + D_shelter	**39.5**	**0.83**	**0.397**
		Null	55.0	16.40	0.000
		D_shelter	55.8	17.18	0.000
	UNMANAGED	**Soils**	**51.1**	**0.00**	**0.268**
		Soils + D_water	**51.5**	**0.42**	**0.217**
		Soils + P_ori	53.2	2.12	0.093
		Soils + D_agri	53.4	2.31	0.084
		Soils + D_agri + D_water	53.5	2.41	0.080
		Soils + D_water + P_ori	54.0	2.89	0.063
		Null	55.0	3.94	0.037
		D_agri + D_water	55.6	4.55	0.028
		Soils + D_agri + P_ori	55.7	4.59	0.027
		Soils + D_agri + D_water + P_ori	56.0	4.88	0.023
		D_agri	56.3	5.18	0.020
		D_water	56.4	5.31	0.019
		P_ori	57.1	6.05	0.013
		D_agri + D_water + P_ori	57.3	6.16	0.012
		D_agri + P_ori	57.7	6.65	0.010
		D_water + P_ori	58.7	7.65	0.006
	SPATIAL	Eigenvector 2 + Eigenvector 6	49.1	–	–
2009	MANAGED	**D_crop**	**42.6**	**0.00**	**0.736**
		D_crop + D_shelter	44.7	2.08	0.261
		D_shelter	53.9	11.27	0.003
		Null	56.7	14.04	0.001
	UNMANAGED	**Null**	**56.7**	**0.00**	**0.219**
		D_water	**57.4**	**0.79**	**0.147**
		D_agri + D_water	**58.2**	**1.52**	**0.102**
		Soils	**58.5**	**1.83**	**0.088**
		D_agri	58.7	2.01	0.080
		P_ori	58.8	2.20	0.073
		Soils + D_water	59.1	2.49	0.063
		D_water + P_ori	59.7	3.09	0.047
		D_agri + D_water + P_ori	60.5	3.89	0.031
		Soils + D_agri + D_water	60.6	3.92	0.031
		Soils + D_agri	60.8	4.13	0.028

Sample	Hypotheses sets	Models	AICc	ΔAICc	w_i
		Soils + P_ori	60.8	4.14	0.028
		D_agri + P_ori	60.8	4.17	0.027
		D_water + P_ori	61.6	4.90	0.019
		Soils + D_agri + D_water + P_ori	63.1	6.47	0.009
		Soils + D_agri + P_ori	63.1	6.50	0.008
	SPATIAL	Eigenvector 2 + Eigenvector 6	47.1	–	–
2012	MANAGED	**D_crop**	**40.2**	**0.00**	**0.582**
		D_crop + D_shelter	**41.0**	**0.78**	**0.395**
		D_shelter	47.4	7.17	0.016
		Null	49.2	8.91	0.007
	UNMANAGED	**D_water**	**48.7**	**0.00**	**0.182**
		D_agri + D_water	**48.9**	**0.23**	**0.163**
		Null	**49.2**	**0.46**	**0.145**
		D_water + P_ori	**50.3**	**1.64**	**0.080**
		Soils + D_water	**50.5**	**1.85**	**0.072**
		Soils	51.1	2.40	0.055
		D_agri	51.2	2.49	0.053
		P_ori	51.3	2.59	0.050
		D_agri + D_water + P_ori	51.3	2.64	0.049
		Soils + D_agri + D_water	51.4	2.67	0.048
		Soils + D_agri + P_ori	52.1	3.44	0.033
		Soils + P_ori	53.4	4.66	0.018
		Soils + D_agri	53.4	4.69	0.017
		D_agri + P_ori	53.5	4.82	0.016
		Soils + D_agri + D_water + P_ori	53.9	5.18	0.014
		D_water + P_ori	55.8	7.13	0.005
	SPATIAL	Eigenvector 2 + Eigenvector 6	47.6	–	–

Chapter 4

Survival and space use of a restocked Iberian rabbit population in a semi-natural enclosure

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Abstract

Restocking is widely used to recover depleted wild rabbit *Oryctolagus cuniculus* populations in the Iberian Peninsula. However, in general, it's costly and unsuccessful. In this work, we developed a wild rabbit restocking protocol based on recommendations from existing literature to enhance its success. We released 75 Iberian rabbits, *Oryctolagus cuniculus algirus*, in a 1.7-ha restocking park, a fenced semi-natural enclosure with similar resources as the surrounding area, in Monchique, southern Portugal. We tracked 22 radio-collared rabbits (1:1 sex ratio) for 6 months. We released some rabbits inside warrens, and others in shrub patches. After a 72-day acclimation period, we opened the restocking park passages to allow the rabbits to disperse. We then assessed rabbit survival and space use. We found that survival rates stabilised 74 days after restocking, with an estimated probability of survival at the end of the study of 35.4%. Predation by birds of prey was the primary cause of death. Regarding space use, the restocked population took 96.364 ± SE 12.615 days to stabilise home ranges. After the acclimation period, the maximum distances travelled by rabbits significantly increased. However, before and after the opening of the passages, the home ranges remained within the limits of the restocking park, indicating that the surviving rabbits settled within the enclosure. Rabbits released within warrens had significantly smaller core areas, while those released in shrubs exhibited more ranging behaviour. Considering our findings, we recommend implementing several measures to improve similar rabbit restocking programs.

Keywords: dispersion, home ranges, *Oryctolagus cuniculus algirus*, predation, restocking park, wildlife management

4.1. Introduction

Translocation is widely used in wildlife management to restore natural ecosystems and communities. Given the rapid destruction of natural habitats and the rising number of threatened species, translocation is emerging as a valuable tool in conservation efforts (Griffith et al., 1989).

Translocation involves moving organisms from one area to another through human intervention. When conducted intentionally, translocations can be done for various reasons, such as political, commercial, recreational, or conservation purposes. It is called reinforcement or restocking when the translocation involves moving and releasing individuals into an area with an existing population, even when densities are low. The aim is to improve population viability by, for instance, increasing population size or genetic diversity (IUCN/SSC, 2013).

Restocking is a common method to increase European rabbit *Oryctolagus cuniculus* populations in Portugal and Spain, whether for conservation or hunting purposes (Calvete et al., 1997; Delibes-Mateos et al., 2008c). The main goal is to establish a self-sustaining breeding core of rabbits with abundant numbers, ensuring they can naturally repopulate the surrounding areas.

In 2019, the International Union for Conservation of Nature (IUCN) classified the European rabbit as a globally Endangered species (Villafuerte and Delibes-Mateos, 2019). This is mainly due to the sharp reduction in the distribution and abundance of its Iberian populations in the last few decades, particularly the southern Iberian subspecies *Oryctolagus cuniculus algirus*. The decline is primarily attributed to outbreaks of a new variant of rabbit haemorrhagic disease virus (RHDV2) (Delibes-Mateos et al., 2014b; Monterroso et al., 2016; Villafuerte and Delibes-Mateos, 2019). In Portugal, this species has recently been classified as Vulnerable, as it was recognised as one of the mammal species with the greatest population decline in the last decade (Mira et al., 2023).

In the Iberian Peninsula, two distinct genetic lineages of rabbits have been associated with two rabbit subspecies: *Oryctolagus cuniculus algirus* and *Oryctolagus cuniculus cuniculus* (Branco et al., 2000; Carneiro et al., 2010). Only the *O. c. algirus* subspecies occurs in Continental Portugal (Branco et al., 2000; Delibes-Mateos et al., 2023; Díaz-Ruiz et al., 2023). As a result, this text will specifically refer to the Iberian rabbit, the common name of the *O. c. algirus* subspecies (Mira et al., 2023).

Given the fundamental role of the Iberian rabbit in Mediterranean ecosystems, its scarcity is a major concern. It acts as an ecosystem engineer (Jones et al., 1994; Gálvez et al., 2008), altering vegetation structure through grazing and seed dispersal, and providing refuge for other animal species that use its warrens (Willot et al., 2000; Gálvez-Bravo et al., 2009; Dellafiore et al., 2010; Bobadilla et al., 2023). Furthermore, the rabbit holds great significance as a game species in the Iberian Peninsula, where hunting holds high socio-economic importance (Villafuerte et al., 1998; Paixão et al., 2009). However, its primary contribution lies in being the main prey for numerous avian and mammalian predators, including endangered species like the Iberian lynx (*Lynx pardinus*) and the Spanish imperial eagle (*Aquila adalberti*) (Delibes and Hiraldo, 1981; Delibes-Mateos et al., 2008a). Consequently, efforts to reinforce rabbit populations are commonly incorporated into predator conservation programs (Moreno et al., 2004; Guil et al., 2014a; Carro et al., 2019).

While successful rabbit restocking programs exist, even in areas where the species was absent, despite suitable habitat (Villafuerte et al., 2008; Guil et al., 2014a), this outcome is unusual. There is an ongoing debate among hunters and conservationists concerning the effectiveness and high economic costs of restocking (Ferreira and Delibes-Mateos, 2010; Guerrero-Casado et al., 2013a; Carro et al., 2019).

Releasing animals into a new habitat can be challenging and often results in high failure rates, especially during the first few days after release (Calvete et al., 1997; Letty et al., 2002; Calvete and Estrada, 2004; Rouco et al., 2010). Early mortality can occur due to transportation and handling stress, adjustment to the new environment, exposure to local viruses and diseases, and predation (Calvete et al., 1997; Letty et al., 2000; Letty et al., 2002; Cabezas et al., 2011). Furthermore, this action presents significant risks to the resident population, including the possibility of sanitary or genetic contamination (Delibes-Mateos et al., 2008c).

Restocking failures often occur due to inadequate planning, which violates critical assumptions necessary for implementing proper management (Calvete et al., 1997; Calvete and Estrada, 2004; Guerrero-Casado et al., 2013a). Despite available information on game management and restocking, many hunting estates, especially those without a game manager, still carry out unplanned restocking operations (Machado et al., 2017).

For successful rabbit restocking, careful planning of all restocking phases is essential. This involves selecting a donor population genetically similar to the native population (Delibes-Mateos et al., 2008c) and individuals in good body condition. Additionally, it is crucial to establish strict guidelines for transportation, handling, and vaccination to minimise initial stress on the rabbits, which can affect their physiological condition (Cabezas and Moreno, 2007), increasing vulnerability to predation or diseases.

Based on practical research, protocols have improved, highlighting good practices and suggestions to increase restocking success. For instance, restocking should only be considered after ensuring the species' habitat requirements are fulfilled, promoting the rapid adaptation of the population relocated to the release area (Moreno and Villafuerte, 1997; Cabezas and Moreno, 2007; Cabezas et al., 2011; Guil et al., 2014a).

Rouco and colleagues (2010) argued that it is important to prevent short-term dispersal. This is usually achieved by releasing the animals in fenced areas that serve as quarantine or acclimation sites. Doing so allows the animals to adapt to the new environment immediately after release when they are most vulnerable. This reduces post-release stress and ensures immediate access to vital resources such as shelter, food, and water, and protection against predation (Calvete and Estrada, 2004; Rouco et al., 2008; Rouco et al., 2010; Cabezas et al., 2011; Machado et al., 2017).

A long acclimation period increases the initial breeding stock and overall restocking viability (Letty et al., 2008; Rouco et al., 2010). Restocking programs should also consider other factors such as release timing, sex ratio, and rabbit age (Cotilla and Villafuerte, 2007; Guerrero-Casado et al., 2013a).

Several authors studied the survival and dispersal of restocked rabbit populations in the short term (Letty et al., 2002; Calvete and Estrada, 2004; Letty et al., 2008; Rouco et al., 2010; Machado et al., 2017). However, the behaviour of a restocked rabbit population in the medium and long term after an extended confinement period is poorly understood (Guerrero-Casado et al., 2013a).

We carried out an Iberian rabbit restocking in southern Portugal. We considered various factors, as described in the literature, that promote the success of rabbit restocking. The primary aim of this work is to assess the survival and space use of a rabbit population released in a restocking park, a semi-natural enclosure.

Specifically, we aimed to answer the following questions:

1. How did the survival rate of the restocked rabbits vary over time? Were there differences in the survival of males and females, rabbits released in warrens versus rabbits released in the shrubs, and rabbits that died due to predation or other causes? We expect higher mortality during the first few days after restocking, due to stress or predation (Calvete et al., 1997; Letty et al., 2000; Letty et al., 2002), as rabbits explore the new environment. Additionally, due to the same reason, we expect higher mortality rates among dispersing animals after the passages are opened. We predict a higher mortality rate for rabbits released in the shrubs than those released in warrens because the former are expected to have higher mobility to find an adequate place to settle (Kolb, 1991). We expect a higher mortality rate in males than females due to males' greater locomotor activity (Donázar and Ceballos, 1989). During the breeding season, male aggression intensifies as they compete for and maintain high social ranks (von Holst et al., 1999).
2. Did the sex of the rabbits, the type of release location, and the time since restocking (before or after the opening of the restocking park passages) influence the mean and maximum distances travelled from the released sites (rabbits' dispersion), and home range and core area sizes? We anticipate that male rabbits would travel longer distances to explore the territory, leading to larger home ranges than females (Parer, 1982). We predict rabbits released in warrens would adjust more quickly and travel shorter distances, resulting in smaller home ranges and core areas than those released in shrubs. Warrens are fundamental

for rabbit populations, providing refuge from predators and extreme climatic conditions, and playing a key role in rabbit reproduction and establishing social ties (Parer and Libke, 1985; Kolb, 1991). Additionally, we hypothesise that, after the passages are opened, the rabbits would travel longer distances from the release site and have bigger home ranges and core areas, assuming some rabbits would disperse and explore the habitat outside the restocking park.

4.2. Materials and methods

4.2.1. Study area

We conducted the study in a hunting estate in Monchique Natura 2000 Special Conservation Area (SAC) (PTCON0037) (Regulatory Decree n. º 1/2020 of 16th March), Southwest Portugal (37° 16’ 33’’ N, 8° 29’ 27’’ W) (Figure 4.1). The weather is characteristic of Mediterranean climates (Rivas-Martinez and Loidi, 1999), with minimum and maximum mean temperatures of 5.6°C and 11.6°C in winter (January), and 17.3°C and 24.0°C in summer (July). Annual rainfall averages 925.5mm (Monchique, 1984 – 2022; SNIRH, 2023). The relief is undulating, with altitudes ranging from 30 to 180 m above sea level (CNA, 1982), and the soils are poor, mainly dominated by incipient soils (IHERA, 1999). The landscape is largely dominated by dense Mediterranean shrubs, occupying about 75% of the area, but eucalyptus (*Eucalyptus globulus*) plantations and agricultural fields (mostly cereal crops and orchards) can also be found, the latter ones, in the valley of the Odelouca river. Previous surveys indicated the presence of Iberian rabbits in the area, with scattered and low-density populations.

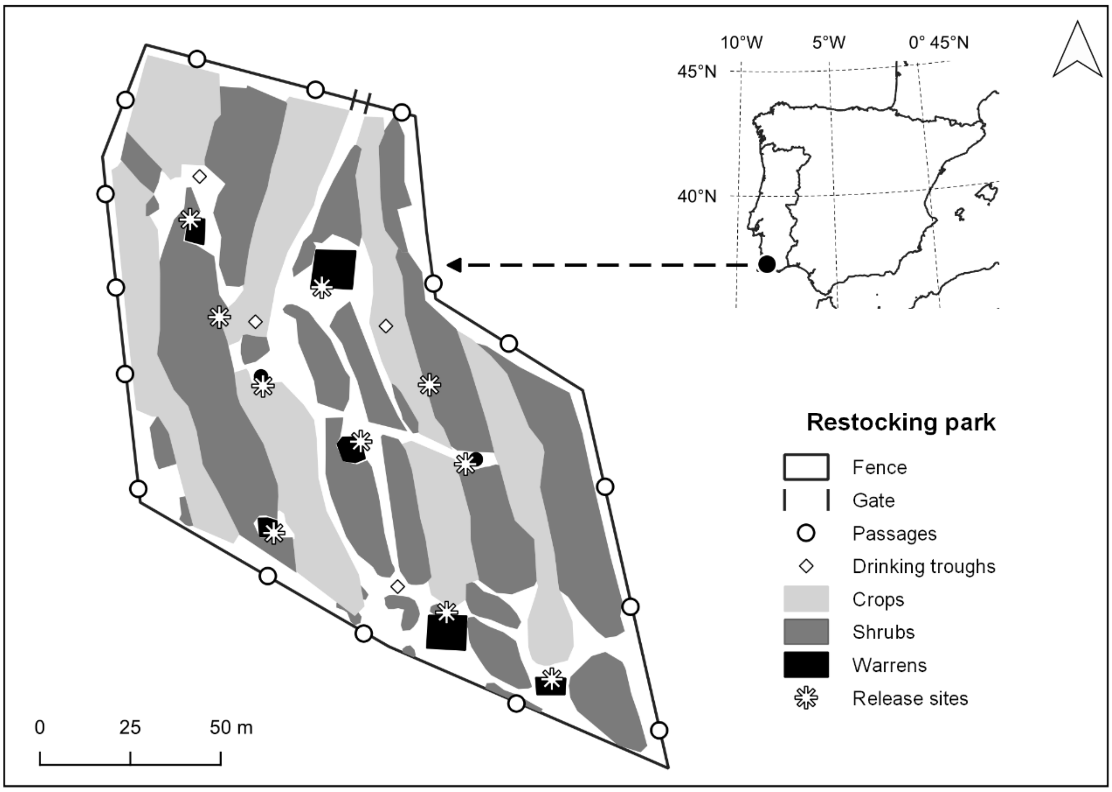

Figure 4.1 Location and schematic representation of the restocking park in Southern Portugal. The release sites of the restocked rabbits are also marked.

4.2.2. Restocking park, a semi-natural enclosure

We built a 1.7-ha restocking park to acclimate the restocked rabbits and prevent the entry of terrestrial carnivores (Figure 4.2). A wire fence with a simple mesh of 40mm, 1.8m high, and 50cm buried underground in an "L-shape" delimited the park (Figure 4.2b). This first fence was reinforced at the base with a second fence, 1m high (15mm mesh), with 50cm below ground to prevent rabbits from getting through. Also, on top of the fence, we added four lines of barbed wire. Under the fence, we installed 16 passages, made of plastic tubes 12.5cm in diameter, to allow rabbit dispersion to the surrounding area (Figure 4.2c).

No measures were taken to exclude aerial predators since the restocking was incorporated in the "Compensatory measures and specific monitoring of the Odelouca's Bonelli eagle couple, arising from the environmental impact assessment process of the Sines-Portimão high-voltage power line" project (REN et al., 2009).

Inside the fenced park, we ensured food, shelter, and water availability (Figures 4.1 and 4.2a). We alternated patches of herbaceous crops, a mixture of Leguminosae and Graminae (food), and patches of Mediterranean shrubs (shelter) and we installed four drinking troughs (water). Additionally, we built eight uniformly spaced (as much as possible) warrens, to increase the availability of shelter and breeding sites. We built four different types of man-made warrens, two of each: logs, Mayoral® – registered trademark, pallets, and tubes.

Figure 4.2 Restocking park limits (a; white line), fence (b) and passages (c).

4.2.3. Rabbit release protocol

We conducted the restocking on 28th October 2007, using adult Iberian rabbits from a certified national breeder, who kept the animals in a semi-natural regime, *i.e.* living outside in enclosures but with food supplementation. We chose a breeder within the natural distribution area of the subspecies *O. c. algirus* (approximately 160 km from the study area) to ensure genetic similarity to the native populations (Branco et al., 2000; Carneiro et al., 2010). Before travelling, the rabbits were fed and vaccinated against rabbit haemorrhagic disease (RHD) and myxomatosis.

Rabbits were transported overnight and arrived at the enclosure at sunrise (e.g., Machado et al., 2017), to minimise the effects of thermal stress, during animal transportation, manipulation and release. Additionally, releasing the rabbits early in the day, when they are less active and more likely to be resting, reduces their movement as they acclimate to their new environment in the initial hours after release. This makes them less vulnerable to stress and predation (Letty et al., 2008).

We conducted a clinical examination of all the animals before their release into the restocking park, ensuring that only healthy rabbits were released. A total of 75 Iberian adult rabbits were released, consisting of 19 males and 56 females, resulting in a sex ratio of 1:2.9. With this sex ratio, we intended to promote the formation of initial family nuclei with enough females for males, thereby minimising the risk of conflicts arising from competition for recruiting females for reproduction (von Holst et al., 2002).

Each rabbit was weighed, sexed, subjected to internal and external deworming, and identified by a small, numbered metal tag placed in the left earflap. We performed all the procedures as quickly as possible to minimise the stress due to handling. A veterinary team oversaw all procedures, ensuring compliance with Portuguese legal regulations. All actions were done following the guidelines of the American Society of Mammalogists for the use of wild mammals in research (Gannon et al., 2007), and the guidelines for the treatment of animals in behavioural research and teaching (ASAB/ABS, 2006) and with the authorisation of the Portuguese Conservation Agency (ICNF).

We then released the rabbits in 10 locations inside the restocking park: inside each of the eight warrens and in two randomly selected locations in shrub patches (Figure 4.1).

At each location, we released groups of 5-8 individuals, maintaining approximately the same ratio of male/female.

To enhance rabbit survival during the initial weeks following restocking, we confined the rabbits within the fenced park by keeping the passages closed. This acclimation period allowed the animals to adjust to the new environment before dispersing into the surroundings (Machado et al., 2017).

Initially, we planned an acclimation period of about four weeks. However, due to insufficient rain for the growth of autumn crops inside and outside the restocking park, we decided to postpone the opening of the passages. Throughout this period, we provided water (see Figure 4.1) and occasionally offered supplementary food (cereal seeds) near the four drinking troughs.

On 8th January 2008, after a confinement period of 72 days, we opened the enclosure passages to facilitate the natural dispersal of rabbits into adjacent areas following their acclimation to the new habitat.

4.2.4. Rabbit survey by radio-tracking

Out of the 75 rabbits released, we randomly selected 22 (11 males and 11 females), approximately 30% of the total released. These rabbits had radio transmitting collars (model: lpm-2,700; weight ≈ 25g; Wildlife Materials, Inc., USA). The collars were designed to add no more than 5% of the animal's weight and to ensure no significant additional energetic costs (Wilson et al., 1996; Sikes et al., 2011). We considered the population wearing radio collars a representative sample of the entire population. The collars had an activity sensor, which generated a different pulse rate after 4 hours of inactivity, ensuring we registered only locations of live rabbits. We released two radio-tagged individuals (one male and one female) in each warren, and three in two randomly selected locations in the shrub patches (one male and two females in one location, and two males and one female in the other).

Monitoring occurred between 30th October 2007 (two days after restocking to allow rabbits to recover from transportation and handling stress; Teixeira et al., 2007), and

24th April 2008. We located the animals daily during the first two weeks after restocking and the first five weeks following the opening of the passages and about three times a week during the rest of the monitoring period.

For each animal, we evenly surveyed six different 4-h radio-tracking intervals covering a complete 24-h cycle (00:00–04:00, 04:00–8:00, 08:00–12:00, 12:00–16:00, 16:00–20:00, 20:00–00:00 hours), so that specific daily patterns of activity would not bias radio locations (Villafuerte et al., 1993). Each tracking session started at least 12 hours after the previous session to minimise autocorrelation in the radio-tracking data.

We used a TS–1 receiver (Telonics, Telemetry – Electronics Consultants, USA), and an external 3-element Yagi directional antenna (Wildlife Materials, Inc., USA) for tracking. The transmitters operated within the 150–152 MHz frequency range. During each tracking session, we first located each radio-collared rabbit using the homing method. As we approached within about 10 to 15 meters, we conducted multiple triangulations. This approach aimed to minimise any disturbance to the rabbits and reduce the margin of error for each location, which could increase if we relied solely on triangulation from a greater distance. A positioning measurement was recorded at each radio location using a handheld GPS. We monitored each radio-collared rabbit until its death or until the end of the battery life of the transmitter. The average duration of the monitoring period per animal was (±SE) 77.4 ± 14.8 days (range: 1–179).

Concerning survival analysis, when a collar emitted a signal of inactivity, the technician searched for the animal and identified the presumed cause of death. We also regularly checked the enclosure and the surroundings for signs of dead rabbits such as carcasses, body parts, ear tags, or tufts of hair. Whenever possible, the carcasses were collected and subjected to veterinary exams to determine the specific cause of death. We categorised the cause of death as predation or other causes. Other causes included dead rabbits with no visible signs of predation, non-recovered carcasses inside warrens, or other unknown reasons. Animals found dead on the nth day after release were considered to have survived n−1 days (Rouco et al., 2010).

4.2.5. Statistical Analysis

4.2.5.1. Survival

We calculated the finite survival rate by dividing the number of individuals alive at the end of the monitoring period by the number of individuals alive at the beginning.

We estimated survival rates for rabbits during the monitoring period with the Kaplan–Meier product limit estimator. This non-parametric technique shows the probability of survival over time (Pollock et al., 1989). Additionally, 95% confidence intervals were computed. We estimated the survival curves for the entire population, and separately for males and females, for rabbits released in warrens and rabbits released in shrubs, and for rabbits that died due to predation or other causes. We used a non-parametric log-rank test to compare survival curves between these pairs of groups. This test compares survival probabilities between two groups, with the null hypothesis stating that the survival functions of the groups being compared do not differ.

We conducted the analysis using the “survival” package (Therneau, 2023) in R software version 4.2.3 (R Core Team, 2023).

4.2.5.2. Space use

We used radio-tracking data to calculate four space use indicators for each rabbit: maximum distance travelled from the release point, mean distance travelled from the release point, home range, and core area. The maximum distance travelled is the Euclidean distance from the release point to the furthest recorded point, while the mean distance travelled is the average Euclidean distance of all locations of each rabbit from the release point (Moreno et al., 2004; Machado et al., 2017). Home range and core area sizes were determined using 95% and 50% minimum convex polygons, respectively (MCP; Mohr, 1947).

Only one rabbit dispersed from the restocking park to the surrounding area. Given the small sample size, we included this rabbit in the analysis. However, we omitted all its locations recorded outside the restocking park, focusing the analysis on the rabbit population within the restocking park.

We chose to use Minimum Convex Polygons (MCPs) for several reasons (Harris et al., 1990; Hemson et al., 2005; Devillard et al., 2008; Ziege et al., 2020):

1. They are typically more robust when the number of locations is small.
2. They are less affected by location density than Kernel or the k-nearest neighbours convex hull methods. Since rabbits inhabit holes, multiple relocations may occur at the same place, potentially causing a lack of convergence in the smoothing parameters.
3. MCPs have also traditionally been the most common metric used in home range studies, allowing for easier comparisons with other studies.

In this case, we estimated a 95% MCP instead of a 100% MCP. We based this decision on the fact that MCPs are highly sensitive to the most extreme locations in space (Burgman and Fox, 2003). By excluding 5% of extreme locations, we improve the standardisation in animal home range calculations. These extreme locations are believed to be more related to the dispersal or exploratory movements of the animals rather than the regular movements that typically define animal home ranges (Harris et al., 1990).

The minimum number of fixes needed for reliable home range estimation was determined by analysing incremental-area plots (Odum and Kuenzler, 1955; Harris et al., 1990; Kenward, 2001) using R software version 4.2.3 (R Core Team, 2023). We considered the number of locations satisfactory for MCP estimation when the relationship between MCP percentages of the total area and the number of fixes reached an asymptote. This refers to the point at which additional locations result in a minimal increase in range size. Defining where asymptotes begin and determining the number of locations required is subjective, so we adopted a criterion of less than a 10% increase in the area to identify the asymptote (e.g., Hayward et al., 2009; Plotz et al., 2016). We only included rabbits with enough locations above this threshold for further analysis.

We used incremental-area plots to estimate the average number of days it took for the rabbit home ranges to stabilise after restocking.

For each of the four space-use indicators, we computed three values for each animal: one for all the locations acquired during the monitoring period, and two by dividing the locations obtained before and after the opening of the passages.

Distance indicators were calculated using QGIS (QGIS Development Team, 2023), and area indicators were determined in R software version 4.2.3 (R Core Team, 2023) using the “adehabitatHR” package (Calenge, 2006).

Due to the small sample size, we used non-parametric statistical tests to compare the space use indicators, determined for the entire monitoring period, for male and female rabbits, and rabbits released in shrubs versus those released in artificial warrens. We employed the Two-sample Mann-Whitney U test for independent samples for this comparison. For the same reason, we compared the space use indicators for locations registered before and after the opening of the passages using the non-parametric Wilcoxon signed-rank test for related samples.

We also evaluated rabbit site fidelity in QGIS by calculating the percentage of overlap between the home ranges and core areas of each rabbit in two different periods: before and after the opening of the passages (Jerosch et al., 2017; Wereszczuk and Zalewski, 2019). The percentage overlap was determined using the formula $(A_{ij}/A_i) \times 100$ where A_{ij} represents the area of overlap between the areas at time i (before) and time j (after), and A_i represents the area in time i (before the opening of the passages) (Jerosch et al., 2017).

4.3. Results

Throughout the study, we recorded 864 rabbit radio locations. On average, each rabbit had 39.1 ± 7.4 locations (range: 1–89). The tracking period for each rabbit varied from 2 to 179 days, with an average of 77.4 ± 14.8 days (Table 4.1).

Table 4.1 Details of the 22 radio-tracked rabbits. For each rabbit, we provide detailed information about sex, release site, number of locations, number of tracking days, rabbits that stabilised home ranges (HR, marked with x), and rabbits with enough locations before and after the opening of the restocking park passages (marked with x).

Rabbit ID	Sex	Release site	Nº of locations	Nº of tracking days	Death cause	Stable HR	Before and after locations
1	Male	Warren	3	6	Other		
2	Male	Warren	25	55	Other	x	
3	Female	Warren	7	10	Predation		
4	Male	Warren	1	3	Predation		
5	Female	Warren	18	37	Predation		
6	Male	Warren	26	62	Predation		
7	Male	Shrubs	84	177	-	x	x
8	Male	Warren	80	163	-	x	x
9	Male	Warren	5	8	Predation		
10	Female	Shrubs	1	2	Other		
11	Female	Warren	12	17	Predation		
12	Female	Shrubs	87	179	-	x	x
13	Female	Warren	28	71	Predation	x	
14	Female	Warren	89	179	-	x	x
15	Female	Warren	32	75	Other	x	
16	Male	Warren	87	174	-	x	x
17	Female	Shrubs	81	174	-	x	x
18	Male	Warren	25	52	Other		
19	Female	Shrubs	83	170	-	x	x
20	Male	Shrubs	12	22	Predation		
21	Female	Warren	1	3	Predation		
22	Female	Warren	77	64	-	x	x

4.3.1. Survival

During the monitoring period, we documented 14 mortality events (Table 4.1). Only eight of the 22 radio-collared rabbits survived (four males and four females), representing an overall finite survival rate of 36.4%.

Predation was the main cause of death. Of the 14 rabbits found dead, nine exhibited signs of predation (64.2%), particularly by birds of prey (Calvete et al., 1997; Lombardi et al., 2003). Indeed, during the monitoring period and near the restocking park, we heard vocalisations of a Eurasian eagle owl (*Bubo bubo*), and we found feathers and regurgitated pellets of this species with metal tags identical to the ones we placed on the rabbits' earflap. Additionally, we found two radiotelemetry collars near a Eurasian eagle owl nest, located about 250m away from the restocking park. The remaining five rabbits died from other causes, two of them during the first week after restocking and three between the middle of December 2007 and the middle of January 2008.

Additionally, we found eight more carcasses or body parts of rabbits (six females and two males) within the restocking park. All were from the individuals we released, and all occurred within the first three weeks after restocking. Four of these carcasses showed signs of predation, while the other four rabbits died from different causes during the initial week after restocking.

The veterinary team conducted a lab examination on the six carcasses showing no signs of predation, found in the first week after restocking and including two radio-collared rabbits. The results revealed that the cause of death may be related to a severe parasite infection, including Helminth (Cestoda, Nematoda) and coccidian.

Regarding rabbits that died more than a month after restocking, lab results revealed that both radio-collared males died of hyperparasitism. As for the other rabbit, despite necropsy examinations suggesting sudden death due to intoxication, the veterinary team remained unable to determine the exact cause of death.

We found no evidence of death caused by myxomatosis or rabbit haemorrhagic disease during the monitoring period.

Survival probability for this population stabilised 74 days after restocking (Figure 4.3). The estimated median survival time was 57.5 days, which means that on average, 50% of the population had died by that point. The probability of survival beyond 74 days was 35.4% (95% CI = 19.9% - 62.9%). Assuming the radio-collared population is representative of the total restocked population, we can estimate there were approximately 27 rabbits alive (75x0.354=26.6; 95% CI = 14.9 – 47.2 rabbits) at the end of the radiotelemetry, out of the 75 restocked.

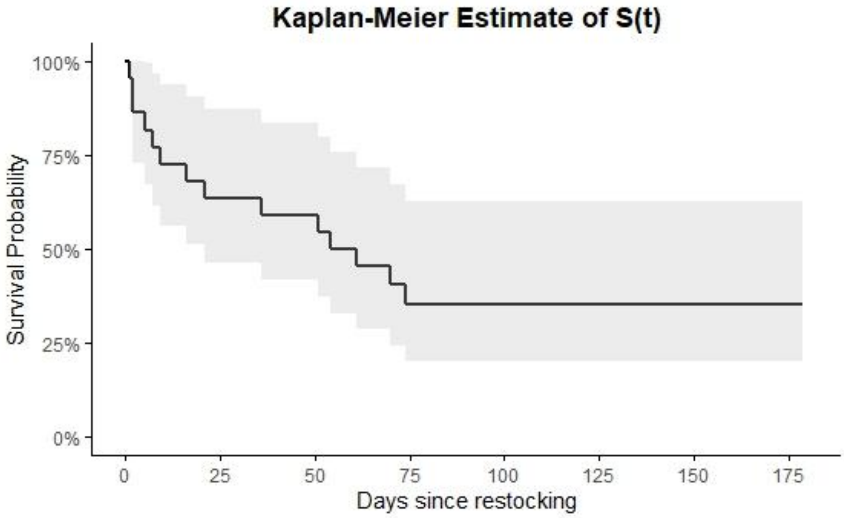

Figure 4.3 Restocked rabbit survival probability curve during radio tracking, in a semi-natural enclosure, based on Kaplan-Meier estimate, with a 95% confidence interval.

We found no significant differences in survival rates between females and males (p=0.653; Figure S4A.1, Supplementary information 4A) or between rabbits released in a warren and rabbits released in shrubs (p=0.151; Figure S4A.2, Supplementary information 4A). Furthermore, we have no evidence to suggest survival rates differ between rabbits that died due to predation or other causes (p=0.484; Figure S4A.3, Supplementary information 4A).

4.3.2. Space use

Eleven rabbits stabilised their home ranges (Table 4.1). On average, this restocked population stabilised home ranges in 96.364 ± SE 12.615 days.

Only 8 rabbits had enough locations to compute space use indicators before and after the opening of the passages (Table 4.1). Before and after core areas overlapped on average 39.503 ± SE 14.143% (n=8), and home ranges overlapped on average 69.709 ± SE 8.578% (n=8).

Regarding space use indicators, the mean maximum distance travelled and the mean distance travelled were 81.304 ± SE 8.097 m (n=11) and 40.289 ± SE 5.420 m (n=11), respectively. Rabbits’ home range size was on average 0.228 ± SE 0.037 ha (n=11), and rabbits' core area size was on average 0.055 ± SE 0.009 ha (n=11). We found no significant differences in space use indicators between males and females.

Only the core areas, determined for the entire monitoring period, of rabbits released in artificial warrens were significantly smaller (p=0.042) than those released in shrub patches (Figure 4.4, Table S4A.1, Supplementary information 4A). The average core area of rabbits released in warrens was less than half the size of those released in shrubs (warrens - 0.040 ± 0.009 ha, n=7; shrubs - 0.082 ± SE 0.012 ha, n=4).

Maximum distance travelled was the only space use indicator significantly higher (p=0.023) after the opening of the restocking park passages. Before the opening of the passages, the maximum distances travelled by rabbits from their release site were on average 76.280 ± SE 5.016 m (n=8), and after the opening of the passages, 93.190 ± SE 5.871 m (n=8) (Figure 4.5, Table S4A.2, Supplementary information 4A).

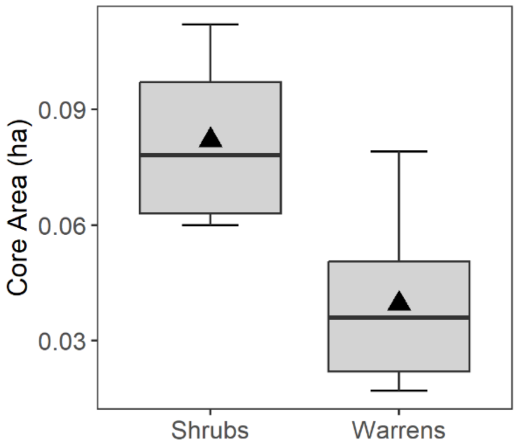

Figure 4.4 Core area size (50% minimum convex polygon) of the restocked Iberian rabbits, determined for the entire monitoring period, according to the type of site they were released, shrubs, or warrens. In each boxplot of the graph, the triangle is the mean, and the darker horizontal line is the median. The length of the box represents the interquartile range (i.e., the difference between the 75th and 25th percentiles). The dots outside the whiskers are outliers.

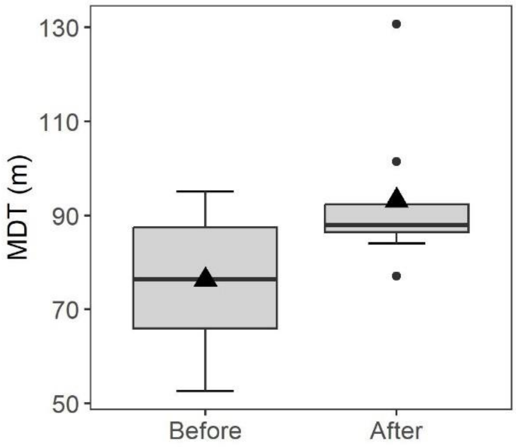

Figure 4.5 Maximum distance travelled (MDT) by the restocked Iberian rabbits, before and after the opening of the restocking park passages. In each boxplot of the graph, the triangle is the mean, and the darker horizontal line is the median. The length of the box represents the interquartile range (i.e., the difference between the 75th and 25th percentiles). The dots outside the whiskers are outliers.

4.4. Discussion

In the southern regions of Europe, conservationists and hunters often invest in rabbit restocking or translocation to areas where their numbers are declining. However, these efforts are sometimes unsuccessful (Calvete et al., 1997; Letty et al., 2002) and require significant economic costs (Ferreira and Delibes-Mateos, 2010). Therefore, it is essential to assess all aspects of restocking efforts to maximise their effectiveness.

Furthermore, most studies involving rabbit restocking or translocations tend to concentrate on the first few weeks after the animals are released (e.g. Letty et al., 2002; Letty et al., 2003; Calvete and Estrada, 2004; Rouco et al., 2008; Rouco et al., 2010) and available data on the long-term outcomes for the restocked rabbits are scarce (e.g., Cabezas et al., 2011; Machado et al., 2017; Tobajas et al., 2021).

In this study, we assessed the long-term outcomes by monitoring the survival and space use of an Iberian rabbit population released in a restocking park, a semi-natural enclosure, for six months. In this permanently enclosed area, surrounded by a fence, released rabbits could roam freely, and the habitat closely resembled the surrounding environment. The purpose of the enclosure was to facilitate rabbit settlement by reducing mortality from terrestrial predators and post-release stress, particularly during acclimation. Additionally, the restocking park aimed to establish a local breeding core of rabbits that expands naturally to the surrounding areas (Rouco et al., 2008; Guerrero-Casado et al., 2013b).

We implemented the rabbit restocking protocol, considering important issues that contribute to the success of rabbit restocking. For example, we ensured the restocking park fulfilled the habitat requirements for the species, namely, in terms of food, shelter and water (Cabezas and Moreno, 2007; Letty et al., 2008), selected a donor population genetically close to the native rabbit populations (Delibes-Mateos et al., 2008c), established strict guidelines for transportation, handling, and vaccination, and implemented a soft-release protocol with a long confinement period (Rouco et al., 2010).

Our findings should be interpreted cautiously due to the limitations of this study and cannot be extrapolated to natural populations. Our research was confined to a single restocking park, with only 1.7ha, which may influence rabbit movements and home ranges. Moreover, the limited number of rabbits could increase the risk of statistical errors, particularly when the sample is divided to make subgroup comparisons. Grouping the data could increase statistical power, allowing for more robust and reliable conclusions. However, we could risk losing statistically relevant distinctions between subgroups, such as those we attained.

Nevertheless, our results provide meaningful preliminary insights, highlighting important issues to consider for enhancing the success of rabbit restocking programs.

We found that rabbit survival was globally low, and that space use only presented punctual differences among rabbits released in shrubs and warrens and between before and after the opening of the restocking park passages.

4.4.1. Survival

Despite implementing a restocking protocol that included measures known to enhance restocking success, and the Iberian rabbits being released in a semi-natural enclosure, at the end of the monitoring period (179 days), only eight out of the 22 radio-tagged rabbits survived, reflecting a finite survival rate of 35.4%.

This survival rate aligns with findings from several studies on rabbit restocking, including those by Letty et al. (2002), Drees et al. (2009), and Tobajas et al. (2021). However, in these studies, rabbits were released in unfenced areas without undergoing a quarantine period before release. Calvete and colleagues (1997) also found similar survival rates. In their study, the rabbits were released in unfenced areas after a two-week confinement period.

On the other hand, other studies, where rabbits also underwent a period of confinement before release, but were released in open areas, contrary to our study, estimated higher survival rates. Moreno and colleagues (2004) evaluated the success of introducing rabbits for predator conservation in Spain. After a 90-day study period, researchers reported survival rates between 70% and 78% for the introduced rabbits, depending on the season in which they were restocked. Rouco and colleagues (2010) estimated a survival rate between 79% and 87% in a study aiming to assess the effect of different confinement periods on the survival of translocated rabbits. However, the authors only monitored the radio-collared rabbits for 10 days.

The survival rates stabilised 74 days after restocking, immediately after the opening of passages on the 72nd day. We had anticipated increased mortality of dispersing animals after the opening of passages, but the results do not support this. This outcome, combined with limited dispersion, suggests the surviving animals have adapted well to the habitat in the restocking park. In this respect, the enclosure partially fulfilled its purpose.

Based on field observations, we found radio-collared rabbits primarily died due to predation by birds of prey, most likely caused by a Eurasian eagle owl (*Bubo bubo*). We believe the sudden release of many rabbits in the small area of the restocking park attracted the owl, leading it to kill more rabbits than needed. This type of behaviour is known as multiple predation or surplus killing (Short et al., 2002). Other authors observed similar predator behaviour following rabbit translocations (Calvete et al., 1997; Moreno et al., 2004; Cabezas et al., 2011; Guerrero et al., 2013b). We found no signs of predation by terrestrial mammal carnivores, suggesting the structure of the restocking park fence was robust enough to prevent the entry of carnivorous mammals.

In the first few weeks after restocking, the mortality rate of rabbits due to causes other than predation, which are usually associated with induced stress (Calvete et al., 1997; Letty et al., 2000; Letty et al., 2002), was relatively low. We only observed two deaths among the radio-collared rabbits in the first week, representing 9.1% of the radio-collared population. Other studies have also reported low rabbit mortality rates due to stress, which were lower than the mortality rates caused by predation (Calvete et al., 1997; Calvete and Estrada, 2004; Drees et al., 2009). We believe the transport and handling methods were appropriate, and the requirements for the animals to acclimatise were met within the enclosure, which helped minimise post-release stress.

The veterinary analysis showed these two rabbits died due to severe parasite infections, even though the initial exams performed on the 1st day after restocking confirmed the low degree of parasitic infection of the animals. This confirms that stress can cause strong immunosuppression in rabbits, making them vulnerable to developing severe parasitism even from low initial infections (Letty et al., 2000).

After these first few weeks of restocking, an additional three rabbits were found dead without any signs of predation. These late deaths cannot be attributed to adaptive stress since they occurred after a considerable amount of time had passed. Post-mortem examinations were conducted, and the veterinary team was unable to determine the exact cause of death for one of the rabbits. However, lab results confirmed that the other two rabbits, both males, died due to hyperparasitism. There could be several reasons behind this diagnosis. One possible cause is the absence of basic nutritional requirements within the restocking park. As mentioned earlier, in the year of the restocking, the lack of rain caused a delay in the germination of crops, both inside and outside the restocking park. Although we occasionally provided supplementary food during acclimation, its quantity and quality may have been insufficient. The shortage of green biomass, rich in nutrients and water content, could have weakened some individuals (Dudzinski and Mykytowycz, 1960; Alves and Moreno, 1996). This could have made them more susceptible to parasitism, leading to mortality even outside the critical period of adaptation (Villafuerte, 1994; Reglero et al., 2007). Increased parasitism may also be caused by intraspecific aggression associated with male social interactions during the reproductive season (von Holst et al., 1999). During this time, the stress caused by the high rabbit concentration inside the restocking park, with rabbits competing for territory and mating partners, can weaken their immune systems and make them more susceptible to parasitic infections (von Holst et al., 1999).

We initially expected that males would have a higher mortality rate than females. However, our results did not support this hypothesis. Several authors also noted the absence of differences between sexes in survival after release (Calvete et al., 1997; Letty et al., 2003; Calvete and Estrada, 2004). Furthermore, our results revealed no significant difference in the survival rates of rabbits that died due to predation and those that died from other causes.

Although the mortality rate of rabbits released in shrubs was not significantly higher than that of those released in warrens, we observed a slight tendency for higher survival rates in rabbits released in artificial warrens (Figure S4A.2, Supplementary information 4A). Warrens are essential in maintaining healthy rabbit populations as they serve as breeding sites and provide refuge from predators (Parer and Libke, 1985; Kolb, 1991). Natural burrows are challenging to excavate in the study area due to the rocky and hard soil (IHERA, 1999). Therefore, we believe the rabbits released in shrubs exhibited more ranging behaviour to find a suitable refuge, making them vulnerable to predation. On the other hand, rabbits released into warrens settled within them and had less need to explore the area.

4.4.2. Space use

The radio-collared rabbits stayed inside the restocking park, except for one male rabbit who dispersed and settled about 200 meters north of the release location. We believe the carrying capacity of the restocking park was not reached due to the mortality that occurred before the passages were opened. As a result, the surviving rabbits established themselves within the park without feeling compelled to explore the nearby areas. Right after restocking, rabbit density within the park was high, at 44 rabbits per hectare. By the end of the monitoring period, considering the final survival rate of the radio-tracked rabbits, we estimated a density of 16 rabbits per hectare. This estimate does not account for the number of rabbits entering or leaving the park, nor the number of newborn rabbits, since we were unable to accurately estimate those numbers.

Rabbits took about 90 days to stabilise their vital areas, in contrast to the 8.3 days reported by Moreno and colleagues (2004). This delay may have been caused by factors such as a lack of nutritious food, aggressive interactions, or the pressure of predation, which can all contribute to erratic behaviour.

Rabbits' home range (HR) and core area (CA) size were relatively smaller than what is reported in the literature (e.g., HR 6.3 ha - Hulbert et al., 1996; HR 2.1 ha - Moseby et al., 2005; HR 1.2 ha and CA 0.4 ha - Devillard et al., 2008; 9.6 ha and CA 1.3 ha - Rouco et al., 2019), which is attributed to the fact that rabbits with radio collars remained within the restocking park.

After the acclimation period, the maximum distances travelled by rabbits significantly increased. However, there was a high overlap between their home ranges before and after the opening of the restocking park. This suggests the surviving rabbits settled within the park and explored the nearby areas around their home ranges when the passages were opened, instead of dispersing to other locations.

As we hypothesised, animals released within warrens had significantly smaller core areas than those released in shrubs. This indicates concentrated activity within and around the warrens. On the other hand, animals released in shrubs exhibited more ranging behaviour, which makes them more vulnerable to predation (Parer and Libke, 1985; Kolb, 1991).

Contrary to our predictions, our study found no significant differences in spatial indicators between males and females. This result aligns with the findings of Rouco and colleagues (2019), who reported similar results regarding home range and core area sizes, and Letty and colleagues (2008), who reported no difference in distance from release warrens between males and females. These findings suggest separate management measures for males and females may be unnecessary for restocking efforts.

4.4.3. Management suggestions

Based on our research findings, we believe we can make recommendations to improve rabbit restocking success in similar operations.

The fence we installed in the semi-natural enclosure prevented terrestrial predators from entering. Protection against predators, namely terrestrial, is essential to ensure the investment in restocking does not merely result in an immediate and short-term food supply for predators. Therefore, we recommend that conservationists and hunting managers involved in rabbit recovery release rabbits preferably in confined, fenced areas. This helps prevent rabbit dispersion and protects them from predation by terrestrial mammals during the initial days after release.

The enclosure effectively protected against predation by terrestrial mammals, but it failed to provide adequate protection from birds of prey. Predation by birds of prey was the main cause of rabbit mortality, especially in the first few weeks after release. We took no measures to exclude aerial predators since the restocking was part of the "Compensatory measures and specific monitoring of the Odelouca's Bonelli eagle couple, arising from the environmental impact assessment process of the Sines-Portimão high-voltage power line" project (REN et al., 2009). The results clearly showed this decision was incorrect. We believe the released rabbit population should be protected from both mammalian predators and birds of prey, at least until the animals are adapted to the new environment. Avoiding predator activity in the release area during the critical period could substantially increase rabbit survival (Calvete et al., 1997).

To prevent predation by birds of prey, a soft net could be installed to cover the top of the restocking park, especially during the acclimation period (Guerrero-Casado et al., 2013b). However, this approach may be expensive and logistically challenging to implement in large-scale restocking parks like ours. It is also advisable to avoid installing fences near large trees that could serve as perches for diurnal or nocturnal birds of prey during their hunting activities.

Considering our findings regarding space use, we recommend releasing rabbits into warrens that offer protection from predators in the most critical period (Parer and Libke, 1985; Kolb, 1991). This will help animals acclimate faster, reduce post-release stress, minimise distances to explore the new and unfamiliar environment, and ultimately decrease predation risk.

After restocking, we suggest long-term monitoring of the released rabbit population thoroughly and continuously for dispersal, mortality, and breeding success. This will allow implementing adaptive management and taking the actions needed to enhance the rabbits' survival and the overall success of the restocking effort whenever necessary.

Finally, given the limitations of our research, we acknowledge the need for future research with larger sample sizes to support the conclusions presented in the study and increase the replicability of these measures. Even though we know that the high costs associated with this type of action may always limit what can be done.

4.5. Conclusions

Our study presents findings on the survival and space use relevant to the recovery plans for the Iberian rabbit populations, based on releasing animals within a semi-natural enclosure and following specific guidelines.

We believe that our findings provide meaningful preliminary insights, even considering the local context and the limitations of this study. Our management recommendations can be applied to similar restocking programs involving the release of rabbits in semi-natural enclosures in the southern Iberian Peninsula. These results and conclusions can be helpful for game managers and conservationists, given the importance of conducting restocking efforts to help recover this declining species that plays a fundamental role in Mediterranean ecosystems.

Ethics approval

Animal transportation and handling were in conformity with Portuguese legal regulations. All applicable international, national and institutional guidelines for the care and use of animals were followed.

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Supplementary information 4A

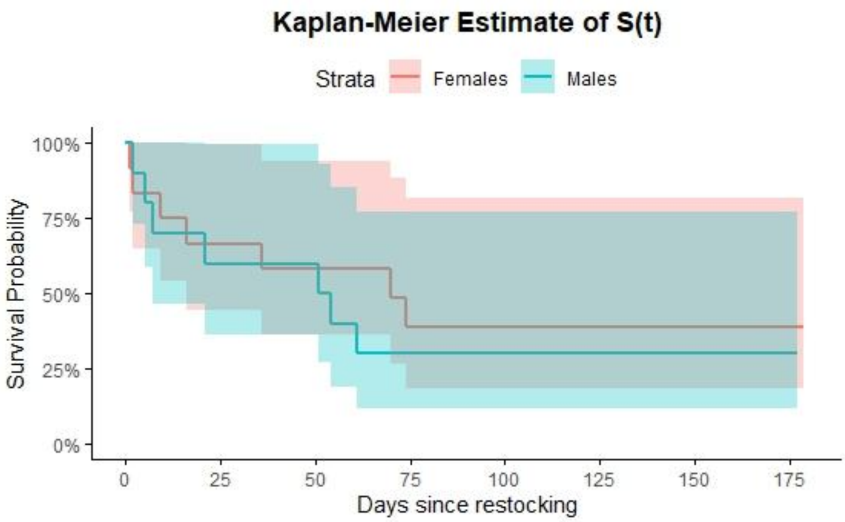

Figure S4A.1 Restocked males and females' survival probability curve during radio tracking, based on Kaplan-Meier estimate, with a 95% confidence interval.

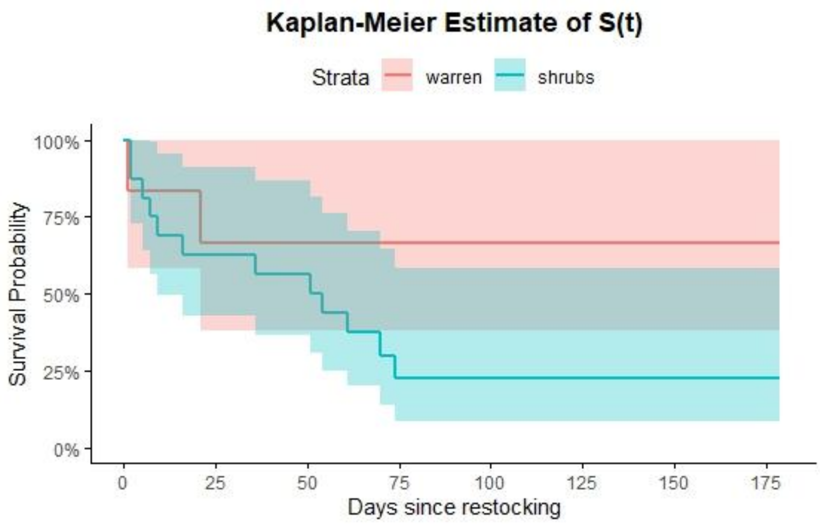

Figure S3A.2 Survival probability curves for both types of release sites, warren or shrubs, during radio tracking, based on Kaplan-Meier estimate, with a 95% confidence interval.

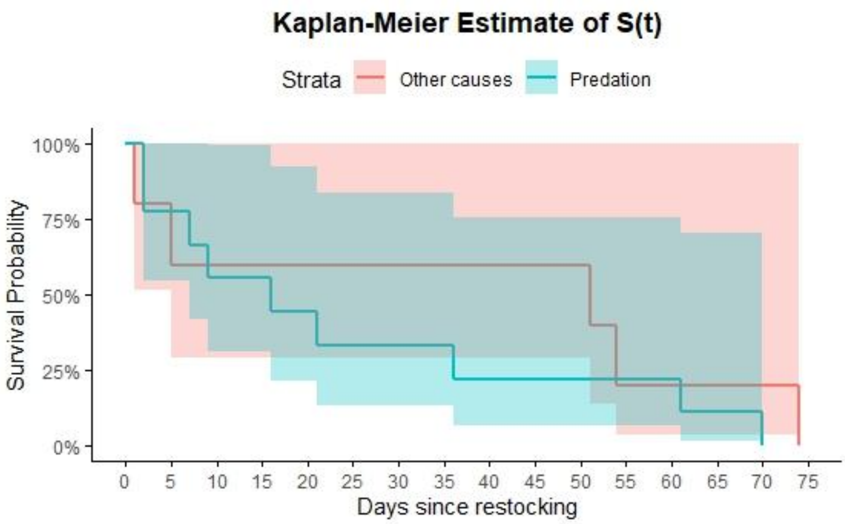

Figure S3A.3 Survival probability curves for both classes of causes of rabbit death, predation or other causes, during radio tracking, based on Kaplan-Meier estimate, with a 95% confidence interval. The length of time axis is limited to a maximum of 75 days because these survival probability curves only considered rabbits that died, and the last death was registered at day 74.

Table S4A.1 Results of the Mann-Whitney test for independent samples comparing spatial use indicators, determined for the entire monitoring period, of males and females, and of rabbits released in warrens and rabbits released in shrubs. Spatial use indicators: MDT – maximum distance travelled, DT – mean distance travelled, CA – Core area (50% minimum convex polygon), and HR – Home range (95% minimum convex polygon). * - Significant for p≤0.05

Spatial use indicator (Unit)	Classes	Mean ± SE	W	p-value
MDT (m)	Females (n=7)	79.526 ± 9.642	14.000	1.000
	Males (n=4)	84.416 ± 19.420		
	Warrens (n=7)	75.203 ± 12,947	21.000	0.230
	Shrubs (n=4)	91.981 ± 3.830		
DT (m)	Females (n=7)	39.190 ± 5.420	17.000	0.648
	Males (n=4)	42,212 ± 14.357		
	Warrens (n=7)	38.396 ±8.259	18.000	0.527
	Shrubs (n=4)	43.601 ± 7.188		
CA (ha)	Females (n=7)	0.056 ± 0.014	15.000	0.927
	Males (n=4)	0.053 ± 0.016		
	Warrens (n=7)	0.040 ± 0.009	**25.000**	**0.042***
	Shrubs (n=4)	0.082 ± 0.012		
HR (ha)	Females (n=7)	0.256 ± 0.058	18.500	0.449
	Males (n=4)	0.180 ± 0.049		
	Warrens (n=7)	0.184 ± 0.046	20.000	0.298
	Shrubs (n=4)	0.306 ± 0.046		

Table S4A.2 Results of the Wilcoxon test for dependent samples comparing spatial use indicators before and after the opening of the restocking park gates. Spatial use indicators: MDT – maximum distance travelled, DT – mean distance travelled, CA – Core area (50% minimum convex polygon), and HR – Home range (95% minimum convex polygon). * - Significant for p≤0.05

Spatial use indicator (Unit)	Classes	Mean ± SE	W	p-value
MDT (m)	Before (n=8)	76.280 ± 5.016	**2.000**	**0.023***
	After (n=8)	93.190 ± 5.871		
DT (m)	Before (n=8)	43.900 ± 5.482	14.000	0.641
	After (n=8)	46.281 ± 7.652		
CA (ha)	Before (n=8)	0.037 ± 0.009	9.000	0.447
	After (n=8)	0.053 ± 0.011		
HR (ha)	Before (n=8)	0.066 ± 0.023	7.000	0.148
	After (n=8)	0.240 ± 0.036		

Chapter 5

Selection of artificial warrens following the restocking of an endangered keystone prey

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Abstract

The European rabbit (*Oryctolagus cuniculus*) is an endangered species native to the Iberian Peninsula, playing a vital ecological role in Mediterranean ecosystems as prey for several threatened predators. Conservation efforts have been implemented to halt its decline, focusing on the Iberian rabbit subspecies (*Oryctolagus cuniculus algirus*). Many conservation programmes involve restocking and habitat management, including artificial warren construction to provide essential refuge sites. In this study, we examined the use of four types of artificial warrens (logs, Mayoral®, pallets and tubes) by a restocked Iberian rabbit population within a fenced park in southern Portugal. We investigated the factors influencing warren use, basing our analysis on faecal pellet counts at the entrances of artificial warrens. We analysed spatial and temporal patterns in warren use using a generalised additive mixed model. Additionally, we determined the efficiency of each type of artificial warren by computing the ratio between the costs of building the warren and the level of warren use by the rabbits. Our results indicate that Mayoral, tube and log warrens are significantly less used compared to pallet warrens (Logs: $\beta=-0.171\pm0.041$; Mayoral: $\beta=-0.149\pm0.058$; Tube: $\beta=-0.240\pm0.071$). Moreover, pallet warrens were found to be more cost-effective compared to other types analysed. Furthermore, rabbits preferred artificial warrens surrounded by a higher proportion of shrubs ($\beta=0.132\pm0.037$). Artificial warren use exhibited seasonal variation, declining gradually during the winter and early spring, and recovering in late spring, coinciding with the expected breeding peak. Based on our findings, we recommend the implementation of pallet warrens in rabbit restocking programmes to provide immediate shelter and breeding sites for the released rabbits. Furthermore, artificial warrens should be strategically located near shrub patches to facilitate safe access to vital resources such as food and water.

Keywords: habitat management, Mediterranean, Iberian rabbit, restocking, warren use

5.1. Introduction

The European rabbit (*Oryctolagus cuniculus*) is a native species of the Iberian Peninsula (Delibes-Mateos et al., 2023). In addition, it has been introduced in numerous countries and can now be found in scattered areas across all continents, except Antarctica (Thompson and King, 1994). Although the species is considered a pest that can cause irreversible economic and ecological damage in many introduced regions (Courchamp et al., 1999; Eldridge and Myers, 2001; Scanlan et al., 2006; Ríos-Saldaña et al., 2013; Delibes-Mateus et al., 2018), it plays a significant ecological and economic role in Mediterranean ecosystems where it is a native species.

In its natural range, as a keystone species within food webs, the European rabbit serves as a fundamental prey for many Iberian predators, some of which are globally threatened, such as the Iberian lynx (*Lynx pardinus*) and the Spanish imperial eagle (*Aquila adalberti*) (Delibes and Hiraldo, 1981; Delibes-Mateos et al., 2008a). Additionally, this lagomorph acts as an ecosystem engineer (Jones et al., 1994; Gálvez et al., 2008), promoting flora diversity and landscape heterogeneity through grazing and seed dispersal. Its faecal pellets contribute to improving soil fertility, and its warrens provide refuge for other animals (Willot et al., 2000; Gálvez-Bravo et al., 2009; Dellafiore et al., 2010). The European rabbit is also one of the most managed small game species and is intensively harvested within its original distribution range in the Iberian Peninsula, where hunting holds high socio-economic importance (Villafuerte et al., 1998; Paixão et al., 2009).

The European rabbit population, particularly the southern Iberian subspecies, *O. c. algirus*, has experienced a decline in its native range since the 1950s, primarily due to human-induced habitat changes and two viral diseases, myxomatosis and rabbit haemorrhagic disease (Villafuerte et al., 1995; Delibes-Mateos et al., 2009a). Between 2009 and 2019, the rabbit suffered an estimated population size reduction of ≥50%, mainly due to outbreaks of a new variant of rabbit haemorrhagic disease virus (RHDV2), resulting in negative consequences for several endangered predator species and ecosystems (Delibes-Mateos et al., 2014b; Monterroso et al., 2016; Villafuerte and Delibes-Mateos, 2019). As a result, the International Union for Conservation of Nature

(IUCN) recently classified *O. cuniculus* as an endangered species (Villafuerte and Delibes-Mateos, 2019).

Wildlife managers and hunters have continuously made efforts to reverse the rabbit population decline through restocking (e.g., Calvete et al., 1997; Moreno et al., 2004; Guil et al., 2014a) and/or increasing habitat carrying capacity by enhancing food and/or shelter availability (e.g., Moreno and Villafuerte, 1995; Ferreira and Alves, 2009; Encarnação et al., 2019).

Rabbits are strongly territorial and form social groups, typically living in burrows they dig out of the ground (Macdonald and Norris, 2001). This behaviour earned the rabbit its scientific name, *Oryctolagus*, meaning "digging hare" (Thompson and King, 1994). Warrens play a fundamental role in maintaining viable rabbit populations, serving as breeding sites and providing refuge from predators (Parer and Libke, 1985; Kolb, 1991). They also optimise the physiological requirements during the most unfavourable climatic periods (Villafuerte et al., 1993) and play a role as an element of cohesion of social relationships (Roberts, 1987).

The provision of artificial warrens has long been used. The initial efforts to provide artificial shelter for the species occurred in the last decades of the previous century within extensive rabbit production farms, aiming to enhance animal health and welfare (Roca, 2009; EFSA AHAW Panel, 2020), using materials such as straw, hay or wood shavings (EFSA AHAW Panel, 2020). Recently, artificial warrens have been frequently employed in rabbit conservation programmes and hunting management, especially in adverse habitat conditions, such as open habitats with no shrub protection or unfavourable soils for digging (Rouco et al., 2011).

Several works have shown the great importance of artificial warrens for rabbit populations, sometimes combined with other habitat management practices (e.g., Cabezas and Moreno 2007; Catalán et al., 2008; Godinho et al., 2013).

Some authors have also studied the factors determining the use of artificial warrens by rabbit populations (e.g., Fernández-Olalla et al., 2010; D'Amico et al., 2014). However, although artificial warrens may provide immediate refuge to released rabbits during the acclimation period, minimising predation, little is known about the selection and use of different types of artificial warrens, particularly in controlled experiments, such as restocking in fenced areas.

Moreover, the materials used and costs involved in artificial warren construction may vary, so it is important to evaluate their efficiency and point to more appropriate conservation strategies that optimise existing funds (Fernández-Olalla et al., 2010; Ferreira et al., 2013).

In this study, we analyse the use of four types of artificial warrens (logs, Mayoral® – registered trademark, pallets, and tubes) by a recently restocked Iberian rabbit population in southern Portugal. To estimate warren use, we conducted pellet counts at the entrances of artificial warrens. To the best of our knowledge, this is the first time such an analysis has been performed, simultaneously comparing the use of four different types of artificial warrens by a restocked population inside a fenced restocking park. The behaviour of the released population may differ from that of natural populations, influenced by the rabbit's adaptation period to the new habitat and the carrying capacity of the restocking park. Additionally, we quantify the costs associated with warren installation and discuss the best options in terms of cost-benefit.

Specifically, we aimed to answer the following four questions and associated hypotheses:

1. Which warren types are the most used by restocked rabbits? We hypothesised that rabbits would prefer artificial warrens built with natural features, such as log warrens or with structures resembling their natural warrens, such as tube warrens (Fernández-Olalla et al., 2010; San Miguel, 2014).
2. What habitat characteristics around artificial warrens promote warren use by the restocked population in the restocking park? We hypothesised that the presence of crops, shrubs, drinking troughs, and/or ecotone around the warren would enhance its use (Rogers and Myers, 1979; Carvalho and Gomes, 2004; Encarnação et al., 2019).

3. Does rabbit artificial warren use vary through the annual life cycle? We anticipated that warren use would be higher after the peak of the breeding period, which generally occurs in late spring (Gonçalves et al., 2002).
4. What is the efficiency of different artificial warrens, considering the financial investment and the level of warren use? We expect that warrens built with natural materials will be cheaper and more utilised by rabbits.

Overall, our results will provide practical guidelines to improve the success of rabbit restocking programmes in the Mediterranean region, particularly those requiring artificial warrens.

5.2. Materials and methods

5.2.1. Study area

We conducted this study in the Algarve region, southern Portugal (37° 16’ 33’’ N, 8° 29’ 27’’ W; Figure 5.1), specifically within a hunting estate located in the Monchique Natura 2000 Special Conservation Area (SAC) (PTCON0037) (Regulatory Decree n. º 1/2020 of 16th March). The area’s climate is characterised by mild and moist winters and hot and dry summers. The mean annual total rainfall is 937.9 mm, and the mean annual daily temperature is 14.3 °C, as recorded in Monchique from 1980 to 2021 (SNIRH, 2022).

The landscape surrounding the restocking park is dominated by dense Mediterranean shrubs, with scattered eucalyptus (*Eucalyptus globulus*) plantations and agricultural fields, primarily consisting of cereal crops and orchards. The terrain is undulating, with elevations reaching approximately 165 m above sea level (CNA, 1982). The soils in the area are poor and mainly dominated by incipient soils, particularly schist or greywacke lithosols of xeric-regime climates (IHERA, 1999).

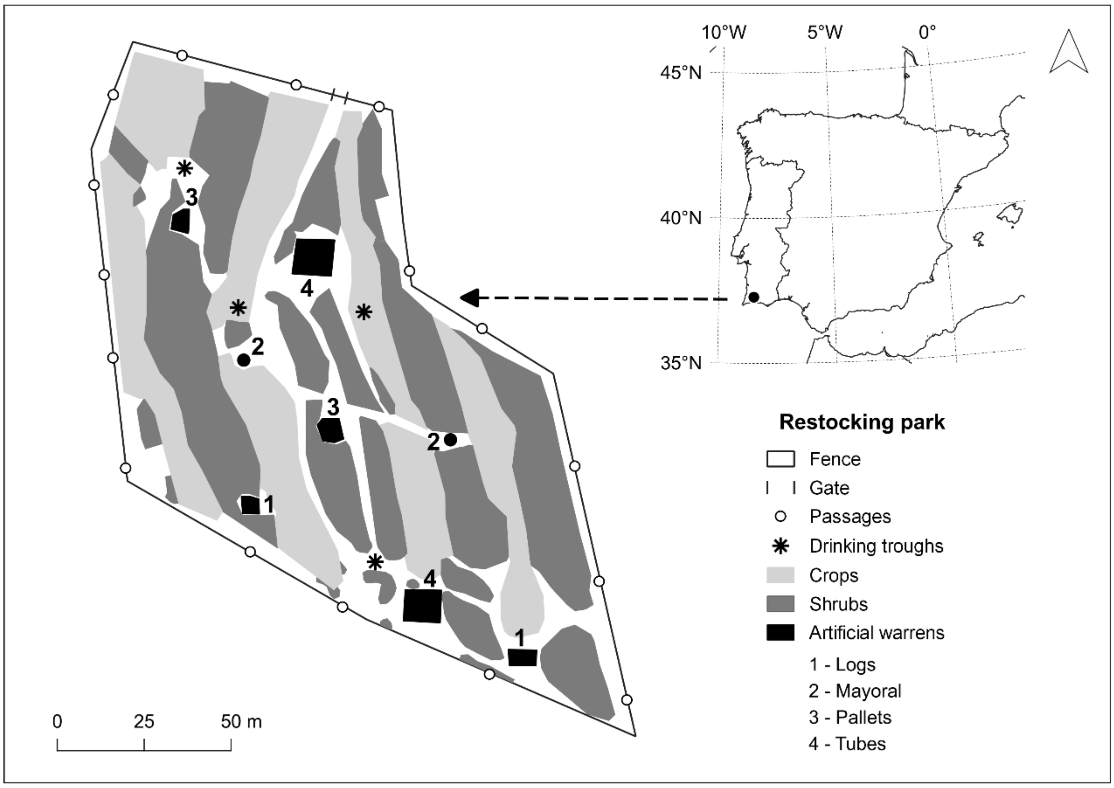

Figure 5.1 Schematic representation of the restocking park in southern Portugal.

5.2.2. Restocking park

A restocking park, covering an area of approximately 1.7 ha, was designed to acclimate and breed reintroduced rabbits that, subsequently, would restock the surrounding area (Figure 5.1). The park was enclosed by a 1.8 m high fence, with an additional 0.5 m buried underground in an "L-shape" configuration, intended to prevent terrestrial carnivores from entering and enhance rabbit survival (Rouco et al., 2008). However, we did not take any measures to exclude aerial predators, as the restocking was conducted as part of the "Compensatory measures and specific monitoring of the Odelouca's Bonelli eagle couple, arising from the environmental impact assessment process of the Sines-Portimão high-voltage power line" project (REN et al., 2009). To facilitate rabbit dispersion, 16 passages made of plastic tubes, each with a diameter of 12.5 cm, were installed under the fence.

Inside the fenced area, we ensured the availability of essential requirements for rabbit survival, including food, water and shelter (Figure 5.1). Initially, the restocking park surface was covered with dense scrubland. To create a suitable habitat for the rabbits, we cleared elongated parcels of shrubs and sowed them with herbaceous crops, a mixture of Leguminosae and Graminae, creating alternating patches of food (crops) and shelter (shrubs). Additionally, we installed four drinking troughs, ensuring water availability.

To further enhance the availability of shelter and breeding sites, we built eight artificial warrens, spaced as uniformly as possible throughout the area. The artificial warrens included two of each type (See Supplementary information 5A for photos):

- Log warren – A warren with a diameter of approximately 4-5 m, constructed using natural materials such as logs, branches and rocks and covered with surrounding soil. The materials were piled to create galleries to facilitate rabbit movement.
- Mayoral® warren – A prefabricated plastic warren specifically designed for rabbits, consisting of several independent modules that form a circular structure measuring 3 m in diameter. The bottom of the structure is open to allow rabbits to construct their galleries. It contains several internal galleries and has six entrances (González and San Miguel, 2004). Each warren was installed on the ground surface, with its perimeter protected by rocks and its top covered with cork boards and bushes to mimic the surrounding area and help regulate internal temperature.
- Pallet warren – A warren constructed by overlapping several wooden pallets on the ground, with nine pallets on the lower level and six on the upper level. We placed rocks inside the pallets to compartmentalise and reinforce the structure, which was then covered with branches and soil.
- Tube warren – A warren developed by the CBD-Habitat Foundation to mimic the labyrinth structure and dimensions of natural warrens, following Kolb's (1985) description. This type of warren consisted of several bottomless PVC chambers for passage or breeding, interconnected by plastic tubes (1 m long and 12.5 cm in diameter), which were perforated to allow drainage. We placed the structure

underground, at approximately 0.60 m in depth, following the layout described by González and San Miguel (2004), and subsequently covered it with soil, with the four entrances at ground level.

The shrubs were initially cleared, and the ground was levelled. Since the artificial warrens were located within the restocking park, they shared similar characteristics in terms of elevation, slope and soil type.

As of 2023, the updated prices for installing each type of artificial warren in this study area are approximately as follows: 260€ for a log warren, 320€ for a pallet warren, 630€ for a tube warren, and 750€ for a Mayoral warren. These estimated prices include costs for backhoe work, materials, transport and the technician's labour. However, the final cost of establishing a warren in a specific area could vary significantly based on factors such as location, materials used and fuel costs.

5.2.3. Rabbit release protocol

On 28th October 2007, 75 adult Iberian rabbits (19 males and 56 females) were released into the restocking park at sunrise. To ensure genetic similarity to native populations (Branco et al., 2000; Carneiro et al., 2010), we carefully selected a certified breeder from the natural distribution area of *O. c. algirus*.

Before release, each rabbit underwent a series of preparatory measures. We weighed and sexed each individual and administered internal and external deworming treatments. Additionally, all rabbits were vaccinated against rabbit haemorrhagic disease and myxomatosis, with the entire process being supervised by a team of veterinarians. All applicable international, national and/or institutional guidelines for the care and use of animals were followed.

Following these preparations, the rabbits were released in groups of 5-8 individuals per release location, approximately maintaining the same sex ratio (2-3 females for each male) across all ten release sites inside the restocking park. Specifically, the release locations comprised each of the eight artificial warrens and two randomly selected spots within the shrub patches. To allow for rabbit dispersion outside the restocking park, the fence passages were opened on 8th January 2008, after an acclimation period of 72 days.

5.2.4. Artificial warren use

Over six months, we conducted weekly estimations of rabbit use for each artificial warren by counting the number of faecal pellets within a 0.5 m^2 radius area outside the entrance of each warren. The sampling started in early January 2008, immediately after the acclimation period following the restocking, to minimise disturbance to the rabbits. Data collection was concluded at the end of June. The number of pellets was used as a proxy for the number of rabbits utilising each warren (Palomares, 2001; Guerrero-Casado et al., 2020). In every visit, we ensured the removal of pellets, thus guaranteeing that we exclusively counted fresh pellets less than one week old (Iborra and Lumaret, 1997). Subsequently, we estimated warren use for each artificial warren by dividing the number of pellets per square metre by the number of days elapsed since the last cleaning (Guerrero-Casado et al., 2020). This methodology allowed for the comparison of abundance values between warrens with different numbers of entrances.

5.2.5. Predictors of warren use

We modelled warren use as a function of the predictors listed in Table 5.1. We assessed the proportion of food patches, shelter patches and ecotone length within a 10m radius buffer around each warren. The ecotone corresponded to the edges between food and shelter patches. To account for the potential impact of rainfall on pellet persistence (Iborra and Lumaret, 1997; Fernández-de-Simon et al., 2011), we included two predictors: mean weekly rainfall and accumulated weekly rainfall (SNIRH, 2022). We extracted distance and proportion predictors, along with ecotone length, from original vegetation cover maps created by the team using QGIS (QGIS Development Team, 2021).

Table 5.1 Predictors used in the analysis of rabbit artificial warren use.

Predictors description (Units)	Mean (± SE)	Range
Sample week	-	1-24
Type of artificial warren: Logs, Mayoral, Pallets*, Tubes	-	-
Ecotone length (m)	73.680±1.036	42.284–89.703
Proportion of food patches	0.175±0.008	0.027–0.320
Proportion of shelter patches	0.319±0.008	0.193–0.536
Distance to the nearest food patch (m)	4.187±0.143	0.976–8.073
Distance to the nearest shelter patch (m)	0.996±0.057	0.300–2.900
Distance to the nearest drinking trough (m)	25.035±1.037	9.711–44.997
Mean weekly rainfall (mm)	2.845±0.272	0.000–13.613
Accumulated weekly rainfall (mm)	24.575±2.464	0.000–111.200

Note. SE - standard error; * Pallets is the reference category for the type of artificial warren predictor.

5.2.6. Data analysis

We analysed spatial and temporal patterns in warren use using a generalised additive mixed model (GAMM), with a Gaussian error distribution and an identity link function (Hastie and Tibshirani, 1990; Wood, 2017). We decided to use GAMM because the exploratory analysis of the data indicated the presence of a non-linear pattern between the response variable and several continuous predictors. To account for multiple surveys of the same warrens, we used the warren identity code of every artificial warren as a random variable.

We subjected the response variable to a logarithmic transformation (log(x+1)) to approach normality, stabilise the variance and reduce the influence of outliers (Zuur et al., 2010). Three predictors, namely the distance to the nearest shelter patch (log x), mean weekly rainfall (log(x+1)) and accumulated weekly rainfall (log(x+1)), were also logarithmically transformed to meet these assumptions. All continuous predictors were standardised to facilitate direct comparisons of regression coefficients (Schielzeth, 2010).

To identify potential collinearity problems, we calculated Spearman correlations (r_s) among all predictors (Zuur et al., 2010). For each pair of highly correlated predictors ($|r_s|>0.7$) (Dormann et al., 2013), only the predictor with the stronger correlation with the response variable was retained for further analysis (Tabachnick and Fidell, 1996). As a result, we removed the ecotone length, the proportion of food patches and the mean weekly rainfall predictors from the analysis.

To evaluate the linearity of non-collinear predictors, we individually tested each predictor against the response variable as a smoothing term. Only predictors showing non-linearity (edf>2; edf - effective degrees of freedom of nonlinear (smooth) terms) and statistical significance ($P<0.05$) were included in the subsequent analysis. We found that the sample week and accumulated weekly rainfall were significant non-linear terms, with the optimal amount of smoothness estimated via generalised cross-validation (Zuur et al., 2009).

Then, for each predictor, we compared the respective univariate model Akaike's Information Criterion corrected for small sample sizes (AICc) with the null model AICc. Only predictors that produced univariate models with an AICc at least four units lower than the null model were considered to have strong support and were retained as candidates for the multivariate model. The selected predictors (sample week, type of artificial warren, proportion of shelter patches and distance to the nearest food patch) were then used to build multivariate mixed models with all possible combinations, including the null (intercept-only) and full models (with all candidate predictors). A multi-model inference procedure was applied to rank the models based on their Akaike weights (wi) (Burnham and Anderson, 2002).

To account for heterogeneity in model residuals, we allowed variances per warren to differ by adding a variance structure (varIdent) to the model (Zuur et al., 2009). This resulted in lower AICc values and improved the model fit.

As no single model was convincingly the most plausible (wi≥0.95), we performed a model averaging approach, basing inferences of the averaged parameters, unconditional standard errors (SE) and 95% confidence interval (CI) on the set of models showing an AICc within four units (ΔAICc<4) of the best model (Burnham and Anderson, 2002). We determined the relative importance of each predictor (w+) by the sum of Akaike weights (wi) of all models where the predictor was included (Burnham and Anderson, 2002). Predictors with 95% CIs including zero were considered to have low support (Burnham and Anderson, 2002). The best model incorporated all predictors of the group of models with ΔAICc<4.

We checked for potential spatial autocorrelation in the best model residuals by computing Moran's I and inspected temporal autocorrelation by plotting the autocorrelation function (ACF) (Zuur et al., 2009). We validated the best model using diagnostic plots (Zuur et al., 2009) and assessed the best model performance through the adjusted R-squared (Wood, 2017).

Additionally, we performed a simple efficiency assessment of each warren type by computing the ratio between the costs of building the warren and the level of warren use by the rabbits for each type. The efficiency of artificial warrens was hierarchised based on these ratios, with lower values indicating higher artificial warren efficiency, implying fewer costs invested to achieve greater warren use.

All the statistical analyses were conducted in R version 4.1.3 (R Core Team, 2022) using the packages: "car" (Fox and Weisberg, 2019) to assess collinearity, "mgcv" (Wood, 2017) for GAMM, "MuMIn" (Barton, 2020) for model averaging and "ape" (Paradis and Schliep, 2019) to check spatial autocorrelation. Plots were generated using "ggplot2" (Wickham, 2016).

5.3. Results

Warren use, as measured by mean pellet abundance, varied significantly among the different types of artificial warrens. Warren use was higher in pallet warrens (0.922 pellets/d/m^2), followed by log warrens (0.411 pellets/d/m^2) and Mayoral warrens (0.403 pellets/d/m^2). Tube warrens were the least used (0.313 pellets/day/m^2).

Pallet warrens had the lowest ratio of cost/warren use value (347.1€/pellets/d/m^2) and tube warrens had the highest (2,012.8€/pellets/d/m^2). Log warrens and Mayoral warrens fell in between, with efficiency ratios of 632.6€/pellets/d/m^2 and 1,861.0€/pellets/d/m^2, respectively.

The best-fitted model explaining artificial warren use had an adjusted R-squared of 0.545. Model residuals did not exhibit any temporal or spatial autocorrelation (Moran's I= –0.0002, P<0.237).

The level of artificial warren use was significantly associated with the type of artificial warren, the proportion of shrub cover, the distance to food patches and the sample week. The sample week and the proportion of shelter patches had the highest relative importance (w+), with a relative importance value of 1.00 for both, indicating that they were included in all the candidate models with ΔAICc<4. The type of artificial warren also had a considerable influence on warren use, with a relative importance value of 0.49. On the other hand, the distance to the nearest food patch had the lowest relative importance (w+=0.33) (Table S5B.1, Supplementary information 5B).

Sample week exhibited a non-linear relationship with warren use (edf=6.840; F=13.350, P=0.000) (Figure 5.2a). Warren use gradually decreased from January onwards, reaching its lowest values in May, specifically between the 16^{th} and 20^{th} sampling weeks. The decrease in warren use was particularly sharp in the first four sampling weeks, followed by a more stable period until the end of March. In June, the last sampling month, there was an inversion of the trend and an increase in warren use was observed.

The proportion of shrubs around the warren positively influenced warren use (β=0.132±0.037) (Figure 5.2b). This means that the higher the proportion of shrubs around warrens, the greater their use by rabbits.

The type of artificial warren also had a significant effect on warren use. Warren use was significantly lower in Mayoral, tube and log warrens than in pallet warrens (Logs: β= –0.171±0.041; Mayoral: β= –0.149±0.058; Tube: β= –0.240±0.071) (Figure 5.2c).

The distance to the nearest food patch did not show a significant effect on warren use, as the unconditional CI for its coefficient included zero (Table SB5.1, Supplementary Information 5B).

All candidate models and the average model describing the estimated effects of predictors on warren use are presented in Table SB5.2, Supplementary Information 5B.

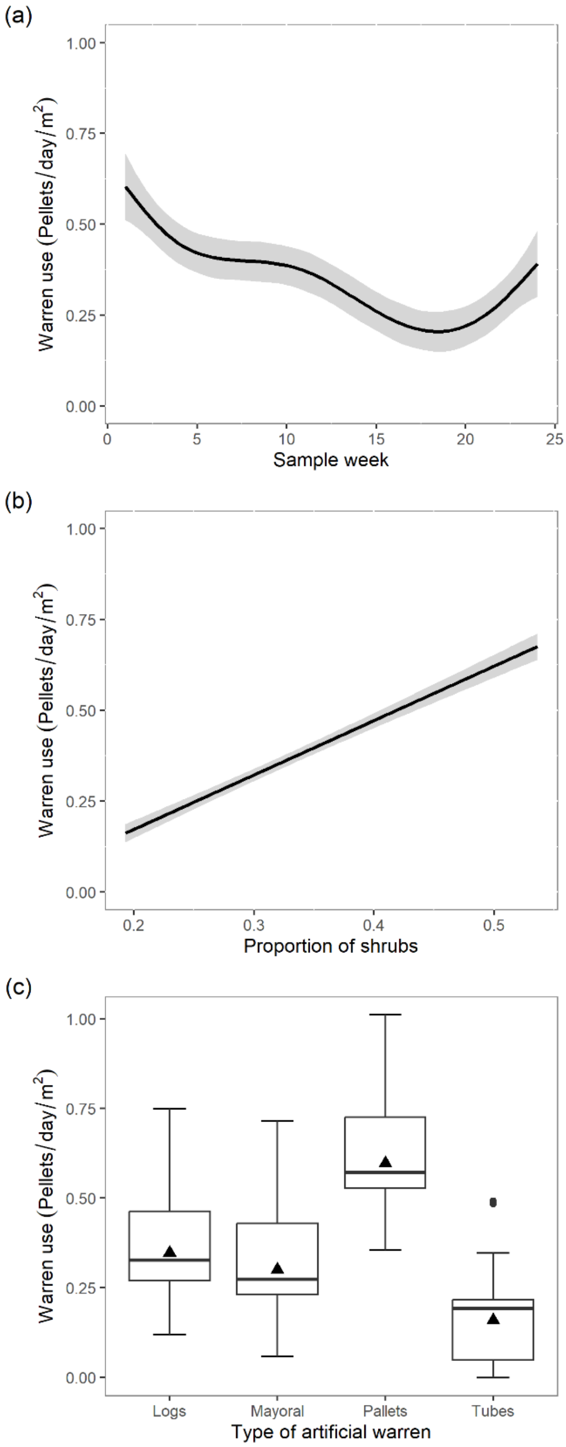

Figure 5.2 Relationship between warren use, expressed as logarithmic mean pellet abundance [log(x+1) (pellets/d/m^2)], and (a) sample week, (b) proportion of shrubs and (c) type of artificial warren. Predicted values of warren use were calculated using the averaged GAMM model. In graphs (a) and (b), the grey zone represents the 95% confidence interval of the predicted values. In each boxplot of graph (c), the triangle is the mean, and the darker horizontal line is the median. The length of the box represents the interquartile range (i.e., the difference between the 75th and 25th percentiles). The dots outside the whiskers are outliers.

5.4. Discussion

In this study, we compared the use of four distinct types of artificial warrens, commonly employed in Iberian rabbit recovery programmes (García, 2003; Fernández-Olalla et al., 2010; San Miguel, 2014). To the best of our knowledge, limited research has been undertaken to compare the use of different artificial warren types (e.g., Fernández-Olalla et al., 2010) and identify the factors influencing the use of artificial (e.g., D'Amico et al., 2014) and natural warrens (e.g., Barrio et al., 2009). Our study provides a novel contribution by examining these aspects in a confined and controlled population, immediately after restocking, evaluating the temporal variation in use and discussing the cost-benefit implications associated with each artificial warren type.

However, it is essential to acknowledge that our findings should be approached with caution, considering the limitations inherent in this study. The research was confined to a singular restocking park, encompassing a relatively small area, and our sampling was limited to two artificial warrens per warren type. Conducting similar studies with a higher number of replicates, including more artificial warrens of each type, and across multiple restocking plots simultaneously, would be ideal to corroborate and reinforce these findings. However, we acknowledge the challenges related to budget constraints, particularly when it comes to fence installation and the construction of certain types of artificial warrens, such as tube and Mayoral warrens. Despite the constraints, we were able to gather statistically meaningful results, which are a promising step to support better choices in rabbit restocking programmes.

Our findings reveal significant variations in the use of the four types of artificial warrens, which is consistent with our initial hypothesis, despite the similar number of animals released in each warren. Iberian rabbits demonstrated a preference for pallet warrens over the other options, contrary to our prediction that they would favour warrens constructed solely with natural materials (logs) or those closely resembling natural warrens (tubes). It is interesting to note that a previous study by Fernández-Olalla and colleagues (2010), which examined three types of artificial warrens in the context of rabbit natural populations occupancy, found that subterranean warrens made of tubes exhibited higher rates of rabbit occupancy. In our case, we speculate that the restocked rabbits showed a higher preference for pallet warrens in our study area due to the robust structure and resistance to collapse offered by the arrangement of pallets (García, 2003). Moreover, the design of pallet warrens seemed to facilitate tunnel excavation, which might have contributed to their increased use. Another noteworthy advantage of pallet warrens is that they cost less than most artificial warren types usually installed for habitat improvement in rabbit recovery programmes. Thus, in this study, they presented the best efficiency ratio.

The use of all other warren types by rabbits was comparatively lower. For instance, tube warrens presented challenges as their structure needed to be buried, requiring the clearance of a larger area of shrubs. This increased the warrens' exposure and potentially reduced the level of protection for rabbits when they came out of the warrens. Additionally, the risk of flooding might have been higher for tube warrens, as they were installed below ground level. However, we were unable to confirm this hypothesis, as the interior of tube warrens was inaccessible for observation.

Contrary to our initial prediction, log warrens did not emerge as one of the most utilised artificial warren types, despite the use of natural materials. The logs used to construct the warrens may have been too large, resulting in limited space between logs filled with dirt, hindering rabbits from effectively building their tunnels (Figure S5A.1, Supplementary Information 5A).

As for Mayoral® warrens, rabbits likely use them less due to their significant structural differences from natural warrens. Being made of plastic and placed on the surface of the soil, the interior of Mayoral warrens could experience higher humidity and temperature levels. Although we attempted to protect against extreme climate conditions by covering them with branches and cork (Villafuerte et al., 1993), this may not have fully buffered against weather conditions, leading to decreased use by rabbits.

Our results revealed a positive association between the proportion of shrub patches surrounding the artificial warrens and the level of warren use by Iberian rabbits. The presence of shrubs near the warrens ensures the availability of suitable conditions for the rabbits to access essential resources, such as food and water, safely. This result aligns with previous studies that also reported similar findings concerning natural warrens

(Palomares, 2003; Gea-Izquierdo et al., 2005; Dellafiore et al., 2008), as well as artificial warrens (Fernández-Olalla et al., 2010).

We observed a decline in the use of warrens by Iberian rabbits over time, following the acclimation period, which is likely related to the digging and use of natural burrows. Although we did not conduct a specific search for natural warrens, we occasionally found them. A fact that may be related to rabbit reproductive activity (Kolb, 1991), which occurs between October and June (Alves and Moreno, 1996).

Another possible explanation for the decline in warren use could be the dispersal of some restocked or young Iberian rabbits to the surrounding areas of the restocking park. While this might explain the reduced warren use observed after the beginning of March (when we noticed signs of activity near the passages installed under the fence), it does not explain the initial decrease observed earlier in the study.

The mortality rate of the restocked rabbits could also explain the decline in warren use, particularly since we did not take any measures to exclude aerial predators from the restocking park. However, no concrete evidence supports this hypothesis, as most recorded deaths occurred during the acclimation period. During our study, we radio-tagged some restocked rabbits and closely monitored them for approximately six months or until their death. We only detected signs of predation from radio-tagged animals and during field surveys conducted inside the restocking park and its surroundings until January 11th, 2008, coinciding with the beginning of artificial warren pellet counts.

As predicted, we observed a slight recovery in warren use in June, coinciding with the period immediately after the breeding peak (Gonçalves et al., 2002). The confirmation of successful reproduction just a few months after restocking indicates that the rabbits successfully adapted to the new habitat, and the restocking park provided suitable conditions for their thriving.

While it is well-documented that rainfall can affect pellet persistence (Fernández-de-Simon et al., 2011), in this study, the influence of precipitation on warren use was negligible. One possible explanation for this finding is that the short intervals between our pellet counts ensured pellet persistence (Moreno and Villafuerte, 1995).

Since 2011, there has been a drastic reduction in Iberian rabbit populations, mainly due to the outbreak of RHDV2. Numerous studies have reported declining trends in wild rabbit populations in both Portugal and Spain after the rapid spread of RHDV2 throughout the Iberian Peninsula (Guerrero-Casado et al., 2016; Monterroso et al., 2016). The ongoing decrease in populations is a cause for concern regarding their survival and its impact on Mediterranean ecosystems (Delibes-Mateos et al., 2014b; Monterroso et al., 2016), given their roles as keystone prey species, ecosystem engineers and small game species (Delibes-Mateos et al., 2008a; Gálvez et al., 2008; Paixão et al., 2009). Therefore, enhancing rabbit populations also benefits the ecosystem and predator species specialised in preying on rabbits, many of which are of conservation concern (Delibes-Mateos et al., 2008a).

In southern Europe, conservationists and hunters often invest in restocking operations to boost rabbit populations. However, such efforts come with significant economic costs (Ferreira and Delibes-Mateos, 2010) and varying success rates (Calvete et al., 1997; Letty et al., 2002). To optimise the effectiveness of restocking interventions, it is crucial to carefully evaluate every aspect of the process, including the design, characteristics, and costs of artificial warrens.

In this context, we believe our study provides valuable insights into the selection and use of artificial warrens by restocked Iberian rabbit populations and contributes with practical recommendations to enhance the success and effectiveness of rabbit restocking efforts, thereby aiding the conservation of Iberian rabbit populations in the Mediterranean region.

5.5. Conclusions

Based on our research findings, we emphasise the importance of installing artificial warrens, even within fenced restocking parks, as they create favourable conditions for the Iberian rabbits' shelter, breeding success and recruitment. These artificial warrens play a crucial role in supporting the initial adaptation of the rabbits to their new environment. We highly recommend the implementation of pallet warrens as a cost-effective and practical option for conservationists and game managers tasked with constructing artificial warrens to support restocking operations. Pallet warrens offer a budget-friendly alternative compared to more intricate and expensive designs. Furthermore, we strongly advise placing artificial warrens strategically near shrub patches. This placement ensures that restocked rabbits can safely access vital resources such as food and water, optimising their chances of survival and successful adaptation to the new habitat. Additionally, to enhance the dispersal and survival of rabbits, we advocate the strategic installation of additional pallet warrens around the restocking parks, providing essential shelter for dispersing rabbits.

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Supplementary information 5A

Photographs of the four types of artificial warrens installed inside the restocking park.

- **Log warren**

Figure S5A.1 Log warren.

- **Mayoral® warren** (registered trademark)

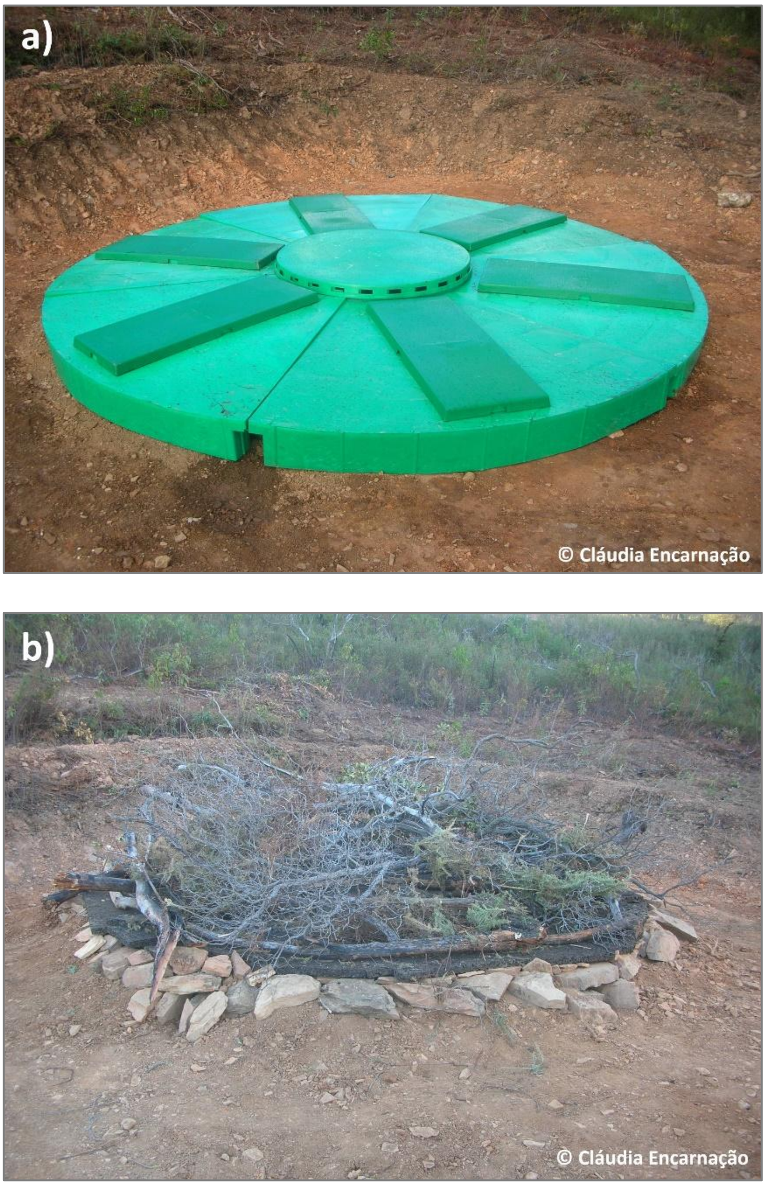

Figure S5A.2 Structure (a) and final appearance (b) of a Mayoral® warren.

- **Pallet warren**

Figure S5A.3 Structure (a) and final appearance (b) of a pallet warren.

- **Tube warren**

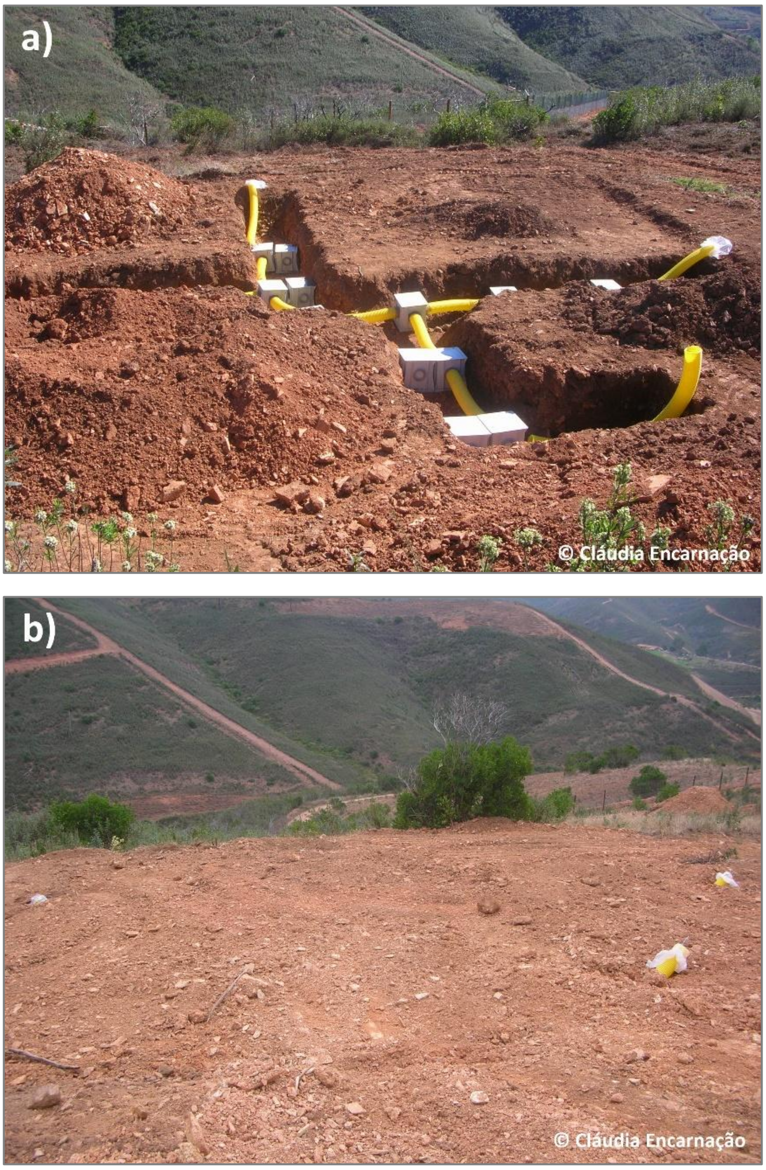

Figure S5A.4 Structure (a) and final appearance (b) of a tube warren.

Supplementary information 5B

Details of model selection.

Table S45.1 Candidate models tested to assess predictors potentially affecting rabbit use of artificial warrens, accounting for “warren” as random effect and allowing for different variances per warren. Models are ranked by AICc. Predictors: WEEK - sample week, TYPE - type of artificial warren, D_FOOD - distance to the nearest food patch and P_SHRUB - proportion of shrub patches in a 10-meter buffer around the warren. Delta are AICc differences to the best model and w_i are Akaike weights based on the entire set of models. The table also shows values for each model's intercept (Int) and degrees of freedom (df). Models are ranked by ΔAICc. Models included in model averaging (confidence set of models at ΔAICc<4 from the best model) are highlighted in bold.

Model	(Int)	s(WEEK)	TYPE	D_FOOD	P_SHRUB	df	AICc	Delta	Wi
12	**0.4824**	**+**	**+**		**+**	**16**	**-40.1**	**0.00**	**0.336**
11	**0.3574**	**+**			**+**	**13**	**-40.1**	**0.30**	**0.289**
15	**0.3602**	**+**		**+**	**+**	**14**	**-39.0**	**1.13**	**0.190**
16	**0.4745**	**+**	**+**	**+**	**+**	**17**	**-38.0**	**2.13**	**0.116**
7	0.3682	+		+		13	-35.2	4.96	0.028
8	0.5134	+	+	+		16	-34.7	5.46	0.022
4	0.6175	+	+			15	-34.2	5.93	0.017
3	0.3663	+				12	-29.6	10.48	0.002
9	0.3557				+	11	3.4	43.51	0.000
10	0.4851		+		+	14	3.9	43.99	0.000
13	0.3578			+	+	12	4.3	44.43	0.000
14	0.4757		+	+	+	15	6.1	46.18	0.000
5	0.3661			+		11	8.2	48.30	0.000
6	0.5158		+	+		14	8.7	48.82	0.000
2	0.6164		+			13	8.9	48.99	0.000
1	0.3651					10	13.6	53.69	0.000

Table S5B.2 Averaged model (GAMM) of the effects of predictors on rabbit use of artificial warrens. Model averaging accounted for "warren" as random effect and allowed for different variances per warren. Model averaging is based on the confidence set of models at ΔAICc<4 from the best model. The table shows standard errors (SE), 95% confidence intervals (CI) and relative importance (w+) of each predictor involved. Estimates whose 95% CI excluded zero are in bold. Predictors: WEEK - sample week, TYPE - type of artificial warren, D_FOOD - distance to the nearest food patch and P_SHRUB - proportion of shrub patches in a 10-meter buffer around the warren. The reference category for TYPE is Pallets.

	Estimate	**SE**	**CI**	**w+**
(Intercept)	0.418	0.071	(0.279, 0.556)	
TYPE				
Logs	**-0.165**	**0.047**	**(-0.258, -0.072)**	
Majano	**-0.144**	**0.061**	**(-0.265, -0.023)**	**0.49**
Tubes	**-0.239**	**0.071**	**(-0.379, -0.099)**	
P_SHRUB	**0.128**	**0.038**	**(0.054, 0.202)**	**1.00**
D_FOOD	0.035	0.037	(-0.039, 0.108)	0.33
s(WEEK).1	0.181	0.094	(-0.006, 0.368)	
s(WEEK).2	**-1.272**	**0.277**	**(-1.819, -0.725)**	
s(WEEK).3	0.109	0.080	(-0.049, 0.266)	
s(WEEK).4	**0.748**	**0.204**	**(0.346, 1.151)**	
s(WEEK).5	**-0.167**	**0.082**	**(-0.329, -0.006)**	**1.00**
s(WEEK).6	**-0.693**	**0.189**	**(-1.066, -0.320)**	
s(WEEK).7	-0.118	0.076	(-0.267, 0.032)	
s(WEEK).8	**-1.906**	**0.427**	**(-2.747, -1.064)**	
s(WEEK).9	-0.217	0.180	(-0.572, 0.138)	

Chapter 6

General conclusions

6.1. Thesis overview and summary of the main findings

This thesis aimed to provide empirical insights and practical guidelines to enhance the effectiveness of management interventions for the Iberian rabbit (*Oryctolagus cuniculus algirus*) in the Mediterranean region. The results are presented in three research papers obtained by examining key aspects of rabbit recovery efforts, focusing on the effectiveness of habitat management (**Chapter 3, Paper I**), the survival and behaviour of restocked individuals (**Chapter 4, Paper II**), and the suitability of artificial warrens (**Chapter 5, Paper III**).

The first study (**Chapter 3**) evaluated the long-term impacts of habitat management interventions on rabbit presence and abundance, covering the periods before (2007), during (2008), immediately after (2009) and three years after post-management cessation.

Results indicate that habitat management can significantly increase the Iberian rabbit presence and abundance; however, these effects are not self-sustaining and require continued intervention. A substantial increase in rabbit distribution and abundance was observed during and immediately after implementing habitat management, largely due to improved environmental conditions, such as greater food availability and a more diverse habitat mosaic (Moreno et al., 1996; Calvete et al., 2004; Carvalho and Gomes, 2004). However, three years after implementing management measures, rabbit abundance had declined to pre-management levels, suggesting that short-term interventions alone are insufficient for long-term population recovery. While habitat management significantly increased rabbit populations, particularly through crop sowing (Sarmento et al., 2012), additional factors, such as the presence of suitable soils for digging, also influenced species distribution. Thus, these results highlight the importance of promoting medium or long-term management measures, at least for establishing stable Iberian rabbit populations. The abandonment of supporting measures to improve rabbit populations after their implementation does not seem appropriate to promote stable rabbit populations.

The second study (**Chapter 4**) addressed the survival and space use of the restocked Iberian rabbit population in the semi-natural enclosure.

Despite implementing known measures to enhance restocking success (Cabezas and Moreno, 2007; Delibes-Mateos et al., 2008c; Letty et al., 2008; Rouco et al., 2010), findings revealed low survival rates, particularly during the first few weeks after release. Predation by avian predators was the primary cause of mortality, whereas deaths from non-predation causes, often linked to stress (Calvete et al., 1997; Letty et al., 2000; Letty et al., 2002), were relatively low.

Restocked rabbits required approximately three months to stabilise their home ranges. Most radio-collared individuals remained inside the semi-natural enclosure, and, probably for this reason, their home range and core area sizes were smaller than those reported in previous studies (e.g., Hulbert et al., 1996; Moseby et al., 2005; Devillard et al., 2008; Rouco et al., 2019).

Space use analyses showed an increase in the maximum distances travelled. However, home ranges remained within the boundaries of the restocking park, suggesting that rabbits settled within the park as they acclimated to their new environment and adapted to local conditions. Moreover, rabbits released into warrens exhibited smaller core areas, while those released in shrubs displayed broader-ranging behaviour, making them more vulnerable to predation (Parer and Libke, 1985; Kolb, 1991).

The third study (**Chapter 5**) evaluated the use of four types of artificial warrens - logs, Mayoral®, pallets, and tubes - and examined the habitat factors that contributed to their use by the restocked Iberian rabbit population in the semi-natural enclosure.

Findings revealed that rabbits favoured pallet warrens, contrary to the initial hypothesis that they would prefer warrens made from natural materials or structures resembling natural burrows (Fernández-Olalla et al., 2010; San Miguel, 2014). The robust structure of pallet warrens facilitated tunnel excavation. Pallet warrens also provided the best cost-benefit ratio, making them a highly effective option for rabbit conservation.

A higher proportion of shrub patches surrounding artificial warrens positively influenced their use by rabbits, reinforcing the idea that vegetation cover is vital for providing refuge, ensuring safe access to vital resources (Moreno et al., 1996; Carvalho and Gomes, 2004). Additionally, seasonal variations in warren usage were observed: a decline during winter and early spring, followed by an increase in late spring, which aligned with the expected peak in breeding activity (Gonçalves et al., 2002).

6.2. Management implications

The decline in Iberian rabbit populations highlights the importance of effectively managing both the subspecies and its habitat, given the rabbits' crucial role in Mediterranean ecosystems (Delibes-Mateos et al., 2008a). The three studies in this thesis emphasise the significance of three key conservation strategies to ensure the sustainability of Iberian rabbit populations: habitat management (**Chapter 3**), restocking efforts (**Chapter 4**), and the provision of artificial warrens (**Chapter 5**).

The findings support several management recommendations to improve the effectiveness of future Iberian rabbit conservation initiatives, benefiting the species and broader ecological communities that depend on it (Delibes-Mateos et al., 2008a).

The results reinforce the fundamental role of habitat quality in determining rabbit conservation success. Habitat management efforts should prioritise maintaining a habitat mosaic to ensure resource availability and protection from predators (Moreno et al., 1996; Carvalho and Gomes, 2004), particularly by sowing crops within continuous scrub patches, as discussed in **Chapter 3**. The findings also underscore the importance of long-term habitat management strategies to sustain favourable conditions for rabbit populations. Furthermore, it is advisable that the management process be subject to continuous review based on monitoring outcomes.

Artificial warren installation is advisable, particularly in areas with unfavourable soil that hinders natural burrow excavation, since they serve as breeding sites and provide protection from predators (Parer and Libke, 1985; Kolb, 1994; **Chapter 5**). Even in enclosed restocking parks, artificial warren installation is recommended, as they provide critical shelter and facilitate the initial acclimation process for restocked rabbits. Among available options, pallet warrens are particularly recommended (**Chapter 4**).

Within semi-natural enclosures, artificial warrens should be placed near shrub patches, as nearby vegetation enhances warren use by providing cover, reducing predation risk, and facilitating access to critical resources, thus further improving the adaptation success of restocked rabbits (Moreno et al., 1996; Carvalho and Gomes, 2004; **Chapter 4**).

Furthermore, we suggest strategically placing additional warrens around the outer boundaries of semi-natural enclosures (**Chapter 5**). This measure aims to support dispersal by providing essential shelter for young rabbits or individuals exploring beyond the park's limits, contributing to successful colonisation and population growth.

In rabbit restocking efforts, acclimation semi-natural enclosures should be built with fences designed as described in **Chapter 4**, as they effectively prevent terrestrial predator entrance. However, further improvements can enhance protection against aerial predators by placing a soft net over the restocking park, at least during rabbit acclimation (Guerrero-Casado et al., 2013b). Whenever possible, enclosures should not be located near large trees, which could serve as perches for birds of prey.

Management strategies like habitat improvement and restocking can be costly, so it is essential to prioritise cost-effective measures. For example, promoting self-regrowing crops can help sustain the food supply for rabbits, without requiring frequent replanting (**Chapter 3**). Additionally, we recommend using pallet warrens in restocking programs, as they are more economical and have a higher usage than more expensive and complex warren designs (**Chapter 5**).

Rabbit populations, especially restocked ones, should undergo regular long-term monitoring to assess survival rates, dispersion patterns, distribution, abundance, and disease incidence (**Chapters 3** and **4**). Continuous evaluation of conservation efforts is key to implementing adaptive management strategies, ensuring solutions are data-driven. This approach will help address emerging challenges and improve outcomes, thereby improving rabbit recovery protocols and ensuring their survival within Mediterranean ecosystems.

6.3. Limitations and future research

While this thesis provides valuable insights into Iberian rabbit management, several limitations were identified across the three studies that may have influenced the results and interpretations. Addressing these gaps will be essential for refining management plans and enhancing conservation outcomes for the Iberian rabbit.

One limitation is the specific geographical context in which the studies were conducted, which may restrict the generalisation of findings to other regions with different ecological conditions.

In the first study (**Chapter 3**), rabbit presence was used as the response variable in the three sampling periods - during habitat management (2008), immediately after (2009) and three years after (2012) - because rabbits were present on too few sites to allow a more robust statistical analysis based on rabbit abundance. In 2007, rabbit presence remained too low, with only five detections, preventing the use of GLM analysis, thereby limiting statistical analysis to the subsequent three sampling periods.

Moreover, the lack of long-term monitoring hindered the assessment of the persistence of trends in rabbit presence and abundance immediately following the cessation of habitat management. Future studies should incorporate extended monitoring periods of at least 7 to 10 years to ensure the robust detection of sustained population trends and the effective evaluation of management interventions (e.g., Moreno et al., 2007; Delibes-Mateos et al., 2009a; Sarmento et al., 2012). Monitoring should be carried out at least once a year, preferably during the peak of the reproductive period. Long-term monitoring is also particularly important for understanding the impacts of key factors such as disease outbreaks and changes in habitat or environmental conditions.

In **Chapters 3 and 5**, rabbit sampling relied on indirect methods, such as detecting presence signs, pellets and latrines, which can, however, degrade due to rainfall or natural decomposition (Iborra and Lumaret, 1997; Fernández-de-Simon et al., 2011). Nevertheless, these methods are widely used in assessing rabbit abundance indices (e.g., Virgós et al., 2003; Calvete et al., 2004; Beja et al., 2007; Godinho et al., 2013) and were considered the most suitable given study conditions at the time and in that study area. In the first study (**Chapter 3**), the low rabbit density and dense vegetation cover would have made direct counting methods ineffective. In the third study (**Chapter 5**), radiotelemetry data from artificial warrens were insufficient for drawing reliable conclusions.

The primary limitation in the second (**Chapter 4**) and third studies (**Chapter 5**) lies in the restricted scope of the research, which was limited to a single restocking park. Moreover, the second study involved a limited sample size of rabbits monitored by radiotelemetry, while the third study included only two replicates per warren type.

Although some results from both studies are statistically significant and provide useful insights for enhancing rabbit restocking success, the limited number of replicates may weaken the conclusions. Therefore, caution is needed when generalising these findings to broader contexts. Ideally, future research should encompass multiple restocking sites, monitor a greater number of rabbits using radio or GPS telemetry, and include additional warrens to validate some of the findings. However, the high financial cost of these measures poses challenges for implementing this approach.

In the second study (**Chapter 4**), due to the "Compensatory measures and specific monitoring of the Odelouca's Bonelli eagle couple, arising from the environmental impact assessment process of the Sines-Portimão high-voltage power line" project goals (REN et al., 2009), no measures were taken to mitigate avian predation, potentially influencing rabbit mortality rates. Future studies should explore cost-effective exclusion methods to reduce aerial predation, particularly during the initial weeks following rabbit restocking (e.g., Guerrero-Casado et al., 2013b). For instance, establishing several smaller restocking parks could mitigate surplus killing (Short et al., 2002), while testing different net types to cover the top of the restocking park, such as wire nets, hard plastic nets or soft and flexible plastic nets could enhance protection.

Although the impact of diseases was not the primary focus of this thesis, it was monitored as part of the project that funded the fieldwork. A veterinary team regularly surveyed the semi-natural enclosure and surrounding area to detect and prevent myxomatosis and rabbit haemorrhagic disease (RHD) outbreaks impacting the rabbit population, searching for dead or sick rabbits and collecting pellets for laboratory analysis. No signs of myxomatosis or RHD were observed in the study area during the study period. At the end of 2008, we found only one rabbit carcass exhibiting symptoms of myxomatosis near the study area (REN et al., 2009). Therefore, it appears that these diseases were not a significant issue in the study area at the time.

However, the ongoing threat of diseases, particularly the variant of the RDH virus known as RHDV2 (Monterroso et al., 2016; Villafuerte and Delibes-Mateos, 2019; Asin et al., 2024), poses a significant risk to Iberian rabbit populations. Therefore, it is essential to establish and implement a well-structured sanitary monitoring plan for rabbits, enabling timely preventive and mitigation actions in response to disease outbreaks. Local plans can be implemented in cooperation with large-scale projects, such as the LIFE Iberconejo project - "Drawing the baselines for the good management of a Mediterranean key species, the wild rabbit" (LIFE20 GIE/ES/000731) or the Portuguese projects "+Coelho" and "+Coelho2", both coordinated by the Portuguese National Institute of Agricultural and Veterinary Research (INIAV) (Duarte et al., 2020).

One of the goals originally set for the semi-natural enclosure was to serve as a rabbit source for local translocations, aiming to establish new populations and improve connectivity between existing ones. The aim was to capture rabbits within the semi-natural acclimation enclosure, but only if the enclosure supported a high density of rabbits capable of long-term self-sustainability. The plan involved soft-release translocations (Rouco et al., 2010) into temporarily fenced areas, providing complete protection against predation and supplying necessary resources such as shelter, food, and water. This process would contribute to expanding Iberian rabbit distribution in the area by installing temporary fenced plots in locations with suitable habitat, or where habitat enhancement is feasible, but where the species is absent. Additionally, the stress associated with transportation would be minimised since the time between capture and release would be reduced. Furthermore, rabbits would face less stress adapting to their new habitat, as they would already be acclimatised to conditions like those at the release site. Unfortunately, the previous actions and goals could not be achieved due to financial constraints associated with the premature conclusion of the project by the financing entity.

In 2018, a large-scale wildfire consumed approximately 27,000 hectares of forest and agricultural land in the Monchique municipality within a week (ICNF, 2018). The fire destroyed dozens of homes and a significant portion of the study area, including the semi-natural enclosure and surrounding areas. Unfortunately, to the best of our knowledge, no studies have assessed the exact impact of this wildfire on local Iberian rabbit populations. Nevertheless, evaluating the status of these populations in the Serra de Monchique is essential.

6.4. Concluding remarks

This thesis contributes significantly to the knowledge required to enhance management strategies for future conservation efforts focused on recovering the Iberian rabbit *Oryctolagus cuniculus algirus*.

The three studies presented emphasise the importance of implementing evidence-based strategies to enhance habitat quality, optimise restocking efforts, and refine the selection and placement of artificial warrens.

The thesis findings suggest that rabbit recovery efforts should prioritise cost-effective and proven strategies, particularly habitat improvements implemented across broad temporal and spatial scales (Carro et al., 2019). Common management practices, such as rabbit restocking—especially traditional restocking methods—frequently exhibit high failure rates (Calvete et al., 1997; Calvete and Estrada, 2004; Tobajas et al., 2021). Therefore, restocking should be considered an exceptional measure, to be implemented only after ensuring that all habitat requirements are fulfilled and all relevant factors known to influence restocking success have been carefully considered (Carro et al., 2019; Delibes-Mateus et al., 2023).

The decline of the Iberian rabbit over the past 15 years has been more severe than ever, largely due to new variant disease outbreaks affecting the Iberian population. Therefore, implementing measures for population management becomes even more critical. The insights provided in this thesis offer valuable guidance for future recovery and conservation efforts, helping to ensure the species' survival within Mediterranean ecosystems. This research provides a solid foundation for future rabbit conservation studies and practical guidelines that can be successfully applied in similar ecological contexts.

Ultimately, the findings presented in the thesis contribute to the Iberian rabbit conservation and, by extension, to the maintenance of broader Mediterranean ecosystems that depend on this keystone species.

Chapter 7

References

Abrantes, J., van der Loo, W., Le Pendu, J., Esteves, P.J. (2012). Rabbit haemorrhagic disease (RHD) and rabbit haemorrhagic disease virus (RHDV): A review*. Veterinary Research*, 43: 12.

Abrantes, J., Lopes, A.M., Dalton, K.P., Melo, P., Correia, J.J., Ramada, M., Alves, P.C., Parra, F., Esteves, P.J. (2013). New variant of rabbit haemorrhagic disease virus, Portugal, 2012–2013. *Emerging Infectious Diseases*, 19: 1900-1902.

Alves, J.M., Carneiro, M., Cheng, J.Y., Lemos de Matos, A., Rahman, M.M., Loog, L., Campos, P.F., Wales, N., Eriksson, A., Manica, A., Strive, T., Graham, S.C., Afonso, S., Bell, D.J., Belmont, L., Day, J.P., Fuller, S.J., Marchandeau, S., Palmer, W.J., Queney, G., Surridge, A.K., Vieira, F.G., McFadden, G., Nielsen, R., Gilbert, M.T.P., Esteves, P.J., Ferrand, N., Jiggins, F.M. (2019). Parallel adaptation of rabbit populations to myxoma virus. *Science*, 363: 1319-1326.

Alves, P.C., Moreno, S. (1996). Estudo da reprodução do coelho-bravo em Portugal. *Revista Florestal*, 9: 149-166.

Angulo, E. (2003). Factores que afectan a la distribución y abundancia del conejo en Andalucía. PhD Thesis, Complutense University, Madrid, Spain.

Angulo, E., Villafuerte, R. (2003). Modelling hunting strategies for the conservation of wild rabbit populations. *Biological Conservation*, 115: 291-301.

APA - Agência Portuguesa do Ambiente, I.P. (2013). Boletim de temperatura. SNIRH (Sistema Nacional de Informação de Recursos Hídricos). http://www.snirh.pt

APA - Agência Portuguesa do Ambiente, I.P. (2018). Massas de água superficiais. Rios de Portugal continental: conjunto de dados geográfico SNIAmb. https://sniamb.apambiente.pt

Argüello, J.L., Llanos, A., Pérez, L.I. (1988). Enfermedad hemorrágica del conejo en España. *Revista de Medicina Veterinaria*, 5: 645-650

Armenteros, J. A., Sánchez-García, C., Alonso, M. E., Larsen, R. T., Gaudioso, V. R. (2015). Use of water troughs by wild rabbits (*Oryctolagus cuniculus*) in a farmland area of north-west Spain. *Animal Biodiversity and Conservation*, 38: 233-240.

ASAB/ABS. (2006). Guidelines for the treatment of animals in behavioural research and teaching. *Animal Behavior*, 71: 245-253.

Asin, J., Calvete, C., Uzal, F.A., Crossley, B.M., Duarte, M.D., Henderson, E.E., Abade Dos Santos, F. (2024). Rabbit hemorrhagic disease virus 2, 2010-2023: a review of global detections and affected species. *Journal of Veterinary Diagnostic Investigation*, 36: 617-637.

Barnett, L.K., Prowse, T.A.A., Peacock, D.E., Mutze, G.J., Sinclair, R.G., Kovaliski, J., Cooke, B.D., Bradshaw, C.J.A. (2018). Previous exposure to myxoma virus reduces survival of European rabbits during outbreaks of rabbit haemorrhagic disease. *Journal of Applied Ecology*, 55: 2954-2962.

Barrio, I.C., Bueno, C.G., Tortosa, F.S. (2009). Improving predictions of the location and use of warrens in sensitive rabbit populations. *Animal Conservation*, 12: 426-433.

Barrio, I.C., Bueno, C.G., Tortosa F.S. (2010). Alternative food and rabbit damage in vineyards of southern Spain. *Agriculture, Ecosystems and Environment*, 138: 51-54.

Barrio, I.C., Bueno, C.G., Villafuerte, R., Tortosa, F.S. (2013). Rabbits, weeds and crops: Can agricultural intensification promote wildlife conflicts in semiarid agro-ecosystems? *Journal of Arid Environments*, 90: 1-4.

Barton, K. (2014). MuMIn: Multi-model inference. R package version 1.10.7/r295. http://R-Forge.R-project.org/projects/mumin/

Barton, K. (2020). MuMIn: Multi-Model Inference. R package version 1.43.17. https://CRAN.R-project.org/package=MuMIn

Beja, P., Pais, M., Palma, L. (2007). Rabbit *Oryctolagus cuniculus* habitats in Mediterranean scrubland: The role of scrub structure and composition. *Wildlife Biology*, 13: 28-37.

Beja, P., Gordinho, L., Reino, L., Loureiro, F., Santos-Reis, M., Borralho, R. (2009). Predator abundance in relation to small game management in southern Portugal: Conservation implications. *European Journal of Wildlife Research*, 55: 227-238.

Blázquez, M.C., Villafuerte, R. (1990). Nesting of the Montpellier snake (*Malpolon monspessulanus*) inside rabbit warrens ate Doñana National Park (SW Spain): phenology and a probable case of communal nesting. *Journal of Zoology*, 222: 692-693.

Bobadilla, S.Y., Olivares, E.T., Jaksic, F.M., Ojeda, R.A., Cuevas, M.F. (2023). European rabbit (*Oryctolagus cuniculus*) as seed disperser in arid ecotones of Argentina: non-native herbivore facilitation of native and non-native plants. *Mammal Research*, 68: 625-635.

Borcard, D., Legendre, P., Drapeau, P. (1992). Partialling out the spatial component of ecological variation. *Ecology*, 73: 1045-1055.

Branco M., Ferrand N., Monnerot N. (2000). Phylogeography of the European rabbit (*Oryctolagus cuniculus*) on the Iberian Peninsula inferred from RFLP analysis of the cytochrome b gene. *Heredity*, 85: 307-317.

Burgman, M.A., Fox, J.C. (2003). Bias in species range estimates from minimum convex polygons: implications for conservation and options for improved planning. *Animal Conservation*, 6: 19-28.

Burnham, K.P., Anderson, D.R. (2002). Model selection and multi-model inference: A practical information—Theoretic approach (2nd ed.). New York, NY: Springer-Verlag. 488 pp.

Cabezas, S., Moreno, S. (2007). An experimental study of translocation success and habitat improvement in wild rabbits. *Animal Conservation*, 10: 340-348.

Cabezas, S., Calvete, C., Moreno, S. (2011). Survival of translocated wild rabbits: importance of habitat, physiological and immune condition. *Animal Conservation*, 14(6): 587-696.

Cabral, M.J. (coord.), Almeida, J., Almeida, P.R., Dellinger, T., Ferrand de Almeida, N., Oliveira, M.E.; Palmeirim, J.M., Queiroz, A.I.; Rogado, L., Santos-Reis, M. (eds.). (2005). Livro Vermelho dos Vertebrados de Portugal. 2ª Edição. Instituto da Conservação da Natureza/Assírio Alvim, Lisboa. 660 pp.

Calenge, C. (2006). The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling*, 197: 516-519.

Calvete, C. (2006). Modelling the effect of population dynamics on the impact of rabbit hemorraghic disease. *Conservation Biology*, 20: 1232-1241.

Calvete, C., Estrada, R. (2004). Short-term survival and dispersal of translocated European wild rabbits. Improving the release protocol. *Biological Conservation*, 120(4): 507-516.

Calvete, C., Villafuerte, R., Lucientes, J., Osacar, J.J. (1997). Effectiveness of traditional wild rabbit restocking in Spain. *Journal of Zoology*, 241: 271-277.

Calvete, C., Estrada, R., Angulo, E., Cabezas-Ruiz, S. (2004). Habitat factors related to wild rabbit conservation in an agricultural landscape. *Landscape Ecology*, 19: 531-542.

Calvete, C., Angulo, E., Estrada, R. (2005). Conservation of European wild rabbit populations when hunting is age and sex selective. *Biological Conservation*, 121: 623-634.

Calvete, C., Pelayo, E., Javier Sampietro, F. (2006). Habitat factors related to wild rabbit population trends after the initial impact of rabbit haemorrhagic disease. *Wildlife Research*, 33: 467-474.

Calvete, C., Sarto, P., Calvo, A.J., Monroy, F., Calvo, J.H. (2014). Could the new rabbit haemorrhagic disease virus variant (RHDVb) be fully replacing classical RHD strains in the Iberian Peninsula? *World Rabbit Science*, 22: 91.

Cancellotti, F.M., Renzi, M. (1991). Epidemiology and current situation of viral haemorrhagic disease of rabbits and the European brown hare syndrome in Italy. *Revue scientifique et technique*, 10: 409-422.

Carneiro, M., Blanco, J.A., Villafuerte, R., Ferrand, N., Nachman, M.W. (2010). Speciation in the European rabbit (*Oryctolagus cuniculus*): islands of differentiation on the X-chromosome and autosomes. *Evolution*, 64: 3443-3460.

Carro, F., Ortega, M., Soriguer, R.C. (2019). Is restocking a useful tool for increasing rabbit densities? *Global Ecology and Conservation*, 17(2): e00560.

Carvalho, J., Hipólito, D., Teixeira, D., Fonseca C., Torres, R.T. (2024). Hunting bag statistics of wild mammals in Portugal (1989–2022): on the need to improve data report and compilation. *European Journal of Wildlife Research*, 70: 96.

Carvalho, J.C., Gomes, P. (2004). Influence of herbaceous cover, shelter and land cover structure on wild rabbit abundance in the NW Portugal. *Acta Theriologica*, 49: 63-74.

Catalán, I., Rodríguez-Hidalgo, P., Tortosa, F.S. (2008). Is habitat management an effective tool for wild rabbit (*Oryctolagus cuniculus*) population reinforcement? *European Journal of Wildlife Research*, 54: 449-453.

CNA - Comissão Nacional do Ambiente. (1982). Carta I.15—Carta hipsométrica, 1:1,000,000. Atlas do Ambiente Digital - Instituto do Ambiente. http://www.apambiente.pt

Cooke, B. (2008). Managing the European rabbit: converging interests between Australian research for rabbit control and European research for their conservation. In: Alves, P.C., Ferrand, N., Hackländer, K. (eds.). Lagomorph Biology:

Evolution, Ecology and Conservation, Springer-Verlag, Berlin, Heidelberg, pp. 317–326.

Cooke, B.D., Flux, J.F.C. and Bonino, N. (2018). Introduced lagomorphs. In: Smith, A.T., Johnston, C.H., Alves, P.C., Hacklander, K. (eds.). Lagomorphs: Pikas, Rabbits, and Hares of the World, Johns Hopkins University Press, Baltimore, Maryland, USA, pp. 13-17.

Cortés-Avizanda, A., Colomer, M.A., Margalida, A., Ceballos, O., Donázar, J.A. (2015). Modeling the consequences of the demise and potential recovery of a keystone-species: Wild rabbits and avian scavengers in Mediterranean landscapes. *Scientific Reports*, 5: 17033.

Cotilla, I., Villafuerte, R. (2007). Rabbit conservation: models to evaluate the effects of timing of restocking on recipient and donor populations. *Wildlife Research*, 34: 247-252.

Courchamp, F., Langlais, M., Sugihara, G. (1999). Control of rabbits to protect island birds from cat predation. *Biological Conservation*, 89: 219-225.

Cushman, S.A., McGarigal, K. (2002). Hierarchical, multi-scale decomposition of species-environment relationships. *Landscape Ecology*, 17: 637-646.

D'Amico, M., Tablado, Z., Revilla, E., Palomares, F. (2014). Free housing for declining populations: Optimizing the provision of artificial breeding structures. *Journal for Nature Conservation*, 22: 369-376.

Dalton, K.P., Nicieza, I., Balseiro, A., Muguerza, M.A., Rosell, J.M., Casais, R., Alvarez, A. L. Parra, F. (2012). Variant rabbit hemorrhagic disease virus in young rabbits, Spain. *Emerging Infectious Diseases*, 18: 2009-2012.

Dalton, K.P., Nicieza, I., Abrantes, J., Esteves, P.J., Parra, F. (2014). Spread of new variant RHDV in domestic rabbits on the Iberian Peninsula. *Veterinary Microbiology*, 169: 67-73.

Delibes, M., Hiraldo, F. (1981). The rabbit as prey in the Iberian Mediterranean ecosystem. In: Myers, K., MacInnes, C.D. (eds.). Proceedings of the World Lagomorph Conference. Ontario: University of Güelph & Wildlife Research, Ministry of Natural Resources, pp. 614-622.

Delibes-Mateos, M., Redpath, S.M., Angulo, E., Ferreras, P., Villafuerte, R. (2007). Rabbits as a keystone species in southern Europe. *Biological Conservation*, 137: 149-156.

Delibes-Mateos, M., Delibes, M., Ferreras, P., Villafuerte, R. (2008a). Key role of European rabbits in the conservation of the Western Mediterranean basin hotspot. *Conservation Biology*, 22: 1106-1117.

Delibes-Mateos, M., Ferreras, P., Villafuerte, R. (2008b). Rabbit populations and game management: The situation after 15 years of rabbit haemorrhagic disease in central-southern Spain. *Biodiversity and Conservation*, 17: 559-574.

Delibes-Mateos, M., Ramírez, E., Ferreras, P., Villafuerte, R. (2008c). Translocations as a risk for the conservation of European wild rabbit *Oryctolagus cuniculus* lineages. *Oryx*, 42(2): 259-264.

Delibes-Mateos, M., Ferreras, P., Villafuerte, R. (2009a). European rabbit population trends and associated factors: a review of the situation in the Iberian Peninsula. *Mammal Review*, 39: 124-140.

Delibes-Mateos, M., Ferreras, P., Villafuerte, R. (2009b). Rabbit (*Oryctolagus cuniculus*) abundance and protected areas in central-southern Spain: why they do not match? *European Journal of Wildlife Research*, 55: 65-69.

Delibes-Mateos, M., Farfán, M.A., Olivero J., Vargas, J.M. (2010). Land use changes as a critical factor for long-term wild rabbit conservation in the Iberian Peninsula. *Environmental Conservation*, 37: 169-176.

Delibes-Mateos, M., Smith, A.T., Slobodchikoff, C.N., Swenson, J.E. (2011). The paradox of keystone species persecuted as pests: a call for the conservation of abundant small mammals in their native range. *Biological Conservation*, 144: 1335-1346.

Delibes-Mateos, M., Díaz-Fernández, S., Ferreras, P., Viñuela, J., Arroyo, B. (2013). The Role of Economic and Social Factors Driving Predator Control in Small-Game Estates in Central Spain. *Ecology and Society*, 18(2): 28.

Delibes-Mateos, M., Ferreira, C., Rouco, C., Villafuerte, R. and Barrio, I.C. (2014a). Conservationists, hunters and farmers: the European rabbit *Oryctolagus cuniculus* management conflict in the Iberian Peninsula. *Mammal Review*, 40: 190-203.

Delibes-Mateos, M., Ferreira, C., Carro, F., Escudero, M.A., Gortázar, C. (2014b). Ecosystem effects of variant rabbit hemorrhagic disease virus, Iberian Peninsula. *Emerging infectious diseases*, 20: 2166-2168.

Delibes-Mateos, M., Farfán, M.A., Rouco, C., Olivero, J., Marquez, A.L., Fa, J., Vargas, J.M., Villafuerte, R. (2018a). A large-scale assessment of European rabbit damage to agriculture in Spain. *Pest Management Science*, 74: 111-118.

Delibes-Mateos, M., Villafuerte, R., Cooke, B.D., Alves, P.C. (2018b). *Oryctolagus cuniculus* (Linnaeus,1758). In: Smith, A.T., Johnston, C.H., Alves, P.C., Hacklander, K. (eds.). Lagomorphs: Pikas, Rabbits, and Hares of the World, Johns Hopkins University Press, Baltimore, Maryland, USA, pp. 99-103.

Delibes-Mateos, M., Arroyo, B.E., Ruiz, J., Garrido, F.E., Redpath, S.M., Villafuerte, R. (2020). Conflict and cooperation in the management of European rabbit *Oryctolagus cuniculus* damage to agriculture in Spain. *People and Nature*, 2(4): 1223-1236.

Delibes-Mateos, M., Rödel, H.G., Rouco, C., Alves, P.C., Carneiro, M., Villafuerte, R. (2023). European Rabbit *Oryctolagus cuniculus* (Linnaeus, 1758). In: Hackländer, K., Alves, P.C. (eds.). Primates and Lagomorpha. Handbook of the Mammals of Europe., Springer, Cham.

Dellafiore, C.M., Gallego Fernández, J.B., Vallés, S.M. (2008). Habitat use for warren building by European rabbits (*Oryctolagus cuniculus*) in relation to landscape structure in a sand dune system. *Acta Oecologica*, 33: 372-379.

Dellafiore, C.M., Gallego Fernández, J.B., Vallés, S.M. (2010). The rabbit (*Oryctolagus cuniculus*) as a seed disperser in a coastal dune system. *Plant Ecology*, 206: 251-261.

Devillard, S., Aubineau, J., Léger, F., Léonard, F., Roobrouck, A., Marchandeau, S. (2008). Home range of the European rabbit (*Oryctolagus cuniculus*) in three contrasting French populations. *Mammalian Biology*, 73: 128-137.

Díaz-Ruiz, F., Vaquerizas, P.H., Márquez, A.L., Delibes-Mateos, M., Piorno, V., Castro, F., Ramírez, E., Farfán, M.Á., Olivero, J., Real, R., Villafuerte, R. (2023). Unravelling the historical biogeography of the European rabbit subspecies in the Iberian Peninsula. *Mammal Review*, 53: 1-14.

Diniz-Filho, J.A.F., Bini, L.M. (2005). Modelling geographical patterns in species richness using eigenvector-based spatial filters. *Global Ecology and Biogeography*, 14: 177-185.

Donázar, J.A., Ceballos, O. (1989). Selective predation by eagle owls Bubo bubo on rabbits *Oryctolagus cuniculus*: age and sex preferences. *Ornis Scandinavica*, 20: 117-122.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36: 27-46.

Drees, M.J.M., Dekker, J.J.A., Wester, L., Olff, H. (2009). The translocation of rabbits in a sand dune habitat: survival, dispersal and predation in relation to food quality and the use of burrows. *Lutra*, 52(2): 109-122.

Duarte, M., Carvalho, C. L., Santos, F. A., Monteiro, J., Gomes, J., Alves, P. C., Esteves, P. J., Abrantes, J., Lopes, A. M., Monterroso P., Serronha, A., Santos, N., Santos, Santos, P.T., Carvalho, J., Pinto, F. C., J. Bernardino, Amaro, J. (2020). "+Coelho2: Desenvolvimento e implementação de medidas práticas impulsionadoras da recuperação dos leporídeos silvestres em Portugal”. Relatório de atividades na época venatória 2018-2019 e 2019-2020. INIAV I.P., DGAV, CIBIO, ANPC, CNCP, FENCAÇA. Fundo Florestal Permanente. ICNF.

Dudzinski, M.L., Mykytowycz, R. (1960). Analysis of weights and growth rates of an experimental colony of wild rabbits, *Oryctolagus cuniculus* (L.). *CSIRO Wildlife Research*, 5(2): 102-115.

Ecosativa (Consultadoria Ambiental, Lda.). (2007). Programa de Gestão de Habitat do Parque Eólico de Madrinha. 2nd Progress report and technical proposal reformulation to EDP—Portuguese Energies. Portimão, Portugal.

EEA - European Environment Agency. (2013). Digital elevation model over Europe (EU-DEM). http://www.eea.europa.eu/data-and-maps/data/eu-dem

EFSA AHAW Panel (EFSA Panel on Animal Health and Welfare), Saxmose, Nielsen S., Alvarez, J., Bicout, D.J., Calistri, P., Depner, K., Drewe, J.A., Garin-Bastuji, B., Gonzales Rojas, J.L., Gortazar Schmidt, C., Michel, V., Miranda Chueca, M.A., Roberts, H.C., Sihvonen, L.H., Spoolder, H., Stahl, K., Velarde Calvo, A., Viltrop, A., Buijs, S., Edwards, S., Candiani, D., Mosbach-Schulz, O., Van der Stede, Y., Winckler, C. (2020). Scientific Opinion on the health and welfare of rabbits farmed in different production systems. *EFSA Journal 2020*, 18: 5944.

Eldridge, D.J., Myers, C.A. (2001). The impact of warrens of the European rabbit (*Oryctolagus cuniculus* L.) on soil and ecological processes in a semi-arid Australian woodland. *Journal of Arid Environments*, 47: 325-337.

Eldridge, D.J., Simpson, R. (2002). Rabbit (*Oryctolagus cuniculus* L.) impacts on vegetation and soils, and implications for management of wooded rangelands. *Basic and Applied Ecology*, 3: 19-29.

Encarnação, C., Medinas, D., Alves, P.C., Mira, A. (2019). Does short-term habitat management for the European rabbit (*Oryctolagus cuniculus*) have lasting effects? *Ecological Research*, 34: 296-308.

Fa, J.E., Sharples, C.M., Bell, D.J., DeAngelis, D. (2001). An individual based model of rabbit viral haemorrhagic disease in European wild rabbits (*Oryctolagus cuniculus*). *Ecological Modelling*, 144: 121-138.

Farfán, M.A., Vargas, J.M., Guerrero, J.C., Barbosa, A.M., Duarte, J., Real, R. (2008). Distribution modelling of wild rabbit hunting yields in its original area (S Iberian Peninsula). *Italian Journal of Zoology*, 75: 161-172.

Fenner, F., Ratcliffe, F.N. (1965). Myxomatosis. Cambridge University Press, Cambridge, UK.

Fenner, F., Ross, J. (1994). Myxomatosis. In: Thompson, H.V., King, C.M. (Eds.), The European Rabbit. The History and Biology of Successful Colonizer. Oxford University Press, Oxford, UK, pp. 205–239.

Fernandez-Ales, R., Martin, A., Ortega, F., Enrique, A. (1992). Recent changes in landscape structure and function in a Mediterranean region of SW of Spain (1950-1984). *Landscape Ecology*, 7: 3-18.

Fernandez-de-Simon, J. (2013). Predation and the recovery of the European rabbit populations in central-southern Iberian Peninsula. An assessment of the predator pit hypothesis (master's thesis). University of Castilla-La Mancha. 192 pp.

Fernandez-de-Simon, J., Díaz-Ruiz, F., Villafuerte, R., Delibes-Mateos, M., Ferreras, P. (2011). Assessing predictors of pellet persistence in European rabbits *Oryctolagus cuniculus*: towards reliable population estimates from pellet counts. *Wildlife Research*, 17: 317-325.

Fernández-Olalla, M., Martínez-Jauregui, M., Guil, F., San, A. (2010). Provision of artificial warrens as a means to enhance native wild rabbit populations: What type of warren and where should they be sited? *European Journal of Wildlife Research*, 56: 829-837.

Ferrand, N. (2008). Inferring the evolutionary history of the European rabbit (*Oryctolagus cuniculus*) from molecular markers. In: Alves, P.C., Ferrand, N., Hackländer, K. (eds.). Lagomorph Biology: Evolution, Ecology and Conservation, Springer-Verlag, Berlin, Heidelberg, pp. 47-63.

Ferreira, C., Alves, P.C. (2005) Impacto da implementação de medidas de gestão do habitat nas populações de coelho-bravo (*Oryctolagus cuniculus algirus*) no Parque Natural do Sudoeste Alentejano e Costa Vicentina. Relatório final do protocolo de colaboração entre ICN/PNSACV e CIBIO-UP. 95 pp.

Ferreira, C., Alves, P.C. (2009). Influence of habitat management on the abundance and diet of wild rabbit (*Oryctolagus cuniculus algirus*) populations in Mediterranean ecosystems. *European Journal of Wildlife Research*, 55: 487-496.

Ferreira, C., Delibes-Mateos, M. (2010). Wild Rabbit Management in the Iberian Peninsula: State of the Art and Future Perspectives for Iberian Lynx Conservation. *Wildlife Biology in Practice*, 6: 48-66.

Ferreira, C., Ramírez, E., Castro, F., Ferreras, P., Alves, P.C., Redpath, S., Villafuerte, R. (2009). Field experimental vaccination campaigns against myxomatosis and their effectiveness in the wild. *Vaccine*, 27: 6998-7002.

Ferreira, C., Paupério, J., Alves, P.C. (2010). The usefulness of field data and hunting statistics in the assessment of wild rabbit (*Oryctolagus cuniculus*) conservation status in Portugal. *Wildlife Research*, 37: 223-229.

Ferreira, C., Touza, J., Rouco, C., Díaz-Ruiz, F., Fernandez-de-Simon, J., Ríos-Saldaña, C.A., Ferreras, P., Villafuerte, R., Delibes-Mateos, M. (2013). Habitat management as a generalized tool to boost European rabbit *Oryctolagus cuniculus* populations in the Iberian Peninsula: a cost-effectiveness analysis. *Mammal Review*, 44: 30-43.

Ferreira, C., Touza, J., Rouco, C., Díaz-Ruiz, F., Fernandez-de-Simon, J., Ríos-Saldaña, C. A., Ferreras, P., Villafuerte, R., Delibes-Mateos, M. (2014). Habitat management as a generalized tool to boost European rabbit *Oryctolagus cuniculus* populations in the Iberian Peninsula: A cost-effectiveness analysis. *Mammal Review*, 44: 30-43.

Ferreira, C., Castro, F., Piorno, V., Barrio, I., Delibes-Mateos, M., Rouco, C., Mínguez L.E., Aparicio F., Blanco-Aguiar J.A., Ramírez E., Iriarte C., Ríos-Saldaña C.A., Cañadilla J., Arias de Reyna L., Ferreras P., Alves P.C., Villafuerte R. (2015). Biometrical analysis reveals major differences between the two subspecies of the European rabbit. *Biological Journal of the Linnean Society*, 116: 106-116.

Ferreira, C.C, Alves, P.C., Lourenço, R., Bencatel, J. (2017). Lagomorfos (Lagomorpha). In Bencatel, J., Alvares, F., Moura, A.E., Barbosa, A.M. (eds.). Atlas de Mamíferos de Portugal. Portugal, Universidade de Évora, pp. 39-59.

Ferrer, M., Penteriani, V., Balbontın, J., Pandolfi, M. (2003). The proportion of immature breeders as a reliable early warning signal of population decline: evidence from the Spanish imperial eagle in Doñana. *Biological Conservation*, 114(3), 463-466.

Ferreras, P., Travaini, A., Zapata, S.C., Delibes, M. (2011). Short-term responses of mammalian carnivores to a sudden collapse of rabbits in Mediterranean Spain. *Basic and Applied Ecology*, 12: 116-124.

Fouchet, D., Guitton, J.S., Marchandeau, S., Pontier, D. (2008). Impact of myxomatosis in relation to local persistence in wild rabbit populations: the role of waning immunity and the reproductive period. *Journal of Theoretical Biology*, 250: 593-605.

Fox, J., Weisberg, S. (2019). An {R} Companion to Applied Regression, 3rd edition. Sage, Thousand Oaks CA. https://socialsciences.mcmaster.ca/jfox/Books/Companion/

Galante, E., Cartagena, M.C. (1999). Comparison of Mediterranean dung beetles (Coleoptera: Scarabaeoidea) in cattle and rabbit dung. *Environmental Entomology*, 28: 420-424.

Gálvez, L., López-Pintor, A., De Miguel, J.M., Alonso, G., Rueda, M., Rebollo, S., Gómez-Sal, A. (2008). Ecosystem engineering effects of European rabbits in a Mediterranean habitat. In: Alves, P.C., Ferrand, N., Hackländer, K. (eds.). Lagomorph Biology: Evolution, Ecology and Conservation, Springer-Verlag, Berlin, Heidelberg, pp. 125-140.

Gálvez-Bravo, L., Belliure, J., Rebollo, S. (2009). European rabbits as ecosystem engineers: warrens increase lizard density and diversity. *Biodiversity Conservation*, 18: 869-885.

Gannon, W. L., Sikes, R. S., Animal Care and Use Committee of the American Society of Mammalogists. (2007). Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy*, 88: 809-823.

García, F. (2003). Revisión de las actuaciones para el fomento de las poblaciones de conejo de monte. 1er Informe anual. Madrid: Dirección General para la Conservación de la Naturaleza - Ministerio de Medio Ambiente. 171 pp.

Gea-Izquierdo, G., Muñoz-Igualada, J., San Miguel-Ayanz, A. (2005). Rabbit warren distribution in relation to pasture communities in Mediterranean habitats: consequences for management of rabbit populations. *Wildlife Research*, 32: 723-731.

Geraldes, A., Carneiro, M., Delibes-Mateos, M., Villafuerte, R., Nachman, M.W., Ferrand, N. (2008). Reduced introgression of the Y chromosome between subspecies of the European rabbit (*Oryctolagus cuniculus*) in the Iberian Peninsula. *Molecular Ecology*, 17: 4489–4499.

Gibb, J. (1993). Sociality, time and space in sparse population of rabbits (*Oryctolagus cuniculus*). *Journal of Zoology*, 229: 581-607.

Godinho, S., Mestre, F., Ferreira, J.P., Machado, R., Santos, P. (2013). Effectiveness of habitat management in the recovery of low-density populations of wild rabbit. *European Journal of Wildlife Research*, 59: 847-858.

Gonçalves, H., Alves, P.C., Rocha, A. (2002). Seasonal variation in the reproductive activity of the wild rabbit (*Oryctolagus cuniculus algirus*) in a Mediterranean ecosystem. Wildlife Research, 29: 165-173.

González, L.M., San Miguel, A. (2004). Manual de gestión de fincas de monte mediterráneo de la Red Natura 2000. Ministerio de Medio Ambiente. Madrid. 327

pp.

Gonzalez-Bernaldez, F. (1991). Ecological consequences of the abandonment of traditional land use systems in central Spain. *CIHEAM—Options Mediterranéennes, Série Séminaires*, 15: 23-29.

GRASS Development Team. (2014). Geographic resources analysis support system (GRASS) software, Version 6.4.4. Beaverton, Oregon: Open Source Geospatial Foundation. https://grass.osgeo.org/home/about-us/

Griffith, B., Scott, J.M., Carpenter, J.W., Reed, C. (1989). Translocation as a species conservation tool: status and strategy. *Science*, 245: 477-480.

Griffith, D.A., Peres-Neto, P.R. (2006). Spatial modelling in ecology: The flexibility of eigenfunction spatial analyses. *Ecology*, 87: 2603-2613.

Guerrero-Casado, J., Letty, J., Tortosa, F.S. (2013a). European rabbit restocking: a critical review in accordance with IUCN (1998) guidelines for re-introduction. *Animal Biodiversity Conservation*, 2: 177-185.

Guerrero-Casado, J., Ruiz-Aizpurua, J., Tortosa, F.S. (2013b). The short-term effect of total predation exclusion on wild rabbit abundance in restocking plots. *Acta Theriologica*, 58: 415-418.

Guerrero-Casado, J., Carpio, A.J., Tortosa, F.S. (2016). Recent negative trends of wild rabbit populations in southern Spain after the arrival of the new variant of the rabbit haemorrhagic disease virus RHDV2. *Mammal Biology*, 81: 361-364.

Guerrero-Casado, J., Ström, H., Hilström, L., Prada, L.M., Carpio, A.J., Tortosa, F.S. (2020). Assessment of the suitability of latrine counts as an indirect method by which to estimate the abundance of European rabbit populations at high and low abundance. *European Journal of Wildlife Research*, 66: 10.

Guil F., Higuero R., Moreno-Opo, R. (2014a). European wild rabbit (*Oryctolagus cuniculus*) restocking: effects on abundance and spatial distribution. *Wildlife Society Bulletin*, 38: 524-529.

Guil, F., Fernandez-Olalla, M., Martinez-Jauregui, M., Moreno-Opo, R., Agudín, S., San M.A. (2014b). Grain sowing aimed at wild rabbit *Oryctolagus cuniculus* L. enhancement in Mediterranean environments. *Journal for Nature Conservation*, 22: 552-558.

Guisan, A., Zimmermann, N.E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling*, 135: 147-186.

Hackländer, K., Ferrand, N., Alves, P.C. (2008). Overview of lagomorph research: what we have learned and what we still need to do. In: Alves, P.C., Ferrand, N., Hackländer, K. (eds.). Lagomorph Biology: Evolution, Ecology and Conservation, Springer-Verlag, Berlin, Heidelberg, pp. 381-391.

Harris, S., Cresswell, W.J., Forde, P.G., Trewalla, W.J., Woolard, T., Wray, S. (1990). Home-range analysis using radiotracking data—a review of problems and techniques particularly as applied to the study of mammals. *Mammal Review*, 20: 97-123.

Harrison, S. (2020). Plant community diversity will decline more than increase under climatic warming. Philosophical Transactions of the Royal Society of London. *Series B, Biological science*, 375(1794): 20190106.

Hastie, T.J., Tibshirani, R.J. (1990). Generalized additive models. Chapman and Hall/CRC, Boca Raton, London, New York, Washington D.C. 352 pp.

Hayward, M.W., Hayward, G.J., Druce, D.J., Kerley, G.I.H. (2009). Do fences constrain predator movements on an evolutionary scale? Home range, food intake and movement patterns of large predators reintroduced to Addo Elephant National Park, South Africa. *Biodiversity Conservation*, 18: 887-904.

Heikkinen, R.K., Luoto, M., Virkkala, R., Rainio, K. (2004). Effects of habitat cover, landscape structure and spatial variables on the abundance of birds in an agricultural–forest mosaic. *Journal of Applied Ecology*, 41: 824-835.

Hemson, G., Johnson, P., South, A., Kenward, R.E., Ripley, R., Macdonald, D. (2005). Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with least-squares cross-validation. *Journal of Animal Ecology*, 74: 455-463.

Hulbert, I.A.R., Iason, G.R., Racey, P.A. (1996). Habitat utilization in a stratified upland landscape by two lagomorphs with different feeding strategies. *Journal of Applied Ecology*, 33(2): 315-324.

Iborra, O.L., Lumaret, J.P. (1997). Validity limits of the pellet group counts in wild rabbit (*Oryctolagus cuniculus*). *Mammalia*, 61: 205-218.

ICN - Instituto de conservação da natureza. (2006). Sítio Monchique PTCON0037. Sítios da lista nacional. Plano sectorial da Rede Natura 2000.

ICNF - Instituto de conservação da natureza e florestas. (2018). 6.º Relatório Provisório de incêndios rurais – 01 de janeiro a 15 de setembro. DGAPPFD - Departamento de Gestão de Áreas Públicas e de Proteção Florestal/DDFVAP - Divisão de Defesa da Floresta e Valorização de Áreas Públicas. Lisbon, Portugal. https://www.icnf.pt/api/file/doc/61e4d0cfc888973b

ICNF - Instituto de conservação da natureza e florestas. (2023). Relatório Actividade Cinegética 2022-2023. Departamento de Gestão e Valorização da Floresta Divisão de Recursos Cinegéticos e Aquícolas. 17 pp.

IHERA - Instituto de hidráulica engenharia rural e ambiente, DSRNAH, Divisão de solos. (1999). Carta dos solos de Portugal, 1:25000.

IUCN/SSC. (2013). Guidelines for Reintroductions and Other Conservation Translocations. Version 1.0. Gland, Switzerland: IUCN Species Survival Commission, viiii + pp. 57.

Jaksic, F.M., Soriguer, R.C. (1981). Predation upon the European rabbit (*Oryctolagus cuniculus*) in Mediterranean habitats of Chile and Spain: A comparative analysis. *Journal of Animal Ecology*, 50: 269-281.

Jerosch, S., Götz, M., Roth, M. (2017). Spatial Organisation of European Wildcats (*Felis Silvestris Silvestris*) in an Agriculturally Dominated Landscape in Central Europe. *Mammalian Biology*, 82: 8-16.

Jones, C.G., Lawton, J.H., Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos*, 69: 373-386.

Kenward, R.E. (2001). A Manual for Wildlife Radio Tagging. Academic Press, London.

Kerr, P.J., Ghedin, E., DePasse, J.V., Fitch, A., Cattadori, I.M., Hudson, P.J, Tscharke, D.C. Read, A.F., Holmes, E.C. (2012). Evolutionary History and Attenuation of Myxoma Virus on Two Continents. *PLOS Pathogens*, 8: e1002950.

Kolb, H.H. (1985). The burrow structure of the European rabbit (*Oryctolagus cuniculus* L). *Journal of Zoology*, 206: 253-262.

Kolb, H.H. (1991). Use of burrows and movements of wild rabbits (*Oryctolagus cuniculus*) in an area of hill grazing and forestry. *Journal of Applied Ecology*, 28: 892-905.

Kolb, H.H. (1994). The use of cover and burrows by a population of rabbits (Mammalia: *Oryctolagus cuniculus*) in eastern Scotland. *Journal of Zoology*, 233: 9-17.

Kontsiotis, V.J., Bakaloudis, D.E., Tsiompanoudis, A.C. (2013). Key factors determining the seasonal population growth rate of European wild rabbits and their implications for management. *European Journal of Wildlife Research*, 59: 495-503.

Krohmer, J., Deil, U. (2003). Paysages dynamiques et conservateurs? Couvert vegetal actuel et changements de l'occupation du sol dans la Serra de Monchique (Portugal). *Phytocoenologia*, 33: 767-799.

Le Gall-Reculé, G., Zwingelstein, F., Boucher, S., Le Normand, B., Plassiart, G., Portejoie, Y., Decors, A., Bertagnoli, S., Guérin, J.L., Marchandeau, S. (2011). Detection of a new variant of rabbit haemorrhagic disease virus in France. *The Veterinary Record*, 168: 137-138.

Le Gall-Reculé, G., Lavazza, A., Marchandeau, S., Bertagnoli, S., Zwingelstein, F., Cavadini, P., Martinelli, N., Lombardi, G., Guérin, J., Lemaitre, E., Decors, A., Boucher, S., Le Normand, B., Capucci, L. (2013). Emergence of a new lagovirus related to rabbit haemorrhagic disease virus. *Veterinary Research*, 44: 81.

Le Pendu, J., Abrantes J, Bertagnoli, S., Guitton, J.S., Le Gall-Reculé, G., Lopes, A.M., Marchandeau, S., Alda, F., Almeida, T., Célio, A.P., Bárcena, J., Burmakina, G., Blanco, E., Calvete, C., Cavadini, P., Cooke, B., Dalton, K., Delibes-Mateos, M., Deptula, W., Eden, J.S., Wang, F., Ferreira, C.C., Ferreira, P., Foronda, P., Gonçalves, D., Gavier-Widén, D., Hall, R., Hukowska-Szematowicz, B., Kerr, P., Kovaliski, J., Lavazza, A., Mahar, J., Malogolovkin, A., Marques, R.M., Marques, S., Martin-Alonso, A., Monterroso, P., Moreno, S., Mutze, G., Neimanis, A., Niedzwiedzka-Rystwej, P., Peacock, D., Parra, F., Rocchi, M., Rouco, C., Ruvoën-Clouet, N., Silva, E., Silvério, D., Strive, T., Thompson, G., Tokarz-Deptula, B., Esteves, P. (2017). Proposal for a unified classification system and nomenclature of lagoviruses. *The Journal of general virology*, *98*(7), 1658–1666.

Lees, A.C., Bell, D.J. (2008). A conservation paradox for the 21st century: The European wild rabbit *Oryctolagus cuniculus*, an invasive alien and an endangered native species. *Mammal Review*, 38: 304-320.

Legendre, P., Legendre, L. (1998). Numerical ecology. 2nd ed. Amsterdam: Elsevier.

Letty, J., Marchandeau, S., Clobert, J., Aubineau, J. (2000). Improving translocation success: an experimental study of anti-stress treatment and release method for wild rabbits. *Animal Conservation*, 3: 211-219.

Letty, J., Marchandeau, S., Reitz, F., Clobert, J., Sarrazin, F. (2002). Survival and movements of translocated wild rabbits (*Oryctolagus cuniculus*). *Game Wildlife Science*, 19: 1-23.

Letty, J., Aubineau, J., Marchandeau, S., Clobert, J. (2003). Effect of translocation on survival in wild rabbit (*Oryctolagus cuniculus*). *Mammalian Biology*, 68: 250-255.

Letty, J., Aubineau, J., Marchandeau, S. (2005). Effect of storage conditions on dispersal and short-term survival of translocated wild rabbits *Oryctolagus cuniculus*. *Wildlife Biology*, 11: 249-255.

Letty, J., Aubineau, J., Marchandeau, S. (2008). Improving rabbit restocking success: a review of field experiments in France. In: Alves, P.C., Ferrand, N., Hackländer, K. (eds.). Lagomorph Biology: Evolution, Ecology and Conservation, Springer-Verlag, Berlin, Heidelberg, pp. 125-140.

LIFE Iberconejo (2022). Jornadas sobre seguimiento sanitaria del conejo de monte. Documento Resumen. Mertola, Portugal. 9 pp.

LIFE Iberconejo (2024). Manual de apoio à formação do protocolo de monitorização das populações de coelho-bravo do LIFE Iberconejo. 19 pp.

LIFE LYNXCONNECT (2021). Protocol for monitoring populations of wild rabbit. 11 pp.

Liu, S.J., Xue, H.P., Pu, B.Q., Qian, N.H. (1984). A new viral disease in rabbit. *Animal Husbandry and Veterinary Medicine*, 16: 253-255.

Lombardi, L., Fernández, N., Moreno, S., Villafuerte, R. (2003). Habitat related differences in rabbit (*Oryctolagus cuniculus*) abundance, distribution and activity. *Journal of Mammal*, 84: 26-36.

Lombardi, L., Fernández, N., Moreno, S. (2007). Habitat use and spatial behaviour in the European rabbit in three Mediterranean environments. *Basic and Applied Ecology*, 8: 453-463.

Lopes, A.M., Correia, J., Abrantes, J., Melo, P., Ramada, M., Magalhães, M.J., Alves, P.C., Esteves, P.J. (2015). Is the New Variant RHDV Replacing Genogroup 1 in Portuguese Wild Rabbit Populations? *Viruses*, 7**:** 27-36.

Lopez-Martinez, N. (2008). The lagomorph fossil record and the origin of the European rabbit. In: Alves, P.C., Ferrand, N., Hackländer, K. (eds.). Lagomorph Biology: Evolution, Ecology and Conservation, Springer-Verlag, Berlin, Heidelberg, pp. 27-46.

Macdonald, D.W., Norris, S. (2001). The new encyclopedia of mammals. Oxford University Press, Oxford. 930 pp.

Machado, R., Magalhães, P., Godinho, S., Santos, P. (2017). Wild rabbit restocking: suitable acclimation conditions foster adaptive behavior and improve survival of captive reared rabbits. *World Rabbit Science*, 25: 407-414.

Marchandeau, S., Bertagnoli, S., Peralta, B., Boucraut-Baralon, C., Letty, J., Reitz, F. (2004). Possible interaction between myxomatosis and calicivirosis related to rabbit haemorrhagic disease affecting the European rabbit. *The Veterinary record*, 155: 589-592.

Melo-Ferreira, J., Alves P.C. (2018). Systematics of Lagomorphs. In: Smith, A.T., Johnston, C.H., Alves, P.C., Hacklander, K. (eds.). Lagomorphs: Pikas, Rabbits, and Hares of the World, Johns Hopkins University Press, Baltimore, Maryland, USA, pp. 9-12.

Ministerio de Agricultura y Medio Ambiente. (2025). Estadística Anual de Caza. Tablas resumen 2005-2019. Secretaría General de Agricultura y Alimentación, Dirección General de Desarrollo Rural y Politica Forestal, Subdirección General de Silvicultura y Montes, Gobierno de España. Available at: https://www.miteco.gob.es/es/biodiversidad/estadisticas/est_anual_caza.html.

Mira, A., Santos, A.E., Alves, P.C. (2023). *Oryctolagus cuniculus* coelho-ibérico. In: Mathias, ML (coord.), Fonseca, C., Rodrigues, L., Grilo, C., Lopes-Fernandes, M., Palmeirim, J.M., Santos-Reis, M., Alves, P.C., Cabral, J.A., Ferreira, M., Mira, A., Eira, C., Negrões, N., Paupério, J., Pita, R., Rainho, A., Rosalino, L.M., Tapisso, J.T., Vingada, J. (eds.). Livro Vermelho dos Mamíferos de Portugal Continental, FCiências.ID, ICNF, Lisboa, pp. 144-145.

Mohr, C.O. (1947). Table of equivalent populations of North American small mammals. *American Midland Naturalist*, 37: 223-249.

Monnerot, M., Vigne, J., Biju-Duval, C., Casane, D., Callou, C., Hardy, C., Mougel, F., Soriger, R., Dennebouy, N., Mounolou, J. (1994). Rabbit and man: genetic and historic approach. *Genetics Selection Evolution*, 26(Suppl 1): 167s-182s.

Monterroso, P., Garrote, G., Serronha, A., Santos, E., Delibes-Mateos, M., Abrantes, J., Ayala, R.P., Silvestre, F., Carvalho, J., Vasco, I., Lopes, A.M., Maio, E., Magalhães, M.J., Mills, L.S., Esteves, P.J., Simón, M.A., Alves, P.C. (2016). Disease-mediated bottom-up regulation: An emergent virus affects a keystone prey, and alters the dynamics of trophic webs. *Scientific Reports*, 6: 6072.

Monzón, A., Fernandes, P., Rodrigues, N. (2004). Vegetation structure descriptors regulating the presence of wild rabbit in the National Park of Peneda-Gerês, Portugal. *European Journal of Wildlife Research*, 50: 1-6.

Moreno, S., Villafuerte, R. (1995). Traditional management of scrubland for the conservation of rabbits *Oryctolagus cuniculus* and their predators in Doñana National Park, Spain. *Biological Conservation*, 73: 81-85.

Moreno, S., Villafuerte, R. (1997). Translocating rabbits (*Oryctolagus cuniculus*): the influence of habitat quality on survival rate and population growth. Proceedings of the XIIth Lagomorph Workshop, Clermont-Ferrand, France, 8-11 July 1996. *Gibier Faune Sauvage*, 14(3): 520-521.

Moreno, S., Villafuerte, R., Delibes, M. (1996). Cover is safe during the day but dangerous at night: The use of vegetation by European wild rabbits. *Canadian Journal of Zoology*, 74: 1656-1660.

Moreno, S., Villafuerte, R., Cabezas, S., Lombardi, L. (2004). Wild rabbit restocking for predator conservation in Spain. *Biological Conservation*, 118: 183-193.

Moreno, S., Beltran, J.F., Cotilla, I., Kuffner, B., Laffite, R., Jordán, G., Ayala, J., Quintero, C., Jiménez, A., Castro, F., Cabezas, S., Villafuerte, R. (2007). Long-term decline of the European wild rabbit (*Oryctolagus cuniculus*) in south-western Spain. *Wildlife Research*, 34: 652-658.

Moseby, K. E., De Jong, S., Munro, N., Pieck, A. (2005). Home range, activity and habitat use of European rabbits (*Oryctolagus cuniculus*) in arid Australia: implications for control. *Wildlife Research*, 32(4): 305-311.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403: 853-858.

Odum, E.P., Kuenzler, E.J. (1955). Measurement of territory and home range size in birds. *The Auk*, 72: 128-137.

Osácar-Jimenez, J.J., Lucientes-Curdi, J., Calvete-Margolles, C. (2001). Abiotic factors influencing the ecology of wild rabbits fleas in north-eastern Spain. *Medical and Veterinary Entomology*, 15: 157-166.

Paixão, R., Godinho, S., Santos, P. (2009). Is the Nature 2000 Network associated with small-game bag results? *European Journal of Wildlife Research*, 55: 553-559.

Palma, L., Beja, P., Tavares, P.C., Monteiro, L.R. (2005). Spatial variation of mercury levels in nesting Bonelli's eagles from Southern Portugal: Effects of diet composition and prey contamination. *Environmental Pollution*, 134: 549-557.

Palomares, F. (2001). Comparison of three methods to estimate rabbit abundance in a Mediterranean environment. *Wildlife Society Bulletin*, 29: 578-585.

Palomares, F. (2003). Warren building by European rabbits (*Oryctolagus cuniculus*) in relation to cover availability in a sandy area. *Journal of Zoology*, 259: 63-67.

Palomares, F., Delibes, M. (1997). Predation upon European rabbits and their use of open and closed patches in Mediterranean habitats. *Oikos*, 80: 407-410.

Palomares, F., Delibes, M., Revilla, E., Calzada, J., Fedriani, J.M. (2001). Spatial ecology of Iberian lynx and abundance of European rabbits in Southwestern Spain. *Wildlife Monographs*, 65: 1–36.

Paradis, E., Schliep, K. (2019). ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, 35: 526-528.

Parer, I. (1982). Dispersal of the Wild Rabbit, *Oryctolagus cuniculus*, at Urana in New South Wales. *Australian Wildlife Research*, 9(3): 427-441.

Parer, I., Libke, J.A. (1985). Distribution of rabbit, *Oryctolagus cuniculus*, warrens in relation to soil type. *Australian Wildlife Research*, 12: 387-405.

Parra, F., Prieto, M. (1990). Purification and characterization of a calicivirus as the causative agent of a lethal hemorrhagic disease in rabbits. *Journal of virology*, 64: 4013-4015.

Pech, R.P., Sinclair, A.R.E., Newsome, A.E., Catling, P.C. (1992). Limits to predator regulation of rabbits in Australia: evidence from predator removal experiments. *Oecologia*, 89: 102-112.

Piorno, V., Villafuerte, R, Branco, M, Carneiro, M., Ferrand, N., Alves, P.C. (2015). Low persistence in nature of captive reared rabbits after restocking operations. *European Journal of Wildlife Research*, 59: 573-580.

Plotz, R.D., Grecian, W.J., Kerley, G.I., Linklater, W.L. (2016). Standardising home range studies for improved management of the critically endangered black rhinoceros. *PLoS One*, 11(3): Article e0150571.

Pollock, K.H., Winterstein, S.R., Bunck, C.M., Curtis, P.D. (1989). Survival analysis in telemetry studies: the staggered entry design. *Journal of Wildlife Management*, 53: 7-15.

Portaria No. 1064/2006. (2006). Diário da República n.º 186/2006, Série I de 2006-09-26. Lisboa, Portugal: Ministério do Ambiente, do Ordenamento do Território e do Desenvolvimento Regional.

Procesl - Engenharia Hidráulica e Ambiental, Lda. (2010). Parque Eólico de Malhanito—Relatório de Conformidade Ambiental do Projecto de Execução. Executive Summary. Amadora, Portugal: Engenharia Hidráulica e Ambiental.

QGIS Development Team. (2014). QGIS geographic information system. Open source geospatial foundation project. https://www.qgis.org

QGIS Development Team. (2021). QGIS geographic information system. Open source geospatial foundation project. https://www.qgis.org

QGIS Development Team. (2023). QGIS geographic information system. Open source. Geospatial Foundation Project. http://qgis.org

R Core Team. (2017). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org/

R Core Team. (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

R Core Team. (2023). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rangel, T.F., Diniz-Filho, J.A.F., Bini, L.M. (2010). SAM: A comprehensive application for spatial analysis in macroecology. *Ecography*, 33: 46-50.

Raposo, M., Nunes, L., Gomes, C. J. (2023). Evolution of land cover in the special area of conservation of Monchique (Southern Portugal): Have the objectives of the Natura 2000 network been achieved (1995–2018)? *Land Degradation and Development*, 34: 1-8.

Reglero, M, Vicente, J, Rouco, C., Villafuerte, R., Gortazar, C. (2007). Trypanosoma spp. infection in wild rabbits (*Oryctolagus cuniculus*) during a restocking program in southern Spain. *Veterinary Parasitology*, 149: 178-184.

REN, EGSP, Ecossistema. (2007). Linha Tunes—Estoi, a 150 kV. Medidas compensatórias e monitorização específica para o casal de águia de Bonelli de Odelouca, decorrentes do processo de Avaliação de Impacte Ambiental. 1st Annual Report. Lisbon, Portugal.

REN, EGSP, Ecossistema. (2009). Linha Sines—Portimão 3 a 400 kV. Medidas compensatórias e monitorização específica para o casal de águia de Bonelli de Odelouca, decorrentes do processo de Avaliação de Impacte Ambiental. Final report. Lisbon, Portugal.

Revilla, E., Palomares, F., Fernandez, N. (2001). Characteristics, location and selection of diurnal resting dens by Eurasian badgers (*Meles meles*) in a low density area.

Journal of Zoology, 255: 291-299.

Ríos-Saldaña, C.A., Delibes-Mateos, M., Castro, F., Martínez, E., Vargas, J.M., Cooke, B.D., Villafuerte, R. (2013). Control of the European rabbit in central Spain. *European Journal of Wildlife Research*, 59: 573–580.

Rivas-Martinez, S., Loidi, J. (1999). Biogeography of the Iberian Peninsula. *Itinera Geobotanica*, 13: 49-67.

Rivas-Martínez, S., Penas, A., del Río, S., González, T.E.D., Rivas-Sáenz, S. (2017). Bioclimatology of the Iberian Peninsula and the Balearic Islands. In: Loidi, J. (eds) The Vegetation of the Iberian Peninsula. Plant and Vegetation, vol 12. Springer, Cham, pp. 29-80.

Roberts, S.C. (1987). Group-living and consortship in two populations of the European rabbit (*Oryctolagus cuniculus*). *Journal of Mammalogy*, 68: 28-38.

Roca, T. (2009). Historia de la cunicultura industrial en España. *Cunicultura*, 35: 9-15.

Rödel, H.G., Starkloff, A., Seltmann, M.W., Prager, G., von Holst, D. (2009). Causes and predictors of nest mortality in a European rabbit population. *Mammalian Biology*, 74: 198-209.

Rogers, P.M., Myers, K. (1979). Ecology of the European wild rabbit, *Oryctolagus cuniculus* (L.), in Mediterranean habitats. I. Distribution in the landscape of the Coto Doñana, S. Spain. *Applied Ecology*, 16: 691-703.

Rouco, C., Ferreras, P., Castro, F., Villafuerte, R. (2008). The effect of exclusion of terrestrial predators on short-term survival of translocated European wild rabbits. *Wildlife Research*, 35: 625-632.

Rouco, C., Ferreras, P., Castro, F., Villafuerte, R. (2010). A longer confinement period favors European wild rabbit (*Oryctolagus cuniculus*) survival during soft releases in low-cover habitats. *European Journal of Wildlife Research*, 56: 215-219.

Rouco, C., Villafuerte, R., Castro, F., Ferreras, P. (2011). Effect of artificial warren size on a restocked European wild rabbit population. *Animal Conservation*, 14: 117-123.

Rouco, C., Moreno, S., Santoro, S. (2016). A case of low success of blind vaccination campaigns against myxomatosis and rabbit haemorrhagic disease on survival of adult European wild rabbits. *Preventive Veterinary Medicine*, 133: 108-113.

Rouco, C., Barrio, I.C., Cirilli, F., Tortosa, F.S., Villafuerte, R. (2019). Supplementary food reduces home ranges of European wild rabbits in an intensive agricultural landscape. *Mammalian Biology*, 95: 35-40.

San Miguel (Coord.). (2014). Manual para la gestión del hábitat el lince ibérico (*Lynx pardinus*) y de su presa principal, el conejo de monte (*Oryctolagus cuniculus*). 2ª Edición. Fundación CBD-Habitat, Madrid, España. 325 pp.

Sánchez, C., Gaudioso, V.R., Alonso, M.E., Bartolomé, D.J., Pérez, J.A., Prieto, R., Valle, C.D., Olmedo, J.A. (2007). Valoración del consumo de agua y presencia de la fauna silvestre en bebederos artificiales en un entorno mediterráneo continental seco. Anales de la Real Academia de Ciencias Veterinarias de Andalucía Oriental, 20: 11-30.

Sánchez-Piñero, F., Ávila, J.M. (1991). Análisis comparativo de los Scarabaeoidea (Coleoptera) coprófagos de las deyecciones de conejo (*Oryctolagus cuniculus* (L.)) y de otros mamíferos: estudio preliminar. *Eos*, 67: 23-24.

Sarmento, P., Cruz, J., Paula, A., Eira, C., Capinha, M., Ambrósio, I., Ferreira, C., Fonseca, C. (2012). Occupancy, colonization and extinction patterns of rabbit populations: Implications for Iberian lynx conservation. *European Journal of Wildlife Research*, 58: 523-533.

Scanlan, J.C., Berman, D.M., Grant, W.E. (2006). Population dynamics of the European rabbit (*Oryctolagus cuniculus*) in northeastern Australia: simulated responses to control. *Ecological Modelling*, 196: 221–236.

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods Ecology Evolution*, 1: 103-113.

Serrano, S., Hidalgo de Trucios, S.J. (2011). Burrow types of the European wild rabbit in southwestern Spain. *Ethology Ecology and Evolution*, 23: 81-90.

Short, J., Kinnear, J.E., Robley, A. (2002). Surplus killing by introduced predators in Australia, evidence for ineffective anti-predator adaptations in native prey species? *Biological Conservation*, 103: 283-301.

Sikes, R.S., Gannon, W.L., the Animal Care and Use Committee of the American Society of Mammalogists. (2011). Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy*, 92(1): 235-253.

Smith, G.C., Prickett, A.J., Cowan, D.P. (2007). Costs and benefits of rabbit control options at the local level. *International Journal of Pest Management*, 53: 317-321.

SNIRH - Sistema nacional de informação de recursos hídricos. (2022). Portal do Sistema nacional de informação de recursos hídricos. https://snirh.apambiente.pt/

SNIRH - Sistema nacional de informação de recursos hídricos. (2023). Portal do Sistema nacional de informação de recursos hídricos. https://snirh.apambiente.pt/

Swets, J. A. (1988). Measuring the accuracy of diagnostic systems. *Science*, 240: 1285-1293.

Tabachnick, B., Fidell, L. (1996). Using Multivariate Statistics. 3rd edition. HarperCollins College Publishers, New York. 880 pp.

Tablado, Z., Revilla. E. (2012). Contrasting Effects of Climate Change on Rabbit Populations through Reproduction. *PLoS ONE*, 7(11): e48988.

Teixeira, C., Azevedo, C., Mendl, M., Cipreste, C., Young, R.J. (2007). Revisiting translocation and reintroduction programmes: the importance of considering stress. *Animal Behaviour*, 73: 1-13.

Therneau, T. (2023). A Package for Survival Analysis in R. R package version 3.5-3, https://CRAN.R-project.org/package=survival

Thompson, H.V., King, C.M. (1994). The European Rabbit: the history and biology of a successful colonizer. Oxford University Press, Great Britain. 245 pp.

Tobajas, J., Descalzo, E., Villafuerte, R., Jimenez, J., Mateo, R., Ferreras, P. (2021). Conditioned odor aversion as a tool for reducing post-release predation during animal translocations. *Animal Conservation*, 24: 373-385.

Trout, R.C., Tittensor, A.M. (1989). Can predators regulate wild Rabbit *Oryctolagus cuniculus* population density in England and Wales? *Mammal Review*, 19: 153-173.

Trout, R.C., Langton, S., Smith, G.C., Haines-Young, R.H. (2000). Factors affecting the abundance of rabbits (*Oryctolagus cuniculus*) in England and Wales. *Journal of Zoology (London)*, 252: 227-238.

Tuszynski, J. (2014). caTools: Tools: Moving window statistics, GIF, Base64, ROC AUC, etc. R package version 1.17.1. http://CRAN.Rproject.org/package=caTools

Van de Vuurst, P., Escobar, L.E. (2023). Climate change and infectious disease: a review of evidence and research trends. *Infectious Diseases of Poverty*, 12: 51.

Vaquerizas, P.H., Delibes-Mateos, M., Piorno, V., Arroyo, B., Castro, F., Villafuerte R. (2020). The paradox of endangered European rabbits regarded as pests in the Iberian Peninsula: subspecies differences in trends matter. Endangered Species Research 43: 99-102.

Villafuerte, R. (1994). Riesgos de predación y estratégias defensivas del conejo (*Oryctolagus cuniculus*) en el Parque Nacional de Doñana. Ph.D. Thesis. University of Córdoba, Spain.

Villafuerte, R., Delibes-Mateos, M. (2019). *Oryctolagus cuniculus* (errata version published in 2020). The IUCN Red List of Threatened Species 2019: e.T41291A170619657.

Villafuerte, R., Kufner, M.B., Delibes, M., Moreno, S. (1993). Environmental factors influencing the seasonal daily activity of the European rabbit (*Oryctolagus cuniculus*) in a Mediterranean area. *Mammalia*, 57: 341-347.

Villafuerte, R., Calvete, C., Gortázar, C., Moreno, S. (1994). First epizootic of rabbit hemorrhagic disease in free living populations of *Oryctolagus cuniculus* at Doñana National Park, Spain. *Journal of wildlife diseases*, 30(2), 176–179.

Villafuerte, R., Calvete, C., Blanco, J.C., Lucientes, J. (1995). Incidence of viral hemorrhagic disease in wild rabbit populations in Spain. *Mammalia*, 59: 651-659.

Villafuerte, R., Viñuela, J., Blanco, J.C. (1998). Extensive predator persecution caused by population crash in a game species: The case of red kites and rabbits in Spain. *Biological Conservation*, 84: 181-188.

Villafuerte, R., Castro, F., Rouco, C., Ferreras, P. (2008). Seguimiento y recuperación de las poblaciones de conejo de monte en el área de compensación del embalse de Los Melonares (Sevilla). In Investigación científica y conservación en el Parque Natural Sierra Norte de Sevilla: pp. 211–226. Menor, A. (Coord.), Cuenca, I (Coord). Ed. Consejería de Medio Ambiente, Junta de Andalucía. isbn: 978-84-96776-50-0.

Villafuerte, R., Castro, F., Ramírez, E., Cotilla, I., Parra, F., Delibes-Mateos, M., Recuerda, P., Rouco, C. (2017). Large-scale assessment of myxomatosis prevalence in European wild rabbits (*Oryctolagus cuniculus*) 60 years after first outbreak in Spain. *Research in veterinary science*, 114: 281-286.

Virgós, E., Cabezas-Días, S., Malo, A., Lozano, J., López-Huertas, D. (2003). Factors shaping European rabbit abundance in continuous and fragmented populations of central Spain. *Acta Theriologica*, 48: 113-122.

Virgós, E., Cabezas-Díaz, S., Lozano, J. (2007). Is the wild rabbit (*Oryctolagus cuniculus*) a threatened species in Spain? Sociological constraints in the conservation of species. *Biodiversity and Conservation*, 16: 3489-3504.

von Holst, D., Hutzelmeyer, H., Kaetzke, P., Khaschei, M., Schönheiter, R. (1999). Social rank, stress, fitness, and life expectancy in wild rabbits. *Naturwissenschaften*, 86: 388-393.

von Holst, D., Hutzelmeyer, H., Kaetzke, P., Khaschei, M., Rödel, H.G., Schrutka, H. (2002). Social rank, fecundity and lifetime reproductive success in wild European rabbits (*Oryctolagus cuniculus*). *Behavioral Ecology and Sociobiology*, 51: 245-254.

Ward, D. (2005). Reversing rabbit decline: One of biggest challenges for mature conservation in Spain and Portugal. IUCN Technical Report. 54 pp.

Wereszczuk, A, Zalewski, A. (2019). Does the matrix matter? Home range sizes and space use strategies in stone marten at sites with differing degrees of isolation. *Mammal Research*, 64: 71-85.

Wickham, H. (2016). ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York.

Williams, C.J., Parer, I., Coman, B.J., Burley, J., Braysher, M.L. (1995). Managing Vertebrate Pests: Rabbits. Canberra: Australian Government Publishing Service.

Williams, D., Acevedo, P., Gortázar, C., Escudero, M., Labarta, J.L., Marco, J., Villafuerte, R. (2007). Hunting for answers: Rabbit (*Oryctolagus cuniculus*) population trends in northeastern Spain. *European Journal of Wildlife Research*, 53: 19-28.

Williams, F., Eschen, R., Harris, A., Djeddour, D., Pratt, C., Shaw, R.S., Varia, S., Lamontagne-Godwin, J., Thomas, S.E., Murphy, S.T. (2010). The economic cost of invasive non-native species on Great Britain. Centre for Agriculture and Bioscience International (CABI), Surrey.

Willott, S.J., Miller, A.J., Incoll, L.D., Compton, S.G. (2000). The contribution of rabbits (*Oryctolagus cuniculus* L.) to soil fertility in semi-arid Spain. *Biology and Fertility of Soils*, 31: 379-384.

Wilson, D.E., Cole, F.R., Nicchols, J.D., Rudran, R., Foster, M.S. (Eds.). (1996). Measuring and monitoring biological diversity. Standard methods for mammals. Washington, DC: Smithsonian Institution Press. 409 pp.

Wood, S. (2017). Generalized Additive Models: An Introduction with R, 2nd edition. Chapman and Hall/CRC, Boca Raton, London, New York. 476 pp.

Ziege, M., Hermann, B.T., Kriesten, S., Merker, S., Ullmann, W., Streit, B., Wenninger, S., Plath, M. (2020). Ranging behavior of European rabbits (*Oryctolagus cuniculus*) in urban and suburban landscapes. *Mammal Research*, 65: 607-614.

Zuur, A.F., Ieno, E.N., Smith, G.M. (2007). Analysing ecological data. New York, NY: Springer. 409 pp.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M. (2009). Mixed-effects model and extensions in ecology with R. New York, NY: Springer. 574 pp.

Zuur, A.F., Ieno, E.N., Elphick, C.S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology Evolution*, 1: 3-14.

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