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SEXUAL SEGREGATION PATTERNS OF RED DEER: DECIPHERING SPECIES-SPECIFIC AND POPULATION-SPECIFIC PATTERNS

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Padrões de segregação sexual do veado: Decifrando padrões específicos da espécie e padrões específicos da população

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Do Choupal até à Lapa foi Coimbra meus amores
A sombra da minha capa deu no chão abriu em flor

- José Afonso, *Saudades de Coimbra*

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ABSTRACT

Sexual segregation is a common phenomenon among social animals. It is characterized by the separation of the sexes outside the breeding season. One of the species to exhibit this phenomenon is the red deer, our study species. This ungulate is known to be vastly distributed around the world, and the largest mammal in both Portugal and Denmark.

In this study, we aim to compare the patterns of sexual segregation of different red deer populations and interconnect them with population and environmental factors. We used camera-traps as our field method and placed them in various sampling points scattered in Lousã Mountain (Portugal) and Central Jutland (Denmark).

Our results showed a significant difference in the mean number of individuals per group and a different aggregation period during the breeding season, in both countries. With the information obtained, we found that when different red deer populations are subjected to distinct environmental factors, changes in the start and duration of the rut season may arise. Globally, our results provide support to both the predation-risk hypothesis and the forage-selection hypothesis, as they provide an explanation for some of the observed sexual segregation patterns.

In conclusion, we recognise that environmental factors, such as latitude, day-length and temperature can be crucial to better understand red deer grouping dynamics. In the future, further research, to comprehend the riddles behind sexual segregation and the triggers to rut, and a better assessment of the species' activity patterns is necessary, as well as a comparative large-scale survey between various populations.

Keywords: Red deer; Sexual segregation; Grouping patterns; Camera-traps; Environmental factors.

RESUMO

A segregação sexual é um fenómeno comum entre animais sociais. É caracterizado por uma separação dos sexos fora da época de reprodução. Uma das espécies a exibir esse fenómeno é o veado, a nossa espécie em estudo. Este ungulado é conhecido por estar amplamente distribuído pelo Mundo, sendo o maior mamífero em Portugal e na Dinamarca.

Neste estudo, pretendemos comparar os padrões de segregação sexual de diferentes populações de veados e interligá-los com fatores populacionais e ambientais. Utilizámos camera-traps como método de campo e colocámo-las em vários pontos de amostragem dispersos na Serra da Lousã (Portugal) e no Centro da Jutlândia (Dinamarca).

Os nossos resultados mostram uma diferença significativa no número médio de indivíduos por grupo e um período de agregação diferente durante a época reprodutiva, em ambos os países. Com as informações obtidas, descobrimos que, quando diferentes populações de veados estão sujeitas a fatores ambientais díspares, podem ocorrer mudanças no início e na duração da brama. Globalmente, os nossos resultados fornecem suporte para a hipótese predation-risk e a hipótese forage-selection uma vez que permitem explicar alguns dos padrões de segregação sexual observados.

Em conclusão, reconhecemos que fatores ambientais como latitude, duração do dia e temperatura podem ser cruciais para entender melhor a dinâmica de agrupamento dos veados. No futuro, pesquisas adicionais, para compreender os enigmas por trás da segregação sexual e os estímulos para a brama. De igual forma, é necessária uma melhor avaliação dos padrões de atividade da espécie, bem como um levantamento comparativo em larga escala entre várias populações.

Palavras-chave: Veado; Segregação sexual; Padrões de agrupamento; Camera-traps; Fatores Ambientais.

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1.1. Sexual segregation

1.1.1. Concept

Sexual segregation is a common phenomenon among social mammals and is described as the male and female separation outside the breeding season (Ruckstuhl, 2007; Ruckstuhl & Neuhaus, 2002). It is a behavioural pattern that occurs at different time and spatial scales and ecological scenarios, on top of having important management and conservation implications (Main, 2008; Main et al., 1996).

Many hypotheses have been proposed to explain sexual segregation in ungulates, but a complete agreement is lacking in the scientific community (Alves et al., 2013b; Bonenfant et al., 2007; Bonenfant, Loe, et al., 2004; Ruckstuhl, 2007). The ability to reach an understanding is delayed by the various terminologies presented, combined with an absence of measurement ability (Bonenfant et al., 2007), and standardized field methodologies.

In polygynous ungulates, like our study species, *Cervus elaphus*, functional and causal explanations can be used to interpret sexual segregation. These are influenced by social, spatial, and temporal factors such as the periodicity of mating opportunities, population densities, resource distribution, and environmental conditions (Main et al., 1996; Ruckstuhl & Neuhaus, 2000). These factors affect the degree of sexual segregation, causing it to be highly variable between populations (Putman & Flueck, 2011).

1.1.2. Hypotheses

Five main hypotheses were described to explain sexual segregation. These hypotheses are mostly based on (1) sex-differences in vulnerability to predation or reproductive strategies (predation-risk or reproductive strategy hypothesis); (2) sex-differences in digestive abilities and consequently forage selection (forage-selection hypothesis); (3) sex-differences in activity budgets (activity-budget hypothesis); (4) differences in social preferences (social-affinity hypothesis) and (5) differences in social-factors (social-factor hypothesis) (Ruckstuhl, 2007).

The predation-risk hypothesis (or reproductive strategy hypothesis – RSH) predicts that male exploit areas where nutritious forage is always abundant (except in the breeding season), even if these areas have a high predation risk (Main et al., 1996; Main

& Coblentz, 1996; Ruckstuhl, 2007). The females, on the other hand, choose areas with higher security to offspring (e.g., areas with vegetation cover or escape habitats), considering that the latter is more vulnerable to predation (Bonenfant, Loe, et al., 2004; Main, 2008; Main et al., 1996; Ruckstuhl & Neuhaus, 2000, 2002). The areas chosen by females also have to present optimal conditions to ensure offspring survival, such as the presence of water during parturition and lactation (Main et al., 1996; Main & Coblentz, 1996). This type of segregation peaks around calving time (birth of offspring) and it is ultimately attributed to sex differences in reproductive strategies (Bonenfant, Loe, et al., 2004; Ruckstuhl, 1998, 2007). The female's reproductive strategy is dictated by the offspring's survival, whereas the male's is dictated by an increase in energy reserves, in preparation for the breeding season (Main et al., 1996; Ruckstuhl & Neuhaus, 2006).

The forage-selection hypothesis (FSH) assumes that the sexes segregate due to differences in body size, which lead to different energy requirements and therefore different forage selection (Ruckstuhl & Neuhaus, 2000). This hypothesis states that females, because of their smaller body size and therefore lower digestive efficiency, need higher quality foods, in opposition to males, that feed on abundant, low-quality, and high-fibre forages (Bowyer, 2004; Han et al., 2020; Main et al., 1996; Main & Coblentz, 1996; Ruckstuhl, 2007). This type of segregation peaks when differences in the spatial distribution of high- and low-quality forages are highest (Main et al., 1996), and can also happen between lactating and non-lactating females (Bowyer, 2004; Main & Coblentz, 1996; Ruckstuhl & Neuhaus, 2006).

The activity-budget hypothesis (ABH) presumes that a social group can only be cohesive if all its members have synchronized activities (e.g. foraging and resting) (Conradt & Roper, 2000). It also expresses that mixed-sex groups have a lower level of activity synchrony between their individuals than single-sex groups, resulting in intersexual differences in activity rhythm (Bonenfant, Loe, et al., 2004; Conradt, 1998). This assumption leads to different activity-budgets in males and females, even when feeding on the same plants and in the same habitat (Ruckstuhl & Neuhaus, 2000). As a consequence, mixed-sex groups are more likely to segregate (except in the breeding season) than single-sex groups, which are more stable in terms of homogeneity in activity patterns (Bonenfant, Loe, et al., 2004; Conradt, 1998). That happens because activities synchronization in mixed-groups may be too costly to maintain, therefore animals with similar body size and energetic needs (same age, sex-classes and reproductive status) form groups to minimize this cost (Bon & Campan, 1996; Ruckstuhl & Neuhaus, 2000, 2006).

The social-affinity hypothesis (SAH) proposes that there is an innate preference for the sexes to group, leading males to interact more with other males and females to do the same with other females (Bon & Campan, 1996; Ruckstuhl, 2007). According to this hypothesis, the sexes display a different social motivation to interact, leading to behavioural incompatibility (Alves et al., 2013b). Even if the group contains individuals with very dissimilar behaviours (e.g. females and offspring), they stay together, because the individuals have a shared motivation and carry their maintenance activities (Ruckstuhl & Neuhaus, 2006). However, even though this assumption increases group cohesion within single-sex groups, similarities in nutritional requirements and activity-budgets are more likely to hold this cohesion (Bon & Campan, 1996; Ruckstuhl, 2007; Ruckstuhl & Neuhaus, 2000).

The social-factor hypothesis (SFH) invokes an aspect of aggression of one sex towards the other (Main et al., 1996; Ruckstuhl, 2007; Ruckstuhl & Neuhaus, 2006), as well as, a necessity, in males, to interact with other males (Alves et al., 2013b; Main et al., 1996). This stems from the fact that males develop fighting skills, evaluate rivals and establish hierarchies, more efficiently, when in only male groups (Wang et al., 2018). In fact, sexual segregation may simply be a consequence of male-group preferences without any direct function (Ruckstuhl, 2007; Ruckstuhl & Neuhaus, 2000). The aggression aspect of this hypothesis explores the fact that males become more aggressive with each other, in the presence of females, therefore becoming less social to avoid costly social interactions with other males (Ruckstuhl, 2007; Ruckstuhl & Neuhaus, 2006; Wang et al., 2018; Weckerly, 2001).

As previously mentioned, the literature has many explanations for sexual segregation in ungulates. To facilitate the understanding process and therefore present a better overview of the hypotheses, a summary of the assumption associated with each of them is shown in Table 1.

Table 1. A review of the sexual segregation hypotheses and its predictions.

Hypotheses	Predictions			Sources
	Intersexual segregation	Intrasexual segregation	Habitat segregation	
Predation Risk (RSH)	Males and females segregate most during calving and lactation	-	Females choose areas that provide food and water resources, and that increase security to offspring	(Main et al., 1996; Main & Coblentz, 1990, 1996)
Forage Selection (FSH)	Males and females segregate because they select different quality food (differences in digestive efficiency)	Non-lactating females segregate from lactating females due to their distinct nutritional needs	Males choose areas with more ubiquitous and fibrous plants than females	(Barboza & Bowyer, 2000; Beier, 1987; Bowyer, 1984; Demment & Soest, 1985)
Activity Budget (ABH)	Males and females have different activity patterns due to differences in body size, energy requirements and digestive efficiency	Females with offspring segregate from other females because they have different activity patterns	Females show a greater proportion of foraging activity, while males spend more time ruminating	(Conradt, 1998; Ruckstuhl, 1998)
Social Affinity (SAH)	Males and females show a preference for the same sex groups outside the breeding season	Females do not segregate due to differences in their reproductive status; Males of different ages segregate into single age groups	-	(Bon & Campan, 1996)
Social Factor (SFH)	Males and females segregate due to aggressive behaviours, which associated with social preferences lead to unisex groups	Males of different ages do not segregate into single age groups	-	(Main et al., 1996)

1.2. Study species – Red deer, *Cervus elaphus*

1.2.1. Species distribution

Of the existing 40 species of deer, 15 live primarily in the temperate and cold zones (30°- 80° latitude) (Gyllensten et al., 1983; Lincoln, 1992).

Red deer is indigenous[1] within the 30º-65° N latitude zone, with a Holarctic[2] but discontinuous distribution (Meiri et al., 2018; Mitchell et al., 1977). It is one of the most widely distributed mammals in the world, occurring naturally in temperate and southern Europe, North America, North Africa, and Central and East Asia (Salazar, 2009). In Europe, red deer occurs throughout most of the continent except in northern Scandinavia, Finland, and Iceland (Zachos & Hartl, 2011).

There are several subspecies of red deer, such as the British red deer (*C. e. scoticus),* Norwegian red deer (*C. e. atlanticus*), Swedish red deer (*C. e. elaphus*), Central European red deer (*C. e. hippelaphus*) and the Iberian red deer (*C. e. hispanicus*) (Baskin & Danell, 2003; Zachos & Hartl, 2011). The subspecies are divided into a western lineage (Europe, North Africa, and Western Asia) and an eastern lineage (Eastern Asia and North America) (Meiri et al., 2018).

The largest wild populations of this species, in Portugal, are found in Alentejo, International Tagus Natural Park, Lousã Mountain, and Montesinho Natural Park (Coelho, 2018). In Denmark, it is known to be dispersed all over the country (Strandgaard & Simonsen, 1993).

1.2.2. Morphology and Ecology

Cervus elaphus, known as red deer, is a mammal of the Cervidae family and an ungulate, meaning that it is a hoofed animal. It is a species characterized by extreme diversity in morphology, physiology, ecology and geographical distribution (Asher et al., 2019).

Red deer is a highly sexually dimorphic species with marked segregation of the sexes (Bonenfant et al., 2007), with males being larger than females. This sexual dimorphism is described as a morphological differentiation of sexually mature males and females (Fairbairn, 1997) and is noticeable by their body size and by the presence of secondary sexual characters. However, sexual size dimorphism is undetectable in

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[1] A species is indigenous to a region if its presence is the result of only natural processes, with no human intervention.
[2] A biogeographic realm that encompasses most habitats found throughout the northern continents of the world.

calves (>1 year old) (Lincoln, 1971a; Mattioli et al., 2003), leading to difficulties in sexing them.

Red deer is the second largest European deer (Peixoto, 2014), varying considerably in weight throughout their world range (Mitchell et al., 1977; Suttie & Hamilton, 1983). The Iberian subspecies differs from others mainly due to its smaller size (Garde et al., 2006).

Males (stags) weigh on average 160 kg, and females (hinds) 108 kg (males are 1.5 bigger than females) (Peters et al., 2019). In Mediterranean regions, stags are approximately 175-250 cm long, weighing 130-180 kg, and hinds are 160-210 cm long, weighing 80-120 kg (Garcia, 2016; Soriguer et al., 1994). These differences express a sexual dimorphism of 37±3% in terms of body size (Alves et al., 2013b). Stags from eastern Europe are the largest of them all, weighing up to 350 kg (Suttie & Hamilton, 1983).

Within this species characteristics, we can identify an elongated body and snout, broad robust head with lateral eyes (Peixoto, 2014). Eastern red deer have longer snouts and shorter foreheads whilst the Danish red deer have larger mandibles (Lowe, 1972). The tail is short and brown in contrast with the perianal area which has a whiter colouration (Soriguer et al., 1994).

Red deer calves, up to 2 months of age, have white dorsal spots, which favour camouflage in the vegetation, as well as a dark streak in the dorsal midline, a characteristic that they lose around six months of age (Peixoto, 2014). We can also discriminate the age of an individual up to 3-4 years of age, by studying the gradual changes in dentition (Azorit et al., 2002).

The individuals of this species alternate between a darker reddish-brown coat colour in summer and a grey or grey-brown woolly coat in winter that they shed in May and June (Kay & Ryder, 1978; Ryder & Kay, 1973). This is also affected by body condition, with impaired animals tending to moult late (Mitchell et al., 1976). The winter moult, in October, is less noticeable considering that the new coat is growing (Ryder, 1977). Moulting has two functions (1) replacement of worn-out hairs and (2) providing different coats for each season, allowing appropriate colour changes (in comparison with the environment) and insulation (Ryder & Kay, 1973).

When mature, stags in good condition cast their antlers in March and April, as the breeding season (rut) approaches, and also lose their "velvet" skin (Hyvärinen et al., 1977; Mitchell et al., 1976). This velvet skin (short hairs), when frayed off, by late July and August, leaves the stags with hard dead headpieces (Goss, 1969a; Kay & Ryder,

1978; Lincoln, 1971b; Mitchell et al., 1976). These antlers are bony structures that grow in stags, during the summer months when food is usually abundant (Hyvärinen et al., 1977; Suttie et al., 1984). Their size is correlated with the males breeding success (Kruuk et al., 2002) and usually start to develop after the first year of age (Lincoln, 1971a), being also related to age. At this time, we can also witness the body becoming more robust, the coat hairier (longer), the neck thicker and the ears more separated than in females of the same age (Peixoto, 2014; Ryder, 1977).

From autumn to spring, when the animal's nutrition is poor, the antler bone remains attached to the pedicle but is now dead and inert (Hyvärinen et al., 1977). It only begins to grow again once the hinds are carrying new foetuses, allowing the males to spend more energy in feeding activities (Georgii & Schröder, 1983).

The maximum lifespan in this species is about 20 years (Mitchell et al., 1977) being the average for males 9-11 years old and for females 11-13 years old (Clutton-Brock et al., 1986). The life of an individual can be, therefore, divided into three phases (1) <5 years, active growth and development; (2) 5-10 years, maximum body size, condition and reproductive efficiency; and (3) >10 years, progressive decline (Mitchell et al., 1976). During the first years of life, while the growth potential is highest, stags grow as large as they can and as fast as they can (Mitchell et al., 1976; Suttie & Hamilton, 1983). Meaning that sexual selection will favour faster early growth rates in males, with a greater allocation of parental resources to juvenile males (Clutton-Brock et al., 1981). This happens because males have to be heavier than females to have the same chance of survival (Loison et al., 1999).

1.2.3. Grouping dynamics

Red deer shows marked sexual segregation, and lives mostly in unisex groups, except in the breeding season (Coelho, 2018; Mitchell et al., 1977; Peixoto, 2014).

Group size is variable between and within populations (Mitchell et al., 1977) and can vary depending on population density (Baskin & Danell, 2003; Jędrzejewski et al., 2006). Most red deer prefer to stay in small groups, varying between 1-3 individuals (Alves, 2013), with the group mean being around 2.4 individuals, in Portugal (Salazar, 2009).

Individuals can be grouped into three age classes (1) calves (<1 year); (2) sub-adult (between 1-2 years in females and 1-3 years in males) and (3) adult (>2 years for females and >3 years for males) (Alves, 2013; Garcia, 2016). Based on group composition (number of animals of each sex and age-class), red deer groups can be

classified into five typologies (1) solitary males; (2) solitary females; (3) bachelor groups; (4) matriarchal groups and (5) mixed groups (formed by at least one adult male and one adult female) (Alves, 2013; Baskin & Danell, 2003).

Matriarchal groups are the most common group outside the breeding season and are formed by adult females, sub-adult females and offspring (<1-2 years old males or females) (Santos, 2009; Soriguer et al., 1994). As soon as mature (adult), females rarely disperse from their natal group, associating with their mothers and other maternal figures throughout their lives, with overlapping territories and feeding areas (Carranza, 2017; Clutton-Brock et al., 1986; Coelho, 2018; Soriguer et al., 1994). The females establish themselves around the territory occupied by their mother, maintaining a high level of relationship with each other, due to the bond formed between family members (Baskin & Danell, 2003; Soriguer et al., 1994).

The opposite happens with males. When they mature, they gradually isolate themselves, until they are independent of their maternal group, and leave their home ranges (Georgii & Schröder, 1983; Soriguer et al., 1994). Males join the so-called bachelor groups, which tend to consist of similarly aged males, fluctuating between 2-7 individuals (Santos, 2009). These males have a strong hierarchy of dominance established (Carranza, 2017) and invest substantial energy to reach a higher rank (Esattore et al., 2020, 2021).

Larger and mixed groups can be expected in the breeding season, due to the species reproductive behaviour. Males and females come together to mate, forming a harem (group of hinds protected and monopolised by a male) (Jędrzejewski et al., 2006; Peña et al., 2021).

Stags aged 7-11 years (prime stags) are the first to hold harems and usually defend them from other stags, for about 2-4 weeks (Clutton-Brock & Albon, 1979). Young stags (2-5 years old) rarely hold harems and if they do, they are the last to do so (Clutton-Brock et al., 1979; Clutton-Brock & Albon, 1979; Gibson & Guinness, 1980a, 1980b; Mitchell et al., 1976). However, they attempt to abduct hinds from the older stags' harems, in a strategy called 'kleptogamy', which has proven to be unsuccessful, considering young stags are unable to control or defend the abducted hinds (Clutton-Brock et al., 1979). Even if unsuccessful, it allows young stags to learn the necessary skills for handling hinds (Clutton-Brock & Albon, 1979).

Females, occasionally, leave and enter harems on their own, while in their oestrus (McComb, 1991). There is also evidence that they join larger harems, so they can experience lower rates of harassment from other males (Sánchez-Prieto et al., 2004).

1.2.4. Reproductive behaviour

Red deer's sexual behaviour has always been a matter of significant historic and scientific interest. However, it is important to recognise that a universal reproductive function does not exist, as it is detected in cool temperate climes, where some cervids exhibit highly seasonal patterns of births, while others are completely unseasonal in equatorial regions (Asher et al., 2019; Lincoln, 1992; Putman & Flueck, 2011).

When living in woodland habitats, red deer females become sexually mature between the 1 ½ and 2-year mark and, when mature, tend to breed every year (Mitchell et al., 1986; Mitchell & Lincoln, 1973; Putman & Flueck, 2011). They can also skip breeding events, depending on the investment in their offspring (Moyes et al., 2006).

Stags are polygamous meaning that is possible to have surplus (more than needed) males in the population (Yalden et al., 1978). The average ratio varies between 1 to 5 females per male (Clutton-Brock & Lonergan, 1994). These species individuals are short-day breeders[3], being essentially continuous breeders, whose reproductive processes are suppressed for part of the year, lapsing into a reproductive quiescence[4] each year (García et al., 2002; García, Landete-Castillejos, Zarazaga, et al., 2003; Lincoln, 1971a, 1971b; Mitchell & Lincoln, 1973). The breeding season, known as the rut, occurs around the autumn equinox, the pregnancies extend to winter and the parturitions take place in late spring/early summer (García, Landete-Castillejos, Zarazaga, et al., 2003; Mitchell & Lincoln, 1973).

Rut is indicated by the presence of disturbed soil, vegetation patches, bathing holes in streams and the roaring of males (Baskin & Danell, 2003). Stags roar loudly and repeatedly during the rut season, maintaining rates of up to 8 roars/min (Charlton et al., 2007b; Clutton-Brock & Albon, 1979; Reby & McComb, 2003b). Roaring repeatedly is costly, in terms of energy expenditure and detection by predators, therefore forming a link with the stags' body condition (Mitchell et al., 1976; Reby et al., 2001). Juvenile stags, even if fertile, don't roar, considering that this secondary sexual feature is not fully developed during the first 3 years of their life (Lincoln, 1971a). Roaring ability declines throughout the breeding season, seeing that the individual's total activity and body condition have a negative correlation (Prebanić & Ugarković, 2015; Reby et al., 2001).

At the beginning of the rut, males move to traditional rutting grounds, attempt to form harems and, once they have one, they move to new feeding and sheltered areas, establishing and defending a territory (Baskin & Danell, 2003; Carranza et al., 1990;

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[3] That breed at times of the year when the day length is shorter, and the night is longer.
[4] Dormancy or inactivity.

Kruuk et al., 2002; Mitchell et al., 1976). The harem holders engage in reciprocal roaring with challengers (Clutton-Brock & Albon, 1979; Davies et al., 2012).

Red deer hinds are seasonally polyoestrous, with oestrous cycles of approximately 18 days from October to March, even if prevented from mating (García, Landete-Castillejos, Gomez-Brunet, et al., 2003; Guinness et al., 1971; Lincoln & Short, 1980). However, the hinds in better condition tend to ovulate or conceive first while the poorer ones conceive later or not at all (Mitchell et al., 1976). A mature hind may be either "milk" (with a current year's calf) or "yeld" (no calf) with the milk hinds generally having later conception dates than yeld hinds (Mitchell et al., 1986; Mitchell & Lincoln, 1973).

Multiple pregnancies are rare, and usually, females give birth to a single calf each year, rearing 0 to 12 calves during their lifetime (Clutton-Brock et al., 1981; Gibson & Guinness, 1980a; Guinness et al., 1971; Mitchell et al., 1977; Mysterud et al., 2000). Conception is followed by a gestation period between 230 and 260 days, the mean being 231 days (Guinness et al., 1971; Lovari et al., 2018; Soriguer et al., 1994).

The offspring are born (calving) in the early summer which appears to be the most favourable time considering that high nutritional food is most abundant , and temperatures are more suitable (Bocci et al., 2012; García et al., 2002; Lincoln, 1992). Late conception, with calving in the late autumn, is associated with lactational failure and can lead to calves not surviving the winter (Clutton-Brock, Major, et al., 1987; Lincoln & Short, 1980; Yalden et al., 1978). Male calves suckle more frequently than females, require longer gestation and are larger at birth, therefore mothers who have successfully reared sons are expected to fail to breed the following year compared to those that reared daughters (Clutton-Brock et al., 1981; Myers, 1983).

Hinds also have a dominance rank, influenced by their age, adult hind body weight as well as birth weight, and usually female calves inherit their mother's dominance rank (Carranza, 1988; Clutton-Brock et al., 1981, 1986; Fløjgaard et al., 2017; Hall, 2010). These dominant hinds tend to be in higher ground, lead the way for other hinds and have close to 10% more calves than subordinates (Carranza, 2017; Clutton-Brock et al., 1986; Mitchell et al., 1986). This can be explained considering that the fertility of females is linked with body condition since heavier hinds have the greatest probability of getting pregnant (Albon et al., 1986).

It was stated that there is no concrete indication that female choice in red deer exits (Carranza et al., 1990). However, there is contradictory evidence, since females can choose between males based on their roaring characteristics, such as moving towards male roars with lower formants (resonance vocal tract frequencies) as they are

expected to be larger and have higher fitness (Charlton et al., 2007a, 2007b; McComb, 1991; Reby et al., 2001; Reby & McComb, 2003a).

1.2.5. Feeding habitats

Satisfying nutritional demands is the most fitness-related task for any animal, and to achieve this goal, ruminants can sustain themselves in most vegetative zones (Kay, 1987). As a ruminant, red deer have a much broader feeding niche than other Cervidae (Baskin & Danell, 2003) and is classified as an intermediate, opportunistic and mixed feeder (Hofmann, 1989; Zweifel-Schielly et al., 2012).

Red deer feed on a broad range of plants (minimum 145 species) (Gebert & Verheyden-Tixier, 2001). Its diet switches between grazing (grass and sedges) mixed with browsing (shrubs, shoots and leaves of broadleaf and coniferous trees) (Ahmad et al., 2016; Alves, 2013; Gebert & Verheyden-Tixier, 2001; Hofmann, 1989; Kay, 1987; Storms et al., 2008). In autumn, red deer's diet may rely on fruits and seeds, varying with food accessibility and seasonality (Hofmann, 1989; Lovari et al., 2018).

The species diet varies between sexes, and it's associated with behaviour plasticity (e.g. foraging behaviour) according to the environmental limitations, such as plant biomass and quality that differ between habitats and seasons (Bugalho et al., 2001; Gebert & Verheyden-Tixier, 2001; Ruckstuhl, 1998; Smolko et al., 2018; Zweifel-Schielly et al., 2012).

Hinds use more productive areas, in terms of soils, due to their richer and more diverse vegetation (Barboza & Bowyer, 2000; Staines et al., 1982; Yalden et al., 1978). Females select these areas as a necessity, as they are lactating or pregnant (higher demands for energy and protein), to secure foetal and early-calf survival (Barboza & Bowyer, 2000; Main et al., 1996; Yalden et al., 1978).

Stags, on the opposite, occupy areas with less grassland, as they are incapable of getting sufficient nutrition from heavily grazed pastures and need to feed on poorer foods but with higher available biomass (abundant) (Barboza & Bowyer, 2000; Main et al., 1996; Staines et al., 1982). This indicates that they must compensate for this lower quality food, by eating in relation to their larger size (Staines et al., 1982).

In Mediterranean environments, shrubs (e.g., *Pterospartum tridentatum* and *Ulex minor*) is expected to be a major component of the red deer's diet, during the hot and dry summers, when most grasses senesce, leading to likely nutritional constraints (Bugalho et al., 2001; Bugalho & Milne, 2003; Garcia, 2016).

1.2.6. Seasonal patterns

Many aspects of behavioural ecology of animals are not fixed elements and show significant variation under different circumstances (Putman & Flueck, 2011). In most terrestrial animals, daily activity is regulated by the endogenous circadian clock and responds directly to light levels (Vazquez et al., 2019).

Red deer, as a seasonal breeder, may be separated into two groups, according to the latitude (north and south of 30ºN), given that the behavioural differences between populations are suggested to be environmental rather than genetic (Bonenfant, Loe, et al., 2004; Fletcher, 2009; García et al., 2002; Lincoln, 1992). Those environmental differences stem from the fact that temperate climates have highly seasonal physiology with an endogenous circannual rhythm (persists under constant conditions) that generate long-term cycles, in contrast with equatorial climates that are unseasonal (Georgii, 1981; Lincoln, 1992).

Day-length has been a point of interest in the regulation of the reproductive cycle of red deer (Goss, 1969a; Lincoln, 1971b, 1992; Loudon et al., 1989; Marshall, 1937). Day-length provides individuals with a code for light and darkness. Resulting in a hormonal code that gives photoperiodic information which entrains seasonality, known as an animal's adaptive response to its environment, that changes cyclically with the season (García et al., 2002; Webster et al., 1991). These day-light fluctuations contribute to the explanation of unseasonality in equatorial and tropical regions, considering that in these regions there is an absence of seasonal fluctuations in day-lengths (Goss, 1969b).

The indicated daily cycle, of light and darkness, acts as a powerful zeitgeber[5], entraining the endogenous circadian rhythm (Daan & Aschoff, 1975; Georgii, 1981), seeing that free-ranging animals adjust their activity to the variation of day-length (Goss, 1969a; Vazquez et al., 2019). An example of this phenomenon is the replacement of antlers (antler cycle), which synchronises with changes in day-length (Goss, 1969a).

Red deer seasonal events have been proven to be responsive to a reduction in the daily photoperiod, supporting the importance of fluctuating photoperiod in the timing of reproductive events (Fletcher, 2009; Webster & Barrell, 1985). Melatonin is responsible for the transfer of photoperiodic information between mother and foetus, as well as the development of foetal tissues, and a change in the environment can affect foetal and prepubertal development (Lowe, 1967; Williams et al., 1997).

Even though photoperiod and day-length are accepted to be the main regulators in the timing of reproductive events in seasonal breeders, it is recognized that other

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[5] Periodically changing environmental stimuli.

factors can deploy modifying pressures (Fletcher, 2009; Fonseca, 1998; Mitchell & Lincoln, 1973). There is evidence of a correlation with factors such as air temperatures along with lunar phases and red deer's activity in the breeding season (Albon et al., 1987; Prebanić & Ugarković, 2015). Their activity patterns also depend on the twilights around dawn and dusk, since they show crepuscular activity (activity peaks around twilight) (Alves et al., 2014; Ensing et al., 2014; Godvik et al., 2009).

1.2.7. Conservation and Management

Red deer are economically and ecologically valuable, with a large impact on forage distribution worldwide, besides being the most important mammal game species in Europe (Mitchell et al., 1976; Seidel & Boyce, 2016; Stergar & Jerina, 2017; Zachos & Hartl, 2011). This importance stems from its large body size, broad distribution and genetic value (Sánchez-Ajofrín et al., 2020; Vilela, 2015).

More than other Cervidae, red deer have been extensively managed throughout their range (Gyllensten et al., 1983). Managements' major goal consists in minimizing economic damage associated with forestry, along with animal-vehicle collisions, and at the same time maximizing the economic gains associated with hunting and ecosystem services (Coppes et al., 2017). The intensity of management depends on the animals' body condition and diet, which can also affect the animals' ecosystem function and the areas of biodiversity conservation (Fløjgaard et al., 2017).

Ultimately, there is a need to improve the availability of quality red deer population data to put in place better sustainable management decisions (Alves et al., 2014; Milner et al., 2006). Understanding and elucidating people's perceptions of red deer is a crucial step in designing socially acceptable management strategies (Valente et al., 2020) since the ecosystem function of the species is versatile and involves more than browsing, as it is a major influence on vegetation and land use on millions of hectares worldwide (Fløjgaard et al., 2017; Mitchell et al., 1976).

When it comes to this study species, the need to improve their conservation leads us to major conservation concerns (1) threatened genetic lineages through translocations and reintroductions; (2) hybridization with other subspecies; (3) selective hunting; and (4) decline of population sizes due to habitat fragmentation (Lovari et al., 2018; Zachos & Hartl, 2011).

In a management hunting setting, the smaller sized deer or with a disease status are selected, since the managed areas can be overcrowded with overabundant species, due to the human intervention in population densities and forest management measures

(Acevedo et al., 2008; Martínez et al., 2005; Stergar & Jerina, 2017). And little is known about the extent of the changes in the genetic profile of managed populations, since the main focus is the body and antler size, and this can represent an incentive for game breeding and hunting industry (Garde et al., 2006; Gyllensten et al., 1983).

Around the world, there is a rapid expansion of red deer farming and hunting industries with commercial purposes (Garde et al., 2006; Sánchez-Ajofrín et al., 2020). They tend to be limited to landowners and their associates (state or private) along with paying leaseholders and hunting clients (Milner et al., 2006). In addition, these industries are divided into two groups, those of temperate areas and those of tropical areas (Asher et al., 2019). They select large antler and body size, in contrast, when with management reasons (Martínez et al., 2005; Mitchell et al., 1976). The antlers are used as a trophy and the meat has commercial purposes, as well as the velvet and tails glands that can be used in Chinese medicine (Baskin & Danell, 2003; Martínez et al., 2005). The increase in game meat commercial demand is due to the fact that consumers perceive free-range animals as a natural meat alternative since they are low in fat with a high protein density, are free from hormones and antibiotics and feed freely (Kudrnáčová et al., 2018; Soriano et al., 2020).

Hunting season allows management entities to identify how red deer react and are influenced by hunter pressure regardless of habitat composition (Amor et al., 2019). The animal reaction triggered by humans (anthropogenic stress) can cause conflicts with other forms of human land use, for instance, agriculture, forestry and transportation (Coppes et al., 2017; Prebanić & Ugarković, 2015). This happens because red deer are unable to distinguish between land recreational users and hunters (Coppes et al., 2017). Therefore, the animals change their activity patterns, avoiding areas with high human use and reducing their activity during the day to avoid diurnally hunters (Coppes et al., 2017; Prebanić & Ugarković, 2015; Sunde et al., 2009; Vilela et al., 2020).

As a consequence of the lack of adequate land cover, there can be an increase in predation risk, that red deer overcome by using shrubs to meet their nutritional requirements and as an anti-predator response (Asher et al., 2019; Carvalho et al., 2012; Torres et al., 2012). And as red deer land cover diminishes, browsing and bark-peeling damage are more often reported, which leads managers to consider improving access to farmland to mitigate impacts on forests (Zweifel-Schielly et al., 2012).

1.3. Aims

Sexual segregation is often associated with habitat preferences, therefore comparing patterns from populations inhabiting different environmental circumstances may help to decipher the factors that model sexual segregation patterns. To this end we aim to compare the patterns of sexual segregation of two different red deer populations (Portugal and Denmark) and interconnect them with population and environmental factors, thus setting the main goal of our study.

To meet this goal, we need to understand if all red deer populations exhibit the same sexual segregation patterns, and if these patterns are influenced by environmental and climatic factors, such as latitude, reproductive cycle stage, season, group heterogeneity and/or dependent on individual sex-age class social motivations, known to contribute to social segregation.

2.1. Study areas

Our study areas are in the central regon of two European countries – Portugal and Denmark (Figure 1). They differ in some characteristics such as latitude, longitude, and weather conditions, to name a few significant factors when studying sexual segregation between locations.

It is also worth noting that both *Cervus elaphus hispanicus* (Iberian Peninsula) and *Cervus elaphus atlanticus* (Norway) are present in the Danish red deer genetics, indicating a close relationship between Scandinavian (Danish and Norwegian) and Western European red deer (Meiri et al., 2018; Nielsen et al., 2008)
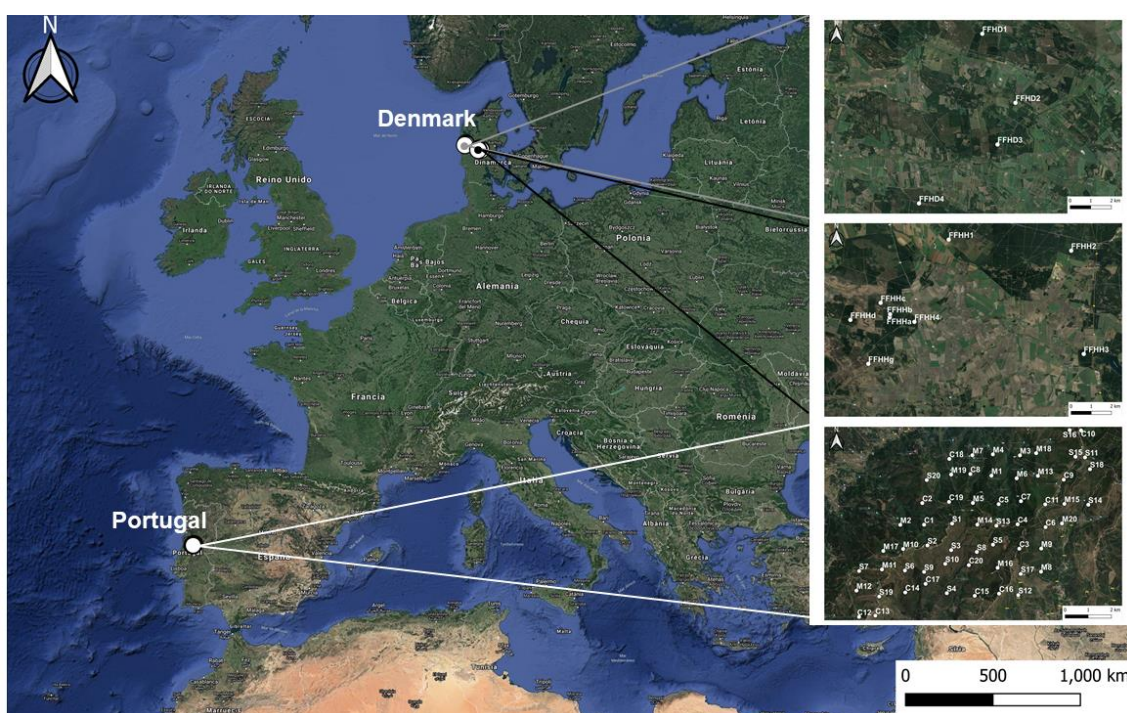
Figure 1. Study areas location. Lousã mountain in Portugal; Hoverdal, Nørlund, Harrild, St. Hjøllund and Gludsted Plantations in Denmak.

2.1.1. Portugal – Lousã Mountain

Red deer, *Cervus elaphus hispanicus*, is the largest Portuguese herbivore (Peixoto, 2014), and its increasing population size, both in number and area in Lousã mountain, can be credited to a reintroduction program, that occurred between 1995 and 1999 (Alves, 2013; Valente et al., 2017). *Cervus elaphus hispanicus*, the Iberian red deer, is a subspecies that only inhabits the Iberian Peninsula, being its largest free-living ruminant (Fonseca et al., 2006; García, Landete-Castillejos, Zarazaga, et al., 2003;

Garde et al., 2006; Sánchez-Ajofrín et al., 2020), in addition to having a higher density, in terms of population, than other ungulates (Acevedo et al., 2008).

The Lousã Mountain is located in the centre of Portugal (40º3'N, 8º15'W), and is characterized by a Mediterranean climate. This type of climate has a strong seasonality, where rainfall concentrates mostly in winter and spring, while summers are extremely hot and dry (Sánchez-Prieto et al., 2004). The medium annual temperature is around 12ºC, with a range between -4.1ºC to 35.9ºC, and the medium annual precipitation is around 827 mm (Alves et al., 2013b, 2014). The mountain altitude varies between 100-1205 m, the most frequent altitudes being 700 m to 1000 m (Alves, 2013). Altitudes below 600 m are common in the surrounding areas, near the villages and agricultural lands (where conflicts between red deer and humans are more evident) (Alves, 2013; Fonseca et al., 2006).

The ecological importance of this region was recognized internationally, for its inclusion in Natura 2000 Network, referring to areas with habitats and species of interest, under the Habitats directive (Fonseca et al., 2006).

Regarding land cover and flora, the region is mainly covered by coniferous and broadleaf trees as well as shrublands (Alves et al., 2014). Therefore, establishing three key habitat types, shrubland, coniferous and mixed forests.

The shrublands have the typical Mediterranean composition, amounting to 47.7% of the area, and being dominated by *Erica* spp. and *Calluna vulgaris* (heathers), *Ulex* spp. and *Pterospartum tridentatum* (known as carqueja) (Alves et al., 2013a). Coniferous forests amount to 34.4% of the area, with a predominance of pine trees (e.g. *Pinus pinaster*, *Pinus sylvestris* and *Pinus nigra*) (Alves et al., 2013a). Lastly mixed forests, that are composed of the conifer and broadleaf trees, amount to 17.9%, being the main broadleaf trees oak *Quercus sp.* and chestnut *Castanea sativa* (Alves et al., 2013a).

The study area also has an array of fauna, such as birds (*Circus pygargus* and *Caprimulgus europaeus*), amphibians (*Chioglossa lusitanica* and *Rana iberica*) and reptiles (*Vipera latastei* and *Lacerta schreiberi*) (Vilela, 2015). Concerning mammal fauna, the area includes populations of carnivores such as the red fox (*Vulpes vulpes*), common genet (*Genetta genetta*), European polecat (*Mustela putorius*) and the marten (*Martes foina*) (Alves, 2013).

Lousã mountain has two other ungulate species, besides red deer, those being the wild boar (*Sus scrofa*) and roe deer (*Capreolus capreolus*), the latter also resulting from the 1990's reintroduction (Salazar, 2009).

Red deer is the most widespread native cervid in Portugal (Carvalho et al., 2018) with a range of 170 km^2 in the Lousã mountain (where rut and reproduction take place) and a total of around 435 km^2 with the surrounding areas (Alves et al., 2014). That was not always the case, considering the species was almost extinct at the end of the XIX century, due to overexploitation (hunting) and habitat fragmentation (degradation caused by human activities) (Alves, 2013; Oliveira, 2018; Santos, 2009). Nowadays, there are 12 hunting zones in the surroundings of the study area, in which the red deer hunting occurs at least from October to February by 'montaria' (Alves, 2013).

With the help of the reintroduction, between 1995 and 1999, as well as the population natural dispersion, the problem no longer exists (Oliveira, 2018). The reintroduction took place with the release of 96 animals, 32 males and 64 females, originally from Vila Viçosa and Herdade da Contenda, areas in south Portugal (Alves, 2013; Valente et al., 2017).

There are no natural predators, in the study area, and red deer are mainly preyed on by feral dogs (mainly abandoned by hunters), that primarily chase young and female deer (Alves, 2013; Vilela et al., 2020).

2.1.2. Denmark – Hoverdal, Nørlund, Harrild, St. Hjøllund and Gludsted Plantations

Red deer is also the largest free-living mammal in Denmark (Nielsen et al., 2008), having immigrated 8,000 years B.C. and dispersed all over the country (Strandgaard & Simonsen, 1993). Nowadays, it is one of the deer with higher population numbers, with more than 24000 individuals (Müller et al., 2017).

Between the 1970s and the 1980s, independent populations were established in Thy and Vendsyssel (Sunde et al., 2008). Also, in the 1970s, red deer hunting started to multiply again all over Denmark (Sunde et al., 2008), since the near extinction of the species due to over-hunting between the XVIII and XIX centuries (Nielsen et al., 2008; Strandgaard & Simonsen, 1993).

In the areas where red deer individuals survived, populations formed and dispersed all over the country (Strandgaard & Simonsen, 1993). One of those places being Central Jutland where populations were established in 1940, with the help of animal releases from Jagersborg Dyrehave (Strandgaard & Simonsen, 1993). Dyrehaven is danish to 'The Deer Park', and this type of deer parks are a legal concept in Denmark where the main focus is biodiversity conservation (Fløjgaard et al., 2017).

Since the 70s, red deer have established permanent populations in several places in Jutland (Sunde et al., 2008).

In Denmark, the hunting season goes from November to January for hinds and calves, and from September to January for stags (Jeppesen, 1987; Sunde et al., 2009). At this time, the owners of properties (>1 ha) and renters of properties (>5 ha) can shoot as many deer as they like (Sunde et al., 2009), resulting in at least 150 stags hunted each year (Fløjgaard et al., 2017).

Hunters and wolves, which prey on red deer, have been the main population regulating agents in the country for over 200 years (Jędrzejewski et al., 2000; Sunde et al., 2009).

Red deer, in Denmark, mainly follow established tracks in the forest and have a relatively stable diurnal rhythm (Trolle-Lassen, 1990). The use of the same tracks can be attributed to changing landscape, which in the last century was heavily modified due to the construction of roads and railways and the clearing of hedgerows, orchards, and small woods (Nielsen et al., 2008).

Central Jutland, our study area located in Denmark, is divided into three smaller regions (1) Hoverdal Plantage; (2) Nørlund Plantage and Harrild Hede, and (3) St. Hjøllund Plantage and Gludsted Plantage. The medium annual temperature, in Central Jutland, is around 7.5ºC with a range between -3.5ºC to 19.7ºC, and the medium annual precipitation is around 802-813 mm (Müller et al., 2017).

This part of Jutland also accounts for two other ungulate species, besides the red deer (*Cervus elaphus*), as the fallow deer (*Dama dama*) and the roe deer (*Capreolus capreolus*) are also present (Müller et al., 2017).

The Hoverdal Plantation (1600 ha) was created on a sandy heathland[6] in 1882 and is own and managed by the Danish Nature Agency. The vegetation includes an abundance of pine (e.g., *Pinus nigra*, *Pinus mugo* and *Pinus sylvestris*) spruce (e.g., *Picea abies* and *Picea sitchensis*), larch (*Larix* sp.), beech (*Fagus sylvatica*) and oak (*Quercus* sp.) punctuated with open areas derived from the initial heathland[7].

Our second region includes Nørlund Plantage (2431 ha), which was planted firstly in 1808, and Harrid Hede (550 ha), a reminiscent of the vast heathland that once covered more than half of Jutland in the 19th century. Together they cover a total area of 30 km^2. The regions are owned and managed by the Danish Nature Agency and are dominated by an array of small vegetation. Wavy hairgrass (*Deschampsia flexuosa*), thyme

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[6] Open and uncultivated land covered with grass or heather, with very few trees.
[7] https://naturstyrelsen.dk/naturoplevelser/naturguider/hoverdal-plantage/dyr-og-planter/

(*Thymus vulgaris*), bell, scotch, and cross-leaved heathers (*Erica cinerea*, *Calluna vulgaris* and *Erica tetralix*), along with black crowberry (*Empetrum nigrum*) are just some examples of species that can be found on this heathland[8].

Lastly, St. Hjøllund Plantage, privately owned, and Gludsted Plantation, owned by the Danish Nature Agency, are connected, making up a total area of 48 km^2. They were established between 1877 and 1900 on a sandy heathland and share the same habitat structure[9]. The regions consist of 98% conifers, mainly Norway spruce (*Pices abies*) and are surrounded by agricultural lands, such as farms, villages and other coniferous plantations (Sunde et al., 2009).

2.2. Methods

2.2.1. Data collection

To understand red deer's spatial, temporal and grouping patterns several camera-traps were deployed to be active 24h/day. Each camera (Bushnell HD) was configured (1) to record only photos or three photos, followed by a video with a duration of 10-60s and (2) to document the date, time, and temperature (Figure 2). The cameras documented this information every time the motion sensor was triggered.

Figure 2. Camera-trap output example with temperature, date and time represented.

[8] https://naturstyrelsen.dk/naturoplevelser/naturguider/harrild-hede-og-noerlund-plantage/dyr-og-planter/
[9] https://naturstyrelsen.dk/naturoplevelser/naturguider/gludsted-plantage/dyr-og-planter/

In Portugal, the monitoring by camera-traps occurred from June 2019 until June 2020 adding to 441 days of recordings, shared amongst 60 sampling points. The sampling points were distributed in Lousã Mountain's central region with three established types of habitats, labelled coniferous forest, mixed forest and shrubland. The labelling was done based on previous studies, followed by field confirmation (Figure 3).
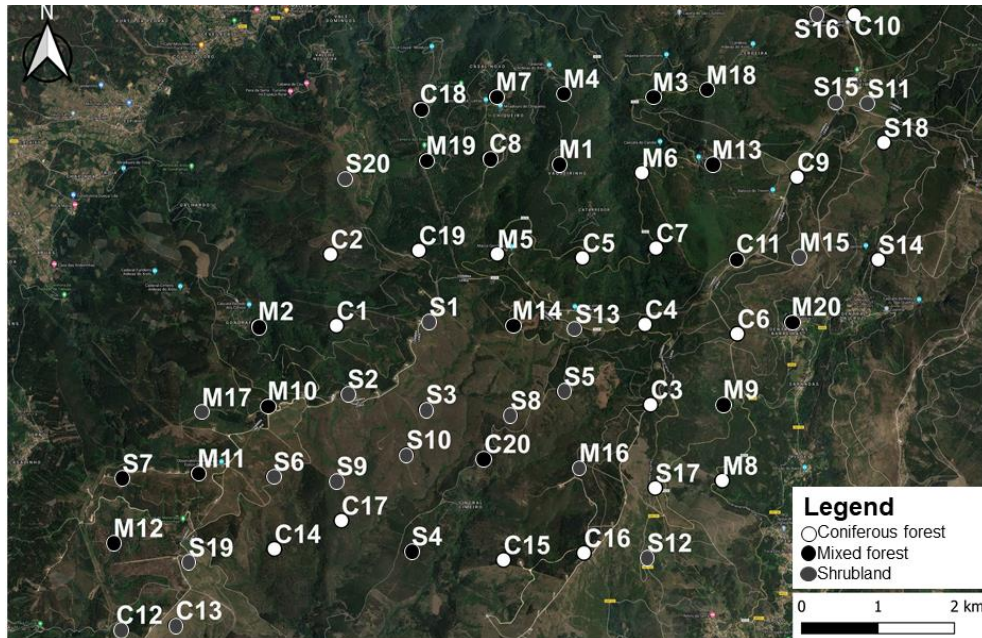
Figure 3. Camera-traps location in Lousã Mountain, Portugal.

Whereas in Denmark, the fieldwork took place between June 2016 and November 2018 accumulating 846 days of monitoring, divided by 13 sampling points. The cameras were scattered all over Central Jutland representing the Hoverdal, Harrild, St. Hjøllund and Gludsted plantations and their surroundings. In these areas, four types of habitats were observed in the field and later confirmed by examining the videos and photos. These types of habitats are coniferous forest, deciduous forest, mixed forest and shrubland (Figure 4).

Figure 4. Camera-traps location in Denmark. (A) Hoverdal Plantage; (B) Nørlund Plantage/Harrild Hede and St. Hjøllund Plantage/Gludsted Plantage.

2.2.2. Data observation

Once the data was exported to the computer, their observation began. The data was then entered into an excel spreadsheet using contacts. A new contact was considered when (1) a new animal (of any species) appeared on screen; (2) the time spent by the animal in front of the camera was ≥ 60 seconds and (3) a new behaviour was detected.

When an individual was captured on camera, the species was inserted, and in the case of an ungulate species, their sex, age-class, behaviour, group type and group composition was logged.

Individual's sex (Figure 5) and age-class were determined based on their body size (stature and neck proportion), antler size (in males), and coat characteristics (amount of hair and hair colour). Ungulate individuals were divided into three age-classes (1) calves – especially small animals and when exhibiting white spots on their body; (2) sub-adults – smaller than adult animals (1-4 years old) and (3) adults – significantly bigger animals (>4-5 years old).
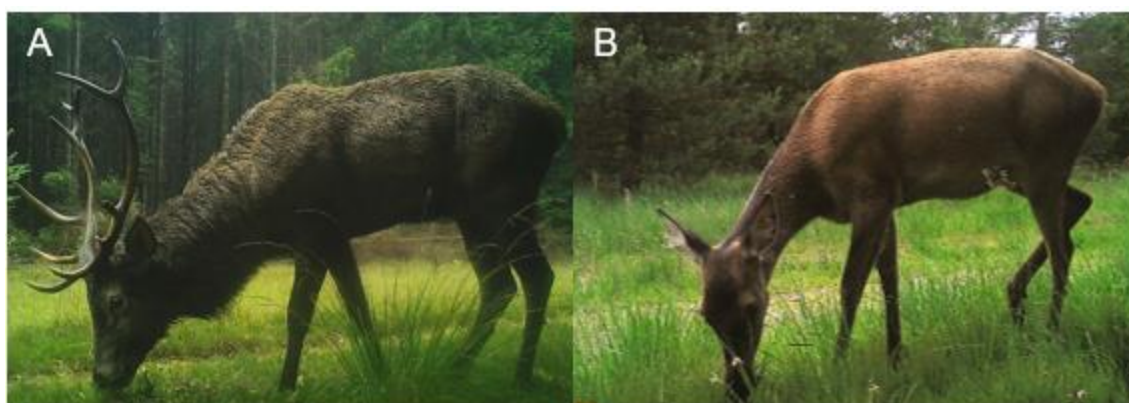
Figure 5. Red deer's recordings showcasing the differences between sexes. (A) Adult male; (B) Adult female.

The animal's behaviour was recorded. Each behaviour was grouped into 6 categories (Table 2) and its start and end (because the animal left or changed behaviour) were documented. Examples that illustrate the descriptions in Table 2 are shown in Figure 6, for a better understanding.

Table 2. Ethogram of the recorded behaviours.

Behaviour	Code	Description
Feeding	FE	Eating or chewing plants.
Walking	WA	Moving, either walking or running.
Standing	ST	Standing without vigilance behaviour.
Lying	LY	Lying on the ground, e.g., resting or sleeping.
Alert State	AS	Raising of head and hears staying static.
Other	OT	Vocalizing, breastfeeding, fighting etc.
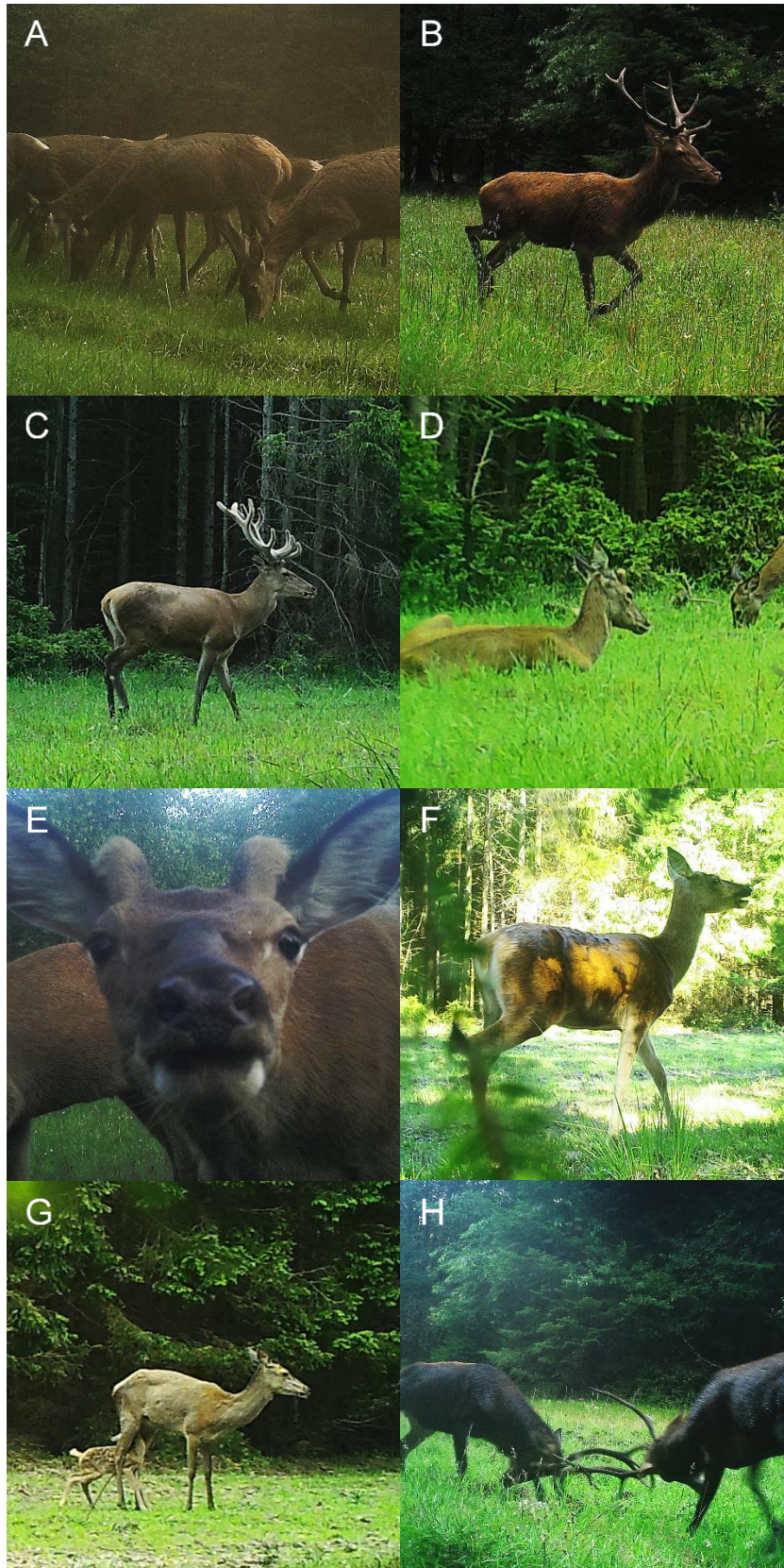
Figure 6. Types of recorded red deer behaviour. (A) FE – adult females feeding; (B) WA – adult male walking; (C) ST – adult male standing; (D) LY – sub-adult male resting; (E) AS – sub-adult male alert; (F) OT – adult female vocalizing; (G) OT – calf breastfeeding on adult female; (H) OT – two adult males fighting.

An important factor to extract from the data is the type of group, which is how we know when the red deer are segregated and therefore understand the population patterns. The different groups' typologies, as previously stated are (1) Solitary – only one individual; (2) Matriarchal – females, calves, and sub-adult males; (3) Bachelor – only males and (4) Mixed – with at least one adult male and one adult female (Figure 7).
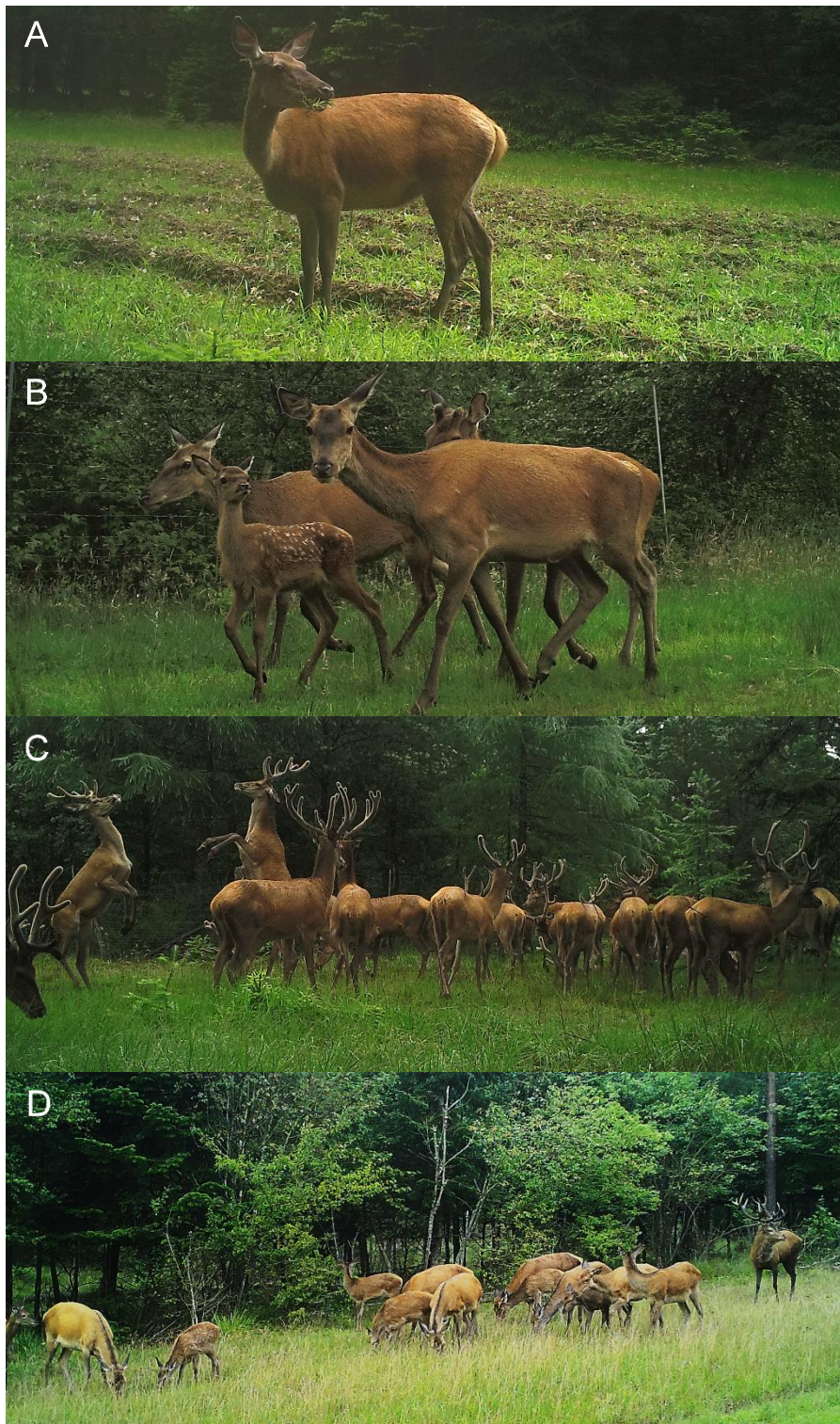
Figure 7. Group typologies shown in recordings. (A) Solitary; (B) Matriarchal; (C) Bachelor; (D) Mixed.

2.2.3. Data treatment

In order to test the observed segregation and aggregation temporal patterns of red deer, we used the sexual segregation and aggregation statistics (SSAS; Bonenfant et al., 2007).

$$SSAS = 1 - \frac{N}{X \cdot Y} \cdot \sum_{i=1}^{k} \frac{X_i \cdot Y_i}{N_i} \quad (1)$$

N – X+Y

X – number of animals of class I

Y – number of animals of class II

k – total number of groups

X_i – number of animals of class I in the ith group

SSAS is a statistic that tests a null hypothesis of a random association between the classes (e.g., females and males), against the two alternative hypotheses (1) segregation (the sex ratio of groups is strongly different from the sex ratio of the population) and (2) aggregation (the proportion of sexes in the group is similar to the proportion of sexes in the population). Therefore, the SSAS accurately determines, when classes are segregated, aggregated or simply randomly distributed.

SSAS varies between 0 and 1 and needs to be interpreted according to the expected values of the confidence intervals. When it is equal to 0 (complete aggregation), the SSAS is lower than expected from a random association, indicating that the individuals occur predominantly in mixed groups (e.g., groups of different age-classes and reproductive states or groups of both sexes). However, when the SSAS is equal to 1 (complete segregation), the SSAS is higher than expected, indicating the presence of mostly unisex (same class) groups.

In addition to using SSAS to obtain temporal sex segregation and aggregation patterns, we also performed SSAS to test segregation between males' and females with different reproductive status (females with offspring and females without offspring).

To access the effect of the environment and land-cover on red deer sexual segregation patterns, we used canonical correspondence analysis (CCA) at monthly timescale. The statistical significance of the eigenvalues of each CCA was obtained by using Monte Carlo permutation tests, based on 999 unrestricted permutations of the residuals from the reduced model (Braak & Smilauer, 2002). CCA was performed using the package 'vegan' (Oksanen et al., 2020),

Furthermore, a generalized linear mixed model (GLMM) with Poisson distribution was used to analyse the effects of month and group type on the size of the of red deer groups. The results from GLMM are expressed as estimated means ± standard error (SE) and 95% confidence intervals. General linear models were used to analyse the monthly fluctuations on proportions of matriarchal groups, bachelor groups, and mixed-sex groups. The statistical analyses were performed using IBM.SPSS Statistics 23 (IBM Corporation, New York, U.S.A.). All statistical tests were considered significant when $p<0.05$.

Between Denmark and Portugal, 223536 photos and videos were analysed. This number amounted to 9762 individuals with 11454 contacts, resulting in 5159 red deer individuals with 5700 contacts.

We detected 12 animal species (Table 3), and in addition to red deer (*Cervus elaphus*), we also identified three additional non-targeted ungulates, namely fallow deer (*Dama dama*), roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*). Besides the ungulates, we came upon other mammals such as the badger (*Meles meles*), hare (*Lepus europaeus*), marten (*Martes foina*), polecat (*Mustela putorius*), red fox (*Vulpes vulpes*), squirrel (*Sciurus vulgaris*) and most importantly, a predator to our study species, the wolf (*Canis lupus lupus*). We also came across a variety of species of birds, but due to the data mostly featuring fast movements, it was hard to identify their exact species, so we decided to put them in the same category. Figure 8 shows an example of the different animal species detected.

Table 3. Number of individuals observed of each species per country.

Species	Denmark	Portugal	Total
Badger	133	-	133
Birds	121	3	124
Fallow deer	346	-	346
Hare	1250	-	1250
Marten	44	13	57
Polecat	11	-	11
Red deer	1881	3282	5163
Red fox	784	131	915
Roe deer	390	372	762
Squirrel	89	10	99
Wild boar	-	902	902
Wolf	4	-	4
Total	**5053**	**4713**	**9766**
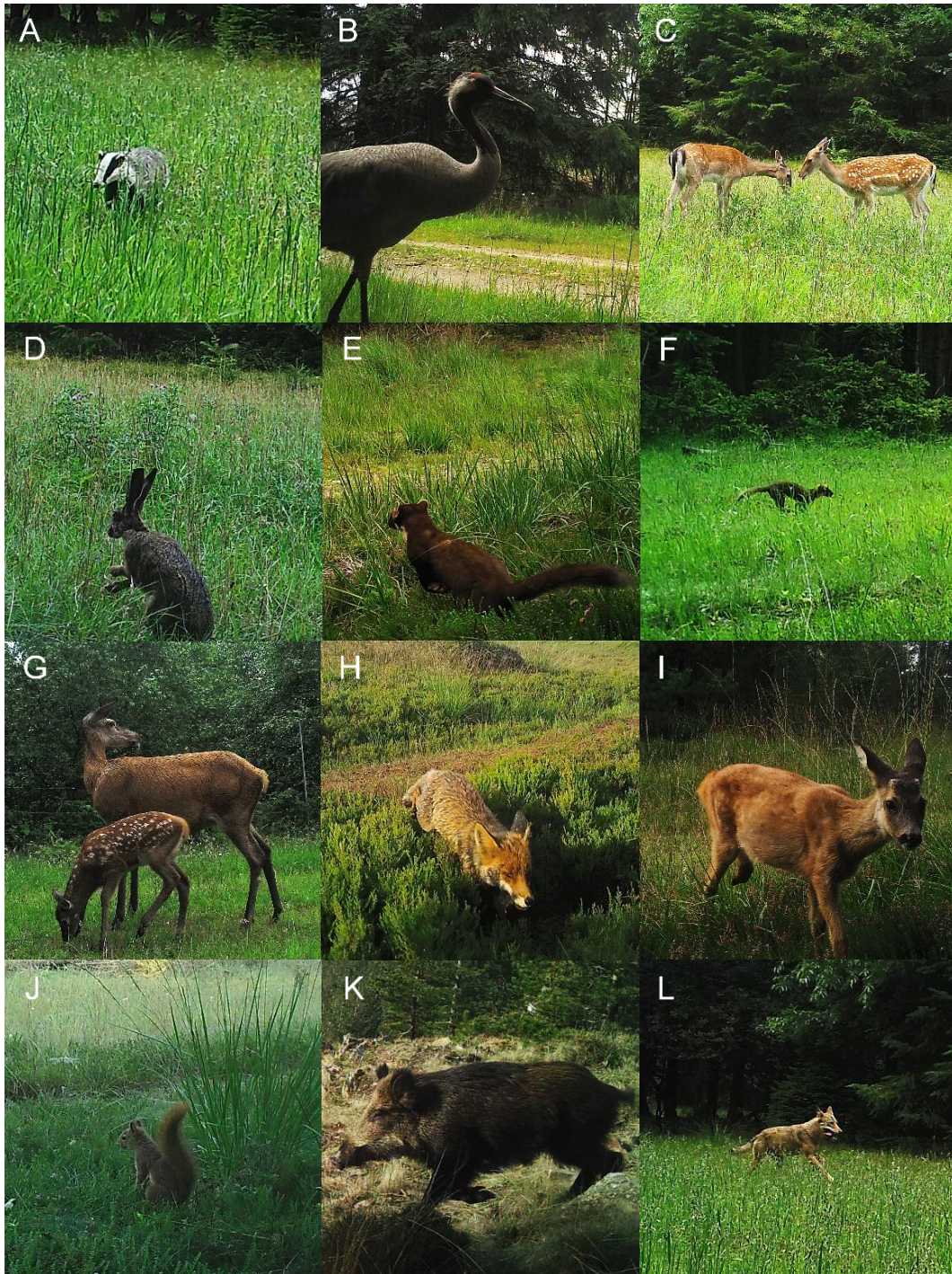
Figure 8. Animal species represented in our sampled data. (A) Badger; (B) Bird; (C) Fallow deer – two adult females feeding; (D) Hare; (E) Marten; (F) Polecat; (G) Red deer – adult female and calf feeding; (H) Red fox; (I) Roe deer – sub-adult male walking; (J) Squirrel; (K) Wild boar – adult female running; (L) Wolf.

3.1. Group size and monthly variation

Throughout our study period, group size in Denmark ranged from 1 to 33 individuals, with the mean being 4.64±0.18 without the solitary. Whereas in Portugal it varied from 1 to 14 individuals, with a mean of 2.60±0.10 when we excluded the solitary. Group size varied significantly between countries (Wald Chi-Square test: χ2 = 119.167, df = 1, p < 0.000). In Figure 9 a better representation of the mean individuals per group is illustrated.
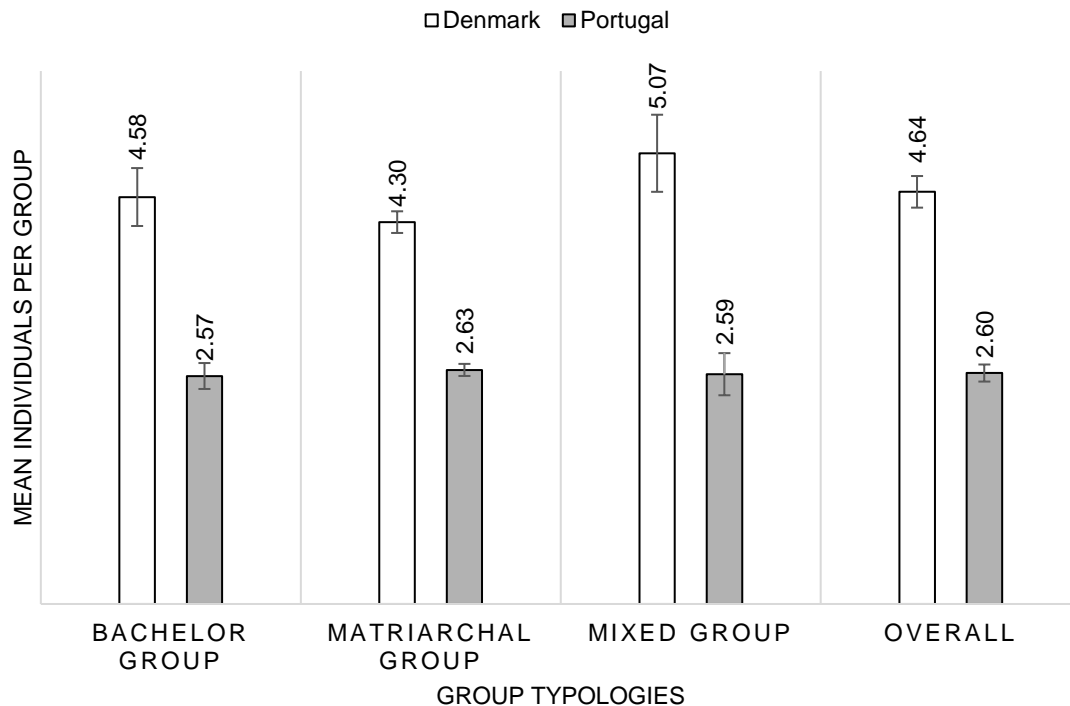
Figure 9. Observed mean ± SE of individuals per group typology in each country.

In Denmark, group size fluctuated significantly between months (Wald Chi-Square test: χ2 = 39.575, df = 11, p<0.000). The interaction between group type and month was also significant (Wald Chi-Square test: χ2 = 29.961, df = 13, p=0.005), meaning that depending on the month, group size fluctuated within the group typology. Matriarchal groups were consistently bigger than other group typologies, except in February (5.67±0.80) and July (3.79±0.28), when bachelor groups had more individuals per group (5.83±0.99 and 5.50±0.96 respectively) (p<0.05). Mixed groups also had more individuals (5.76±0.59) than matriarchal (3.37±0.38) ones in the month of October (p<0.05).

On the contrary, in Portugal, group size didn't fluctuate significantly between months (Wald Chi-Square test: χ2 = 10.040, df = 11, p = 0.527). The highest mean value of individuals per group was observed in December for bachelor groups (3.70±0.61) and November for both matriarchal groups (3.11±0.26) and mixed groups (2.88±0.60).

Overall, in this Portuguese area, matriarchal groups are mostly bigger in terms of mean individuals than the other groups, but there are no significant differences in the interaction between group type and month. However mixed groups were bigger in September (2.50±0.31) and October (2.58±0.46), when compared with matriarchal ones (2.36±0.22 and 2.52±0.19 respectively).

3.2. Group typologies

In our sample design, as stated, 2717 groups were observed, this is a sum between the groups in Denmark that amounted to 654 groups and Portugal with 2063 groups.

Singleton (solitary individuals) were the most abundant group type in both countries, 45% in Denmark and 64% in Portugal, followed by the matriarchal groups with 44% and 28% respectively. The group typologies with lower percentages were bachelor groups 7% in Denmark and 6% in Portugal, and the staple group of the rutting season, mixed-sex groups with 4% in Denmark and 2% in Portugal.

The matriarchal groups were most often observed outside the rutting season (January to August). The occurrence of mixed-sex groups increased quickly during the rutting season (September to November) and then declined gradually after the rut.

Male groups (bachelor) occurrence reached its maximum in January (Portugal 41%) and February (Denmark 33%) and decreased to its minimum in September (Denmark 1%) and October (Portugal 2%). Relatively to solitary individuals, Portugal had a steady higher percentage throughout the months than Denmark (Figure 10).

To have a clear understanding of the different group typologies, we can compare the group overall behaviour. In Denmark, feeding was the main behaviour observed in all group typologies (60% to 80%). Whereas in Portugal, all group typologies exhibited walking as the main behaviour (30% to 45%). In both countries, matriarchal groups were the ones exhibiting higher alert states, having twice the percentage when comparing with bachelor groups.

A
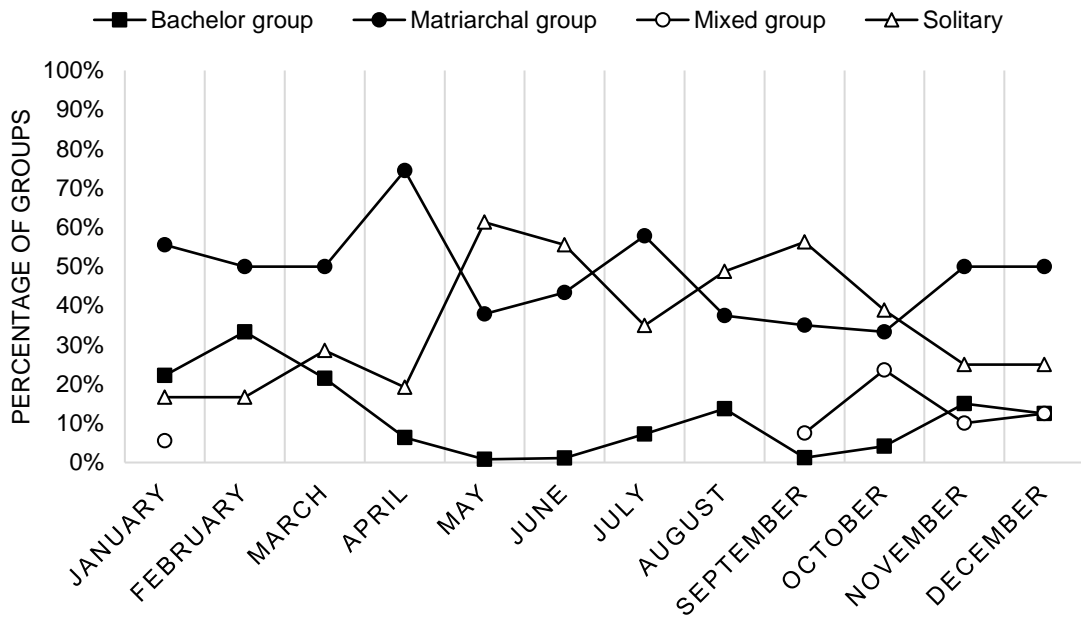
B
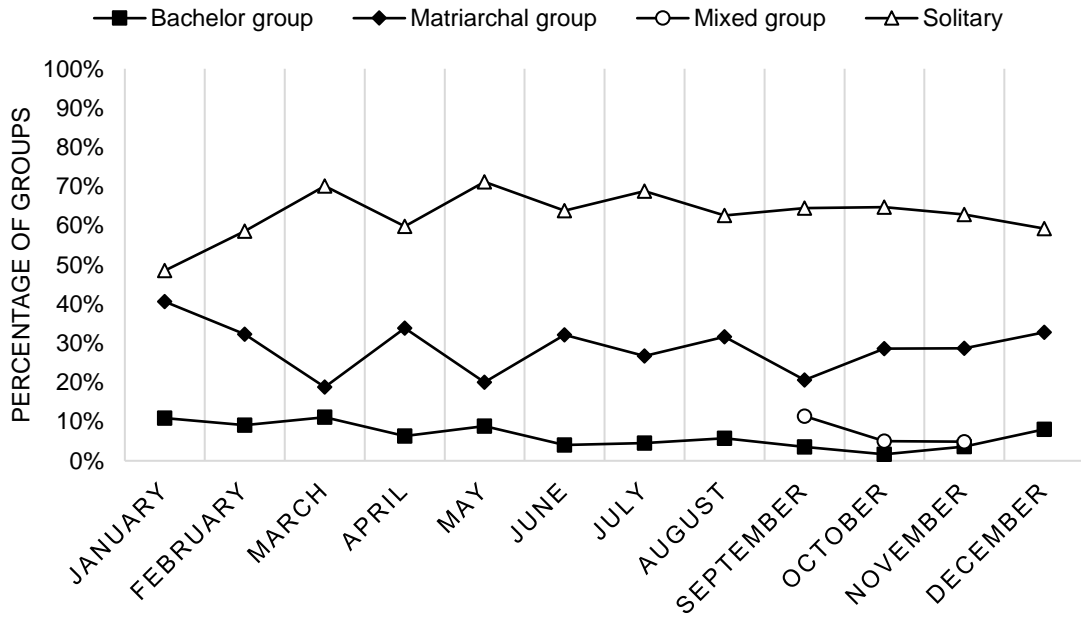
Figure 10. Percentage of groups typologies over the months in the two countries. (A) Denmark; (B) Portugal.

3.3. Sexual segregation patterns

The grouping dynamics, and consequently the social structure of our study species, the red deer, changed throughout the sampled months.

All year, in both countries, sexual segregation was at its maximum (SSAS=1), except in rut (breeding season) and surrounding months, as we can see in Figure 11. Meaning that red deer form mixed-sex groups at the rut season, and same-sex groups in the rest of the year marked by the different reproductive stages (1) winter dispersal; (2) calving (calves' birthing) and (3) lactation.

In Denmark the lowest peak of SSAS was in October (SSAS=0.54, SSAS interval=0.33–0.55) and in Portugal, this peak was in September (SSAS=0.77, SSAS interval=0.77–0.87).

For a better overview of the results and a better understating of the sexual segregation dynamics between the sexes, a shorter timeframe was used (15-day intervals) in the breeding season (Figure 12). This includes pre-rut, rut, and post-rut, uncovering a more detailed analysis of how SSAS adjusts in this season.

The pre-rut marks the beginning of the breeding season, at this time the animals start to shift from their original groups, assuming a random association, that leads to a change in the SSAS, from 1 (complete segregation) to a lower value, due to the few emerging mixed groups. The lowest values of SSAS are documented once the rut begins and the peak of aggregation between females and males is established. In the post-rut, the individuals assume a random association again, and they do so until the end of the breeding season. Once the breeding season ends, females and males progressively segregate, and return to form matriarchal and bachelor groups, reaching the maximum SSAS during the winter dispersal.
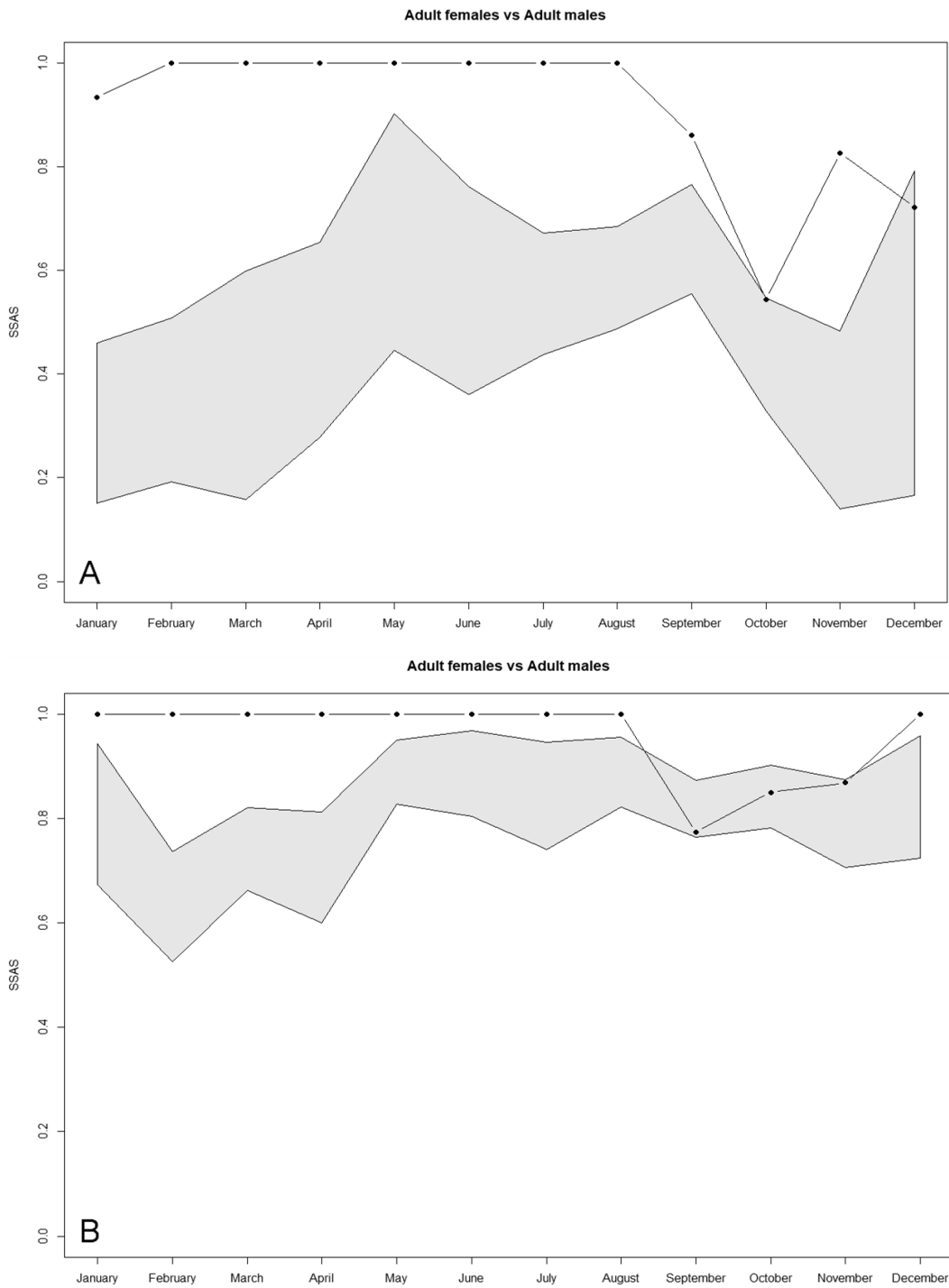
Figure 11. Monthly sexual segregation patterns of red deer adult males and adult females in our two study areas. (A) Denmark; (B) Portugal. Black dots – level of SSAS observed between the sexes; Grey area – levels of SSAS that would be expected if the sexes were randomly associated. Values above the grey area indicate significant segregation and values below it indicate significant aggregation (p<0.05).

Adult females vs Adult males

Adult females vs Adult males
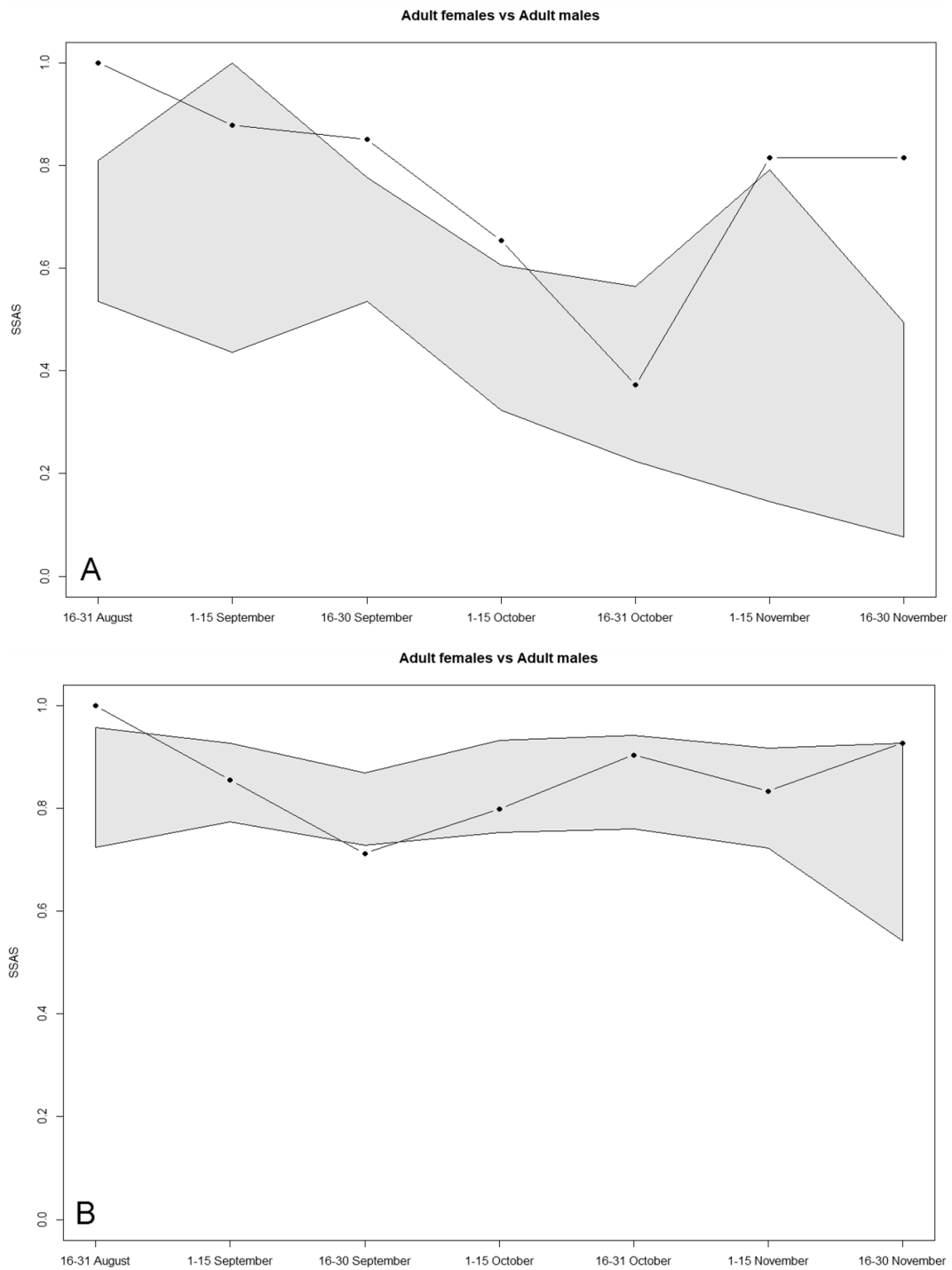
Figure 12. Sexual segregation and aggregation patters of red deer adult males and adult females in our two study areas, at a two-week timescale. (A) Denmark; (B) Portugal. Black dots – level of SSAS observed between the sexes; Grey area – levels of SSAS that would be expected if the sexes were randomly associated. Values above the grey area indicate significant segregation and values below it indicate significant aggregation (p<0.05).

The effect of females' reproductive stage and consequently the presence of young during the breeding season was analysed. The results show that calf absence promotes more pronounced segregation outside the rut and a prominent aggregation during the rut. The segregation between males and females with calves seems to be more pronounced (higher SSAS values) when compared to the females without calf, in both countries (Figures 13 and 14).

When we go into detail, between countries, Denmark demonstrated more peaks of segregation (SSAS=1) as well as Portugal (SSAS≈1), when using females with calves. This is a sign that males aggregated more over time with yeld[10] hinds, meaning that they were associated with males a longer period of time and with lower values of SSAS, consequentially leading to a more pronounced aggregation.

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[10] Females without calves.

Adult females with calf vs Adult males

Barren females vs Adult males
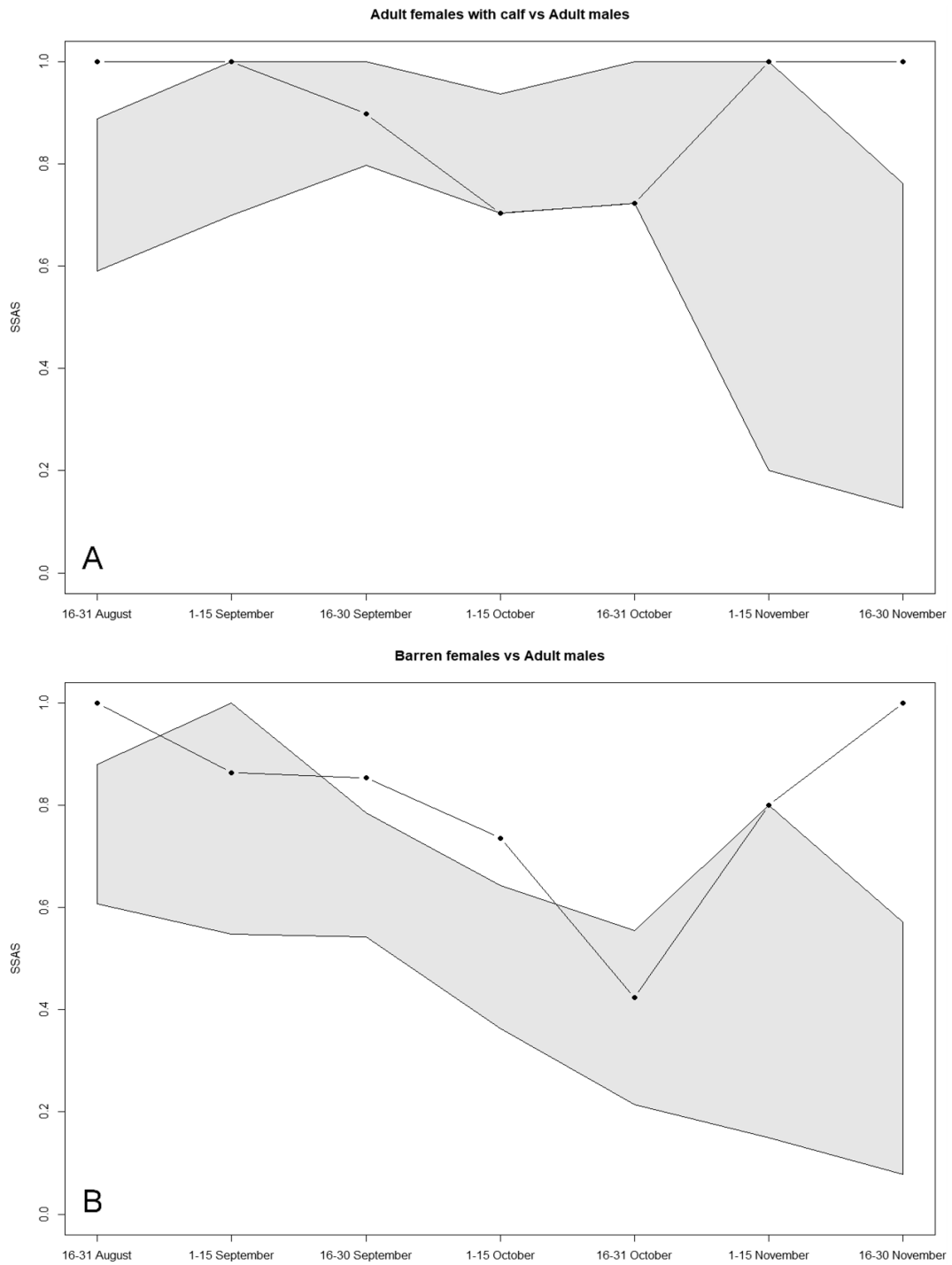
Figure 13. Sexual segregation and aggregation patters of red deer adult male and adult female with different reproductive conditions in Denmark, at a two-week timescale. (A) Adult males and adult females with calf; (B) Adult males and barren adult females. Black dots – level of SSAS observed between the sexes; Grey area – levels of SSAS that would be expected if the sexes were randomly associated. Values above the grey area indicate significant segregation and values below it indicate significant aggregation (p<0.05).

Adult females with calf vs Adult males

Barren females vs Adult males
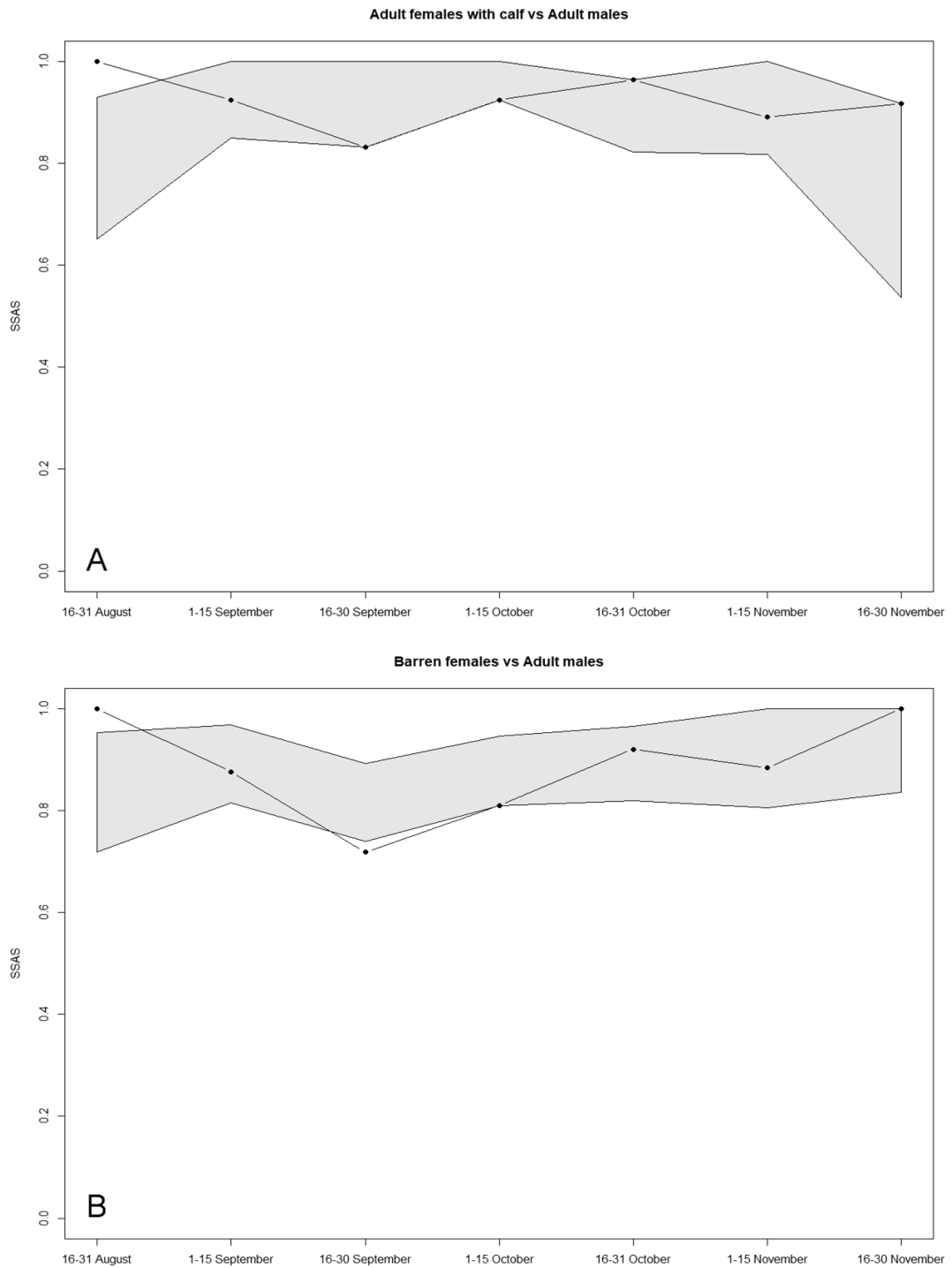
Figure 14. Sexual segregation and aggregation patters of red deer adult male and adult female with different reproductive conditions in Portugal, at a two-week timescale. (A) Adult males and adult females with calf; (B) Adult males and barren adult females. Black dots – level of SSAS observed between the sexes; Grey area – levels of SSAS that would be expected if the sexes were randomly associated. Values above the grey area indicate significant segregation and values below it indicate significant aggregation (p<0.05).

3.4. Environmental segregation

Considering the total number of groups observed, 2723 red deer groups were recorded, as previously mentioned. This number decreased to 1106 when excluding the solitary individuals. Of the observed 1106 red deer groups, 894 were within the forest habitats (81%), while the remaining 212 (19%) were out in open areas, such as shrublands.

Table 4 illustrates how much the environment can explain the sexual segregation and aggregation patterns of each red deer population. For the Danish red deer population, environment contributes significantly to the observed patterns of SSAS in June, July, October, and November. The latter has the highest percentage amounting to approximately 64%. Considering the Portuguese red deer population, on the other hand, the percentage of the observed patterns of SSAS explained by the environment was significant in all months, except for November.

Table 4. Percentage of SSAS (male vs female) variability explained by environment (habitat and spatial components). Statistically significant values (p<0.05) are highlighted in grey. NA – males and females never appeared together in the same point/habitats.

| Month	Denmark			Portugal		
	% SSAS explained by environment	$F_{df1,df2}$	p	% SSAS explained by environment	$F_{df1,df2}$	p
January	37.92	$F_{3,13}=2.65$	0.075	64.40	$F_{28,42}=2.71$	0.003
February	21.33	$F_{3,13}=1.18$	0.337	100.00	NA	NA
March	18.15	$F_{3,9}=0.67$	0.612	66.60	$F_{31,54}=3.47$	0.001
April	6.52	$F_{2,44}=1.53$	0.224	66.10	$F_{42,93}=4.32$	0.001
May	10.57	$F_{4,104}=3.07$	0.078	66.70	$F_{51,110}=4.33$	0.001
June	31.85	$F_{4,75}=8.76$	0.004	47.50	$F_{38,129}=3.08$	0.003
July	33.92	$F_{7,64}=4.69$	0.021	40.60	$F_{31,85}=1.87$	0.029
August	5.81	$F_{5,61}=0.75$	0.645	59.10	$F_{35,72}=2.97$	0.001
September	5.49	$F_{4,66}=0.96$	0.425	37.50	$F_{36,140}=2.33$	0.001
October	11.41	$F_{3,61}=2.62$	0.044	43.00	$F_{35,134}=2.89$	0.001
November	63.68	$F_{2,14}=12.27$	0.014	36.80	$F_{34,75}=1.29$	0.166
December	40.93	$F_{3,3}=0.69$	0.623	49.50	$F_{28,58}=2.03$	0.020

Considering the contribution of the environment (Table 4) and comparing it to the contribution of land cover alone (Table 5), the results show that the factors behind the habitat segregation include more than land-cover. Considering land cover alone (Table 5), it significantly explained 10% of the observed pattern of sexual segregation in July in the Danish red deer population and 4% to 15% of SSAS in various months in Portugal, outside of the rut.

Table 5. Percentage of SSAS (male vs female) variability explained by land cover. Statistically significant values (p<0.05) are highlighted in grey. NA – all observations were in the same habitat type.

Month	Denmark			Portugal		
	% SSAS explained by land-cover	$F_{df1,df2}$	p	% SSAS explained by land-cover	$F_{df1,df2}$	p
January	9.97	$F_{1,15}=1.66$	0.197	5.50	$F_{2,68}=1.98$	0.114
February	7.24	$F_{1,15}=1.17$	0.388	15.07	$F_{2,80}=7.10$	0.004
March	11.84	$F_{1,11}=1.48$	0.136	9.22	$F_{2,83}=4.21$	0.018
April	0.00	NA	NA	5.19	$F_{2,133}=3.64$	0.024
May	0.04	$F_{1,107}=0.04$	0.139	4.53	$F_{2,159}=3.78$	0.025
June	0.15	$F_{1,78}=0.12$	0.727	1.54	$F_{2,165}=1.29$	0.262
July	10.05	$F_{1,70}=7.82$	0.005	6.16	$F_{2,114}=3.74$	0.032
August	1.97	$F_{1,65}=1.30$	0.324	2.61	$F_{2,105}=1.41$	0.242
September	0.99	$F_{1,69}=0.69$	0.490	5.53	$F_{2,174}=5.10$	0.007
October	0.00	NA	NA	4.38	$F_{2,167}=3.83$	0.025
November	0.00	NA	NA	1.61	$F_{2,107}=0.88$	0.433
December	0.00	NA	NA	5.07	$F_{2,84}=2.24$	0.098

CHAPTER 4 – DISCUSSION

In this study, we addressed the differences between two countries, by studying two of their populations of red deer. This species that has been in the centre of conservation and evolutive studies in the recent past (Niedziałkowska et al., 2011).

Red deer grouping patterns are subject to seasonal variations (Gillich et al., 2021). In our study areas group size fluctuated between countries, with the Danish mean being 4.64 individuals (range 1-33) and the Portuguese mean being 2.60 (range 1-14). In Portugal, the results go along with previous Portuguese studies. In the past decade, red der mean group size was around 2.37, with red deer preferring to stay in small groups of up to three individuals (Alves, 2013; Salazar, 2009). Whereas Denmark differs from a former investigation which was in a similar area in Jutland. In this work, the mean individuals per group was around 6.7 (ranging from 1 to 95) (Jeppesen, 1987). The recorded decrease can be attributed to the rising hunter percentage and the establishment of populations of wolves.

When talking about hunting in Denmark, we have to take into account that it is one of the countries with the highest percentage of hunters in the population, with an average of 3 to 5% (Milner et al., 2006). That aligned to the presence of wolves can justify the larger groups and the presence of less solitary individuals. Larger groups are beneficial to vigilant behaviours, meaning that each individual can spend less time being vigilant and more time conducting fitness-enhancing behaviours, such as foraging (Rowe et al., 2021).

Harem size is very different between countries, and it is known to be related to rut dominance and rutting area (Gibson & Guinness, 1980a). Previously reported harem size varies between 1.43 to 2.50 (Bonenfant, Gaillard, et al., 2004), whereas the values in Denmark and Portugal are 5.07 and 2.59 respectively. In Lousã Mountain, harem size did not vary along time, suggesting a high number of harem-holders leading to an escalation in the costs of mating for males (Bonenfant, Gaillard, et al., 2004). This can imply that in Denmark, the level of competition is lower, therefore the optimal group size can increase (e.g., to improve the benefits of vigilance) (Carranza, 1988). It is unclear if the males in both populations use the same breeding strategy during the rutting season, defending a territory or defending a group of hinds (Carranza, 1995; Carranza et al., 1990; Putman & Flueck, 2011).

Our findings confirm that red deer grouping is not static, and it changes according to predator cues as well as different habitat structures. As expected, the grouping

dynamics varied significantly during the breeding season, with an increasing number of individuals in mixed groups while a decrease was detected in the other group typologies.

Red deer sexes are separated for most of the year, and their reproductive success promotes sexual segregation (Bocci et al., 2012; Hall, 2010). In our discoveries, SSAS obtained was conforming to our expectations. Sexual segregation reached its peak outside of the breeding season, marking a time where males and females live separately. During the rut season, males and females tend to significantly aggregate, as shown by our results. Rut is the time with the lowest SSAS values and marks a time when males and females come together for breeding.

When looking at a shorter timescale, 15-day intervals in the breeding season, we could attest to differences between countries. Therefore, Portugal and Denmark have different times for their aggregation peak. The 15-day intervals contribute to a better assessment of the time of pre-rut, rut, and post-rut. Pre-rut showed random associations between sexes, which was expected given that males start to search for female groups and try to establish a hierarchy. This means that males become more aggressive towards each other and start to roar (Davies et al., 2012). After the random association, males and females create mixed-sex groups and mating behaviours take place. Our study species reproductive cycle is highly synchronised and conception occurs in a short period of time to increase calf survival (Alves et al., 2013b).

In Portugal, both sexes stayed randomly associated for about 5 weeks, and the aggregation peak happened between 16-30 of September (statistically significant), which was corroborated by previous studies in Lousã mountain, with the same population (Alves et al., 2013b; Relvas, 2020). On the other hand, in Denmark, we did not notice a clear aggregation between the sexes, but instead more of random association, and the peak of lowest SSAS was on 16-31 of October. This result can be associated to the existence of larger groups. Larger groups have a difficult time synchronising their behaviours (Ruckstuhl & Neuhaus, 2000) and therefore can cause the aggregation to be shorter than two weeks.

When talking about segregation between males and females with and without young, we can see that males aggregated more with barren females in both countries. This was contrary to expected (Alves et al., 2013b), since females with calves provide males with a cue to their reproductive potential. However, females with calves have lower physical condition and ovulate later than females without offspring (Albon et al., 1986; Mitchell et al., 1986; Mitchell & Lincoln, 1973), which may result in more of a random association during a longer period of time due to a less synchronized oestrous. This

happens because the investment in the current years' calf causes a drop in females condition, therefore lowering their ability to ovulate at the right time to ensure the calf birth in the following spring (Langvatn et al., 2004). Another explanation to the difference between what was expected and what we observed can be explained by the simultaneous presence of both females with and without calves in the same harem. This situation can result in a less synchronized and continuous aggregation.

Regarding the timing of the rut season in both countries, the results show that the rut happens with a two-week difference between Portugal and Denmark, corroborated by an increase in the number of individuals per mixed group in September and October respectively. This can be explained by previous studies that showed that countries in different latitudes show a variance in reproductive cycle dates (Bonenfant, Loe, et al., 2004; Fletcher, 2009; Langvatn et al., 2004; Loe et al., 2005). The shift in the rut season can be caused by variances in day-length and temperature. Considering the variation of temperature between latitudes, we can argue that this climatic factor is crucial to plant growth as well as precipitation (Loe et al., 2005). Temperature is a limiting factor at northern latitudes (e.g., Denmark) and precipitation can be limiting in southern regions in Europe, such as the Mediterranean ecosystems (e.g., Portugal) (Loe et al., 2005; Sánchez-Prieto et al., 2004). Therefore, the plant growing season is delayed in northern latitudes, deriving from snow depth and negative temperatures (Benton et al., 1995; Mysterud et al., 2008; Sánchez-Prieto et al., 2004). This leads to a scarcity of food and an uneven distribution of resources that increases the chances of modifying behaviour in red deer grouping dynamics (Benton et al., 1995; Carranza et al., 1990; Forchhammer et al., 1998; Loison et al., 1999; Sánchez-Prieto et al., 2004). Since male reproductive strategy is to have the best fitness during rut, and female is to ensure calf survival (Ruckstuhl & Neuhaus, 2006), we can deduce that this species reproduction season starts later at high latitudes (Loe et al., 2005). The lack of resources can also surge a higher competition which affects reproductive performance and rut duration, through an influence in males' physical characteristics (Clutton-Brock, Albon, et al., 1987; Gibson & Guinness, 1980b).

Day-length, as previously stated, is also an important factor when comparing breeding seasons in seasonal areas, as it varies between latitudes (Vazquez et al., 2019). The antler cycle in red deer is known to respond to increasing photoperiod stimuli (Goss, 1969b; Webster et al., 1991). In this case, in our two study areas, rut occurred with a two-week difference. Given that different latitudes exhibit different day-lengths (Fletcher, 2009; Vazquez et al., 2019) and that an increase in photoperiod (and melatonin) leads to an early onset of the breeding season (Lincoln, 1992; Loudon &

Brinklow, 1992; Suttie et al., 1984; Webster & Barrell, 1985), we can include this variable as a cause of the delay of the breeding season in Denmark.

Climatic factors are also important to calving date and calf body condition (Albon et al., 1987). Late-born calves are more likely to succumb to winter, as they are smaller animals and cannot meet their energy requirements (Clutton-Brock, Major, et al., 1987; Langvatn et al., 2004; Loudon & Brinklow, 1992). Similarly, high temperatures are known to be a stress-inducing factor in the rate-growth of red deer calves (Pérez-Barbería et al., 2020). Consequently, calving must happen on an optimal date to make sure that females' fitness, related to their forage behaviour (they must have sufficient pastures), and milk production does not affect their calves growth (Garde et al., 2006; Godvik et al., 2009; Langvatn et al., 2004; Loudon et al., 1984).

When analysing the environmental and habitat input in the SSAS, we can say that environmental variables and land-cover explain a large portion of the segregation. The remaining variance in percentage could be explained by social factors. Males and females are possibly segregated into different parts of the land cover or in the same land cover but in different microhabitats (e.g., feeding on the same vegetation section but with disparate environmental conditions).

As previously stated, social and habitat components are not mutually exclusive and complement each other, in terms of sexual segregation. From this study results, support can be given to more than one hypothesis postulated to explain sexual segregation. The predation-risk hypothesis (RSH), states that sexes have different reproductive strategies (Bocci et al., 2012). The females focus on the offspring survival, (using secluded areas to hide) whereas the males emphasise on increasing energy reserves, in preparation for the breeding season (Godvik et al., 2009; Main et al., 1996). We can find that in Denmark, females and males use different habitats in the presence of predators. The considerable habitat segregation can also be attributed to the forage-selection hypothesis (FSH), which assumes the sexes segregate due to differences in energy requirements and therefore, different forage selection (Ruckstuhl & Neuhaus, 2000). This type of segregation peaks when differences in the spatial distribution of forages are highest (Main et al., 1996).

Addressing the activity-budget hypothesis (ABH), global results show that males and females, both in Denmark and Portugal, spent presented similar times performing similar behaviours. In Denmark the individuals spent most of their time feeding, while in Portugal, animals were mostly observed walking. This difference may be related with the distribution of the feeding patches across the landscape, or due to the differential quality

of the forage available, that may increase or decrease the time spent feeding. Nevertheless, in both countries a sexual difference in the alert state was noticed, where females were alert more times than males. This can be relevant and linked to the ABH and RSH. ABH assumes that a social group can only be cohesive if all its members have synchronizing activities (Conradt & Roper, 2000). As a consequence, mixed groups are more likely to separate than same-sex groups, which are more stable in terms of homogeneity in activity patterns (Bonenfant, Loe, et al., 2004; Conradt, 1998). Considering RSH, females depend on the survival of the young, and for that reason will exhibit more alert behaviours even at the expense of energy, which may lead to mixed-sex groups to segregate sooner in the presence of young.

Considering the methodology and sampling approach employed in the two countries, the difference in the animals recorded in each one may have some implications on the observed results, and for that reason must be interpreted taking this into account. The strategy employed in Portugal was fully developed for red deer monitoring, resulting in a higher recording rate but also in a larger number of camera-traps per sampling day (21 cameras/day). In Denmark, the sampling approach was developed to respond to a multitude of objectives (monitoring of different animal species), which resulted in a lower number of red deer detected by camera-traps (4 cameras/day). Camera-traps are known to be a better option in these types of studies, as other methods like spotlight surveys, roadside counts and on-site observation may mislead the estimations of population traits (e.g., individuals age and sex) (Jarnemo et al., 2017). Even though this is a preferred method, standardized techniques for field and laboratory analysis are needed to allow a better comparison of results between different populations or even different species. This will be crucial to decipher the factors behind sexual segregation.

So, are red deer sexual segregation patterns species-specific or population-specific? Segregation and aggregation patterns are similar between populations, demonstrating that it is species-specific, however, these patterns can have temporal shifts, which are population-specific. These shifts are derived from the populations' habitat, which exhibits different environmental conditions (e.g., day-length and temperature) that define calving season and consequently the grouping dynamics of the rut season. Furthermore, to better comprehend the factors that lead to differences in red deer patterns between populations, a large-scale survey about climate and photoperiod is needed. These surveys could be essential to understand and unravel sexual segregation patterns as well as to recognize the triggers to the rut.

CHAPTER 5 – FINAL REMARKS

This research focused on studying the patterns of red deer sexual segregation and aggregation in two different populations from two different countries. Considering the group size, the two populations differ in terms mean group size. The mean of individuals of each group can help to discover the effects of hunters (anthropogenic stress) and predator importance to the grouping dynamics of red deer populations, as well as group individuals' adjustments at the breeding season.

From our results, it is possible to conclude that rut occurred with a two-week difference and that can be attributed to changes in latitude between our study countries. These changes entail variance in temperature and day-length (population-specific). Even though a shift in the start of the rut was detected between populations, sexual segregation patterns were similar (species-specific) and support more than one hypothesis. In this study we found support for the predator-risk hypothesis and the forage-selection hypothesis.

This thesis is one of the first and few studies, to our knowledge, that compares red deer populations at a sexual segregation level, using a long-term sampling survey and methodology that enables the detection and recording of red deer 24 hours/day, 365 days of the year. This methodology resulted in a robust and detailed dataset, which would be very difficult to obtain using other methods. Therefore, our method contributes with solid data to the factors that triggers rut and the dynamics of sexual segregation and aggregation in populations with disparate environmental and ecological realities. However, it is also important to notice that camera-traps constitute fixed and static observation positions, and for that reason missing or lack of detection of some members of the groups can occur. This can lead to incomplete information in terms of group composition. Nevertheless, performed preliminary tests with more than one camera per point, show that the number of animals missing is quite low and cause no implications on the overall results.

Based on our results, we can conclude that other studies must be performed, namely a detailed analysis of the activity patterns and a comparative large-scale survey on environmental variables between populations. These studies can be crucial to unravel the factors associated with habitat segregation, which significantly contributed to the SSAS obtained. In addition to decisively complement the decisions on species conservation and management, of their ecosystems and on the provision of ecosystems services, in which they have an influence on.

CHAPTER 6 – REFERENCES

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