



UNIVERSIDADE D
COIMBRA

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**ACTIVITY PATTERNS OF RED AND
ROE DEER: DIFFERENCES BETWEEN
SEXES**

**Dissertation under the Master of Ecology supervised by Professor
Doctor José Paulo Filipe Afonso de Sousa and by Doctor Joana
Alexandra da Silva Alves presented to Department of Life Sciences of
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Padrões de atividade de veado e corço: diferenças entre sexos

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Resumo

A grande maioria dos Ungulados, especialmente os pertencentes à família *Cervidae* apresentam um elevado grau de dimorfismo sexual, em termos de tamanho corporal, onde machos são maiores que as fêmeas. Além do tamanho, os machos apresentam outros caracteres sexuais secundários que os distingue das fêmeas, como é o caso das hastes.

Associado ao dimorfismo sexual de tamanho corporal surge a segregação sexual, que parece ser inevitável em espécies com mais de 20 % de dimorfismo sexual no tamanho corporal, levando a que varias hipóteses tenham sido propostas para entender este complexo fenómeno. De entre as várias hipóteses propostas, a hipótese da sincronia de atividade, surge como estando diretamente ligada ao dimorfismo sexual de tamanho corporal, e propôs que os machos sendo maiores do que as fêmeas, apresentam maior eficiência digestiva, devido a terem um rúmen maior o que leva a uma mais lenta passagem dos alimentos, permitindo-lhes estarem mais tempo inativos, quer seja a ruminar ou descansar. Pelo contrário, as fêmeas, sendo menores tem um rúmen menor, e, portanto, os alimentos passam pelo trato digestivo mais rapidamente. Esta característica, obriga-as a estarem mais tempo a alimentarem-se, compensando a sua baixa eficiência digestiva.

Recorrendo a armadilhas fotográficas, colocadas na Serra da Lousã, foi possível obter resultados relativamente aos padrões de atividade, de veado e de corço. Os resultados demonstraram que os machos e fêmeas de veado diferem no tempo despendido na maioria dos comportamentos analisados, ocorrendo maior sobreposição dos seus comportamentos na época do acasalamento, na altura em que se juntam em grupos mistos para acasalar. Para corço, verificou-se que num modo geral o tempo despendido na maioria dos comportamentos, entre machos e fêmeas, foi semelhante, no entanto maiores assincronias foram detetadas face ao esperado.

Apesar da maioria dos resultados obtidos estarem de acordo com a hipótese da sincronia da atividade, o facto de os resultados revelarem níveis de sincronia semelhantes em espécies com níveis de dimorfismo sexual de tamanho corporal tão distinto, pode indicar que as diferenças nos padrões de atividade dos sexos não se devem apenas às diferenças de tamanho corporal, podendo ser resultado de outros fatores sociais ou ambientais. Os resultados evidenciam ainda necessidade de estudos futuros incluindo não só os ecossistemas naturais, mas também os humanizados (*i.e.* áreas agrícolas), como nos quais a presença de corço pode ser mais relevante do que o esperado.

Palavras-chave: *Cervus elaphus*, *Capreolus capreolus*, dimorfismo sexual de tamanho corporal, hipótese da sincronia de atividade, padrões de atividade, armadilhas fotográficas

Abstract

Most ungulates, especially those belonging to *Cervidae* family, display an elevated degree of sexual body-size dimorphism, where males are larger than females. Besides the size, males present other secondary sexual characters that distinguish them from females, as is the case of the antlers.

Associated with sexual body size dimorphism arises sexual segregation, which seems to be inevitable in species with more than 20% of sexual body size dimorphism. Several hypotheses have been proposed to understand this complex phenomenon. Among them, the activity budget hypothesis, arises as being directly linked to sexual body size dimorphism, and proposed that males being larger than females, present higher digestive efficiency, due a larger rumen that leads to a slow passage of food, allowing them to be more time inactive, either ruminating or resting. Contrary, females, being smaller have smaller rumen, and, so, the food passes through the digestive system faster. This characteristic, leads them to be more time feeding, balance their low digestive efficiency.

Using camera traps, placed in the Serra da Lousã, it was possible to obtain results regarding the patterns of activity of red and roe deer. The results demonstrated that males and females of red deer differed in time spent in most of the analysed behaviours, occurring a greater overlap of their behaviours in the rut season when sexes gather in mixed sex groups to mate. For roe deer, was verified that in general, the time spent in most behaviours, between sexes, was similar, however, greater asynchronies were detected contrary to our expectations.

Although most of the results obtained are in the line with hypothesized by the the activity budget hypothesis. Similar synchrony levels obtained for red and roe deer, species with so distinct levels of sexual body-size dimorphism, may indicate that the differences in gender activity patterns are not only due to their differences in body-size, and may be the result of other social or environmental factors. The results also show the need for future studies including not only natural ecosystems, but also humanized ones (*i.e.* agricultural areas), as in which the presence of roe deer may be more relevant than expected.

Key words: *Cervus elaphus*, *Capreolus capreolus*, sexual body-size dimorphism, activity budget hypothesis, activity patterns, camera-trap

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Chapter I - General Introduction

1.1. Sexual Body Size Dimorphism

Males of the most mammal species are usually larger than females (Webster 1992; Lindenfors et al. 2005), and this difference between the two sexes it's known as sexual size dimorphism (SSD). One reason, and probably the major one explaining the occurrence of this phenomenon in mammals is the sexual selection (Loison et al. 1999, Pérez-Barbería et al. 2002, Lindenfors et al. 2005, Vanpé et al. 2008; McPherson and Chenoweth 2012; Roylance-Casson 2021), which occur in two different forms: intrasexual and/or intersexual selection pressures (Roylance-Casson 2021). Intrasexual selection happens through male-male combat to get access to females; when females choose among all males available to mate it is called intersexual selection (Moore 1990, Pérez-Barbería et al. 2002).

The selection pressures and, consequently the degree of sexual body-size dimorphism are measured throughout the social structure of the species (Pérez-Barbería et al. 2002, Roylance-Casson 2021). Jarman's (1974) proposed that the first antelopes that lived in closed forests and that were monogamous species, migrated to more open habitats that give the possibility to create larger groups favouring the polygyny (Jarman, 1974; Pérez-Barbería et al. 2002; Szemán et al. 2021). However, smaller body size ungulates need a higher quality of food that grows in closed habitats compared to larger ones that feed in high quantity but lower quality, and so are forced to live in more open habitats (Szemán et al. 2021). And so, ungulates living in open habitats tend to form larger groups (Ruckstuhl 1998) that offer some protection against predators (Månsson et al. 2017).

Generally, in polygynous species, intrasexual pressures occur through combats between males to get access to females. A social order is established with larger males, and so the most dominant ones, being more successful in reproduction (Roylance-Casson 2021). Secondary sexual characteristics, as antlers or horns, evolved to maximize the possibility of a male with good ornamentation winning the combat or even preventing one (McPherson and Chenoweth 2012, Bowyer et al. 2020, Peña et al. 2021).

1.1.1 Sexual body-size dimorphism: the role to Sexual segregation

Sexual segregation is described by habitat or social segregation. It is known that habitat segregation always guides to social segregation of a group (Conradt 1999, Ruckstuhl and Neuhaus 2006), the contrary, social segregation can happen independently of habitat segregation. In sexually dimorphic ungulates is very common to see segregation of sexes, usually more evident among the Cervidae family (Main et al. 1996, Mysterud 2000, Bowyer et al. 2002, Bowyer 2004). This particular event can also occur in many other non-dimorphic species like birds, fish, whales, seals, monkeys and elephants (Myers 1981, Ruckstuhl and Neuhaus 2000, Stokke and Du Toit 2002, Catry et al. 2006, Laidre et al. 2009).

Generally, sexual segregation is defined as a different use of space by the sexes outside the rut season (Main et al. 1996) what leads to the formation of two different groups types: adult males or sub-adult males - Bachelor groups; and other groups of females and their young - Matriarchal groups (Ruckstuhl 2007, Ruckstuhl and Neuhaus 2016, Roylance-Casson 2021).

In social segregation, both sexes inhabit the same place yet in different social groups, *i.e.*, males and females occur in different social groups. In terms of habitat segregation, both sexes have different distribution and use habitats in different ways (Conradt 1998a, 1999). Sexual segregation can occur due to factors such as sexual dimorphism degree, activity budget, predation risk, digestion ability or foraging efficiency (Main et al. 1996).

Over time many hypotheses have been proposed to explain sexual segregation, however many have been rejected. Some remained over time and, among those, there are three that are gaining support in terms of its ability to explain how and why sexual segregation happens, which are the Reproductive Strategy Hypothesis (RSH), also called Predation Risk Hypothesis; Forage Selection Hypothesis (FSH) and Activity Budget Hypothesis (ABH) (Ruckstuhl and Neuhaus 2002, Yearsley and Javier Pérez-Barbería 2005). These three hypotheses are associated with the concept of sexual dimorphism (sexual body size differences). Predation Risk and Forage Selection Hypothesis attempt to explain sexual segregation through the use of different habitat space used by both sexes and Activity Budget Hypothesis attempt it over habitat but also social component (Bowyer 2004, Ruckstuhl and Neuhaus 2006).

Females use most of their energy for breeding and rising their young until they become self-independent. Contrarily, males use it for their reproductive success (Ruckstuhl 1998). And so, the predation Risk Hypothesis states that females are more susceptible to be predated when they have young at their care, and in this case, females select a habitat where could ensure the security of offspring (Ruckstuhl and Neuhaus 2000, Pęksa and Ciach 2018). While bigger males choose habitats with great resources even when the predation risk is high (Main and Coblentz 1996, Main et al. 1996). This hard choice is made to improve energy reserves and body conditions, essential to the mating season, and important to individual reproductive success, which gives them better chances when facing rivals (Main and Coblentz 1996, Main et al. 1996). In harsh winters and dry summers, food resources are scarce that is why pre-rut is so relevant for the survival and reproductive ability of males.

Forage Selection Hypothesis predicts that smaller animals are expected to choose food of higher quality when compared to larger ones that can extract enough energy from resources with lower quality, *i.e.*, smaller individuals will compensate for their low digestive efficiency by foraging longer, while larger individuals will spend more time ruminating (Ruckstuhl 1998). This hypothesis is common in species where the differences between sexes are evident, being the

females the smaller sex (Pełksa and Ciach 2018). However, in non-dimorphic species is expected that both sexes choose the same quality resources, except lactating females that need a higher quality of food. So, it is predicted that in non-dimorphic species males and lactating females would segregate, due to different energy demands. Segregation also occurs between non-lactating and lactating females considering that at this point lactating females have high energy requirements (Main and Coblentz 1996, Bowyer 2004, Alves 2013).

Distinct nutritional requirements lead each sex to use habitat differently, causing different foraging behaviour of the sexes (Conradt 1998a, Mysterud 2000, Ruckstuhl and Neuhaus 2000). As a result, males and females are incapable of sharing the same habitat, and therefore activity synchronization turns to be nearly impossible, which makes sexual segregation unavoidable (Garcia 2016).

Is it known that in polygynous ruminants social segregation of sexes can also happen, with the formation of different social groups (Ruckstuhl 1998, Kie and Terry Bowyer 1999). The activity budget hypothesis (ABS) predicts that high degrees of sexual body-size dimorphism lead to greater differences in activity patterns between males and females, especially when SSD exceeds the threshold of 20 % (Ruckstuhl and Neuhaus 2002). It also predicts that single-sex groups have higher levels of activity synchrony between individuals than in mixed-sex group (Conradt 1998b, 1998a)

Differences in the activity patterns between sexes lead to sexual segregation. This is probably due to the difficulty of animals to live in a group where there are no similar body sizes and, as consequence, different needs that enhances the costs of synchrony. So, living in a group, where most have different needs will bring many costs for all individuals in the group, and this leads to the necessity to form groups with individuals of similar body sizes (Ruckstuhl and Neuhaus 2000). Differences in time spent active or inactive between sexes is one of the reason point out as leading to sexual segregation (Ruckstuhl and Kokko 2002).

Two primary assumptions are key in the activity budget hypothesis. The first one says that the smaller rumen size and fast passage of food in smaller animals makes them less efficient to digest food, while bigger animals, being more efficient, spend less time foraging (Demment 1982). The second assumption says that differences in activity budget between animals with different body sizes makes behavioural synchrony too costly (Conradt 1998a, Yearsley and Javier Pérez-Barbería 2005). The predictions of activity budget hypothesis are: (1) due to smaller body-size of females and consequently, lower efficiency of digest food they need to spend more time active (feeding or walking). On the contrary males being larger and with higher digestive efficiency can spend more time inactive (ruminating or resting); (2) animals with similar activity budget tend to aggregate, while animals tend to segregate when different

activity budget is present (Ruckstuhl and Neuhaus 2002, Yearsley and Javier Pérez-Barbería 2005). Species where males and females present an equal or superior percentage of 20 % in body size dimorphism are expected to form distinct groups (single size groups) due to differences in the activity patterns (Ruckstuhl 1998, 1999, Alves et al. 2013).

1.2. Ecology and behaviour of red deer

From all ungulates that live presently in the Iberian Peninsula, red deer (*Cervus elaphus*, Linnaeus 1758) is the largest one, and one of the largest in the world. This ungulate belongs to the Cervidae family and the Cetartiodactyla order. According to the IUCN Red List, the red deer is in category and criteria: “Least Concern” (Lovari et al. 2018).

1.2.1. Distribution and habitat

Red deer has a wide distribution around the world, and we can encounter it in meridian and temperate Europe, North America, North of Africa, and Minor Asia, Central and Oriental Asia, near east, occurring naturally (Salazar 2009). Over the last few years, many cervids had enlarged their populations in Europe and this is due to changes in habitat and management practices (Alves 2013).

Red deer has a widespread distribution over our country mostly in the centre and south. Populations of red deer can be found in protected areas as Montesinho Natural Park and Internacional Tagus Natural Park; and in other areas such as Lousã Mountain, Tapada Nacional de Mafra and Tapada Real de Vila Viçosa due to reintroductions programs (Oliveira 2013).

The quality of habitat, human activities, food availability and predation influenced the space used by red deer, and also their seasonal and daily activities (Carvalho 2013). These species use more preferentially ecotones areas, which are transitional zones (Alves et al. 2014) characterized by areas between forest (used for refuge and rest) and open areas or grasslands (used for feed).

1.2.2. Morphology, Activity and Behaviour

Red deer has an elongated body, a large and robust head and a short tail (Baskin and Danell 2003, Santos 2009). During summer this species presents a reddish-brown coat and a dark brown coat in winter, this colouration differs over the year due to climate variation. Calves up to 2 months of age show a dorsal white mark that provides camouflage against predators, weighing around 15 kg when they are born (Peixoto 2014).

The primary characteristic differing females and males are the antlers in males, bone

formation, which fall after the mating season and grow again in the same year (Peixoto 2014). The number of stubs can indicate the age of males but this is not secure because it is influenced by other factors, such as the quality of food (Santos 2009). High nutrition demands are necessary for the great growth of antlers in red deer males, so factor age is not so important as the quality of food in this process (Santos 2009, Peixoto 2014). Males present larger necks, unlike females who have thinner/smaller ones. Adult females reach 90kg when not lactating and 70kg when lactating, and males weigh an average of 180kg (Mitchell et al. 1977), reaching 250kg (Santos 2009). About the length, adult males ranges from 160 to 220 cm and adult females range from 160 to 195 cm (Alves 2013).

Sexual dimorphism plays an important role in differentiating patterns of activity between red deer males and females. Due to it is high dimorphism (50%) males and females (Catchpole et al. 2004) cannot synchronize their activity patterns (Wang et al. 2018a), so they only gather during the mating season (Ruckstuhl and Neuhaus 2002).

We can see this species active 24h a day, however, they are more active at dawn and dusk. The seasonal activity of red deer show a huge variation, with activity increasing during the summer and decreasing in winter (Pépin et al. 2001, 2006, Arnold et al. 2004). These differences in seasonal activity probably reflect changes in daylight hours, deer metabolism, quantity and quality of food (Georgii 1981, Green and Bear 1990).

Males and females usually differ in their activity patterns probably because of their different energetic requirements (Georgii and Schröder 1983) due to body size differences between them. A study made by Pépin et al. 2009 has shown that both females and males travel less in winter, but males travel less than females due to their larger body size. However, during the breeding season, males showed more activity than females and this is probably due to the competition between males or even due to searching multiple for females to breed (Peña et al. 2021). After this period males need to recover their energy, and so they register a decrease in their activity.

1.2.3. Feeding ecology

The habitat has a great influence on the diversity of food intake (Cornelis et al. 1999), *i.e.* the availability of food is habitat dependent. Moreover, food resources also vary seasonally (Gaudry et al. 2015). Based on that, in temperate regions, larger herbivores tend to migrate from the low-elevation winter range to the high-elevation summer range (Mysterud et al. 2001)

The food quality and its digestion define the level of nutritional physiology of a species (Maloiy and Kay 1971). Ruminants can be classified, as browsers (feed mostly on woody and non-woody dicotyledonous plants); grazers (feeding on Gramineae species) and mixed/intermediate feeders that consume a mixture of the two, which is the case of red deer

(Hofmann 1995, Clauss et al. 2003, Gordon 2003, Zweifel-Schielly et al. 2012). Food quantity and quality differ over the year, so ungulates need to adapt their diet to these annual changes (Bugalho and Milne 2003). Intermediate feeders are known to avoid fibre, and prefer concentrate foods (browse, forbs, fruits) when quality and availability are high (Dumont et al. 2005). In a Mediterranean environment, they eventually, change to a diet based on browse species, in winter (Bugalho et al. 2001, Bugalho and Milne 2003). In spring, red deer turns to be more selective due to an abundant and high quality of resources. While, in summer they avoid open areas, where heat dries the vegetation (Lovari et al. 2007). Better conditions in autumn, when rainfall brings the regrowth of vegetation, seems to have great importance in the body condition of deer (Millán et al. 2021).

According to the results obtained by Garcia 2016, in Lousã Mountain, red deer feed mostly on shrub species (e.g. *Pterospartum tridentatum*, *Erica spp.*, *Ulex minor*), and this is a consequence of its high nutritional value. Although around 45% of the red deer diet is also composed by tree vegetation (e.g., *Pseudotsuga menziesii*) and herbaceous plants (mostly grass).

1.2.4. Social structure and reproduction

Red deer is a polygamous species, with gregarious behaviour influenced by sexual segregation (Alves et al. 2013). Outside mating season, red deer females form familiar matriarchal groups, which can be composed by the older female that is the leader (Peixoto 2014), a calf of the year, calf male or female from the year before and other related females. Sub-adult males leave the group after two years of age, forming other groups with of similar age, called bachelor groups. The sub-adult females leave the group to form their own group, however, they still share the same area with their origin group. During rut season males and females are frequently seen in mixed-sex groups.

Red deer species are polygynous, where males mate with several females, and one female only mates with one male. This occurs in most mammals because of the lower parental care provided by males, and females take care of their young all alone (Vanpé 2007). Males use a harem defence strategy where they follow and defence one or a group of females. However, depending on some environmental conditions, red deer males can adjust their strategy by defending a feeding area instead of defending a harem (Pépin et al. 2009). Males opt to defend some areas from potential rivals and from intruders males, to ensure their reproductive success (Carranza 1990).

Red deer males' behaviour differs enormously in rut season compared to other times of the year. Outside mating season males tend to form bachelor groups or live alone, while in rut season they became intolerant to each other and each individual moves to traditional rut areas

(Clutton-Brock et al. 1979, Pépin et al. 2001). Rut season occurs between September and October, and for males this period usually become a challenge where they spend most of their time active, leading to a great mass loss (Carvalho 2013). Red deer males emit sounds, called “roaring” - similar to snoring, to attract females and even when facing with potential rivals, protecting their rut territories (Pépin et al. 2001, Reby and McComb 2003).

Gestation lasts about 240-262 days, and calving takes place between May and beginning of June. Usually, females have just one calf per year. The lactation period occurs after birth, ending in September (Pépin et al. 2009, Alves et al. 2013).

1.3. Ecology and behaviour of roe deer

Roe deer is the most abundant and widespread ungulate in Europe (Tixier et al. 1997), and is capable of occupying a variety of habitats. Roe deer belongs to the Cervidae family and the Cetartiodactyla order, and is listed as “Least concern” in IUCN Red List (Lovari et al. 2016)

1.3.1. Distribution and habitat

In Europe, roe deer is broadly distributed and abundant. It can be found in the north of Scandinavia and north of the Mediterranean area, Denmark, Sweden, Norway and Finland (Salazar 2009).

Roe deer is native to Portugal, and there was an increase of its distribution between 1990 and 2000 (Salazar 2009). It is present in the North, namely in Alfândega da Fé, Miranda do Douro, Mirandela, Vimioso; in the Centre, like Lousã Mountain, Manteigas e São Macário and even in the South due to well succeed introductions. Between 2000 and 2009 occurred an expansion on its distribution, being present in Vila Nova de Foz Côa, São João da Pesqueira, Tabuaço, Fundão e Vila Velha de Rodão.

They can be found in a great variety of habitats, such as coniferous, and deciduous forests, marshes and even agricultural areas (Vanpé 2007). Some factors affect the daily activities and space used by this species, such as food availability, vegetation cover, and characteristics of the terrain, climate factors, human disturbance, and predation risk. As so roe deer prefer mountainous areas preferentially more close to watercourses, with big covers and with low shrub density, and with a low presence of red deer and humans (Torres et al. 2015).

1.3.2. Morphology, Activity and Behaviour

Roe deer has a short head with large ears (12-14 cm), a long neck, a short trunk, and long limbs (front legs shorter than hind ones) (Sempere et al. 1996). It is a small ungulate weighting 18-49kg (Lister et al. 1998) with a body length of 95-135cm (Vanpé 2007). The most visible differences between the two sexes are the antlers in males, which fall in autumn or early winter,

regrowing within a week (Sempere et al. 1996), between October and November and remain untouched during the rut season (Froehlich et al. 2016, Cappelli et al. 2020).

Every year there are two moults of the hair. In winter they present a grey dense hair pelage. Contrary, in summer the pelage is thinner, between reddish and red-brown. A short and rudimentary tail, with no more than 4 cm, is surrounded by a white caudal disc, being less visible in summer or even absent (Lister et al. 1998). The distinctive caudal disc seems to have the shape of a kidney in males and in females looks like an inverted heart. Fawns are spotted, with dorsal white marks (Sempere et al. 1996), furred and weight 1-1.7 kg. Growing very fast, where in 2 weeks of age fawns double their birth mass. In the biggening of the second year of age, males reach puberty (Stache et al. 2013)

Individual factors, such as age and sex influence the activity patterns of roe deer (Stache et al. 2013). Other factors such as photoperiod and thermoperiod use to influence also the activity patterns (Pagon et al. 2013). In roe deer, males weigh about 5% more than females, so the sexual dimorphism is very low (Yearsley and Javier Pérez-Barbería 2005, Vanpé 2007) and for that reason is not expected big differences in the activity patterns between sex (Pagon et al. 2013). However, there is different request on the environment between the two sexes which leads to different sizes in their home range (Stache et al. 2013)

Roe deer females and males show similar activity patterns over the year, however in spring, males become territorial increasing their activity levels (Pagon et al. 2013). Rut season brings many costs for both males and females, which leads them to increase their activity (Stache et al. 2013). For females, gestation and lactation periods, also request higher energetic levels which leads them to also increase their activity during these periods.

1.3.3. Feeding ecology

Roe deer is a browser (Rautiainen 2017) and a selective feeder, so they feed mostly on woody and non-woody dicotyledonous plants. In the summer, this species shows a preference for fruits and seeds (Wallach et al. 2010) and in winter prefer herbs (Baskin and Danell 2003). They eat a huge variety of species that belong to the major taxonomic groups of plants (conifers, deciduous trees and shrubs, cultivated plants, grasses, sedges and fruits), fungi and lichens. (Duncan et al. 1998). The small capacity of the rumen, small stomach and the rapid digestion process leads to a regular food intake (Pagon et al. 2013), so roe deer feed between five and eleven times a day (Sempere et al. 1996, Cornelis et al. 1999).

Small ungulates are known for having high energy requirements and similar gut capacity when compared with large ungulates. In the case of roe deer, it must select food easily digestible (Tixier et al. 1997). Roe is predicted to choose high concentrate cell soluble resources, avoiding species with a high concentration of fibres (Rautiainen 2017).

Another factor interfering in nutritional requirements is the reproductive strategy. Different energy requirements depend on the number of offspring's, *i.e.*, a female with more than one fawns needs more energy intake than one female with only one fawn (Rautiainen 2017). Energy requirements also depend on lactating and no-lactating females, *i.e.*, a lactating female require more energy due to milk production than a non-lactating one (Rautiainen 2017).

1.3.4. Social structure and reproduction

Females in summer used to be solitary, while in winter form matriarchal groups composed of one or more adult females and their calves, accompanied by one or two males (Vanpé 2007). Males are solitary due it's high territorial behaviour, they become aggressive to other males. When faced with intruders they threaten, warn, and even fight against others. In winter they become non-territorial (Sempere et al. 1996).

Females become sexually active at 14 months old, and males sexually mature at the end of their first year old. (Sempere et al. 1996). There is a peculiarity on the female of this species, due to their rare reproductive cycle, occurring a delay of five months in embryonic implantation. The rut begins between mid-July and mid-August (Sempere et al. 1996) and calving occurs in May-June, and their young become independent with one year of age (Vanpé 2007, Rautiainen 2017). Roe deer is a polytocous species, and females can give birth between 1-3 fawns (Vanpé et al. 2009, Rautiainen et al. 2021).

Roe deer males are polygamous and use a resource defence strategy where they access females by defending a local against rivals (Liberg et al. 1992). Males are capable of protecting one territory from rivals, during months (March until September), to secure females until the breeding season. In a study made by Vanpé et al. 2009, they concluded that both males and females mate with several partners, describing their mating tactics as promiscuous.

1.4. Aims

Our study species are the *Cervus elaphus* (Red deer) and *Capreolus capreolus* (Roe deer). Red deer is considered the largest ungulate of Peninsula Iberia, while roe deer is a smaller ungulate, with both species having a wide distribution over Lousã Mountain. Taking in mind that activity budget is known as the amount of time that one individual spends in each activity (Fawzy et al. 2019) it is intended to understand the activity patterns of both species.

Considering the Activity Budget hypothesis, it is predicted that considering red deer, since females due to their smaller size and low digestive efficiency when compared with males, will spend more time active (feeding or walking). The opposite is expected for males, as they are larger and more efficient at digesting food, they will spend more time inactive (resting or ruminating). In the case of red deer males, they tend to adjust their activity patterns to the ones of females, to increase mate probability, during rut season. Contrarily, considering roe deer, which have a low degree of sexual size dimorphism (below 5%) (Yearsley and Javier Pérez-Barbería 2005), females and males are expected to have similar and more synchronized activity patterns, due to a similar body size between sexes, excluding when males initiate a territorial behaviour in rut season.

The main goal of the present project was to analyse the differences in the activity patterns of females and males in both species, red and roe deer, and relate it with biological characteristics, namely with body size dimorphism. To achieve this, three hypotheses were designated: 1) Activity of males and females of roe deer is more synchronized than in red deer; 2) Activity patterns of roe deer males and females are similar across the year; 3) Activity patterns of red deer males and females change across the year.

Chapter II - Methodology

2.1. Study Area

The area of this study was the Lousã Mountain (40° 3"N, 8° 15"W), in the Centre of Portugal, an area of about 170 Km². This area has a Mediterranean climate, where the summer is hot and dry and the winter is cold and with rain (Alves 2013). Temperatures range from – 4.1 °C to 35.9 °C, and an annual mean of 12 °C. The annual medium precipitation is about 827 mm and can reach 1600 mm in the highest altitudes (Alves et al. 2014). Relative to topography, the terrain is characterized by rugged terrain, composed of deep valleys and rounded hilltops, and with an altitude range from 100 to 1205 meters (Alves 2013, Alves et al. 2014), reached at “Pico do Trevim” (Oliveira 2013).

Lousã Mountain has a great variety of vegetation characterized by coniferous plantations and broad-leaf trees, resulting in mixed habitats, but also with shrubland present in a vast area. (Alves 2013, Alves et al. 2014). Coniferous forests are dominated by genus *Pinus* namely *Pinus pinaster*, *Pinus sylvestris* e *Pinus Nigra*. The forests of broadleaf trees are dominated by many species of *Quercus* sp., and also by *Castanea sativa*, *Prunus lusitanica* and *Ilex aquifolium* (Oliveira 2013).

Lousã Mountain is surrounded by an extensive road network with more than 500 km of length. Generally, it is characterized by low levels of traffic, with further disturbance registered in the beginning and end of the day (Alves 2013).

Our study area has a vast avifauna, such as *Circus cyaneus* and *Circus pugargus*; relevant communities of amphibians, *Chioglossa lusitanica*: reptiles like *Vipera latastei* and even mammals such as *Vulpes vulpes*, *Sus scrofa*, *Genetta genetta*, *Martes foina*, etc. (Alves 2013). Lousã Mountain was inserted in the National List of Natura 2000 sites, due to the huge richness of biodiversity in this mountainous region (Alves 2013).

The presence of red and roe deer populations in Lousã Mountain is due to a reintroduction program (Salazar 2009). The red deer reintroduction program occurred between 1995 to 1999, with the release of 96 individuals (Alves 2013). In the case of roe deer, this program started a year before, in 1994 and extent until 1997, with a total of 54 individuals released (Ribeiro 2018).

Although there are no natural predators in Lousã Mountain, stray dogs, abandoned usually by hunters, are the main predator attacking firstly young, sub-adults and even adult females (Alves 2013, Alves et al. 2014, Vilela 2015, Ribeiro 2018). Populations of red and roe deer live in sympatry way with wild boar- *Sus scrofa* (Alves 2013).

2.2. Sampling design

In the central region of Lousã Mountain, between May 2019 and June 2020, were selected 60 different sampling points, with, approximately, 1 km between each other (Figure 1). Based on previous studies for the same population, 3 different habitat types were considered: mixed-forest, coniferous forest and shrublands. This habitat characterization became possible due to aerial photographs and field visualization. From the 60 sampling points, there are 20 points covered by coniferous forests, with the presence of trees of genus *Pinus* and *Chamaecyparis*, other 20 points composed of mixed forests, characterized by the presence of broadleaf trees together with coniferous trees and, 20 points of shrublands.

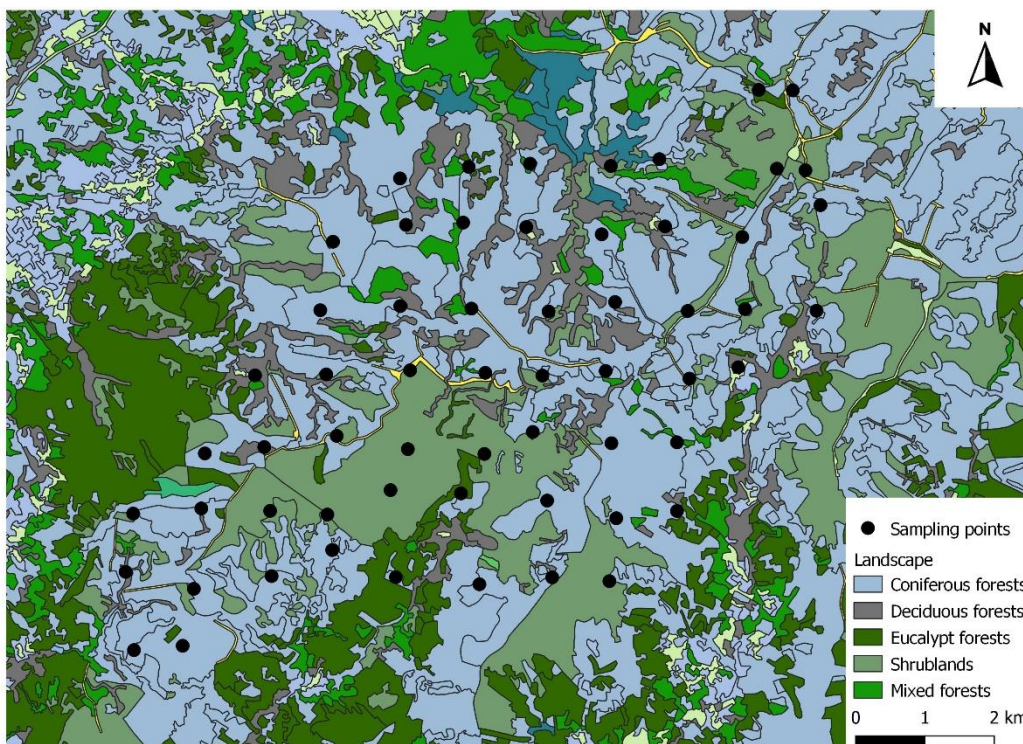


Figure 1 - Camera traps location in Lousã Mountain, by each habitat type.

To register the behaviour, sex, age and even composition of groups in the two species in study, it was analysed photos and videos from camera traps (Bushnell Natureview Cam HD). We trapped these cameras in trees approximately 1 m above the ground. Our camera-traps were programmed to record 24/per day, with a proper configuration: when activated take 3 pictures, followed by a video of 1 minute; high image quality (14 MP) and the sensitivity of the sensor on medium. The cameras are activated when movement is detected by the sensor and registered the date, time, and temperature.

2.3. Data collection

Every time an animal of any species triggered the camera, it was considered a new contact and inserted into a excel dataset. For each contact, individual characteristics of animals and, their movement and behaviour were used to distinguish between individuals. If the same individual stays activating the camera for more than 1 min, it was recorded with the same animal ID, and only when a new individual trigger the camera the animal ID changed. In the case of ungulates, the age-class, sex, behaviour, group type and group composition were registered. Individuals' age-class and sex were determined based on the body size, antler size and colour of the coat. In both our study species, fawns have a dorsal white-spotted marks, being red deer ones bigger than roe deer yearlings. Red deer sub-adults were considered all individuals which have between one and three years old or four in the case of males. Adults are much larger and comprised animals with four years or five in the case of males (Figure 2). Regarding roe deer, sub-adults were considered individuals which have until two years of age and adults three or more years old (figure 3) (Melis et al. 2005).

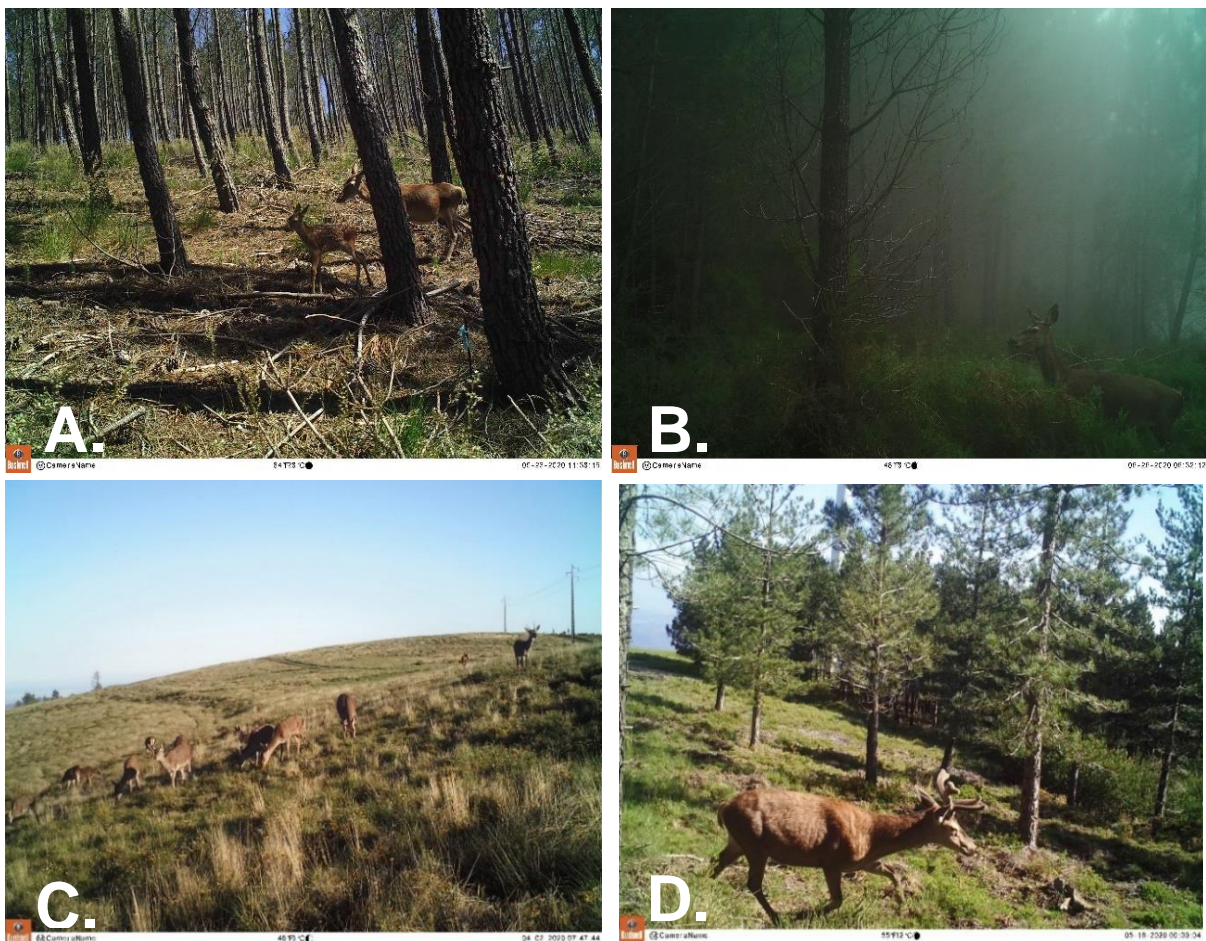


Figure 2 - Photographs of Red deer exhibiting different characteristics between sexes and ages in Lousã Mountain. A - Female and calf; B – Solitary adult female; C – Matriarchal group; D – Solitary adult male.

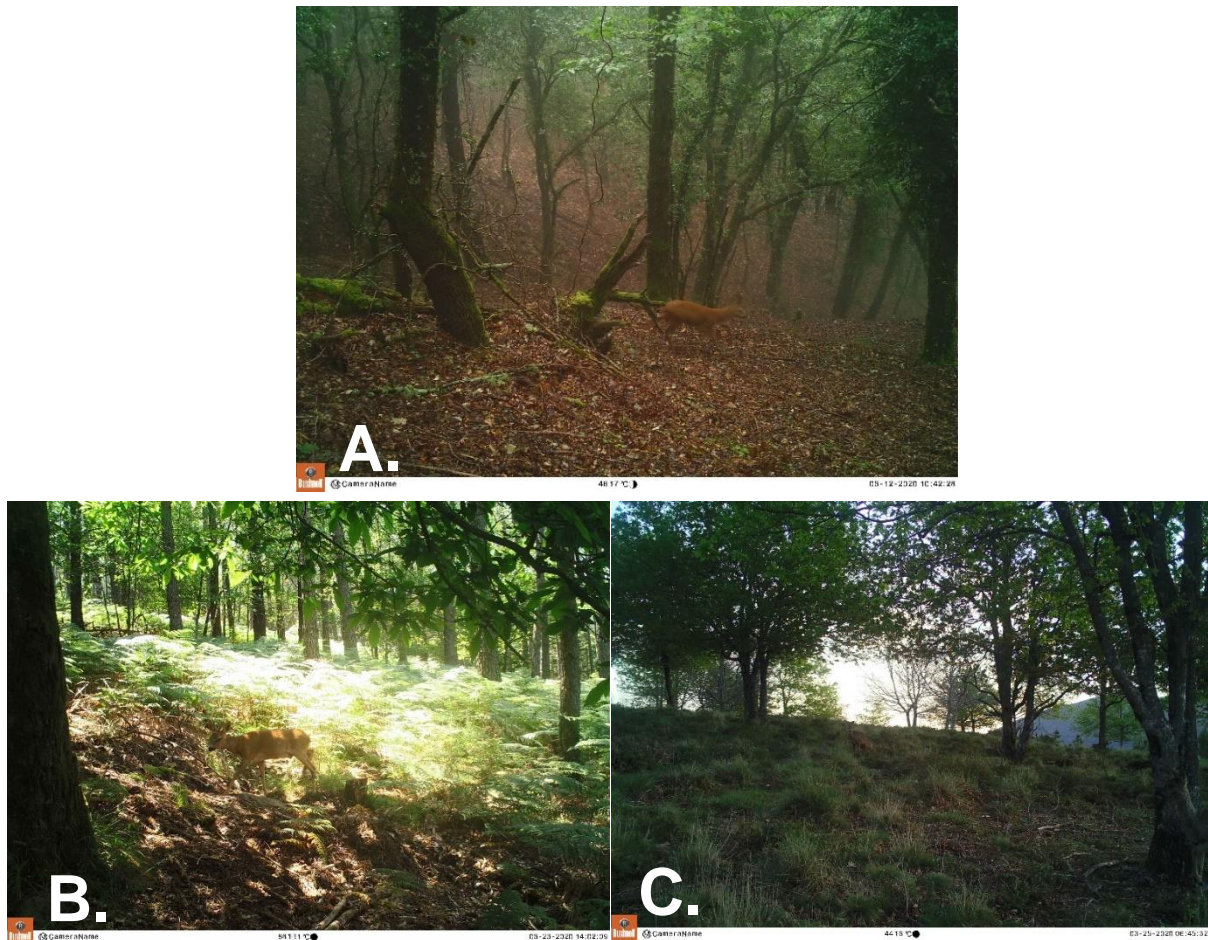


Figure 3 - Photographs of Roe deer exhibiting different characteristics between sexes and ages in Lousã Mountain. A – Solitary adult male; B – Solitary sub-adult male; C – Female and calf.

For this study, three temporal time scales were considered: annual, comprising the complete dataset; seasonal, divided into Spring (March 20 - June 20), Summer (June 21 - September 21), Autumn (September 22 - December 20) and Winter (December 21 – March 19); and monthly. From the analysis of the camera traps, activity patterns for each of the timescales were estimated.

The behaviour of each individual and its duration were noted. We characterized the behaviours into alert state, feeding, lying, olfactory control, ruminating, standing, walking – as seen in table 1. All mentioned behaviours were considered active behaviours. For the analyses, we compiled behaviours like lying, olfactory control, ruminating, roaring and others all in a category of general behaviours named – “Others”, due to its low occurrence in the observed records.

Table 1 - Ethogram of red and roe deer behaviours

Code	Behavior	Description
AS	Alert state	Individual interrupt its behavior and raises the head and ears
FE	Feeding	With their head down, individuals are eating or chewing plants
LY	Lying	Individuals lying on the ground
OC	Olfactory control	Sense of smell. The mouth stays closed and chewing motion is missing
RU	Ruminating	Individuals regurgitate the food, and then chew and eat again
ST	Standing	Individuals without vigilance behavior
WA	Walking	Individuals are in movement - walking or running
OT	Others	Drinking, Fighting, Jumping, Scraping, Urinating, Defecating, Roaring, Breastfeeding, etc....

2.4. Data analysis

Ridout and Linkie 2009 had spread a statistical calculation to determine the synchronization of activities between males and females of a species, using behaviour analyses of photographs from camera traps. As so, the overlap of activity patterns between sexes was calculated through a nonparametric technique - kernel density analysis (Ridout and Linkie 2009). To discover differences in activity patterns between sexes of a species, we measured the coefficient of overlap Δ , which varies between 0 (without overlapping) and 1 (total overlap). A kernel density activity function had to be adjusted to the daily temporal pattern of each sex, in each behaviour type, at each timescale. The grey area corresponds to the overlap between two kernel density functions of each sex. We estimated the confidence intervals using bootstraps. All the statistical analyses were performed in the program R 3.5.0 (R core Team 2019) with the package “overlap”.

The percentage that males and females differed in time spent performing each behaviour, was measured by the calculation of the Sexual difference in Activity Budget, following the formula:

$$SDAB = 100 - \left(\frac{MA*100}{FA}\right);$$

where MA = % of time active of males and FA = % of time active of females, adapted from Ruckstuhl and Neuhaus 2002. This calculation was made for each behaviour – Alert state, Walking, Feeding, Standing and Others. Values close to 0 means fewer differences in time spent in each activity between the sexes. Positive values mean that females spent more time performing a behaviour, while negative values say that males spent more time in that behaviour.

Chapter III - Results

From 1 year of study (May 2019 – June 2020) in Lousã Mountain, more than 12 000 files were analysed. Besides the target species, other species were detected and registered, such as wild boar (*Sus scrofa*), stone marten (*Martes foina*), common genet (*Genetta genetta*); red fox (*Vulpes vulpes*). From 8769 photographs and 1981 videos of red deer, a total of 5744 individual contacts were detected, comprising 3103 individuals (Table 2) and 744 groups (120 bachelor groups, 578 matriarchal groups, 46 mixed groups). From those contacts, 2687 were of adult females, 475 of sub-adult females, 294 of calves, 596 of adult males, 1500 of sub-adult males and 192 of individuals non-identifiable.

From 1247 photographs and 249 videos in which roe deer was detected, a total of 449 contacts of roe deer, were determined, including 354 individuals (Table 2) and 24 groups (7 mixed groups and 16 matriarchal groups). The contacts consisted of 207 contacts of adult females, 25 of sub-adult females, 2 of calves, 165 of adult males, 32 of sub-adult males and 18 of non-identifiable.

Table 2 - Number of individuals observed in each species.

	Red deer	Roe deer
Adult females	1364	152
Sub-adult females	384	21
Calf	414	12
Adult males	450	143
Sub-adult males	491	26
Total	3103	354

Red deer was detected in the three studied habitats, being the highest number of animals of this species detected in shrublands (41.07%), where roe deer was practically absent (2.45%). Roe deer were more present in mixed (55.01%) and coniferous forests (42,54%) (Table 3).

Table 3 - Percentage of individuals of red and roe deer detected in each habitat type.

	Red deer	Roe deer
Coniferous forest	24.79	42.54
Mixed forest	34.14	55.01
Shrubland	41.07	2.45

3.1. Temporal differences in Activity budget?

Red deer activity pattern over the year presented a bimodal activity, with two separate peaks corresponding to sunrise (dawn) and sunset (dusk) (Fig. 4). In general, males' higher daily activity at sunrise and during day, while for females it was during night and at sunset. Considering activity overlap, females and males of red deer presented a high synchrony at annual timescale ($\Delta=0.91$).

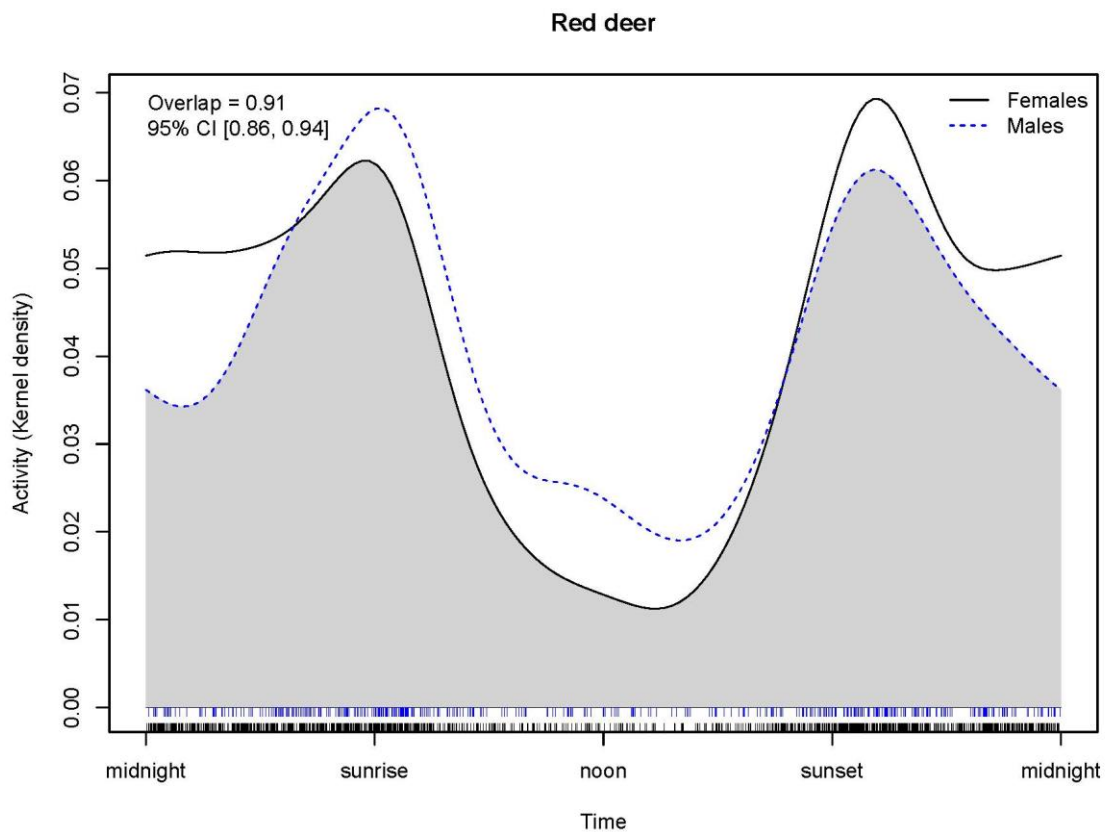


Figure 4 – Annual activity patterns of red deer males (dashed lines) and females (solid line), in Lousã Mountain. Overlap between males and females is represented by the grey areas. Values of overlaps ranges from 0 (no overlap) to 1 (total overlap).

Roe deer showed also two distinct peaks of activity at annual timescale, over the year, at sunrise and sunset. In general, females concentrate their daily activity during the night, right after sunset, and at sunrise. Contrary, males concentrate their daily activity at sunrise and during the day. Estimates of overlap over the year showed high synchrony on the activity patterns of roe deer males and females ($\Delta=0.85$) (Fig. 5).

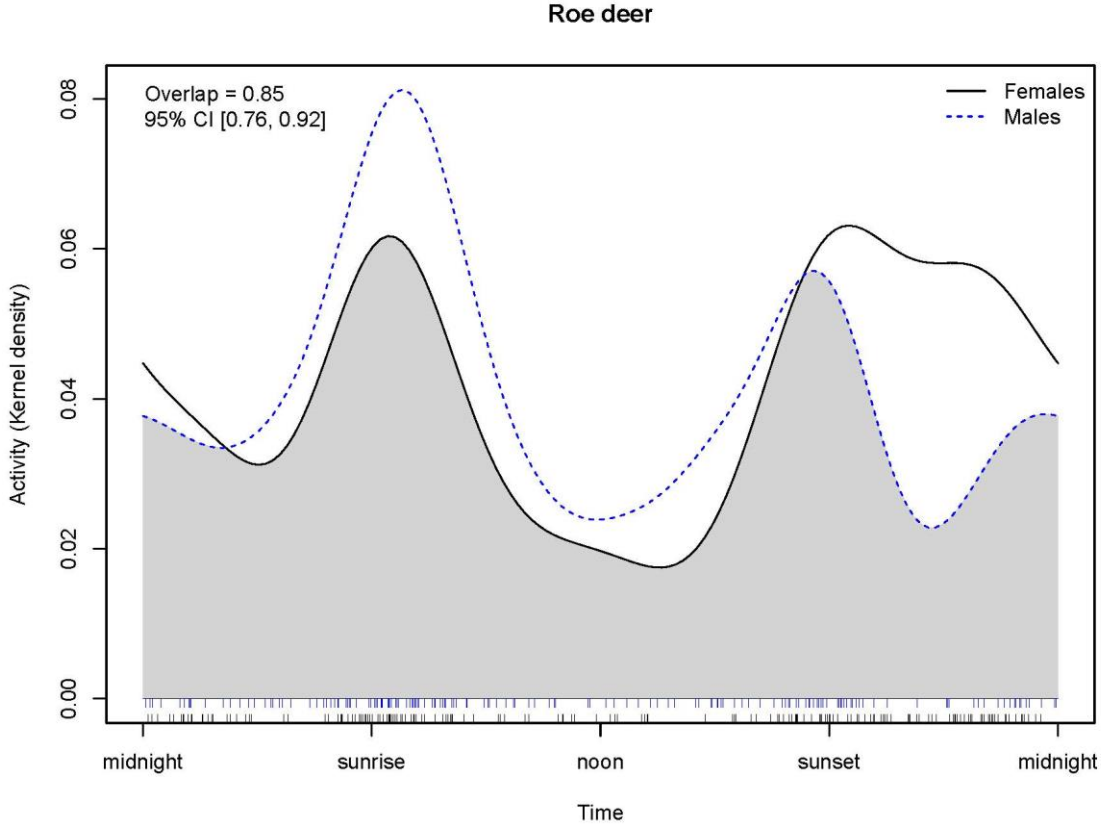


Figure 5 – Annual activity patterns of roe deer males (dashed lines) and females (solid line), in Lousã Mountain. Overlap between males and females is represented by the grey areas. Values of overlaps ranges from 0 (no overlap) to 1 (total overlap).

3.1.1. Seasonal activity patterns

- Red deer

Considering the seasonal timescale, red deer males and females presented a high synchrony in all seasons, with the lowest values occurring in Spring ($\Delta=0,82$) (Fig. 6)

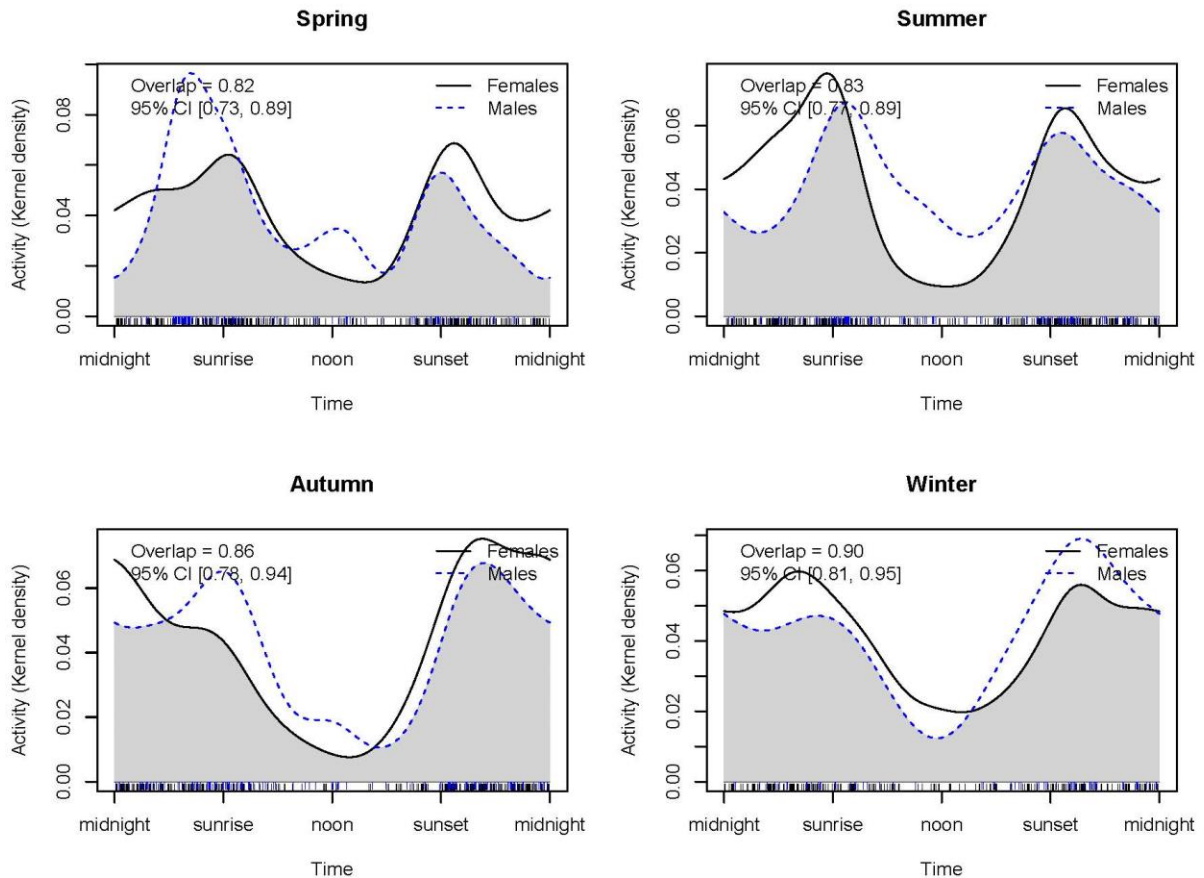


Figure 6 - Seasonal activity patterns of red deer males (dashed line) and females (solid line), in Lousã Mountain, in Lousã Mountain. Overlap between males and females is represented by the grey areas. Values of overlaps ranges from 0 (no overlap) to 1 (total overlap).

In seasonal observations, both red deer males and females spent more time feeding over the year, with higher percentages seen in spring (females – 58.78% and males – 60.08%). Both moved almost similarly, in autumn and summer, but in winter females (9.52%) moved less than males (15.59%). Looking specifically to the alert state, females were more vigilant than males, especially in autumn (15.68%) (Table 4).

Table 4 - Percentage of time spent by red deer females and males performing each behaviour, by seasons

	Females					Males				
	WA	FE	AS	ST	OT	WA	FE	AS	ST	OT
Autumn	18.27	32.94	15.68	9.14	23.97	18.55	28.81	6.20	18.13	28.31
Spring	13.20	58.78	11.51	3.60	12.92	10.91	60.08	4.15	3.41	21.44
Summer	14.15	47.30	7.50	5.39	25.65	13.70	42.49	4.85	7.37	31.59
Winter	9.52	54.61	6.96	3.90	25.01	15.59	51.52	4.43	6.63	21.82
Global	13.50	49.61	10.08	5.23	21.58	14.52	44.95	4.95	9.00	26.58

Considering the two major behaviours observed, feeding (Fig. 7) and walking (Fig. 8) overlap revealed some specificities.

For feeding behaviour, males and females of red deer demonstrated a lower activity synchrony in autumn ($\Delta=0.67$) and a higher overlap rate in spring ($\Delta=0.86$). In autumn females and males formed a peak after sunset, and males formed more two peaks, one at sunrise and the other at noon. Activity patterns over winter were more linear (Fig. 7).

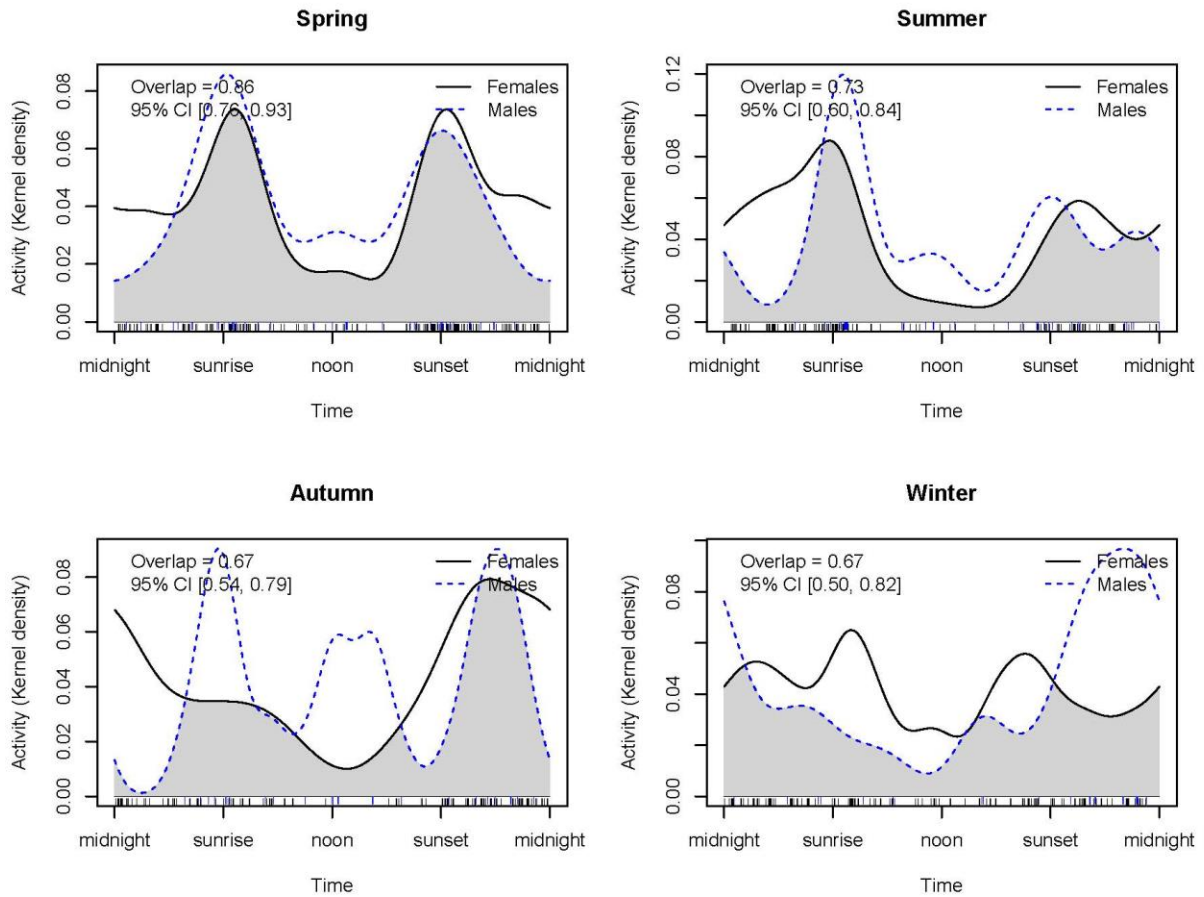


Figure 7 - Seasonal analyses in feeding activity patterns of red deer females (solid line) and males (dashed line), in Lousã Mountain. Overlap between males and females is represented by the grey areas. Values of overlaps ranges from 0 (no overlap) to 1 (total overlap).

Compared with feeding behaviour, walking brought higher degrees of activity overlap (spring - $\Delta=0.81$; summer - $\Delta=0.88$; autumn - $\Delta=0.86$; winter - $\Delta=0.91$), translating into greater activity synchrony between males and females. Two well-separated peaks at sunrise and sunset are demonstrated in all seasons (Fig. 8).

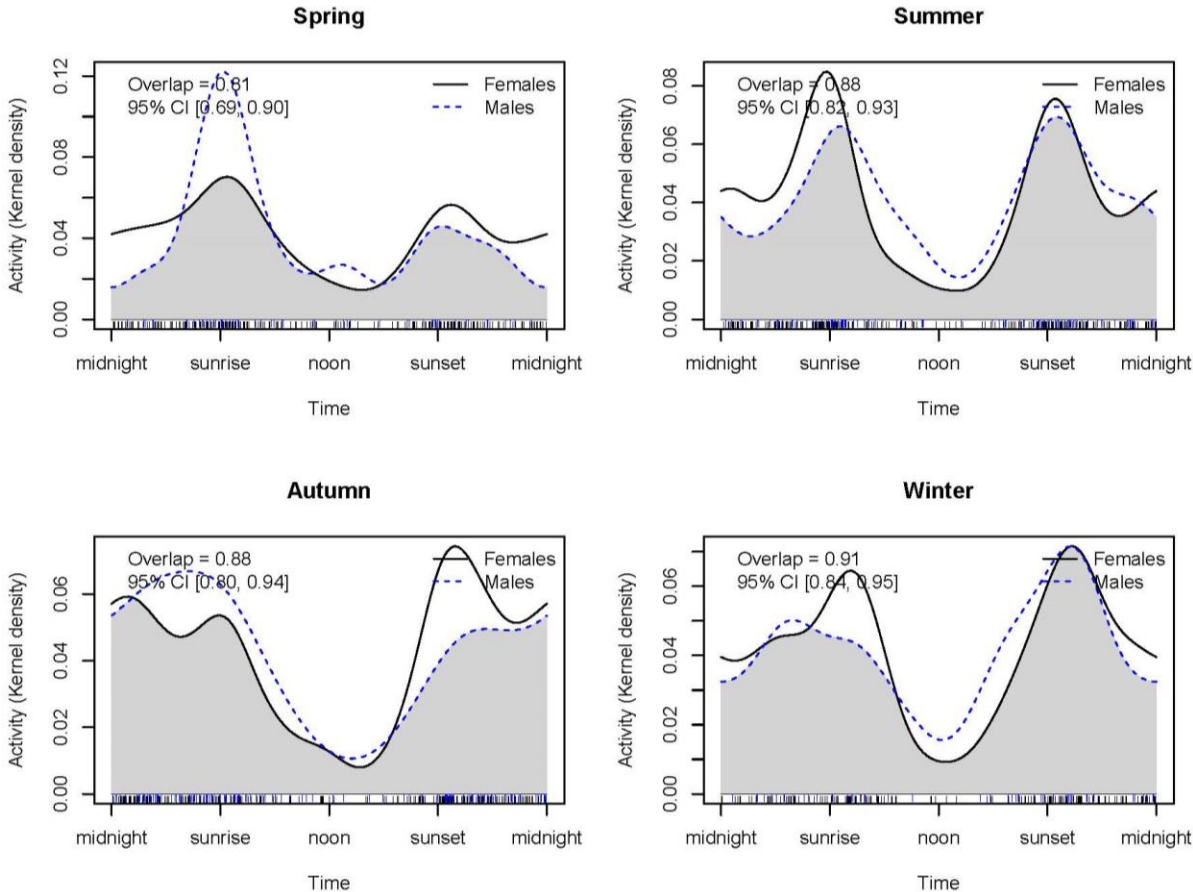


Figure 8 - Seasonal analyses in walking activity patterns of red deer females (solid line) and males (dashed line), in Lousã Mountain. Overlap between males and females is represented by the grey areas. Values of overlaps ranges from 0 (no overlap) to 1 (total overlap).

- **Roe deer**

Regarding roe deer, a higher activity overlap occurred in spring ($\Delta=0.82$) and summer ($\Delta=0.85$), with greater synchrony of activity patterns between roe deer females and males. In autumn females and males become less synchronized ($\Delta=0.69$). In winter, roe deer presence at the Lousã mountain decreased, reason why we indicate the information of “Low data” in winter panel (Fig. 9).

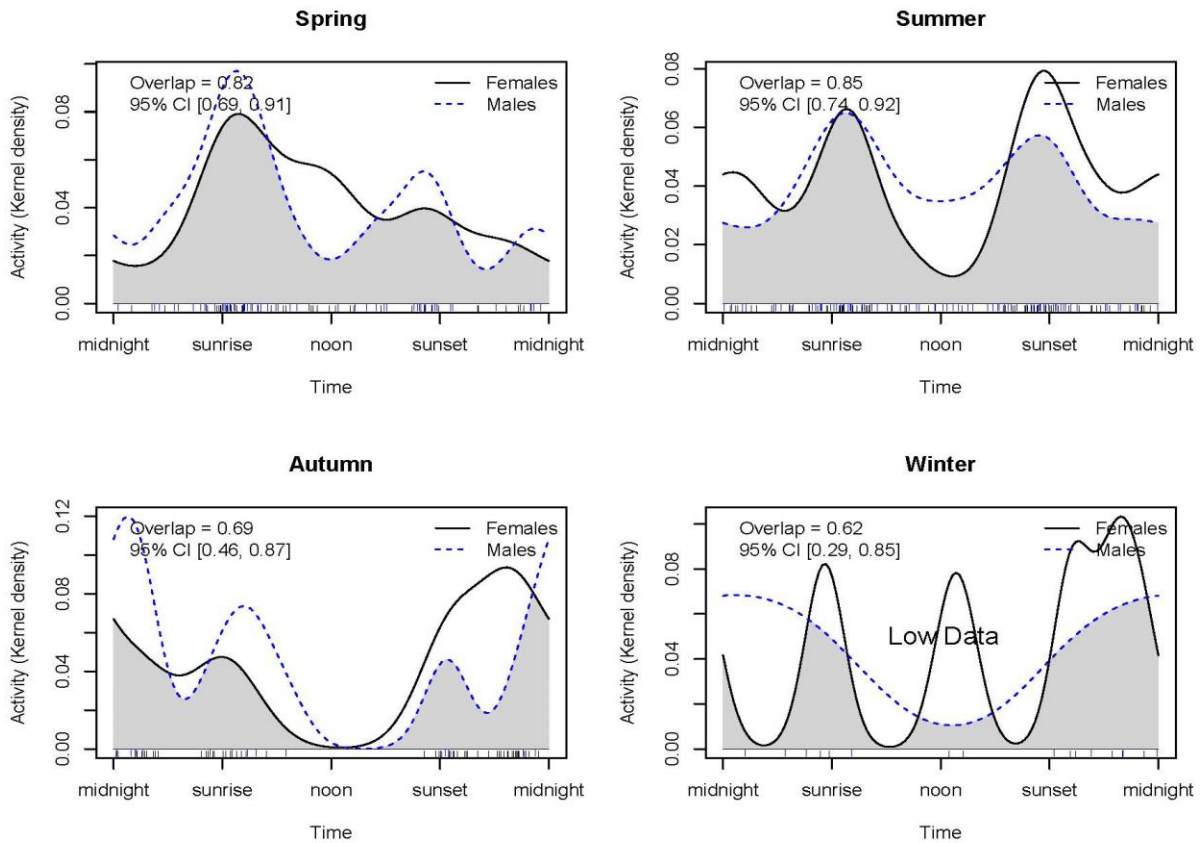


Figure 9 - Seasonal activity patterns of roe deer males (dashed line) and females (solid line), in Lousã Mountain. Overlap between males and females is represented by the grey areas. Values of overlaps ranges from 0 (no overlap) to 1 (total overlap).

When considering specific behaviours females increased their time spent feeding (66.99%) during spring. Seasonal observations showed that in winter, roe deer females spent most of their time vigilante (61.36%), while roe deer males were feeding (42.77%) and moving (34.68%) (Table 5).

Table 5 - Percentage of time spent by roe deer females and males performing each behaviour, by seasons

	Females					Males				
	WA	FE	AS	ST	OT	WA	FE	AS	ST	OT
Autumn	23.88	34.50	9.97	3.34	28.31	18.07	23.37	22.41	4.34	31.81
Spring	25.63	66.99	4.60	0.00	2.79	30.11	42.24	14.67	2.37	10.60
Summer	29.29	43.41	12.07	5.39	9.84	28.32	43.57	2.74	9.37	16.01
Winter	28.41	10.23	61.36	0.00	0.00	34.68	42.77	14.45	0.00	8.09
Total	26.66	42.94	11.05	3.70	15.65	28.00	40.45	10.25	5.67	15.64

Looking specifically to the two major behaviours observed in roe deer, and although for some season the data available is quite low or even inexistant, the feeding (Fig. 10) and walking (Fig. 11) overlap revealed some specificities.

In terms of feeding, summer brought higher activity synchrony ($\Delta=0.80$), where both males and females spent similar time feeding. Lower values were observed in spring, indicating a lower synchrony in terms of feeding behaviour in this season ($\Delta=0.70$) (Fig. 10).

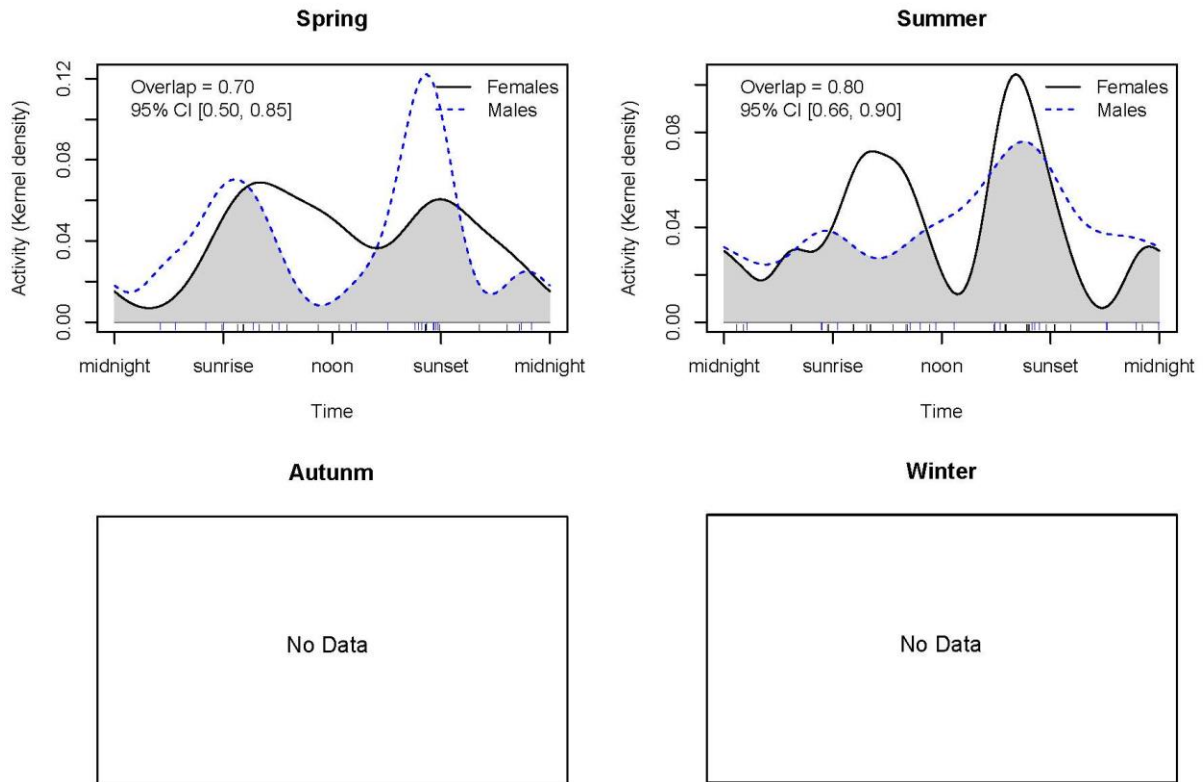


Figure 10 - Seasonal analyses in feeding activity patterns of roe deer females (solid line) and males (dashed line), in Lousã Mountain. Overlap between males and females represented with grey areas. Values of overlaps ranges from 0 (no overlap) to 1 (total overlap).

For walking behaviour, roe deer females and males demonstrated high degrees of synchrony in spring ($\Delta=0.82$) and summer ($\Delta=0.85$). In spring, there was only one peak during the day, at sunrise, after that, both sexes significantly decreased their walking activity. In summer, males concentrate their daily movements at sunrise and during the day, while females concentrate their movements at sunset and during the night. Autumn and winter results showed a low overlap degree. However, due to the low data available of roe deer, these results cannot be interpreted (Fig. 11).

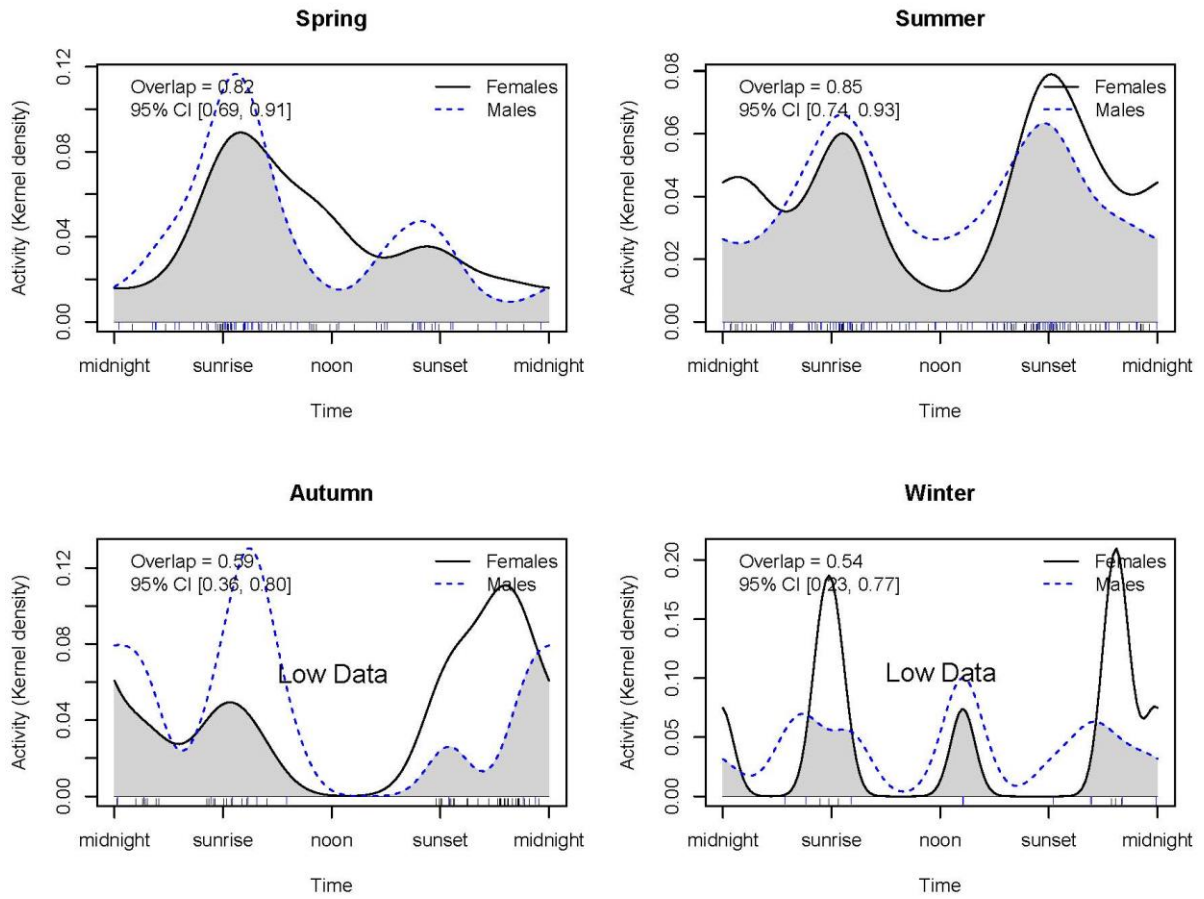


Figure 11 - Seasonal analyses, in walking activity patterns of roe deer females (solid line) and males (dashed line), in Lousã Mountain. Overlap between males and females is represented by the grey areas. Values of overlaps range from 0 (no overlap) to 1 (total overlap).

3.1.2. Monthly activity patterns

- **Red deer**

Activity budget changed seasonally, with each sex showing a different percentage of time spent in each behaviour. Feeding was the prevailed behaviour, where both sexes spent most of their time feeding (Table 6).

Looking specifically to the alert state, red deer females were more vigilante than males, especially between March and July, and after rut season. Males spent more time (26.58%) than females (21.6%) in other behaviours, with the highest percentage observed in April (46.65%) and September (46.54%) for males. The total percentage of time spent in walking behaviour was similar for both sexes, where females decreased a lot their movements between December and February (Table 6).

Table 6 - Percentage of time spent by males and females red deer performing each behaviour, by months

	Females					Males				
	WA	FE	AS	ST	OT	WA	FE	AS	ST	OT
Jan.	6.57	46.41	4.46	5.85	9.36	20.45	28.85	2.19	13.66	34.84
Feb.	11.55	63.59	9.78	2.14	12.94	10.64	57.07	3.66	5.43	23.20
Mar.	30.46	40.63	25.83	2.77	0.31	10.65	42.15	5.78	0.77	40.65
Apr.	9.59	67.47	11.75	1.19	9.99	11.62	75.75	2.70	0.37	46.65
May	14.16	57.98	8.75	2.45	12.61	12.56	70.31	5.25	3.97	7.91
June	18.57	51.46	11.37	6.66	11.94	10.59	62.84	3.52	9.26	13.80
July	15.75	40.74	8.71	6.98	27.82	16.09	45.99	3.99	4.15	29.77
Aug.	12.35	53.62	4.98	6.99	22.07	10.69	42.63	6.36	5.88	34.44
Sept.	13.65	36.77	7.64	4.11	37.84	18.85	18.38	3.85	12.38	46.54
Oct.	22.32	31.39	11.00	10.92	24.37	26.77	18.45	8.71	13.84	32.23
Nov.	15.50	28.46	21.68	10.58	23.78	15.71	27.02	9.82	33.97	13.47
Dec.	9.01	63.03	6.87	2.69	18.39	15.95	50.79	3.74	8.71	20.81

At the peak of winter, January and February showed that males concentrate their daily activity at sunrise and sunset. Greatest asynchronies in daily activity of males and females were detected in both months (January: $\Delta=0.62$; February: $\Delta=0.77$).

At the peak of the rut season, between September and October, males and females were more synchronized in their activities ($\Delta=0.86$ in September and $\Delta=0.82$ in October). After the rut ends, at the point where mixed-sex groups were dissolved, it was detected a decreased of overlap values ($\Delta\leq 0.65$), until January. At the calving, that occurs in May, mid-June, it was also demonstrated a lower synchronization in the daily activity of males and females, with $\Delta=0.76$ in April and $\Delta=0.79$ in May (Fig. 6).

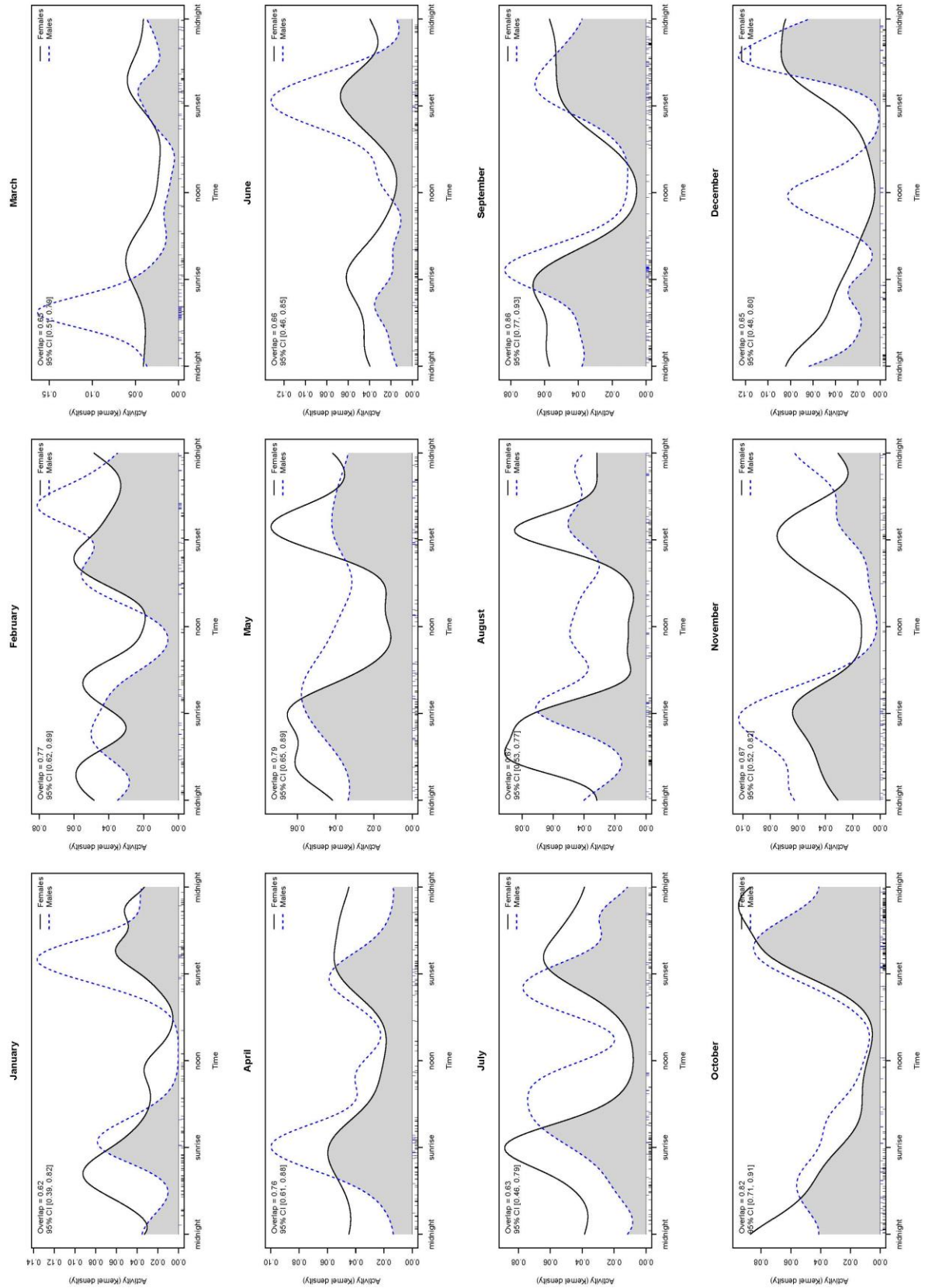


Figure 12 - Activity patterns of red deer males (dashed line) and females (solid line) between January and December, in Lousã Mountain. Overlap between males and females is represented by the grey areas. Values of overlaps ranges from 0 (no overlap) to 1 (total overlap).

- **Roe deer**

Activity patterns of roe deer changed seasonally, with each sex showing a different percentage of time spent in each behaviour. Feeding is the prevailed behaviour, where both sexes spent most of their time feeding (Table 7). However, higher percentage of time spent at feeding behaviour was detected in April and May for females, and in August for males. In September, roe deer males increased their time spent walking and decreased it in August, October, and during winter (Table 7)

There were few observations in the first month of the year, with only females being detected in January, and always walking (Table 7).

Table 7 - Percentage of time spent by males and females of roe deer performing each behaviour, by months.

	Females					Males				
	WA	FE	AS	ST	OT	WA	FE	AS	ST	OT
Jan.	100.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb.	70.00	30.00	0.00	0.00	0.00	29.17	51.39	13.19	0.00	6.25
Mar.	9.91	56.03	25.43	0.00	8.62	18.61	48.18	1.82	0.00	31.39
Apr.	24.59	68.85	6.56	0.00	0.00	15.56	48.89	33.02	0.00	2.54
May	20.88	78.11	1.01	0.00	0.00	52.81	29.59	11.48	3.83	2.30
June	55.16	38.10	6.75	0.00	0.00	19.48	58.43	7.12	4.87	10.11
July	18.47	48.65	23.87	0.90	8.11	35.66	27.62	4.20	6.29	26.22
Aug.	34.57	43.76	7.39	10.49	3.80	12.45	68.27	0.80	16.67	1.81
Sept.	21.13	45.75	10.31	2.45	20.36	76.19	0.00	23.81	0.00	0.00
Oct.	16.90	26.14	3.84	3.98	49.15	12.02	38.20	13.30	7.73	28.76
Nov.	29.61	32.47	19.35	2.73	15.84	21.13	0.00	33.10	0.00	45.77
Dec.	37.04	41.36	3.70	0.00	17.90	67.44	18.60	13.95	0.00	0.00

Territorial behaviour in males started in March, when was detected low activity synchronization between males and females ($\Delta=0.69$). This month presented a peak at the sunrise for both sexes, while the second mentioned peak (sunset) was dissolved.

Until rut season ends (August), the higher synchronization was maintained, with higher overlap values been detected in June ($\Delta=0.78$), July ($\Delta=0.84$) and August ($\Delta=0.77$).

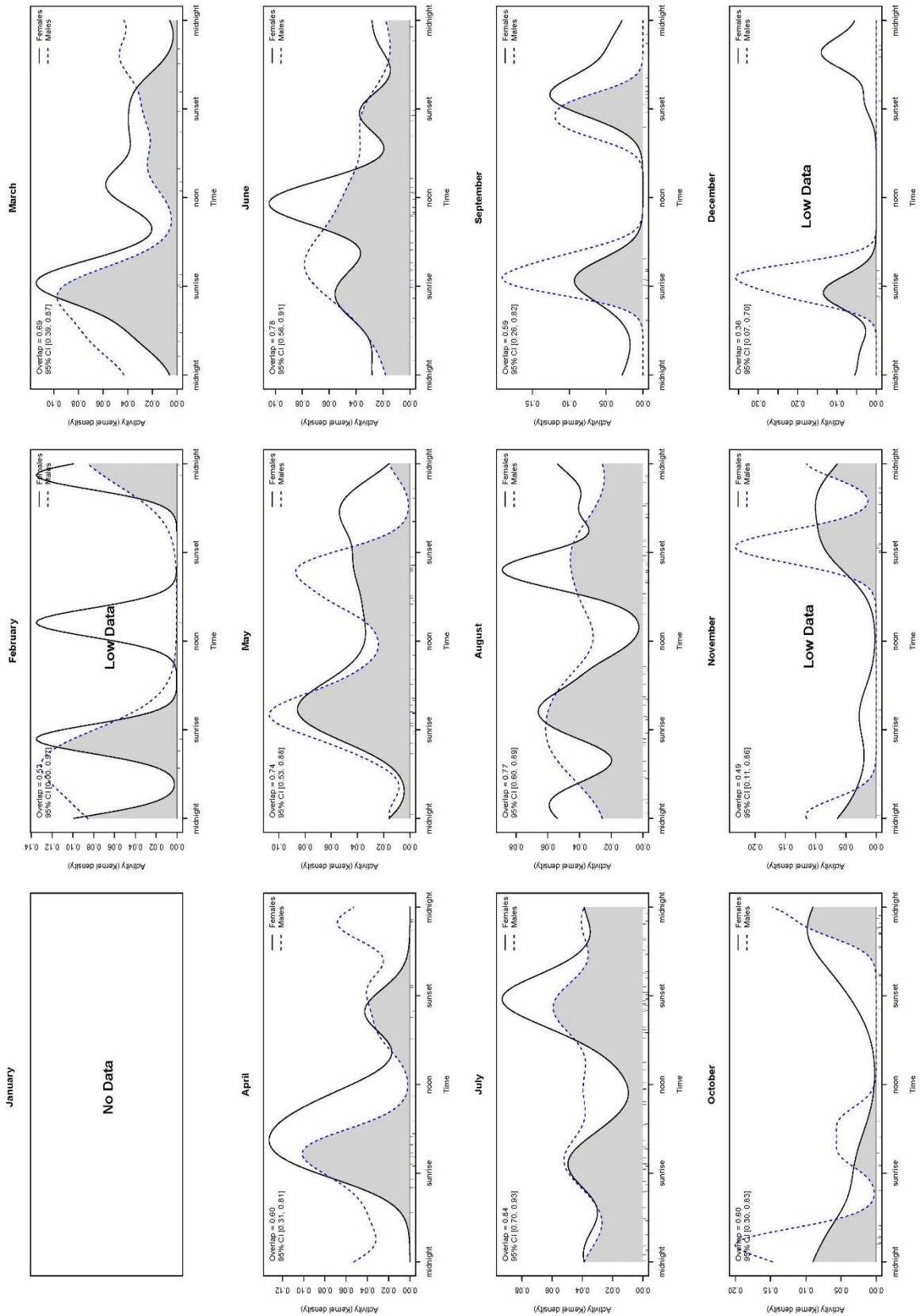


Figure 13 - Activity patterns of roe deer males (dashed line) and females (solid line) between January and December, in Lousã Mountain. Overlap between males and females represented with grey areas. Values of overlaps ranges from 0 (no overlap) to 1 (total overlap).

3.2. Sexual differences in Activity Budget

Considering the sexual difference in activity budget (SDAB) the results shown that males and females of red deer, spent a similar time feeding and walking, resulting in low values of SDAB (9.41 and -7.55 values, respectively). Standing behaviour shows the most sexual difference in activity budget, being males, the ones standing for the longest time (-72.00). Followed by alert state, showing red deer females were more vigilante (50.84) than red deer males. While males spent more time performing other behaviours (-23.19) (Table 8).

For roe deer, standing behaviour had the most significant difference in time spent between sexes, with a negative value (-53.24), meaning that males spent more time doing this activity. Behaviours designated as “others” represent the less difference in time spent (0.07). The remaining behaviours were close to zero, and so there were no significant differences in time spent by males and females, in each of the observed behaviours. Even so, females spent a little bit more time being vigilant (7.26) and feeding (5.80), while males moved more (-5.01) (Table 8).

Table 8 - Sexual difference in Activity budget (SDAB), for each species in each behaviour type.

Behaviour type	SDAB (Red deer)	SDAB (Roe deer)
AS	50.84	7.26
FE	9.41	5.80
ST	-72.00	-53.24
OT	-23.19	0.07
WA	-7.55	-5.01

Chapter IV – Discussion

Nowadays, one of the most popular methods of studying animal behaviour is camera traps (Caravaggi et al. 2020). Their primary advantages are being non-invasive, the possibility of being used in a huge variety of habitats and to study a great diversity of species, and its labour costs are lower than other methods (Rowcliffe et al. 2014). A disadvantage of this tool, however, is that the activity of individuals is only detected within the camera location since these devices have a continuous position (Ogurtsov et al. 2018). However, with longer sampling periods and wide coverage of the study areas, it is possible to mitigate this problem and obtain representative data. In this study, the number of cameras placed, and the sampling design employed were robust enough to ensure the proper coverage of the central area of the Lousã Mountain, and so the data obtained for this area is representative. However, an considering the low number of detections of roe deer in some months, it is important to highlight that it can be due to the low occurrence of the species in the mountain region during winter.

Individuals of the same species are under the same external factors (variation day/night, resources availability, climate condition, human disturbance) when living in the same study area. Cited factors influence, significantly the activity patterns of species, others, individual ones, such as sex, age and body-size, cause great variations in the activity budget of each individual as well (Stache et al. 2013).

Meteorological constraints of the environment, create big difficulties for individuals, changing their ecological, physiological, and behavioural responses. Temperature is not constant, varying yearly and in the 24h hours of the day, which influence significantly the activity patterns of each individual (Beier and McCullough 1990, Signer et al. 2011). In summer, with high temperatures is expected that animals lower their activity rhythm during the day, where the temperature is usually elevated. So it is normal to see more activity from individuals, during the crepuscular time and during night in summer season (Beier and McCullough 1990, Scheibe et al. 2009). Contrarily, in late autumn and during winter, lower temperatures tend to slow the daily activity rhythm of animals, especially during winter night and before the sunrise, for both red deer (Arnold et al. 2004), and roe deer (Krop-Benesch et al. 2013), which is the time of the year where the temperatures reach their lowest rate (Pagon et al. 2013). These previous studies are in agreement with the results obtained in our study for both species. For the two species in study, it was obtained less activity at late autumn (November) and during winter months (December to February). Indeed, roe deer had a low detection rate in autumn and was not detected in the peak of winter, when only some females were observed walking. These climate constraints, may have provoked the migration of roe deer species to lower areas of

Lousã Mountain outside of the study area, probably to agricultural areas (Ribeiro 2018) where the availability of food seems to be higher.

Besides temperature variation, the availability of food resources can limit the proportion of time active of each individual (Pęksa and Ciach 2018). In spring, when occurs a great regrowth of huge variety plant species, both red and roe deer increased their feeding activity (also obtained by Ribeiro 2018). Although in summer when the food quality decreased, both species increased their feeding behaviour. In the case of roe deer, the rut season occurs mid-July and mid-August and, they need to have a greater body condition to face the hard constraints that rut brings. In the case of red deer, the increasing of feeding behaviour, can be also explained by the constraints of the rut season, which happens between September and October, leading them to prepare their physical condition for that period of the year. Both species, seek to be at the maximum of their body conditions to ensure the reproductive success and the survival of offspring. In fact, these results are in agreement with previous studies on red deer in the same study area, in which males moved to areas with better food during the months before the rut season to ensure their physical conditions (Alves et al. 2013, 2014).

The diet of red deer is usually different from that of the roe deer, and, usually, they choose distinct food resources over the year. However, when food availability is low, both species overlap their diet (Ribeiro 2018). In winter and summer, the availability and quality of food decrease, and for that reason, red and roe deer compete for the same food resources (Storms et al. 2008). This competition between the species may have led the roe deer to move to other areas, avoiding areas with a higher presence of red deer.

The results obtained about the presence of both species in each habitat demonstrate that red deer had a higher presence in the shrublands, while roe deer were almost not detected in this habitat type. Other study made in Lousã Mountain demonstrated that the presence of roe deer in this habitat type was low or even null (Ribeiro 2018), indicating that roe deer avoided areas where the presence of red deer was higher. Other study made in Słowiński National Park (SNP), in Poland, revealed also some competition between these two species (Borkowski et al. 2021). The absence of roe deer in the shrublands may not be only due to the presence of red deer, but also due to their morphology and height, that makes harder for roe deer to move in areas where the shrublands are dense and with more than 50cm of height.

As seen in many other species, especially in ungulates, like in *Axis axis*, *Ovis aries musimon* (Centore et al. 2018) and *Capra ibex* (Signer et al. 2011), red and roe deer also demonstrated two distinct peaks in their daily activity rhythm in most months, one at sunrise and other at sunset. These well-separated peaks for the species in study were demonstrated in other studies, for roe deer (Krop-Benesch et al. 2013, Pagon et al. 2013, Stache et al. 2013) and red

deer (Kamler et al. 2007, Relvas 2020). The activity patterns of both species (red and roe deer) varied significantly throughout all study year and during day/night.

The activity budget hypothesis (ABH) predicts that sexual body-size dimorphism induces different energy demands between animals, which leads to different activity patterns. Sexual differences in activity budget vary with body size dimorphism, and high degrees of sexual dimorphism ($\geq 20\%$) leads to distinct activity patterns between males and females (Ruckstuhl and Neuhaus 2002). In non-dimorphic species with low body size dimorphism ($<20\%$), males and females are expected to be more synchronized in their activity patterns.

In Lousã Mountain, both species in study were observed under the same conditions and same external factors. However, red and roe deer display different levels of sexual body-size dimorphism and, so, it was expected higher differences in synchronization of each species. In red deer, with higher rates of body-size dimorphism (50%), it was expected greater differences in time spent active between males and females. Contrary, roe deer, with lower degrees of sexual body-size dimorphism ($<5\%$), it was expected greater synchronies of activity between females and males.

Within-year time window, red deer males and females seemed to be synchronized in their activities. However, looking to the finer scales (monthly) the synchronization changed across the year. Indeed, red deer's synchronization reached its peak in the rut season (September/October), decreasing in the following months. Females spent more time feeding than males during breeding season, at the point where males increased their movement activity (also obtained by Relvas 2020), probably to search for possible mates, to protect females against mating rivals, or even to protect an area from intruders (Pépin et al. 2009). Nevertheless, this may be a "false" synchronization, and a results of both sexes being active, although not performing the same behaviour at the same time (Ruckstuhl and Neuhaus 2002).

For roe deer, results showed a lower synchrony on a broad scale (year) comparatively with red deer. This result must be carefully interpreted since it is mainly reflecting spring and summer, and no other periods where a higher asynchrony was expected for roe deer, like the post-rut or winter dispersal. In March, when males' territorial defence strategy began, the activity overlap between sexes was lower. In the following month, males and females tended to be more synchronized, when territorial males succeeded in driving out rival males. These results are in agreement with those obtained by Villerette et al. 2006. Until late August (peak of rut) the synchronization of males and females were maintained, after this period occurred a decreased in the activity overlap, at the point when male's territoriality ended. Males' movement was intensified in September, probably when they left the rutting areas. This was

followed by an increase in their feeding, in October, probably to obtain favourable body conditions for winter.

Smaller animals are characterized by a fast passage of food, due to their small rumen, consequently, they spent more time feeding to compensate for the low digestive efficiency. On the opposite, bigger animals, with big rumen size, can digest efficient food, passing more time in an inactive state (resting or ruminating) (Ruckstuhl and Neuhaus 2002). These assumptions are consistent with the forage-selection hypothesis for body-size dimorphic species, that states that females need more food intake and so spent more time feeding, and males being larger, spend more time ruminating or resting (lying) (Ruckstuhl 1998, Pęksa and Ciach 2018). Furthermore, lactating females, that show high energy demands, have distinct feeding behaviour from males and even from non-lactating females (Ruckstuhl and Neuhaus 2002). Less differences are expected in non-dimorphic species or even in less dimorphic species, as it is the case of roe deer.

The sexual differences in the activity budget over the study year showed that red deer females spent more time than males in feeding behaviour, and males spent more time performing other behaviours, which included lying, ruminating, olfactory control and roaring. Indeed, this seems to be related to both forage-selection hypothesis and activity budget hypothesis. Studies on other ungulates (Xu et al. 2012, Wang et al. 2018b, Fawzy et al. 2019) with more than 20% of sexual body-size dimorphism also showed a similar results, supporting the assumption of energetic demands.

Red deer dispended some time in vigilant behaviours, while roe deer seemed to be less vigilant. This can be explained by their small size and the agility to escape. Indeed, the low number of contacts of roe deer can be explained also considering this. Camera traps, when detect movement, are activated, and take 3 photographs, followed by a video of 1 minute, and roe deer, being fast and with a slippery behaviour, could activate the camera however not being present enough time to be detected. Other reason for this difference in vigilant behaviour can be explained by the habitat type preferred by each species. For instance, red deer used more shrublands (open habitats) that makes them more exposed than in closed habitats, which are the preferred habitat of roe deer (Alves et al. 2014, Keten 2016).

Both red and roe deer females give birth in the same season (end of May until mid-June) when their nutrient demands increase. In fact, females' from both species increased feeding behaviour during this months, avoiding losing body mass due to lactation periods (Stache et al. 2013). A study made in China with *Moschus chrysogaster* (Xiaofeng et al. 2010), reported that feeding behaviour in females increased in lactation periods. At the breeding season females tend to be more isolated from other individuals, moving to habitats where the safety

of offspring is ensured. Contrary, males being free from parental care gives them the possibility of maximizing their body conditions (Wang et al. 2021), supporting the assumptions of the predation-risk hypothesis.

Despite the robust data obtained for red deer species, giving good knowledge of their behaviour, the low number of contacts of roe deer in some of the study period compromised results and conclusion driven from this study for this species in Lousã Mountain. In this case, and for a greater comparison between activity patterns of red and roe deer, it became clear the need to enlarge the study area, extending it to include other habitats, namely the agricultural areas on the surroundings of the Lousã Mountain, and where it seems to be the place where roe deer migrate specially during the winter.

The results of this project are in line with our expectations. Despite the misleading synchronization observed on a large time scale, for red deer species, the results at a fine time scale were able to demystify the apparent activity overlap. For roe deer, further studies are necessary, with a big coverage of area and habitat types, to ensure the proper surveying of this species.

Chapter V - General conclusions

This project aimed to relate a biological characteristic - the sexual body size dimorphism - with the activity patterns of each sex, following predictions on the base of the Activity-budget hypothesis. It was intended to explain if dimorphic species, such as red deer, are less synchronized due to different activity budgets when comparing with a non-dimorphic species, like roe deer, which was expected to be more synchronized.

In the line with assumption of the activity budget hypothesis, red deer were more synchronized at an expected season, namely the rut season when they join in groups to reproduction. During the rest of the year, they were less synchronized, with females being more active at feeding while males spend more time performing other behaviours. The limited data of roe deer species interfered in more robust analyses about the synchrony of males and females. However, in the line of expectation, both sexes had a similar percentage of time performing each behaviour. Comparing with red deer species, roe deer spent much less of their time in other behaviours. Results agreed with expectations, that smaller animals must be more active, to compensate lower digestive efficiencies.

In general, our results provide support to activity budget hypothesis, but it seems that the threshold of the 20% of body-size dimorphism and their associated differences in terms of energetic demands are not the only factors shaping the differences in activity patterns. Furthermore, our results are also in line with those expected by reproductive strategy hypothesis and forage selection hypothesis, which in fact helped to explain some of the behavioural patterns observed in both species.

Sexual body-size dimorphism alone cannot explain the differences in the activity budget of a species, either dimorphic or non-dimorphic ones. Other external factors seem to shape the differences in the activity patterns observed for these species, such as temperature daylight hours, rainfall, quality and quantity of resources, predation, habitat type, among others.

Further studies are needed, specifically, those with longer sampling periods to be enable a large number of contacts of both species, especially of roe deer. The use of more cameras to cover habitats often chosen by roe deer, in lower altitudes, near agricultural areas seems also a good strategy for future works.

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