Universidade de Évora - Escola de Ciências e Tecnologia

Universidade de Lisboa - Instituto Superior de Agronomia

Mestrado em Gestão e Conservação de Recursos Naturais

Dissertação

Linking population trends of wild herbivores harvested in Portugal and Hunting Zone characteristics: Effects of location, management, interspecific competition and land use dynamics

Sofia de Sousa Gorgulho

Orientador(es) | Miguel Nuno do Sacramento Monteiro Bugalho

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A dissertação foi objeto de apreciação e discussão pública pelo seguinte júri nomeado pelo Diretor da Escola de Ciências e Tecnologia:

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Abstract

Wild herbivores affect the ecology of ecosystems and, as game species, are relevant for the socio-economy of various countries. Thus, management of its populations is crucial and can benefit from hunting bag monitoring across time and space. This dissertation assesses the usefulness of data on hunting bags to get insights on wild rabbit (*Oryctolagus cuniculus*), Iberian hare (*Lepus granatensis*) and red deer (*Cervus elaphus*) distribution and population trends in Portugal, assessing the effects of location, administrative type, land-use dynamics and co-occurrence of species on the population dynamics of each species. The density of wild rabbit, Iberian hare and red deer hunting bags from 1989-2017 in Portugal were analysed using ANOVA to ascertain the influence of hunting region, administrative type and hunting season. Population tendencies were calculated for each hunting zone and maps of occurrence were projected in ArcGis to verify whether hunting bag data showed the same trends as other data sources. A primary analysis on the relationship between deer and lagomorphs was made through correlation analysis of populations densities of both species. The occurrence maps obtained for rabbit and hare showed a wider distribution across Portugal as compared to data on species distribution from the Atlas of Mammals of Portugal. Main core areas for deer populations had a scarcer distribution across the country. Hunting bag density is linked to region, administrative type and fluctuates throughout the years. Overall, rabbit and hare hunting bags decreased but deer hunting bags increased across time. There is correlation between deer and lagomorphs, mostly negative but also positive. Results suggest that hunting bags are useful indicators of game population abundances, but extrapolation of results must be assessed critically. Efforts on improving the efficiency of survey methods are advisable. The present dissertation contributes to understand distributions and tendencies of main herbivore game species in Portugal.

Keywords: Hunting statistics, population dynamics, lagomorphs, deer, territory management

Relação entre tendências populacionais de herbívoros selvagens caçados em Portugal com características de Zonas de Caça: Efeito da localização, gestão, competição interespecífica e dinâmicas de uso do solo

Resumo

Os herbívoros silvestres afetam a ecologia dos ecossistemas, sendo também espécies cinegéticas com importância socio-económica. A gestão das suas populações é essencial, estando a caça diretamente relacionada. Esta providencia os números de animais abatidos anualmente nas explorações cinegéticas. A presente dissertação tem como objetivo avaliar o potencial de bases de dados de animais abatidos como indicadores das tendências populacionais das espécies cinegéticas, averiguando ainda como estas podem ser afetadas. Os dados de caça ao coelho bravo, lebre e veado em Portugal foram analisados entre 1989-2017 através de ANOVA usando como fatores fixos: região cinegética, tipo administrativo e época de caça. A tendência populacional foi calculada para cada zona de caça usando os dados de abate e projetaram-se em ArcGIS mapas de ocorrência de espécies, cujos dados foram comparados com outros estudos. Foi também investigada a ocorrência de correlações entre abates de veado e lagomorfos. Os mapas de ocorrência obtidos a partir dos dados de caça ao coelho e lebre sugerem que a distribuição destas espécies é mais ampla do que a sugerida pelo Atlas de Mamíferos de Portugal. O mapa de distribuição do veado identificou os principais núcleos populacionais da espécie. A densidade de animais caçados varia com a região cinegética e tipo de zona de caça, oscilando ao longo dos anos. Em geral, a densidade de coelho e lebre caçados diminuiu ao longo do período de estudo, enquanto que a de veado aumentou, o que é concordante com outros estudos. Foi encontrada uma correlação, maioritariamente negativa, mas também positiva, entre a densidade de lagomorfos e veados. Os resultados da exploração cinegética são um potencial indicador de abundância, mas deve ser avaliado com cuidado. É essencial uma melhoria no método de declaração dos resultados cinegéticos anuais. Esta dissertação contribui para melhorar o conhecimento sobre distribuição e tendências das espécies estudadas.

Palavras-chave: Cinegética, dinâmica populacional, lagomorfos, veado, gestão do território

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1. Introduction

1.1 Wild herbivores

Wild herbivores, by interacting directly or indirectly with soil, vegetation and fauna, may cause a profound impact on the ecosystems, namely on their structure and dynamics (Hester *et al.,* 2000; Reimoser & Putman, 2011, Lecomte *et al.,* 2019).

The composition and structure of the vegetation are transformed through herbivore feeding habits, implying that herbivory intensity determines not only plant species abundance and diversity, but also community canopy structure and ecosystem primary productivity (Milchunas *et al.,* 1988; Milchunas & Lauenroth, 1993; Bugalho *et al.,* 2006; Bugalho *et al*., 2013; Mutze *et al.,* 2016). By modifying flora, herbivores also have an impact on animal communities (Stewart, 2001; Bugalho *et al.,* 2006) and can, this way, regulate the abundance, richness and diversity of different faunistic groups, such as lagomorphs, rodents, birds, arthropods and nematodes. These effects differ, however, between faunistic groups and herbivory intensity (Sumption & Flowerdew, 2008; Bugalho *et al*., 2011). Changes in vegetation communities by herbivores also affect soil's structure and composition, having consequences in soil's carbon and nitrogen reservoirs (Milchunas & Lauenroth, 1993), namely Soil Organic Carbon (SOC) stocks (Piñeiro *et al.,* 2010). Additionally, herbivory contributes to changes in frequency and intensity of fires by helping to reduce vegetation loads (Oesterheld *et al.,* 1999; Bond & Keeley, 2005; Lecomte *et al*., 2019), which will also contribute to modifications in SOC accumulation (Piñeiro *et al.,* 2006) and, consequentially, determine the soil fertility, water retention and structure (Lal, 2004). This makes the relationship herbivores-flora-fauna quite complex, inducing an event cascade with a variety of consequences to the ecosystems (Milchunas *et al.,* 1998).

Wild herbivores play another important role in ecosystems, as they are frequently the basis of food chains. Some herbivorous species play a special role as prey due to their predators' specialization, particularly when these predators have an unfavourable conservation status. The wild rabbit (*Oryctolagus cuniculus*) and the Iberian hare (*Lepus granatensis*) are good examples of this situation, being preyed by numerous species in the Mediterranean ecosystem (Delibes-Mateos *et al.,* 2008; Tapia *et al.,* 2010). Some of these predators evolved as "super-specialists" in rabbit hunting, such as the Imperial eagle (*Aquila adalberti*) and the Iberian lynx (*Lynx pardinus*), both endemic to the Mediterranean region and sharing a high conservation status (Delibes-Mateos *et al.,* 2008). Other facultative or opportunistic predators of the wild rabbit are also endangered species, like the Bonelli's eagle (*Hieraaetus fasciatus*), the Golden eagle (*Aquila chrysaetos*), the Red kite (*Milvus milvus*), the Montagu's harrier (*Circus pygargus*), the Egyptian vulture (*Neophron percnopterus*), the Black vulture (*Aegypius monachus*) and the Bearded vulture (*Gypaetus barbatus*) (Fernàndez, 1993; Villafuerte *et al.,* 1998; Delibes-Mateos *et al.,* 2008). In addition, there are several other predators that also include the wild rabbit in their diet to a greater or lesser extent, depending on its abundance, such as the Black kite (*Milvus migrans*), the Wild cat (*Felis silvestris*) and the Fox (*Vulpes vulpes*) (Delibes-Mateos *et al.,* 2008).

Likewise, red deer (*Cervus elaphus*), namely calves and juveniles, may be part of the diet of various top predators, thus playing a vital role in conservation of protected species such as the Iberian lynx, (Okarma *et al.,* 1997), the Golden eagle (Watson *et al.,* 1992), the Black vulture (Costillo *et al.,* 2007) and the Wolf (*Canis lupus*) (Jędrzejewski *et al.,* 2000; Salazar, 2009).

On top of influencing the structure of predator communities, prey availability also has consequences on their survival and reproductive success (Watson *et al.,* 1992; Fernàndez, 1993; Serrano, 2000). Thus, the study of the distribution and abundance of those herbivorous species will support a proper management of natural prey populations, which is crucial to the success of their predator's conservation programs.

Besides their ecological relevance, wild herbivores also have a significant role on the socio-economy of different countries, either positive or negative, depending on the implementation and success of population management plans. There are several cases of poorly animal population management, often leading to high densities of wild herbivores that conflict with land use objectives and create imbalances for biodiversity and ecosystems, causing environmental and economic impacts (Williams *et al.,* 1995; Putman *et al.,* 2011; Reimoser & Putman, 2011). When introduced in a new habitat, or due to changes in land use and human presence, some species can become a pest, inflicting damages in agriculture (Putman, 1986; Norbury & Norbury, 1996; Fleming *et al.,* 2002; Schley & Roper, 2003; Wilson *et al.,* 2009), forestry (Ratcliffe, 1989; Gill, 1992) and habitats of conservation concern (Henzell & Lay, 1981; Mitchell & Kirby, 1990; Cooke & Farrell, 2001; Lecomte *et al.*, 2016). It is also important to notice the potential risk to public safety due to vehicle collisions (Langbein *et al.,* 2011) and transmission of diseases to humans, domestic livestock and pets (Simpson, 2002; Froliche *et al.,* 2002; Bohm *et al.,* 2007). For example, millions of dollars are used annually for control of the wild rabbit in Australia (Williams *et al.,* 1995), both by the public and private sector. The consequences of the infestation led to severe economic damage due to losses on the agriculture, livestock and forestry sector, reaching millions of dollars annually (e.g., $135 million in Australia) (Gordon *et al.,* 2004).

However, when populations are well managed, wild herbivores bring numerous social-economic benefits, having a high economic value. They are a popular touristic attraction, especially for public interested in wildlife observation (ecotourism) (Salazar, 2009), thus generating revenue in natural parks where tours are specially designed to observe these animals, usually the largest and most abundant, such as the deer and the wild boar (Maciejewski & Kerley, 2014). Hunting is also an important source of income in different regions, namely of marginal agricultural activity. Hunting is one of the main sources of income in various rural areas, generating employment and moving hunters to these regions worldwide (Mulero, 1991; Lovelock, 2007), in this way contributing to the improvement of life conditions for the underprivileged populations (Conover, 1997; Salazar, 2009). For example, in the United States, over one billion dollars is spent on deer sport hunting (Gordon *et al.,* 2004) and, in Portugal, game activity engages an estimated value of around 330 million euros for the annual economy (Paiva *et al.,* 2016). Hunting can also be a viable and sustainable solution to deal with over-abundance species, with additional economic benefits for the local population through indirect impacts in subsidiary activities (e.g., hotels, restaurants and transportation used by the tourist hunters) (Gordon *et al.,* 2004; Vasios *et al.*, 2020). Hunting plays one other key role in communities, both utilitarian, recreational and cultural, by strengthening social bonds and being a source of food resources (Lovelock, 2007).

Wild herbivores are, therefore, of extreme importance, at ecologic, social and economic levels. Hence, an effective population management is crucial, be it driven by economic or conservation goals. The success of such management plans relies on sound knowledge on species distribution and abundance, across space and time, and on the factors affecting it (Thomas & Martin, 1996; Fewster *et al.,* 2000; Croose *et al.,* 2019).

1.2 Abundance and distribution study

Monitoring the distribution and abundance of wild herbivore species assists in the evaluation of population trends, which is essential for implementing protective measures and allows adaptive management (Hellawell, 1991; Thomas & Martin, 1996; Gibbs *et al.,* 1999; Fewster *et al.,* 2000; Croose *et al.,* 2019). For example, species with declining populations, such as the wild rabbit (Martins *et al.,* 2002; Ferreira *et al.*, 2010), need conservation measures, while other species proliferating ominously, as the wild boar (Fernández-Llario *et al.,* 2003), need control measures in order to keep the ecosystem's balance.

Population monitoring takes a crucial role in various areas (Lindenmayer & Likens, 2009), namely:

a) when evaluating a species' conservation status or the progress of its recovery plan (Witmer, 2005; Virgós, 2007);
b) in detecting decreases of population numbers, allowing to redirect research and management efforts before the species is endangered;
c) in containing the spread of pests and their capacity to cause agricultural, sanitary or environmental damages (Witmer, 2005);
d) evaluating intra and interspecific competition when facing limited resources;
e) and by assuring a desirable population structure for game species subject to sustainable exploration (Delibes-Mateos et al*.,* 2009).

In addition, linking population trends with environmental factors and land-use management allows the evaluation of species habitat preferences and somehow predict how it will react to future changes (Gibbs et al., 1999; Witmer, 2005).

Monitoring animal populations may be performed by various methods, some needing direct observation of individuals (e.g., in transects, camera and live trapping, for mark-recapture and tracking with radio-telemetry). There are also a variety of indirect methods, which instead of relying on directly seeing or hearing animals merely observe signs of presence, such as faecal counts, hair tubes, food removal, burrow counts, runway counts or track stations (Witmer, 2005; Croose *et al.*, 2019). Accurate collection of data can be challenging on many wildlife species, either because of their small size, secretive or nocturnal habits, large home ranges or low population densities (Milner-Guilland & Rowcliffe, 2007). Also, personality traits may influence detectability, causing under-sampling of less exploratory individuals if a sampling method requires potentially risky behaviour, such as entering a trap. All methods have advantages and disadvantages, a combined sampling approach is the most effective for estimating and monitoring animal populations (Witmer, 2005; Croose *et al.*, 2019).

Hunting bags statistics, by reporting date, local and some information about the hunted specimen, can be a tool for monitoring and study population trends (Myrberget, 1988; Besnard *et al.*, 2010). For instance, in the UK, many estates have monitored local game abundance in the last two centuries, through numbers of culled animals annually (Whitlock *et al.,* 2003; Aebischer & Baines, 2008). Potts *et al.* (1984) analysed population fluctuations in the red-grouse *(Lagopus lagopus)* through the analysis of bag records and Cattadori *et al.* (2003) calculated the index of their population density. Virgós *et al.* (2007) used hunting bag data as the source of wild rabbit abundance across years and analysed population trends in order to identify its conservation status in Spain. It is also worthy of mention that Kitson (2004) used the harvest rate of sooty shearwaters (*Puffinus griseus)* as a tool for monitoring population trends. Using hunting bags as source of information for monitoring programs has numerous advantages compared to other methods, such as (Witmer, 2005; Aebischer & Baines, 2008; Croose et al., 2019):

- Covering a wide span of time and space, providing national scale vision and unique insight into historical trends;
- Covering a great range of species;
- Absence of common limitations like challenging fieldwork, secretive habits of species, high financial and team investment, space and time limitations.

The main challenge of working with hunting bags is finding a plausible link between the number of animals culled and trends of game populations. This is particularly challenging if there is missing data, such as spatial and/or temporal gaps in records, hunting efforts or in the absence of a systematic method to record hunting data (Ferreira *et al.,* 2010). Studies with a large dataset tend to perform well and obtain better estimates, even in the absence of accurate hunting effort information (Whitlock *et al.,* 2003; Aebischer & Baines, 2008).

1.3 Hunting in Portugal

Since pre-historical times, hunting has been part of human's lifestyle, both as a way to find food and to strengthen social bonds (Gallego, 2010). Small mammals, like the wild rabbit, were a major component of humans' diet in the Iberian Peninsula since the Palaeolithic, and they still remain a valuable resource nowadays, although less than before due to the domestication of the species (Delibes-Mateos, 2008). Humans have also hunted several other animals since primordial times, namely the deer. Centuries ago, in Europe, big game hunting was restricted to the upper classes, such as the royalty and nobility (Salazar, 2009), but with the passing of times, deer hunting steadily increased in popularity and became a universal sport, under specific regulations and fees (e.g., Ordinance n.º 105/2018, of April 18) To minimise over-hunting, pressure on game species and conflicts between hunting and other ecological and agricultural goals, the implementation of hunting management legislation was crucial. In Portugal, since 1959, is forbidden to hunt endangered species (Salazar, 2009) and from 1986 onwards hunting zones were created to allow adequate management and sustainable hunting of game species, generating additional sources of income mainly in depressed rural areas. After the law nº30/86, of 27 August, it was possible to establish "Zones of Special Hunting Regime" (ZSHR), where game management is allowed, and hunting effort regulated according to availability of game species. The law aimed to reconcile the principle of hunting freedom with the right of game exploitation, resulting in the obligation to negotiate agreements with landowners and the establishment of rules in favour of resident hunters. In addition, management entities were entitled to monetary compensation, based on their contribution to breeding, promotion and conservation of game species, thereby encouraging their protection. ZSHR are created by the Government according to several administrative types: National Hunting Zone (NHZ), Social Hunting Zone (SHZ), Associative Hunting Zone (AHZ) and Touristic Hunting Zone (THZ). There are also hunting zones that belong to the military or to the justice ministry; however, these are very uncommon and will not be discussed in detail. What differs between ZSHR is the management entity, payment options and the modalities of hunting plans and exploitation (Law nº 30/86).

NHZs are established in areas whose physical and biological characteristics allow the formation and preservation of important game resources or when, by public safety reasons, it is justified being the State the only responsible for its management. SHZs aimed to provide all national hunters the possibility to hunt in affordable conditions. In 1999, Municipal Hunting Zone (MHZ) replaced the SHZ (Law nº 173/99, of 21 September). In a similar concept, MHZ favours the local resident hunters and hunting depends on a special permit, obtained by public lottery to ensure equal accessibility. Management of MHZs may be performed by farmers, forestry producers, environmental NGOs, local authorities or other collective entities. AHZs encourage partnership between hunters, with game management done by associations, societies or hunting clubs with intention on carrying out actions towards the sustainability of hunting and game resources. It is the hunter’s association responsibility to elaborate the management and exploration plans and hunting is reserved for its members and their guests. Finally, THZs aim essentially to provide a touristic service by exploring game resources. This may be done by the State, local authorities, tourist companies or societies of landowners. Hunting is offered equally both to national and foreign hunters.

The implementation of ZSHRs in Portugal increased steadily until the point where almost all-available land was under a specific management plan (game included) which happened around 2006 (Figure 1). Currently, national authorities consider that the designation of “Zone of Special Hunting Regime” is outdated given the large dissemination (coverage) of the different types of game management across the country. As such, the designation in use is simply Hunting Zone (HZ).

Besides HZs, there are also areas of land under no management plan but where hunting is permitted, according to general limitations by law. These are referred as “unordered hunting lands” (Law nº 173/99, of 21 September).

In 2018 there were 4977 HZs covering around 7 million hectares, corresponding to 79% of national mainland territory (INE, 2018). Portugal is organised in five hunting regions, I - North, II - Centre, III – Lisbon and Tagus Valley (LTV), IV – Alentejo and V – Algarve (Figure 2). Most of HZs are located in Alentejo and AHZ dominate in all regions (over 50% in number and area). MHZs are more abundant in the North where THZs are only vestigial, while in Alentejo and Algarve the opposite occurs. In central Portugal (regions II and III) MHZ and THZ have similar abundance (Lopes, 2015; Santos *et al.*, 2015). Military and justice ministry HZs are scarce and together with NHZs, represent only 0.3% of the total number of HZs (INE, 2016).

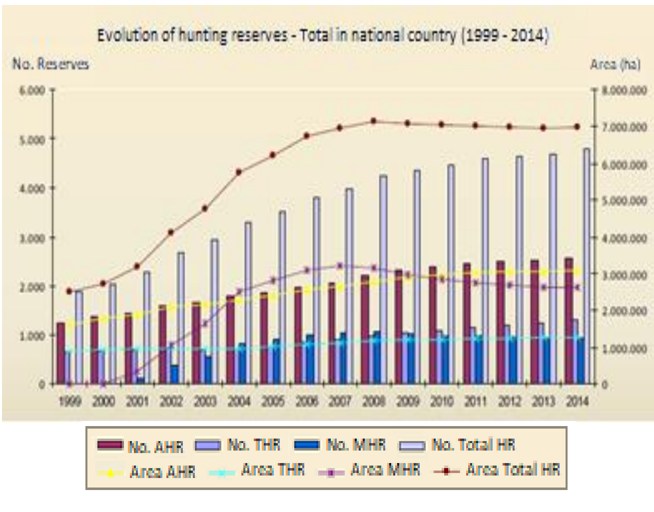


Figure 1 - Evolution of the number and area of total HZs in Portugal from 1999 to 2014 *(adapted from Lopes, 2015)*

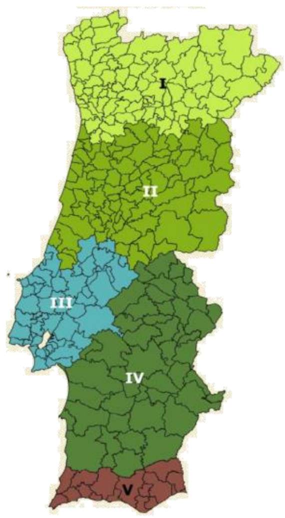


Figure 2 - Hunting regions in Portugal: I - North, II - Centre, III - Lisbon and Tagus Valley, IV - Alentejo, V – Algarve *(adapted from Lopes, 2015)*

Since 1989, each HZ needs to report annual game results to the institution in charge (currently, ICNF - *Instituto da Conservação da Natureza e das Florestas* – Institute for Nature Conservation and Forests). These reports include the number of hunters, hunting days and animals that were culled (*Decreto-lei* nº 202/2004). ICNF compiles these data, allowing information on the number of animals culled by species in each HZ and hunting season.

Current legislation requires for each HZ the establishment of multi-annual hunting plans. These contain relevant components for the conservation, promotion and exploration of game, such as land use and water resources cartography, game species inventory, qualitative estimation of game populations (e.g., age and sex structure), conservation measures and processes of population estimation. It also defines goals such as to minimize negative impacts for the game fauna, to increase habitat carrying capacity or to enhance maximum sustained productivity, and establishes the actions to reach them, including habitat and population management.

Habitat management measures can be oriented for improving food resources and water availability (e.g., establishing game crops, defining sowing and grazing periods, installing water points), for improving availability of shelter (creating refugee areas) or for improving habitat quality (increasing structure complexity). Population management encompasses restocking, translocations, selective shooting, predator control, population estimation and monitoring and determination of harvesting rates (Bugalho & Carvalho, 2001).

The hunting calendar is another tool for game management, stating the species, processes and periods reserved to hunting activity, taking into consideration reproductive cycles and migration periods of the game species. Currently, this calendar is established every 3 years and applied at national level. The number of culled specimens of each species and the expected number of hunting days are defined in the annual hunting plan, according to the population management measures undertaken.

Hunting effort is also a main factor that influences animal populations and can be measured either by the number of hunters, time spent hunting, area covered by hunters or even hunting methods used (Rist *et al*., 2008). These parameters influence population age and sex structure and animal behaviour, especially in big game species since hunters tend to prefer trophy animals, turning hunting more selective (Hutchings & Harris, 1995; Torres-Porras *et al*., 2008; Braga *et al*., 2010). However, hunters or landowners seldom measure or are required to supply this information. As such, hunting effort is evaluated trough results of questionnaires and interviews (Brøseth & Pedersen, 2001) and to economic results on the number of registered hunters. In Portugal, data on the total number of emitted hunting licences per hunting season depict a decrease between 2000/01 to 2014/15 (from ca. 225 000 to 115 000 emitted licences). It is also known that the majority of current licenced hunters are of old age – in 2014, 69% were above 50 years old and only 3.3% were under 30 years (Santos *et al.*, 2015). This abandonment on hunting activity, linked with the low recruitment of young people and the high rate of old age hunters who simply cease hunting, is expected to continue unless there is an effort to entice young hunters and/or tourists (Paiva *et al.*, 2017). This conjures a problem for the economy and to the management of HZs, due to lack of financial income. Also, over-abundant game populations, such as the wild boar, will increase without the population control from hunting, thus enhancing the negative effects it has on ecosystems.

Concluding, hunting, as a bio-economic activity, is directly related to animal population management, influencing it strongly and conditioning distribution and abundance of game species (Fisher *et al.,* 2013).

This dissertation addresses the three species of wild herbivores previously mentioned: the wild rabbit, the Iberian hare and the red deer. All these herbivores are game species by law in Portugal (e.g. Annex I of *Decreto-Lei* nº 202/2004, of 18 August 2004, amended by *Decreto-Lei* nº 201/2005, of 24 November 2004).

1.4 Deer-rabbit/hare interactions

Normally, different feeding niches contribute to ecological segregation and coexistence among herbivores within the same habitat. Herbivores have developed different digestive systems and ways to digest the plant food, and therefore have different diets. The main difference among herbivore digestive systems are polygastric and monogastric, or ruminant and non-ruminant herbivores. These animals also tend to differ largely in body size and behaviour (Duncan *et al.,* 1990), which leads to a resource's partition through selection of food items with different height above ground level ("feeding-height-separation" hypothesis (Du Toit, 1990; Bugalho, 1995; Sangiuliano *et al.,* 2016). This means that the smaller herbivores can feed on vegetation closer to the ground, while larger herbivores feed higher on vegetation, thus causing segregation between species, or even between males and females of dimorphic species such as deer (Bugalho *et al.,* 2001). However, this hypothesis is not yet completely confirmed (see, for example, Telfer, 1972a, b; Belovsky, 1984; Hulbert & Andersen, 2001).

Increased herbivore population density and dispersion may trigger interspecific competition for resources or cause habitat changes that affect other animal and plant populations (Lecomte *et al.*, 2017). An example is the "overabundance" of ungulates (such as wild boar and red deer) which cause several negative effects on wildlife, vegetation and soil dynamics through over-foraging (Carpio *et al.,* 2014; Lecomte *et al.*, 2016). In this situation, it is hypothesised that deer (large ruminants) and lagomorphs (small non-ruminants), sharing the same food stratum, may compete for food resources. Lagomorphs are expected to have a competitive advantage under large ruminants, since they have a digestive system more tolerant to poor quality foods (Sangiuliano *et al.,* 2016) and the relation between metabolic needs and body size allows them to survive with limited food resources (Illius & Gordon, 1987). However, when food is scarce, both species may prefer to feed on vegetation closer to the ground, since younger plants are more nutritious, empowering interspecific competition (Belovsky, 1984; Hulbert & Andersen, 2001).

Despite lack of information on the subject, some studies report overlapping diets in deer and lagomorphs. Dodds (1960), Telfer (1972a) and Belovsky (1984) found an overlap in the diet of the Moose (*Alces alces*) and the Snowshoe hare (*Lepus americanus*), suggesting competition between them, and Telfer (1972b) also found a diet overlap between the White-tailed deer (*Odocoileus virginianus*) and the Snowshoe hare. Hulbert & Andersen (2001) suggest that when coexisting in the same habitat, roe deer (*Capreolus capreolus*) and the European hare (*Lepus europaeus),* which are both browser species, preferentially feeding on woody vegetation, compete between themselves, with the hare having a poorer diet. In the Mediterranean climate, Sangiuliano *et al.* (2016) also reports this situation between the roe deer and European hare, although of minor significance and only during winter.

In the last decades, big game species, such as deer, have increased across their areas of distribution, mainly due to favourable habitat changes (e.g. agricultural abandonment and consequent increase of woody habitat types) and lack of large predators (Lecomte *et al.*, 2016). Additionally, particularly in Portugal, there were various areas where deer was reintroduced, mainly for hunting purposes (Salazar, 2009). While previously decreasing, deer populations are now responding positively to these conservation actions (Bugalho *et al.*, 2006; Salazar, 2009; Burbaite & Csányi, 2010). Overabundant deer populations, however, may negatively impact ecosystems and eventually other herbivores due to interspecific competition for food (Carpio *et al.,* 2014).

In the present thesis, within the context of competition and facilitation among different body size herbivores species, we aim to assess, as a preliminary step of future research, if there are significant correlations between density of red deer and wild rabbit/Iberian hare harvest in hunting zones in Portugal.

1.5 Objectives

Monitoring distribution and abundance of wild herbivores is crucial for managing their populations. For game management purposes, in particular, it is also important to know how HZ's characteristics may affect game populations. Given that HZs report the numbers of harvested animals, this data may be useful to inform monitoring and management plans for game species populations.

The main objective of the present dissertation is to explore hunting bag data as a complement of other sources of information on the distribution and abundance of game populations, using wild herbivores as an example. Additionally, it addresses how hunting bags vary with location and administrative type of HZs. Therefore, annual density of wild rabbit, Iberian hare and red deer harvested in HZs of continental Portugal, between 1989-2018, are analysed to (i) generate maps of occurrence/distribution for the analysed species, which is compared with distributional data reported by the Atlas of Mammals of Portugal (Bencatel *et al*., 2019); (ii) ascertain the influence of HZ's characteristics on density of hunted animals; (iii) determine the hunting bag trends in the analysed HZs; (iv) investigate potential correlation between hunting bags of red deer and wild rabbit and between red deer and hare.

Specific objectives can be synthesized in the following questions:

(i) Do hunting bags reported for red deer, wild rabbit and hare across the country, support distributional data reported by the Atlas of Mammals of Portugal for these species?

(ii) Are there differences in hunting bag densities among regions, administrative types and years?

(iii) Do trends of hunting bags vary with administrative type and hunting region?

(iv) Are there significant correlations, either positive or negative, between annual density trends of wild rabbits and red deer and between hare and red deer?

Each topic is address as a specific section of the results in chapter 3 of this dissertation. Discussion and main conclusions are presented in chapter 4 and final considerations in chapter 5. The bibliography cited throughout the document are listed in chapter 6. Supplementary information regarding data analyses can be found in annexes I to VI.

2. Materials and Methods

2.1 Study area

This study is conducted at the national level, covering the whole territory of Continental Portugal. Biogeographically, Continental Portugal is divided in two Holarctic Regions: Eurosiberian and Mediterranean. The north-west of Portugal belongs to the Eurosiberian Region, characterized by a temperate and rainy climate, strongly influenced by the Atlantic Ocean (Aguiar *et al.,* 2008). Mean annual temperature varies between 19°C in summer and 3°C in winter, while mean annual rainfall is usually over 1,000 mm (IPMA, 2015). North-east, centre and south Portugal belong to the Mediterranean Region, characterized by mild winters and a dry period in summer that lasts at least two months, where temperatures are high and rain is scarce (Aguiar *et al.,* 2008). In the north-east rainfall averages around 1,000-800 mm annually, going below 400 mm in some areas, while mean annual temperatures vary between 20°C in summer and 4°C in winter (Ferreira, 2000; IPMA, 2015). In the central and southern areas of Portugal, most of the territory receives around 500-700 mm of rainfall per year, with some areas in Algarve receiving less than 400 mm (Ferreira, 2000). The exception occurs in mountainous areas were annual rainfall goes above 800 mm in the south and reaches 2800 mm in the Central System (*Serra da Estrela*) (Ferreira, 2000). In the centre of Portugal average temperature reaches 21°C in summer and 7°C in winter, while in the south it varies between 24°C in summer and 9°C in winter (IPMA, 2015).

The northern and centre areas are the more mountainous regions of Portugal (Aguiar *et al*., 2009) with four main mountain complexes: the *Serras Galaico-Portuguesas* (1,544 m at *Serras do Gerês*)*, Serras Galaico-Duriences* (1,486 m at *Serra de* Montesinho)*, Serras Beira-Durienses* (1,381 m at *Serra de Montemuro*) and the Central System that includes *Serras da Malcata, Gardunha, Açor, Lousã* and *Estrela,* where the highest point of continental Portugal occurs (1,993 m) (Aguiar & Vila-Viçosa, 2016). At the centre-southern Portugal there are some lower mountains, such as *Serra de São Mamede* (1,027 m) in the east, and *Serras de Aire e Candeeiros* (675 m) and *Serra de Sintra* (528 m) in the west (Rebelo, 1992). Southern Portugal is mainly plain, with relevant elevations at *Serra de Monchique* (902 m) and *Serra do Caldeirão* (577 m) (Ferreira, 2000).

The north-west forest communities are characteristic of the Eurosiberian climate, such as woods dominated by deciduous trees, mainly the European (*Quercus robur*) and Pyrenean-oak (*Quercus pyrenaica*), and low scrubs of gorses (*Ulex* sp.), heathers (*Erica* sp.) and brooms (*Cytisus* sp.). Typical of the Mediterranean area are the woods and scrubland composed of sclerophyllus shrubs and trees like the holm-oak (*Quercus rotundifolia*), cork-oak (*Quercus suber*), kermes-oak (*Quercus coccifera*) and wild olive tree (*Olea europaea*). Annual meadows of cistus (*Cistus* spp.), heathers and gorses are frequent in brushland clearings.

The vegetation at the north-east of Portugal consists of mixed woods of cork-oaks, holm-oaks and juniper trees (*Juniperus* sp.) and a landscape dominated by bushlands of heathers and brooms. The plains of interior Alentejo are dominated by *montados* of cork and holms oaks, being common in low areas several types of reeds and meadows typical of wet soils. Also, scattered across the territory, it is possible to observe mosaics of these oaks with a diversity of scrubland (e.g. strawberry tree *Arbutus unedo*, kermes-oak) and low bushes (heathers, cistus). In the littoral areas of center and southern Portugal vegetation is quite complex, with a diversity of oaks and wild olive woods. Near water lines it is common to find ash trees (*Fraxinus* spp.), willows (*Salix* spp.), poplars (*Populus* spp.), elms (*Ulmus* spp.) and brambles (*Rubus* spp.). This primitive vegetation is, however, often replaced by crops, meadows or vineyards. It is also possible to find low brushlands and scrublands typical of dunes and coastal cliffs, such as juniper, seagrass and gall-oak (*Quercus lusitanica*). In Algarve and southern Alentejo, besides the woods previously mentioned, it can also be found carob trees (*Ceratonia siliqua*) and low brushlands of cistus and thymes (*Thymus* sp.) (Aguiar *et al.,* 2008).

2.2 Hunting bag statistics

The hunting bag data was obtained from ICNF, under a protocol with CEABN (*Centro de Ecologia Aplicada "Professor Baeta Neves"* – Centre for Applied Ecology "Professor Baeta Neves"), School of Agriculture, University of Lisbon. Dataset consists on the number of animals harvested (per hectare) during each hunting season as well as information related to HZ administrative type (associative, touristic, municipal), HZ location (expressed by the administrative hunting region, see Figure 2) and by the centroid coordinates of the HZ area (which were used for projection in ArcGis maps). Hunting bag data covered the period between hunting season of 1989/1990 and 2017/2018. Throughout the text, hunting seasons will be identified by the first year of the season, e.g. 1989/1990 = 1989 or 89. Deer hunting is allowed all year, however a hunting season initiates in June and ends in May of the following year. Rabbit and hare game seasons are open from September to December, although hares may be hunted until February with specific methods (Ordinance n.º 105/2018, of April 18).

This dissertation addresses three species: the wild rabbit, Iberian hare and red deer. A first exploratory analysis revealed that hunting bags for other species, such as roe deer and fallow deer, did not have enough data for national coverage and analysis. Although hunting bag data of red deer are considerably less than of rabbit and hare (see Table 1), this species was kept as a representative of big game, namely to analyse the relationship between this animal and the lagomorphs.

Rabbit, hare and deer data

For rabbit and hare there are 27 years of data, from 1989/90 to 2015/16, while for deer there are two additional years, until 2017/18. All available data with known location of animal harvest were used to describe species distribution, whereas a subset of the data was applied to assess hunting bag trends (Virgós *et al.*, 2007). This latter subset includes HZs with 13 or more years of records for rabbit and hare (corresponding to at least 50% of hunting seasons in the study period) and with 8 or more years of records for red deer.

Table 1 - Number of HZs with record of at least one hunting season in the period 1989-2015(7) in Portugal, specified by game species, hunting region and administrative type.

Region	Rabbit	Hare	Deer
North	843	484	10
Centre	969	678	121
LTV	688	545	22
Alentejo	2283	2516	195
Algarve	261	243	42
Total	5044	4466	390

Type	Rabbit	Hare	Deer
Associative	2760	2551	195
Municipal	1160	719	40
National	13	12	3
Touristic	1080	1155	150
Military	4	3	1
Social	24	24	1
Ministry of Justice	3	2	0
Total	5044	4466	390

Table 2 - Number of HZs with 13 or more recorded hunting seasons for rabbit and hare, and with 8 or more recorded hunting seasons of deer, between 1989-2015(7) in Portugal, specified by game species, hunting region and administrative type.

Region	Rabbit	Hare	Deer
North	198	97	0
Centre	238	140	28
LTV	288	102	3
Alentejo	443	493	39
Algarve	61	42	4
Total	1228	874	74

Type	Rabbit	Hare	Deer
Associative	959	636	28
Municipal	28	3	1
National	0	0	2
Touristic	240	235	43
Military	1	0	0
Total	1228	874	74

Rabbit hunting data refer to 5044 HZs, of which 1228 HZs have 13 or more registered years. The Military HZ type was removed from analysis on the effect of administrative type, due to the lack of representativeness in the dataset, and only associative, municipal and touristic HZs were considered (1227 HZs).

Data of annual hare bags was reported by 4466 HZs, of which 874 HZs have 13 or more registered years. Given that there is just three MHZs, only AHZs and THZs were considered for evaluating the effect of administrative type on hare trends (871 HZs).

Deer hunting was reported by 390 HZs, of which 74 HZs have 8 or more registered years. There is only one municipal and two national HZs, which is not enough data to take conclusions on these management types, so only AHZs and THZs were considered for evaluating the effect of administrative type on deer trends (71 HZs). Also, since there are no HZs in north region, and only three in LTV region and four in Algarve, these regions were not included in the analysis for effect of hunting regions (67 HZs).

2.3 Methods

2.3.1 Comparison between hunting bag locations and species distribution reported in Atlas of Mammals of Portugal (2019)

Systematic surveys of species covering all national territory are challenging, time-consuming and imply considerable investment of financial resources. The Atlas of Mammals of Portugal (Bencatel *et al.*, 2019) resulted from an exhaustive compilation of bibliographic sources, complemented with direct personal records from individuals, associations and companies, news, naturalistic photographs, public databases and various information available online. Works of this nature, similar to that of most mammal Atlas in other countries (Palomo *et al.*, 2007), are essential for mapping and analysing general patterns of the known distribution of species at the national scale, being an important starting point for further investigation. For the purposes of this dissertation, the Atlas of Mammals of Portugal (hereafter mention as Atlas)was considered the most complete work on the distribution of mammals in Portugal. Additional sources of information, however, may contribute to improve and complement large scale distribution maps (Bencatel *et al.*, 2019). Such is the case of information regarding species hunting bags.

In the Atlas, distribution maps were constructed by converting the records of species presence to the respective square of the UTM-29 (Universal Transverse Mercator) 10x10km^2 grid, in national territory (Bencatel *et al.*, 2019). Similarly, for comparing hunting bag locations with Atlas species distribution data, the centroid of each HZ was projected in ArcMap (from ESRI ArcGIS 10.6.1) and the UTM-29 10x10km^2 grid was applied to the map of continental Portugal, with the difference that the Atlas used R software for projection. With the purpose of displaying hunting occurrence of each species in a given period, thus representing species presence in mainland Portugal, all HZs were considered in this analysis.

A filled-in grid square means that a species was detected and harvested at least once in that area, during the period considered. In the Atlas, areas with no indication whether the species is present or not are identified as "No data" (Bencatel *et al.*, 2019). In the maps constructed in this dissertation, it corresponds to areas where there are no records of HZs. The Atlas distinguishes "Old" records from "Recent", considering old data from 1990 - 1999 and recent from 2000 – 2018, so this legend was used was well in this dissertation's maps. There is also unconfirmed data in the Atlas' maps, corresponding to records of occurrence from vocalizations, records of indirect signs of presence not confirmed genetically or records with no indication of how they were obtained (Bencatel *et al.*, 2019). The maps constructed from the hunting bags comprise only confirmed records, since each corresponds to a culled animal.

To compare Atlas distribution maps with hunting bag locations, the number and percentage of grid squares common to both sources of information were assessed and their frequencies compared.

2.3.2 Differences in species hunting bags among regions, hunting zone types and across years

The effect of hunting region, administrative type and year on the harvest density of each study species was analysed with ANOVA on transformed data (see below). A three-way ANOVA with hunting region, administrative type and year as independent factors and hunting bags density as dependent variable, was performed. Tukey post-hoc HSD test were used to assess the differences between groups (see section 2.2 Hunting statistics).

Kolmogorov-Smirnov test showed that the original density values of rabbit, hare and deer do not follow a normal distribution neither in regions, types nor years and histograms and normal Q-Q plots displayed a right-skewed distribution (see Annex I). Hence a logarithmic (log_{10}) transformation was performed (the most suitable transformation for right-skewed distributions, see Kirchner, 2001; McDonald, 2008) to reach normality and homoscedasticity. Log transformed data distribution was shown to be very close to normal and therefore parametric analysis were used as this approach is more robust to slight violations of their assumptions (Blanca et al., 2017) and can perform well with non-normal data if sample size is satisfied (Frost, 2015).

The density logarithmic values are not very informative so it would not be wise to report means in transformed units (McDonald, 2008). The marginal means of hunting bags density (m) for each level of each factor, as well as the lower and upper bounds of 95% confidence interval (CI), of the log-transformed values were back-transformed and displayed in graphics.

Non-parametric Kruskal-Wallis tests were performed on the original data and are available in Annex III, as well as statistical information of the original data (Annex II).

The level of statistical significance considered for all analysis was at p-value < 0.05. Data were analysed using the SPSS software (IBM SPSS Statistics version 25) and graphics were constructed in Microsoft Excel.

2.3.3 Trends in density of hunting bags across regions and hunting zone types

To assess the trend in density of bagged species across the period of study period, each HZ was classified according to annual changes in the density of harvested animals using adapted criteria from other studies (e.g., Pannekoek & van Strien, 2005; PECBMS, 2012; Dias, 2016). A general linear model for bag density with year as explaining variable was used to determine slope values and R^2 significance. R^2 significance was calculated through variance analysis, considering a 0.05 (p) significance level. Annual relative variation (k) was determined by dividing slope value obtained with the model, by the mean of annual values. Hence, each population tendency in each HZ was categorized from k and p values (Table 3).

***Table 3 - Tendency categories criteria**. Adapted from other European studies on population status evaluation (e.g. Dias, 2016)*

Annual relative variation (k)	Significance (p)	
	p < 0.05	**p ≥ 0.05**
k ≥ 0.05	SG - Significant growth	UG - Unstable growth
0.00 < k < 0.05	G - Growth (moderate)	U – Unstable
-0.05 < k < 0.00	D - Decline (moderate)	
k ≤ -0.05	SD - Significant decline	UD - Unstable decline

Contingency tables were performed for each one of the three species in study, one with the variables region/tendency and other with type/tendency. A contingency table displays the frequency distribution of two categorical variables as well as the proportion of a variable within the other, providing a general picture of the relation between them. Furthermore, a chi-square test was conducted as it determines whether there is a relationship between categorical variables (if they are dependent or not) (Van Den Berg, 2014).

Adjustments on the criteria for population tendency categories were performed after first analysis so that no cells on the contingency table had zero counts (Weaver, 2013). Original categories SG/G were merged as G (growth), categories SD/D were merged as D (decline) (Table 4). The results for rabbit populations considering these five tendency categories are available in Annex IV.

Table 4 - Adjusted tendency categories

Annual relative variation (k)	Significance (p)	
	p < 0.05	**p ≥ 0.05**
k ≥ 0.05	G - Growth	UG - Unstable growth
0.00 < k < 0.05		U – Unstable
-0.05 < k < 0.00	D - Decline	
k ≤ -0.05		UD - Unstable decline

A second adjustment was performed since hare and deer contingency tables still displayed cells with zero counts. Original categories UG/U/UD were merged as U (unstable) (Table 5).

Table 5 – Second adjustment of tendency categories

Annual relative variation (k)	Significance (p)	
	$p < 0.05$	**$p \geq 0.05$**
k > 0.00	G - Growth	U – Unstable
k < 0.00	D - Decline	

Graphics with the proportion (in %) of each population tendency category across hunting regions and administrative types were constructed in Excel. HZs' centroid were projected in ArcMap (from ESRI ArcGIS 10.6.1) within each hunting regions.

2.3.4 Correlations between species harvests

HZs with records of both lagomorphs and deer were selected to evaluate the link between species trends. Correlation analyses were performed between hunting bag densities of red deer and wild rabbit and between red deer and hare for each HZ. Five types of correlations were considered: strongly negative or positive (p-value < 0.01), negative or positive (p-value < 0.05) or neutral (p-value > 0.05). A negative correlation means that both species density trends run in opposite directions trough time (e.g., one increasing while other decreases), whilst a positive correlation indicates a similar pattern between hunting bag density trends (i.e., both increasing or decreasing).If no significant correlation was found the relationship is classified as neutral.

To visualize correlations, the HZs' centroids were projected in ArcMap (from ESRI ArcGIS 10.6.1) together with administrative hunting regions borders and information on correlation tendencies.

Factors influencing Pearson correlation values were explored using a set of variables, reflecting changes in landscape composition between 1995 and 2018, in terms of dominant land use/cover categories identified by GIS. The geographic limits of each HZ were used to extract the area of each land-use class from the land-use/cover maps available for 1995 and 2018 (COS 1995 and COS 2018 form IGP). The amount (in hectares) and the proportion (in %) of change for each land-use and of transition between major land-uses classes were synthetized in a transition matrix (from 1995 to 2018). The small number of HZs with significant Pearson values prevent further analysis and modelling using land-use changes as explanatory variables. Therefore, the discussion on potential links between Pearson correlation and changes in main land-use classes were supported by visual inspection of average proportion of change (and corresponding 95% CI) according to correlation types. Differences are highlighted when no 95% CI overlap between different land-use categories (classes) were observed.

3. Results

3.1 Species occurrence and comparison with Atlas of Mammals of Portugal (2019)

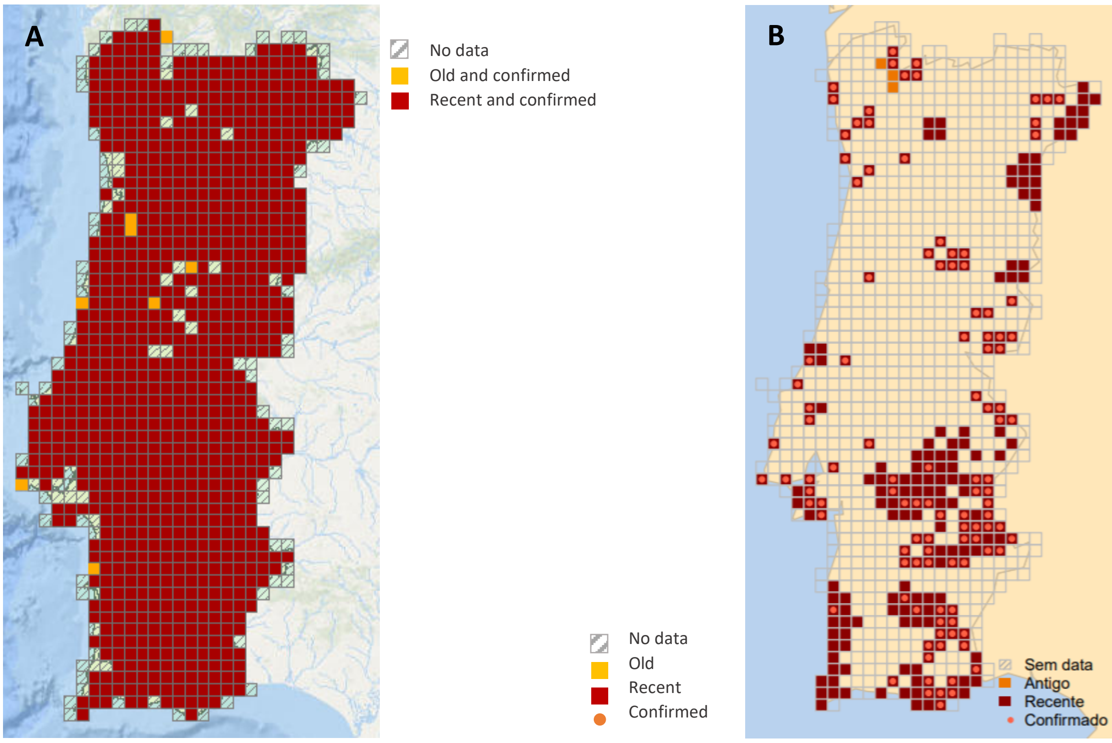
3.1.1 Wild rabbit

Hunting bag data shows that the wild rabbit is widely distributed across continental Portugal (Figure 3A). The 5044 records of rabbit occurrence, from 1989 to 2016, cover 89.6% of national territory (904 grid squares out of 1009) (Figure 3A'). Eight of these squares regards "old" data (no records after the year 1999/00). The map of the Atlas of Mammals of Portugal (Figure 3B) shows a very different distribution of the wild rabbit, with 1790 records, of which 45.3% are verified, covering 23.0% of the national territory (232 grid squares) (Figure 3B').

The Atlas' and the hunting bags' maps have overlapped 994 grip squares (Table 6, 7 and 8). The records of recent occurrence from hunting bags not only confirm most recent records from the Atlas (91%) but also add 686 grid squares (88.5%) where the rabbit is considered as absent (Table 6). Moreover, most old records from hunting bags fill grid squares where rabbit was considered absent in the Atlas (Table 6). However, according to the information provided by the Atlas, wild rabbit is present in about 10% of national territory where there is no data from hunting records (Table 6).

Table 6 - Number of grid squares overlapping in the two maps of wild rabbit occurrence. *ATLAS: records regarding the Atlas of Mammals of Portugal. HUNTING BAGS: records regarding the map constructed from hunting bags. Absent (blank): no records of occurrence. For more info, see Figure 3*

ATLAS / *HUNTING BAGS*	*No data*	*Old*	*Recent*	*Recent confirmed*	*Absent (blank)*	*TOTAL HUNTING BAGS*
No data	0	0	9	10	69	88
Old confirmed	0	0	0	1	7	8
Recent confirmed	0	3	114	94	686	897
Absent (blank)	0	0	0	0	1	1
TOTAL ATLAS	0	3	123	105	763	**994**



Adapted from Atlas of Mammals of Portugal (Bencatel et al.*, 2019)*

A’

	Hunting Bags *No. grid squares (%)*
Old	8 (0.8%)
Recent	896 (88.8%)
Confirmed	904 of 904 (100%)

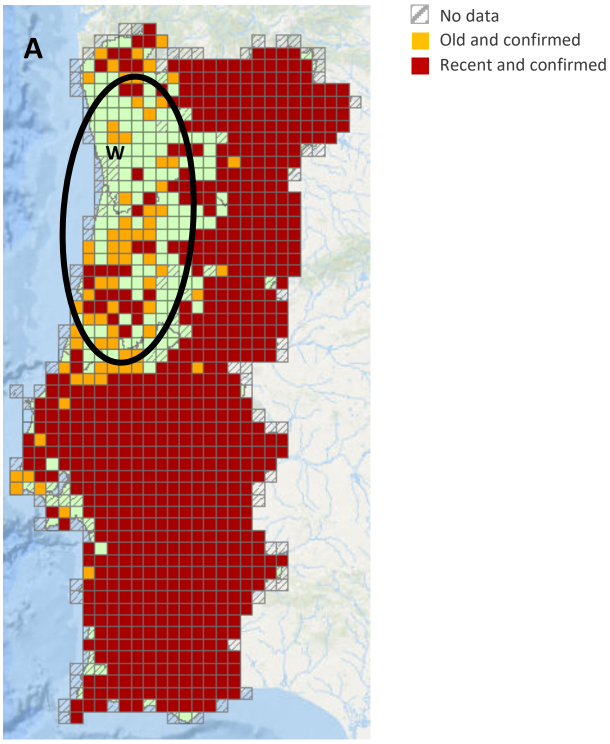
B’

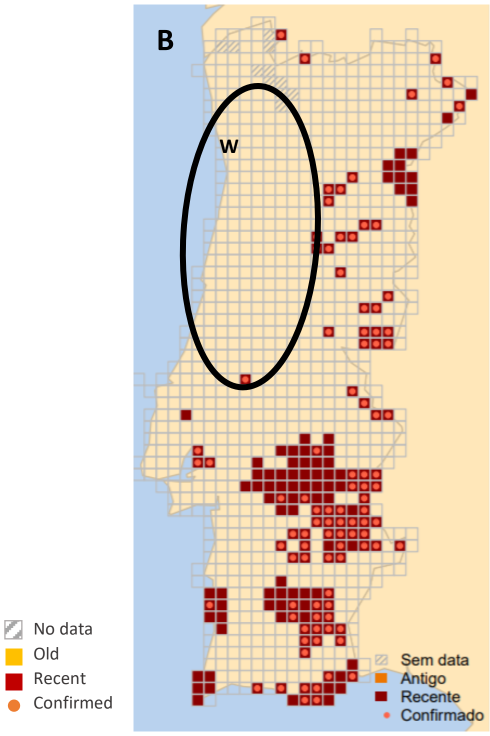
	Mammals of Portugal Atlas *No. grid squares (%)*
Old	3 (0.3%)
Recent	229 (23%)
Confirmed	105 of 229 (45.3%)

Figure 3 - Rabbit distribution across continental Portugal. *A filled-in grid square means that the species was detected at least once in that area during the time period considered. A. Hunting bags data; A’. Number and percentage of grid squares, regarding the hunting bags data, with registered presence of rabbit. B. Atlas of Mammals of Portugal (adapted image); B’. Number and percentage of grid squares, regarding the Atlas of Mammals of Portugal data, with registered presence of rabbit. Sem data – no available data. Old* (Antigo) *- data obtained from 1990 – 1999. Recent* (Recente) *- data obtained from 2000 – 2018. Confirmed* (Confirmado) *– excludes records of occurrence from vocalizations, records of indirect signs of presence not confirmed genetically or records with no indication of how they were obtained. All the data from the hunting bags comprises only confirmed records, since there was an animal kill.*

3.1.2 Hare

The maps of hunting bags show that hares are widely distributed across continental Portugal, with the exception of west part of north and centre regions (Figure 4A, circled area W). The 4466 records of hare occurrence, from 1989 to 2016, cover 76.5% of national territory (776 grid squares out of 1009) (Figure 4A'). Seventy-two of these squares do not have records after the year 1999/00 and thus were considered as "old" data. In the Atlas there are 402 records of hare occurrence (Figure 4B), 169 squared grids (16.8% of continental Portugal) of which only 53.8% are confirmed data (Figure 4B').





Adapted from Mammals of Portugal Atlas (Bencatel et al.*, 2019)*

A'

	Hunting Bags *No. grid squares (%)*
Old	72 (7.1%)
Recent	700 (69.4%)
Confirmed	772 of 772 (100%)

B'

	Mammals of Portugal Atlas *No. grid squares (%)*
Old	0 (0%)
Recent	169 (16.8%)
Confirmed	91 of 169 (53.8%)

***Figure 4** - **Hare distribution across continental Portugal.** A filled-in grid square means that the species was detected at least once in that area during the time period considered. A. Hunting bags data; A'. Number and percentage of grid squares, regarding the hunting bags data, with registered presence of hare. B. Atlas of Mammals of Portugal (adapted image); B'. Number and percentage of grid squares, regarding the Atlas of Mammals of Portugal data, with registered presence of hare. For more info, see Figure 3*

The overlap of both maps allows to see that the hunting bags confirm recent occurrence of hare in 540 grid squares (65.3%), identified by the Atlas as absent and old occurrence in 8.2% (Table 7). More so, almost all recent (unconfirmed) occurrences stated by the Atlas are confirmed by these results (92%) and 4 grid squares with no data in the Atlas are also confirmed as recent occurrence of hare (Table 7).

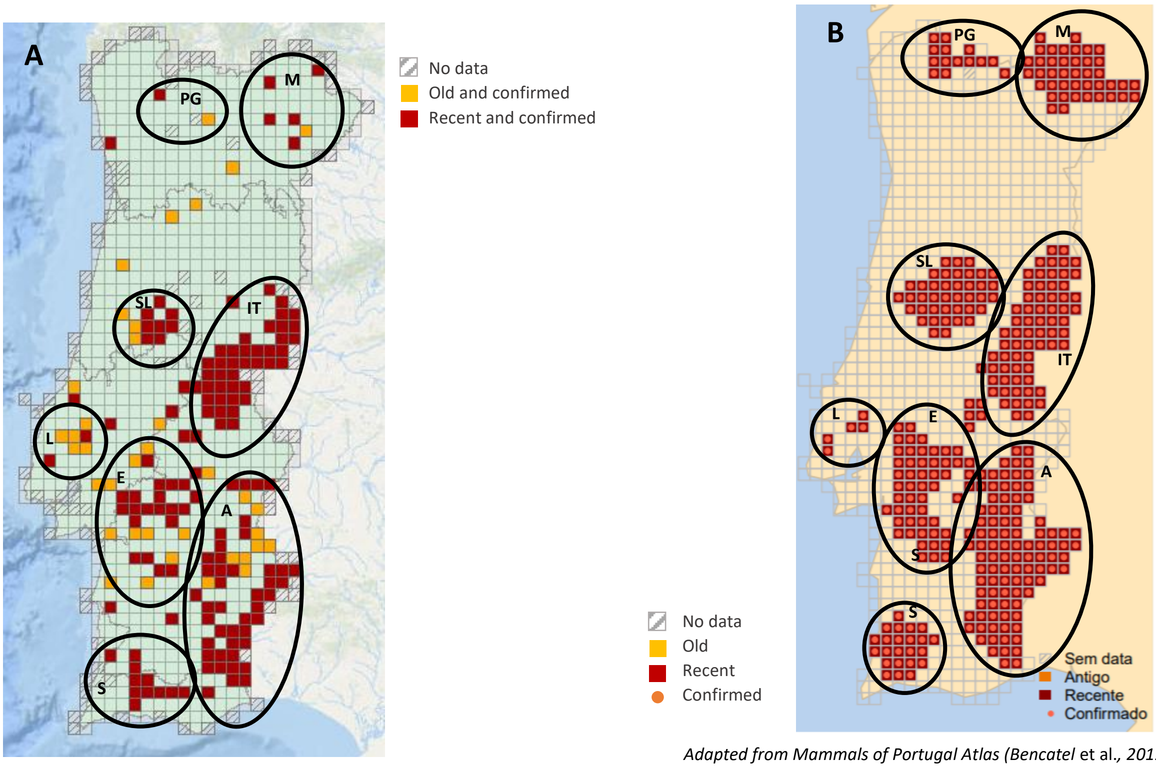
Table 7 - Number of grid squares overlapping in the two maps of hare occurrence. *ATLAS: records regarding the Atlas of Mammals of Portugal. HUNTING BAGS: records regarding the map constructed from hunting bags. For more info, see Table 6*

ATLAS / *HUNTING BAGS*	*No data*	*Old*	*Recent*	*Recent confirmed*	*Absent (blank)*	*TOTAL HUNTING BAGS*
No data	0	0	4	5	81	90
Old confirmed	3	0	0	1	68	72
Recent confirmed	4	0	72	84	540	700
Absent (blank)	4	0	1	1	126	132
TOTAL ATLAS	11	0	77	91	815	**994**

3.1.3 Red deer

The hunting bags register 390 occurrences of hunted deer in the study period, occupying 179 grid cells (ca. 17.7% of the total national area), of which 37 grid squares are "old" records. The deer distribution map in the Atlas comprises 484 records in 345 grid squares (34.4%) of which all is confirmed data. According to the data provided by the Atlas, the map constructed from the hunting records does not show the whole distribution of the red deer in Portugal. However, although in a scarcer distribution, it is possible to identify the main deer population groups displayed in the Atlas map (Peneda-Gerês National Park - PG, Montesinho Natural Park - M, *Serra da Lousã* - SL, International Tagus - IT, Lisbon (district) - L, east Alentejo - A, Évora – E, Silves - S; Figure 5A/B).

Analysing the overlap of both maps, it is seen that where the Atlas considered absence of deer, the hunting bags confirm recent occurrence in 29 grid squares (4.4%) and old occurrence in 20 (3%) (Table 8). The hunting bags also extends in time the occurrence of deer in 17 grid squares of the Atlas (Table 8).



Adapted from Mammals of Portugal Atlas (Bencatel et al.*, 2019)*

A’

	Hunting Bags *No. grid squares (%)*
Old	37 (3.7 %)
Recent	142 (14.1%)
Confirmed	179 of 179 (100%)

B’

	Mammals of Portugal Atlas *No. grid squares (%)*
Old	0 (0%)
Recent	345 (34.4%)
Confirmed	345 of 345 (100%)

Figure 5 - Deer distribution across continental Portugal. *A filled-in grid square means that the species was detected at least once in that area during the time period considered. A. Hunting bags data; A’. Number and percentage of grid squares, regarding the hunting bags data, with registered presence of deer. B. Atlas of Mammals of Portugal (adapted image); B’. Number and percentage of grid squares, regarding the Atlas of Mammals of Portugal data, with registered presence of hare. Peneda-Gerês National Park - PG, Montesinho Natural Park - M,* Serra da Lousã *- SL, International Tagus - IT, Lisbon (district) - L, east Alentejo - A, Évora - E, Silves - S. For more info, see Figure 3*

Table 8 - Number of grid squares overlapping in the two maps of red deer occurrence. *ATLAS: records regarding the Atlas of Mammals of Portugal. HUNTING BAGS: records regarding the map constructed from hunting bags. For more info, see Table 6*

ATLAS / *HUNTING BAGS*	*No data*	*Old*	*Recent*	*Recent confirmed*	*Absent (blank)*	*TOTAL HUNTING BAGS*
No data	0	0	0	34	60	94
Old confirmed	0	0	0	17	20	37
Recent confirmed	0	0	0	110	29	139
Absent (blank)	1	0	0	181	543	724
TOTAL ATLAS	1	0	0	342	652	**994**

3.2 Hunting bag differences among regions, hunting zone types and across years

3.2.1 Wild rabbit

The three-way ANOVA indicates that the effects of region, type and year on density of harvested rabbits were statistically significant at the .05 level [region: $F_{(4, 21031)} = 85.036$, $p < 0.001$; type: $F_{(2, 21031)} = 52.082$, $p < 0.001$; year: $F_{(26, 21031)} = 4.854$, $p < 0.001$]. Also, there was a statistically significant interaction between the effects of region and type on density of harvested rabbits [region*type: $F_{(7, 21031)} = 47.919$, $p < 0.001$] as well as between region and year [region*year: $F_{(103, 21031)} = 3.014$, $p < 0.001$.

The density of harvested rabbits in Algarve was not statistically different from any region other than LTV [Algarve: M = 0.089, CI = 0.075, 0.106; north: M = 0.086, CI = 0.073, 0.103, p = 0.938; centre: M = 0.049, CI = 0.042, 0.057, p = 0.506; LTV: M = 0.260, CI = 0.236, 0.287, p < 0.001; Alentejo: M = 0.088, CI = 0.075, 0.103, p = 0.303]. Besides, there are also no statistical differences between the centre region and Alentejo (p = 0.983). LTV region clearly stands out with a higher density of harvested rabbits than any other region (Figure 6). The post-hoc test on type effect shows that AHZs have a statistically significant higher density of harvested rabbits than MHZs and THZs (p < 0.001), which have similar values of mean density (p = 0.214) [associative: M = 0.142, CI = 0.135, 0.149; municipal: M = 0.082, CI = 0.065, 0.103; touristic: M = 0.073, CI = 0.065, 0.083] (Figure 6).

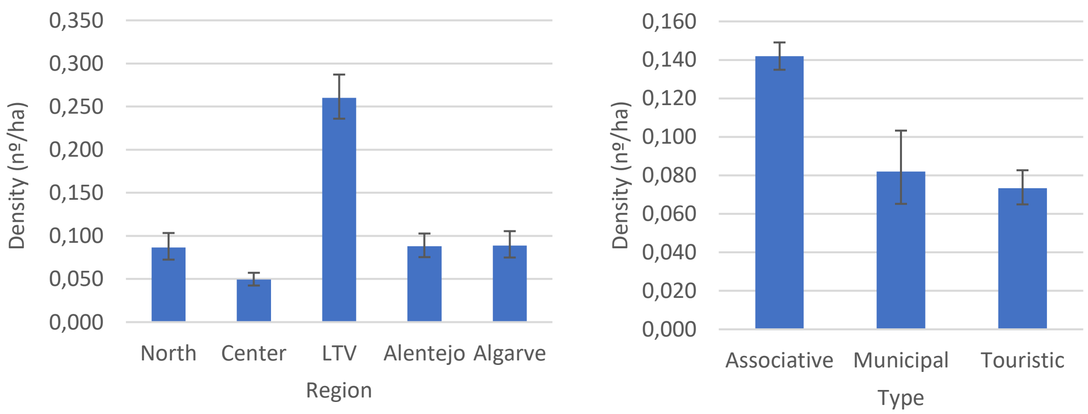


Figure 6 - Mean harvested rabbits per hectare (density) on each hunting region and administrative type. *Values are the mean of all values reported in hunt bags from 1889/90 to 2015/16 from HZs with thirteen or more records. Values were back-transformed from logarithmic transformation. Error bars display 95% CI*

The interaction between the effects region and type show that in the north, Alentejo and Algarve THZs have a density of harvested rabbits higher than MHZ and similar to AHZ, contrary to what happens both in centre region and LTV (Figure 7).

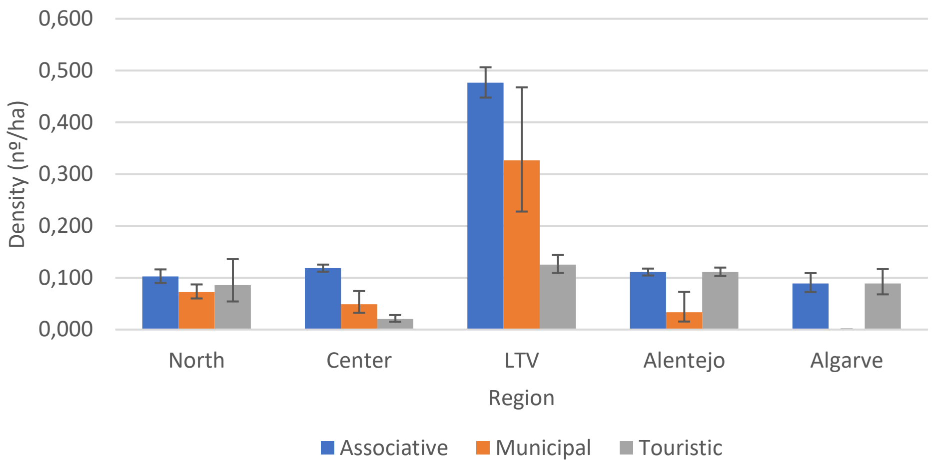


***Figure 7 – Mean density of harvested rabbits in each administrative type across the five hunting regions.** Error bars display 95% CI.*

Non-parametric test Kruskal-Wallis performed on untransformed data corroborates major effects of hunting regions [$H_{(4)}$ = 2572.040, p < 0.001] and administrative types [$H_{(2)}$ = 117.354, p < 0.001] on the density of hunted rabbits. Furthermore, Dunn's pairwise tests also highlights the higher density values in LVT region (for detailed information, see Annex III)

Mean density of hunted rabbits in Portugal shows a decrease between 1989/90 to 2015/16 with a tendency of -3% per year, resulting in ca. 50% reduction in 27 years. The highest density was registered in 1996/97 [M = 0.167, CI = 0.126, 0.222] and the lowest in 2015/16 [M = 0.036, CI = 0.025, 0.054]. The first years of data have a wide 95% CI since the density values of HZs for those years are very disperse. It is noticeable two considerable drops in density values, one in 1999/00 [M = 0.096, CI = 0.071, 0.131] and another in 2012/13 [M = 0.036, CI = 0.026, 0.050]. The year after the first drop was followed by a recuperation [M = 0.120, CI = 0.087, 0.166] but it dropped again the flowing year [M = 0.087, CI = 0.061, 0.124] (Figure 8).

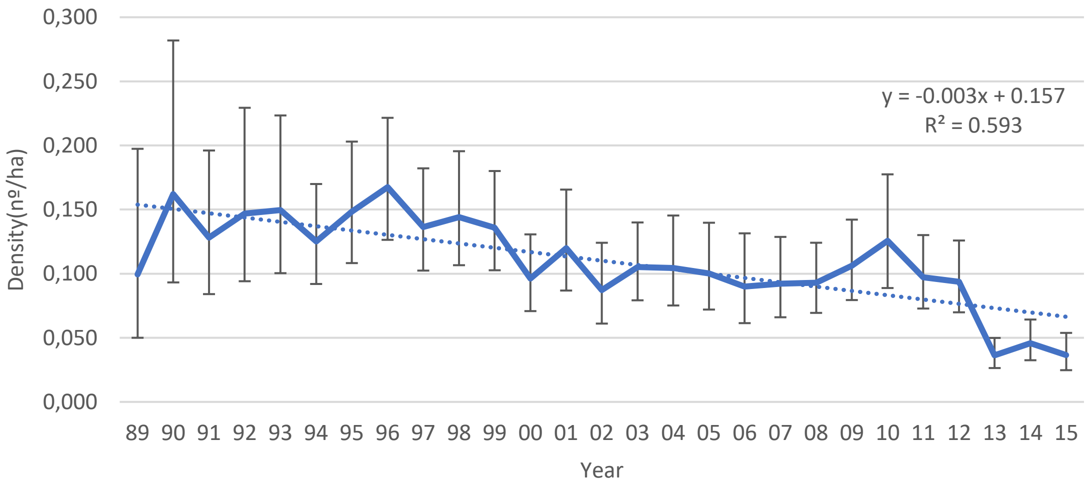


***Figure 8 – Mean density of harvested rabbits in Portugal per hunting season since 1989/90 (89) until 2015/16 (15).** Error bars display 95% CI. Trendline is displayed, as well as the equation and R-squared value.*

Looking at the graphic of the interaction between region and year (Figure 9) it is visible that the decrease in density of hunted rabbits is common in all five regions. In Algarve there was a period of increase between 2002/03 and 2007/08. The LTV region suffered the most severe decline. This region has the highest density of hunted rabbits the majority of the time but decreased to a point where, in the last three years of data, all regions have a similar density.

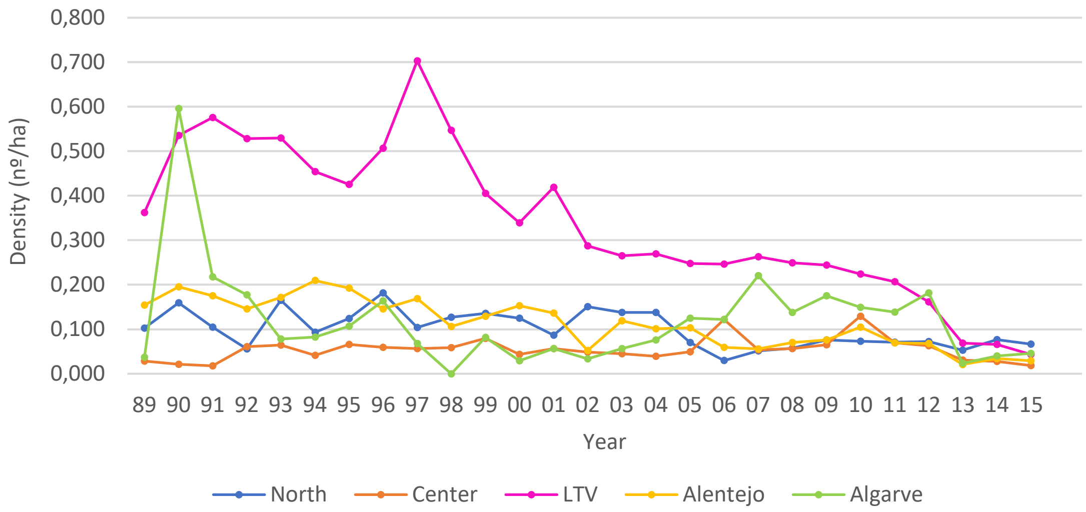


Figure 9 - Mean density of harvested rabbits per hunting season in each region*. 95% Confidence intervals are available in annex V*

Unusually high values of rabbit hunting bags were found in the dataset. Some of the HZs with these unusual high values were investigated, showing that at given years there is an exponential growth of culled rabbits, followed by a drastic drop the in the next hunting season (Figure 10).

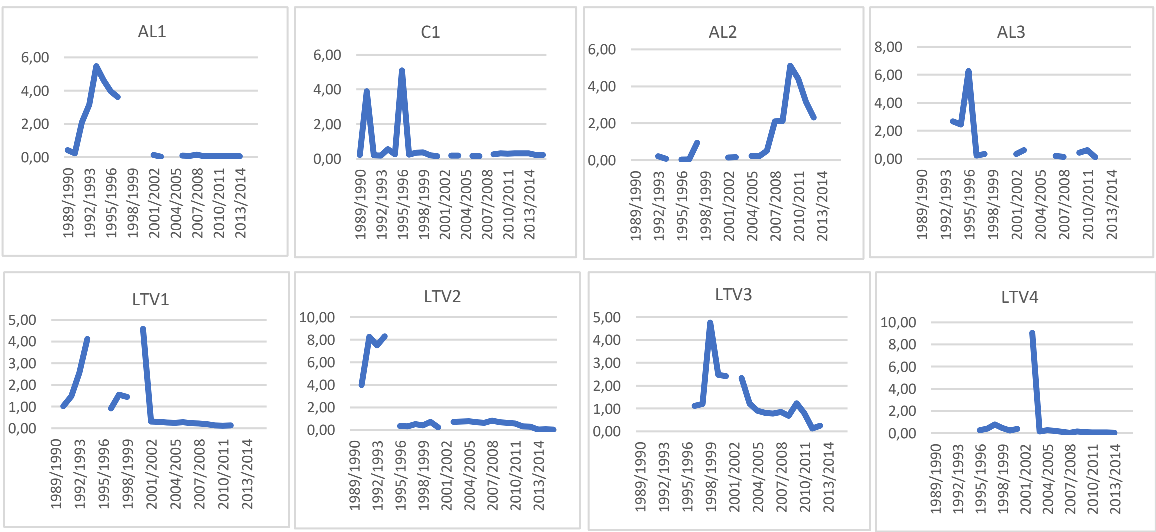


Figure 10 – Unusual high values of rabbit density. *Rabbit harvest density (nº hunted rabbits per ha, y-axis) at each hunting season (x-axis) in eight HZs, as example. Graphic titles state HZ code per region: AL – Alentejo; C – Centre; LTV – Lisbon and Tagus Valley. Scales are not standardized.*

3.2.2 Hare

The effects region, type and year on density of harvested hares were statistically significant at the .05 level [region: $F_{(4, 14272)} = 148.063$, $p < 0.001$; type: $F_{(1, 14272)} = 4.694$, $p = 0.030$; year: $F_{(26, 14272)} = 5.096$, $p < 0.001$], as well as the interaction between region and type [region*type: $F_{(4, 14272)} = 15.218$, $p < 0.001$] and between region and year [region*year: $F_{(98, 14272)} = 2.038$, $p < 0.001$].

The Alentejo region has the highest density of all regions [M = 0.030, CI = 0.029, 0.031], followed up by Algarve [M = 0.021, CI = 0.018, 0.023]. The density registered in the centre region is not statistically different from LTV [centre: M = 0.012, CI = 0.011, 0.013; LTV: M = 0.014, CI = 0.013, 0.016; p = 0.951] and is similar to the density registered in the north region [north: M = 0.011, CI = 0.009, 0.014] (Figure 11). There is a statistically difference in density of harvested hares between HZs administrative types, AHZs have records of a slighter higher density than THZs [associative: M = 0.018, CI = 0.017, 0.018; touristic: M = 0.016, CI = 0.014, 0.017; p = 0.030] (Figure 11).

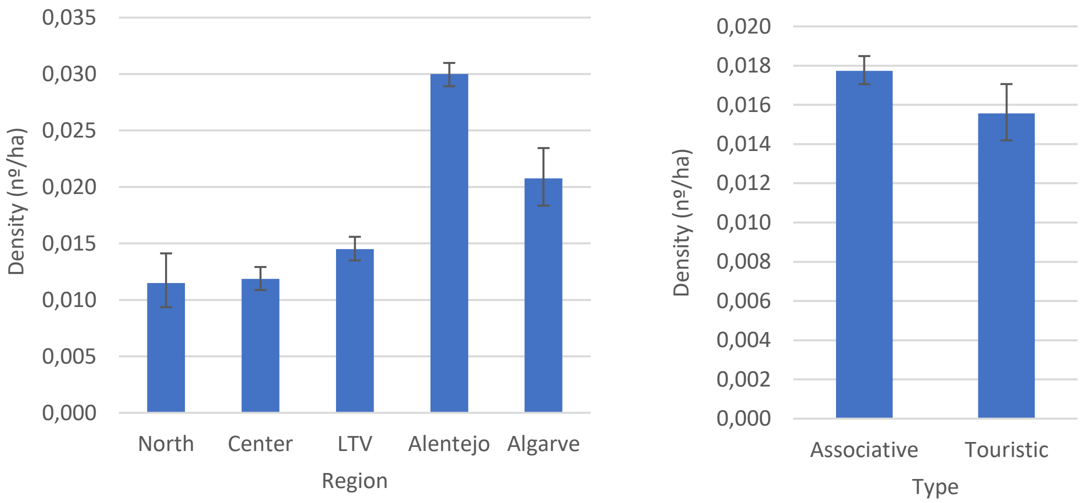


Figure 11 - Mean harvest hares per hectare (density) on each hunting region and administrative type*. Error bars display 95% CI*

The interaction between the effects of region and administrative type occurs in the north region and Algarve, were THZs have a slightly higher density, contrary to what happens in all other regions (Figure 12).

Non-parametric test Kruskal-Wallis performed on untransformed data corroborates major effects of hunting regions [$H_{(4)} = 2214.358$, $p < 0.001$] on density of hunted hares. Furthermore, Dunn's pairwise tests also indicate that density of hunted hares in LTV does not differ from centre region (for detailed information, see Annex III).

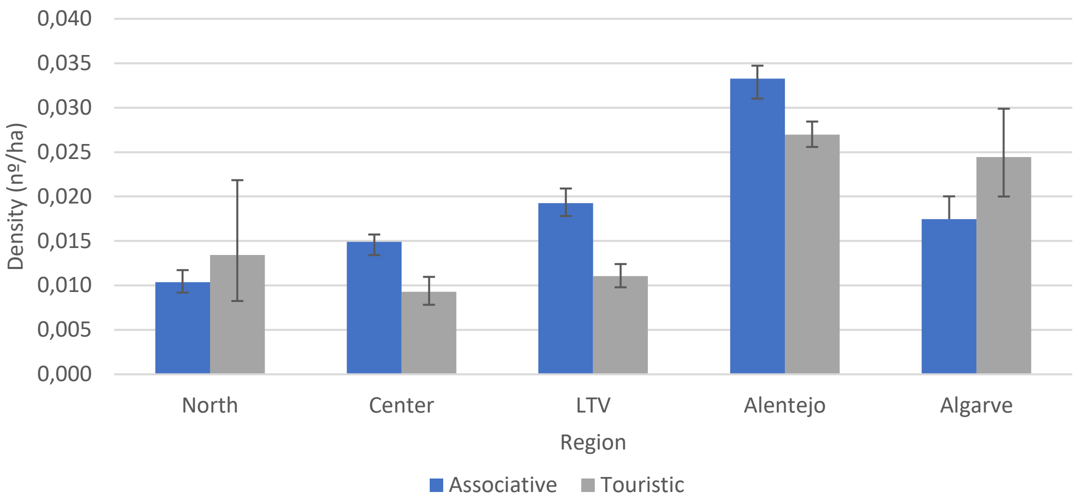


Figure 12 – Mean density of harvested hares in each administrative type across the five hunting regions. *Error bars display 95% CI*

Density of harvested hares in Portugal declined during the study period at a rate of -0.2% per year. The highest density occurs in the year 1995/96 [M = 0.027, CI = 0.020, 0.038] and the lowest happens to be the most recent, in 2015/16 [M = 0.008, CI = 0.007, 0.011]. In the first years there was some growth, followed by a drop in 1995, and then a recuperation until around 2004. Then the population seems to stabilize for about four years, before a steady decline since 2008 to the most recent records. In general, data depicted a reduction of ca. 50% in hare bagged density along the last 27 years (Figure 13).

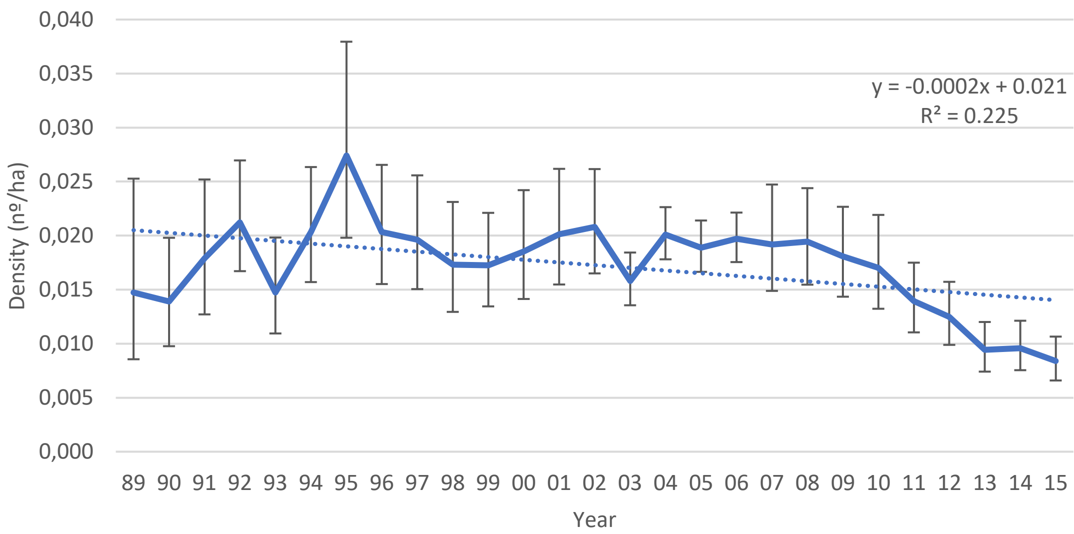


Figure 13 – Mean density of hunted hares in Portugal in each hunting season since 1989/90 (89) until 2015/16 (15). *Error bars display 95% CI. Trendline is displayed, as well as the equation and R-squared value.*

In Alentejo and Algarve the density of hunted hares only started to drop considerably after 2008/09, until then there was an unstable increase, with a minor drop in the period 2001/02 – 2003/04. North, LTV and centre register an increase until 95, 96 and 97, respectively, from which point the densities started to decrease until nowadays, with records of very similar densities since 1999/00. For the last three years of data, all five regions have proximate densities (Figure 14).

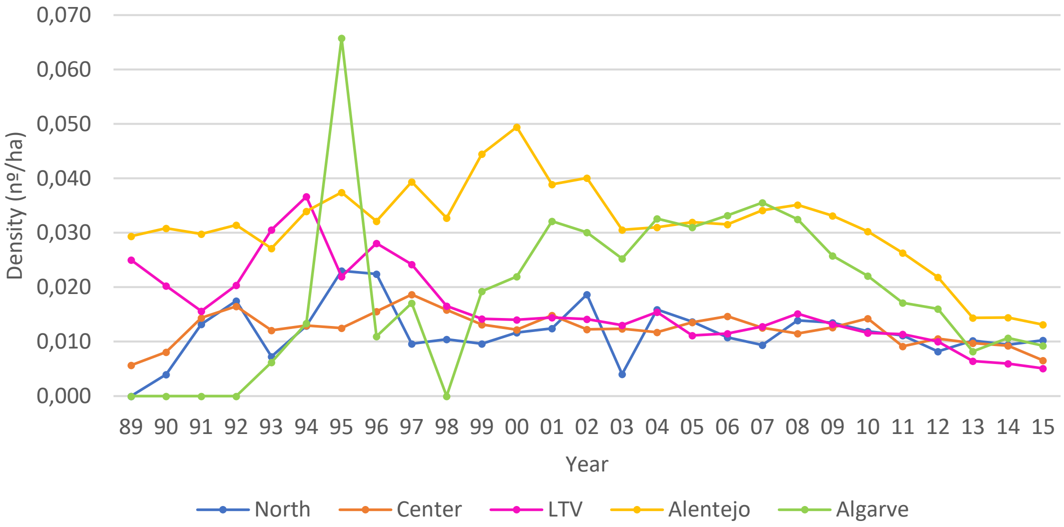


***Figure 14 - Mean density of harvested hares per hunting season in each region**. 95% Confidence intervals are available in annex V*

3.2.3 Red deer

The difference between regions was detected with Kruskal-Wallis performed with untransformed data [H(1) = 4.921, p = 0.027]. However, only the statistically significance of the effects "type" and "year" on density of harvested deer was detected by the parametric approach at the .05 level [type: $F_{(1, 756)} = 11.220$, $p < 0.001$; year: $F_{(28, 756)} = 1.543$, $p = 0.037$]. According to the ANOVA outputs, in the centre region there is a non-significant higher density of hunted deer per hectare than in Alentejo [centre: M = 0.010, CI = 0.008, 0.012; Alentejo: M = 0.008, CI = 0.007, 0.010; p = 0.097). Harvested deer per hectare in THZs is higher than in AHZs [touristic: M = 0.011, CI = 0.010, 0.013; associative: M = 0.007, CI = 0.006, 0.009; p = 0.001] (Figure 15).

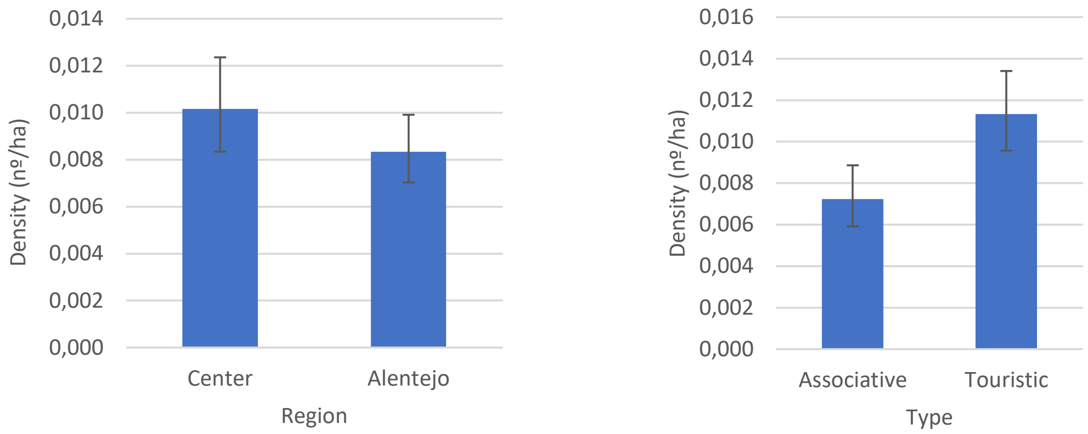


Figure 15 - Mean density of harvested deer in the period 1989-2017 in each hunting region and administrative type. *Error bars display 95% CI*

During the study period, between 1989/90 and 2017/18, there was a slight increase in the density of harvested deer in Portugal (0.3% per year). The first years of data have a wide 95% CI since the density values reported by the HZs for those years are very disperse. The first four years of data show a decrease in density of hunted deer [1998/97: M = 0.013, CI = 0.002, 0.077; 1992/93: M = 0.002, CI = 0.001, 0.033] and the following years register an unstable increase, with the highest density value occurring in 2011/12 (M = 0.017, CI = 0.012, 0.024) (Figure 16).

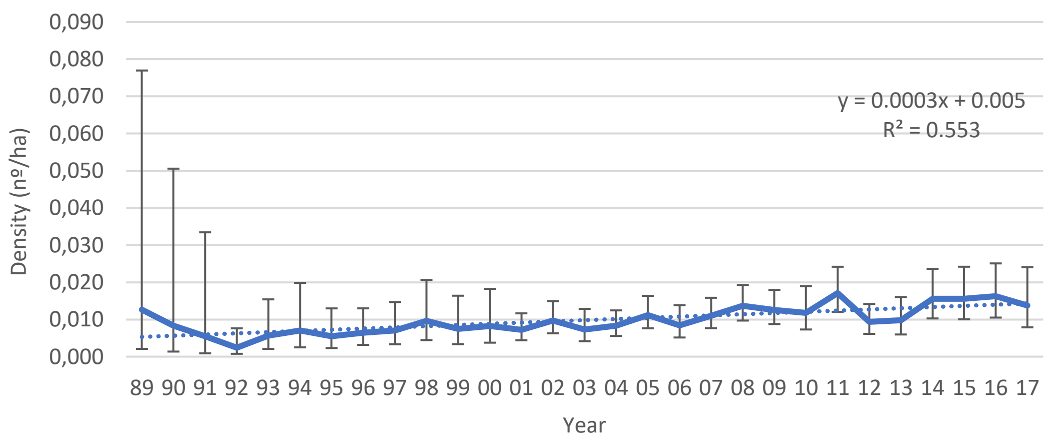


Figure 16 - Mean density of harvested deer in Portugal in each hunting season since 1989/90 (89) until 2017/18 (17). *Error bars display 95% CI. Trendline is displayed, as well as the equation and R-squared value.*

3.3 Hunting bag trends

3.3.1 Wild rabbit

The Pearson chi-square test showed that there is a significant association between hunting region and rabbit population tendency, X^2 (8, N = 1227) = 99.281, p < 0.001. Figure 17 shows that rabbit populations are either unstable or declining. LTV region has the highest proportion (65.9%) of declining populations and the lowest proportion of growth (1.7%). The region with less HZs reporting declining populations is Algarve (18.0%) but there is a very high proportion of unstableness (77.0%), so an accurate conclusion on this premise cannot be made.

There is also a significant association between administrative type and population tendency, X^2 (4, N = 1227) = 44.227, p < 0.001 (Figure 17). The proportion of unstableness is similar between the three administrative types (Associative - 52.1%; Municipal - 57.1%; Touristic - 46.3%). In MHZs there are more populations with a growth tendency than decline, contrary to what happens on the other two types. AHZs have the lowest proportion of growth (4.2%) and an equal proportion of decline populations as touristic ones (43.7%).

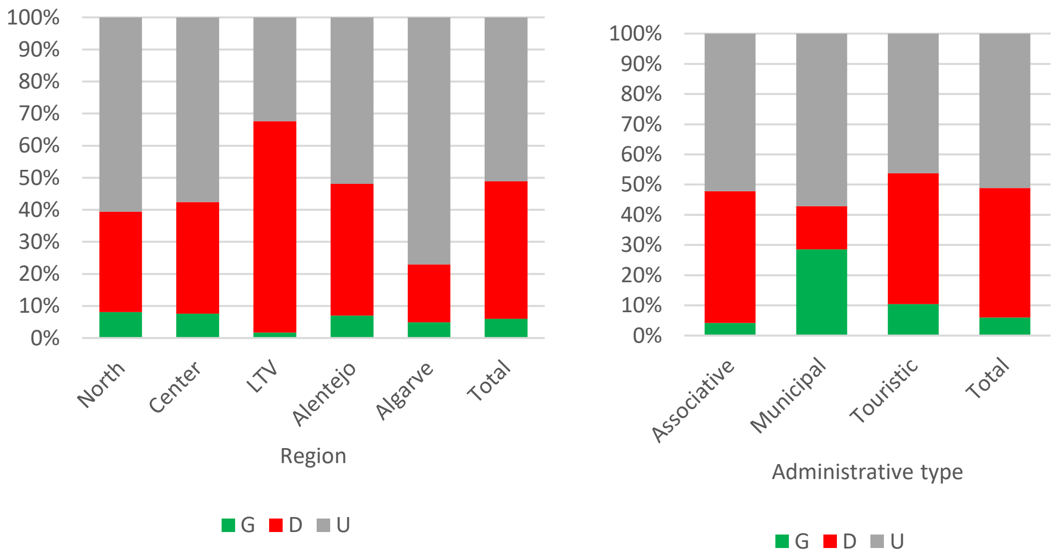


Figure 17 - Proportion (%) of rabbit population tendency category across hunting regions and administrative types. *G – growth; D – decline; U – unstable.*

A visual representation of this information shows two main zones of rabbit population growth, one in northwest (Figure 18A, circle NW) where most MHZs are located (Figure 17B, circle NW), and another in southeast (Figure 18A, circle GV) (*Guadiana Valley Natural Park),* consisting of mainly THZs (Figure 18B, circle GV).

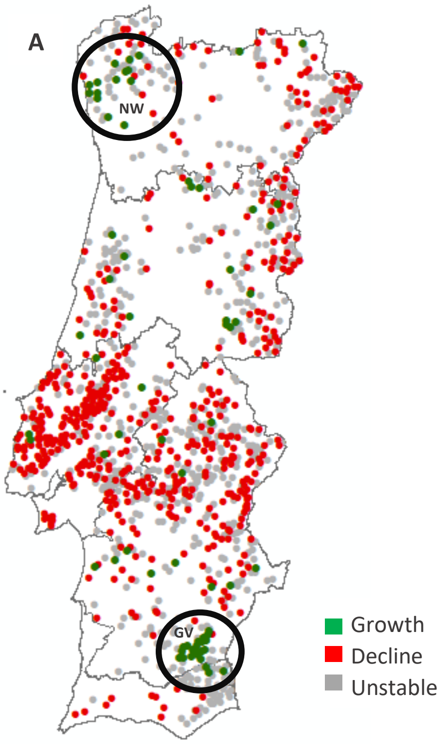


Figure 18 - HZs with rabbit hunts across Portugal*. A: HZ tendency category; B: HZ administrative type. NW – area of rabbit population growth in the northwest of Portugal; GV – area of rabbit population growth in the Guadiana Valley.*

3.3.2 Hare

The relation between hare populations tendency and hunting regions is significant, X^2 (8, N = 871) = 18.401, p = 0.018. The tendency category in higher proportion is unstable (57.2%) followed up by decline (35.9%) (Figure 19). The centre region has the highest proportion of growing populations (9.4%) while Algarve has the lowest (2.4%) (Figure19). The Pearson chi-square test showed that there is no relationship between tendency categories and administrative types for hare populations, X^2 (2, N = 871) = 3.398, p = 0.183. Looking at Figure 19, it is noticeable that the proportion of tendency categories is indeed very similar between associative and touristic HZs with no significant differences.

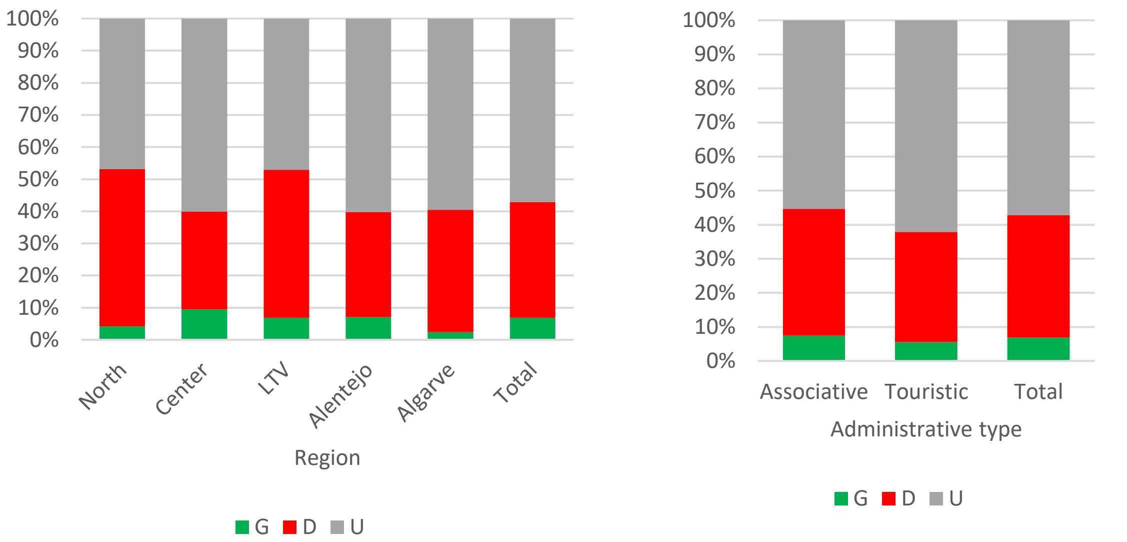


Figure 19 - Proportion (%) of hare population tendency category across hunting regions and administrative types. *G – growth; D – decline; U – unstable.*

There are no areas in continental Portugal with a visible population tendency, contrary to the results found for the rabbit. Growing, declining and unstable populations appear to be dispersed throughout the territory (Figure 20).

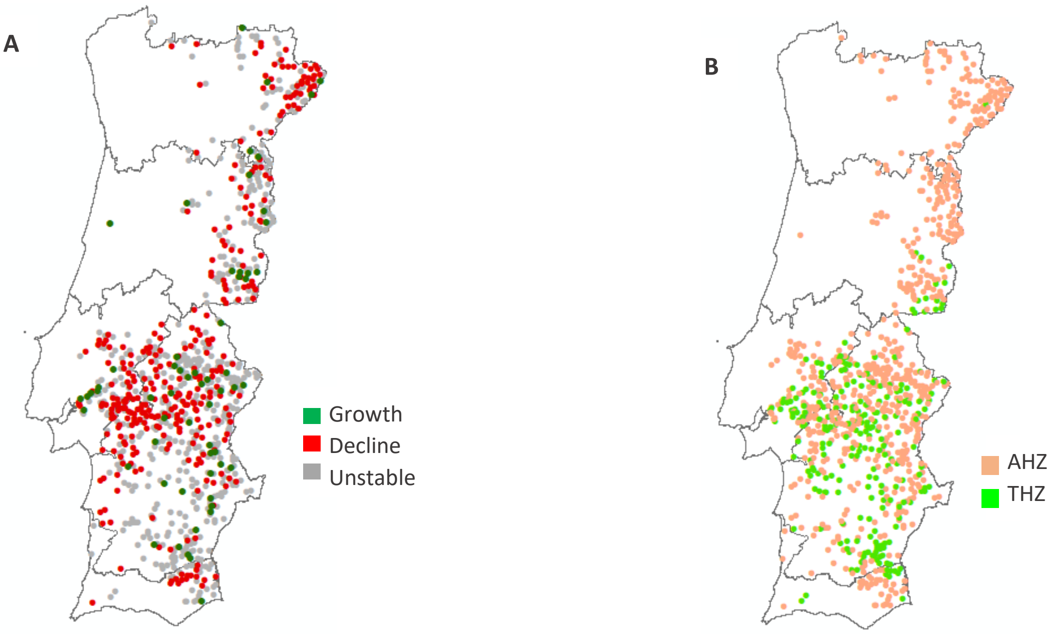


Figure 20 - HZs with hare hunts across Portugal*. A: HZ tendency category; B: HZ administrative type.*

3.3.3 Red deer

The tendency categories of deer populations do not have a significant relationship with hunting regions, X^2 (2, N = 70) = 1.030, p = 0.597, nor with administrative types, X^2 (2, N = 70) = 0.355, p = 0.837. Most deer populations in HZs are either growing (44.3%) or unstable (51.4%) and a very low proportion has a tendency of decline (4.3%) (Figure 21). Despite not being significant, there is a slightly higher proportion of growing tendency in Alentejo (48.8%) comparing with the centre region (37.9%) and also in associative (48.3%) HZs comparing with touristic (41.5%) (Figure 21).

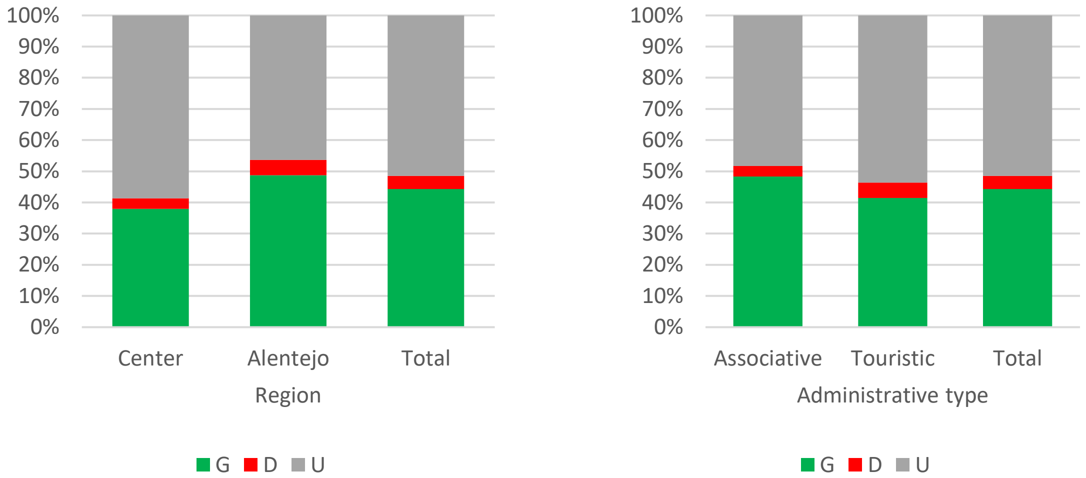


Figure 21 - Proportion (%) of deer population tendency category across hunting regions and administrative types. G – growth; D – decline; U – unstable.

HZs with deer hunts are concentrated mainly in a centre-east area of Portugal, the International Tagus Natural Park (Figure 22A and B, circle IT), thus this is where most growing populations of deer are located.

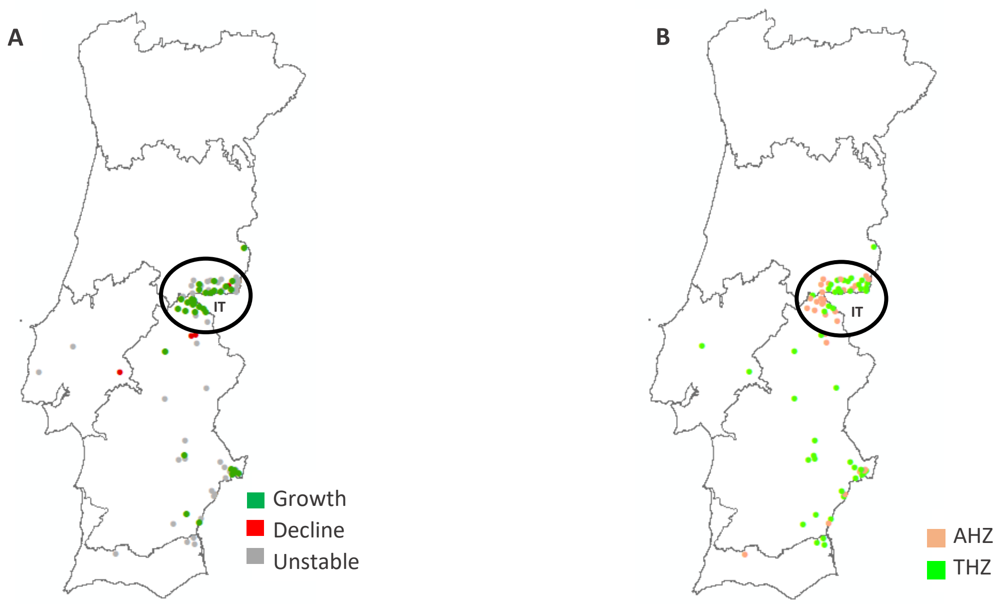


Figure 22 - HZs with deer hunts across Portugal. A: deer population tendency category; B: HZ administrative type. IT – area where most HZs with deer hunts are located.

3.4 Correlations between species hunting bags

From the HZs in study, only thirty-one have records of both deer and rabbit hunts. From these, only nine depicted a significant correlation between the two species densities, of which seven were negative and two were positive (Table 9). There are also four HZs that reported a negative correlation close to significant, thus worth of careful investigation.

Table 9 - HZs where both rabbits and deer were hunted between 1989-2015 for N hunting seasons. *Significant (Sig.) correlation was admitted * at p<0.05 and ** at p<0.01. Positive correlations were admitted at Pearson's r > 0 and negative at Pearson's r < 0. Strongly negative - ↓ ; Negative - ↘ ; Strongly positive - ↑ ; Positive - ↗ ; Neutral — . HZ are coded per region: AL – Alentejo, C – Centre, LTV – Lisbon and Tagus Valey, Alg - Algarve*

HZ	Pearson's r	Sig.	N	Relationship	Region	Type
Al1	-0.529	0.071	9	—	Alentejo	Associative
C1	0.356	0.128	12	—	Center	Touristic
Al2	-0.105	0.350	16	—	Alentejo	Touristic
Al3	0.071	0.413	12	—	Alentejo	Touristic
AL4	-0.575	0.068	8	—	Alentejo	Touristic
Al5	-0.442	0.228	5	—	Alentejo	Associative
C3	-0.175	0.293	12	—	Center	Associative
C4	-0.445	0.085	11	—	Center	Associative
Al6	0.119	0.331	16	—	Alentejo	Touristic
Al7	-0.018	0.482	9	—	Alentejo	Associative
C5	-.700*	0.018	9	↘	Center	Touristic
Al8	0.168	0.301	12	—	Alentejo	Associative
C6	-.731*	0.013	9	↘	Center	Associative
C7	-.487*	0.039	14	↘	Center	Touristic
LVT1	0.004	0.495	12	—	LTV	Touristic
C8	-0.002	0.498	8	—	Center	Touristic
Al9	0.062	0.432	10	—	Alentejo	Touristic
C9	.927**	0.000	13	↑	Center	Touristic
C10	-0.337	0.110	15	—	Center	Associative
Al10	-.736**	0.003	12	↓	Alentejo	Associative
Al11	0.043	0.463	7	—	Alentejo	Touristic
Al12	0.083	0.376	17	—	Alentejo	Touristic

C11	-.858**	0.003	8	↓	Center	Touristic
C12	-.662*	0.018	10	↘	Center	Associative
Al13	-0.282	0.215	10	—	Alentejo	Associative
C11	-0.402	0.077	14	—	Center	Associative
C12	.599*	0.020	12	↗	Center	Touristic
C13	0.339	0.129	13	—	Center	Touristic
Alg 1	-.796*	0.029	6	↘	Algarve	Touristic
C14	0.368	0.185	8	—	Center	Associative
Alg2	-0.043	0.459	8	—	Algarve	Touristic

Most negative correlations happen in the center region, as well as the positive correlations. As for administrative type, positive correlations happen in THZs and negative correlations appear to be equally distributed as three of them occur in associative type and four in touristic. Negative correlations close to significant occur mostly in center region and in AHZs.

Regarding the analysis on hare-deer relationship, there are thirty-three HZs with records of both deer and hare hunts, of which ten show a significant correlation. From these, eight were a negative correlation and two were positive (Table 10). There are also five HZs that reported a correlation close to significant, thus worth of careful investigation.

***Table 10 - HZs where both hares and deer were hunted between 1989-2015 for N hunting seasons**. Significant (Sig.) correlation was admitted * at p<0.05 and ** at p<0.01. Positive correlations were admitted at Pearson's r > 0 and negative at Pearson's r < 0. . Strongly negative - ↓ ; Negative - ↘ ; Strongly positive - ↑ ; Positive - ↗ ; Neutral - —. HZ are coded per region: AL – Alentejo, C – Centre, LTV – Lisbon and Tagus Valey, Alg - Algarve*

ZRCE	Pearson's r	Sig.	N	Relationship	Region	Type
Al1	-.657*	0.019	10	↘	Alentejo	Associative
C1	-0.001	0.499	14	—	Center	Touristic
Al2	0.407	0.059	16	—	Alentejo	Touristic
Al3	-0.095	0.404	9	—	Alentejo	Touristic
Al3	-0.470	0.062	12	—	Alentejo	Touristic
Al4	-0.020	0.479	9	—	Alentejo	Touristic
Al5	-0.518	0.094	8	—	Alentejo	Associative
Al6	-.823**	0.002	10	↓	Alentejo	Touristic

C2	0.282	0.187	12	—	Center	Associative
C3	0.067	0.422	11	—	Center	Associative
Al7	-0.067	0.403	16	—	Alentejo	Touristic
Al8	0.090	0.402	10	—	Alentejo	Associative
C4	-.564*	0.045	10	↘	Center	Touristic
Al9	0.019	0.477	12	—	Alentejo	Associative
C5	.486*	0.033	15	↗	Center	Associative
C6	-.575*	0.025	12	↘	Center	Touristic
C7	-.506*	0.032	14	↘	Center	Touristic
LVT1	-0.388	0.106	12	—	LTV	Touristic
C8	-0.466	0.122	8	—	Center	Touristic
C9	-0.408	0.066	15	—	Center	Touristic
Al10	0.483	0.079	10	—	Alentejo	Touristic
C11	0.063	0.412	15	—	Center	Associative
Al12	-.793**	0.001	12	↓	Alentejo	Associative
Al13	-.809*	0.014	7	↘	Alentejo	Touristic
Al14	.705**	0.001	17	↑	Alentejo	Touristic
C12	-0.307	0.230	8	—	Center	Touristic
C13	-0.186	0.316	9	—	Center	Associative
Al15	-0.273	0.223	10	—	Alentejo	Associative
C14	-.545*	0.022	14	↘	Center	Associative
C15	-0.086	0.390	13	—	Center	Touristic
C16	0.014	0.483	13	—	Center	Touristic
Alg1	0.557	0.165	5	—	Algarve	Touristic
Alg2	-0.390	0.170	8	—	Algarve	Touristic

Half the negative correlations occur in the center region while the other half occurs in Alentejo and the same happens for the positive correlations. As for administrative types, most negative correlations occur in THZs (five against three in associative) and positive correlations occur equally in both types.

There are no noticeable patterns of positive, negative or neutral correlation between lagomorphs and deer across the national territory (Figure 23A and B).

***Figure 23 – Correlation between lagomorphs and deer found in HZs across Portugal**. A: HZs with both rabbit and deer hunts; B: HZs with both hare and deer hunts.*

The overall transition matrix (from 1995 to 2018) of main land-use classes, done with data from 36 HZs shared by red deer and wild rabbits and/or hares, depicted a variety of situations (Table 19, Annex VI). The most stable land-uses are forested habitats, preserving over 90% of the area during decades. On the contrary, agricultural habitats and shrublands experienced relevant changes in the area initially occupied (1995). A general pattern towards the increase of more closed forested habitats (mainly with broadleaved, conifers and scrublands) can be recognised in some HZs. This change was mainly due to a reduction of agroforestry systems (mainly cork and holm oak "montado") and herbaceous habitats (e.g., annual crops and pastures). Another identifiable pattern is the transition between pastures and other agricultural areas, often associated with an increase in area occupied by agroforestry systems. Between 1995 and 2018 no relevant changes (>5%) were detected in habitats with lower representation in the study area (e.g., complex patches, urban, aquatic, rocky or open habitats). Further detailed information is available in Annex VI.

The resulted variables regarding major landuse changes did not show any evident effect on the relationship trend (Pearson correlation categories) between red deer and the two lagomorphs species (Figure 24).

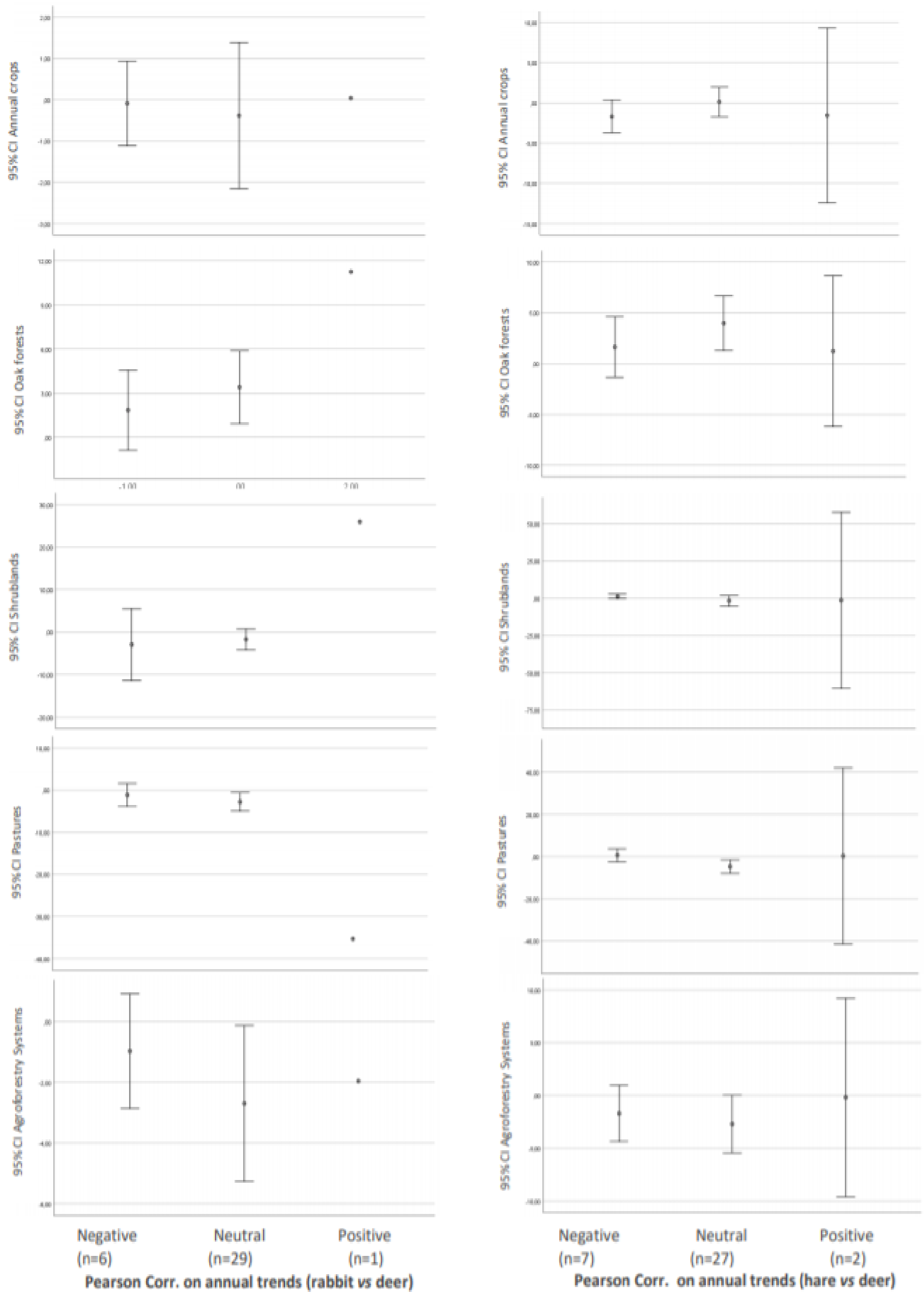


Figure 24 - Proportion change (mean and 95%CI) of major land-use classes between 1995 and 2018 for the three Pearson correlation categories (negative, neutral and positive) for reed deer and rabbit (left side graphs) and red deer and hare (right side graphs)

4. Discussion

4.1 Hunting bag data and Atlas of mammal species distribution

Although apparently there is only a difference of 2 grid squares between the maps in the Atlas (total of 1007) and the ones constructed in this dissertation (total of 1009), there are actually fewer grid squares overlapping (994). This is due to the different software used for map projecting between the Atlas of Mammals of Portugal and this dissertation. However, the grid squares that fall out of the overlap occur in the borders on national territory, mainly the east border, thus covering mostly Spain territory and not Portugal's. A limitation in the maps constructed from hunting bags is the amount areas with unavailable data, which is considerably higher than in the Atlas. Although most fall in areas of absence, in some cases leaves out relevant animal occurrences (Table 6, 7 and 8).

Hunting bags show a much wider geographic distribution of the wild rabbit, as compared with data from the Atlas of Mammals of Portugal. In fact, it shows that the wild rabbit is hunted, and therefore occurs, in almost every part of continental Portugal, 89.6% of the territory and not just 23.0%, as the Atlas states (Figure 3A/B)

Similarly, the map obtained for hare hunting bags shows a more extensive distribution of this species than the Atlas, confirming that the center-north west region of Portugal is an area where hares may not be found, since most data is considered "old" (Figure 4A/B).

Even though Atlas data collection was based on an exhaustive bibliographic research, hunters end up covering a wider area through their ongoing leisure activity than scientific researcher teams, who tend to collect data in limited areas, thus creating a geographically dispersed distribution.

Deer hunting bags, however, show a different pattern from that of the wild rabbit and hare. Indeed, only 17.7% of national territory is occupied, as compared to the 34.4% stated by the Atlas (Figure 5A/B). This might be due to the fact that red deer also occurs in non-hunting areas, which would not be accountable in a study based on hunting statistics. However, it is possible to identify the main deer population nuclei at the Peneda-Gerês National Park, Montesinho Natural Park, *Serra da Lousã*, International Tagus, Lisbon district, east Alentejo, Évora and Silves.

Thesis results suggest that the hunting bags can be a good indicator of species occurrence and this data would complement a source of information such as the Atlas of Mammals. Indeed, an animal kill is a confirmed and absolute occurrence, unlike some of the indirect methods used in the Atlas of Mammals of Portugal. Additionally, because hunting bags are provided by hunters, this is a relatively effortless gathering of data, requiring no additional field work such as transect-based counts, performed either by direct observation or from indirect presence indicators (e.g. footprints, burrows or faecal counts). The potential for the study of species abundance is, however, very limited. Although there is information on the density of animals harvested per hectare, there is no data on hunting efforts and therefore care is needed when considering this data. Nevertheless, efforts should be done in order to relate information from hunting bags with information on species distribution from Atlas of Mammals of Portugal.

4.2 Differences in density of hunted animals between hunting regions, administrative types and across hunting seasons

The results in this study show that the density of hunted animals differ according to the hunting region and administrative type of the HZ, as well as between hunting seasons, for the period considered in this study.

Wild rabbits are hunted in higher density in the LTV region and in AHZs (Figure 6). Higher densities in this administrative type were expected, as rabbit is one of the most popular game species in Portugal and has a significant history in hunting tradition (Virgós *et al.*, 2007). Additionally, AHZs are managed by associations of hunters where tradition is very well rooted, since most hunters are of old age Lima-Santos *et al.*, 2015). Hunters prefer AHZs for the opportunity to take part in the HZ management and for social bonding. A survey conducted in 2001 stated that approximately 90% of the Portuguese hunters prefer to hunt small game, being the wild rabbit the most hunted species in AHZ (65%) (Bugalho & Carvalho, 2001; Virgós *et al.*, 2007).

A higher density of hunted rabbits in the LTV region might be due to favourable habitats and productive systems for rabbits in this area. Indeed, according to Lima-Santos *et al.* (2015), there is a considerable area of high game productivity in this region.

Interestingly, in Alentejo and Algarve, THZs appear to have more rabbits hunted per hectare than MHZs, contrary to what happens in the rest of the country (Figure 7). MHZs have a high popularity of rabbit hunting since most hunters who attend them do so for the economical accessibility, and thus they probably do not have enough economic resources to access game species other than rabbit (Virgós *et al.*, 2007). However, the south of Portugal is the most proactive region in hunting tourism. The only touristic entity that promotes hunting as an activity in Portugal is *Turismo do Alentejo e Ribatejo* (Tourism of Alentejo and Ribatejo), which developed a strategic plan for the touristic operation of game hunting, the PETCAR (Gamito, 2018; Pereira *et al.* 2015). Since the rabbit is one of the most appreciated small game in the south of Portugal, high densities of this species is a common goal of THZs in these regions (Serronha, 2014). Therefore, more financial resources and target management are applied in these regions, with the goal of improving the wild rabbit living conditions, which result in an increase of its abundance in these THZs, higher than in other regions where the investment in management and game productivity is considerably lower.

The prioritization for tourism in these regions can also explain the higher densities registered for hare in THZs of Algarve, contrary to what happens in the other regions of Portugal, where AHZs register higher hare densities (Figure 11). The Alentejo region is where the highest mean density of hunted hares can be found, followed by Algarve (Figure 10). Studies on hare distribution and abundance (Acevedo *et al.* 2012; Almeida *et al.* 2004) showed that the south of Portugal, and particularly the Alentejo region, is indeed where this species is most found, according to its habitat preferences, so the higher density of hunted hares in these regions is as expected. The analysis on the administrative type shows that there is a significative difference between them, being the associative type the one with higher density of harvested hares, although this difference is not as evidential (Figure 11) as what was recorded for the wild rabbit and for the deer (Figure 6 and 15, respectively). The hare is not as popular nor as traditional as the wild rabbit and other small game species, such as the red-legged-partridge (*Alectoris rufa*) (Bugalho & Carvalho, 2001) so it is probably not specifically pursued by hunters and is instead hunted as an extra if it comes by during a hunt. If that is the case, there should not be a big difference between an associative or tourist HZ and the slightly lower density in THZ may be explained by the fact that tourist hunters are more commonly in search for big game.

Mean densities of hunted deer do not differ significantly between the Alentejo and center region. The p-value, thought, is close to significance (0.097), so a tendency for higher deer densities in the center region can be speculated. The density values of hunted deer are very low in the whole country and the available data is scarce, so significant differences are difficult to find and may become significant with more data and larger sample sizes. The wild boar (*Sus scrofa*) is more common and possibly more popular as a game species than red deer (Pereira *et al.* 2015). Also, prices for hunting red deer, either by “montaria” or, mainly, for trophy, can be more expensive than rabbits or hares (Paiva *et al.*, 2017). Deer trophy hunting is particularly expensive, with prices as high as 3000 Euros per trophy. As expected, the results show a significant higher density of deer in THZs than in AHZs, as THZs can be managed for trophy hunting (Figure 15).

In general, density of hunted lagomorphs decreased along the study period while the density of hunted deer increased (Figure 8, 13 and 16), which is coincident with results from other studies (Santilli & Galardi, 2006; Delibes-Mateos *et al.*, 2009). Across the years of the study period there are fluctuations in density of harvested animals in all three species, both positive and negative, and at some points quite considerable. Also, it is noticeable that confidence intervals are relatively wide, which means there is a substantial discrepancy between the lowest and highest density reported of the same species on the given hunting season. Annual density means might be marked substantially by particular events, such as the health status or reproductive success of a species in a hunting season, and even in a specific HZ (Ferreira *et al.*, 2010; Lima-Santos *et al.*, 2015). Rabbit and hare populations have been victims of severe burst of diseases, like the myxomatosis and the rabbit haemorrhagic disease (RHD). The myxomatosis virus was introduced intentionally in France in the decade of 1950 and entered in the Iberian Peninsula in 1954. It rapidly spread, killing up to 90% of the European rabbit populations (San Miguel, 2014). Myxomatosis also affects the hare, in 2018 the first outbreak of myxomatosis in hares was recorded in Spain (García-Bocanegra *et al.,* 2019) and there is also an indirect impact since the drastic reduction of rabbit populations directed hunting pressure to other game species (Ferreira, 2003). The rabbit haemorrhagic disease appeared in Europe a few decades later, in the late 1988, with an initial impact of up to 75% of rabbits perished in the Iberian Peninsula (San Miguel, 2014). There is also the equivalent disease in hares, the European brown hare syndrome (EBHS), first reported in the Iberian Peninsula in 1995. Despite being very similar, these two diseases are restricted to their natural hosts, or so was thought until 2014 when evidence of RHD was found in hares (Lopes *et al.*, 2014). Myxomatosis and RHD incidence in populations fluctuates, with higher mortality in the first outbreaks than in the subsequent years, where some resistance and recuperation occur, but with new strains appearing causing again more severe outbreaks (San Miguel, 2014). These fluctuations are probably influencing the density of hunted rabbits and hares, with hunting seasons scarcer in game than others where populations recovered (Ferreira *et al.*, 2010). For example, in 2012 a new variant of RHD occurred in Portugal (Abrantes *et al.*, 2013) and it is noticeable the effect it had on rabbit populations in the results shown in Figure 8, as there is a generalised drop in density of hunted rabbits in this hunting season. Monterroso *et al.* (2016) also found declining rates of rabbit populations highly coherent and coincident with the arrival of the new RHD strain in 2012. Likewise, Virgós *et al.* (2007) reports a good correlation between significant rabbit population declines and the appearance of RHD in multiple areas in Spain. Actions of restocking are responsible for considerable fluctuations in game populations' density as well, normally occurring when a population has reached a very low density or has extinguished (San Miguel, 2014; Monterroso *et al.*, 2016). Translocations or release of captive animals need to be accompanied by careful monitoring of habitat quality because if species requirements are not satisfied population re-stockings are ineffective. Frequently, re-stockings are not successful in the long term, but may lead to an occasional increase in hunting bags, since most times individuals are released just a few days prior to being hunted (Ferreira, 2003; Delibes-Mateos *et al.*, 2009; Ferreira *et al.,* 2010). There were some HZs, where unusual high numbers of hunted animals per hectare were reported followed by sharp decreases. Either diseases or factors related to re-stocking conducted without habitat management may contribute to explain these results, particularly for the wild rabbit (Figure 10).

Other explanation for the oscillations and wideness of confidence intervals, both in the lagomorphs and in deer, may be related to inaccurate reporting of hunting bags

(Ferreira *et al.*, 2010). Some HZs may even not fill annual bag reports for a specific hunting season, either to pay less taxes or simply by inconvenience. For example, it is also known that THZs report less hunts, since the payment is done per number of hunted animals, unlike AHZs where payment consists on annual quotas or MHZs where payment is done by day of hunting and is exempt of taxes (Paiva *et al.*, 2017).

The results also show that density of hunted rabbits and hares fluctuates, across the years, differently among hunting regions. Overall, the regions that had a higher density of hunted animals in the first hunting seasons is where a more notorious decrease of density was found, as by the most recent years all hunting regions display a similar value of hunted animals per hectare (Figure 9 and 14). Besides punctual occurrences of hunting bags increasing at given years, some hunting regions had periods of a more continuous growth, in particular, rabbit hunting bags in Algarve, from 2002 to 2007, and hare hunting bags in Alentejo, from 1993 to 2000, and in Algarve, from 1998 to 2007. This might be due to slight recuperation of populations after bursts of diseases, as said before, or special investment in populations recovery, either by habitat management measures or successful actions of re-stocking. Land-use modifications or even climate events might also explain these results, which could be material for future investigations.

4.3 Hunting bag trends

Approximately fifty percent of the populations of the three species in this study were found to have an unstable tendency, which means that it is unclear whether there was a growth or a decline over time. This high proportion of uncertainty might be because most HZs do not have a steady report of their hunting bags (discussed in chapter 4.2).

As expected, hunting bags of wild rabbit populations are mostly in decline, which may indicate that populations are also declining (Figure 17). Rabbit populations have dramatically declined over the past century in the Iberian Peninsula, as a consequence of different factors, mainly viral diseases. Other factors include habitat fragmentation, predation and hunting pressure (Ferreira, 2003; Delibes-Mateos *et al.*, 2009; Ferreira *et al.*, 2010; Gonçalves, 2015). In Portugal, a study conducted in 2002 estimated a 30% reduction of rabbit populations in the previous decade (Ferreira, 2003), and the species is now classified as Near Threatened (NT) in the Portuguese Red List of Vertebrates (Ferreira *et al.,* 2010).

In the LTV region it was found an interesting result. Although this region was the one with higher density of harvested rabbits, it was also the one with higher proportion of declining tendency and lower growth. The highest impacts of RHD have been frequently associated with higher population densities, probably because high densities favour the transmission of the virus (Delibes-Mateos *et al.*, 2009; San Miguel, 2014). If the LTV region has a higher rabbit population density, it makes sense that the impact of RHD was higher in this area, with a higher mortality of animals to the disease. Another explanation could be a greater (unfavourable) change in habitats of this particular region.

The municipal administrative type is the only one with a higher proportion of rabbit population growth than decline. However, when looking in detail at Figure 18, it is noticeable that it might be a misleading result. Most MHZs are concentrated in a small area in northwest Portugal (Figure 18B, circle NW). This area is also where a concentration of HZs (mostly municipal, but also associative) with growth of rabbit populations is found (Figure 18A, circle NW). MHZ located out of the delimited area do not have a growth tendency. Being so, it is likely that this rabbit population growth is related to that specific area and not necessarily to the municipal administrative type. A possible explanation can be personal interests of the hunting managers in this area, who invested particularly in rabbit populations. Because there are only 28 MHZs in analyses, compared to 959 AHZs, these MHZs with growth tendency had more weight in the results, thus creating a higher proportion of growth than decline. However, there is a possibility that MHZs have more efficient management measures for rabbit populations. A need for a deeper investigation on municipal hunting management is left, as there might be relevant differences in how management is performed compared to other administrative types. Likewise, as the observed growth tendency could be related to that particular region, it would also be worth investigating if the management policies applied in that region are responsible for the tendency for the increase in rabbit population.

There is one other area of rabbit population growth, in the southeast of Portugal, more precisely in the region of the Guadiana Valley (Figure 18A, circle GV). This region is known to have some of the highest densities of rabbit in Portugal. Indeed, in this region ZCTs are managing different populations of game species, and particularly the wild rabbit, which led to high population densities of the species. This is also the main reason explaining the re-introducing of the Iberian lynx in these areas, in agreement with game managers and the land-owners (Sarmento *et al.*, 2009; Serronha, 2014; Monterroso *et al.*, 2016). Sarmento *et al.* (2009) report the South Guadiana to be one of the regions that fosters a vital population of Iberian lynx. Since prey availability is essential for the survival and reproductive success of the Iberian lynx, a special care for the rabbit population in this area has been taken (LIFE10NAT/ES/570, 2011). From 2004 to 2010, the rabbit population in Guadiana Valley increased intensely, but in 2013 the new strain of RHD reduced drastically rabbit populations, which took a severe impact in lynx reproduction. Emergency management actions were carried out, namely rabbit restocking operations (Monterroso *et al.*, 2016).

Hare population tendency results were expected as well, as most hare populations fall in the category of decline (Figure 19). Although not as drastically as the wild rabbit, studies show that European hare populations have been declining since the 1960s, mainly due to loss of habitat, agricultural intensification, predators, excessive hunting and, with a minor role, diseases such as the EBHV and pseudotuberculosis (Paupério, 2003; Santilli & Galardi, 2006). The results show that the centre region has the highest proportion of hare population growth, although not distinguishable from other regions so this might be due to slightly successful re-stock actions or better habitat conditions in some HZs of this region. It was not found a significant difference in proportion of tendency categories between administrative types, which suggests that there are no relevant differences in management measures applied to this game species between AHZs or THZs.

The results on deer population tendency show that most populations have grown during the period analysed, independently of the hunting region or administrative type (Figure 21). This was expected, since there is evidence that deer populations have been increasing across the world, due to favourable habitat changes, lack of large predators, population reintroductions and natural dispersion (Bugalho *et al.*, 2006; Salazar, 2009; Burbaite & Csányi, 2010). Red deer populations recovered from near extinction in XIX century in Portugal to become abundant across their areas of distribution (Salazar, 2009; Carvalho, 2013). Also, deer hunting has been gaining popularity, not only because tourism hunting has been greatly promoted, but also because the scarcity of small game (namely the wild rabbit) has led hunters to dedicate more to big game (Delibes-Mateos *et al.*, 2009; Paiva *et al.,* 2017), which explains why the growth was observed in equal proportions between AHZs and THZs.

4.4 Correlations between species hunting bags

The results on the correlation between the lagomorphs and deer were not completely conclusive, mainly due to data scarcity. However, it was possible to find correlations in some of the HZs analysed, more negative than positive, but mostly non-significant.

There were no significant patterns to whether the correlations found are related to hunting region or administrative type. Although most correlations were non-significant, it was found a number of significant correlations and, within these, a higher number of negative rather than positive correlations between hunting bags of deer and lagomorphs. Testing these correlations is a first step to investigate potential competition among these groups of species. A more detailed analysis, in the future, on the characteristics (size, land-use changes, implemented management practices) of estates where significant relationships occurs may contribute to explain potential interactions among these species. There are various possibly relevant factors not taken in consideration by this approach, as the information provided by hunting bags is limited.

As mentioned above, the information on the number of animals harvested per hectare, without data on hunting effort, is not sufficient to calculate abundance of animals accurately. Some areas may report a lower number of harvested animals simply because less hunters went to that HZ in that hunting season, and vice-versa.

Looking at the evolution of density of harvested animals across the study period in each HZ where a correlation was found, it could be speculated that deer density generally increased along the time, while rabbit and hare density decreased (Figure 16, 8, 13, respectively), thus creating a negative correlation. It is left unknown if this happened due to the influence of a species on the other or simply because this is the general pattern found, as seen in the previous results of population trends (chapter 3.3 and 4.3). Positive relationships are more difficult to explain but they may correspond to areas of very good habitat and adequate management directed both for deer and the rabbit/hare, allowing positively related hunting bags of either species.

A more profound study on the possibility of competition between lagomorphs and deer is necessary, where a local approach is applied. Indeed, most studies suggest that small bodied herbivores may have competitive advantages over large bodied animals, mainly if they preferentially feed on herbaceous and grass vegetation ("grazers"). There are, however, studies in northern Europe, where winter is a nutritional stressed season and woody plants are the preferred food, that show potential feeding completion between hares and roe deer (e.g. Hulbert & Andersen, 2001; Carpio *et al.*, 2014). An investigation on the effects each species has on vegetation in the HZs where a negative correlation was found could be carried out in future studies. To address this subject, manipulative studies should be conducted, for example, using selective fenced plots where only rabbits could have access compared with plots where both red deer and wild rabbit could feed. Furthermore, a more detailed study on the species distribution within each HZ could also provide more relevant results, as at a smaller scale species might find refugee from one another.

4.5 Limitations of hunting bags data

Some considerations must be made due to the nature of the data set used, as there are probably significant sources of variation in the results due to inaccurate report of hunting bags from various reasons. Moreover, the dataset used compiles information on both currently active and inactive HZs. Some of the inactive HZs did not cease to exist but instead changed administrative type and/or owners, for example, the same area of land may have been a MHZ and later converted into associative. As a result, potential useful data on animal populations for that area of land may be lost in this process. If there are ten years of MHZ records plus ten years of AHZ records, these were not used in analyses since HZs with less than thirteen years of records, for rabbit or hare as example, were excluded. However, for that area of land, there was in fact twenty useful years of data, at least for hunting region and population tendency analyses. In addition, besides most of national territory being ordered as a HZ, there are still “non-managed game land”, where hunting occurs but under no management or supervision, and, hence, there are no available records of hunting. Being so, a considerable area of land is left unstudied concerning game population trends.

One other failure in this data set is the lack of information on hunting effort. Hunting effort is an essential measure to take in consideration when using hunting records as an index of abundance (Acevedo *et al.,* 2005), however, this information is not available and thus not taken in consideration for this study. The only information available is the number of hunters and emitted hunting licenses in Portugal per year since 1999, though that is not sufficiently relevant for the study as it does not reflect the number of rabbit, hare or deer hunters. In theory, the law requires the HZ’s managers to report the number of hunters and days of hunting in their annual report but the data available only has the number of animals hunted per year.

Virgós *et al.* (2007) assume that rabbit hunting method did not considerably change in Spain during their study period (1937-2002) and thus consider that the relationship between hunting bags and rabbit density did not differ between years. If it was assumed that the same occurred in Portugal, the results of this dissertation would gain substantial meaning. However, there is no tangible proof of this happening, neither for rabbit hunting, hare or deer. In fact, information available points in the direction that hunting effort towards small game has been decreasing as hunters are switching their preferences to big game. As Ferreira *et al.* (2010) concluded as well, hunting statistics are not yet sufficiently thorough to access game population trends in Portugal accurately, due to a lack of supervision and efficient survey methods of the records provided by hunters and HZ’s managers. With improvements on the quality of the information regarding hunting statistics, being gathered in a more systematic and rigorous format, the usefulness of these records would increase greatly.

4.6 Linking wildlife conservation and hunting

Hunters, researches and environmentalists are united by the shared goal of protecting and promoting wildlife fauna. The Wildlife Game Summit 2019 brought together these entities with a special focus on the need to break the distrust between environmental non-governmental organizations (NGOs) and hunting organizations, pointing that the increase in synergies between hunting and nature conservation is beneficial for both sectors and that who most benefits from it is wild fauna and biodiversity. As said before, game monitoring is crucial for the prosperity of these populations, and hunters could have a more active role on it by providing vital information.

Some projects are taking this initiative of synergy, such as the monitoring of woodcock in western Europe (Gonçalves *et al.*, 2019), the demographic study of wild boars in Portugal (Fonseca *et al.*, 2019), the ENMANO project (Guzmán *et al.*, 2019) and the website ENETWILD (Vicente, 2019). In general, it is unanimous that hunting statistics need to be standardise in a more rigorous and systematic report, thus increasing trustworthiness, easiness of application and comparability, not only within but also between countries and regions (Consortium *et al.,* 2018).

Suggestions include the development of digital tools for data collected by hunters, such as apps, websites, reporting via WhatsApp, so that hunters may have at their fingertips not only the opportunity of inputting information but also accessing it, thus making it easier and more rewarding to report hunting bags. Also, hunting bags are lacking vital information that could effortlessly be collected by hunters, such as the day of the hunting, localization, duration of the event, area covered, number of hunters participating, hunting method and, in addition to the number of animals hunted, the number of animals observed. With this data available the accuracy of studies on abundance, tendency and distribution of game populations through hunting bags would increase greatly, facilitating monitoring and management plans and decreasing significantly the need for additional effort on direct sampling, thus saving financial and team resources (Wildlife Game Summit 2019).

5. Final considerations

Wild herbivores are particularly relevant for the ecology of ecosystems, affecting the structure of flora, fauna and soil, with the ability to induce a cascade of events. They also play a significant role in human society at the socio-economic level, specially through the hunting sector. Hunting takes a significant part in management of animal populations and its habitats through various actions of game protection, promotion and culling, so an understanding on the impacts that hunting management has on these animals is fundamental. A successful management of wild herbivores populations is vital to achieve either economic or conservation goals and thus a knowledge of their distribution and abundance is needed.

Being so, population estimation based on hunting data emerges as a good complement, or eventual alternative, to direct population monitoring (higher human and financial resource demands) and has become a generalized practice in many countries and been used in several studies (Bosch *et al.*, 2012). Indeed, in Portugal, and other countries, hunting statistics may be an important source of data to assess temporal and spatial trends of game species. Moreover, such information is available from 1989, covering most of the country. It is crucial that efforts on rigorous collection of this information are done, namely by explaining to game managers and hunters the importance of reliable data on hunting bags for adequate game management. Further research on calibration of hunting bag information, with real data on game population densities, may increase the usefulness of hunting bags as population trend indicators. Also, managers and researchers must be careful when using hunting bag information and be aware of the limitation of this information.

This dissertation has contributed to relate the information on hunting bags with information on the geographical distribution of the wild rabbit, hare and red deer, as well as its populations tendencies on the past thirty years in continental Portugal, using hunting bags as an indicator of game species population trends. It also gives relevant information on how hunting management affects game populations, based on HZ's administrative type, thus suggesting that it is a factor worth of concern when developing monitoring and management plans. The present thesis also provides, albeit correlational, data on the potential relationship between deer and lagomorphs population trends. This is a first step to address eventual food competition between these groups of herbivores.

The associations found to hunting region, HZ's administrative type and hunting season are coherent with other sources and, in general, were as expected, thus validating this source of data. Being so, it can be concluded that hunting bags are worthy of exploration for the study of game populations' distribution, tendency and its constrictors. These results may prove useful for guiding management and monitoring plans of the wild rabbit, European hare and red deer and the approach used in this dissertation may be applicable to other game species and countries, providing there is enough hunting bags data across time and regions. This would allow to generate global game population density and distribution maps, as well as identify impacts of hunting management on populations trends, especially if efforts on standardising hunting reports are put into action.

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Annex I – Data distribution before and after logarithmic transformation

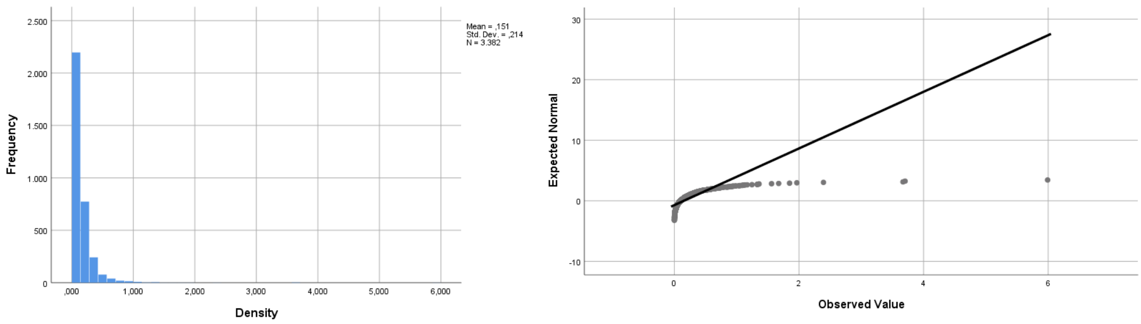


Figure 25 - Histogram and Normal Q-Q plot of rabbit density values in north region. *Serves as an example of the right-skewed distribution the density values of rabbit, hare and deer show for all regions and administrative types in study.*

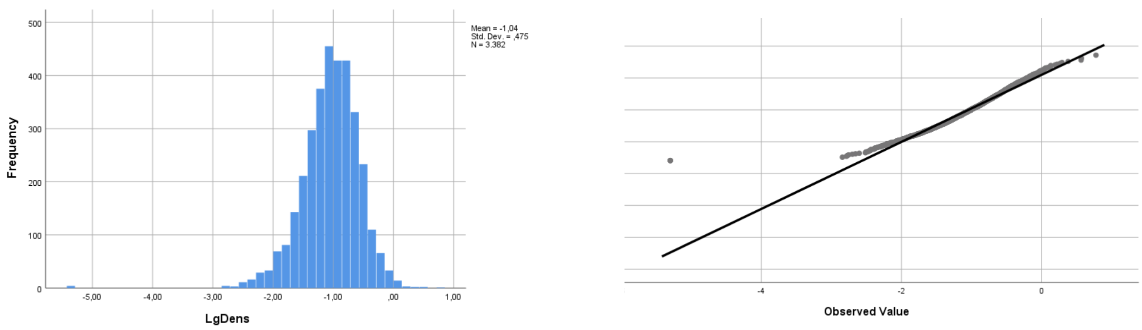


Figure 26 - Histogram and Normal Q-Q plot of rabbit logarithmic density values (Log_{10} (x)) in north region. *Serves as an example of the normal distribution that the log-density values of rabbit, hare and deer show for all regions and administrative types in study.*

Annex II – Original (untransformed) data

Table 11 - Original data (untransformed): mean density of hunted rabbit, hare and deer in each hunting region for the period in study. *Mean: number of hunted animals per hectare; Lower/Upper: lower and upper bounds of 95% confidence interval.*

	Rabbit			***Hare***			***Deer***		
Region	Mean	Lower	Upper	Mean	Lower	Upper	Mean	Lower	Upper
North	0.151	0.126	0.176	0.016	0.013	0.019	-	-	-
Center	0.248	0.227	0.270	0.021	0.019	0.024	0.024	0.021	0.028
LTV	0.823	0.803	0.843	0.026	0.023	0.029	-	-	-
Alentejo	0.356	0.339	0.373	0.054	0.052	0.055	0.025	0.022	0.028
Algarve	0.278	0.229	0.326	0.038	0.033	0.043	-	-	-

Table 12 - Original data (untransformed): mean density of hunted rabbit, hare and deer in each administrative type for the period in study. *Mean: number of hunted animals per hectare; Lower/Upper: lower and upper bounds of 95% confidence interval.*

	Rabbit			***Hare***			***Deer***		
Type	Mean	Lower	Upper	Mean	Lower	Upper	Mean	Lower	Upper
Associative	0.431	0.419	0.443	0.038	0.036	0.039	0.018	0.014	0.022
Municipal	0.229	0.150	0.308	-	-	-	-	-	-
Touristic	0.360	0.335	0.384	0.046	0.044	0.048	0.029	0.026	0.032

Table 13 - Original data (untransformed): mean density of hunted rabbit, hare and deer in each hunting season for the period in study. *Mean: number of hunted animals per hectare; Lower/Upper: lower and upper bounds of 95% confidence interval.*

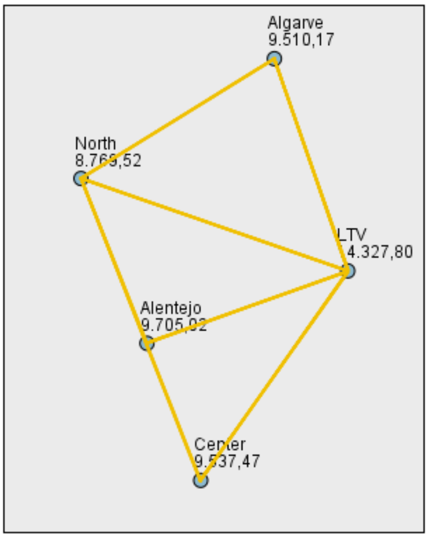
	Rabbit			***Hare***			***Deer***		
Year	Mean	Lower	Upper	Mean	Lower	Upper	Mean	Lower	Upper
89	0.454	0.258	0.649	0.053	0.033	0.073	0.024	-0.025	0.073
90	0.757	0.646	0.869	0.073	0.061	0.086	0.014	-0.035	0.064
91	0.822	0.712	0.931	0.055	0.043	0.067	0.009	-0.041	0.058
92	0.683	0.603	0.764	0.072	0.063	0.081	0.003	-0.025	0.032
93	0.826	0.766	0.887	0.044	0.038	0.051	0.010	-0.010	0.030
94	0.627	0.565	0.690	0.049	0.042	0.056	0.007	-0.013	0.027
95	0.787	0.732	0.843	0.054	0.049	0.060	0.013	-0.003	0.029
96	0.608	0.555	0.662	0.045	0.040	0.051	0.011	-0.006	0.029
97	0.714	0.664	0.765	0.049	0.043	0.054	0.015	-0.001	0.031
98	0.700	0.638	0.762	0.027	0.019	0.035	0.017	-0.003	0.036
99	0.569	0.519	0.618	0.046	0.041	0.052	0.029	0.015	0.043
00	0.536	0.478	0.595	0.026	0.019	0.033	0.015	-0.003	0.033
01	0.382	0.329	0.434	0.049	0.043	0.054	0.016	0.005	0.028
02	0.365	0.319	0.411	0.045	0.040	0.050	0.020	0.009	0.031
03	0.387	0.338	0.437	0.037	0.031	0.042	0.023	0.012	0.035
04	0.369	0.323	0.415	0.038	0.034	0.043	0.018	0.007	0.029
05	0.349	0.304	0.394	0.038	0.033	0.042	0.027	0.017	0.037
06	0.303	0.257	0.349	0.040	0.035	0.045	0.024	0.012	0.037
07	0.389	0.341	0.437	0.048	0.043	0.053	0.022	0.012	0.032
08	0.330	0.285	0.376	0.048	0.044	0.053	0.029	0.020	0.038
09	0.332	0.287	0.377	0.042	0.037	0.046	0.027	0.017	0.036
10	0.322	0.277	0.367	0.040	0.035	0.045	0.031	0.020	0.042
11	0.321	0.276	0.366	0.035	0.030	0.039	0.039	0.030	0.048
12	0.279	0.234	0.325	0.028	0.023	0.033	0.020	0.010	0.031
13	0.123	0.072	0.174	0.020	0.015	0.025	0.019	0.007	0.032
14	0.117	0.068	0.167	0.020	0.014	0.025	0.031	0.020	0.041
15	0.102	0.049	0.154	0.018	0.013	0.023	0.033	0.022	0.044
16	-	-	-	-	-	-	0.031	0.020	0.042
17	-	-	-	-	-	-	0.037	0.022	0.052

Annex III – Nonparametric tests

➔ Kruskal-Wallis test indicates that there are differences in density of hunted rabbits between hunting regions (north, centre, LTV, Alentejo, Algarve), $H(4) = 2572.040$, $p < 0.001$

Table 14 - Dunn's pairwise test on density of wild rabbit between hunting regions. *Highlighted: groups with significant difference (p < 0.05, adjusted using the Bonferroni correction)*

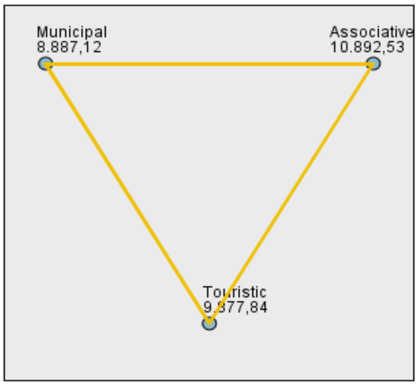
Sample1-Sample2	Test Statistic	Std. Error	Std. Test Statistic	Sig.	Adj.Sig.
North-Algarve	740,649	230,947	3,207	,001	,013
North-Center	767,949	139,991	5,486	,000	,000
North-Alentejo	935,502	128,583	7,275	,000	,000
North-LTV	5.558,279	135,316	41,076	,000	,000
Algarve-Center	-27,300	224,664	-,122	,903	1,000
Algarve-Alentejo	194,853	217,738	,895	,371	1,000
Algarve-LTV	-4.817,630	221,781	-21,722	,000	,000
Center-Alentejo	167,554	116,924	1,433	,152	1,000
Center-LTV	-4.790,330	124,290	-38,542	,000	,000
Alentejo-LTV	-4.622,776	111,284	-41,540	,000	,000



➔ Kruskal-Wallis test indicates that there are differences in density of hunted rabbits between administrative types (associative, municipal, touristic), $H(2) = 117.354$, $p < 0.001$

Table 15 - Dunn's pairwise test on density of wild rabbit between administrative types. *Highlighted: groups with significant difference (p < 0.05, adjusted using the Bonferroni correction)*

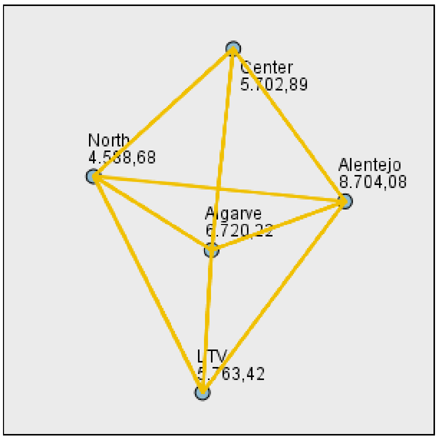
Sample1-Sample2	Test Statistic	Std. Error	Std. Test Statistic	Sig.	Adj.Sig.
Municipal-Touristic	-990,716	332,608	-2,979	,003	,009
Municipal-Associative	2.005,410	320,873	6,250	,000	,000
Touristic-Associative	1.014,694	110,012	9,223	,000	,000



→ Kruskal-Wallis test indicates that there are differences in density of hunted hares between hunting regions (north, centre, LTV, Alentejo, Algarve), H(4) = 2214.358, $p < 0.001$

Table 16 - Dunn's pairwaise test on density of hare between hunting regions. *Highlighted: groups with significant difference (p < 0.05, adjusted using the Bonferroni correction)*

Sample1-Sample2	Test Statistic	Std. Error	Std. Test Statistic	Sig.	Adj.Sig.
North-Center	1.114,214	131,082	8,500	,000	,000
North-LTV	1.174,738	143,242	8,201	,000	,000
North-Algarve	2.131,542	196,588	10,843	,000	,000
North-Alentejo	4.115,405	111,975	36,753	,000	,000
Center-LTV	-60,524	130,624	-,463	,643	1,000
Center-Algarve	1.017,328	187,593	5,423	,000	,000
Center-Alentejo	3.001,191	95,302	31,491	,000	,000
LTV-Algarve	956,803	196,283	4,875	,000	,000
LTV-Alentejo	2.940,667	111,438	26,388	,000	,000
Algarve-Alentejo	1.983,864	174,777	11,351	,000	,000



→ Kruskal-Wallis test indicates that there are no differences in density of hunted hares between administrative types (associative, touristic), H(1) = 0.844, p = 0.358

→ Kruskal-Wallis test indicates that there are differences in density of hunted deer between hunting regions (centre, Alentejo), H(1) = 4.921, p = 0.027

→ Kruskal-Wallis test indicates that there are differences in density of hunted deer between administrative types (associative, touristic), H(1) = 19.687, $p < 0.001$

Annex IV – Tendency categories in rabbit populations

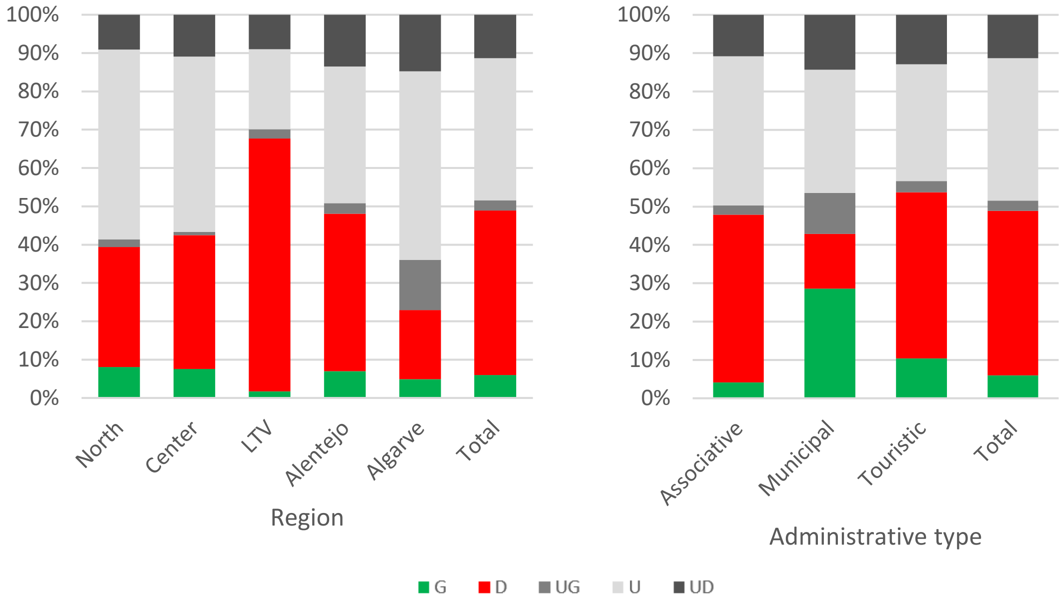


Figure 27 - Proportion (%) of rabbit population tendency category (extended) across hunting regions and administrative types. *G - growth, D - decline, UG – unstable growth, U – unstable, UD – unstable decline*

Annex V – Density of hunted rabbit and hare per hunting season among hunting region (95% CI)

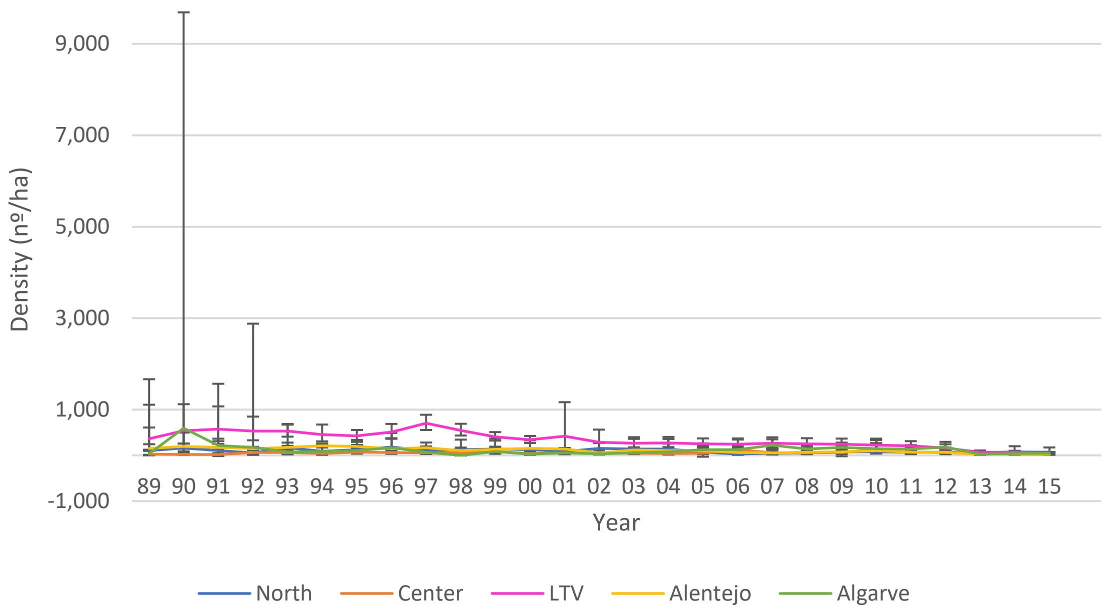


Figure 28 - Mean density of harvested rabbits per hunting season in each region. *Error bars display 95% CI*

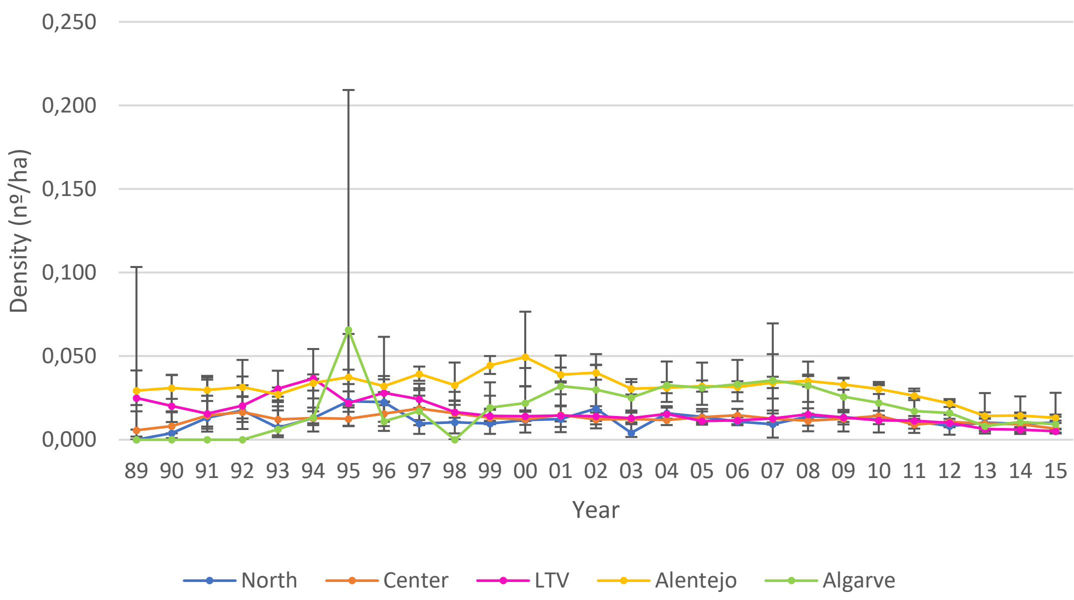


Figure 29 - Mean density of harvested hares per hunting season in each region. *Error bars display 95% CI*

Annex VI – Transition matrixes resuming changes between major land use classes between 1995 and 2018

Table 17 - Transition matrix resuming changes between major land use classes between 1995 and 2018 for the all HZ where red deer and rabbit or hare coexist in the hunting bag statistics, in percentage (%)

Landuse in 2018 (%) / Landuse in 1995 (%)	Exposed areas	Annual crops	Permanent crops	Cork and holm oak forests	Exotic forests	Other broadleaved forest	Conifer forests	Shrubland	Patchy habitats	Pastures	Agroforestry systems	Aquatic habitats	Urban	Total % in 1995
Exposed areas	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
Annual crops	0.00	0.47	0.02	0.04	0.00	0.00	0.03	0.02	0.00	0.36	0.01	0.03	0.00	1.00
Permanent crops	0.00	0.05	0.77	0.02	0.00	0.00	0.03	0.08	0.00	0.03	0.00	0.00	0.00	1.00
Cork and holm oak forests	0.00	0.00	0.00	0.94	0.00	0.00	0.01	0.01	0.00	0.00	0.04	0.00	0.00	1.00
Exotic forests	0.00	0.01	0.00	0.03	0.94	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	1.00
Other broadleaved forest	0.00	0.00	0.03	0.01	0.01	0.93	0.01	0.01	0.00	0.00	0.00	0.00	0.00	1.00
Conifer forests	0.00	0.00	0.00	0.02	0.02	0.00	0.92	0.01	0.00	0.01	0.01	0.00	0.00	1.00
Shrubland	0.00	0.02	0.00	0.03	0.02	0.00	0.17	0.69	0.00	0.07	0.00	0.00	0.00	1.00
Patchy habitats	0.00	0.06	0.05	0.03	0.00	0.00	0.06	0.03	0.64	0.09	0.00	0.00	0.04	1.00
Pastures	0.00	0.07	0.01	0.08	0.00	0.00	0.08	0.11	0.00	0.63	0.01	0.01	0.00	1.00
Agroforestry systems	0.00	0.00	0.00	0.16	0.00	0.00	0.00	0.00	0.00	0.03	0.79	0.00	0.00	1.00
Aquatic habitats	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	1.00
Urban	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.07	0.91	1.00
Total % in 2018	**0.00**	**0.04**	**0.03**	**0.26**	**0.11**	**0.00**	**0.14**	**0.11**	**0.00**	**0.14**	**0.14**	**0.01**	**0.00**	**1.00**

Table 18 - Transition matrix resuming changes between major land use classes between 1995 and 2018 for the all HZ where red deer and rabbit or hare coexist in the hunting bag statistics, in hectares (ha)

Landuse in 2018 (ha) / Landuse in 1995 (ha)	Exposed areas	Annual crops	Permanent crops	Cork and holm oak forests	Exotic forests	Other broadleaved forest	Conifer forests	Shrubland	Patchy habitats	Pastures	Agroforestry systems	Aquatic habitats	Urban
Exposed areas	78.96												
Annual crops		2039.88	103.94	163.94	11.76		142.64	98.77		1562.26	48.44	113.84	20.43
Permanent crops		127.22	1972.31	48.22	2.95		79.00	213.58	6.85	82.87	8.16	1.28	3.06
Cork and holm oak forests		3.76	4.19	16970.66	47.52	1.52	146.81	154.21		55.46	673.46	64.87	14.54
Exotic forests		64.60	0.65	267.67	8335.06		64.35	39.33	4.35	94.50	0.16	19.84	3.07
Other broadleaved forest			7.11	2.45	1.31	214.90	3.00	1.41			0.17		
Conifer forests		9.12	3.10	164.29	196.19		7898.84	115.14	1.60	77.94	68.84		24.07
Shrubland		168.20	19.49	344.14	175.16		1728.88	7155.13	1.40	729.77	4.89	8.09	41.19
Patchy habitats		7.36	6.29	3.45	0.33		7.36	3.22	77.23	10.37	0.24		4.79
Pastures		877.34	112.02	1041.11	50.89	1.57	1050.05	1450.44	10.17	8349.12	189.93	84.65	59.56
Agroforestry systems		38.31	15.76	2242.59	0.94		62.50	31.16	4.32	455.53	10725.25	18.78	18.16
Aquatic habitats												689.09	0.02
Urban		0.05	0.23		0.03				0.03	1.88		11.60	142.54
Total in 2018 (ha)	**78.96**	**3335.84**	**2245.08**	**21248.51**	**8822.14**	**217.99**	**11183.43**	**9262.39**	**105.95**	**11419.70**	**11719.54**	**1012.05**	**331.43**
% in 2018	0.10	4.12	2.77	26.24	10.89	0.27	13.81	11.44	0.13	14.10	14.47	1.25	0.41

***Table 19 – Land-use change between 1995 and 2018 (in %) for the all HZ where red deer and rabbit or hare coexist in the hunting bag statistics**. HZ are coded per region: AL – Alentejo, C – Centre, LTV – Lisbon and Tagus Valey, Alg - Algarve. Major changes are highlighted*

HZ	Exposed areas	Annual crops	Permanent crops	Cork and holm oak forests	Exotic forests	Other broadleaved forest	Conifer forests	Shrubland	Patchy habitats	Pastures	Agroforestry systems	Aquatic habitats	Urban
Al1	0.000	0.2	-2.2	0.0	0.0	0.0	0.0	2.2	0.0	-0.2	0.0	0.0	0.0
C1	0.000	-0.4	0.0	3.3	-0.4	0.0	0.0	-0.8	0.0	2.3	-4.0	0.1	0.1
Al2	0.000	-5.6	1.6	0.0	0.0	0.0	13.0	-2.8	0.0	-6.8	0.0	0.6	0.1
Al3	0.000	-4.5	-1.6	10.7	-5.3	0.0	-0.7	-0.5	0.0	0.4	-3.1	4.6	0.1
AL4	0.000	-8.0	5.1	9.0	-0.1	0.0	0.0	0.0	0.0	-6.4	0.4	0.0	0.0
Al5	0.000	1.6	-1.7	3.6	0.1	0.0	0.0	-0.1	0.0	-4.4	-0.8	0.2	1.4
C3	0.000	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	-0.5
C4	0.000	-4.3	-0.7	7.4	-0.1	0.0	0.5	0.0	-0.1	4.0	-7.1	0.2	0.1
Al6	0.000	19.0	0.0	4.4	-3.8	0.0	0.0	2.5	0.0	-22.1	0.0	0.0	0.0
Al7	0.000	-2.5	-1.6	8.9	0.7	0.0	0.3	1.9	-0.4	0.3	-8.0	0.1	0.3
C5	0.000	1.3	0.5	3.9	0.0	0.0	7.7	-0.1	0.0	-9.0	-4.6	0.1	0.1
Al8	0.000	-0.9	0.0	30.7	0.0	0.0	0.8	0.6	-0.1	0.2	-31.6	0.1	0.3
C6	0.000	-0.6	-0.6	0.4	1.1	0.0	0.6	-1.2	0.0	-1.0	1.1	0.1	0.0
C7	0.000	0.0	0.0	-7.4	0.0	0.0	42.9	-21.7	0.0	0.5	-14.3	0.0	0.0
LVT1	0.000	-0.7	-0.6	0.6	0.0	0.0	1.3	3.2	0.0	-3.0	-0.9	0.0	0.0
C8	0.000	0.0	0.0	-2.7	-0.1	0.0	0.0	2.3	0.0	0.4	0.2	0.1	-0.1
Al9	0.000	0.7	-0.3	4.0	0.0	0.0	-2.2	-0.2	0.0	-4.7	2.8	0.0	0.0
C9	0.000	3.0	0.3	-4.9	0.0	0.0	3.7	-0.7	0.0	-8.5	5.8	1.4	0.0
C10	0.000	0.2	0.4	3.2	0.0	0.0	0.0	3.7	0.0	-5.7	-2.0	0.1	0.1
Al10	0.000	-1.4	2.2	4.8	0.0	0.0	12.8	-1.0	-0.1	-12.9	-5.8	1.1	0.4
Al11	0.000	2.6	0.0	0.7	0.0	0.0	-3.1	-3.4	0.0	-1.2	4.3	0.0	0.0
Al12	0.000	-0.7	-0.3	2.5	0.0	0.0	-0.2	2.0	0.0	1.0	-4.2	0.0	0.0
C11	0.000	-5.4	0.0	0.3	0.0	0.0	0.0	0.0	0.0	5.0	-0.8	0.7	0.2
C12	0.000	-2.4	-1.3	1.8	0.0	0.0	3.8	-6.1	0.0	3.5	0.5	0.0	0.0
Al13	0.000	1.7	0.1	-0.3	-4.5	-0.1	1.5	0.1	0.0	1.4	0.0	0.0	0.0
C11	0.000	-0.6	-0.9	6.8	2.0	0.0	-2.5	-3.1	-0.2	0.0	-1.5	0.0	0.0