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RED AND ROE DEER IN LOUSÃ MOUNTAIN: ARE THEY USING THE SAME ECOLOGICAL RESOURCES?

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Resumo

Os recursos ecológicos referem-se de uma forma simplificada ao refúgio e ao alimento. Desta forma, para identificar os recursos ecológicos usados por uma espécie é necessário estudar o uso do habitat bem como o seu comportamento alimentar. O estudo do uso comparativo de recursos (em termos de habitat e alimento) permite identificar interacções interespecíficas assim como o seu modo de operação. São cada vez mais as situações por toda a Europa em que veado e corço ocorrem simpatricamente. Tal ocorre na Serra da Lousã (Portugal) como resultado de programas de reintrodução. No entanto, as interacções interespecíficas entre estes dois cervídeos nunca foram estudadas após a sua reintrodução. No entanto, o seu conhecimento é crucial para a gestão e conservação de ambas as espécies e dos seus habitats. Assim, este trabalho tem como objectivo avaliar os recursos ecológicos usados sazonalmente pelo veado e pelo corço na Serra da Lousã, de forma a perceber como uma espécie se comporta na presença da outra. Contagens de grupos de excrementos através de transectos lineares com amostragem à distância foram realizadas de modo a identificar os padrões do uso de habitat por ambas as espécies. Durante a realização dos transectos também foram recolhidas amostras de excrementos frescos de ambas as espécies que foram posteriormente analisadas por meio da técnica microhistológica. Esta permitiu identificar as espécies de plantas consumidas pelo veado e pelo corço.

Deste modo através de ambos os métodos pretendeu-se determinar as interacções interespecíficas entre o veado e o corço e averiguar se a presença de ambas as espécies não acarreta problemas para nenhuma delas, resultando em coexistência, ou se pelo contrário a presença de uma compromete a presença da outra, resultando em competição. Os resultados deste estudo mostraram que o veado e o corço coexistem na Serra da Lousã, apresentando baixa competição quer em termos de ocupação de habitat quer por recursos alimentares.

Palavras-chave: *Cervus elaphus*, *Capreolus capreolus*, uso do habitat, comportamento alimentar, contagens de grupos de pellets, técnica microhistológica

Abstract

The ecological resources, in simple terms, refers to cover and food. Hence, to identify the ecological resources used by a species it is necessary to study their habitat use as well as their feeding behavior. The study of the comparative use of resources (in terms of habitat and food) allows the identification of interspecific interactions as well as how they function. It is becoming more common for the red and roe deer to occur sympatrically through all Europe, which also happens in Lousã Mountain (Portugal) as the result of reintroduction programs. However, the interspecific interactions between these two deer species was never been studied after their reintroduction. Such study is crucial for the management and conservation of both species and their habitats. Therefore, the aim of this study is to evaluate the ecological resources used seasonally by the red and roe deer in Lousã Mountain, to understand the behavior of each species in the presence of the other. Pellet group counts through line transects with distance sampling was made to identify the patterns of the habitat used by both species. When making the transects, fresh fecal samples of both species were collected for posterior analysis using the microhistological technique. The latter allowed the identification of the plant species consumed by the red and roe deer.

Thus, through the use of both methods the aim was to determine the interspecific interactions between the red and roe deer, and to verify if the presence of both species is not posing a problem for neither, resulting in coexistence, or on the contrary, if the presence of one species affects the other, resulting in competition. The results of this study demonstrate that the red and roe deer coexist in Lousã Mountain, presenting little competition either for habitat or food.

Key words: *Cervus elaphus*, *Capreolus capreolus*, habitat use, feeding behavior, pellet group counts, microhistological technique

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Chapter I – General introduction

When considering sympatric species, whom coexist and may or not compete, there are several concepts that need to be defined to provide their correct utilization and interpretation throughout the thesis.

1.1 Important ecological concepts and its definition

Ecological resources

Understand how animals answer to the environment allows identifying the essential resources, how and when they are used (Manly et al. 2002; Alves et al. 2014). Ecological resources correspond to resources requirements which are, in a simplified way, the food and cover (Borkowski 2004; Manly et al. 2002). These two continuous habitat variables, related with fitness of an individual (Clark 1994), are very important because when different habitats confer opposing benefits, as food quality or quantity versus protection against predation (Brown 1999; Godvik et al. 2009; Panzacchi et al. 2010), the animals have to make behavioral trade-offs (Dupke et al. 2017). In accordance with the relative influence of the different limiting factors, the strength and magnitude of trade-offs can vary in time and space (Dupke et al. 2017). Limiting factor is an environmental factor of such importance that limits the size of the population (Jie 2017).

Habitat use and selection

Habitat can be defined as the set of resources and conditions present in an area that will allow the occupation of a given area, and to determine the survival and reproduction of organisms (Hall et al. 1997; Hirzel and Le Lay 2008). Two important concepts should be considering when talking about habitat for a species, the habitat use and habitat selection. Habitat use corresponds to how animals use the resources to satisfy their requirements (Block and Brennan 1993). This is selective when resources are used disproportionately to their availability (Johnson 1980). It's influenced by biotic, abiotic, species and social factors. As biotic factors can be mentioned the quality, quantity and dispersion of resources (MacDonald 1983; Anderson et al. 2005; Van Beest et al. 2011); as abiotic factors the climate and topography (Kie et al. 2005; Rivrud et al. 2010); of species the age, sex, physiology and reproductive state (Dahle and Swenson 2003; Saïd et al. 2009) and finally the social factors as the intraspecific competition by resources (Kjellander et al. 2004). The habitat selection is a hierarchical process in space and time that occurs at multiple scales and is related with the process of choosing a resource (Johnson 1980). It is influenced by several factors such as the behavior, nutrition, competition, predation but also the scale at which selection occurs (Johnson 1980; Senft et al. 1987; Wiens 1989; Manly et al. 2002; Hirzel and Le Lay 2008). In turn, it indirectly affects the population dynamics and distribution of species and directly the survival and the reproductive success of individuals (Holt 2003;

Gaillard et al. 2010). So a lot of ecological factors can modulate habitat selection by species, changing the benefits and costs supplied by the habitat (Lima and Dill 1990).

It is possible that animals develop trade-offs between the optimization of energy balances and the need to use habitats with less food availability to increase the opportunities for mating or safety (in relation to predators, for instance) (Hardenberg et al. 2000; Ciuti et al. 2006; Panzacchi et al. 2009). In addition, the seasonality and climate conditions may be a limiting factor for herbivorous (e.g. ungulates) which strongly influences the space use (Shackleton and Bunnell 1987). As previously mentioned, sex influences the use of space. In fact, males and females have different constraints, for example the availability of high-quality food in case of females and availability of high quantity in case of males. As seasonality and climate conditions, these constraints will be influencing the space use too (Emlen and Oring 1977; Clutton-Brock 1989).

Ecological niche

The ecological niche happens when a mutual relationship between organisms and environment is present, meaning, when an organism needs and/or shape the environment (Hutchinson 1957). Ecological niche includes a variety of small and large processes, ranging from resource competition, predation, stress to community structure as well as biodiversity and ecosystem function (Chase and Leibold 2003).

Niche overlap and niche breadth

The niche overlap is a measure of the extent of sharing of resources between species (Giller 1984), and niche breadth is a measure of variety of items used within a resource category (Latham 1999). Through the measure of niche breadth and niche overlap it's possible to quantify the comparative resources used and to infer about the interspecific interactions.

It is important to be careful and take into consideration the density of individuals (Abrams 1980) and the abundance of resources (in space and time), when interpreting of the quantification of niche overlap throughout the existing indices, since it will determine when the overlap will lead to competition (Latham 1999). In fact, both niche overlap and density will determine the magnitude of the competitive interactions (Abrams 1980). This implies that high values of niche overlap may be found when resources are superabundant, so the species can use the same resources without competition. On the other hand, high values of niche overlap may also be found when resources are scarce leading the species to use the same resources and compete, which can lead to the exclusion of one of the species (Wiens 1993).

In addition, it's also important take into consideration the scale at which resources are measured. This is because if the resources are divided into large groups (for example in relation to diet, if plants are divided in forbs, shrubs and grasses) a greater value of niche overlap are expected than if the resources are measure at small scales (for example in also relation to diet, if plants are considered at the species level or subdivided into different parts of the same plant) (Latham 1999). It's also important to describe the overlap in resources in different times of the year, when resources are numerous and when they are limited, and to infer about the existence of competition if and when overlap decreases in the lean season (Smith et al. 1978; Gordon and Illius 1989). This is based on the presupposition that grazing ungulates begin to use lower-quality forage when outcompeted from mutually preferred swards (Illius and Gordon 1987).

Home-range

The home-range is the area in which a species lives and moves, meaning, the area of residence of a species. It's possible to define the home-range fidelity as the fixed location of home-range over time (Greenwood 1980). Home-range fidelity depends, besides its location in space, of the variation of its size. This causes to an individual being able to stay in the same place and to present high home-range fidelity by changing the size of home-range, which leads to changes in the degree of overlap (Richard et al. 2014). The overlap occurs when species' home-ranges coincide. The home-range size it's determined by the resources that are used by each animal within this. On the other hand, the variation of home-range size between individuals is determined by their energy requirements (McNab 1963; Harestad and Bunnel 1979), age (Saïd et al. 2009), body size (Harestad and Bunnel 1979) and by the amount of resources available (Richard et al. 2011). These, in turn, are influenced by population density (Kjellander et al. 2004) and by habitat quality (Wahlstrom and Kjellander 1995).

Sympatry

The first definition of sympatry is given by Poulton (1904) in which species are called sympatric if found together in certain geographical areas. Later, Mayr (1942) redefined sympatry whenever two forms or species occurs together, that is, whenever its distribution areas overlap or match.

The occurrence of two species in same geographical area is the result of the different adaptations of each species to local conditions, that is, since resources are found in different conditions or at different moments, each species can adapt to these conditions in different way, resulting in different behavior and preferences, allowing the occurrence of both species in the same area (Darwin 1859).

Interspecific competition

Regarding interspecific interactions, in herbivorous these interactions depend on factors such as: resources availability, animal density and the extent of overlap in the resources used (De Boer and Prins 1990). Habitat heterogeneity it terms of resources may allow species to coexist, especially if species differ in their feeding behavior, as well as body size (Owen-Smith 2002). However, habitat heterogeneity may lead to junction of animals into resources hotspots, which lead to increased local competition as well to grouped distribution of the species that are upper competitors. This can lead to the absence or origin of competition refuges (patches with reduced densities) for species that are bottom competitors (Begon et al. 1996; Durant 1998; Hobbs and Gordon 2010).

In fact, for ungulates the most important interaction and that is more times described is competition. Competition is understood by all interactions where one species negatively affects the fitness of another species (Latham 1999). There are two types of competition: resource competition and interference competition (Birch 1957). The first type of competition occurs when species uses and compete for shared resources, such as food or space. The interference competition happens when one species causes slight effects on the environment, reducing its quality for the other species. Therefore, it's expected if two species interact they can influence the way how each of species uses the resources (Latham 1999).

So, the studies which compare the use of resources (habitat and food) of two sympatric species at a range of densities allow identifying the interspecific interactions and how they act (Latham 1999). According Putman (1996), it's common that two sympatric species have resource partitioning, possibly has evolved of competition in past. This implies that if species have currently the differential use of resources may not mean that these species interacts, but if resources use of a species can be demonstrated based on the character displacement, it's likely that these species interacts (Latham 1999).

To understand the interspecific competition is necessary to have information on overlap in resources used (Schoener 1974; Abrams 1980). The exploitation competition is a crucial mechanism of interaction between large herbivores (Sinclair and Norton-Griffiths 1982; Sinclair 1985; Putman 1986; Putman 1996; Illius and Gordon 1987; Gordon and Illius 1989). To interspecific exploitation competition takes place is crucial occur overlap in habitat use and in diet, and also the shared resources are limited (De Boer and Prins 1990; Tokeshi 1999).

Nevertheless, there is disagreement about the role of interspecific competition in the establishment of food niches (Wiens 1977; Diamond 1978; Connell 1980; Schoener 1982). It is admitted that there is segregation of at least one dimension of spatial niche when sympatric species coexist in long term. This is denominated "Competitive exclusive principle" (Gause 1934; Hardin 1960). What this principle means is that species with similar ecological niche cannot coexist at long term due to the pressure exercised by the competition between the species. In this way one of species lead to the

displacement of the ecological niche of the other species, leading to behavioral changes or even to the extinction to the other species. In conclusion, this principle implies that long-standing competitors cannot coexist.

Feeding behavior

The natural selection shapes the species in terms of their morphology and physiology, defining the limits of their fundamental food niches (Hutchinson 1957; Hanley 1982; Chase and Leibold 2003). In this way, the diet of an animal depends on: intrinsic limitations, essentially the body size; morphological/physiological characteristics which dictate the range of food that is better tolerated; environmental constraints, such as seasonality (variations in resources availability in short periods of time (Schwartz and Ellis 1981)) and of interspecific interactions which determine the resources availability (Storms et al. 2008).

Ungulates feed on plant species which differ in nutritional quality (Hanley 1982). The cells of plant tissues vary in the ratio between slowly digestible cell walls and the facility of assimilation of cellular constituents. Therefore differ in the rate of digestion by ungulates (Demment and Van Soest 1985). In relation to vegetal fiber contents, grasses, sedges, heathers and ferns have high fiber contents whereas the leaves of trees and shrubs have medium to high fiber contents and forbs have lower fiber contents. The fibers (sclerenchyma) are slowly digested because they consist of structural cells with thick-walled (Raven & al. 1992).

The capacity that individuals have to use these fibers in their diets is determined by body size and consequently by their gut capacity. These capacities will determine the retention time of the ingested in the gastrointestinal tract which determine the capacity of individuals to use fibrous forage (Demment and Van Soest 1985; Gordon and Illius 1994; Robbins et al. 1995; Van Soest 1996). In this way, the interspecific morphological/physiological differences are assigned to the tolerance to the fibrous forage (Hofmann and Stewart 1972; Hofmann 1989; Clauss and Lechner-Doll 2001; Clauss et al. 2003).

1.2 Study species

1.2.1   Red deer *Cervus elaphus* - Ecology and behavior

The red deer (*Cervus elaphus*, Linnaeus, 1758) belongs to the family Cervidae and to the order Cetardiodactyla, according to the classification adopted by IUCN (Lovari et al. 2016). Is the one of the largest cervids in world (Oliveira 2013), being one of the mammals with the largest global distribution (Salazar 2009). Is widely distributed throughout Europe (Fig.1) (Koubek and Zima 1999) and is currently the largest ungulate in the Iberian Peninsula (Oliveira 2013). The red deer distribution also extends to North Africa and the Middle East (Corbet 1978; Koubek and Zima 1999; Wilson and Ruff 1999; Wilson and Mittermeier 2011).
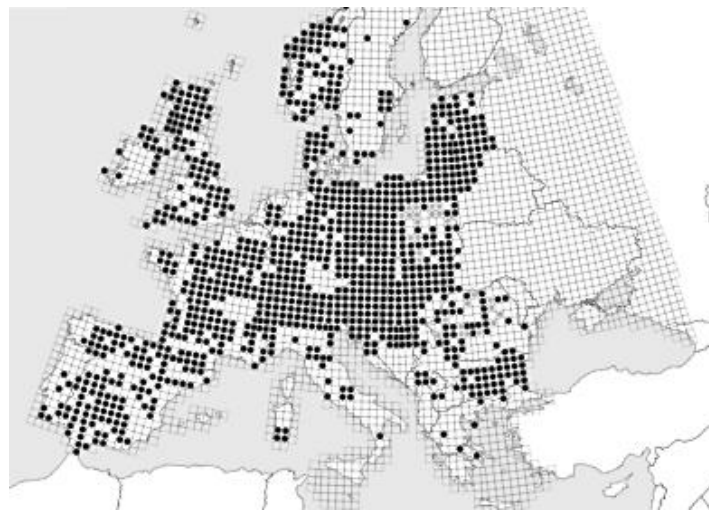
Fig 1: Distribution of red deer populations in Europe (adapted from ©Societas Europaea Mammalogica 2018).

In Portugal, existing populations of red deer resulted from reintroduction programs or from natural expansion of the populations from Spain, where were reintroduced after being close to extinction (Lovari et al. 2016). This has led to an increase of populations in numbers and geographical area (Alves 2013) and this trend is currently not only in Portugal (Lovari et al. 2016). This increase was due not only to management actions but also to changes in habitats (Alves 2013).

Fig 2: Distribution of red deer populations in Portugal (adapted from (Salazar 2009)).

Red deer populations in Portugal (Fig.2) occur in several areas from the North to the South of the country, such as: the Montesinho Natural Park; Peneda-Gerês National Park; Lousã Mountain; International Tagus Natural Park; Tapada Nacional de Mafra; Tapada Real de Vila Viçosa; Moura; Mourão; Barrancos and Monchique (Salazar 2009).

In Mediterranean environments, red deer uses a high variety of habitats, including coniferous and mixed forests, shrublands, agricultural lands, grasslands as well as areas close to the ecotone (transition between two different biomes) and water sources (Koubek and Zima 1999; Alves et al. 2014) Thus, this species has a high plasticity in terms of habitat use but shows preference for habitats that simultaneously provide food and some refuge as shown by their preference for shrublands (Alves et al. 2014). Red deer also presents preference for forestall areas with dense coverings (60-80%) as well as with a diverse tree layer (more than three species) (Prokešová et al. 2006). Red deer positively use areas with small covers and open spaces (e.g. grasslands and shrublands) as proved by their positive use of ecotone zones (Alves et al. 2014).

Apart from these variables, human activity also influences the use of space. Legal hunting (for instance) of red deer is allowed and lead to the avoidance of human settlements, since hunting tends to promote various behavioral responses such as escape behavior (Torres et al. 2014). Another anthropogenic factor is the roads.

This ruminant mammal shows a diphasic activity, once feed during the night to avoid human disturbances (Richard et al. 2014) returning to their covers during the morning (Georgii 1980; Licoppe 2006). So the night home-range is greater than the day home-range (Richard et al. 2014) because red deer during the day are, for safety

reasons, in their covers and only leave during the night when they can go feeding in safety in open areas (Walter et al. 2011).

In terms of feeding behavior, red deer is considered as an intermediate feeder (Hofmann 1989) whereby they are able to be grazer with a mixed diet of grasses, whose forage have a high fiber content, but also browser, feeding on herbaceous and shrub foliage and trees (Bugalho et al. 2001; Gebert and Verheyden-Tixier 2001; Bugalho and Milne 2003; Szemethy et al. 2003; Ruckstuhl and Neuhaus 2005; Dumont et al. 2005). This depends on food availability (Hofmann 1989). The red deer has the capacity to adapt their diet to seasonal changes in food quality and quantity, which leads to changes in their diet composition (Dumont et al. 2005). In periods of reduced availability and quality of food but with high energy requirements, red deer needs to resort to alternative food such as agricultural species (Prokešová 2004; Putman and Staines 2004; Dumont et al. 2005), fruits (Suter et al. 2004; Ferreira 2004; Putman and Staines 2004; Dumont et al. 2005; Cortez 2010; Koda and Fujita 2011) but also browse on trees as a complementary diet (Bugalho et al. 2001; Bugalho et al. 2005). This happens in summer, when most of herbaceous species become senescent. This is a limiting period in Mediterranean areas (dry and hot weather) which can leads to nutritional restrictions (Alves 2013). Thus, red deer is an opportunistic species choosing the more digestible and palatable foods according to environment availability (Hofmann 1989; Ferreira 2004; Dumont et al. 2005; Cortez 2010). In the study area (Lousã Mountain, Portugal) shrubs are the main food resource of red deer throughout the year such as *Erica* sp., *Pterospartum tridentatum*, *Ulex* sp., *Rubus* sp. (Alves 2013). Nonetheless, red deer can also look for Gramineae species and arboreous species, such as *Quercus* sp., *Castanea sativa* and *Pinus pinaster* (Alves 2013; Garcia 2016). This herbivore prefer leaves and sprouts of trees (Prokešová 2004; Dumont et al. 2005; Lovari et al. 2008; Bugalho et al. 2001; Koda and Fujita 2011), leafy young branches of shrub and arboreous species (Suter et al. 2004; Szemethy et al. 2003) as well aerial parts of herbaceous plants and grasses (Milne et al. 1978; Suter et al. 2004; Szemethy et al. 2003; Prokešová 2004; Dumont et al. 2005; Cortez 2010). However, depending on phenology and availability of plants, this ungulate eat different structures of plants (roots, stems, leaves, flowers, fruits, sprouts and seeds), depending on the time of the year (Garcia 2016).

Also, the nutritional requirements change between seasons because the reproductive cycle is synchronized, so this species, as well others ungulates, presents a partial migration (Qviller et al. 2013) to choose the best locals to minimize energetic losses and maximize gains. This partial migration includes altitudinal movements throughout the year according to food quality and availability (Clutton-Brock et al. 1982). Aiming to found food of high quality, this species in summer migrates to high altitudes (Bonenfant et al. 2004; Qviller et al. 2013) especially in locals with snow melt.

1.2.2 Roe deer *Capreolus capreolus* - Ecology and behavior

The roe deer (*Capreolus capreolus*, Linnaeus, 1758) also belongs to the family Cervidae and to the order Cetardiodactyla, according to the classification adopted by IUCN (Lovari et al. 2016). This species are considered the cervid with higher amplitude in terms of geographical range (Aragon et al. 1998) and the most abundance of Europe (Apollonio et al. 2010). It's a forest species that occupies a high variety of habitats, occurring in the majority of the European landscapes (Apollonio et al. 2010; González et al. 2013), with the exception of Ireland, Cyprus, Corsica, Sardinia and the majority of small islands (Fig.3) (Lovari et al. 2016). Besides Europe, occurs in Turkey, northern Syria, northern Iraq, northern Iran and in Caucasus (Wilson and Reeder 2005). However, along the Black Sea coast and in region of Aegean Sea in northern of Turkey, the Mediterranean sub-populations are close to the extinction (Lovari et al. 2016).

Fig 3: Distribution of roe deer populations in Europe (adapted from ©Societas Europaea Mammalogica 2018).

In Portugal in last four decades their distribution as well as their density has increased (Vingada et al. 2010) and this trend is not only present in our country (Lovari et al. 2016). This trend resulted from the change in soil use practices and from partial replacement of agricultural lands by forests, which led to a renaturation of habitats with a consequent increase of landscape domain, in terms of surface area, from 66% in 1960 to 75% currently (Beilin et al. 2014). The increase of these ungulates was also due to reintroduction programs and to the increase of accuracy in hunting legislation and management policies (Torres et al. 2015).

Fig 4: Distribution of roe deer populations in Portugal (adapted from (Salazar 2009))

The populations of roe deer in Portugal (Fig.4) occur in the northern of the country, like in Gerês, Marão, Montesinho and Nogueira Mountains (Salazar 2009). In the center of Portugal, the roe deer is present in Lousã Mountain (Salazar 2009). Even in center of the country but more close to the radius, their existence derive from the movement of roe deer originating from the Spain (Salazar 2009). In addition, their presence also occurs in south of the country as the result of introductions mainly in privates enclosures (Salazar 2009).

The roe deer have a great adaptability and behavioral flexibility that is reflected in high success of this species, since they can use a wide range of habitats (Linnell et al. 1998): deciduous, mixed or coniferous forests, Mediterranean forests, moorland, pastures, arable land, suburban areas with large gardens as well as high latitudes and altitudes (Jepsen and Topping 2004; Lovari et al. 2016). The forests that are used by roe deer essentially have *Rubus* spp., Gramineae, *Erica* spp. and *Ulex* spp. (Mancinelli et al. 2015). However, preferred landscapes include a mosaic of woodland and farmland (Stubbe 1999), and they are also well adapted to modern agricultural landscapes (Andersen et al. 1998; Danilkin 1996; Sempéré et al. 1996). In fact, the human modifications have been reported to be beneficial for this cervid in regions with low snow cover, such as the cutting of trees, formation of croplands and meadows, as well as intensive agriculture (Sempéré et al. 1996). Even so, roe deer can survive in semi-desert environments and seasonally above the tree line (Lovari et al. 2016). Thus, roe deer uses woodlands but also agricultural lands.

Although being a generalist species with a large fundamental niche, roe deer is favored by heterogeneous or mixed habitats, which concurrently promote cover through

the tree canopy against predators and humans, as well as high quality of food resources (Cederlund et al. 1998; Duncan et al. 1998; Mysterud and Ostbye 1999; Said and Servanty 2005; Saïd et al. 2005). In contrast to red deer, roe deer is favored by habitats with big covers and, contrarily, is favored by habitats with small herb layer, dominated by brambles (Prokešová et al. 2006). Nonetheless, the roe deer also uses high-grass meadows with some shrubs (Sempéré et al. 1996). Thus, the two main habitat requisites for the roe deer are food (Duncan et al. 1998a) and cover (Cederlund et al. 1998). Using big covers, this species gets simultaneously protection as well as the decrease of thermal stress during the summer, which leads to energy saving (Mysterud 1996). Consequently, roe deer opt for use more habitats with big covers and small herb layer.

Thus, this species has adapted to a high variety of habitats and environments and it's known that these factors influence the social structure and spatial behavior of their populations (Hewison et al. 1998). In fact, in mountainous habitats mainly in winter, the roe deer spatial behavior changes in function of food availability and snow cover (Cederlund 1983; Mysterud 1999; Lamberti et al. 2001; 2004). Alternatively, in agricultural landscapes their social and spatial behavior changes in function of human activity and woodland fragmentation (Lamberti et al. 2006). So, the strong link to woodlands is the key factor that stays constant in all populations, therefore implying that high fragmentation and low mean patch sizes of woodlands lead to a larger group and home-range size (Lovari and San José 1997; Hewison et al. 2001; Cargnelutti et al. 2002).

This ungulate shows a polyphasic activity with alternative stages of feeding and rest. Thus, the home-range fidelity between night and day is higher in the case of roe deer than red deer, because the roe deer have in the same place food and cover. This means that the size of night home-range is not different from size of day home-range for roe deer (Richard et al. 2014).

Anciaux et al. (1991) suggested that the presence of red deer influences the habitat use by roe deer since roe deer are territorial and many times solitary (Dzięciołowski 1979), and they can be intimidated by red deer since red deer gather in herds and in absence of natural predators their densities are artificially high (Latham 1999).

In terms of feeding behavior, this species is considered a browser (Clauss et al. 2003) and a selective feeder, so they feed selectively and preferably on the most digestible plant material (low fiber content) (Hofmann 1989) that is rich in energy and have high moisture content (Cornelis et al. 1999; Danilkin 1996; Sempéré et al. 1996; Tixier and Duncan 1996), such as tree leaves, seedlings and forbs (Latham 1999). They need a regular food intake (Dupke et al. 2017) because their stomach is small and have a rapid digestion process (Hofmann 1989). As a consequence, this ungulate usually has between five and eleven separate feeding periods in a day, feeding at hour intervals during periods of optimal availability of food (Cornelis et al. 1999; Danilkin 1996; Sempéré et al. 1996). The types of plants and individual species that are consumed by

roe deer vary according to seasons and habitats (Cornelis et al. 1999; Danilkin 1996; Sempéré et al. 1996). 1,000 is the estimated number of plants species that are consume by roe deer, of these species the percentage of breakdown of plant type is 25% for woody plants, 54% for herbaceous dicotyledons and 16% for monocotyledons (Cornelis et al. 1999; Danilkin 1996; Sempéré et al. 1996).

In addition, in winter, when there are less availability of other food sources, roe deer can eat the needles of coniferous trees (Cornelis et al. 1999; Danilkin 1996; Sempéré et al. 1996). Nonetheless, in various parts of Europe, the brambles are an important resource for roe deer in winter (Siuda et al. 1969; Hearney and Jennings 1983; Homolka 1991; Tixier and Duncan 1996) because of their high nutritional value (Prokešová et al. 2006). In this way, the diet of roe deer becomes less varied in winter, as the forage reserves reduce which leads to a decline of metabolic rate and food intake. On other hand, in spring this metabolic rate and food intake increases since the energy requirements and digestion process also increases. In autumn, this cervid opt for concentrate food resources, eating seeds and fruits (Cornelis et al. 1999; Danilkin 1996; Sempéré et al. 1996).

1.3 Study area

1.3.1   Location, climate and topography

The Lousã Mountain (40°3′ N, 8°15′ W) is the study area and is located in the centre of Portugal whose area is around 170km^2 (Alves 2013). The climate is Mediterranean, with hot and dry summers and rainy winters practically without snow (Archibold 1995). The annual temperatures range from -4.1°C to 35.9°C and the annual mean temperature is 12°C. The annual precipitation is approximately 827mm but can reach 1600mm for the highest elevations. However, the patterns of temperature and precipitation fluctuate because of the mountain topography as a consequence of slope, altitude and landscape, which lead to climatic differences inside the mountain (Alves 2013). In relation to topography, the terrains are hilly with deep valleys and marked hilltops. Although the majority of elevations have an altitude that range from 700m to 1000m, this can range from 100m to 1205m. Due to drainage basins of the Mondego and Tejo rivers, the study area has a large hydrologic network (Alves 2013). The road network have more than 500km but have a low traffic level, although in the beginning and in the end of the day (with accentuated traffic) the area is much more disturbed (Alves 2013).

1.3.2   Land cover and flora

Regarding to land cover, the Lousã Mountain is characterized by coniferous and broadleaf tree plantations, constituting the mixed habitats, but also with large areas of

shrublands. The coniferous forests are composed by species of pine trees, as *Pinus pinaster*, *Pinus sylvestris* and *Pinus nigra* but also by Douglas fir (*Pseudotsuga menziesii*) and Mexican cypress (*Cupressus lusitanica*). These coniferous forests have a sparse understory with shrub species, such as *Rubus* spp. (brambles), Erica spp. and *Calluna vulgaris* (L.) Hull (heathers) but also with *Ulex* spp. (gorses). The broadleaf trees are composed by *Quercus* sp. (oak), *Castanea sativa* Miller (Chestnut), *Prunus lusitanica* (Portugal laurel) and *Ilex aquifolium* (common holly). However, these areas are less common and are located close to the water courses, whose understory is also sparse mainly with brambles. In shrublands, the most common and abundant species are: *Erica* spp.; *Calluna vulgaris*; *Ulex minor*; *Rubus ulmifolius*; *Pterospartum tridentatum* (L.) ("carqueja"); the brooms *Genista triacanthos* and *Cytisus striatus* and various Gramineae species, such as *Agrostis* spp. and *Festuca* spp.. Mainly in these areas during springtime occurs a boom of herbaceous species. However, no significant changes occur between seasons in the land cover units constituted by evergreen species.

Forb species are also present in Lousã Mountain and they are diverse, although less abundant. *Anarrhinum bellidifolium*, *Carduus tenuiflorus*, *Crepis vesicaria*, *Digitalis purpurea*, *Juncus effusus*, *Lepidophorum repandum*, *Lepidophorum officinale*, *Tuberaria lignosa* and *Genista triacanthos* are some examples of these (Alves 2013; Alves et al. 2014; Garcia 2016).

In some lowest elevations, outside the mountainous region, the plantations of eucalyptus trees are common, especially of *Eucalyptus globulus* Labill., alone or mixed with maritime pine (*Pinus pinaster*). In addition, the abundance of exotic species (*Acacia melanoxylon* and *Acacia dealbata*) increased during recent years (Alves 2013).

The land cover outside the mountain region has a greater human presence with small villages and with an accentuated traffic level, where the mortality of deer caused by the collision with a motor vehicle is more likely. In these areas, the agricultural lands, close to urbanized areas, are an important stratum. In these small patches is common to find several crops that are possible to divide into two principal groups: Irrigated annual crops and non-irrigated crops. As example of the first group of crops are the potatoes, several vegetables (e.g. *Brassica* sp.) and maize. The rye, wheat and oats represent the non-irrigated crops, frequently associated with olives and fruit trees. Here, the conflicts between humans and deer become more accentuated (Alves 2013).

Due to variety and great richness of fauna and flora, the Lousã Mountain was inserted in the National List of Natura 2000 sites and it is classified as a Natura 2000 Site, due to the presence of reliquial ecosystems (Alves 2013).

1.3.3   Red and roe deer presence

The presence of red and roe deer in Lousã Mountain is the result of reintroduction programs (Salazar 2009). In case of red deer, the reintroduction began in

March 1995 with the reintroduction of four males and three females from Tapada de Vila Viçosa and Herdade da Contenda (Barrancos) (Vingada et al. 1997). The animals were released in the central part of the mountain and no adaptation paddocks were used (Salazar 2009). This reintroduction continued until 1999, originating a total of 96 individuals (32 males and 64 females) released (Alves 2013).

In case of roe deer, the reintroduction began in February 1994 when three individuals were reintroduced: one male, female and calf from Nogueira Mountain paddock (Bragança) (Jesus 2002). This reintroduction was possible because in November of the previous year was finished the construction of a paddock, for acclimatization of the roe deer, with about 20 hectares in northern slope of Lousã Mountain (Salazar 2009). From here, several reintroductions followed until 1997, resulting in a total of 54 roe deer reintroduced (including young and adult females and young and adult males) that was released in zone of Social Hunting of Lousã Mountain (Salazar 2009), currently known as National Hunting Area of the Lousã Mountain.

Consequently, these populations began to occupy new territories, increasing in distribution area and number. Currently the red deer populations occupy an estimated area of about 435km^2 including not only the Lousã Mountain (170km^2) but also the surrounding areas. Nevertheless, the central area of Lousã Mountain (120km^2) is the most important local for activities of red deer. The density in the period between 2005 and 2009 was estimated at 5.6 red deer/km^2 (Alves 2013). Regarding to roe deer, in an area of 14.88km^2 in the Lousã Mountain was reported an increase from about 32 animals in 2004 to about 44 animals in 2005 (Carvalho 2007). The mean density in 2004 was 2.2 individuals/km^2 and in 2005 was 3.0 individuals/km^2 (Carvalho 2007).

In the study area, the occurrence of domestic ungulates is restricted to known areas, and the wild ungulates show noticeable differences, being thus possible to distinguish their pellets. In addition, their natural predators are inexistent, but the stray dogs assume this role by attacking mainly young, sub-adults and adult females. The populations of red and roe deer live in sympatry with wild boar (*Sus scrofa*) (Alves 2013).

1.4 Aims

After the reintroduction plan of red and roe deer and their consequent demographic and geographic expansion, it's important to assess if red and roe deer are in fact two sympatric species, and are using the same ecological niche, or if they are using different ecological resources. This allows to understand if the coexistence of both species poses a threats to each other, or if one species is affected by the presence of the other and to what extent, resulting in interspecific competition. If the species uses different ecological resources is expected that they coexist, but if they use the same ecological resources is expected that the species will compete. Thus, to evaluate the ecological

resources used by each species when they occur sympatrically, it's necessary to study the habitat use as well as the feeding behavior of both species.

According to body dimorphism (Richard et al. 2011) and traits of life stories (Peters and Wassenberg 1983), it is expected that red and roe deer use the habitat differentially since they are markedly different in body size, behavior, morphology, having thus large differences in energy requirements (McNab 1963). Furthermore, it is also expected that red and roe deer have more differences in diet composition than in diet diversity since both species have the capacity to feed on a large number of different plant species. However, it is expected that the proportion of each of these plant species in red and roe deer diet to be different, given the differences in red and roe deer feeding strategies. In this way is expected that red and roe deer do not compete for space and food, allowing their coexistence in Lousã Mountain, since is expected that they use different ecological resources (in terms of habitat and food).

Chapter II – Red and roe deer in the Lousã Mountain: Are they using the same ecological resources?

2.1 Introduction

One of the principles in ecology is to understand how animals react to the nature (Manly et al. 2002). These responses, in turn, allow knowing the ecological resources needed, how and when they are used (Alves et al. 2014). For this it's necessary to study habitat use as well as the feeding behavior of red and roe deer since the ecological resources may be described as food and cover (Borkowski 2004; Manly et al. 2002). Thus, the study of comparative use of resources (habitat and diet) is important because allow identifying the interspecific interactions as well as their mode of operation (Latham 1999). The analysis of interactions between feeding strategies of red deer (intermediate feeder) and roe deer (concentrate feeder) it's important because indicate the probably direction of competition between these species. Nonetheless, it's crucial to take into consideration the densities in which these interactions start to operate (Latham 1999).

The interactions between species shape their communities (Gause 1934; Hutchinson 1959). These interactions can be competitive, when species of same trophic level (e.g. red and roe deer) uses the same resources which availability is limited (De Boer and Prins 1990), and where one of the species reduce the shared resources below the level that can be efficiently used by the other (Illius and Gordon 1987; Murray and Illius 1996; Prins and Olff 1998). Such competition may be avoided by coevolved species, through resources partitioning, but the overlap in the resources used can still occur (Hutchinson 1959; MacArthur 1972; Pianka 1973; Schoener 1974). Various factors can enhance the competition such as the spatiotemporal variation in resources availability, habitat modifications caused by man, patterns of resources availability or even the composition of animal communities (Arsenault and Owen-Smith 2002; Gurnell et al. 2004; Robertson et al. 2013).

Nonetheless, when overlap in the use of resources by individual animals occurs does not inevitably imply competition. It depends on the extent to which these resources limit the abundance of the populations (Wiens 1989; Putman 1996). That is why it is important take into consideration the evaluation of niche breath as well as the niche overlap to quantify the comparative use of resources as well as to obtain findings about interspecific interactions (Latham 1999).

The way how animals use their resources essentially depends on the way how they handle with potential competitors (Namgail et al. 2009; Razgour et al. 2011; Vanak et al. 2013). In fact, if species compete they influence the way how each one use the resources (Latham 1999). For instance, an ungulate that have an intermediate feeding strategy can feed on higher range of food resources than an ungulate that have concentrate feeding strategy. In this case, the first ungulate have advantage over the second because it is competitively superior (Latham 1999). Just as Latham et al. (in

press) suggested this for Scottish red and roe deer, this may occur in our study area for the study species. Is important to study this because the competition can affect the individuals of inferior competitor capacity (in this case the roe deer) in terms of their behavior and/or their growth/survival (Durant 1998; Harris and Siefferman 2014), leading to effects on population at local and global scales (Bertolino 2008; Hamel et al. 2013) and consequently on communities (Levi and Wilmers 2012; Robertson et al. 2013). In addition, there is a suspicion that interspecific competition between wild herbivores can affect the resources used, population trends and/or species distribution, in temperate and savannahs ecosystems (Sinclair and Norton-Griffiths 1982; Putman 1996; Latham 1999; Murray and Illius 2000; Arsenault and Owen-Smith 2002; Focardi et al. 2006; Namgail et al. 2009). In this way the behavioral interactions between ungulates are important because are these interspecific interactions that causes alterations in behavior and consequently in populations, leading one species to use other foraging ground because their preferred has been impoverished by a competitor (Latham 1999).

Interspecific interactions may be particularly important between reintroduced species (Lovari et al. 2014), which need to adapt to new environments, as is the case of red and roe deer in the Lousã Mountain. However, the competition mechanisms resultant of these reintroductions have never been studied. The need to study the interspecific interactions between roe and red deer in Portugal was recently highlighted by Torres et al. (2015). Furthermore, Anciaux et al. (1991) suggested that the presence of red deer influences the use of habitat by roe deer because this last species is territorial and many times solitary (Dzięciołowski 1979). Moreover, roe deer may be intimidated by red deer because this species come together in herds and many times in artificially high densities when natural predators are absent (Latham 1999). In addition, there are studies that prove that reintroduction of *Cervus elaphus* in Italy can affect the quality and quantity of food available to Apennine chamois (*Rupicapra pyrenaica ornata*) having negative effects in dynamic of its populations (Ferretti et al. 2015). Contrarily, Bartos et al. (2002) verified that the four sympatric species of cervids in Czech Republic, including the *Cervus elaphus* and the *Capreolus capreolus*, do not compete with each other.

In relation to wild ungulates, it has been suggested that the competition occurs between pairs of species in which at least one of them is alien (Putman 1996; Forsyth and Hickling 1998; Focardi et al. 2006; Ferretti et al. 2011; Ferretti and Lovari 2014). This happen because the species not had time to develop strategies that allowed them to coexist. The red and the roe deer lived in Lousã Mountain for over 200 years until their extinction. So, when red and roe deer were reintroduced in 1995/1996, the dispersion of resources as well as the availability of resources for both species was partially modified by man in comparison to those present when species coevolved (Ferretti et al. 2015). In turn, the majority of those changes in landscape promoted by anthropogenic pressures

can lead to the junction of the roe deer in the feeding areas of red deer, limiting the availability of food for roe deer (Lovari et al. 2014; Ferretti et al. 2015).

As so, it's necessary to evaluate which are the consequences of interspecific interactions in restored communities in ecosystems modified by man. This can have negative effects to the conservation of both species (Lovari et al. 2014) since that coevolved species can compete relatively to the level of modification of native biological diversity (Ferretti et al. 2015). However, the competition is decreased through the morphophysiological differences between species which will lead to differences in energetic requirements and consequently to different preferences in relation to habitat use (Richard et al. 2014) as well as feeding behavior (Bell 1970; Jarman 1974; Demment and Van Soest 1985; Owen-Smith 1985; Illius and Gordon 1987; Owen-Smith 1989; Prins and Olff 1998).

Although the interspecific competition is more likely to occur during dormant season (in this case in dry season - summer), because the availability of food of high quality is lower, this can be minimized due to facilitation phenomena. For instance, the biggest species can beneficiate the smaller species through their grazing during the season of vegetation growth, improving the forage quality as well as facilitate the access to the resources through the removal of occlusive structures of grass. This can improve the reproductive success. Contrarily, it can led to a reduction of food quantity available for the populations during the dormant season, which can lead to the increase of mortality (Arsenault and Owen-Smith 2002).

Thus, the consequences at the population level cannot be seen only in a specific season of the year. These consequences will be dependent on trade-offs between competition and facilitation, highlighting the importance of the study being performed seasonally, since what is verified in one season may not be what happen in next season. Although competition and facilitation may have consequences in grazing efficiency in short-time, their effects in population dynamic can be masked through seasonal trade-offs and spatial location. The result will depend on what happen during annual cycle. However, the facilitation, namely of feeding during growing season, can promote the coexistence of herbivores species through the improvement of the exploitation competition that occur during dormant season (Arsenault and Owen-Smith 2002).

Since that roe deer is increasing their range through the Europe as well the situations in which they occur in sympatry with red deer (Gill 1990), it's crucial to study the interspecific interactions between these species since there is evidences that roe deer is susceptible to compete with other ungulate species, being displaced or out-competed, evidencing the priority of this study (Latham 1999). There are other studies that evaluate the habitat use (e.g. Prokešová et al. 2006; Borkowski and Ukalska 2008; Borkowski 2004; San José et al. 1997; Heurich et al. 2015) and the feeding behavior (e.g. Latham 1999) of both species but not in same context. Thus, this study of both habitat use and feeding behavior is crucial to the management and the conservation of

both species. The results are expected to evidence to what extent both species are using the same ecological resources and what consequences may occur as consequence. As so, the main goal of this study is to evaluate the ecological resources seasonally used by red and roe deer. Based on fecal pellet group counts through line transects with distance sampling we expect to identify the patterns of habitat use by each species. Furthermore, using the microhistological technique we expect to identify the species of plants that were consumed by red and roe deer.

Based on red deer habitat preferences evidenced in previous studies (Koubek and Zima 1999; Prokešová et al. 2006; Alves et al. 2014), it is expected that red deer preferably use shrublands and areas with high plant heterogeneity with big and diverse herb layer, representing areas with high food availability, like shrublands. However, due to the hunting pressure to which red deer is exposed in the study area, is expected that red deer tends to avoid settlements. In this way, is expected that the red deer diet is mainly constituted by shrub species but also by herbaceous and arboreous species, given that red deer is considered an intermediate feeder (Hofmann 1989; Ferreira 2004; Dumont et al. 2005; Cortez 2010).

Regarding to roe deer habitat preferences, it is expected that it positively uses forests whose herb layer is dominated by brambles, but also agricultural areas given their adaptability to agricultural landscapes (Andersen et al. 1998; Danilkin 1996; Sempéré et al. 1996). Based on their feeding strategy, it is expected that roe deer feed selectively and preferably on leaves and sprouts of dicotyledon species, since these species have low fiber content, but also on brambles given their nutritional value (Prokešová et al. 2006) and high abundance in the habitats used by roe deer. Since it is assumed that browsers are obligatorily non-grazers (Wieren 1996; Clauss et al. 2003), avoiding grasses with high fiber contents in comparison to grazers, preference by plants with less fiber content (forbs and leaves of trees and shrubs) (Storms et al. 2008) is also expected.

Furthermore, it is also expected that in periods with low food resources available, each species will become less selective. This is based on the optimal foraging theory, in which in periods with low availability of food the animals become less selective (Schoener 1971; Owen-Smith and Novellie 1982). Since it's know that in growing season the plants have lower fiber contents that increases in lean season (summer, in this case) (González-Hernández and Silva-Pando 1999) because plants become senescent. Consequently, it's expected that the diets of both red and roe deer present higher proportions of fibrous forage in summer because is this season that the quality and availability of food is lower (Dzieciolowski 1969; Bobek 1977).

2.2 Materials and methods

2.2.1   Study area and study species

The study took place in Lousã Mountain (40° 3'N, 8° 15'W) which presents a Mediterranean climate (Archibold 1995). Is mainly constituted by mixed forests but also by large areas of shrublands (Alves 2013; Alves et al. 2014). Outside the mountain region has a greater human presence with small villages and agricultural areas (Alves 2013). The presence of red deer (*Cervus elaphus*, Linnaeus, 1758) and roe deer (*Capreolus capreolus*, Linnaeus, 1758) in the study area is the result of reintroduction programs (Salazar 2009).

Besides the studied species, red and roe deer, wild boar is also present in the study area. In terms of predation, no natural predators are present, so both species are mainly preyed by feral dogs and foxes. Another important stressor is the anthropogenic pressure, mainly related to game hunting to which both species are exposed (Alves 2013).

2.2.2   Field methods

To study the habitat use of red and roe deer, fecal pellet counts through line transects with distance sampling were done. This method has been adapted from Mayle et al. (1999) and Marques et al. (2001). The term "distance sampling" is based on the fact that is necessary to register all perpendicular distances from the center of excrements until to the center of transect line (Mayle et al. 1999). For this, the study area (3500 ha) was divided into 35 quadrants which contained 70 transects each with 100 meters. The transects were randomly marked in the study area, to avoid a relation between the line transect and the cervids distribution across the study areas (avoiding the occurrence of attraction or avoidance to the line) (Mayle et al. 1999). The study area was centered in the municipal hunting area of Vila Nova, Miranda do Corvo (Fig.5).
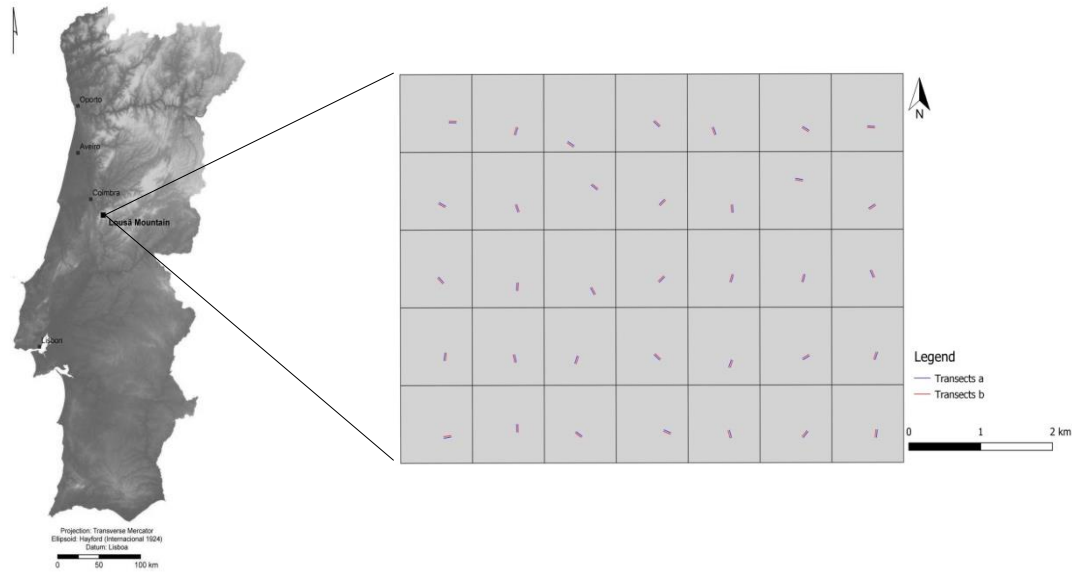
Fig 5: Map of the study area with the line transects of fecal pellet counts.

The study was performed seasonally starting in November 2016 until December 2017. A GPS (hTC with ArcPad) with the region map was used to reach to the tip of each transect that indicated, apart from the location, their direction through the indication of the angle that has been introduced in compass. 70 transects with 100 meters in length and a maximum width of 5 meters were done. Transects has been delimited with a tape measure. In each transect one person walked close to the line, i.e. in center of transect, and the other person walked in zigzag, distancing itself a maximum of five meters from center of the transect for both sides of tape. Along the transects, all feces found were registered together with the identification of transect, species, perpendicular distance to the line transect, linear distance from the starting point, age-class of excrements (i.e. fresh, old or very old) and size (number of pellets).

With line transects with distance sampling it was intended to understand the influence of several habitat variables on the habitat used by red and roe deer in the Lousã Mountain, considering the combination between topographic variables and land cover. These variables were land cover, proximity to areas more urbanized (artificial surfaces), proximity to agricultural areas, presence of water bodies and altitude. The inclusion of the variables proximity to areas more urbanized, proximity to agricultural areas and presence of water bodies it's based on the possibility that those variables influence the red and roe deer distribution as well as the availability of resources and their safety (Alves et al. 2014). In case of the variable altitude this was also considered because have influence on land cover, so affecting the growth of plants consumed by red and roe deer (Stage and Salas 2007).

Regarding land cover, despite the stratification performed using QGIS, the habitat characterization along the transects was also made in the field, together with the collection of the other environmental variables previously defined. Thus, the study area

was divided into six different land cover units, being them shrublands, coniferous forests, broadleaf forests, mixed forests, eucalyptus forests and agricultural areas, which may be subdivided into open areas (feeding) and closed areas (protection) (Alves et al. 2014).

2.2.3   Feces collection and microhistological analysis

To obtain the epidermis of plants that were consumed by red and roe deer, the feces of both species were collected simultaneously to the realization of the line transects. Each fecal sample was constituted just by the fresh pellets.. Then, each fecal pellet group was stored in a plastic bag properly labeled. The fecal samples were frozen in laboratory at -20°C. This fecal material collection and subsequent analysis will allow to determine the diet of each deer species.

The microhistological technique applied to the analysis of diet composition of red and roe deer was done following the technique described by Sparks and Malechek (1968). In this way, after defrost fecal samples five pellets were selected and to these 400ml of water was added and putted into an electrical blender, for mixing by applying three pulses of ten seconds each (Sanders et al. 1980; Vavra and Holechek 1980; Holechek and Vavra 1981; de Jong et al. 1995; Maia et al. 2003; Szemethy et al. 2003). This automatic maceration allow epidermis to easily separate itself from the other tissues, and makes the fragments as homogeneous as possible in terms of size and their distribution in the prepared mixture (Maia et al. 2003). After, the mixture was washed through a sieve with a 0.075mm of mesh, to discard all the fragments smaller and residuals, since the minimal dimension of epidermis that allow their identification is $1mm^2$ (Maia et al. 2003).

Afterwards, the prepared was putted in a Petri dish with sodium hypochlorite to facilitate the observation and identification of epidermis, since this chemical compound help to lighten the epidermis (Butet 1985; Maia et al. 2003). In order to obtain random microscope slides, the Petri dish was placed on a matrix duly identified with numbers and letters and with a pipette the mixture sample was selected through a random algorithm (de Jong et al. 1995; Maia et al. 2003; Garcia 2016). Hereinafter, 20 microscopic slides were prepared for each sample, identifying ten fragments in each, originating a total of 200 plants fragments per sample (Garcia 2016). To avoid duplicate fragments, the slides were observed from one side to the other along the microscopic slide through alternate and systematic transects (de Jong et al. 1995; Maia et al. 2003; Shrestha and Wegge 2006). The observations as well as the photographs of plants fragments were made using an amplification of 100x and 400x using the Optika Vision Pro program.

Finally, the identification of epidermic fragments of plants preserved in fecal samples was made through comparison with the reference collection of epidermis and using a dichotomous key, both elaborated by Garcia (2016). Currently this collection

has 50 species of plants, including arboreous, shrub and herbaceous species (dicotyledons and monocotyledons) (Garcia 2016).

The plant's epidermis are constituted by common epidermic cells and by specialized epidermic cells, such as stomata and trichomes (Ferri 1999; Erickson et al. 2003; Toral et al. 2010; Oliveira 2013). These cells can varied in form, number, size, organization, presence/absence and position in different structures of plants as well as in different plant species (Sparks and Malechek 1968; Sanders et al. 1980; Holechek and Gross 1982; Fahn 1990; Butet 1985; Giuletti et al. 1992; Adulyanukosol and Poovachiranon 2003; Erickson et al. 2003; Barclay et al. 2007; Ahmed and Chandan 2015). Thus, and by comparison with the reference collection, the different plant structures consumed by red and roe deer were identified. Several characteristics were taken into account to enable the identification like the form of common epidermic cells (e.g. rectangular, polygonal and in puzzle); presence/absence, position and type of stomata (e.g. anomocytic and paracytic) and the presence/absence, size and form of trichomes (e.g. tector and starry trichomes). Both stomata and trichomes, when present, are indispensable to identify the epidermic fragments (Garcia 2016).

Based on the use of these individual and morphologic characteristics of epidermis as discriminating characteristics, it's possible to use the reference collection of epidermis and the dichotomous key to identify the epidermic fragments preserved in fecal samples (Garcia 2016).

Only fragments of plants with appropriate dimensions (equal or higher than four cells) and with sufficient discriminating characteristics were considered (Bauer et al. 2005; Oliveira 2013). The epidermic fragments identified were classified according to the structure of plant (leaf, stem, sprout, flower or fruit) and according to the plant group, i.e. in arboreous species, shrubs, herbaceous (dicotyledons and monocotyledons) and agricultural species. This allow to determinate the importance that each plant group and structure have in the diet of these deer species.

2.2.4 Data analysis

Regarding the habitat used by both species, a spatial representation of the number of pellets count in each quadrant of the study area was performed. Beside the pellets counts, the maps present the different habitat types of the study area: forests, shrublands, sparse vegetation areas, agricultural areas, water bodies and artificial surfaces, that correspond to the human settlements. Maps with the total number of pellets of each species and the number of species per season were made for red and roe deer. All maps were performed in QGIS 3.2.1 software.

Furthermore, the spatial overlap was evaluated using the symmetric niche overlap coefficient. The Pianka's index (Pianka 1973) is given by:

$$\Phi = \frac{\sum_{j=1}^{p} \overline{p}_J \, \overline{q}_J}{\sqrt{\sum_{j=1}^{p} \overline{p_J}^2 \sum_{j=1}^{p} \overline{q_J}^2}}$$

where $\overline{p}_j = 1/n \sum_{i=1}^{n} pij$ is the mean proportion of feces in quadrant j^{th} of roe deer and $\overline{q}_J = 1/n \sum_{i=1}^{n} qij$ is the mean proportion of feces in quadrant j^{th} of red deer. The Pianka's index varies between 0 (no spatial resources used in common) to 1 (complete overlap of spatial resource use).

Regarding feeding behavior, and aiming to quantify the diet of both species, the absolute frequency of occurrence (AF) and the relative frequency of occurrence (RF) of each plant species consumed for each type (arboreous, shrub, herbaceous and agricultural species), structure of plant (leaf, stem, sprout, flower and fruit), season and species was calculated.

Those frequencies were calculated according to following formulas:

$$AF = (n_i/N_f) \times 100$$
$$RF = (n_{ei}/N_e) \times 100$$

where n_i is the number of epidermic fragments of the species i, N_f is the total number of fragments of the sample, n_{ei} is the number of feceswith the epidermic fragments of the species i and N_e is the total number of feces (Oliveira 2013; Garcia 2016).

To evaluate the differences between the diet composition of red and roe deer as well as of the other relevant factors, such as the season, a multivariate analysis was used. This approach was used because have the capacity to detect and represent the adjacent structure of the data relating this same structure with the explanatory variables, having the capacity to discriminate the different groups. The analysis was composed by the PCA - Principal Component Analyses (ordination method) (Lepš and Šmilauer 2003), and by a permutation multivariate analysis of variance (PERMANOVA). These statistical analyses were realized using Canoco 5 and Primer 6+PERMANOVA software.

The diversity of plants species present in red and roe deer diet was evaluated through the calculation of species richness (S) (number of different species that are present in the sample), Shannon-Weaver diversity index (H') (predict the sample diversity being the measure of the number of common species (Brewer and Williamson 1994)) (Shannon 2001; Spellerberg and Fedor 2003) and the Pielou's evenness index (J') (represent the uniformity of data) (Pielou 1966).

The Shannon-Weaver diversity index is given by:

$$H' = -\sum p_i \times \ln(p_i)$$

where $p_i = n_i/N_f$ being n_i the number of epidermic fragments of species i and N_f the total number of fragments of the sample.

The Pielou's evenness index is given by:

$$J' = H'/H'_{max}$$

where $H'_{max} = \ln(S)$.

Through the transformation of the Shannon-Weaver diversity index (H') was possible to interpret the food amplitude ($e^{H'}$) in order to represent the effective number of species of plants, according to Jost (2006).

The statistical differences between red and roe deer in terms of richness, evenness, diversity and food amplitude (dependent variables) along the several seasons were analyzed using generalized linear models (GLM). Pairwise comparisons were performed using the Boferroni correction. The statistical analyses were performed using the program IBM.SPSS version 23. The statistical analyses were considered significant when $p < 0.05$. The results are presented as estimated mean ± SE (standard error).

In addition, was evaluated the food overlap using the symmetric niche overlap coefficient- Pianka's index (Pianka 1973). Is given by:

$$\Phi = \frac{\sum_{j=1}^{p} \bar{p}_J \, \bar{q}_J}{\sqrt{\sum_{j=1}^{p} \overline{p_J}^2 \sum_{j=1}^{p} \overline{q_J}^2}}$$

where $\bar{p}_J = 1/n \sum_{i=1}^{n} pij$ is the mean proportion of food item j^{th} of roe deer and $\bar{q}_J = 1/n \sum_{i=1}^{n} qij$ is the mean proportion of food item j^{th} of red deer. The Pianka's index varies between 0 (no food resources used in common) to 1 (complete overlap of food resource use).

2.3 Results

2.3.1 Habitat use

At a general level, our results showed that the red deer was present throughout the study area, since pellet counts for each habitat type were recorded in all habitat types considering all seasons (mixed forests=827 pellets, shrublands=626 pellets, coniferous forests=115 pellets, agricultural areas=92 pellets and eucalyptus forests=14 pellets). However, the higher densities of red deer feces were found in ecotone zones between forests and shrublands that correspond to areas in higher altitudes, far from urbanized areas (artificial surfaces) and agricultural lands (Fig. 6).
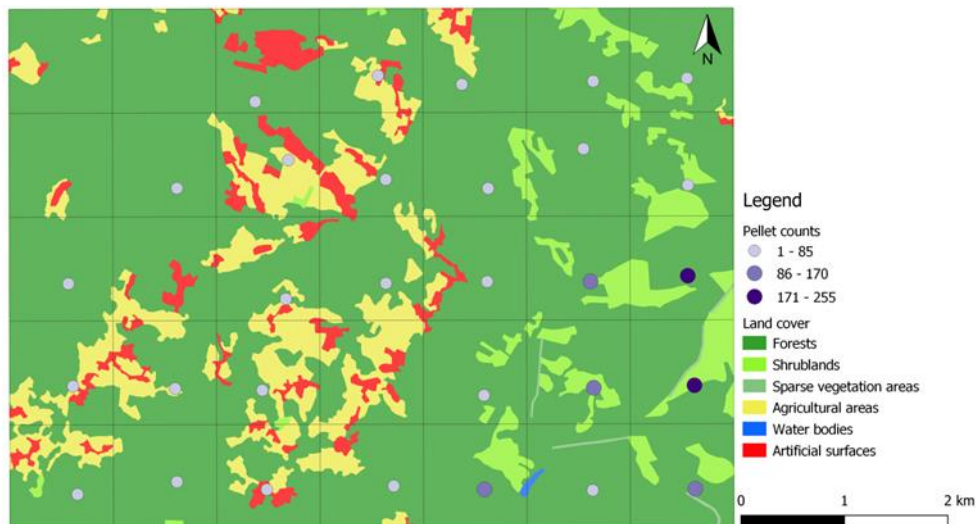
Fig 6: Map of the pellet counts of red deer in each quadrant of the study area throughout the year.

Regarding each season, in winter (Fig. 7a) the presence of red deer was higher in mixed forests (258 pellets) and in shrublands (166 pellets). The presence of red deer in coniferous forests was low (46 pellets) but not as low as in agricultural areas (13 pellets) and eucalyptus forest (1 pellets). As in the winter, in spring (Fig. 7b) the higher values of red deer pellet counts were found in mixed forests (147 pellets) and shrublands (116 pellets), being lower in coniferous forests (25 pellets), agricultural areas (6 pellets) and eucalyptus forests (3 pellets).

The pattern verified in previous seasons was also verified in summer (Fig. 7c), where the presence of red deer was higher in mixed forests (187 pellets) and shrublands (126 pellets). In contrast to winter and spring, in summer the values of pellet counts of red deer were higher in agricultural areas (34 pellets) than in coniferous forests (19 pellets). The lower value continued to be found in eucalyptus forests (3 pellets). In comparison with spring, in this season there was a significantly reduction of the density of pellet counts of red deer in the transects close to the sparse vegetation areas (Fig. 7c). Autumn was also similar to summer, with higher values in mixed forests (235 pellets) followed by shrublands (218 pellets). As verified in summer, in autumn the presence of red deer continued higher in agricultural areas (39 pellets) than in coniferous forests (25 pellets), and very low in eucalyptus forests (7 pellets). In this season, the density of pellet counts of red deer in the transects close to the sparse vegetation areas increased (Fig. 7d).

Fig 7: Map of the pellet counts of red deer in each quadrant of the study area in a) winter, b) spring, c) summer and d) autumn.

The presence of roe deer, in opposition to the one of red deer, was higher in the areas with lower altitudes, with a preference for forest areas close to the agricultural lands (ecotone zones) and urbanized areas throughout the year (Fig. 8). Contrarily to red deer, no roe deer feces were found in shrublands (Fig. 8). So, the pellet counts of roe deer by each habitat type was 128 pellets in mixed forests; 106 pellets in agricultural areas; 5 pellets in eucalyptus forests and 0 pellets in coniferous forests and shrublands.
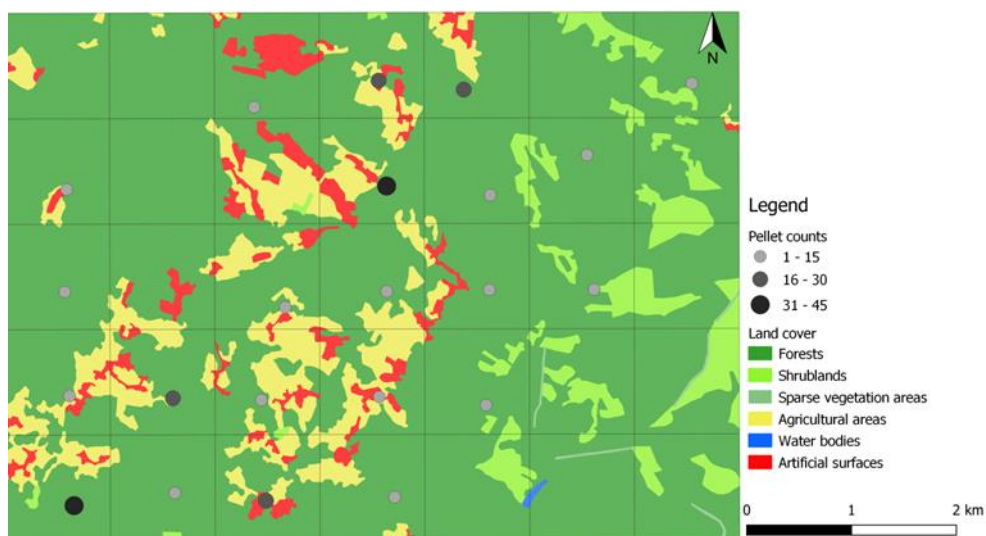
Fig 8: Map of the pellet counts of roe deer in each quadrant of the study area throughout the year.

In winter (Fig. 9a) the presence of roe deer was just verified in agricultural areas (39 pellets) and in mixed forests (26 pellets). The winter was the only case in which the presence of roe deer in agricultural areas was higher than in mixed forests. In spring (Fig. 9b) the pattern of pellet counts of roe deer by each habitat type was similar to winter, in which were just found pellets of roe deer in mixed forests (29 pellets) and in agricultural areas (11 pellets). As in red deer in spring, the value of pellet counts of roe deer in agricultural areas in spring reduced more than half in comparison with winter. In summer (Fig. 9c), the presence of roe deer increased in agricultural areas (16 pellets) and was similar to the presence of roe deer in mixed forests (18 pellets). Only in this season were found roe deer feces in eucalyptus forests (5 pellets). The autumn (Fig. 9d), in comparison with previous seasons, was the season with the highest values of pellet counts of roe deer by each habitat type (mixed forests=55 pellets, agricultural areas=40 pellets), being this last value very similar to the value of pellet counts of roe deer found in agricultural areas in winter (39 pellets).
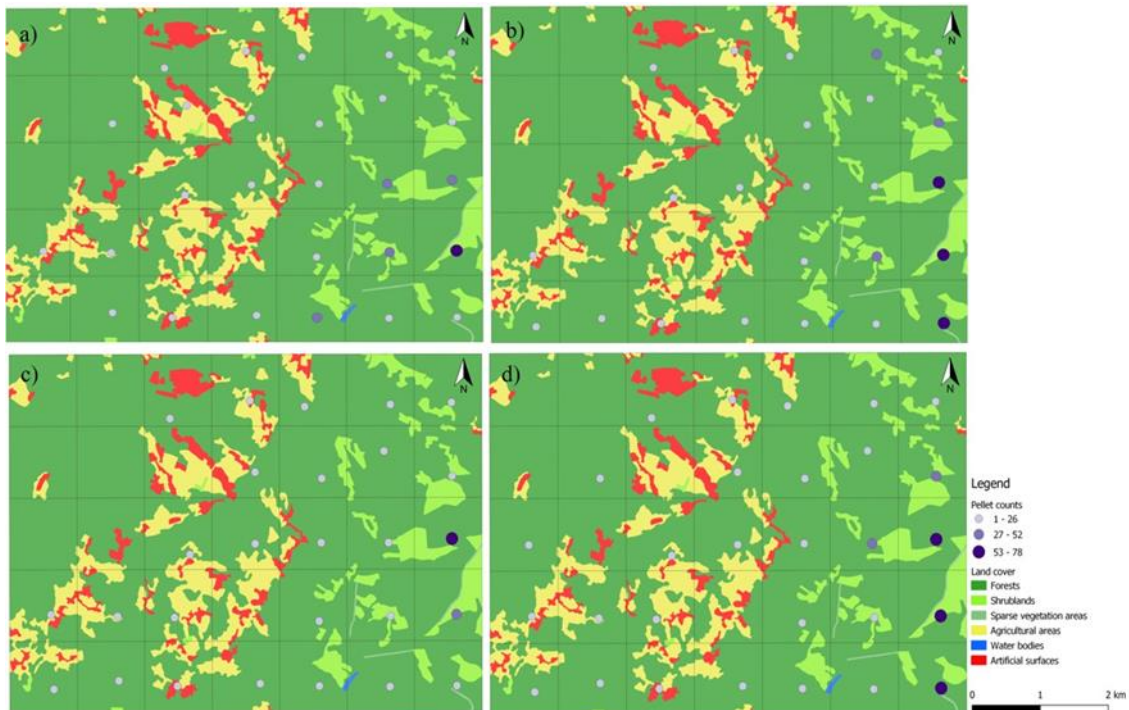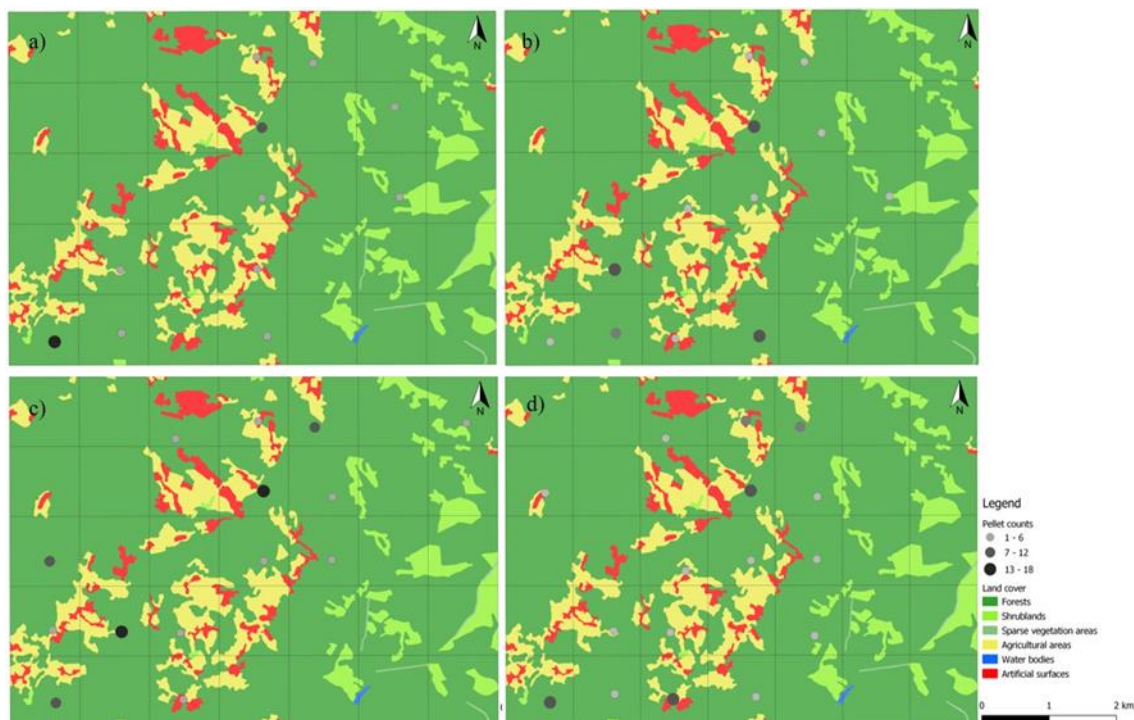

Fig 9: Map of the pellet counts of roe deer in each quadrant of the study area in a) winter, b) spring, c) summer and d) autumn.

Analyzing the results from the Pianka's index (Table 1), the spatial overlap of resources used by red and roe deer was very low. Our results demonstrated that in winter the spatial overlap between red and roe deer is the lowest, having started to increase in the following seasons.

Table 1: Pianka's index representing spatial overlap between red and roe deer.

|	Pianka's index	Confidence interval
Winter	0.066	0.007-0.125
Spring	0.147	0.088-0.206
Summer	0.221	0.162-0.280
Autumn	0.256	0.197-0.315
Global	0.211	0.152-0.270

2.3.2   Feeding behavior

The absolute and relative frequencies of occurrence were calculated for the red deer (Table 2) and for roe deer (Table 3) by each season.

In case of red deer, in all seasons shrub species were the most consumed group of plants (winter: 59.22%; spring: 72.92%; summer: 67.85%; autumn: 62.61%) followed by the monocotyledons (winter: 19.21%; spring: 14.77%; summer: 12.91%; autumn: 18.27%), arboreous (winter: 11.17%; spring: 7.39%; summer: 11.11%; autumn: 10.39%) and dicotyledons species (winter: 7.06%; spring: 1.73%; summer: 5.20%; autumn: 7.14%). In all seasons, the most representative shrub species was *Pterospartum tridentatum* with the exception of spring in which was *Ulex minor* (28.26%). In the case of monocotyledons species, *Arrhenatherum elatius* was the most representative species in all seasons, except in winter that was *Festuca* sp. (12.52%). Regarding to arboreous species the most consumed species changed over the seasons: in winter was *Fraxinus* sp. (3.41%), in spring was *Castanea sativa* (2.00%), in summer was again *Fraxinus* sp. (2.97%) but also *Quercus robur* (2.95%) and in autumn was *Betula pubescens* (3.08%). Finally, in the group of dicotyledons species, *Athyrium filix-femina* was the most representative species in winter (3.51%) and summer (3.69%). In spring was *Trifolium* sp. (1.01%) and in autumn was *Lepidophorum repandum* (4.32%).

Table 2: Diet composition of red deer (N=61) per season in terms of absolute frequency of occurrence (AF) and relative frequency of occurrence (RF).

Red deer	Winter		Spring		Summer		Autumn	
	AF(%)	RF(%)	AF(%)	RF(%)	AF(%)	RF(%)	AF(%)	RF(%)
Arboreous species	**11.17**	**62.86**	**7.39**	**41.76**	**11.11**	**50.79**	**10.39**	**53.33**
Acacia melanoxylon	2.54	73.33	1.63	53.85	0.99	33.33	2.05	66.67
Betula pubescens	0.89	80.00	0.18	30.77	0.19	22.22	3.08	60.00
Castanea sativa	0.60	53.33	2.00	46.15	2.57	77.78	0.91	60.00
Chamaecyparis lawsoniana	0.67	66.67	0.41	30.77	1.12	55.56	0.90	53.33
Fraxinus sp.	3.41	73.33	1.70	46.15	2.97	66.67	1.27	66.67
Laurus nobilis	2.62	53.33	0.11	15.38	0.32	22.22	1.80	40.00
Quercus robur	0.44	40.00	1.36	69.23	2.95	77.78	0.38	26.67
Herbaceous species-Dicots	**7.06**	**40.00**	**1.73**	**36.54**	**5.20**	**41.67**	**7.14**	**46.67**
Athyrium filix-femina	3.51	66.67	0.55	61.54	3.69	88.89	2.33	73.33
Lepidophorum repandum	2.89	33.33	0.00	0.00	0.19	11.11	4.32	53.33
Pteridium aquilinum	0.18	26.67	0.17	23.08	1.22	50.00	0.27	40.00
Trifolium sp.	0.48	33.33	1.01	61.54	0.10	16.67	0.22	20.00
Herbaceous species-Monocots	**19.21**	**70.67**	**14.77**	**81.54**	**12.91**	**54.44**	**18.27**	**72.00**
Agrostis castellana	1.10	60.00	1.61	76.92	4.13	61.11	6.45	93.33
Arrhenatherum elatius	2.10	66.67	5.66	100.00	4.15	72.22	6.49	73.33
Dactylis glomerata	2.13	80.00	5.13	92.31	3.71	94.44	3.81	86.67
Festuca sp.	12.52	86.67	1.65	84.62	0.92	44.44	0.27	46.67
Graminae NI	1.36	60.00	0.72	53.85	0.00	0.00	1.25	60.00
Shrub species	**59.22**	**77.04**	**72.92**	**68.38**	**67.85**	**75.93**	**62.61**	**80.74**
Calluna vulgaris	5.83	86.67	0.14	23.08	2.08	66.67	3.10	73.33
Cytisus striatus	7.18	73.33	15.89	84.62	3.59	83.33	8.39	93.33
Erica arborea	4.79	86.67	6.67	92.31	4.34	83.33	4.99	86.67
Erica australis	8.12	93.33	1.42	69.23	9.87	83.33	4.31	86.67
Erica umbellata	3.59	73.33	1.27	84.62	1.68	83.33	2.60	80.00
Ilex aquifolium	2.24	66.67	0.04	7.69	0.13	22.22	0.62	53.33
Pterospartum tridentatum	17.60	60.00	13.91	92.31	25.33	88.89	23.21	93.33
Rubus ulmifolius	4.00	80.00	5.32	61.54	12.46	88.89	3.08	73.33
Ulex minor	5.87	73.33	28.26	100.00	8.37	83.33	12.31	86.67

Table 3: Diet composition of roe deer (N=35) per season in terms of absolute frequency of occurrence (AF) and relative frequency of occurrence (RF).

Roe deer	Winter		Spring		Summer		Autumn	
	AF(%)	RF(%)	AF(%)	RF(%)	AF(%)	RF(%)	AF(%)	RF(%)
Arboreous species	**19.86**	**68.57**	**54.87**	**71.43**	**52.20**	**50.00**	**37.31**	**78.10**
Acacia melanoxylon	1.00	46.67	0.29	33.33	2.81	100.00	2.49	80.00
Betula pubescens	1.29	80.00	0.47	33.33	0.22	50.00	12.71	100.00
Castanea sativa	1.10	66.67	20.52	100.00	0.44	50.00	3.10	86.67
Chamaecyparis lawsoniana	0.13	26.67	0.61	66.67	0.00	0.00	0.19	20.00
Fraxinus sp.	6.55	100.00	14.41	100.00	48.53	100.00	8.22	100.00
Laurus nobilis	8.99	93.33	0.45	66.67	0.20	50.00	7.43	80.00
Quercus robur	0.81	66.67	18.12	100.00	0.00	0.00	3.17	80.00
Herbaceous species-Dicots	**13.22**	**55.00**	**1.90**	**25.00**	**0.00**	**0.00**	**18.71**	**66.67**
Athyrium filix-femina	1.78	80.00	1.61	66.67	0.00	0.00	1.41	86.67
Lepidophorum repandum	10.94	86.67	0.00	0.00	0.00	0.00	13.34	93.33
Pteridium aquilinum	0.11	20.00	0.00	0.00	0.00	0.00	0.08	13.33
Trifolium sp.	0.40	33.33	0.29	33.33	0.00	0.00	3.88	73.33
Herbaceous species-Monocots	**34.20**	**38.67**	**2.20**	**26.67**	**3.32**	**20.00**	**4.75**	**56.00**
Agrostis castellana	0.15	26.67	0.00	0.00	0.00	0.00	0.22	40.00
Arrhenatherum elatius	0.02	6.67	0.14	33.33	0.00	0.00	0.11	20.00
Dactylis glomerata	0.42	33.33	0.81	33.33	0.22	50.00	1.14	80.00
Festuca sp.	32.20	100.00	1.25	66.67	3.10	50.00	2.81	73.33
Graminae NI	0.40	26.67	0.00	0.00	0.00	0.00	0.47	66.67
Shrub species	**27.75**	**57.78**	**38.63**	**55.56**	**43.21**	**61.11**	**35.65**	**65.19**
Calluna vulgaris	6.34	100.00	2.30	100.00	34.54	100.00	8.12	100.00
Cytisus striatus	0.24	33.33	0.47	33.33	0.22	50.00	0.24	33.33
Erica arborea	0.28	40.00	0.46	66.67	0.42	100.00	0.51	46.67
Erica australis	3.30	80.00	8.06	100.00	4.06	100.00	4.05	93.33
Erica umbellata	0.18	26.67	0.14	33.33	0.00	0.00	0.42	20.00
Ilex aquifolium	1.67	86.67	0.14	33.33	0.20	50.00	1.30	80.00
Pterospartum tridentatum	0.00	0.00	0.27	33.33	0.88	50.00	1.52	13.33
Rubus ulmifolius	14.96	100.00	26.78	100.00	2.88	100.00	11.85	100.00
Ulex minor	0.77	53.33	0.00	0.00	0.00	0.00	7.65	100.00

In the case of roe deer, the groups of plants that were more consumed varied according to the season. The monocotyledons was the most consumed group of plants in winter (34.20%) followed by shrub species (27.75%), arboreous species (19.86%) and dicotyledons species (13.22%). Spring and summer were similar, in which the most consumed group of plants was arboreous species (spring: 54.20%; summer: 52.20%) followed by shrub species (spring: 38.63%; summer: 43.21%), monocotyledons species (spring: 2.20%; summer: 3.32%) and by dicotyledons species (spring: 1.90%; summer: 0%). In autumn, the arboreous species was the most consumed group (37.31%) followed by shrub species (35.65%), dicotyledons species (18.71%) and by monocotyledons species (4.75%). In all seasons the most representative monocotyledon species was *Festuca* sp.. *Rubus ulmifolius* was the most consumed shrub species in all seasons, except in summer that was *Calluna vulgaris* (34.54%). In relation to arboreous species, in winter the most representative species was *Laurus nobilis* (8.99%), in spring was *Castanea sativa* (20.52%), *Fraxinus* sp. in summer (48.53%) and in autumn *Betula pubescens* (12.71%). Lastly, *Lepidophorum repandum* was the most representative dicotyledon species consumed in winter and autumn, while in spring was *Athyrium filix-femina* (1.61%) and in summer were not found dicotyledons species in the roe deer feces.

Our results showed significant differences between the species of deer (pseudo-$F_{(1,88)}$=13.796; p=0.001) in terms of diet composition. Considering the differences between the species, diet composition of red deer was significantly different from diet composition of roe deer for all seasons (winter: t=2.373; p=0.003, spring: t=2.442; p=0.006, summer: t=2.752; p=0.004, autumn: t=2.866; p=0.001). In the winter season, the species that contributed more to differentiate the diet composition of red and roe deer was *Pterospartum tridentatum* and *Festuca* sp. (Fig. 10). Is possible to observe that in spring, *Ulex minor* is of great importance for red deer diet and *Rubus ulmifolius* for roe deer (Fig. 10). In summer, *Pterospartum tridentatum* was again the most important plant species for red deer, followed by *Ulex minor*, whereas for roe deer was *Fraxinus* sp. (Fig. 10). In autumn, red deer consumed more *Pterospartum tridentatum*, *Arrhenatherum elatius* and *Cytisus striatus* whereas *Rubus ulmifolius* was the most important plant species for roe deer in this season (Fig. 10).

Regarding seasons, our results demonstrate significantly differences between the seasons (pseudo-$F_{(3,88)}$=5.456; p=0.001). The diet of red deer in winter was significantly different from the diet in spring (t=2.010; p=0.001) but not in summer (t=1.469; p=0.055) and autumn (t=1.272; p=0.127). In spring, the diet of red deer was significantly different from the diet in summer (t=2.469; p=0.001) and autumn (t=1.740; p=0.016). However, were not verified significant differences in the diet composition of red deer between summer and autumn (t=1.301; p=0.114). Regarding to diet composition of roe der was verified significant differences between all seasons, except between spring and summer (t=2.473; p=0.093).

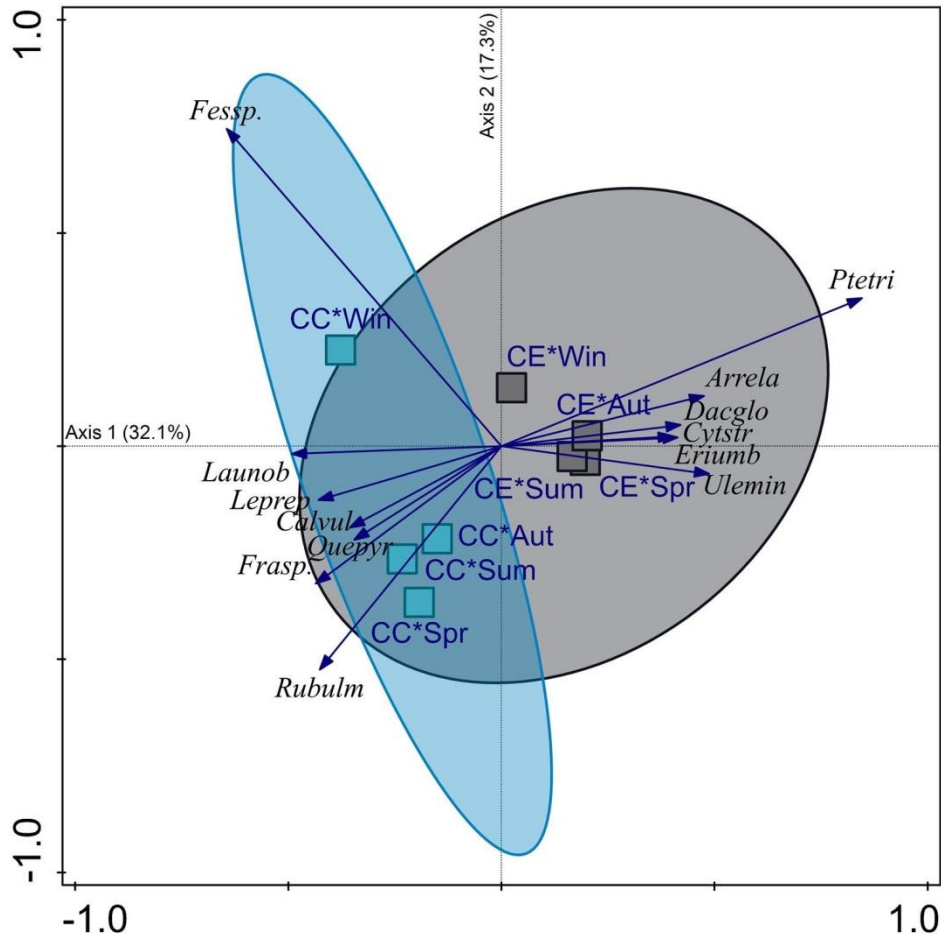Fig 10: PCA biplot for winter (Win), spring (Spr), summer (Sum) and autumn (Aut), showing the differences between the deer species. Grey squares represent red deer (N=61) and blue squares the roe deer (N=35).

Regarding the structures of plants (i.e. leaf, stem, sprout, fruit and flower) consumed by both deer species, in figures 11 and 12 is possible to observe plants structures consumed in each season (Fig. 11 and Fig. 12).
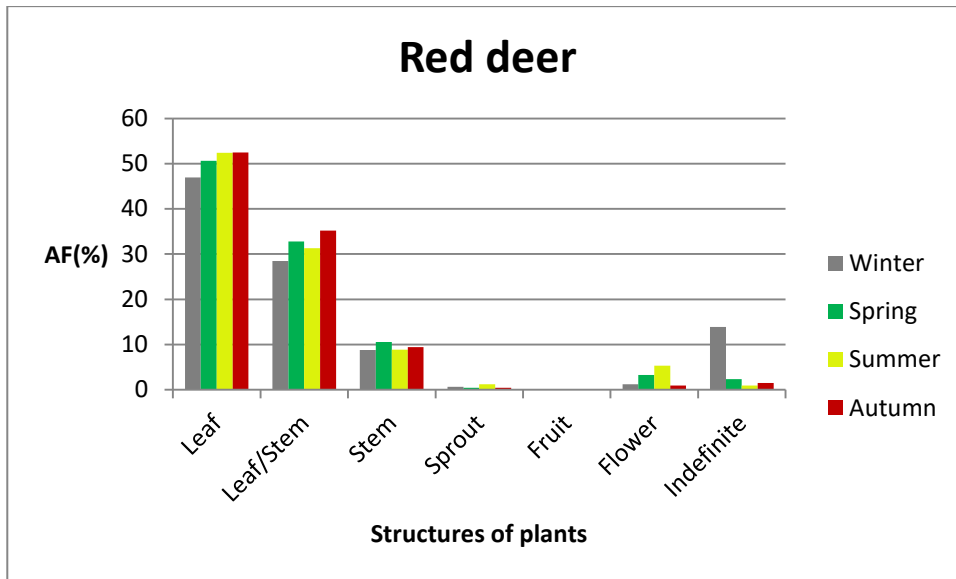
Fig 11: Absolute frequency of occurrence of the different structures of plants on the diet of red deer (N=61) in the different seasons.

Leaves of plants was the most consumed structure by red deer in all seasons reaching the higher value in summer and autumn (52.41% and 52.44%, respectively) (Fig.11). The second group of structures that was more consumed constituted the group named "Leaf/Stem", that correspond to the plants in which the epidermis of leaves and stems are similar. The values were similar in all seasons. Stem was little consumed in all seasons (winter: 8.78%; spring: 10.56%; summer: 8.89% and autumn: 9.41%) (Fig.11). The intake of sprout was vestigial (maximum 1.19% in summer) and the fruits did not arise in the red deer feces (Fig.11). Flowers were more consumed in spring and summer (3.25% and 5.29%, respectively) (Fig.11). The indefinite structure of plants corresponds to the monocotyledons species in which the structure of plant that was consumed isn't clear (e.g. *Festuca* sp. and Graminae NI). In this case, was in winter that this structure was more consumed (13.88%) (Fig.11).
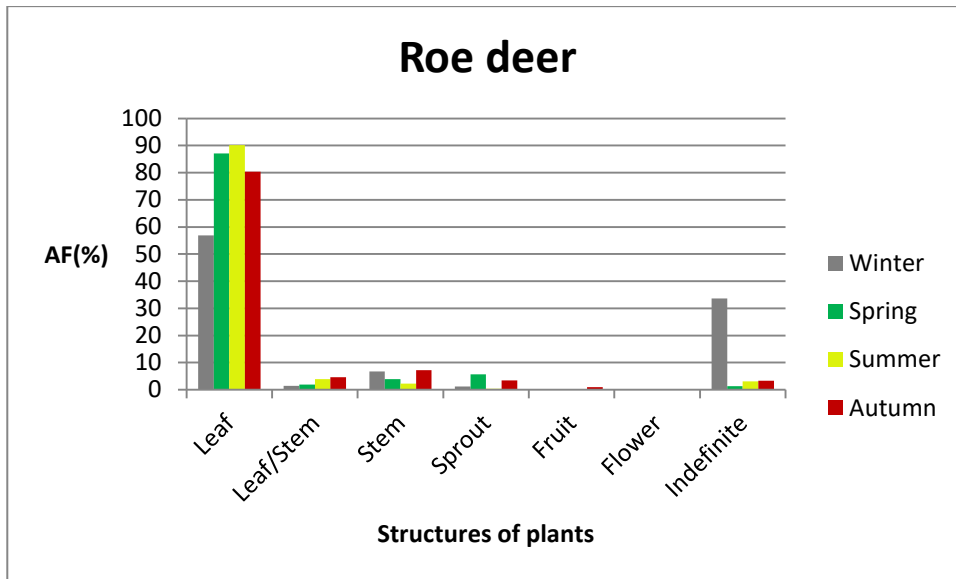
Fig 12: Absolute frequency of occurrence of the different structures of plants on the diet of roe deer (N=35) in the different seasons.

Regarding to roe deer, leaves were the structure that was more consumed in all seasons, having the higher value in the summer (Fig.12). In contrast to red deer, leaf/stem and stem were not highly consumed by roe deer (Fig.12). The sprouts were more consumed by roe deer than by red deer, except in summer (0.40% for roe deer) (Fig.12). Although the small value, in autumn the fruits occurred in roe deer feces (0.96%) (Fig.12). In the opposite to red deer, flowers epidermis did not appear in roe deer feces (Fig.12). The indefinite structures of monocotyledons species were more consumed in winter (33.60%) (Fig.12).

In relation to diet diversity analyzed by the species richness(S), Shannon-Weaver diversity index (H'), Pielou's evenness index (J') and by the food amplitude ($e^{H'}$), our results demonstrate significantly differences between seasons for all of them (S: p=0.003; H': p=0.002; J': p=0.004; $e^{H'}$: p=0.002). However, no significant differences between red and roe deer were found for all indexes of diversity (p>0.05).

Since the results for these indexes of diversity were similar, we opted for only present the food amplitude ($e^{H'}$) (Fig.13). In this case, the pairwise comparisons between seasons showed significantly differences between the food amplitude in autumn (9.17 ± 0.469) and spring (6.62 ±0.822) with p= 0.042, and between autumn (9.17 ± 0.469) and summer (5.97 ±0.956) with p=0.016 (Fig.13). Regarding food amplitude, no differences were found between species (p=0.085), nor in the interaction between species and seasons (p=0.071).
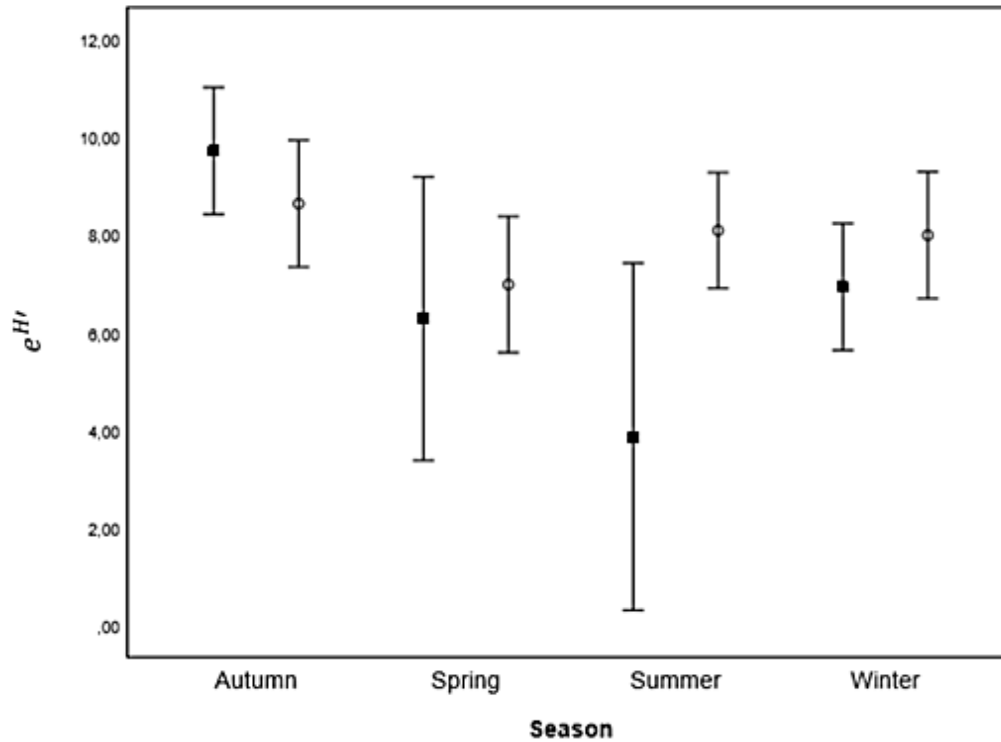
Fig 13: Mean food amplitude index by season between red deer (open circles, N=61) and roe deer (black squares, N=35).

Analyzing the food overlap using Pianka's index is possible to observe a low food overlap between deer species. Our results demonstrated that in winter and autumn the food overlap between red and roe deer was higher, decreasing in spring and summer.

Table 4: Pianka's index representing food overlap between red and roe deer.

	Pianka's index	Confidence interval
Winter	0.573	0.417-0.729
Spring	0.171	0.015-0.327
Summer	0.164	0.008-0.320
Autumn	0.404	0.248-0.560
Global	0.399	0.244-0.555

2.4 Discussion

2.4.1   Habitat use

Independently of the sampling season, red deer used preferentially ecotone zones between forests and shrublands at high altitudes, away from agricultural and urbanized areas. This was also reported by Alves et al. (2014) for Lousã Mountain and by Torres et al. (2014) in northeast Portugal, both for red deer. The same pattern was found in Czech Republic in winter, in which the distribution of red deer in monitoring plots situated away from fields distant to the villages, was higher than in plots close to the fields (Prokešová et al. 2006). Also in China was verified that red deer, subspecies *Cervus elaphus xanthopygus*, during winter occurred in habitats with mature mixed coniferous at higher elevations far from human settlements and croplands (Jiang et al. 2008).

Our results demonstrate the need of red deer to use habitats that provide simultaneously food, in quantity and quality, and some cover (Alves et al. 2014). As has been reported by Borkowski (2004) and Borkowski and Ukalska (2008) in Poland, the cover is the habitat requirement more important to large species, as is the case of red deer, than to smaller species like roe deer. For large species is more difficult to find an adequate cover than for small species. In this way, the differences between body sizes lead to differences in habitat requirements, and consequently lead to a differential habitat use by red and roe deer.

The use of ecotone zones reflects the necessity of red deer to use open areas (Alves et al. 2014). Furthermore, the use of areas in forest habitats close to the edge allow to maximize the gains and minimize the costs, allowing minimize the travel time between food and cover (Thomas and Taylor 2006). In addition, Alves et al. (2014) reported that near the edge in closed areas the understory became dense, providing adequate food linked to cover. Similar results were found in Czech Republic, where red deer preferred forest areas with dense cover and diversified shrub layer (Prokešová et al. 2006).

Contrarily to our results, in Alves et al. (2014) the results of pellet group counts and direct observations disclose that red deer used less mixed forests than coniferous forests. These two types of forests have a low (or even absence) understory (Alves et al. 2014) because the tree canopy is closed, increasing the competition for light, nutrients and water, affecting the ground layers and consequently the growth of shrubs (Nabuurs 1996), that are the main food resources for red deer (Garcia 2016). So, these forests cannot by itself satisfy entirely the red deer requirements (Alves et al. 2014), and consequently red deer used forests close to shrublands. The same explanation can be used for the low number of pellet counts of red deer in eucalyptus forests, being the understory absent in the majority of patches (Alves et al. 2014), and for that reason not having the adequate quality for red deer, resulting in its avoidance.

As reported by Alves et al. (2014), the fact that no pellet counts were found in broadleaf forests may be due to the small size of its patches and to the low abundance of

understory. These results demonstrate a selective use of available habitat by red deer according to land cover, water bodies, distance to ecotone zones, distance to agricultural areas and settlements and as well as topographic features like altitude. The topographic characteristics, such as altitude, influence the composition of the vegetation in terms of plant species and its size (Stage and Salas 2007). So, this can influence the distribution of the red deer, that prefer to use the spaces with the best climatic conditions allowing the intake of high quality of food (Alves et al. 2014).

In Mediterranean areas, the limiting period is the summer due its dry and hot weather which can lead to nutritional restrictions (Bugalho and Milne 2003). This fact can explain the increase of the number of red deer pellets in the summer in agricultural areas (low altitudes), since these areas can operate as complementary food source. Thus, in this season the availability of food in human-impacted areas may encourage the red deer to use these open areas (Zhang et al. 2013). Also, in southern Spain throughout most of the summer, red deer selected low altitudes (San José et al. 1997). The reverse pattern was found in Helan Mountains, China for a subspecies of red deer (*Cervus elaphus alxaicus*), in which red deer preferred open areas in winter and spring but not in summer and autumn (Zhang et al. 2013). This is because in this region the limiting period is not the summer but the winter (low precipitation) (Zhang et al. 2013).

In summer was also verified a reduction in densities of pellets counts in the transects close to the sparse vegetation areas. These areas correspond to the firebreaks in the high altitudes of the study area, so these areas do not have adequate food nor thermal cover (Peek et al. 1982) for red deer in this season, so these areas became less used by red deer in comparison with spring or autumn. Red deer in Tapada Nacional de Mafra (Portugal) during summer uses more the shrublands and cork oak stands, proving their necessity for areas with low sun exposure and low temperatures (Macedo 2015).

In autumn was verified a higher red deer presence in agricultural areas. These pellet counts found in lower altitudes close to the agricultural areas may correspond to the males of red deer (Alves et al. 2014). Consequently, after rut season, males segregate from females and choose to move to higher quality patches to recover from the physical condition lost in the previous month. In opposition, females prefer to continuing using habitats located in high altitudes close to the ecotone zones and water bodies, due to their new condition that requires more safety, the pregnancy (Alves et al. 2014).

Contrarily to the red deer, the presence of roe deer was higher in low altitudinal areas, mainly in forest areas close to the agricultural lands (ecotone zones) and urbanized areas. These results can be explain once again by the combination of food and cover that determines the habitat attractiveness (Borkowski and Ukalska 2008). Since roe deer is smaller than red deer, they can satisfy more easily their requirements of cover (Borkowski 2004; Borkowski and Ukalska 2008), resulting in the higher use of areas with human presence. Similar results was found by Torres et al. (2012b) for roe deer in Norway and by Heurich et al. (2015) for roe deer in the Bohemian Forest Ecosystem, situated along the border between Bavaria(Germany), the Czech Republic

and Austria. The greater tolerance of roe deer to the proximity to humans at low altitudinal areas was also verified by Jiang et al. (2008) for *Capreolus pygargus bedfordi* in China.

Contrarily to red deer, no roe deer feces were found in shrublands. Our results evidenced that red deer is present in all habitats even in the ones with higher density of roe deer, but the opposite does not happen, and roe deer avoid the areas where the red deer density is higher. This evidence a level of spatial segregation between both species, and previous verified by Wildash (1951). The occurrence of roe deer in areas with low red deer presence was also highlighted in various studies (e.g. Aragón et al. 1995; Tellería and Virgós 1997; Virgós and Tellería 1998; Torres et al. 2011, 2012a, 2012b).

Roe deer is a concentrate feeder (Tixier and Duncan 1996) with low body reserves (income breeder) (Jönsson 1997) depending on immediate energy acquisition for reproduction (Richard et al. 2014) through frequent and regular food intakes (Dupke et al. 2017) in comparison with red deer (capital breeder) (Jönsson 1997) that has the capacity of storing energy for reproduction through body reserves construction (Stearns 1992; Festa-Bianchet et al. 1998), having the ability of use the stored energy to raise their young (Dupke et al. 2017). This implies that roe deer have the necessity to use constantly habitats that simultaneously have food and cover in the same area in order to increase the intake of food with high quality and simultaneously have cover in the proximity to these feeding areas, to minimize the travels between feeding areas and covers (thermal and hiding covers) (Peek et al. 1982). This is possible using ecotone zones between forests and agricultural areas.

In fact, the use of areas close to the settlements and ecotone zones between forests and agricultural areas maximize the food intake of roe deer. This positive correlation can be related with soil fertility since human settlements are generally situated close to naturally fertile soils or fertilized soils (Pautasso 2007). In this way the agricultural lands provide extra sources with high-quality forage (Torres et al. 2012b). Furthermore the forests edges close to the agricultural areas have a high diversity of plant species, being an alternative food resource to the scarcity of preferred food resources, providing simultaneously hiding cover in close proximity (Torres et al. 2012b). Thus edges provide good diversity of food resources and as well adequate cover for roe deer (Torres et al. 2012b). This attractiveness of areas close to the forest edges was also verified by Mysterud and Ostbye (1999).

Winter was the single season in which the presence of roe deer in agricultural areas was higher than in mixed forests. In winter, the availability of vegetative parts (leaves) of deciduous trees, shrubs and annual plants is low (Faria 1999), which are the most important plant structure for roe deer diet. So, roe deer needs to find complementary food resources mainly in agricultural areas (Torres et al. 2012b). In addition, in the opposite to red deer, the winter fat reserves of roe deer are small and the food availability is the mainly source of winter energy (Holand et al. 1998), so the

winter habitat used by roe deer is more influenced by food supply than in the case for red deer (Borkowski and Ukalska 2008).

As for red deer, in spring the number of roe deer pellets in agricultural areas reduced more than half in comparison with winter. The spring is the period of vegetative growth, in which occurs the sprouting and flowering of different plant species, increasing the food availability. In this period, the majority of plant species are available and presenting green leaves (Faria 1999). Consequently, red and roe deer do not need so much of find food resources in agricultural areas because in spring the plant's availability is no longer limiting factor (Faria 1999).

In summer, the presence of roe deer increased in agricultural areas. In this season, the herbaceous (Bugalho and Milne 2003) and grass species become senescent due to hydric stress (Leite et al. 1997). The majority of leaves become dry (Faria 1999) and of poor quality, so the roe der needs to find some alternative food resources, mainly in agricultural areas (Torres et al. 2012b). Also, in Spain the roe deer selected the more productive patches (e.g. pastures) in summer (Virgós and Tellería 1998), and large agricultural patches were also important in the expansion process of roe deer across the Iberian Mountains in Spain (Acevedo et al. 2005).

Roe deer feces in eucalyptus forests were only found in the summer. As mentioned for red deer, the understory of eucalyptus forests is practically absence in the majority of patches (Alves et al. 2014), not having the adequate food availability and quality, resulting in its avoidance. However, it can operate as complementary thermal cover (Peek et al. 1982) in this dry and hot season for roe deer, and it may be the reason why roe deer feces were only found in eucalyptus forests in the summer.

In the autumn, the number of roe deer pellets in agricultural areas was very similar to winter. In autumn, the majority of plants have dry leaves, although some plants still have some green leaves such as *Rubus* sp. (Faria 1999). The availability in this season in terms of quality of vegetative parts of plants is low, but in opposition occurs the increase in the availability of dried fruit (e.g. chestnuts and acorns), that are rich in amide and minerals, being an important energy source (Faria 1999). This makes the agricultural areas even more attractive for roe deer during autumn and winter.

Regarding to spatial overlap between red and roe deer, the overlap between deer species was very low. This result also visible in the maps of the number of pellets of each deer species, in which is possible to observed a marked spatial segregation between red and roe deer. Roe deer was mainly present at the lowest elevations with high human presence mainly in ecotone zones between forests and agricultural areas, whereas red deer selected the highest elevations in ecotone zones between forests and shrublands away from settlements and agricultural areas. These results were also verified by Jiang et al. (2008) in China for *Cervus elaphus xanthopygus* and for *Capreolus pygargus bedfordi.* Since vegetation cover varies with altitude, the habitat use of red and roe deer reflects these altitudinal differences, whereas red deer mainly used shrublands that are abundant in high altitudes, and roe deer mainly used vegetation

types that are present in low altitudes. Thus, these differences in the altitudinal ranges used by red and roe deer allow the habitat segregation of deer species and consequently their coexistence (Jiang et al. 2008).

Our findings are in agreement to what was expected in terms of habitat used by deer species, since both species are markedly different in terms of body size, behavior, morphology, having thus large differences in energy and habitat requirements (McNab 1963), resulting in interspecific differences in habitat use (Richard et al. 2014). However, the spatial overlap between red and roe deer in winter was the lowest, having started to increase during the following seasons, attaining the highest value in autumn. Analyzing the number of pellets in agricultural areas of both red and roe deer (areas occupied by both species), mainly in autumn these values were the highest, very similar for both species, resulting in the higher value of spatial overlap. The same trend was found during winter in Poland, in which the winter habitat used by red and roe deer was similar (Borkowski and Ukalska 2008). This is because in this region the limiting period (with particular conditions and with low food available) is the winter, so the feeding behavior and habitat use are more similar between red and roe deer than in other seasons (Borkowski and Ukalska 2008).

2.4.2 Feeding behavior

Shrubs were the most consumed group of plants by red deer in all seasons, as also described by Garcia (2016) for Lousã Mountain. Also Gebert and Verheyden-Tixier (2001) confirmed the shrubs as a key plant species group for European red deer. These results are in accordance with what was expected, since shrublands are one of the most used habitats by red deer in all seasons, consequently red deer's diet is mainly composed by shrubs. This fact was also described by other authors (Tixier and Duncan 1996; Cornelis et al. 1999; Gebert and Verheyden-Tixier 2001) that verified that diet composition is mainly explained by the habitat in which species feed. This implies that the availability of food in the habitats used by the species can be a key determinant of their diet composition (Duncan et al. 1998b).

The most representative shrub species was *Pterospartum tridentatum* in all seasons, except in spring that was *Ulex minor*. In spring (between May and June), the sprouting and flowering of *Ulex minor* start to increase which can explain the higher consume of this species specially in this season. Furthermore, the high consume of these two species can be explained based on their high availability in whole study area (Garcia 2016) and based on the high preference of *Pterospartum tridentatum* for high altitudes where mainly red deer are present. In addition, they are two evergreen shrubs so can be consumed throughout the year. These results are in accordance with fact that red deer feed on plants proportionally to their availability, suggesting a non-selective grazing behavior. This was also verified by Lathman et al. (1999) for red deer feeding behavior in the Scottish forests.

Monocotyledon species were the second group of plants more consumed by red deer in all seasons. *Arrhenatherum elatius* was the most representative species, except in winter that was *Festuca* sp.. Since the flowering of *Festuca* sp. occurs in spring/summer, in winter this species appears at high quantities, being more consumed in this season.

However, red deer also feed on arboreous and dicotyledons species as verified by Garcia (2016). These results are in accordance with what was expected because red deer is considered as an intermediate feeder (Hofmann 1989), whereby they are able to be grazers presenting a mixed of grasses in their diet, whose forage have a high fiber content, but also browsers, feeding on herbaceous and shrub foliage and trees (Garcia 2016). This evidences the changes in diet composition according to food availability (Hofmann 1989). This implies that large animals such as red deer have the capacity to select diets of lower digestibility than smaller animals, such as roe deer (Clutton-Brock and Harvey 1983; Demment and Van Soest 1985). Consequently, the red deer diet is diverse and might be constituted by forages with high fiber content.

In the case of roe deer, the groups of plants more consumed varied according to the season. The monocotyledon species was the most consumed group of plants in winter being *Festuca* sp. the most consumed species. As previously mentioned, the flowering

of *Festuca* sp. occurs in spring/summer, so is in winter that this species presents the higher quantity, so is more consumed. Besides, in winter the availability of vegetative parts of deciduous trees and shrubs and annual plants is low (Faria 1999), so leaves that are an important structure of plants in roe deer diet are less abundant. This result is in agreement with optimal foraging theory, in which in periods of low food resources, the species become less selective (Schoener 1971; Owen-Smith and Novellie 1982). Also, in Italy, Minder (2012) found that grass was typical found in roe deer diet during winter. The high consume of grass in winter can be explained through the increase of new growth availability at the beginning of their vegetative cycle after the first autumn rains (Minder 2012). So roe deer seems to optimize their feeding behavior in periods of low availability of food, by including species of plants which are generally less consumed and by selecting of species with relatively higher quality (Minder 2012).

Spring and summer diets were similar, in which the most consumed group of plants was arboreous species followed by shrub species, monocotyledons species and by dicotyledons species. Also, Faria (1999) verified that the roe deer diet in spring and summer in the Lousã Mountain was similar, and mainly composed by brambles (*Rubus* sp.) and arboreous species such as *Castanea sativa*. As previously mentioned, in spring the most part of plants are available and presenting green leaves (Faria 1999). Consequently, arboreous and shrub species were the most consumed group of plants in this season. Furthermore, in summer the grasses (Leite et al. 1997) and herbaceous species (Bugalho and Milne 2003) become senescent. Consequently, were less consumed (or even not consumed such as the dicotyledons species) by roe deer because in this season these plant species have higher fiber content (González-Hernández and Silva-Pando 1999) resulting in its avoidance by roe deer.

Dicotyledons species were less consumed by roe deer than was expected since have lower fiber contents. However, these results were also found in other studies (Maizeret and Sung 1984; Fandos et al. 1987; Maillard and Picard 1987; Guilhem et al. 1995; Homolka 1995). According to Maizeret and Sung (1984), the herbaceous dicotyledons constitute an ancillary food item in forest habitats. In addition, Homolka (1995) verified in Czech Republic that herbaceous dicotyledons are not an important food resources in forests habitats. Consequently, and as mentioned by Faria (1999), the low importance of herbaceous dicotyledons in diet can be a consequence of its low availability in forests habitats although its high diversity in the study area (Alves 2013; Alves et al. 2014; Garcia 2016). Another possible explanation for this result arises from the major problem of the application of microhistological technique. Different species of plants have differences in digestibility (Fitzgerald and Waddington, 1979) which can lead to errors in quantitative determination of the diet (Maizeret et al. 1986). The leaves and stems of woody species and grasses have thicker epidermic cuticles so can be overestimated in fecal analysis, whereas vegetal components with less cutinized epidermis, such as leaves of herbaceous species might be underestimated (Dearden et al. 1975; Vavra et al. 1980; Holechek et al. 1982).

Rubus ulmifolius was the most representative shrub species in all seasons, except in summer that was *Calluna vulgaris*. This result can be related with the flowering of *Calluna vulgaris* that occurs in summer and the maturation of fruits occurs in sequence of flowering. This results in high attractiveness of this species in summer. In addition, in Mediterranean areas the limiting period is the summer which can lead to nutritional restrictions (Bugalho and Milne 2003). *Calluna vulgaris* belong to the family Ericaceae and the increase in consume of this plant species in summer was also verified by Faria (1999) for roe deer diet in northeast Portugal. This species are usually consumed in periods with low availability of food resources because their leaves have a low nutritional value, high fiber content and consequently low digestibility of its organic matter (Maizeret and Sung 1984). This in agreement with optimal foraging theory. (Schoener 1971; Owen-Smith and Novellie 1982). Nonetheless, the importance of *Rubus ulmifolius* for roe deer was also verified in other parts of Europe (Siuda et al. 1969; Hearney and Jennings 1983; Homolka 1991; Tixier and Duncan 1996; Storms et al. 2008) because of their high nutritional value (Prokešová et al. 2006).

In relation to arboreous species, in winter the most representative species was *Laurus nobilis*, in spring was *Castanea sativa*, *Fraxinus* sp. in summer and in autumn *Betula pubescens*. These results can be related with the phenology of the species. The flowering of *Laurus nobilis* start in January peaking in March, whereas the flowering of chestnut tree (*Castanea sativa*) occur in spring, having the flowering peak in June. The highest consume of *Fraxinus* sp. in summer can be related with the fact that this arboreous species mainly occur in moist soils and have the capacity withstand droughts due to their extent radicular system. Furthermore, the leaves of this species fall in autumn resulting in low consume of this species in autumn and winter and high consume in summer, when the leaves are green and the flowering already occurred. Regarding to *Betula pubescens*, is in the autumn that gathers all conditions for being more consumed.

These results are in accordance with our expectations for roe deer feeding behavior. In fact, the eating habits of roe deer can quickly change (Tixier and Duncan 1996; Cornelis et al. 1999) according to modifications in spatial and temporal availability of food resources, which leads to a strong specialization of the seasonal diet (Duncan et al. 1998a). This species is a browser (Clauss et al. 2003) and a selective feeder, feeding selectively and preferably on the most digestible plant material present in their habitats, which are rich in energy and have high moisture content (Cornelis et al. 1999; Danilkin 1996; Sempéré et al. 1996), such as tree leaves, seedlings and forbs (Latham 1999). This ungulate chooses to forage on plants with highly accessible cellular contents (lower fiber content) (Hofmann 1989). In this way is verified the prediction that browsers are obligatorily non-grazers (Wieren 1996; Clauss et al. 2003) because in winter the most consumed group of plants by roe deer was monocotyledon species, and was more consumed than red deer in this season. However, at a general level, roe deer avoid grasses with high fiber contents in comparison to grazers, preferring plants with less fiber content (leaves of trees and shrubs) (Storms et al. 2008). Consequently, the

roe deer diet had less fiber content than red deer diet. However, we cannot support the prediction that the diets of red and roe deer have more fibrous forage in summer, since nor red or roe deer diet had a high value of absolute frequency of occurrence of monocotyledons species in comparison with other groups of plants in this season.

As our results showed, the diet composition of red and roe deer was significantly different in all seasons, as verified by Storms et al. (2008). Thus, roe deer occupy a niche which is clearly different from red deer, as previous verified by Tixier and Duncan (1996). Regarding to the seasonality of diet composition, our results demonstrated significantly differences in the food items present in the feces. These differences were principally due to the phenology of the plants in the study area, however can also reflects the availability of preferred species (Garcia, 2016).

In relation to the structures of plants consumed by red and roe deer, leaves were the structure that was more consumed by both species in all seasons, whereas stem was little consumed for the same period. The leaves provide a better quality diet for red and roe deer than stems, since the green portions of plants are the most nutritive for animal diet (Leite et al. 1997). In addition, the leaves are the principal component of the photosynthesis of the forage, determining the capacity of dry matter production by the plant (Leite et al. 1997). The sprouts were more consumed by roe deer than for red deer, except in summer. This result can be related with the feeding strategy of roe deer (Cornelis et al. 1999; Danilkin 1996; Sempéré et al. 1996). In spring, takes place the vegetative growth and sprouting of plants (Faria 1999), explaining the higher consume of this structure in this season than in other seasons.

The fruits did not appear in the red deer feces but appeared in roe deer feces in autumn, even with small percentage. However, Garcia (2016) mentioned that fruits can be eaten by red deer depending on phenology and availability of plants and consequently in that the time of the year. In autumn, occurs an increase in the dried fruits availability that are rich in amide and minerals being an important energy source (Faria 1999), explaining the consume of fruits in this season. Also, Cornelis et al. (1999), Danilkin (1996) and Sempéré et al. (1996) concluded that roe deer in autumn opted for use concentrate food resources, such as fruits. The absence of fruits in red deer feces and the low percentage in roe deer feces can be due to the absence of the cuticle in this vegetal component, thus they can be totally digested not being detected in feces with the microhistological technique (Voth and Black 1973; Maizeret et al. 1986). In addition, it is possible that animals ingest the fruits without ectocarp not being detected through microscopic fecal analysis (Faria 1999). Thus, is necessary to use complementary methods to detect this structure in diet, such as the analysis of the seeds present in feces and through the identification of germinated seeds in feces cultures as made by Faria (1999) to roe deer diet in center and northeast Portugal.

Flowers were more consumed in spring and summer by red deer. In the opposite to the red deer, flowers did not appear in roe deer feces. The majority of plants flourish in spring and summer resulting in higher consume of the flowers in these seasons.

Furthermore, flowers are rich in nectar and pollen grains constituting important sources of energy and nutrients (Faria 1999). So, its absence in roe deer diet was unexpected. However, the importance of flowers in roe deer diet is not well documented (Faria 1999), although several studies referred the consume of flowers by roe deer (Holisová et al. 1982; Holisová et al. 1984; Holisová et al. 1986; Fandos et al. 1987).

Regarding to diet diversity, no significant differences were found between red and roe deer, although significantly differences were found between the seasons. These results are in accordance with what was expected since more differences in diet composition of red and roe deer than in diet diversity were predicted, since both species eat high number of different plant species but those plants are consumed in different quantities by each species. Differences on the diet diversity over the seasons reflect the phenology of the plants in the study area, however can also reflects the availability of preferred species (Garcia, 2016). In fact, in the periods with high food availability (e.g. spring), the food amplitude is lower. This result indicates that in spring the animals are feeding on their preferred food items (Garcia, 2016), resulting in lower food amplitude. Conversely, the higher value of food amplitude indicates that species need to use a larger variety of food items to suppress their energetic requirements (Garcia, 2016).

Regarding food overlap, the diet overlap between deer species was low, indicating that these deer species use different food resources across seasons. The highest value of food overlap was found in winter, as also reported by Storms et al. (2008) for red and roe deer in France. The higher value of food overlap in winter was due to *Festuca* sp. that was largely consumed by both species in this season. Also Tixier and Duncan (1996) in mixed coniferous Scottish plantations found that dietary overlap between red and roe deer increased in winter with the main overlap for *Calluna vulgaris* and *Vaccinium myrtillus*. Conversely, in spring and summer food overlap decreases because in these seasons each species is feeding on their preferred food items due its availability (Garcia, 2016), which results in lower food overlap. In autumn, the food overlap increases probably due to the decrease in food availability, that result in the use of larger variety of food items by red and roe deer to supply their energy requirements (Garcia, 2016). As so, our results confirm the segregation of both deer species in terms of diet composition, as previously verified by Storms et al. (2008).

2.4.3 Evaluating ecological resources used by red and roe deer

Based on the results of spatial and food overlap, the results indicate a low overlap between red and roe deer, both in terms of spatial niche and trophic niche. In this way, red and roe deer can coexist in Lousã Mountain with low competition between them, both in terms of space and food resources. Also in other studies, no competition was found between red and roe deer, allowing the coexistence of both species (e.g. Prokešová et al. 2006; Borkowski and Ukalska 2008; Melis et al. 2009; Storms et al. 2008).

The differences between body size and consequently energy requirements explain the interspecific differences in the habitat use (Richard et al. 2014) in terms of space and feeding behavior. These differences in body size as well as the segregation of niche allow the coexistence of red and roe deer in Lousã Mountain. These differences allow the resource partitioning (Putman 1996; Bell 1971; Jarman 1974) between these sympatric species, that results in subtle interactions due to the species co-evolution (Latham 1999).

Red deer can feed on the preferred food items of roe deer, and consequently reduce their abundance, although they do not depend on them. Conversely, roe deer are strongly selective and physiologically unable to supply their necessities based on a diet that is mainly bulk forage. Consequently, roe deer is not able to decrease the abundance of the principal food resources of red deer. Thus, red deer are able to exploit the majority of the roe deer food niche, but the opposite does not occur, since roe deer can only exploit a small part of the red deer food niche. These different digestive physiologies between red and roe deer have implications for the potential competition between these two species, being any competition for food resources between red and roe deer probably be asymmetric (Latham 1999). In conclusion, red deer occurs in habitats where roe deer occurs, but the opposite is less frequent.

Chapter III-General conclusions

The study of habitat use and feeding behavior in same context allowed to conclude if red and roe deer after their reintroduction in Lousã Mountain are feeding on same food resources in same area or if are feeding on same food resources but in different areas. The findings obtained through both studies demonstrate that whereas red deer mainly use ecotone zones between forests and shrublands, which occur at high altitudes away from settlements, roe deer preferably uses ecotone zones between forests and agricultural areas at low altitudes and close to human settlements. Besides the differences in terms of habitat use, their diet composition is also different. Therefore, red and roe deer are using different ecological resources (habitat and food) and ecological niches. In this way, red and roe can coexist in the Lousã Mountain, occurring a low competition between them, either by space or food resources.

The results of this study appear to be crucial for the correct management and conservation of both species and their habitats, having future implications. The fact that roe deer are using more the open areas, such as agricultural areas, than red deer, close to the settlements, may have two future implications. Roe deer may increase the quality of its diet by feeding in these areas, that have consequences at demographic level because this allow to improve the reproductive capacity of young females and increase the offspring survival, leading to the increase in number and geographical area of roe deer as verify throughout Europe (Tixier and Duncan 1996). However, such habitat selection leads to a higher conflict with human population, increasing the damages in agricultural areas caused by roe deer.

Chapter IV-References

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