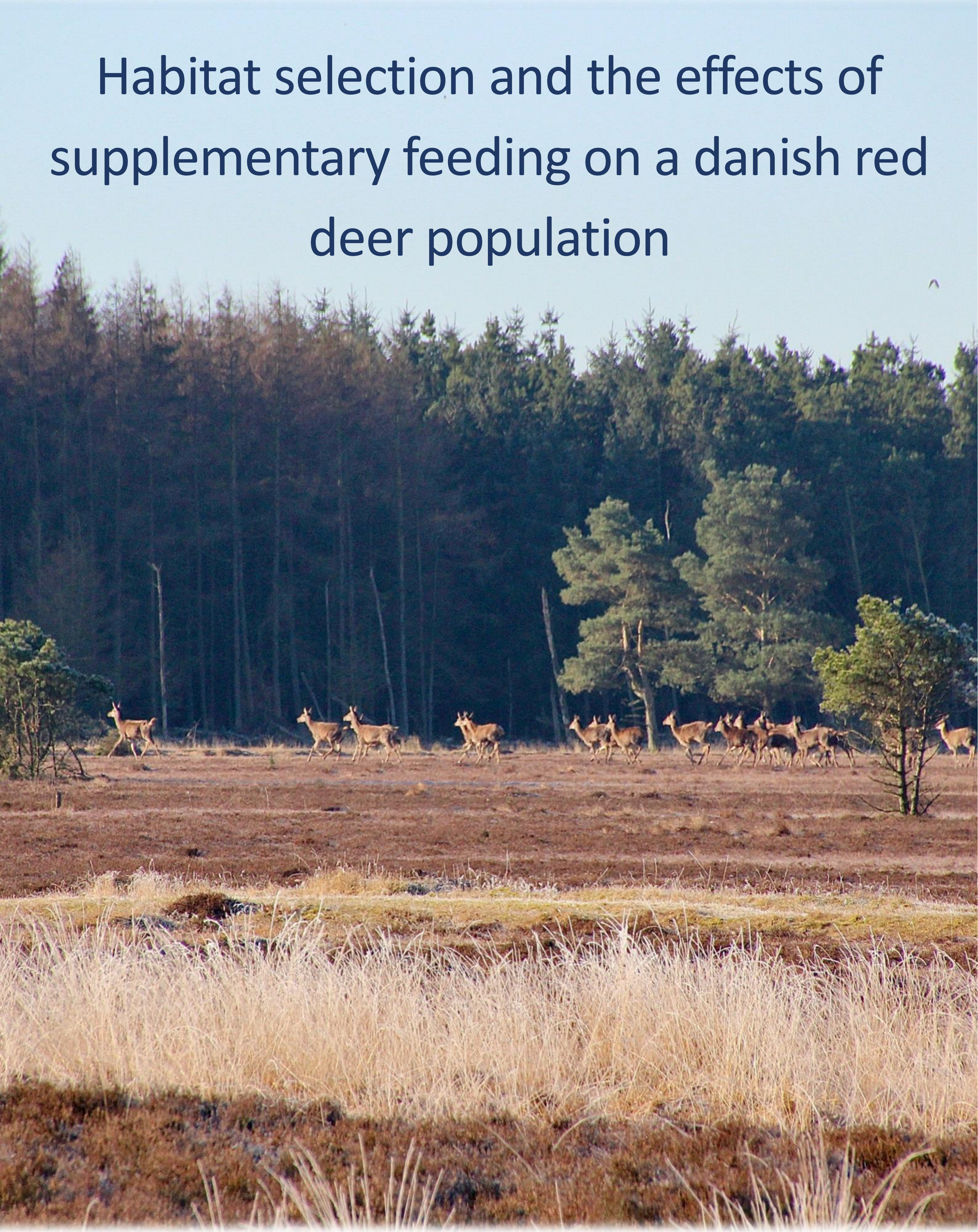
Habitat selection and the effects of supplementary feeding on a danish red deer population



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Habitat selection and the effects of supplementary feeding on a danish red deer population

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Frontpage: Red deer herd on Ovstrup Heathland
Backpage: Ovstrup Heathland
Credit: Camilla Kjær

Content

Preface

This thesis is the product of 10 months (60 ECTS) work, including approximately three weeks of fieldwork at Ovstrup Heathland and surrounding areas. This research will contribute to better knowledge of the red deer's movements and be useful for the future red deer management in Ovstrup Heathland and potentially in Denmark.

During the last week of February and the 19th of March, I participated in the GPS tagging of additional 9 female red der as part of a broader project. Thank you, Lars Haugaard for trusting me to be part of your team and thank you to all involved from Aage V. Jensen Nature foundation, Aarhus university and to veterinarian Monica Lønborg Frederiksen and chief veterinarian Carsten Grøndahl from Copenhagen Zoo.

Additionally, I was lucky to attend the 35th Congress of the International Union of Game Biologists in Budapest from the 20th to 25th September 2021, along with Peter Sunde, two former fellow biology students and other colleagues from the Department of Ecoscience. It was a great honour to present my poster summarizing this thesis – Thank you Hans Peter Hansen and Peter Sunde for this opportunity and to Department of Ecoscience, Wildlife Ecology for the funding.

A special thank you to my two supervisors Robert Buitenwerf and Peter Sunde, for help with both technical and theoretical questions, the development of this project and constructive criticism throughout the entire process.

The thesis consists of two parts. The first part, Part A, is a literature-based study exploring the ecological role of ungulates and why it is important to study this a species like red deer. Further, a description and introduction to habitat selection and pellet counts, along with an assessment some of the anthropogenic factors that can affect the red deer's habitat use and selection. Part A ends with a description of the specific management project in which my Master's thesis has its roots. Part B is an article manuscript – "*Winter feeding affects habitat selection of red deer in a mixed landscape*", investigating the red deers habitat use and selection on Ovstrup Heathland and surrounding areas, whilst also exploring how supplementary feeding sites in the area, could influence the red deer's behaviour and habitat selection.

Those days in the field, helping with the GPS-tagging and the IUGB conference, will always be a highlight during my time at Aarhus University.

Acknowledgements

This study is a contribution to the project “Red Deer - Knowledge, values and management”. A special thank you to project manager Hans Peter Hansen, for all his guidance and help during these 10 months and to Martin Mayer, for his valued support with the statistical analyses in R. I would additionally like to thank the landowners, farmers and hunters that were willing to participate. Without their cooperation, the fieldwork would not have been possible. Lastly, I would like to send my gratitude to Aage V. Jensen Nature Foundation for allowing me to use the area of Ovstrup heathland so freely during this study.

Part A – Literature review

1 Ecological role of ungulates

It has been shown that year round grazing from large herbivores such as ungulates, helps to counteract succession of open habitats towards shrub and create larger diversity of plants as result from the grazing pressure (Vera, 2009). Additionally, grazing and trampling influence the vegetation structure and composition in forest ecosystems (Krojerova-Prokesova, Barančeková, Šustr, & Heurich, 2010), as their browsing on shrubs and tree seedlings can reduce stem densities and limit height growth and therefore create a more open undergrowth (Gill & Beardall, 2001). Ungulates are thus important for management efforts, as they can play major role in landscape structure because their grazing enhances light availability for ground level i.e., creates vegetation openness and eases light competition (Riesch, Tonn, Meißner, Balkenhol, & Isselstein, 2019). Making them important ecosystem engineers (Müller et al., 2017). However, ungulates' browsing and grazing, that is beneficial in certain areas due to their grazing pressure, may be seen unfavourable in others such as the agricultural landscape. Their feeding on crops cause considerable damage to the agricultural fields and results in large yield loss (Trdan & Vidrtrih, 2008).

Ungulates are a ruminant, so their digestive system allows them to chew and swallow their food and afterwards regurgitate it, to get all the available nutrients. This an important foraging-safety trade-off for the ungulates, as they can shorten their foraging time in risky habitats and thus seek safety while ruminating (Van Wieren, 1995). Further, most ungulates have a highly diverse social system and tend organise in groups. These formations are beneficial in defence against and detectability of predators, can enhance feeding efficiency and provide access to potential males (Szemán, Liker, & Székely, 2021).

Humans have impacted large herbivores for thousands of years e.g., by degradation of natural habitats to conversion into agricultural areas (Müller et al., 2017) and through size-biased extinction, leading to smaller herbivore species in present day (Smith, Elliott Smith, Lyons, & Payne, 2018). Moreover, anthropogenic activity influence ungulate behaviour (i.e., habitat use, daily activities and spatial distribution) in multiple ways: 1) Indirect via nonlethal activities such as hiking and other recreational activities. This presence of humans can induce strong fear, which may then alter activity and movement patterns to avoid human contact, 2) direct and lethal effect such as hunting activities, which cause an increase of nocturnality in wild animals and 3) the provision of food provided by humans, which may also cause fear of humans and increase nocturnal activity (Gaynor et al., 2018; Jeppesen, 1987).

Abovementioned indicates how human disturbances have impacted large herbivores in various ways. And as landscapes continues to change due to human interference, especially in a highly populated continent such as Europe, human-wildlife coexistence can be challenging (Cretois et al., 2021). However, Cretois et al., (2021) found that biophysical factors had a larger impact on the species distribution of large herbivores than human disturbances did. Therefore, they suggest that coexistence in modified landscapes is possible if conservation authorities adopt a land-sharing strategy. Landscapes where human and wildlife interactions are allowed, managed, and sustained, as large herbivores are already present in areas of high human disturbance (Cretois et al., 2021).

A specific ungulate species that is of great value to both nature areas and biodiversity in Europe and has been shown to be a key species in nature management through its effect on vegetation, is the red deer (Riesch et al., 2019). However, many issues may arise when dealing with management of red deer, which will be further described throughout the rest of Part A, following the arrangement in figure 1.

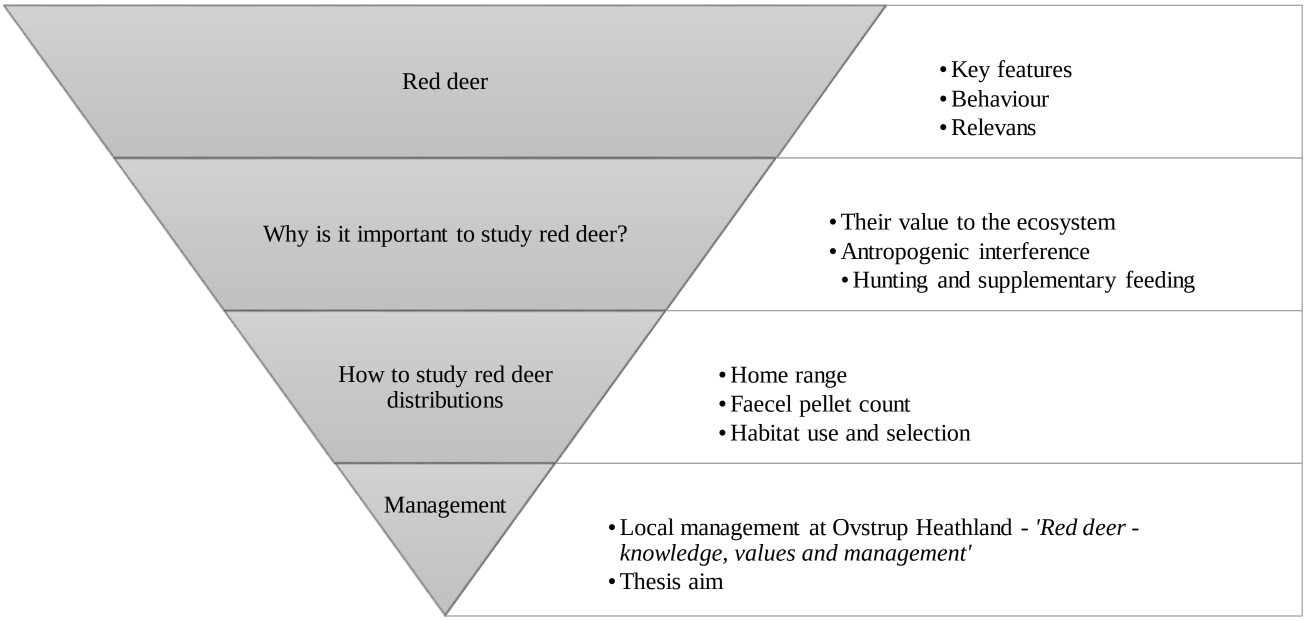

Figure 1. Graphical explanation of the content in Part A, section 2-5, summarizing the study species; why it is important to study it, what analytical approaches can be used, what affects it and lastly how it can be used for management.

2 Red deer (*Cervus elaphus*)

2.1 Red deer ecology and biology

Cervus elaphus, the red deer, is part of the deer family *Cervidae* (Lovari et al., 2016) and is the most widespread existent large autochthonous herbivore in Central Europe (Riesch et al., 2019). It has further been introduced to numerous parts of the world, primarily for hunting and/or farming purposes. The International Union for Conservation of Nature (IUCN) lists red deer as “Least Concern” due to the wide distributions and abundant populations (Lovari et al., 2016). A study from 2010 reported the European population estimate to be 1.7 million individuals and a hunting bag of 429 thousand individuals, with increasing tendency. Estimates are based on data from 32 European countries (Burbaitė & Csányi, 2010). Because red deer are very vulnerable to disturbances, areas without disturbances and habitats such as woodlands are essential for this species to thrive properly (B. Mitchell, Staines, & Welch, 1977).

2.1.1 Habitat requirements and foraging behaviour

Red deer inhabit lowlands, woodlands, natural grasslands and pastures, meadows and mountain areas (Lovari et al., 2016). They are classified as an intermediate feeder and feed opportunistically on mixed diet of grasses (Krojerova-Prokesova et al., 2010), shrub and three shoots. Their diet shifts during seasons and amongst habitats e.g., in autumn fruit and seeds are important (Lovari et al., 2016). It has been shown that the red deer adapts its feeding choices or foraging behaviour to the surrounding environment and food availability. However, grasses remain a large part of their diet (Mitchell et al., 1977). A Danish study from 1950’s of the rumen content in red deer showed that grasses and herbs constitute up to 75% during summer. Whereas heather, conifers and others were the substantial food scource during winter (Jensen, 1968). However, as the environment changes – so does the red deers diet. A more recently study indicated that the amount of grasses and herbs were cut in half and now replaced with at higher content of arable crops along with needles from pine and spruce (Buttenschøn, R. M., 2007).

In areas where they are hunted, red deer are nocturnal animals and are therefore mostly active in the periods from sunset to sunrise (Alves, Alves da Silva, Soares, & Fonseca, 2014; Kamler, Jędrzejewska, & Jędrzejewski, 2007). They are present in close forests during the day, hence why they are rarely seen in the open lands. Experiences from Germany shows that if the animals have access to undisturbed habitats a long way from roads etc., they will wander and forages such places during the light hours of the day (Riesch et al., 2019). During the dark hours of the day they forage on cultivated fields, upon which they could inflict large damage (Fattebert, Morelle, Jurkiewicz, Ukalska, & Borkowski, 2019).

2.1.2 Social organisation

Red deer have a highly developed social behaviour pattern. They live in herds based on a hierarchy, composed of individual animals of different social structures. These herds can consist of both large and small family sizes, where stags and hinds live separately most of the year and gather only during rut season (Mitchell et al., 1977). Stags can form herds in summer but may choose to live alone, until they gather in harems during rut season (Lovari et al., 2016). The stags are polygamous; hence they mate with several hinds. It is therefore unlikely that the conception rate in natural population is limited by stags not finding fertile hinds (Mitchell et al., 1977). In polygamous mating systems with high mating stakes and competition based mating choice, the male-male conflicts are expected to intensify leading to increasing male body size (Szemán et al., 2021). However, stags do not compete with other males until they reach social maturity at age six (Lovari et al., 2016). Hinds are sexually mature at age 1.5-2.5 years, whereas stags obtain this maturity already at yearlings (Lovari et al., 2016).

Social rank in the herds, has furthermore been shown to correlate with age and body weight in both males and females (Veiberg, Loe, Mysterud, Langvatn, & Stenseth, 2004). Older hinds i.e., the leading hind have the responsibility for the safety of the herd of which she leads. However, it is possible that a larger herd can have several hinds as leading hinds (Mitchell et al., 1977). Calves are born from end of May to beginning of June. When the calf can keep up with her mother without difficulties, the hind’s home range expands. At this time the two joins the last season’s calf and thus a matriarchal family herd is made. During this time the family herd can be seen with other related or distant related hinds along with their calves and young adults (Clutton-Brock & Guinness, 1975). This means the leading hinds are also controlling the behaviour of the herd, as they teach the calves important life lessons.

Their herds further have relatively large home ranges, and as their diets shifts during the year, so does their habitat demands and use of particular areas (Reinecke et al., 2014).

2.2 Distribution in Denmark

Red deer are Denmarks largest terrestrial mammals that roams freely throughout the country. The species has been present since the last ice age approximately 10.000 years ago. It differs from other danish wild species, in their ability to cover great distances in a short time (Naturstyrelsen & Vildtforvaltningsrådet, n.d.). The species almost became extinct due to over-hunting in the 1800-

hundreds. However, they managed to recover within remote areas of Denmark along with the introduction of new individuals to several other locations (Nielsen et al., 2008). From 1984 to early 2000s the danish red deer population had a 200% increase in population size (Burbaitė & Csányi, 2010) and according to the annual overview from Danish National Hunters' Association, the total count of red deer in spring 2020 was estimated to be 28.530 individuals (Flinterup, 2020). The largest populations are found in West and Central Jutland, where they live in areas with large coniferous forests used as refuge during the day (Miljøstyrelsen, n.d.-a).

3 Why is it important to study red deer?

In their search for food, red deer wander onto neighbouring heathlands, agricultural areas, pastures and high moors (Miljøstyrelsen, n.d.-a). In the natural ecosystems they play a role in the structure and dynamics through their grazing and trampling, as herbivores commonly remove <10% of the above ground primary production (Reimoser & Putman, 2011). It is recognised that this grazing may be helping the increase in plant diversity, by altering the species composition and removing species that are sensitive to damage. Nevertheless, in areas where populations densities are high, the increased grazing and browsing intensity may cause severe damage to agriculture and forestry, creating conflicts with human interest and management objectives (Reimoser & Putman, 2011).

These animals show great mobility and it is therefore almost certain both civilians, hunters and landowners encounter the same individuals. Consequently, it is important to understand the influence human disturbances have on red deer populations (Jeppesen, 1987). Many types of human disturbances could be mentioned, such as tourism, recreational activities etc., however the following section will focus on hunting and supplementary feeding.

3.1 Hunting

For game management to be effective it is important that the goals and objectives are clearly defined and practically feasible (Sunde & Haugaard, 2014). Through removal of individuals from certain groups (sex or age classes), it is possible to realise several objectives for a game population e.g., reduction in crop damages or high proportion of old males. Consequently, there must be an understanding of density limits to have a functional management practice and through that achieve the given management goals (Sunde & Haugaard, 2014). Especially as the ‘tolerable’ density in forest context might be very different from densities ‘acceptable’ in another context such as the threshold for tolerable impacts on crops or increased risk of traffic accidents (Reimoser & Putman, 2011).

Red deer is in many areas regulated via hunting, as many of the red deers predators have been removed or does not occur in densities that can control a population by themselves (Lovari et al., 2016). Hunting activities has a direct effect on which individuals are removed from the population and indirect effect on the population structure, their behaviour and the genetic variation (Allendorf & Hard, 2009). Furthermore, human disturbances has direct effect on the individual's energy needs and behaviour (Jayakody et al., 2011). Conversely, areas where red deer are not affected by hunting, they thrive in the open and does not show the same flight response to human activities (Sunde, Asferg, Nygaard Andersen, & Riis Olesen, 2008).

The occurrence of red deer, their population densities, and population structure is dependent on the habitat composition, but also the hunting pressure. Red deer are highly affected by hunting disturbances. So, a large hunting pressure can limit the population growth and dispersal. Further, it can act as a stressor introducing shyness, causing the animals to avoid habitats where they feel threatened by humans. Hence, affecting the red deer's habitat use and increasing their need to seek cover and thus making large forests areas of great importance (Sunde et al., 2008). Hunting activities can also force the animals to gather into large herds, as these provide safety possibilities and shared vigilance efforts (Jayakody, Sibbald, Gordon, & Lambin, 2008). The risk of being hunted or killed, causes them to stay away from open areas until nightfall. Then at night the red deer will have a determined, though unhurried flight pattern, as the fear of being hunted is lessened. The deer often leave their home ranges after hunting disturbances and stay away for a few days, until returning to their known habitats inside their home ranges (Kanstrup, Asferg, Flinterup, Thorsen, & Jensen, 2009).

When hunting a species like red deer, that has great mobility and hence most likely wanders across several farms, it is important that the hunters learn to manage it (Naturstyrelsen & Vildtforvaltningsrådet, n.d.). Further, it is favourable for neighbours to have a joint management and communication, as a single action would otherwise not be effective for management purposes (Leopold, 1986).

Overhunting (i.e., excessive and harmful hunting) in some places pressures the populations, however IUCN (International Union for Conservation of Nature) states that this is not seen to be a major threat in present day. Other factors that can pressure red deer populations are agricultural intensification and urbanisation, as these have resulted in habitat loss and fragmentation (Lovari et al., 2016).

3.2 Supplementary feeding

As all other organisms, red deer seek to optimize foraging by maximising calorie intake and nutritional value (Krojerova-Prokesova et al., 2010). With the current human dominated landscape, supplementary winter feeding of red deer has become a common practice in Europe and North America. The intentions of feeding however, varies, and only few consider the consequences feeding may have on red deer populations, as well as non-target species. Further, the surrounding environment that is dependent on a certain grazing pressure, may also face consequences from a possible lack of grazing (Ossi, Ranc, Moorcroft, Bonanni, & Cagnacci, 2020; Putman & Staines, 2004).

Most often supplementary feeding is associated with maintaining high densities of deer for hunting, as feeding may improve overwinter survival, reproductive performance, and fertility as well as body weight. It is also associated with prevention of agricultural and forestry damage (Putman & Staines, 2004). Wishing to maintain the deer densities at a high level, increases the risk of diseases and infections due to increased contact rates and spatial aggregation. Further, the effectiveness of the supplementary feeding depends on the proportion of individuals using the feeding sites (Milner, Beest, Schmidt, Brook, & Storaas, 2014). This is found to be extremely uneven, as the dominant stags may oust the younger individuals (Putman & Staines, 2004).

No matter the cause and effectiveness of supplementary feeding programs, there will most likely always follow unintended effect such as certain health risks (Milner et al., 2014). Deer are ruminants, and their digestive system is adapted to the seasonal diets. During spring and summer, the food available is easily digestible, whereas during winter the plant material has high fibre content and therefore low digestibility (Danmarks Jægerforbund, n.d.-a). Therefore, this sudden access to easy digestible carbohydrates, can cause the rumen environment to become acidified, leading to stomach ulcer, infection and digestive problems. Worst case scenario the deer dies, all because they are not used to this diet during winter (Felton et al., 2017; Putman & Staines, 2004)

If deciding to provide supplementary feed, a general suggestion is that one does not simply stop after the end of hunting season but has a continuous feeding protocol, that can be phased out as availability of plant growth increases. If not, and the feeding is inconsistent or suddenly stops, the animals that were once accustomed to foraging of feeding sites, now need to forage elsewhere. This can result in damages to forestry such as bark stripping (Putman & Staines, 2004). Also, if the animals are familiar with regular feeding, and it suddenly stops, could require a dramatic reduction to the population size, so the natural habitat can support the population (Milner et al., 2014). Or it could lead to a loss in body condition, as they will continue to go to the now empty feeding site and therefore not forage on the surrounding natural vegetation, or wander in the search for food (Putman & Staines, 2004).

In Denmark it is against the law to feed any deer in with sole intension of hunting (Danmarks Jægerforbund, n.d.-b). In 2018 new rules introduce a ban against feeding the red deer with compound feed and rolled grain, as this type of food could cause digestive problems. Another rule introduced in 2018 states, it is only allowed to feed the red deer from a minimum of 130 meters away from hunting towers and shooting ladders, to minimize supplementary feeding on smaller areas (Miljøstyrelsen, n.d.-b). Furthermore, it is against the law to shoot them in close proximity to feeding sites. The definition of what is "close proximity", has been set to be between 25-50 meters. Therefore, a consequence of feeding is that the hunters has prohibited themselves from shooting the animals within a radius of 25 meters from the feeding site (Danmarks Jægerforbund, n.d.-b).

As an alternative to supplementary feeding, it is possible to recreate natural forage with forage potential all year around. Areas such as heathland with sufficient winterfeed would not only benefit red deer populations but would enhance the biological diversity in the given area. Another possibility is to create forest with clearings and natural meadows. By promoting forests with old oaks and beech's, the animals will have nutrient rich food source during winter in form of the fruits from the old trees (Naturstyrelsen & Vildtforvaltningsrådet, n.d.). This furthermore means that unintended effects of feeding, such as increased population density, change in demography, restricted foraging (reduced home range size) and shifts in core area within the home range would possibly decline over time. However, the reversibility of the unintended effects still requires further investigation (Milner et al., 2014).

4 How to study red deer distributions

4.1 Home range estimation methods

Home range behaviour is the emerging pattern of a range of decision-making process, as the individual demonstrate familiarity within the area they live in, knowing the locations of possible mates and locations of resources (Mitchell & Powell, 2004). The concept of home range can be defined as:

> "*that area traversed by the animal during its normal activities of food gathering, mating and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered part of the home range.*"
>
> \- (Burt, 1943)

As a response to mating possibilities and resource availability home range size can change seasonally (Mayer et al., 2019). This applies to not only mammals but also fish, reptiles and birds (Mitchell & Powell, 2004).

There is no standardised method to estimate home range, as several home range estimation methods have been developed: 1) Minimum convex polygon, 2) Kernel density estimation and 3) Local convex hull (Gregory, 2017). However, the following will focus only on kernel density estimation.

Kernel density estimation (KDE) is one of the most commonly used method within home range analysis (David, W., Baruch-Mordo, & C., 2011). This estimation method uses location data to create the utilization distribution (UD), which is a bivariate probability density function that considers the animals use of space (Calenge, 2020). The KDE output is a raster, in which values can be thought of as a the probability of finding an animal in a given location (Gregory, 2017). The 50% and 95% probability of used areas are the most used with this estimation method, where 50% is seen as the animal's core area (Chirima & Owen-Smith, 2017).

This estimation method requires the user to decide on how to incorporate bandwidth. The choice of bandwidth (*h*) when working with this method is extremely important since the bandwidth can change the shape of the kernel. A high *h* will lead to a shallow kernel where very distant points will contribute to the home range estimate. One the other hand, a low *h* only allows very close points to contribute to the estimate, making it narrow. The optimal bandwidth will depend on the data (David et al., 2011).

Complications can occur in relation to overestimation, due to KDE including areas not used by the individual. Also, in relation to the abovementioned selection of bandwidth. In essence, the KDE assumes use of the whole area, but can extrapolate beyond the location of the outside points and therefore give a better understanding of the use of landscape (Gregory, 2017).

4.2 Faecal pellet group count

Faecal pellet count is an indirect census method that can be used to estimate population densities and habitat use for various species and is particularly used in ungulate studies and for management objectives. There are many ways to design a pellet count survey and it all comes down to what the topic of investigation is, the area of investigation and duration of the study (Mayle, Peace, Gill, Britain., & Commission., 1999). There are two main techniques of gathering pellet data; 1) Faecal accumulation rate (FAR) and 2) faecal standing crop (FSC) (Campbell, Swanson, & Sales, 2004). To estimate abundance both FSC and FAR requires a known defecation rate. The animals defecate a certain amount per day and this knowledge allows us to estimate the population size in an area. It is a very basic and easy estimation method that requires very few tools. Tools can vary depending on which method used for a survey and the survey's design (Mayle et al., 1999).

FAR measures the daily accumulation rate of pellet groups and FSC measures overall pellet density. (Campbell et al., 2004). The FAR technique consists of estimates obtained from accumulation of new pellets in-between known time periods e.g., seasons and requires the removal of all pellets in the study plots between each period. Whereas the FSC technique uses density estimates from all pellets found and therefore no need for prior removal. It also requires an estimate of pellet decomposition rate (Periago & Leynaud, 2009). Calculation of deer densities with FSC can be done using equation 1 and with FAR, equation 2 (Mayle et al., 1999):

$$Density_{species} = \frac{Density_{Pellet\ groups}}{Decay\ rate * Defecation\ rate} \qquad \text{(eq.1)}$$

$$Density_{species} = \frac{Density_{Pellet\ groups}}{Time\ between\ visits\ (days) * Defecation\ rate} \qquad \text{(eq.2)}$$

Neither FAR nor FSC can be said as a better method than the other. Both have been evaluated through various studies and neither shown to be more accurate than the other. It all comes down to the research question, the species, and the environment. However, the FAR technique requires more time, as the survey plots need to be stripped of pellet after each count (Campbell et al., 2004; Periago & Leynaud, 2009).

A combination of methods and techniques are possible and previously studied, often with the use of distance sampling as this can easily be adapted to either technique (Alves, Alves da Silva, Soares, & Fonseca, 2013). Distance sampling involves using line transects or point transects in the search of pellet groups. With line-transect sampling several lines with a given distance are used for the count of pellets. Point-transects on the other hand, uses random selected points for the study. This method has the advantage that the observer only needs to focus on each point plot without having to navigate along a line (Marques, Borchers, Borchers, Rexstad, & Thomas, 2002).

Faecal pellet survey methods are prone to observer bias, misinterpretation of pellets and instances of groups not being counted. Missed groups are often influenced by vegetation type and height, plot size and fatigue. Furthermore, as pellets serve as nutrients for several insects, this may at certain times of the year be a reason for pellet loss. Also, the weather plays a part in pellet loss e.g. heavy rainfall (Neff, 1968).

4.3 Habitat selection and resource selection functions

An animals habitat selection is a behavioural consequence of their decision-making process, in which they may actively select for certain areas to inhabit based on resources and/or reproduction possibilities (Boyce & McDonald, 1999). Therefore, habitat selection analyses are central to many ecological studies wishing to understand and predict the relationship between probability of animal occurrences and environmental conditions (Avgar, Lele, Keim, & Boyce, 2017). Selection can be defined as the process of using resources non-randomly in relation to its availability (Lele, Merrill, Keim, & Boyce, 2013; Manly, McDonald, & Thomas, 2002).

Habitat selection analyses include two types of models. The resource probability function (RSPF) that predicts the probability of selection. In contrast, the resource selection function (RSF) yields predictions that are proportional to the probability of selection and can be referred to as relative probability of use (Avgar et al., 2017; Tamstorf, Aastrup, & Cuyler, 2005). They differ in their estimation procedure and therefore also in the predictions they create. The RSPF is scaled and can only be determined if the available units and unused units during a selection period are known (Avgar et al., 2017; Tamstorf et al., 2005) and RSF can be determined when the sampling for used and available units is separate (Manly et al., 2002).

Resource selection functions (RSF) act as a fundamental tool for quantifying ecology and is the most commonly used of the two (Avgar et al., 2017; Boyce & McDonald, 1999). The goal with RSF is to link animal occurrences to resources, risk and environmental conditions i.e., evaluate the relationship between the locations used by an animal and environmental characteristics of this location. Consequently, investigating what animals need to survive and reproduce, what they avoid and how environmental factors e.g. temperature or precipitation may influence their need for resources (Griffin et al., 2021; Spitz, Hebblewhite, & Stephenson, 2020). Further, they can be used to predict situations in the future e.g. how climate change would affect population distribution and habitat availability (Durner, Douglas, Nielson, Amstrup, & Mcdonald, 1985). The selection ratio is the origin of the concept of resource selection functions and is defined as use relative to availability; $w(\underline{x}) = \left(\frac{use\ distribution}{available\ distribution}\right)$ (Lele et al., 2013; Manly et al., 2002).

Much confusion can occur when deciding on which methods to use and how to use certain terms such as selection, use, preference etc. Many practitioners encounter this confusion of concepts and differences, which can in the end effect the management purpose of the investigation (Lele et al., 2013). This thesis will only investigate habitat selection as relative probability of use using RSF.

Several assumptions have to be fulfilled for a RSF to determine the relative probability of use, in a given habitat are: 1) all significant key factors are included in the analysis, 2) free and ready access to available resources, 3) each resource unit is sampled randomly and independently (Boyce & McDonald, 1999)

Resource selection functions can be modelled using many statistical approaches, however fitting a logistic regression function for the probability of use versus available area, is one of the simplest and most frequently used approaches (Manly et al., 2002). Resource selection functions are built using logistic regression for binary response i.e. 0 or 1. Logistic regression assumes that the relative probability of an individual using a given unit is determined by: $w(x) = \exp(ß_1x_1 + \ldots..\ ß_px_p),$ where $ß_1$ to $ß_p$ are constants that can be estimated from the data and x_1 to x_p are variables that *w*, the relative probability of use is to be related to (Manly et al., 2002; Tamstorf et al., 2005).

The models compare known occurrences with available locations i.e., other locations the animal could have been. How availability is defined matters for the output as, how selection is quantified, depends on the definition of availability (Johnson, 1980). Availability can be considered in four different scales: First order selection, second order selection, third order selection (Fig. 2) and fourth order selection.

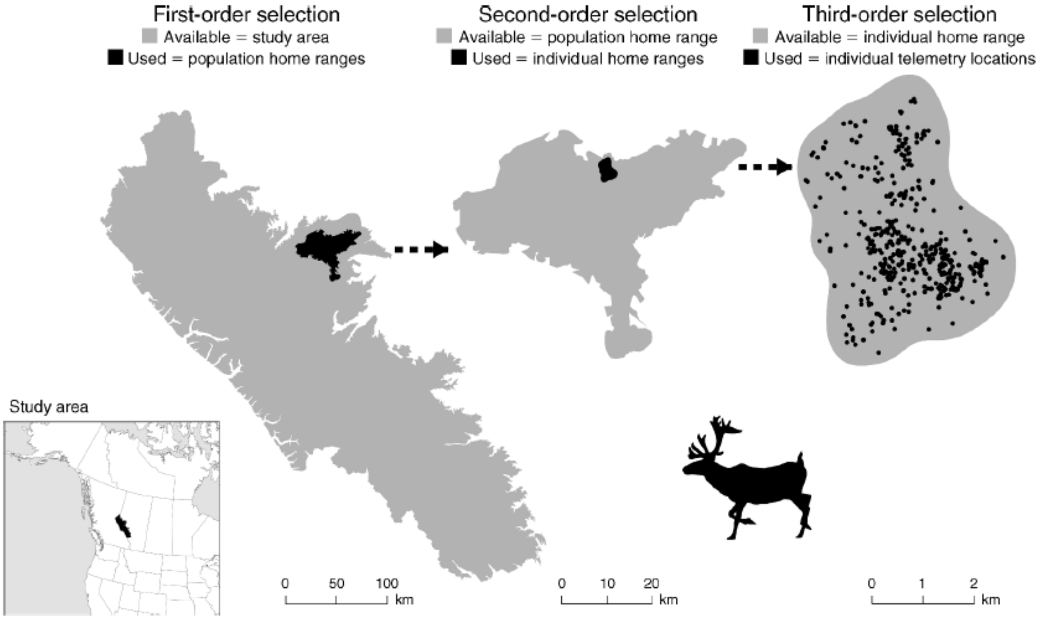

Figure 2. Example of the three scales of selection from (DeCesare et al., 2012). *The two first scales consist of used locations (black polygons) and available locations (grey polygon). In the third order selection, it is the GPS locations that defines the used locations and the home range the available.*

First order selection occurs at a larger scale where availability is the entire study area, and the used area is the populations home range size. Here, selection is investigated at a broad level e.g., why it is important that a given population is found in an area relative to the remaining study area. With second order selection, habitat selection is investigated within population scale. The available area is now the populations home range and the used the individual home range sizes. At this scale it can be investigated why a certain individual has its home range at a given area, compared to where the whole population is found. The third order selection, where the GPS positions are investigated as the used and the available is the individual home ranges. With the third order selection one can study why an individual choose the exact locations in relation to other available locations within its home range (DeCesare et al., 2012; Manly et al., 2002). Lastly, fourth order selection is selection of a specific resource such as food item at the area of the third order selection (Johnson, 1980). Therefore, with resource selection functions we model the spatial distribution of locations as a function of spatial covariates, while accounting for what is available.

As mentioned previously, an animals habitat selection is a consequence of a decision-making process. This decision-making process can be affected by many factors such as human interference e.g hunting, recreative disturbances and supplementary feeding. This suggest that human interference plays a role in the red deers habitat use (Coppes, Burghardt, Hagen, Suchant, & Braunisch, 2017). Thus, making it important to understand how to manage and coexist with this species. Especially in areas where stakeholders' opinions of red deer may not see eye to eye.

5 Management of red deer in an around Ovstrup Heathland

5.1 Red deer on Ovstrup Heathland

The heathlands of Denmark cover approximately 2% (85.000 ha) of Denmark's total area (Buttenschøn, 2007).The area of Ovstrup Heathland with its 490 ha is owned by Aage V. Jensen Nature Foundation. Ovstrup Heathland is a Natura 2000-area which means there are special requirements regarding the protecting of the nature in the heathland (Miljøstyrelsen, 2020). Natura 2000 is a cooperative network between EU member states, which aims to ensure a favourable conservation status for rare, endangered or characteristic species and habitat types in Europe (European Commission, n.d.). This specific Natura 2000 area has been appointed to protect the large occurrences of dry and wet heathland and well as streams with otter and brook lamprey. Ovstrup Heathland consists of areas with well-developed heath vegetation and borders primarily to cultivated nature. There are large areas dominated by heather, cross-leaved heath or crowberry. Ovstrup

Heathland is characterized by its large heath plains with dry heath and large connected areas where the habitat wet heath dominates (Miljøstyrelsen, 2020).

The heathland provides an area of low disturbance that attracts game populations, such as red deer and fallow deer (Aage V. Jensen Naturfond, n.d.-b). The red deer population has increased significantly throughout the recent years. Today the population on and around Ovstrup has a vast majority of hinds and younglings. Problems can occur when old and mature hinds are being shot from their respective herd. This leaves the herds with few experienced hinds and as outcome, large herds consisting of calves and younglings will gather with other inexperienced individuals (Aage V. Jensen Naturfond, n.d.-a).

This thesis revolves upon a management project of the red deer in and around Ovstrup Heathland called “Red Deer – knowledge, values and management”. The project is funded by Aage V. Jensen Nature foundation and managed by researchers from Aarhus University, Centre for Adaptive Nature Management. This management project includes the involvement of citizens around the heathland to explore their role in the future sustainable red deer management in the area. The project deals with four stakeholders: Aage V. Jensen Nature Foundation, landowners, farmers and hunters. These stakeholders’ interests may overlap e.g., a landowner may also have the interest of a hunter. The landowners and farmers that cultivates their land in proximity to the heathland, may see these large red deer population in a more negative way, as they forage on the fields and thus diminish the yield. Whereas Aage V. Jensen’s Nature foundation aims to maintain a certain population size of red deer on the heathland, since their presence and foraging habits plays an evident role in keeping the vegetation down and thus maintaining the light-open nature and a thriving biodiversity (Skriver & Steinar, 2019). Further, joint management of the red deer population aims to result in more fully mature stags and an improved population structure (Aage V. Jensen Naturfond, n.d.-a).

5.2 This study

This study focused on the habitat use and habitat selection by the red deer population on Ovstrup Heathland. By means of telemetry data from GPS collars and faecal pellet count, I studied how supplementary feeding affected the spatial distribution and habitat selection. To see how the deer selected between different habitat categories throughout the year, seasonal and temporal variation was analysed. Furthermore, pellet count data was used to reflect deer presence around feeding sites during winter and used for density estimates.

Accordingly, I predicted that **1)** the red deer would forage on agricultural fields during night and maintain in safety in the forest during the day and **2)** that during winter the red deer would maintain near the feeding sites as they are an easy food source. Finally, **3)** that pellet densities would be higher on the heathland and close to feeding sites, compared to remaining habitats.

The results and perspectives of this study can be read in the article manuscript “Winter feeding affects habitat selection of red deer in a mixed landscape”, Part B of this Master’s thesis.

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Part B - Article manuscript

Winter feeding affects habitat selection of red deer (*Cervus elaphus)* in a mixed landscape

Abstract

In Denmark, massive provisioning of artificial food supply e.g., carrots and beets, is a common practice by landowners to attract red deer (*Cervus elaphus*) and thereby increase hunting opportunities in the hunting season, keep deer in good shape through the winter, or to prevent damage to cultivated fields and tree plantations. As feeding sites of hundreds of kilos of food, represent an overabundant food source of high caloric values, this food provisioning in winter may potentially influence the spatial distribution of red deer in the landscape, as a significant energetic pull factor. Consequently, grazing pressure in nature types reliant on ungulate grazing, such as nearby heathland may be reduced. Knowledge on the red deers habitat selection in areas with supplementary feeding and usage of these feeding sites may be essential for future nature conservation and for the management of red deer populations. I analysed habitat use and habitat selection by red deer in a Danish landscape, with a mosaic of protected heathland, farmland, and forest (conifers). I did this with location data from four GPS-tagged hinds during an observation period of 719 days (~ 2 years). Further, I studied how supplementary feeding affected deer spatial distribution and habitat selection. Faecal pellet counts on transects in different directions from the feeding sites were used as an independent measure of habitat-specific deer activity in winter. GPS data showed that the red deer strongly selected for proximity (0-50m) to feeding sites during winter. This selection was reduced in summer and spring. Also, it was only during winter that a proximity of 50-200m was selected for. Independent of season the red deer only selected for nearness at night. Further, faecal pellet counts were highest within 60 meters from the feeding sites. Additionally, I found that throughout the year, GPS-tagged hinds selected forest more than heathland, grassland and arable land, especially during daytime. Finally, faecal pellet counts were higher in heathland than in other habitat categories. In conclusion, I found indications that supplementary feeding plays a central role in shaping the spatial distribution of red deer in winter, as red deer strongly selected for feeding locations during winter. As a result, the grazing pressure on the adjacent heathland that is maintained through natural grazing may be reduced accordingly.

Key words • Habitat selection • Red deer • Supplementary feeding • Management •

Vinterfodring påvirker habitatvalget hos kronvildt i et mosaiklandskab

Resumé

I Danmark er store mængder af supplerende foder som f.eks. gulerødder og roer, en almindelig praksis blandt lodsejere for at tiltrække krondyr. Dette kan være med til at øge jagtmulighederne, holde dyrene i god form gennem vinteren eller forebygge skader på dyrkede marker og plantager. Da foderpladser repræsenterer en fødekilde med høje kalorieværdier og derfor agerer som tiltrækningsfaktorer, kan vinterfodring potentielt påvirke hvor krondyrene befinder sig i landskabet. Som følge heraf kan græsningstrykket på naturtyper som f.eks. hede arealer, der er afhængige af afgræsning, reduceres. Viden om krondyrenes habitatvalg i områder med fodring og anvendelse af disse foderpladser kan være afgørende for fremtidig naturforvaltning og for forvaltningen af kronvildtbestandene. Jeg analyserede habitatbrug og habitatvalg hos krondyr i et dansk mosaiklandskab af beskyttet hede, landbrug og skov. Dette blev undersøgt med data fra fire GPS-mærkede hinder i en observationsperiode på omkring 2 år. Yderligere undersøgte jeg, hvordan fodring påvirkede krondyrenes fordeling og habitatvalg. Faldtællinger på transekter i forskellige retninger fra foderpladserne blev brugt som et mål for habitatspecifik krondyr aktivitet om vinteren. Resultaterne fra GPS-data viste, at krondyrene særdeles valgte for nærhed (0-50m) til foderpladser om vinteren. Dette var reduceret om sommeren og foråret. Derudover var det også kun om vinteren, at der blev valgt nærhed på 50-200m til pladserne. Uafhængigt af sæson valgte krondyrene kun for nærhed til pladserne om natten. Derudover fandt jeg ud af, at GPS-mærkede hinder gennem hele året og især i dagtimerne, valgte skov mere end hede, græsarealer og dyrkede marker. Desuden, var antallet af faldhobe (ekskrementer) højest inden for 60 meter fra fodringspladserne, samt højere på heden end i andre naturtyper. Afslutningsvis så fandt jeg stærke indikationer på, at fodring spiller en central rolle i hvor krondyrene befinder sig i landskabet om vinteren, da de meget tydeligt valgte for nærhed (0-200m) til fodringspladser om vinteren. Som følge heraf kan græsningstrykket på den nærliggende hede, der opretholdes gennem naturgræsning, reduceres.

Nøgleord ● Habitatvalg ● Krondyr ● Fodring ● Forvaltning ●

1. Introduction

An animals habitat choice is the result of the need to balance the access to resources with predation risk and human disturbance, the so called foraging-safety trade-off (Fattebert, Morelle, Jurkiewicz, Ukalska, & Borkowski, 2019). Spatial heterogeneous landscapes offer solutions to this trade-off, as such landscapes make it possible for the animals to shift between risky habitat rich in high-valued resources and safer habitats with potentially less such resources (Fattebert et al., 2019). However, landscape changes due to agricultural intensification, resulting in loss of habitats, can influence animal behavior, making human-wildlife coexistence challenging (Linnell et al., 2020; Riesch, Tonn, Meißner, Balkenhol, & Isselstein, 2019). Red deer is highly mobile species and thus may come into contact with various stakeholders such as hunters and landowners. All with different opinions on how red deer populaitions are best managed and to which extent coexistence and thus the possibility of land-sharing is of interest (Linnell et al., 2020).

As red deer use habitats differently throughout the year, their large-scale movements can lead to management problems, such as economic losses within agri- and silviculture (Reimoser & Putman, 2011; Szemán, Liker, & Székely, 2021). When red deer do not gain enough food from the natural areas, they forage on cultivated areas, fields and young tree stands in tree plantations, resulting in damage to the crops and reduction of the harvest potential. Also, when stands of older trees are exposed to bark stripping, this reduces their economic value as timber (Reimoser & Putman, 2011; Trdan & Vidrih, 2008). Aside from the negative impacts, these large herbivores' grazing and trampling make them important ecosystem engineers (Müller et al., 2017), as they contribute to creating vegetation diversity and thus, promote biodiversity (Fløjgaard et al., 2017). Furthermore, grazing pressure from large herds of red deer helps keep the areas of heathland open (Jørgen, 2016). Therefore, understanding their habitat requirements is essential (Kneib, Knauer, & Küchenhoff, 2011). Assessing habitat requirements of a species can be done by examining their habitat selection (Sun, Yu, Guo, & Zhang, 2020), i.e., relating habitat use to its availability in a given area or restricted to the animals home range (Mysterud & Ims, 1998).

Additionally, grazing intensity from red deer may be reduced by factors such as supplementary feeding, as this can alter the natural grazing pattern (Fløjgaard et al., 2017). Supplementary feeding, especially during winter, is a common practice, as this can enhance the animal's survival and reproduction success. In other cases, feeding is done with the intention to prevent damage to cultivated fields or forests by relocating the animals (Putman & Staines, 2004). In this sense, feeding sites can be beneficial in terms of manipulating migration routes and habitat selection. Massive provisioning of artificial food supply during winter may also have a short-term benefit for hunters, by increasing their personal hunting opportunities. However, the sites may increase disease transmission, since more animals are gathered at a small area (Felton et al., 2017). It is furthermore important to think about the composition and protocol of the supplementary feed provided, as the red deer's winter diet may be influenced by feed of different nutritional values e.g., hay, silage or sugar beets. If feeding is inconsistent, deer once accustomed to foraging on feeding sites now need to forage elsewhere, which can lead to an increase in bark stripping. On the other hand, supplementary feed with high fibre content may lead to a decrease in bark stripping (Putman & Staines, 2004; Rajský et al., 2008). Finally, supplementary feeding can trigger digestive problems leading ruminal acidosis which cause amongst others weight loss, poor general condition and in worst case death (Felton et al., 2017)

The management of red deer (*Cervus elaphus*) is currently and has for decades been a highly debated issue within wildlife management in Denmark, and there is currently no national red deer management plan (Sunde, Haugaard, & Hansen, 2018). The Danish red deer population became nearly extinct in the 1800s due to over-hunting (Nielsen et al., 2008). However, the last remaining small populations managed to survive during in the 1900s (Naturstyrelsen & Vildtforvaltningsrådet, n.d.), and have since been steadily increasing (Sunde & Haugaard, 2014).

Quantifying the habitat use, locating and mapping supplementary feeding sites and conducting faecal pellet group counts, will provide new information and awareness of the effects that supplementary feeding sites may have on red deer populations. Here, I intend to uncover the red deer's movement patterns under different circumstances, such as seasonal and temporal variation and around nearby feeding sites. Examining the red deer's habitat use will make it possible to see how they use the different areas for grazing, browsing and shelter. The following research questions will be investigated:

1) Do the red deer select for feeding sites? I hypothesise to see seasonal variation in selection for feeding sites, with red deer near feeding sites during winter, as they are an easy food source, compared to the natural foraging habitats, with less food available during winter. During summer, I hypothesise the deer will spend less time near feeding sites, as the heathland and forest will provide sufficient amounts of food and since the feeding sites are not active.

2) How do red deer use and select between different habitat categories across seasons and time of day in relation to availability? I hypothesise that during the day and in winter especially, the red deer would spend more time in cover and most likely forage in the forest because of the foraging-safety trade-off. Whereas at night, I anticipate the red deer to forage on neighbouring fields, the heathland and around feeding stations, as they would be safe from hunters during these hours.

3) What is the habitat specific density of red deer and how does the pellet density differ in different habitat categories and near feeding sites in winter? I hypothesise to find higher densities of pellets groups on the heathland, in the forest and close to feeding sites compared to open habitat. I expect these habitats and areas around feeding sites to be used most in the winter season, due to cover possibility in the forest and safety from hunters on the heathland while foraging.

2. Methods

2.1. Study area and capture procedure

This study was performed at Ovstrup Heathland (490 ha) located in central Jutland along with neighbouring areas (Figure 1).

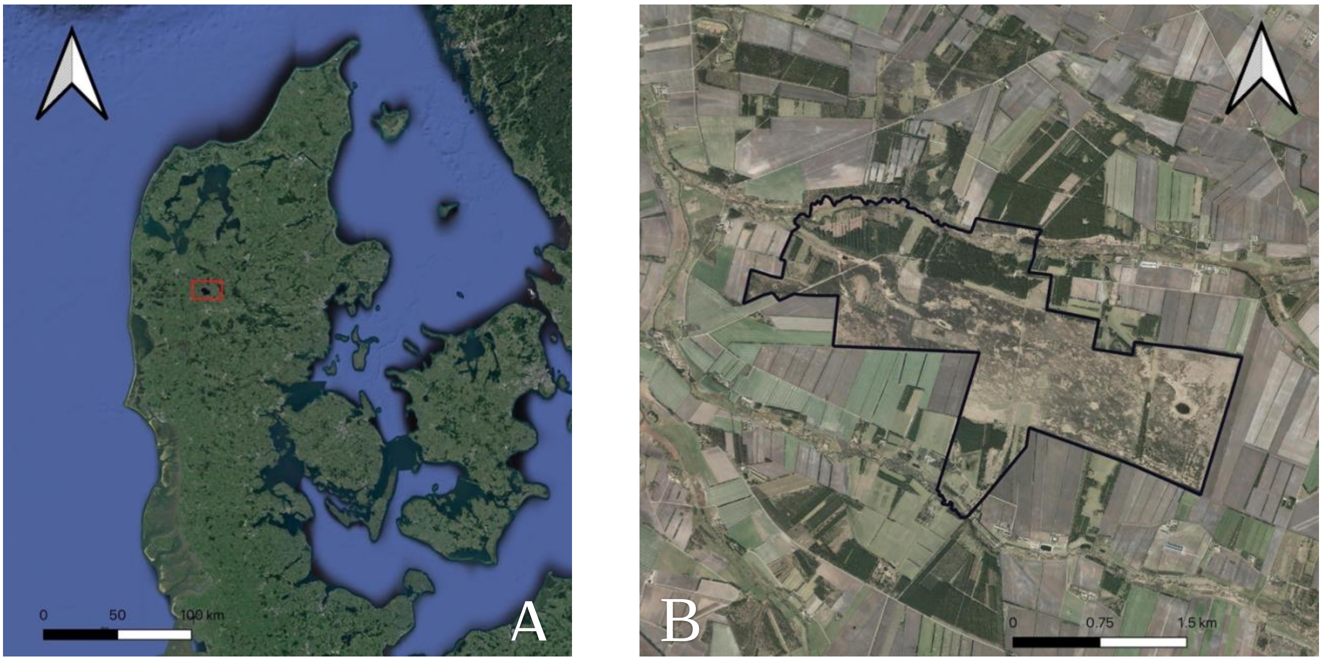

Figure 1. (A) Map of the study area location in Denmark and (B) enhanced map of the study area, Ovstrup heathland (black outline) and the surrounding areas. Both maps are created using Qgis ver. 3.16.0-Hannover.

In 2019, five adult female red deer were captured using a 14x14 meter drop-net. They were put under anaesthetisation and marked with GPS collars and yellow ear tags. Due to technical problems with

GMS-transmission of one collar, only the data from four deer was available for this project. Table 1 presents information about the individual red deer, date of marking, observations period and the different recording intervals.

Table 1. Individual information on the four red deer.

Red deer		**Date of marking**	**Observation period end date**	**Number of GPS locations**
ID	Sex			Hourly recordings
13878	♀	13/3/19	1/3/21 (719 days)	15.977
13879	♀	13/3/19	1/3/21 (719 days)	15.917
13880	♀	13/3/19	1/3/21 (719 days)	16.002
36912	♀	14/3/19	1/3/21 (718 days)	15.940
				63.836

2.2. Habitat data

The landcover types used in the analysis are forest, heathland, agricultural fields, and built-up areas. Fields were split into two categories; 1) Grasses: grass all year round and small newly planted trees without cover for the red deer and 2) Arable: fields that are cultivated with e.g., cereal, maize, and potatoes. See Appendix B1 for the sources from where vector data of landcover types were obtained.

2.3. Field procedure - locating supplementary feeding sites

A total of 16 supplementary feeding sites were actively located during February and March 2021 with help from various landowners. All but two were situated south of the heathland. Locating the feeding sites were done during the winter period, as this is the period the hunters and landowners lay out feed. During each visit, the locations were recorded with a Garmin GPSMAP 64 GPS unit.

Out of the 16 supplementary feeding sites, 11 had available feed whilst mapping the locations. Two of the 16 sites were only used occasionally, when feed was available to the landowner/hunter, two sites had not been used in the 20/21 season and one location was provided by the landowner, and thus I did not see or mark the location myself. The remaining were used regularly from September/November to April. Feeding station design and types of feed differed amongst locations. However, the same type of feed was used in cases where the landowner had more than one site. Types of feed ranged from hay and silage to sugar beets. One site fed all year round with waste soil containing potato leftovers.

2.4. Faecal pellet group count

Faecal pellet counts on transects in different directions from the feeding sites are used as an independent measure of habitat specific red deer activity and density estimates during winter. Data collection of faecal pellet groups was conducted during February and March 2021. Faecal standing crop count (FSC) in combination with distance sampling with a line transect method, was used to obtain an index of deer densities and usage around the supplementary feeding sites and to validate habitat preference estimates retrieved from the GPS collar. Data was collected on 5 of the 16 sites, as the other sites were no longer in use nor available for the pellet group count during the time of data collection. Feeding sites were given individual ID's: F1, F2, F3, F4 and F5. Transects were sampled using a 1m^2 measurement ring, placed at 10-meter intervals along 500 meters from each feeding site. Transects length was measured with a Garmin GPSMAP 64s. Depending on possible directions and property boundaries, two or three transects pr. site were sampled and given direction ID *a, b,* or *c*. To ensure a sampling method with randomised sampling plots, the procedure was to throw the measurement circle approx. 10 meters in the given direction. The position of the circle represented the plot in which pellet groups were counted. From 0-100 meters the circle was thrown once every 10 meters, from 100-200 it was thrown twice every 10 meters, etc. This provided a maximum of 150 plots per transect. Only active feeding sites were used during data collection, active meaning feed is frequently placed at the feeding site.

The definition of a pellet group is a cluster of six or more pellets at the same defecation spot (Mayle, Peace, Gill, Britain., & Commission., 1999). For this study, a minimum of 10 pellets were considered to form a pellet group, when pellets were fully formed with no sign of breakdown. If there were signs of breakdown the group was defined as in Mayle et al., (1999). The groups could have different spatial distributions i.e., scattered individually, clustered or in a line. If a group of pellets were found to be both in and outside of the measurement circle, the group was counted as part of the plot. Furthermore, the habitat of each counting plot was registered as either forest, heathland, or open area. Open area was defined as areas not providing cover/shelter for the red deer and not heathland.

2.5. Statistical analyses

All statistical analyses were done in the in the open-source program R version 4.0.2 (R Core Team, 2020), with extension RStudio version 1.4.1106. (RStudio Team, 2021).

2.5.1. Home range calculation

Fixed kernel method with bandwidth h_{ref}, was used, as it computes an optimal h, fixed across the whole dataset (Gregory, 2017). The entire observation period and seasonal home range sizes were calculated based on 95% kernel density estimation (KDE) using the R package *´adehabitatHR´*(Calenge, 2020). For each individual I calculated four seasonal home ranges and one for the entire observation period. Seasonal home ranges followed the 3-month biological division of seasons in table 2. KDE was used as this method creates concave boundaries and is more accurate with larger datasets, compared to the Minimum convex polygon method (MCP) (Chirima & Owen-Smith, 2017).

2.5.2. Habitat selection

To understand the shifts in habitat selection for different seasons and the effects of supplementary feeding sites, I modelled the relative probability that habitats were selected in relation to the available landcover types and distance to nearest feeding site. To get a measure of habitat availability for the habitat selection analysis, random positions were generated with a 1:5 used-available ratio and located within the individual's home range for the whole observation period, as in Mayer et al., (2019) whom also investigated seasonal selection using the entire home range estimate. The entire home range, even though not used to the same amount during some parts of the year, will still be available.

As the ratio between used and random positions are 1:5, the threshold for selection is drawn at 0.2. Thus, values above 0.2 is selected for and below 0.2 avoided in relation to availability.

I used resource selection functions (RSF) that determine the relative probability of use (Manly, McDonald, & Thomas, 2002), to investigate the four red deer's third order habitat selection i.e., selection of habitat within individuals' home range (Johnson, 1980). Further, generalized linear mixed models (GLMM's) using the R package 'lme4' were built with red deer occurrences as a binomially distributed dependent variable, where 0 = random position vs. 1 = used position.

A landcover map containing all habitat types was created for the analysis and intersected with both used and random positions. Some positions were located outside the defined habitat types. Those positions as well as duplicates created by overlapping landcovers were removed. This intersect resulted in a total loss of 13.70% random positions and 15.99% used positions from the whole observation period. Several land cover types were excluded from the analysis because the red deer never or only rarely used them. Red deer never used the industrial areas and the two nature types "hængesæk" and "kildevæld". Further, only 36 used positions were in areas of low-density housing and 18 positions in acid grassland.

To investigate sensitivity for the analyses to the selected landcover map, the same investigation was performed using another landcover map with lower land cover accuracy. This only produced a 9.02% loss of used points, compared to the 15.99%. However, it was decided that higher accuracy in landcover types at the cost of a slightly higher loss of positions, would yield more reliable interpretations regarding habitat selection. Therefore, I used the initial map with 15.99% loss. An overview of the intersect and the final amount of random and used points can be found, can be found in Appendix B2 and B3.

To analyse if the supplementary feeding sites have an impact on the red deer's behaviour, distance to each feeding site was calculated from all locations and was further grouped into three categories: 0-50 m (at feeding site), 50-200 m (near feeding sites) and > 200 m (away from feeding sites).

Habitat selection was visualised via effect plots generated from the best fit model, since this allows us to see how the effect of one variable change according to another variable e.g., season vs habitat.

For the analysis of habitat selection in different seasons, four biologically meaningful periods were defined (Table 2). To test if habitat selection differs during the day, time of day (TOD) was calculated and split into following categories: day and night. Dusk and dawn were both included in the night variable as they are active during that time.

Table 2. Biological division of the season for the habitat selection.

Season	Period	Information	Reference
Early winter (Hereafter; winter)	November - January	Hunting season ends 31st of January.	(Asferg et al., 2016)
Early Spring (Hereafter; spring)	February - April	Hinds are energy conserving for the calving season. Interest in optimising their conditions.	(Mitchell, Staines, & Welch, 1977)
Summer / Calving season (Hereafter; summer)	May - July	Giving birth to their calf May/June. In July the calf is still very small and not yet completely mobile.	(Mitchell et al., 1977)
Fall / Hunting activity begins (Hereafter; fall)	August - October	The calf is now mobile and there is plenty of food in the environment. Hunting activity begins and mating season begins in September.	(Asferg et al., 2016; Mitchell et al., 1977)

2.5.3. Faecal pellet group count

I made a graphical exploration of the count including habitat as a variable (Appendix A1-A5).

Data was analysed for each habitat type and the overall density. Further, a subset was created for densities near feeding sites defined between 0-200m from the feeding stations. Pellet densities were calculated using following equation:

$$Density_{Pellets} = \frac{No.of\ pellet\ groups\ conted}{Total\ area\ counted} \quad \text{(eq. 1)}$$

Red deer densities was calculated using the below equation from Mayle et al., (1999), which is based on the method FSC (faecal standing crop count) and widely used in various studies of animal densities calculated from pellet counts (Alves, Alves da Silva, Soares, & Fonseca, 2013; Periago & Leynaud, 2009).

$$Density_{Deer} = \frac{Density_{Pellet\ groups}}{Decay\ rate * Defecation\ rate} \quad \text{(eq. 2)}$$

Decay rates depends on weather conditions and habitat. Therefore, for each habitat I used the decay rates from Mayle et al., (1999): forest: 96 days, open areas (bare ground): 81 days and heathland: 146 days. The pellet densities used was the ones calculated from eq.1.

To calculate the overall population estimate on Ovstrup heathland, I did the following: 1) As the heathland covers 490 ha, hereof 312 ha heath (Aage V. Jensen Naturfond. n.d.-b), I calculated that as a separate, 2) I did not know the exact hectares forest and open areas covered of the remaining 178 ha. Therefore, I used the average pellet density of forest and open areas along with the average decay rate of the two. The decay rate used for this population estimate was consequently 88.5 ~ 89 days and 3) I added the two density estimates together.

For the deer density at and near the feeding sites (0-200m), I used the average decay rate of the three habitats, as the feeding sites were in all three habitats. Therefore, it was set to 108 days.

A defecation rate of 25 pellet groups per day (Mayle et al., 1999) was used for all the above density calculations.

2.5.4. Modelling

For habitat selection CollarID was included as a random effect while habitat type, season, distance to feeding site and TOD were included as fixed effects. The two-way interactions of the habitat type with season and habitat type with time of day (TOD), were used to investigate seasonal and daily changes. Further, two-way interactions of distance to feeding sites with season and TOD, were used to investigate the effects of feeding sites.

Model selection was based on a stepwise AIC selection, using the MuMIN package (Barton, 2020), selecting the model with the lowest AIC.

For pellet count the package "glmmTMB" was used to account for zero inflation and non-normal distribution of the count data (Brooks et al. 2017). The transects were nested within feeding site (ID) and included as random effects. Further, optimizers were used to account for convergence issues. Model selection was used to distinguish among a set of possible models by using AIC and selecting the model with the lowest score.

3. Results

3.1. Home range size

I calculated 16 seasonal home ranges from the four individuals, plus four home ranges covering the entire observation period. Home range sizes varied between 705 ha and 2992 ha (mean ± SD = 1674 ± 597 ha). Seasonal home range sizes showed the largest variation in size during summer 1452 ± 602 ha and winter 1286 ± 276 ha, the smallest. During fall 1774 ± 347 ha and spring 1792 ± 527 ha.

Table 3. Individual home range sizes for the observation period and seasons.

CollarID	Home range size (ha)	Season
13878	2992	Observation period
13879	2924	Observation period
13880	1786	Observation period
36912	1168	Observation period
13878	2424	Fall
13879	1889	Fall
13880	1708	Fall
36912	1147	Fall
13878	1529	Spring
13879	1629	Spring
13880	1958	Spring
36912	1363	Spring
13878	2175	Summer
13879	1514	Summer
13880	1415	Summer
36912	705	Summer
13878	1261	Winter
13879	1141	Winter
13880	1603	Winter
36912	1054	Winter

3.2. Habitat use

The red deer hinds used forest as their primary habitat in all four seasons and during the day. The use of all other habitat categories and proximity to feeding sites was highest during night in all seasons, with exception of heathland and feeding sites during summer. This is purely use of the different categories and not in relation to what is available (Fig. 2).

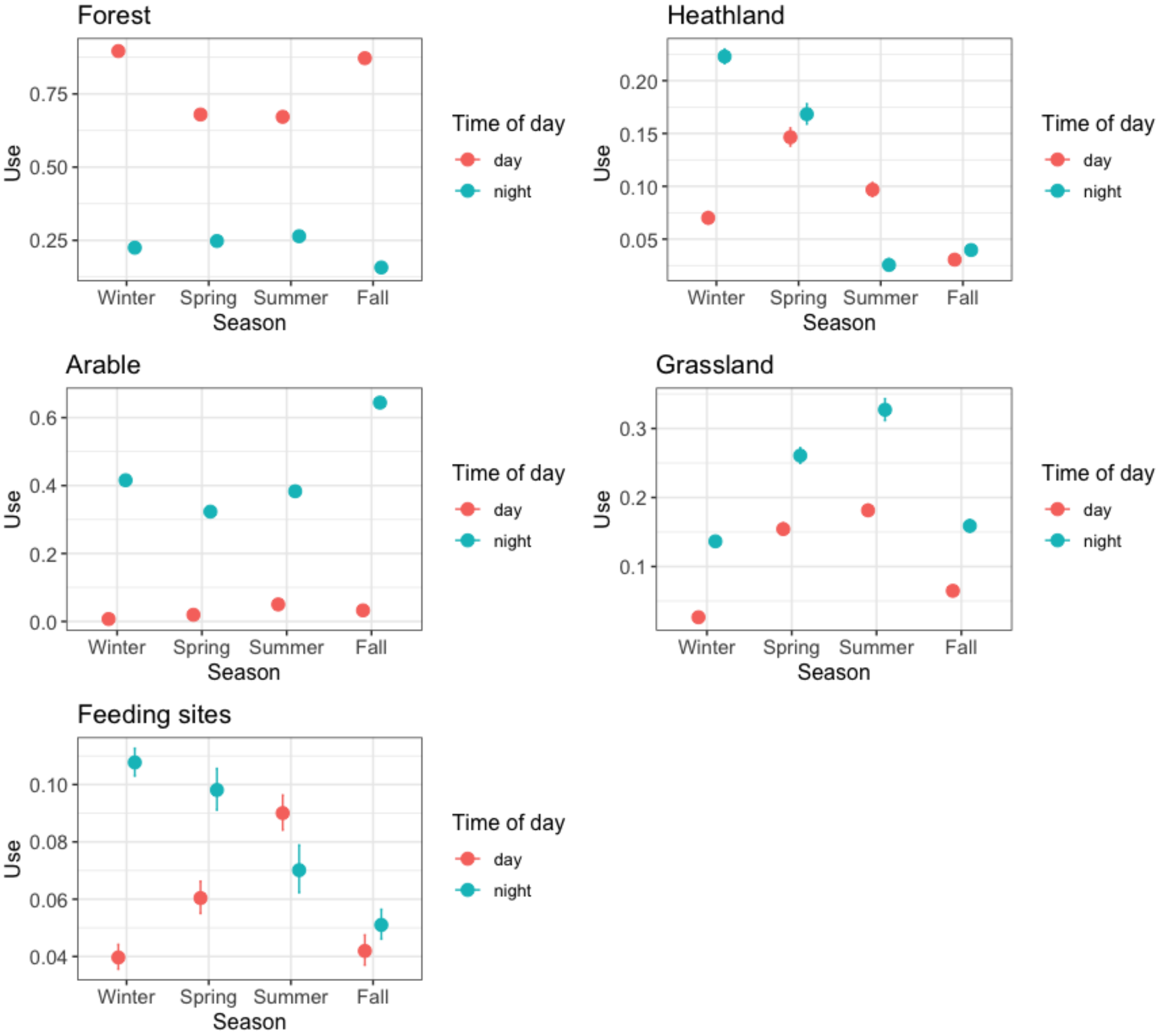

Figure 2. Percentage of use in the four habitat categories and near the feeding sites (0-200m) in different season and during day and night. 95% confidence intervals are given as bars. The four habitat categories are calculated from everything >200m, as everything below is defined as "near the feeding sites" and here we are not interested in the habitat choice itself, but more that they choose to be near the feeding sites.

3.3. Habitat selection

AIC selection showed that the model containing all variables as fixed effect, was the best fit model (Table 4). The parameter estimates for the model can be found in appendix B4

Table 4. Results from model selection explaining use (presence) or unused (absence) of habitat categories and distance to feeding site of the four red deer including interactions. Type: habitat type, Season: the four seasons, feed_cat: distance categories to the feeding site (0-50, 50-200, >200), TOD: time of day, (1|CollarID): individual ID of the hinds.

Model	AICc	Delta	Weight
Use ~ Type + Season + feed_cat + TOD + Type:Season + Type:TOD + Season:feed_cat + feed_cat:TOD+ (1|CollarID)	254852.3	0.00	1
Use ~ Type + Season + TOD + Type:Season + Type:TOD + (1|CollarID)	256164.6	1312.33	0
Use ~ Season + feed_cat + TOD + Season:feed_cat + feed_cat:TOD + (1|CollarID)	288506.8	33654.54	0

Independent of season and time of day (TOD) red deer had a higher relative probability of using (hereafter referred to as selection) forest, whilst a lower relative probability of using (hereafter referred to as avoidance) arable fields, heathland, and grasslands. Following Avgar et al., (2017) and Mayer et al., (2019) this is how I use my terminology throughout this section.

Habitat selection varied seasonally. The red deer did not use a large percentage of arable land and therefore in relation to availability is avoided all year round, thus to a lesser degree in fall. The selection and avoidance for the grasses shows a very distinctive pattern in seasonal use, where they are selected during spring and summer, whilst avoided fall and winter. During winter and fall the red deer selected for forest whilst avoiding the other habitats. The heathland was avoided from spring to fall, but the red deer neither selected nor avoided heathland during winter (Fig. 3). The interaction with TOD clearly shows how arable areas are primarily used during the night, however not selected for (compared to availability). The deer selected for grasslands during night and avoided these areas during the day. Further, the only habitat selected for during day was forest cover. The heathland was not selected for at either time of day (Fig. 3).

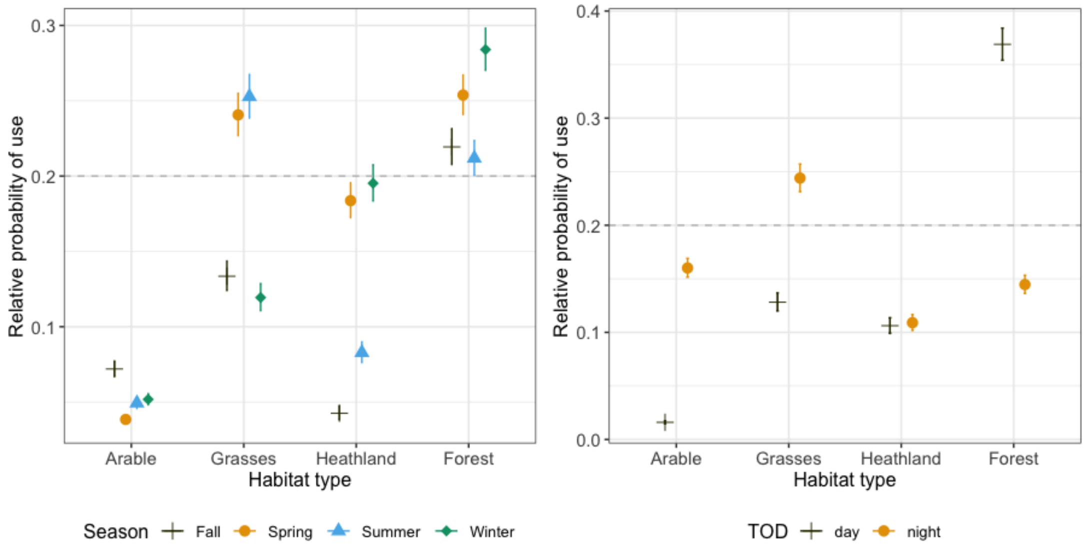

Figure 3. Cross-individual analysis of the effect of seasons (left) and TOD (right) on habitat selection. Colour division for season: Winter (green), spring (orange), summer (blue) and fall (black), and for TOD: day (black) and night (orange). Values > 0.2 (horizontal dotted line) indicate selection and < 0.2 avoidance. Values overlapping 0.2 represent use proportional to availability. 95% confidence intervals are given as bars.

Cross-individual analysis showed selection proximity (0-50m) to the 16 feeding sites during winter and summer and avoidance in fall. There was no selection nor avoidance during spring. Only in winter did the red deer select for 50-200 m proximity to feeding sites. They avoided distances >200 m to feeding sites during all seasons. It was only during night proximity to feeding sites was selected for, with selection strongest close to the feeding sites (0-50 m) and to a lesser degree at 50-200 meters. Distances further away were avoided during both day and night, however usage was higher during night. Day time activity near the feeding site were avoided at all distances (Fig. 4).

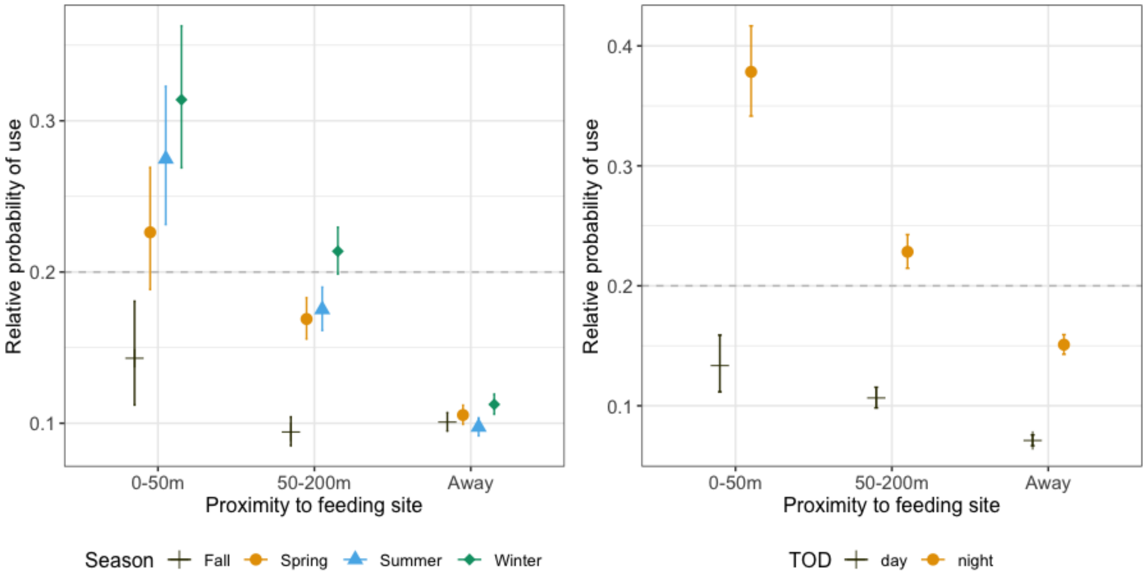

Figure 4. Seasonal effect on selection for proximity to feeding sites (left) and effects of time of day (right). Colour division for season: Winter (green), spring (orange), summer (blue) and fall (black), and for TOD: day (black) and night (orange). Values > 0.2 (horizontal dotted line) indicate selection and < 0.2 avoidance. Values overlapping 0.2 represent use proportional to availability. 95% confidence intervals are given as bars.

3.4. *Faecal pellet group count*

Looking at the AIC and delta values, the model with interaction only had a delta value at 2.03 and was not significant. Meaning, the difference in AIC score between the model with and without the interaction is very low, and the interaction didn't really improve the model nor had anything to say. Therefore, it was discarded. The best-fit model included all variables (Table 5). Parameter estimates are shown in table 6.

Table 5. Results from pellet count model selection with distance to feeding site and habitat category explaining the pellet group density. Log(Distance): distance to feeding site 10-meter intervals, Habitat: habitat categories, (1|ID/ID_com): transects nested within feeding site ID.

Model	AICc	Delta	Weight
Count ~ log(Distance) + Habitat + (1|ID/ID_com)	2396.2	0.00	0.946
Count ~ Habitat + (1|ID/ID_com)	2401.9	5.72	0.054
Count ~ log(Distance) + (1|ID/ID_com)	2419.6	23.36	0.000

*Table 6. Parameter estimates from the best model from table 5.. Signif. codes: 0 '***' 0.001 '**' 0.01 '*'.*

Variable	Estimate	Standard error	95% CI	Z value	P value
(Intercept)	0.73722	0.29873	(0.157, 1.227)	2.468	*
log(Distance)	-0.27052	0.05073	(-0.370, -0.171)	-5.332	***
HabitatHeahtland	0.39949	0.16318	(0.0797, 0.719)	2.448	*
HabitatOpen area	-0.01818	0.1365	(-0.286, 0.249)	-0.133	0.8941

Faecal pellet counts densities were higher in heathland than in the other two habitat categories, forest having the lowest. However, investigating only near feeding sites (0-200m) as a subset, showed the highest pellet densities of 0.75 pellet group per m^2 (Table 7)

Table 7. Calculation of pellet group densities per m^2 across the three habitats and near feeding sites. Calculated based on amount of pellet groups counted per area and the total area counted.

Pellet group densities for each habitat and near feeding sites			
Habitat	*No. of pellet groups*	*Area (m^2) counted*	*Pellet groups density per m^2*
Forest	108	199	0.54
Heathland	470	691	0.68
Open areas	190	310	0.61
Total	768	1200	0.64
Subset			
At and near feeding site (0-200m)	240	320	0.75

The 1200 pellet counts from five different sites with 11 transects, provided a mean ± SD = 0.62 ± 0.75 pellet groups per m^2. Pellet density was highest close to feeding sites, with a large drop at 10 meters (Fig. 5). From 60 meters and onward the density was seen to be consistent, though with a slight increase around 300 meters and the again from 400 meters. In the distances closest to the feeding sites, several more 1m^2 plots contained 3-4 pellet groups, compared to distances furthest away (Fig. 5).

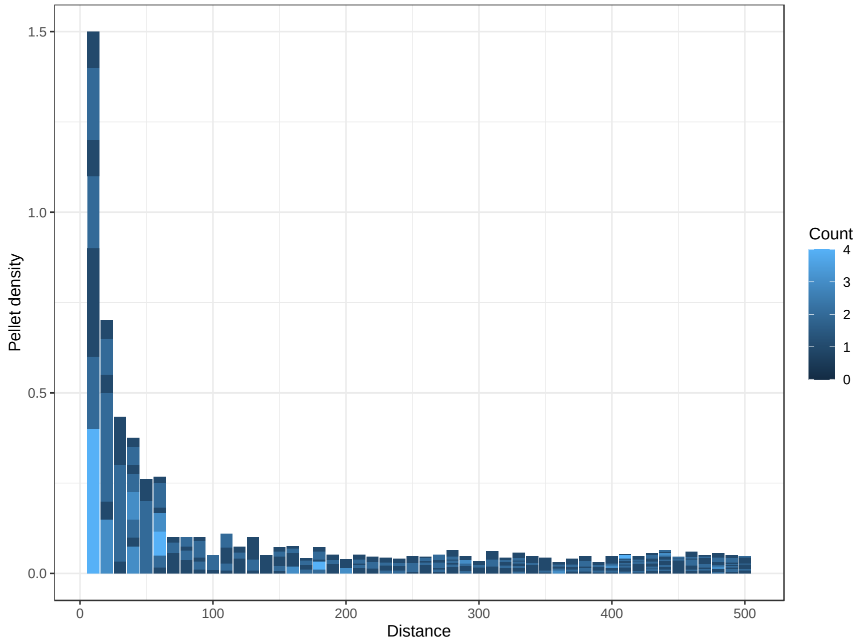

Figure 5. Plot of the overall pellet density across 500 meters from feeding sites. The bars are colour coded according to pellet group counts 0 to a maximum of 4 groups per count.

As an example, pellet counts from feeding site F5 (Figure 6), demonstrates a very clear change in habitats across the two transects, where transect "a" experiences a change from open area to forest. In both transects, the pellet group densities begin to increase approx. 100 meters before the new habitat occurs. Similar patterns appear for the other feeding sites (Appendix A1-A5).

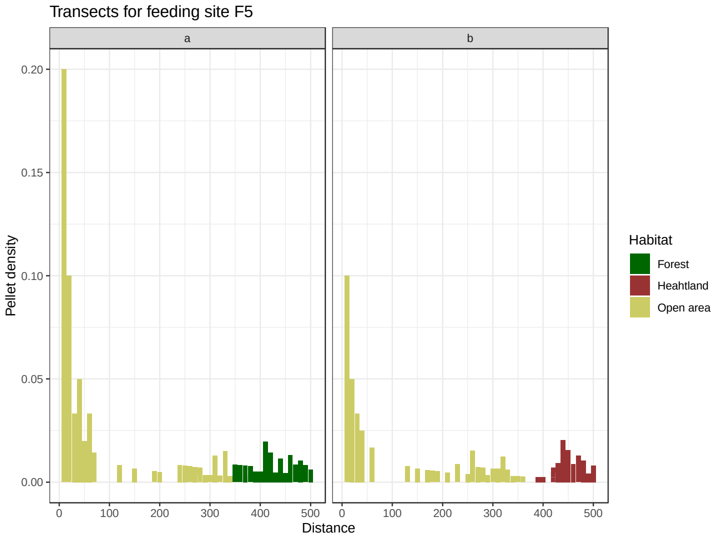

Figure 6. A closer investigation of feeding station F5 and its two transects (a and b).

The population density on the 490-ha Ovstrup heathland was as following, using estimates in table 8. Population density for the 312-ha heath:

$$Deer\ density_{Heath} = 1.86 * 312 = 581.41 \sim 581 \text{ red deer}$$

Population density for the remaining 178-ha mixed habitat (forest and open areas):

$$Deer\ density_{mixed} = 2.59 * 178 = 462.24 \sim 462 \text{ red deer}$$

Thus, the population estimate obtained for Ovstrup Heathland is 1043 red deer (213 red deer per km^2).

Table 8 shows population densities for the three habitats, for the 178-ha mixed habitat, near feeding site (0-200m) and the total per square meter and hectare. All pellet count results can only be seen as a winter estimate as the pellet data was sampled in February and beginning of March.

Table 8. Red deer density calculations of the three habitats and at/near feeding sites. Calculations based on the density estimates from table 7.

Red deer density calculation for each habitat and near feeding sites		
Habitat	*Density per m^2*	*Density per ha*
Forest	0.00023	2.26
Open areas	0.00030	3.01
Heathland	0.00019	1.86
At and near feeding site (0-200m)	0.00028	2.78
Average for the 178 mixed habitat	0.00026	2.59
Total	0.00024	2.37

4. Discussion

The current study assessed habitat use and habitat selection in a danish red deer population and the effect supplementary feeding may have on the spatial distribution and habitat selection. Habitat selection showed seasonal variation and habitats that serve as cover and protection i.e., forest, was selected for during day whereas grass fields were selected for during night. Supplementary winter-feeding led to deer selecting for proximity to the feeding grounds during winter and to lesser degree in summer and only during night.

4.1. Do red deer select for proximity to feeding sites?

During winter red deer actively selected habitat that would allow them to be in 0-50 m proximity to feeding sites. Furthermore, there is also selection to be within 50-200m, confirming the first hypothesis. This indicates that they occupy a larger area around the feeding sites 0-200 meters. On the contrary the avoidance of being far from feeding sites (>200 m) all seasons, shows that feeding sites have a "pull effect". Thus, supplementary feeding plays a part in shaping the spatial distribution of red deer in winter. The findings are consistent with Reinecke et al. (2014) that found that in areas with substantial winter supplementary feeding, red deer restricted their foraging to relatively small areas. The same goes for our individuals that restricted their foraging to areas close to the heathland and had a small home range during winter and were thus closer to feeding sites. Whereas red deer not provided this abundance of food, expanded their home range during winter in search for food (Reinecke et al., 2014). Another study also found unintended effects of feeding such as change in demography and alteration in the natural foraging behaviour, leading to increased local densities (Milner, Beest, Schmidt, Brook, & Storaas, 2014), like the large population seen around Ovstrup Heathland, which both landowners, hunters and Aage V Jensen Nature foundation want to reduce (Aage V. Jensen Naturfond, n.d.-a). Additionally, the red deer use of feeding sites can reduce grazing pressure in grazing reliant habitats e.g., the heathland, as supplementary feeding may lower the intake of natural forages as the deer become accustomed to feeding sites and dependent on this artificial food source (Putman & Staines, 2004). A reduction of grazing pressure can moreover lead to reduced nesting possibilities for bird species associated with open land e.g., heathland habitats, since they prefer short vegetation. Contrary, it is possible that the increase in red deer populations, that do graze on open areas and heathlands have played a part in the growth of some bird populations (Meltofte, Dinesen, Boertmann, & Hald-Mortensen, 2021).

Red deer are social animals and learning is inherited from hind to calf (Mitchell et al., 1977). This suggests the hinds possibly teach the calves where the feeding sites are located and thus when the calf grows up, will forward that knowledge to her own calves. This too is an unintended effect, as the feeding sites would then not only change the spatial distribution of the current population but also the following populations.

Unexpectedly and contradicting to the first hypothesis, proximity to feeding sites was also selected for during summer. When comparing with the habitat use, we see that they use the feeding site more during the day than night in this season, opposite to all other seasons. It is possible to assume that one of the hinds gave birth to her calf in that area and during the first few weeks the hind will stay close to her calf i.e., shorten her range, as it is still immobile (Clutton-Brock & Guinness, 1975). This could therefore influence the inferences made about selection for feeding sites during summer. Moreover, selection for proximity to feeding sites during summer could also reflect the highly discussed local issue, namely red deer foraging on landowners and farmers agricultural fields. The results then indicate that is not only during winter supplementary feeding can cause unintended effect but possibly also during summer, when the landowners particularly do not want the deer to forage on their fields.

4.2. Seasonal and temporal habitat selection

The red deer in this study selected for forest all year round and especially during the day, which support the second hypothesis. The high selection for forest in winter and during the day, is likely to avoid open areas such as agricultural fields as they would feel threatened by humans due to hunting disturbances, particularly during winter (Sunde, Asferg, Nygaard Andersen, & Riis Olesen, 2008). Similar selection for forest habitats during daytime has also been found earlier in red deer in Norway (Godvik et al., 2009). In addition, the red deer actively selected for forest in all seasons, likely due human activity acting as a stressor, inducing fear which may lead to a change in activity pattern to avoid humans (Gaynor, Hojnowski, Carter, & Brashares, 2018). Or because forests act as protection against weather conditions and provides the combination of food and cover (J. Borkowski & Ukalska, 2008). Seasonal differences in selection are consistent with changes in forage quality and quantity, such as the selection for grasses during night and in spring and summer, while using arable land more in fall. Previous studies have also found this link in seasonal variation in relation to forage quality, with selection for pastures during night and spring (Godvik et al., 2009). Furthermore, Zhang, Liu, & Teng, (2013) found seasonal selection for higher or lower elevation relative to forage availability, with higher elevation selected for during summer and fall and lower during winter and spring.

Previous studies show that if red deer have access to undisturbed habitats they will wander and forage these places during the light hours of the day (Riesch, Tonn, Meißner, Balkenhol, & Isselstein, 2019). Hence, a reason the heathland would be a desired habitat due to the peace and protection it can offer the deer. Summer is the only season the deer is seen to use the heathland more during the day than the night. A possible reason would be because they should not be afraid to forage in the daytime as hunting season has not yet started. During the beginning of hunting season, Corgatelli et al., (2019) found that red deer densities where seen to increase in a reserve areas, in order to find protection from hunters. This pattern along with the habitat selection can be interpreted as a behavioural response to predator threats (Godvik et al., 2009) and therefore also as a trade-off between foraging in areas with poor cover opportunities compared to good cover opportunities but low forage possibilities (Mysterud & Ims, 1998).

4.3. Faecal pellet count

The pellet group data supports the third hypothesis that pellet densities were expected to be highest on the heathland during the survey period (winter) and close to the feeding sites. Also, the connection between high pellet densities on the heathland and near feeding sites, could indicate that after using the feeding sites, the deer wander back to the heathland to digest. In most cases the 500 meters stretch in one of the directions from feeding sites enters the heathland. On the heathland the deer are safe from predation i.e., hunting and can maintain in safety in the open (Aage V. Jensen Naturfond, n.d.-b) and thus would seem a desired place to lie and digest the feed. This also correlates with the increase seen in pellet count every time the habitat changed from open to heathland or forest and in general when sampling on the heathland. Furthermore, the habitat use showed the heathland is used most in winter compared to the other seasons, which also correlates with the faecal pellet count results. However, the findings do not show higher pellet densities in forest compared to open areas, as hypothesised.

Density estimates may vary as, the daily defecation rate and decay rate used for the calculations are particularly sensitive to geographic regions and environmental conditions such as weather (Periago & Leynaud, 2009). Compared to a drone count conducted in March by Aarhus university, the density calculated from pellet is larger by 402 animals, as the drone count showed 641 red deer, primarily hinds and calves (pers. comm. Lars Haugaard), in relation to our density result of 1043 animals (213 per km^2). A possible explanation to why my estimate is so much higher could be due to pellets taken longer time to decay than presumed, as the decay rate was not precisely estimated for this specific area and perhaps due to cold weather conditions. Hence resulting in overestimating the deer density. Or as I did not know the exact hectares open areas and forest covered, could make the estimate inaccurate and thus result in overestimation. Another reason is that I have sampled on hot spots in the study area i.e., close to feeding sites. Regardless, both my estimate and the drone estimate indicate a very high population density around Ovstrup Heathland. Especially when compared to other studies that found red deer densities of 29.5 red deer per km^2, which was even said to be particularly high for their study area (Borkowski et al., 2019). Borkowski et. al., (2019) also conducted their pellet count survey in the winter period using FSC method, in a national park where hunting is prohibited. Though, outside the park boundary lies forest and agricultural areas where hunting is allowed, similar to my study.

This pellet count survey could not say anything about sex ratio; however, Sá Nchez-Rojas et al. (2004) showed, that it is possible to differentiate between sex and age classes of mule deer, by examining the morphometry.

Previous studies have found FSC (faecal standing crop) useful and suitable methods to estimate densities (Alves et al., 2013) and habitat use (Alves, Alves da Silva, Soares, & Fonseca, 2014). However, as with many other methods, the validity of faecal pellet count techniques for calculation densities, has been questioned and compared, especially due to the flexibility this method has. I chose to define a pellet group as a cluster of at least 10 pellets and if signs of breakdown follow Mayle et al., (1999). Others have chosen to increase the pellet group size to 20 (Acevedo et al., 2008) or 30 (Neff, 1968). This can ultimately yield different results. Therefore, it is important to be clear about how to define a pellet group cluster that is realistic in relation to decay rate and defecation rate, which are also estimates that vary greatly in studies and depending on environment (Alves et al., 2013; Mayle et al., 1999; Neff, 1968).

In this study, pellet count and GPS locations were both used to investigate red deer presence around feeding sites. Månsson et al. (2011) compared results from pellet count to results obtained from GPS data and found that use of pellet count accurately described habitat selection of moose (*Alces Alces)* and provided similar results as those obtained from 15 GPS collared individuals.

4.4. Limitations

The feeding sites in this study were located with help from farmers, hunters and landowners taking part in the management project “Red deer – Knowledge, values and management”. Consequently, there could be a possible bias towards participants wanting to reveal feeding site locations. This may have provided some gaps in the data due to unknown feeding site locations. Moreover, I have not separated the years (2019 and 2020) in the analysis and thus only calculated as a whole. This furthermore means that for the seasons division in habitat selection and selection for proximity to feeding sites, there are two years of seasons combined to one. Thus, I have not considered year to year variation. Furthermore, this means I have calculated seasonal selection from the entire home range and not seasonal range. Finally, with only four individuals tagged with GPS collars, it is not possible to conclude on population level since my sample size is so low.

4.5. Perspective

A deeper understanding of the effects of supplementary feeding sites would be desirable for joint management plans. A possible way of obtaining more knowledge in this area is to end/ban the supplementary feeding in the areas and locations where feed has already been provided and after approx. 2 years do the exact same analysis, to see how the animals have changed their habitat selection, spatial distribution, and preference for proximity to the locations of previous feeding sites. Then it is possible to investigate what makes those exact sites special and why they would be of interest to the animals e.g., was it the habitat or was it due to an easy food source.

5. Conclusion

Investigating the foraging-safety trade-off and likely effects from supplementary feeding is important to understand the behavioural drivers of the red deer’s habitat use. I found indications that supplementary feeding plays a central role in shaping the spatial distribution of red deer in winter, as red deer strongly selected for adjacency to feeding locations. As consequence, the grazing intensity on the heathland might be reduced accordingly. Local consensus exists in that the red deer population should be reduced to minimise crop damages. This study could possibly benefit future management proposals and strategies, since an improved understanding of red deer’s whereabouts, their movements and relationship to feeding sites, will help accommodate all involved stakeholders.

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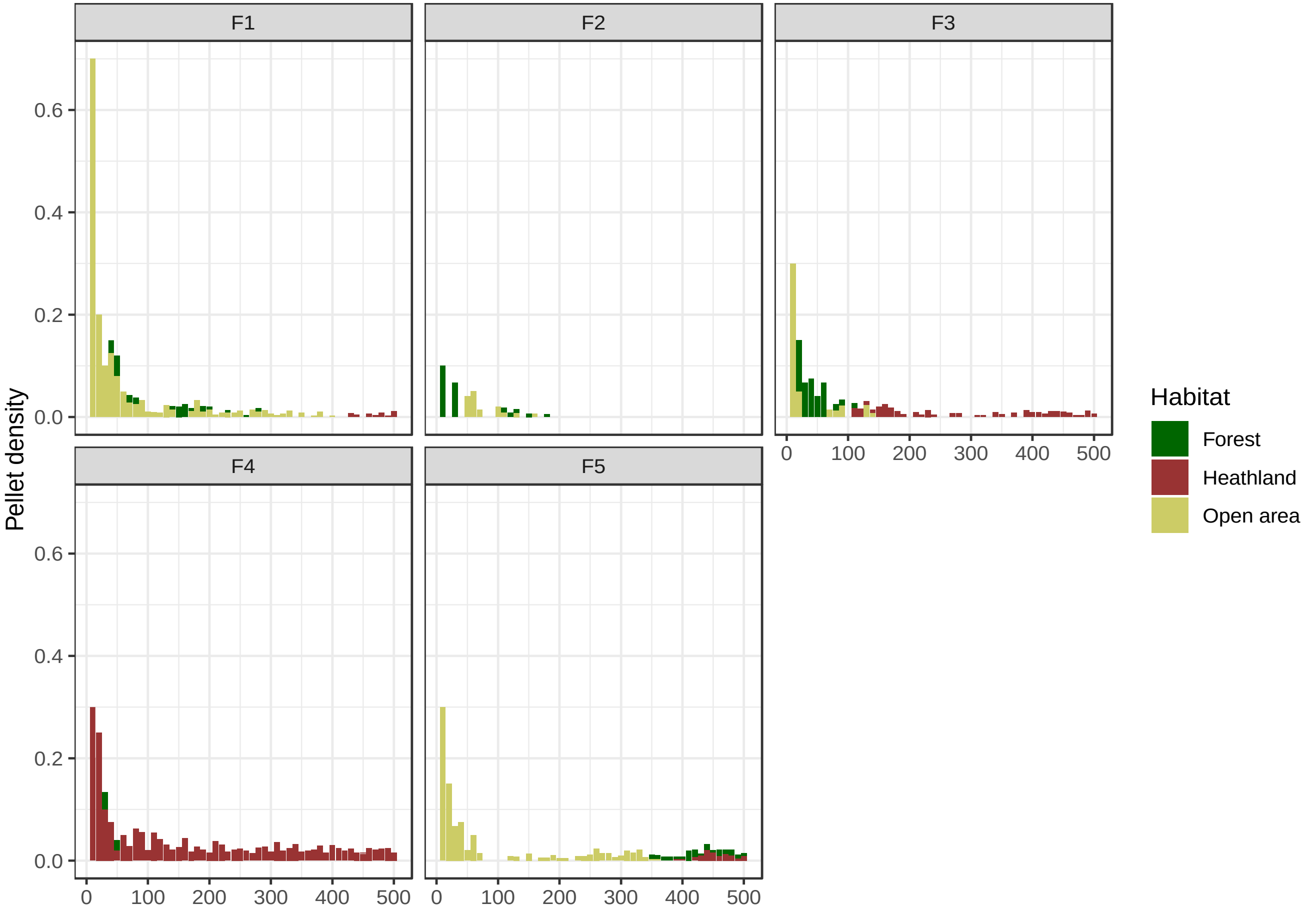
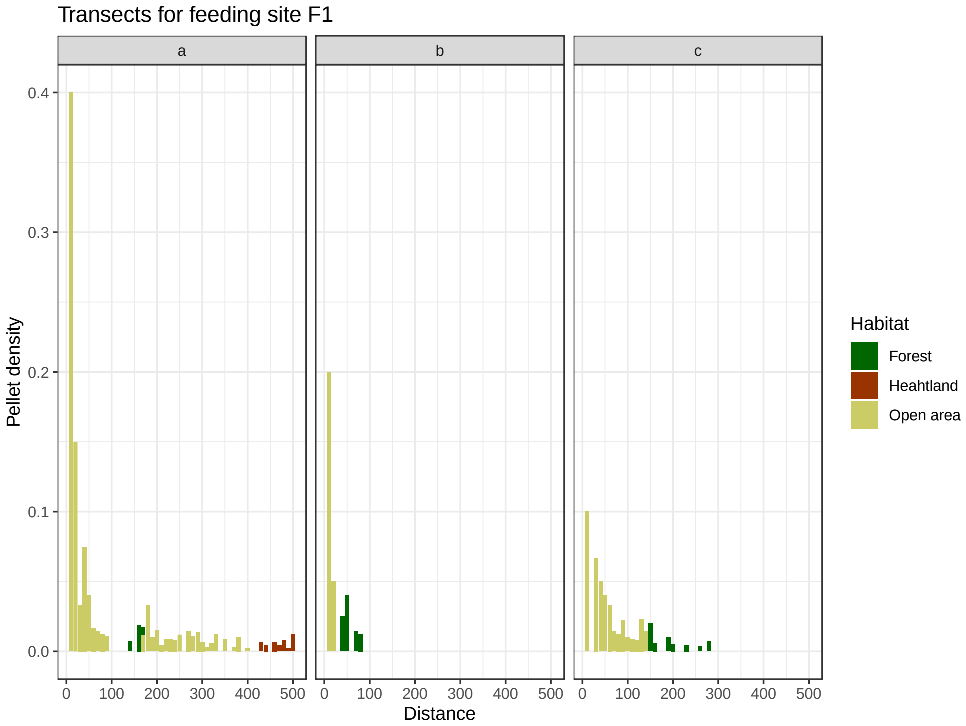
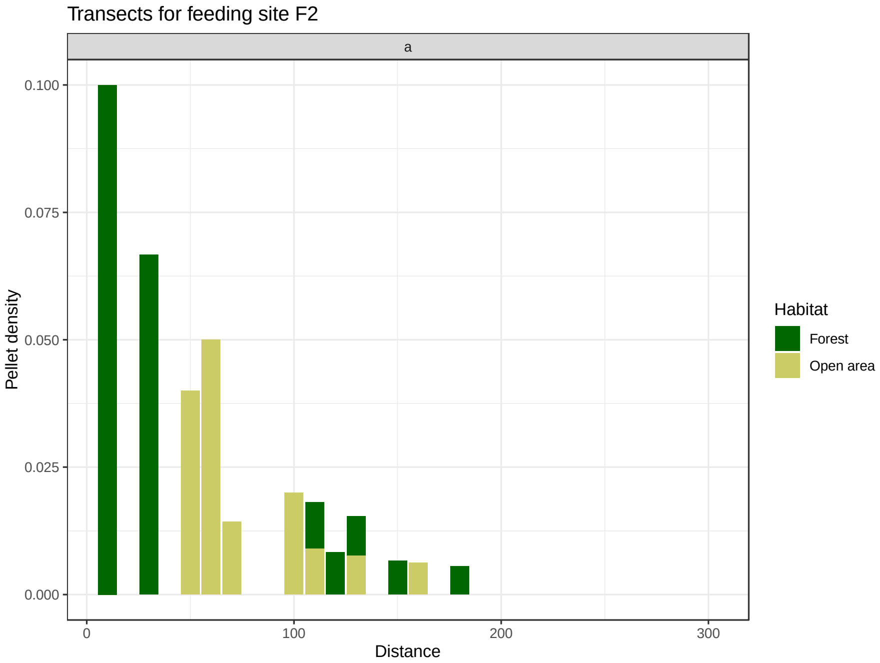
Appendix | A Figures



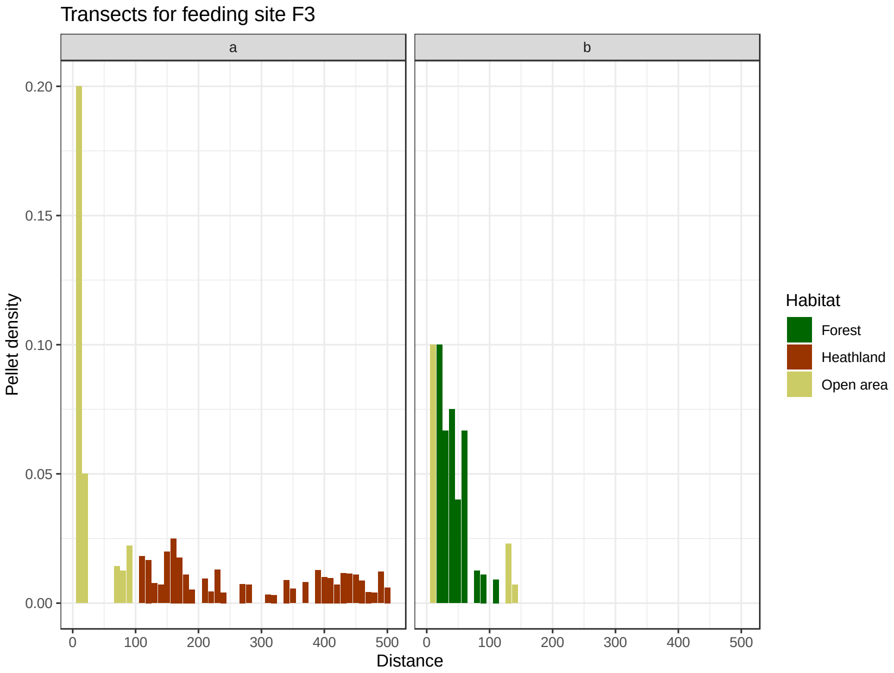
Appendix A1. Pellet density plots across the 500-meter distance from each feeding site. The feeding site F4 is 100% situated on the heathland – at this site, like the rest, we see a drop in density close to the site. Afterwards however, the count appears to be consistent throughout the remaining distance. Three of the feeding sites (F1, F3 and F5) have in common that the pellet density begins to increase again at around 250-400 meters. Also, in common is the fact that at those distances Ovstrup Heathland is located.



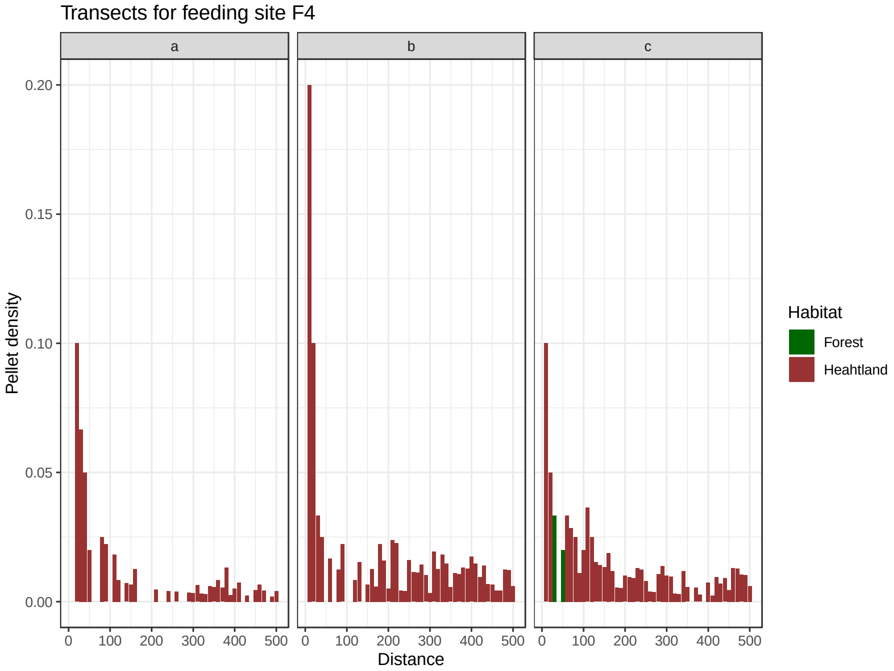
Appendix A 2. Transects for feeding site F1. At this site it was only possible to reach the maximum distance at transect "a". The remaining two were limited due to property boundaries. Transect "a" shows an increase in pellet densities when entering the heathland at approx. 400 meters and at approx. 150 meters when in forest cover. Further it follows the pattern as the others, with highest densities close to the site and a decrease in such, when distance increases.



Appendix A 3. Feeding site F2 was the smallest sampled site with only one transect at 300 meters. It was cut short due to property boundaries and was surrounded by newly ploughed fields that could therefore not be sampled. However, this site also displays the tendencies seen in the other sites, with highest densities close to the feeding site and a drop around 50-60 meters.



Appendix A 4. To very different transects for feeding site F3. At transect "a" no pellet groups were found until entering the heathland. Transect "b" shows high densities very close to the site, with forest as the primary habitat. However, this transect was limited to 140 meters due to property boundaries.



Appendix A 5. Feeding site F4 with its three transects, all situated on the heathland. Within 30-50 meters in transect "c", forest cover was present and thus the plots were noted as "forest" in habitat even though it is situated on the heathland itself. Pellet densities for all three transects increases around 300-400 meters. Further, both transect "b" and "c" illustrates consistency in pellet densities throughout the transect length.

Appendix | B Tables

Appendix B 1. Vector data sources and additional information.

Habitat	Data source	Information
Fields	https://kortdata.fvm.dk/download/Index?page=Markblokke_Marker	"*Marker_2019_CVR*"
Heathland	https://mst.dk/service/miljoegis/	"*Natura 2000-Basisanalyse 2022-27*" → " *Lysåbne naturtyper (2016 - 2019) – Naturtilstand*"
Forest	Forest landcover was extracted from *basemap03* and transformed into smooth polygons.	Shapefile retrieved from Astrid Holm Andersen, master student af Department of Biology, Section of Ecoinformatics and Biodiversity. I created additional polygons and merged them with this file.
Built up areas	https://download.kortforsyningen.dk/content/geodanmark	Kortforsyningen, Styrelsen for Dataforsyning og Effektivisering

Appendix B 2. Amount of used and random positions before and after intersecting

	0 = random	1 = used	Total
Before intersecting with landcover	373.215	74.643	447.858
After intersecting with landcover	322.083	62.707	384.790

Appendix B 3. Overall pattern of the final used vs random points used for the habitat selection analysis.

	Arable	Grasses	Forest	Heathland	Total
0 = random	130.849	32.603	66.380	41.902	271.734
1 = used	13.900	8.026	25.124	6.311	53.361
Percentage of use	26.05%	15.04 %	47.08%	11.83%	100%

*Appendix B 4. Parameter estimates from the best model. Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’*

Variable	Estimate	Standard error	Z value	P value	95% CI
(Intercept)	-3.628	0.165	-21.923	***	(-3.952, -3.303)
TypeForest	3.111	0.037	84.441	***	(3.039, 3.183)
TypeGrasses	1.512	0.048	31.737	***	(1.418, 1.605)
TypeHeathland	0.643	0.059	10.931	***	(0.528, 0.758)
SeasonSpring	-0.19	0.179	-1.065	0.287	(-0.54, 0.160)
SeasonSummer	0.406	0.182	2.228	*	(0.049, 0.764)
SeasonWinter	0.482	0.171	2.817	**	(0.147, 0.817)
feed_cat50-200m	-0.243	0.168	-1.445	0.148	(-0.573, 0.087)
feed_catAway	-0.137	0.160	-0.854	0.393	(-0.45, 0.177)
TODnight	2.986	0.133	22.519	***	(2.726, 3.246)
Interaction w. season and habitat type					
TypeForest:SeasonSpring	0.853	0.035	24.461	***	(0.785, 0.921)
TypeGrasses:SeasonSpring	1.383	0.046	30.117	***	(1.293, 1.473)
TypeHeathland:SeasonSpring	2.283	0.059	39.01	***	(2.168, 2.397)
TypeForest:SeasonSummer	0.358	0.036	9.995	***	(0.288, 0.428)
TypeGrasses:SeasonSummer	1.188	0.047	25.168	***	(1.096, 1.281)
TypeHeathland:SeasonSummer	1.11	0.064	17.363	***	(0.985, 1.235)
TypeForest:SeasonWinter	0.695	0.032	21.7	***	(0.632, 0.758)
TypeGrasses:SeasonWinter	0.222	0.047	4.706	***	(0.130, 0.315)
TypeHeathland:SeasonWinter	2.046	0.057	36.134	***	(1.935, 2.157)
Interaction w. TOD and habitat type					
TypeForest:TODnight	-3.702	0.037	-101.237	***	(-3.774, -3.631)
TypeGrasses:TODnight	-1.675	0.042	-39.752	***	(-1.758, -1.592)
TypeHeathland:TODnight	-2.432	0.043	-56.171	***	(-2.517, -2.348)
Interaction w. season and distance to feeding site					
SeasonSpring:feed_cat50-200m	0.108	0.187	0.58	0.562	(-0.258, 0.475)
SeasonSummer:feed_cat50-200m	-0.107	0.191	-0.559	0.576	(-0.481, 0.267)
SeasonWinter:feed_cat50-200m	-0.049	0.179	-0.273	0.785	(-0.400, 0.303)
SeasonSpring:feed_catAway	-0.51	0.178	-2.874	**	(-0.859, -0.162)
SeasonSummer:feed_catAway	-0.857	0.181	-4.726	***	(-1.212, -0.502)
SeasonWinter:feed_catAway	-0.886	0.171	-5.193	***	(-1.221, -0.552)
Interaction w. TOD and distance to feeding site					
feed_cat50-200m:TODnight	-0.465	0.136	-3.43	***	(-0.730, -0.199)
feed_catAway:TODnight	-0.531	0.130	-4.098	***	(-0.785, -0.277)