Sharing space with a larger relative

- examining interspecific effects of fallow deer on roe deer performance

John-Christophe Hessler Frelinckx

Master's thesis in Biology • 30 hp
Swedish University of Agricultural Sciences, SLU
Faculty of Natural Resources and Agricultural Sciences (NJ)/Department of Ecology
Grimsö 2023

Sharing space with a larger relative - Examining interspecific effects of fallow deer on roe deer performance

John-Christophe Hessler Frelinckx

Supervisor:	Petter Kjellander, SLU, Department of Ecology
Examiner:	Gunnar Jansson, SLU, Department of Ecology

Credits:	30 credits
Level:	A2E
Course title:	Master's thesis in biology, A2E – Ecology
Course code:	EX0953
Course coordinating dept:	Department of Ecology
Place of publication:	Grimsö
Year of publication:	2023
Cover picture:	By the author just outside the Grimsö wildlife research station from "Loftstugan"
Keywords:	roe deer, fallow deer, interspecific competition, population densities

Swedish University of Agricultural Sciences
Faculty of Natural Resources and Agricultural Sciences (NJ)
Department of Ecology
Grimsö Wildlife Research Station

Abstract

Interspecific competition of some form is a part of life for most species across the world. For some species it can be part of their evolutionary history over many thousands of years, while for others it is a more recent experience, as is the case of roe deer (*Capreolus capreolus*) and fallow deer (*Dama dama*), in Scandinavia. In Sweden the number of fallow deer have shown a strong increase in the last 30 years, bringing more attention to the potential competition between the two related species. This study aimed to compare two areas, Bogesund and Koberg, which have contrasting densities of fallow deer, and to examine if indices of roe deer fitness differ between the two.

Bogesund having no resident fallow deer and being an area with much prior research on roe deer. Koberg being an area divided into two by a wildlife fenced road and housing contrasting densities of fallow deer after a deliberate reduction of the population in one of the areas (north) while keeping it more constant in the other (south). This creates a good opportunity for comparative studies between high and low fallow deer density populations. The data used came primarily from hunting statistics at the two study areas, starting in the same year (2006). Physiological indices believed to be relevant and related to fitness were used to examine potential signs of reduced fitness in the roe deer population. The indices were fawn body mass, female ovulation rate and male antler length.

The results showed a clear effect of study area in the expected direction, in three out of four possible model selection procedures, namely a potentially negative effect of high fallow deer density on roe deer in two of the investigated fitness traits (fawn body mass and ovulation rate). However, the pattern was reversed when regarding the antler length between study areas (Koberg and Bogesund). But this trait differed between the two contrasting (high/south vs low/north) areas in Koberg, where male antler length was greater in the area with low fallow deer density. The unexpected and reversed result between Koberg and Bogesund antler length is discussed in terms of genetics, non-random sampling and effects of supplemental winter feeding during the time when antlers are growing and still in velvet.

This study suggests that there is an interspecific competition relationship between the two deer species and that this could have a negative impact on roe deer fitness, with possible management implication in areas where both species occur. Overall, I believe further studies are required to be able to gain better insight into the field of deer management but that this study functions to illustrate the interspecific competitive relationship between roe deer and fallow deer.

Keywords: Interspecific competition, physiological indices, fitness, population densities

Table of contents

List of tables

List of figures

1. Introduction

1.1 Background

Competition might be one of the earliest forms of interaction two organisms had at the inception of life and a powerful force of evolution to drive specialization and speciation (Krebs 2013). Darwin famously stated, “survival of the fittest” (Darwin 1859), or as it can also be expressed “Death of the unfittest”.
This becomes reality when species interact over a commonly shared finite resource, such as food, mating opportunity or desirable territory. Competition in the world of ecology can be divided into two distinct groups depending on the number of species involved, intraspecific and interspecific competition (Krebs 2013). Intraspecific refers to competition between conspecifics, which for example can take the form of competition between males for mating opportunities, be it through straight forward fighting or more indirect forms such as displays or posturing (Tinghitella et al 2018). Further examples of this are fights using elaborate antlers among certain species of deer (Clutton-Brock 1982) or the famous leks among black grouse (*Lyrurus tetrix*) (Hovi et al 1995).
Interspecific competition is when different species compete over the same resource. While intraspecific competition is mainly affecting the individual, interspecific competition can be systematically detrimental for an entire group of individuals or even whole species which results in potentially more harmful consequences. When a new source of competition suddenly arises in an area, typically from an alien species, it can result in very unfavourable conditions for one or several sympatric species. Such as when new species of fish being introduced to otherwise isolated lakes (Mehner & Brucet, 2022), competition for resources when alien plants invade an area (Gioria & Osborne 2014) or when a mixture of intraspecific and interspecific competition drives specialization as observed in the Galapagos finches (Abbot et al 1977). Interspecific competition typically revolves around a common food resource or habitat, but exceptions happen, such as with the recently discovered occurrence of hybridization between Mountain hare (*Lepus timidus*) and European hare (*Lepus europaeus*) (La Morgia & Venturino 2017). Which

highlights that interspecific competition can take different forms and target several different aspects of a species fitness.

This paper focuses on the *Cervidae* family, more specifically on the roe deer (*Capreolus capreolus*) and fallow deer (*Dama dama*) case and their relationship in the northern distributional range in Sweden. Roe deer being a native species to almost all of mainland Europe with a historically fluctuating range (Linnell & Zachos, 2011), with lows in the 19^{th} – early 20^{th} century. More recently seeing an expansion from a reduced range as well as increasing numbers of roe deer across Europe, both naturally and with human help (Andersen et al 2004; Baker & Hoelzel 2012). In Sweden the roe deer has existed since at least the last ice age 10000 – 12000 years ago, reaching near extinction in the 1830's due to a change in laws leading to over extensive hunting (Cederlund & Liberg 1995). Today being at a non-threatened status with an annual harvest of over 100 000 animals in 2020 (Svenska Jägareförbundet 2022).

Fallow deer have existed in parts of mainland Europe for several thousands of years, attributed to a spread aided by humans in a semi-domestic relationship, from an assumed native range around modern day eastern Turkey and western Iran (Chapman & Chapman 1975). In Sweden this introduction is presumed to have happened later with records suggesting introduction at least in the late 1500's (Carlström & Nyman 2005).

Hofmann (1989) divided various ruminants into different categories depending on their morphophysiological adaptions to different types of digestible plants, where in one end there are the selective feeders (also known as browsers), adapted to more protein rich less fibrous foods such as herbs, shoots or leaves (Hofmann 1989). Roe deer being considered a browser or selective feeder (Rautiainen et al 2021). In the "opposite" end to the selective browser is a grazer or bulk feeder such as a domestic cow, which primarily ingests large amounts of less nutritious and more fibrous food such as grass. Then there are intermediate types which are not as specific about what to eat, where the fallow deer is categorized (Rautiainen et al 2021). This possible overlap in food choice between the species have become more relevant in Sweden as the population size of fallow deer grows closer in number to the native roe deer, with the latest hunting data showing an increasing harvest of fallow deer, to approximately 72 000 in 2020 (Svenska Jägareförbundet 2022). The gap between the two species have been narrowing since the peak of the roe deer population in 1993, when the numbers of harvested roe deer was approximately 382 000 and fallow deer at only 2638 (Svenska Jägareförbundet 2022).

Fallow deer competing for the same food, living in groups and being much larger compared to a roe deer could cause difficulties in both availability of and facility to utilize high quality food for a selective feeder as the roe deer. Competition could also result in feeding displacement and even though there are no systematic reports of direct fights between the two species, the competition for food might be detrimental. With an average fallow deer estimated to have a metabolic rate approximately twice that of a roe deer (Kjellander unpublished). Which could lead to high exertion for the roe deer to find enough food to sustain themselves, in turn meaning lower body mass (Richard et al 2010) and possibly less energy spent on reproduction (Flajšman et al 2017; Vanpé et al 2007). Body size and age will also be considered as they have been observed to influence fitness and both female and male reproductive effort in roe deer (Flajšman et al 2017, 2018; Vanpé et al 2007).

1.2 Research question

This study aims to examine whether the presence of fallow deer influence roe deer fitness. This is done by examining the following physiological indices closely related to fitness:

(1) Roe deer fawn body mass
Hypothesis 1: Body mass is a very common general indicator of fitness. When examining this in fawns it gives a reliable point of reference of the current environments quality and ability to sustain roe deer. It is therefore assumed that an area with low access to high quality food will result in low body mass in fawns (Richard et al 2010; Skogland 1984).

(2) Female ovulation rate

Hypothesis 2: The ovulation rate or number of observed corpora lutea is an indication of the energy invested into reproduction during the last mating season. This is assumed to be lower if the levels of competition for food is high (Flajšman et al 2007). Thus, I predict that in areas with more competition and as a result lesser availability and/or quality of food, there will be a lower ovulation rate/fawns born.

(3) Male antler size

Hypothesis 3: The length and shape of the antlers is believed to be a good male specific indication of fitness, showing their investment into competing for mates that particular year (Zahavi 1977; Vanpé et al 2007). It is in a similar manner believed to reflect if the male is subject to competition for food or otherwise lacks energy. In this case mainly during winter/early spring when the antlers are growing. Therefore, I assume that smaller antlers would be a sign of lowered fitness.

These three physiological indices mentioned above have been chosen as they are believed to best reflect the current quality and conditions in the specified study areas.
Body size will in this instance be reflected by the length of the metatarsus and work as a complement to body mass as they are closely correlated.
To the best effect possible indices will be compared between a control area without presence of fallow deer and an area that can be divided into a high- and low-density area of fallow deer.

2. Method

2.1 Study areas

2.1.1 Koberg

The data used was gathered from two localities in Sweden. The primary location being the Koberg estate (58°N, 12°E), located in southwestern Sweden, Västra Götaland county. The estate is divided into two main parts by a wildlife fenced road, creating two distinctive areas with hindered movements between them. The northern area being 27.1 km^2 and the southern area being 54.0 km^2. Fallow deer density differs between the northern and the southern area, with the northern housing fewer fallow deer due to deliberate efforts to keep the population low in this area. Compared to each other, the northern area is considered a low-density area and the southern a high-density area, with average densities of fallow deer during the study period being 11,43/ km^2 in the northern area and 30,76/ km^2 in the southern area (Kjellander unpublished). The first fallow deer, approximately 20 animals, were released from a small enclosure at the estate at the end of the 1920's (Silfverschiöld unpublished). The roe deer is also a valued game at the estate and long-term records on antlers are available from the early 1900's (Agnrud 2011). During the timeframe of this study the estimated average densities of roe deer in the areas were 1.5/ km^2 in the northern area and 0.5/ km^2 in the southern area (Kjellander unpublished). The land surrounding the estate is mainly covered by forest (79%). Arable land and pastures cover 16%, mires and marshes 2% and lakes, ponds, parks and properties represent 3% of the land (Kjellander et al 2012). Supplementary feed is given during winter through early spring to support the large populations of fallow deer and other game (Garrido et al. 2014). Largescale hunts are performed regularly every year, with Swedish hunting season for this type of game being 16th of August until 31st of January, with stricter specifications for age, species and sex of the animal during certain smaller periods.

2.1.2 Bogesund

The other locality was at Bogesund, an approximately 26 km^2 peninsula, located (59 24`N, 18 12`E) a few km north of Stockholm. Proximity to the sea results in a milder climate than might be expected from other areas at the same latitude. The landscape roughly consists of forest (65%), farmland (25%), bogs and rocky ground (10%). A majority of the forest habitats consisting of spruce and pine, with some mixed coniferous trees. Agriculture occurs on the peninsula to a smaller degree, with some farmland being used as pastures mainly for horses and sheep (Jarnemo 2004).

The area has been subject to roe deer research for a long time and is considered a high-density area for roe deer, with an estimated average density of 10/km^2 (Kjellander unpublished). There have been a few observations of young male fallow deer in the area, but there is no known reproducing population. While the surrounding region have local populations of fallow deer, it is assumed that Bogesund remains relatively isolated due to it being a peninsula.

2.2 Data

The data used is part of larger projects being conducted at the two study sites by SLU, both of which spans several years. The data collection at Koberg began in 2006 and thus, is also the start year of the Bogesund data set in this study.

The dataset primarily contains information collected from harvested animals, but also from traffic accidents and animals found injured or dead. Certain measurements were taken by the hunters themselves, such as determining sex, measuring antler length, length of the hind foot (metatarsus) along with weighing the animal (total body mass and dressed weight). The rest of data gathering is handled by SLU in a laboratory setting where several more datapoints are gathered. Data from these processes are more accurate on age than what can be determined in the field, as also the counts of number of corpora lutea. Age was determined by cross-referencing the jaw and teeth with a jaw board made from animals of known age, with which accurate estimates (± 1 year) can be obtained (Cederlund et al 1991). Corpora lutea is what is left in the ovary after successful ovulation and are counted in laboratory settings from ovary samples sent to SLU.

Data from animals involved in traffic accidents can in most cases be used as this is considered as random sampling. When it comes to animals that are found injured or dead for unknown reasons, certain data such as body size (metatarsus) or the length of the antlers can often be used. While body mass is considered to not represent a random sample as the animal might be in an altered state of sickness.

Consequently, the raw data files required some cleaning and removal of animals where either the necessary data were lacking or the validity of the data came into question, such as unrealistic weights/measurements.
Due to the Koberg dataset being the smallest in scope, with a total of 202 animals, some additions and assumptions were necessary. Animals where only dressed weights (eviscerated body weight) had been reported constituted approximately a quarter of the total (n = 63). To increase the data available a linear regression analysis was performed between total body mass and dressed weight for the remaining 139 animals where both measures had been taken. The increase in weight being 25,4 %, was then added to the 63 animals lacking a total weight. The larger dataset from Bogesund with 685 animals in total, contained only a small number of missing total weights. There were 18 animals for which an estimated total weight was derived. The corresponding regression (as above) for the Bogesund data showed that the average weight increase was 33,3 % and these were also added to the dataset.
Age was divided into three classes, being deemed as the best option for analysis. The categories were juveniles (0 years old), yearlings (1-year olds) and full adults (2 years or older). Month was also compiled into classes, merging two months into each class, Swedish hunting season for roe deer beginning in mid-August and finishing in the end of January. The six months of hunting season leading to 3 classes: Month1 (August/September), Month2 (October/November) and Month3 (December/January).

2.3 Statistics

The statistical analyses were performed using Rstudio (RStudio Team 2021) in the "Ghost orchid" release (2021 09-20).

The data was run through R and compiled into several general linear models (GLMs) to yield representations and potential relationships between various portions of the data. Variables included were Body mass, Area, Age, Month, Metatarsus, Corpora Lutea/Antler length. All candidate models and interactions believed to be biologically relevant were considered when processing data (Appendix 1, Table 1-8). Akaike's information criteria (AIC) were used to determine the models with the best fit. Models containing sample sizes <10 were not considered.

3. Results

3.1 Fawn body mass

The data for comparison between the northern and southern area of Koberg were insufficient for analysis, with too few fawns (Sample size North (6); South (9)). Analysis on the larger scale between Koberg and Bogesund was however possible (sample size Koberg (15); Bogesund (135). The model with the lowest AIC (AIC weight 0.63) included study area, sex, month and metatarsus, the second best model had an AIC weight of 0.25 (Appendix 1, Table 5). The effect of study area was not significant in the GLM-model ($P > 0.05$; Appendix 1, Table 1). The absolute uncorrected difference in body mass showed that fawns in Koberg were on average 0.186 kilogram lighter than those in Bogesund.

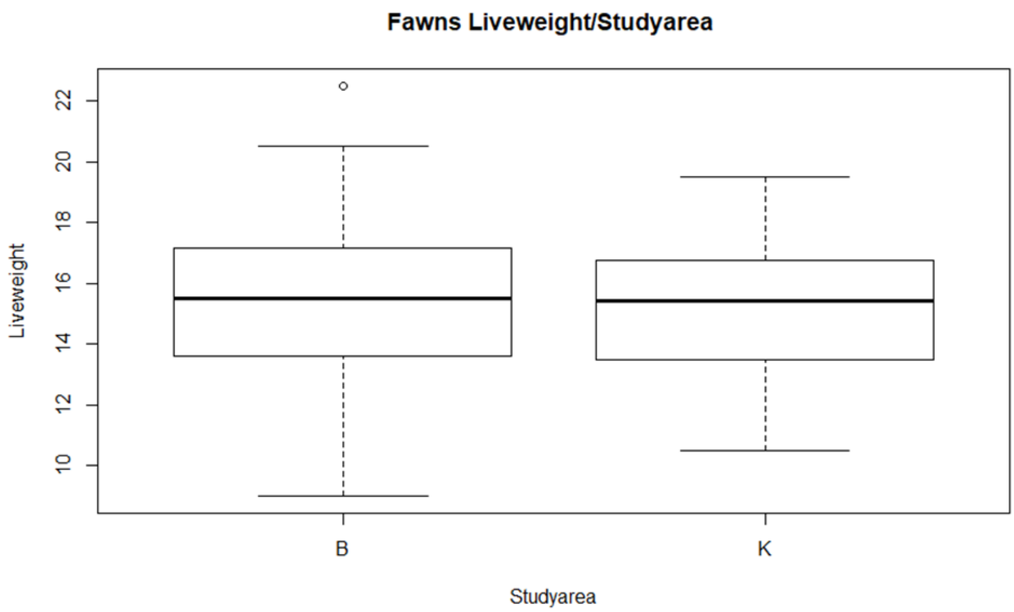

Figure 1. Boxplot illustrating fawn body mass (in kilograms) uncorrected for sex, month and body size as compared between Bogesund (B) and Koberg (K). The difference being approximately 0,2 kilogram

3.2 Ovulation rate / Corpora lutea

The data for comparison between the northern and southern area of Koberg were insufficient for analysis, with too few samples (Sample size North (9); South (13)). Analysis on the larger scale between Koberg and Bogesund was however possible (Sample size Koberg (22); Bogesund (103). The model with the lowest AIC (AIC weight 0.49) included study area, age and body mass, the second best model had an AIC weight of 0.24 (Appendix 1, Table 6). The effect of study area was significant in the GLM-model ($P < 0.05$; Appendix 1, Table 2). Bogesund having a higher mean of 2.28 and Koberg a mean of 1.63 uncorrected for age and body mass but showed the same median of 2 (Figure 2).

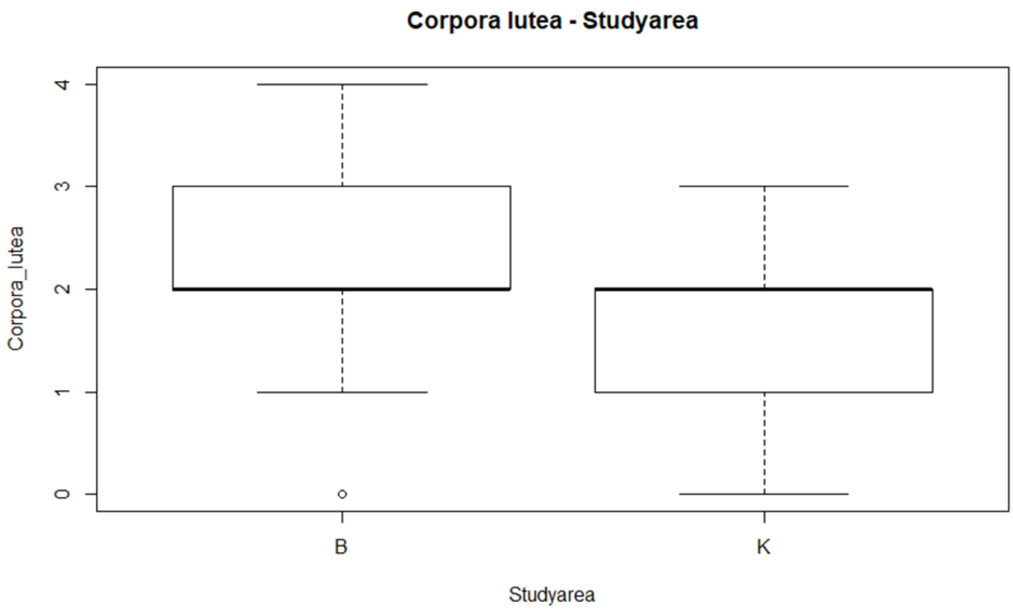

Figure 2. Boxplot illustrating the average number of corpora lutea uncorrected for age and body mass in the two study areas Bogesund (B) and Koberg (K).

3.3 Antlers

3.3.1 Koberg north & south

For the antlers there was enough data to be able to make a comparison within Koberg, thus yielding a comparison of high and low fallow deer density. The sample size is 41 for the north area and 17 for the south area. The model with the lowest AIC (AIC weight 0.46) included area, age and body mass. The second lowest AIC was quite close in weight at 0.33 and excluded body mass but retained age and area (Appendix 1, Table 7). The effect of study area was not significant in the GLM-model ($P > 0.05$; Appendix 1, Table 3). The mean difference in antler length between areas uncorrected for age and body mass being 3 millimetres ($P = 0.804$).

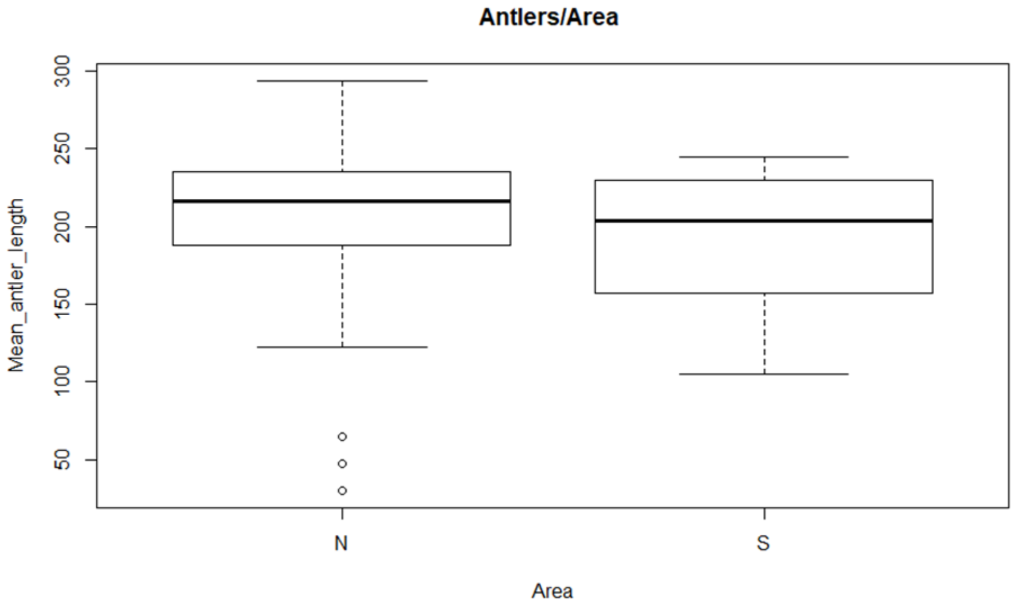

Figure 3. Boxplot illustrating the mean length of antlers (mm) compared between the northern and southern area of Koberg. With a mean difference of 3 millimetres, uncorrected for age and body mass.

3.3.2 Bogesund & Koberg

Data on the analyses of antler lengths between Bogesund and Koberg had the largest sample sizes, Koberg (61) and Bogesund (221). The model with the lowest AIC (AIC weight = 0.56) included study area, age and body mass, the second best model had a AIC weight of 0.24 (Appendix 1, Table 8). The GLM yielded significant results for all variables of the model, study area, age and body mass ($P< 0.05$; Appendix1, Table 4). The uncorrected means for each area being 197 millimetres for Koberg and 175 millimetres for Bogesund (Figure 4 - 5).

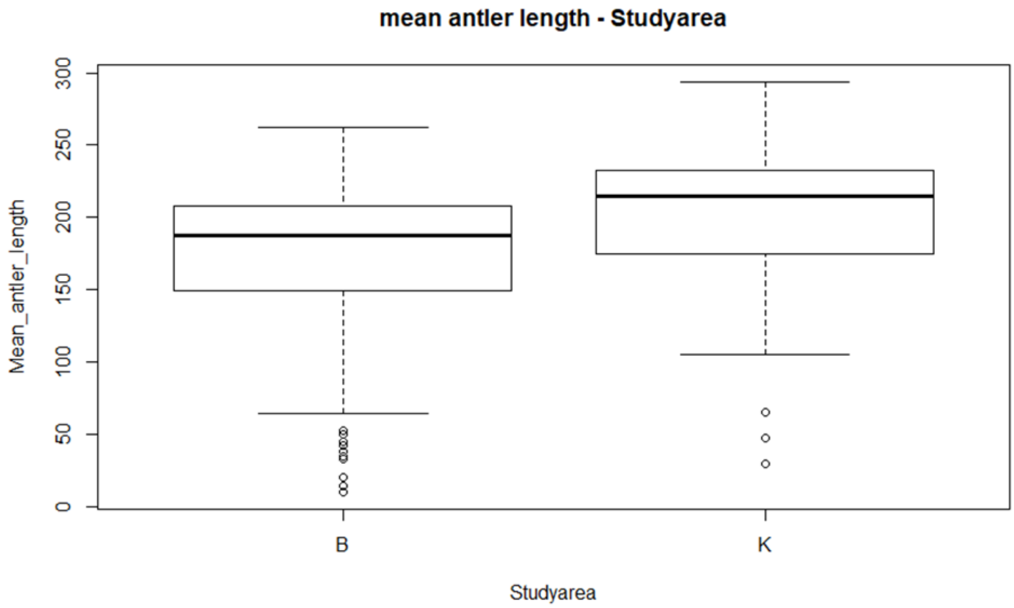

Figure 4. Boxplot illustrating the mean length of antlers (mm) in the two study areas uncorrected for age and body mass compared between Bogesund (B) and Koberg (K). The mean of Bogesund being 175 mm and Koberg 197 mm.

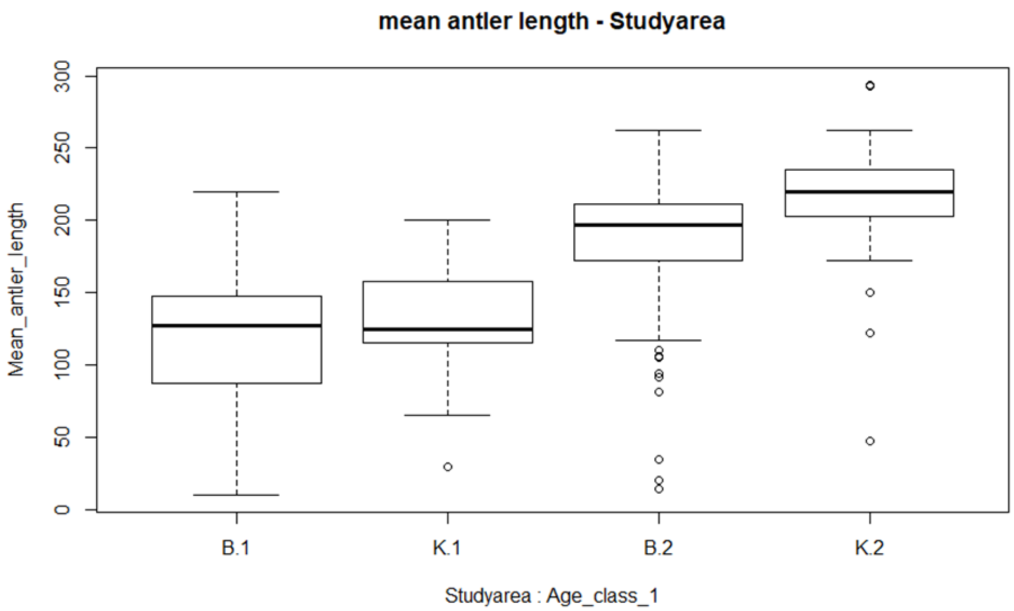

Figure 5. Boxplot illustrating the mean length of antlers (mm) uncorrected for body mass in the two study areas and two age classes between Bogesund (B) and Koberg (K). Age class 1 being yearlings and age class 2 being 2 years or older.

4. Discussion

The study found that regardless of which dependant variable that was analysed, the best model always contained an effect of study area (Bogesund vs Koberg, or Koberg N vs S). With one exception, they all supported the prediction that roe deer populations in areas with high density of fallow deer seems to perform poorer than population with low densities or no fallow deer present. Below I will interpret and discuss the results in more detail.

The result and premise can be further strengthened by the densities of roe deer for the three areas examined, with Bogesund, the area which lacks fallow deer, having higher densities of roe deer (approximately 10/km^2). The carrying capacity for roe deer at Bogesund is estimated at 35/km^2 (Elofsson et al 2017) and using the assumption that the metabolic rate of an adult fallow deer is approximately twice that of an adult roe deer, the theoretical carrying capacity for roe deer alone at Koberg would be in the broad range of 20 to 65 roe deer/ km^2 based on current average densities of fallow deer. That is well above the currently observed densities of roe deer at 0.5/km^2 and 1.5/km^2, highlighting that Koberg should be capable to host more roe deer even with the conservative densities the assumptions are based on after the culling of the fallow deer population in 2006.

The choice of examining body mass in fawns more or less guarantees that the animals are not migrants from the nearby environments, giving more credibility to the data concerning body mass. While seasonal migration occurs to a certain extent in roe deer (Ramanzin et al 2007), it is perhaps not very likely in this case as it is assumed that Koberg is a highly competitive area, based on fallow deer densities, with possible difficulty in finding high quality food and Bogesund is a semi-isolated on a peninsula, but we can never be certain besides of the fawn data. The fenced road of Koberg is also a factor which is assumed to give a degree of separation, but to what extent it is effective in this area is not fully known. The data contains some animals which are involved in car accidents, highlighting that movements between the areas occurs to a certain extent.

The result that contradicted the hypothesis was the Koberg roe deer having longer antlers (mean antler length). The genetic factor is one we cannot fully dismiss, and research in the related red deer (*Cervus elaphus*) suggests that there is indeed a heritable factor for antler length, but that the nutritional state of an animal is more important (Kruuk et al 2002). Other research into antler length finds that the density of roe deer in an area influences antlers, with lower density leading to an increased size (Vanpé et al 2007). This effect is however attributed not to density/number of animals itself, but the effect higher population density can have on food availability and body mass. Without taking into consideration the possible effect of interspecific competition, thus realigning the findings to my current hypothesis that food availability influences antler growth.

This leads to an aspect which could better help explain this slightly surprising result, which is the human factor. In this study it is assumed that the harvest is basically random, meaning that the trophy samples investigated are randomly collected regardless of size. However, since Koberg engages in commercial hunting, there is an apparent risk that a selective hunting could influence the data gathered, with a stronger interest in focusing on bucks with larger antlers. Which is an aspect that might be hard to correct for, but an idea could be to examine older data as a reference for if the length of antlers has changed over time in the area, with antlers from previous hunts available at the Koberg estate according to a previous study (Agnrud 2011). Overall, it adds some uncertainty to the data. Another human factor is that of supplemental feeding, with Koberg having large scale supplemental feeding in both areas of several 100's of tons each year (Garrido et al 2014), with much less notable supplemental feeding in Bogesund during the study. The effect of good nutrition and supplemental winter feeding during the time when antlers are in velvet is clearly positive for antler size (Cappelli et al 2020; Peláez et al 2022).

Ovulation rate was the physiological index which seemed to indicate most strongly that something is different between the areas, with a lower average of approximately 0.6 corpora lutea less in Koberg. Thus, indicating that reproductive effort appears to be lower. The number of fawns born would accordingly be lower and although corpora lutea counts does not completely translate to the number of fawns born, as implantation failure does occur, it is a good indicator when direct counts of fetuses is not feasible (Chirichella et al 2019). To take into account is that roe deer are considered as income breeders (*sensu* Jönsson 1997), meaning that they balance the number of offspring (0-4) in relation to available resources and under normal conditions invest in more than one offspring per year (Andersen et al 2000). In contrast, fallow deer normally only have one offspring, even under poor conditions. Being an income breeder entails that during periods of high food abundance, the extra energy can be capitalized upon to increase reproduction significantly, but also during less rich conditions being able to conserve energy by reproducing less. It can therefore be inferred that a lowered ovulation rate in the Koberg roe deer could be due to a lower amount of food available and thus, more fawns could very likely result in lowered body mass in the adult females. The

Koberg fawns also showed lower body mass highlighting that despite having on average less siblings to share food with, they still do not reach the same body mass as observed in Bogesund. Other studies have shown that in areas with high density of red deer, a negative effect on roe deer fawn body mass occurs (Richard et al 2010), emphasizing the interspecific effect that red deer, another larger cervid, can have on roe deer fitness.

The competition between roe deer and fallow deer have previously been observed, for example at feeding sites (Ferreti et al 2008) and inducing a separation in their spread in a commonly shared habitat (Ferreti et al 2011), not because of direct conflict but rather an observed avoidant behaviour from the roe deer. Strongly suggesting that an interspecific interference relationship exists between the two species and possibly leading to a situation where roe deer are relegated to poorer habitats due to their avoidance of higher quality areas where the fallow deer feed (Focardi et al 2006). The same pattern of interspecific interference has in fact been observed at Koberg in a previous study (Agnrud 2011). But to entirely consider the competition to be interference I think is faulty due to the large overlap in diet and where to draw the line between interference competition and exploitative competition might be a little unclear. But it seems likely that both can occur at the same time.

The management implications of interspecific competition have been discussed in a previous study, which considers the possible economic implications of poor or faulty management in roe deer and fallow deer (Elofsson et al 2017). Establishing that management influences harvest, with possibly reduced harvests of roe deer if fallow deer densities are not taken into consideration. My study does not quantify population growth or include harvest related economy, but rather strengthens the notion of what appears to be an observable interspecific competition relationship with a negative impact on roe deer fitness. Suggesting that if an area have a high density of fallow deer, the local roe deer are likely to have a reduced fitness. Thus, if the goal of a management strategy is to increase fitness and population density of roe deer, the reduction or even complete absence of fallow deer is probably to prefer.

In a concluding remark I would like to note that not all intended comparisons could be conducted due to low sample sizes when dividing it into the two areas of Koberg, which is very regrettable as I think it could have made for much more ideal results with a gradual change with different fallow deer densities. My suggestions for further refining this kind of study could be the use of GPS collared animals of both species to assure whether they spend their time in the study area and comparing areas closer to each other to avoid potential environmental factors. What could also work well as a supplement is better estimations of each areas carrying capacity as this study in some cases uses rather broad estimations.

Better standardization of data gathering to avoid faulty data and minimizing the unknown factors overall is also desirable. Hopefully this study can and will be used for further understanding of the interspecific competition between roe deer and fallow deer.

References

Abbott, I., Abbott, L.K. and Grant, P.R. (1977), Comparative Ecology of Galapagos Ground Finches (Geospiza Gould): Evaluation of the Importance of Floristic Diversity and Interspecific Competition. *Ecological Monographs*, 47: 151-184.

Agnrud A. (2011). Konkurrens mellan rådjur och dovhjort. - Examensarbete, SLUSkogsmästarskolan, Skinnskatteberg.

Andersen, R., Gaillard, J.-M., Linnell, J.D.C. and Duncan, P. (2000), Factors affecting maternal care in an income breeder, the European roe deer. *Journal of Animal Ecology*, 69: 672-682.

Andersen, R., Herfindal, I., Sæther, B.-E., John D. C. Linnell, Odden, J., & Liberg, O. (2004). When Range Expansion Rate Is Faster in Marginal Habitats. *Oikos*, *107*(1), 210–214.

Baker, K., & Rus Hoelzel, A. (2012). Evolution of population genetic structure of the British roe deer by natural and anthropogenic processes (Capreolus capreolus). *Ecology and Evolution, 3*, 89 - 102.

Cappelli, J., Ceacero, F., Landete-Castillejos, T., Gallego, L. and García, A. (2020), Smaller does not mean worse: variation of roe deer antlers from two distant populations in their mechanical and structural properties and mineral profile. *J Zool*, 311: 66-75.

Carlström L & Nyman M. 2005. *Dovhjort*. Kristianstads boktryckeri. Kristianstad.

Cederlund G & Liberg O. (1995). *Rådjuret: viltet, ekologin och jakten*. Almqvist & Wiksell tryckeri. Uppsala

Cederlund G, Kjellander P, Stålfelt F. (1991). Age determination of roe deer by tooth wear and cementum layers--tests with known age material. XXth Congress of the International Union of Game Biologists, Gödöllö: 540-545

Chapman, D., & Chapman, N.G. (1975). *Fallow deer: Their history, distribution, and biology.* Terrence Dalton, Lavenham.

Chirichella, R., Pokorny, B., Bottero, E., Flajšman, K., Mattioli, L. and Apollonio, M. (2019), Factors affecting implantation failure in roe deer. *Jour. Wild. Mgmt.*, 83: 599-609.

Clutton-Brock, T. H. (1982). The Functions of Antlers. *Behaviour*, *79*(2/4), 108–125.

Darwin, C. 1859. *On the origin of species by means of natural selection*. J. Murray, London.

Elofsson, K, Mensah, JT, Kjellander, P. (2017). Optimal management of two ecologically interacting deer species—reality matters, beliefs don't. *Natural Resource Modeling*.; 30: e12137.

Ferretti, F., Bertoldi, G., Sforzi, A. Fattorini, L. (2011). Roe and fallow deer: are they compatible neighbours? *Eur J Wildl Res* **57**, 775–783.

Ferretti, F., Sforzi, A., & Lovari, S. (2008). Intolerance amongst deer species at feeding: Roe deer are uneasy banqueters. *Behavioural Processes, 78*, 487-491.

Flajšman, K., Borowik, T., Pokorny, B., & Jędrzejewska, B. (2018). Effects of population density and female body mass on litter size in European roe deer at a continental scale. *Mammal Research, 63*, 91-98.

Flajšman, K., Jerina, K., & Pokorny, B. (2017). Age-related effects of body mass on fertility and litter size in roe deer. *PloS one*, *12*(4), e0175579.

Focardi, S., Aragno, P., Montanaro, P., & Riga, F. (2006). Inter-Specific Competition from Fallow Deer Dama dama Reduces Habitat Quality for the Italian Roe Deer Capreolus capreolus italicus. *Ecography*, *29*(3), 407–417.

Garrido, P., Lindqvist, S. & Kjellander, P. (2014): Natural forage composition decreases deer browsing on Picea abies around supplemental feeding sites. *Scandinavian Journal of Forest Research* 29: 234-242.

Gioria M, Osborne BA. (2014) Resource competition in plant invasions: emerging patterns and research needs. *Front Plant Sci*. 2014 Sep 29; 5:501.

Hofmann R. R. (1989). Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia*, *78*(4), 443–457.

Hovi, M., Alatalo, R. V., & Siikamäki, P. (1995). Black Grouse Leks on Ice: Female Mate Sampling by Incitation of Male Competition? *Behavioral Ecology and Sociobiology*, *37*(4), 283–288.

Jarnemo, A. 2004. Neonatal mortality in roe deer. Doctoral thesis, Silvestria 321, Swedish University of Agricultural Sciences, Uppsala.

Jönsson K.I. 1997. Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos* 78: 57–66

Kjellander, P., Svartholm, I., Bergvall, U.A. & Jarnemo, A. (2012): Habitat use, bedsite selection and mortality rate in neonate fallow deer Dama dama. - *Wildlife Biology* 18:280-291.

Krebs, C.J. (2013) *Ecology: The experimental analysis of distribution and abundance*. Sixth Edition, Pearson, London.

Kruuk, L.E.B., Slate, J., Pemberton, J.M., Brotherstone, S., Guinness, F. and Clutton-Brock, T. (2002), Antler size in red deer: heritability and selection but no evolution. *Evolution*, 56: 1683-1695.

La Morgia, V. & Venturino, E., (2017). "Understanding hybridization and competition processes between hare species: Implications for conservation and management on the basis of a mathematical model," *Ecological Modelling,* Elsevier, vol. 364(C), pages 13-24.

Linnell, J., & Zachos, F. (2011). Status and distribution patterns of European ungulates: Genetics, population history and conservation. *Ungulate Management in Europe: Problems and Practices* (pp. 12-53). Cambridge: Cambridge University Press.

Mehner, T. & Brucet, S. (2022). Structure of Fish Communities in Lakes and Its Abiotic and Biotic Determinants. *Encyclopedia of Inland Waters* Volume 2, 2022, Pages 77-88

Peláez, M., Sanuy, I., Peral, J. C., Esteban, J. L. Á., Lavín, S., Serrano, E., & Perea, R. (2022). Early life investment in antlers and body growth reflects adult performance in roe deer population under supplementary feeding conditions. *Integrative zoology*, *17*(3), 396–407.

Ramanzin, M., Sturaro E., & Zanon, D. (2007) Seasonal migration and home range of roe deer (*Capreolus capreolus*) in the Italian eastern Alps. *Canadian Journal of Zoology* 85(2):280–289

Rautiainen, H., A Bergvall, U., Felton, AM., Tigabu, M. & Kjellander, P. (2021). Nutritional niche separation between native roe deer and the nonnative fallow deer—a test of interspecific competition. *Mammal Research*, 66: 443–455.

Richard, E., Gaillard, J. M., Saïd, S., Hamann, J. L., & Klein, F. (2010). High red deer density depresses body mass of roe deer fawns. *Oecologia*, *163*(1), 91–97.

Robin M Tinghitella, Alycia C R Lackey, Michael Martin, Peter D Dijkstra, Jonathan P Drury, Robert Heathcote, Jason Keagy, Elizabeth S C Scordato, Alexandra M Tyers, (2018) On the role of male competition in speciation: a review and research agenda, *Behavioral Ecology*, Volume 29, Issue 4, July/August 2018, Pages 783–797

RStudio Team (2021). RStudio: Integrated Development Environment for R. Boston, MA: RStudio, PBC. http://www.rstudio.com/

Skogland, T. (1984). The effects of food and maternal conditions in fetal growth and size in wild reindeer. *Rangifer*, *4*(2), 39–46.

Svenska Jägarförbundet (2022) *Viltdata*, https://rapport.viltdata.se/statistik/ [2022-11-13]

Vanpé, C., Gaillard, J.-M., Kjellander, P., Mysterud, A., Magnien, P., Delorme, D., Laere, G. V., Klein, F., Liberg, O., & Mark Hewison, A J (2007). Antler size provides an honest signal of male phenotypic quality in roe deer. *The American Naturalist*, 169, 481–493.

Zahavi A. (1977). The cost of honesty (further remarks on the handicap principle). *Journal of theoretical biology*, *67*(3), 603–605.

Populärvetenskaplig sammanfattning

Att dela område med en större släkting – en undersökning av dovhjortsförekomst på rådjurs kondition

Rådjur (*Capreolus capreolus*) och dovhjort (*Dama dama*) är två arter som inte helt ovanligen kan skymtas på fält, till skogs och i trädgårdar. Men att de båda förekommer i Sverige tillsammans har inte alltid varit den självklarhet det lätt kan misstas för att vara i nutid. Rådjur har funnits i Sverige sedan istidens slut för cirka 10 000 år sedan, men dovhjorten kan ha kommit till Sverige så sent som på 1500-talet. På senare tid har deras antal i landet närmat sig varandra och vid senaste mätningen 2020 låg rådjursavskjutningen kring 100 000 och antalet dovhjortar cirka 72 000. Detta i kontrast mot antalen 1993 då avskjutningen av rådjur var som högst och uppmättes till 382 000 medan det endast fälldes 2 638 dovhjortar.
Denna studie ämnar undersöka om rådjur uppvisar en mätbart försämrad kondition i områden med olika tätheter av dovhjort, då båda hjortdjuren förväntas nyttja och eventuellt även tävla om samma proteinrika växter och örter. Kondition avser i denna studie, kidvikt, ovulationstakt (hur många kid som förväntas födas) samt hornlängd hos bockarna. Detta mäts med hjälp av data insamlade efter jakt från två platser i landet, Bogesund (inga dovhjortar) nära Stockholms skärgård och Koberg (med dovhjortar) nära Trollhättan. Koberg är uppdelat i två delar av en bilväg (nord och syd), med olika tätheter av dovhjort på vardera sidan, nord lägre och syd högre täthet. Detta tillåter en bra jämförelse för att undersöka om mellanartskonkurrens sker mellan rådjur och dovhjort och med olika tätheter se om fler dovhjortar innebär sämre kondition för rådjur.

Resultaten visade, i tre av fyra utförda mätningar, att kiden på Koberg (där dovhjortar finns) vägde lite mindre (0,2 kg mindre), att getternas ovulationstakt var lägre (i medeltal cirka 0,6 färre kid förväntade per år) samt att hornlängden var lite längre (3 mm) på norra Koberg jämfört mot södra Koberg. Den fjärde mätningen fann ett oväntat resultat i att rådjuren på Koberg i medeltal hade betydligt längre horn jämfört med dem på Bogesund (cirka 22 mm), vilket skulle kunna bero på den vinterutfodring som sker på Koberg, genetiska faktorer samt en möjlig effekt av urvalsjakt.

Sammanfattningsvis indikerar studien att dovhjort kan ha en negativ effekt på rådjur och att detta bör tas i beaktande vid framtida förvaltning och skötsel av hjortdjurs populationer.

Acknowledgements

A big thank you to my supervisor Petter Kjellander for being very patient with me and being very generous with his time, I'm very thankful.
I'd also like to thank my late grandfather for leading me into a life with close connection to nature, and now a greater understanding of it as an ecologist.

Appendix 1

Table 1. Results from GLM with lowest AIC value for fawn body mass comparing Koberg and Bogesund populations. Bold values are significant.

Variables	Estimate	Std.error	T value	P value
(Intercept)	-26.588	3.595	-7.396	**<0.05**
Study area: K	-0.186	0.499	-0.373	0.709
Sex: M	-0.088	0.308	-0.285	0.776
Month:Oct/Nov	0.322	1.093	0.294	0.796
Month:Dec/Jan	-0.085	1.119	-0.076	0.939
Metatarsus	1.293	0.115	11.173	**<0.05**

Table 2. Results from GLM with lowest AIC value for ovulation rate / Corpora lutea comparing Koberg and Bogesund populations. Age class 2 meaning individuals 2 years or older, Bold values are significant.

Variables	Estimate	Std.error	T value	P value
(Intercept)	0.615	0.614	1.001	0.318
Study area: K	-0.652	0.185	-3.518	**<0.05**
Age class: 2	0.227	0.215	1.057	0.292
Body mass	0.060	0.025	2.343	**0.020**

Table 3. Results from GLM with lowest AIC value for mean antler length comparing the northern and southern areas of Koberg, age class 2 meaning individuals 2 years or older. Bold values are significant.

Variables	Estimate	Std.error	T value	P value
(Intercept)	44.046	51.901	0.849	0.399
Area:S	-3.005	12.072	-0.249	0.804
Age class: 2	69.045	17.413	3.965	**<0.05**
Body mass	4.013	2.345	1.712	0.092

Table 4. Results from GLM with lowest AIC value for mean antler length comparing Koberg and Bogesund populations, age class 2 meaning individuals 2 years or older. Bold values are significant.

Variables	Estimate	Std.error	T value	P value
(Intercept)	6.607	20.582	0.321	0.748
Study area: K	24.534	5.635	4.354	**<0.05**
Age class: 2	61.153	6.030	10.141	**<0.05**
Body mass	4.759	0.871	5.458	**<0.05**

Table 5. AIC-table showing all interactions used for fawn body mass comparing Koberg and Bogesund populations, Model with lowest AIC/AIC-weight in bold.

Fawn body mass (Koberg vs Bogesund)														
Model no.	**Study area (K/B)**	**Sex**	**Month**	**Metatarsus**	**Stusy area (K/B)*Sex**	**Study area (K/B)*Month**	**Study area(K/B)*Metatarsus**	**Sex*Month**	**Sex*Metatarsus**	**Month*Metatarsus**	**K**	**AIC**	**ΔAIC**	**AIC-wt**
1	1	1	1	0	0	0	0	0	0	0	6	702.64	91.44	0.00
2	**1**	**1**	**1**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**7**	**611.20**	**0.00**	**0.63**
3	1	1	1	1	1	0	0	0	0	0	8	613.07	1.87	0.25
4	1	1	1	1	1	1	0	0	0	0	9	615.14	3.95	0.09
5	1	1	1	1	1	1	1	0	0	0	10	617.41	6.22	0.03
6	1	1	1	1	1	1	1	1	0	0	12	621.48	10.28	0.00
7	1	1	1	1	1	1	1	1	1	0	13	623.51	12.31	0.00
8	1	1	1	1	1	1	1	1	1	1	15	627.73	16.54	0.00

Table 6. AIC-table showing all interactions used for ovulation rate comparing between Koberg and Bogesund populations. Model with lowest AIC/AIC-weight in bold.

Ovulation rate (Koberg vs Bogesund)														
Model no.	**Study area (K/B)**	**Age class**	**Body mass**	**Metatarsus**	**Study area*Age class**	**Study area*Body mass**	**Study area*Metatarsus**	**Age class*Body mass**	**Age class*Metatarsus**	**Body mass*Metatarsus**	**K**	**AIC**	**ΔAIC**	**AIC-wt**
1	1	1	0	0	0	0	0	0	0	0	4	286.09	3.37	0.09
2	**1**	**1**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**5**	**282.72**	**0.00**	**0.49**
3	1	1	1	1	0	0	0	0	0	0	6	284.17	1.44	0.24
4	1	1	1	1	1	0	0	0	0	0	7	285.70	2.97	0.11
5	1	1	1	1	1	1	0	0	0	0	8	287.22	4.50	0.05
6	1	1	1	1	1	1	1	0	0	0	9	289.47	6.75	0.02
7	1	1	1	1	1	1	1	1	0	0	10	291.60	8.88	0.01
8	1	1	1	1	1	1	1	1	1	0	11	293.73	11.00	0.00
9	1	1	1	1	1	1	1	1	1	1	12	296.13	13.41	0.00

Table 7. AIC-table showing all interactions used for mean antler length comparing between populations in areas of Koberg (North/South). Model with lowest AIC/AIC-weight in bold.

Antlers Koberg (North/south)														
Model no.	**Area (N/S)**	**Age class**	**Body mass**	**Metatarsus**	**Area*Age class**	**Area*Body mass**	**Area*Metatarsus**	**Age class*Body mass**	**Age class*Metatarsus**	**Body mass*Metatarsus**	**K**	**AIC**	**ΔAIC**	**AIC-wt**
1	1	1	0	0	0	0	0	0	0	0	4	606.34	0.67	0.33
2	**1**	**1**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**5**	**605.68**	**0.00**	**0.46**
3	1	1	1	1	0	0	0	0	0	0	6	608.07	2.39	0.14
4	1	1	1	1	1	0	0	0	0	0	7	610.66	4.98	0.04
5	1	1	1	1	1	1	0	0	0	0	8	612.15	6.47	0.02
6	1	1	1	1	1	1	1	0	0	0	9	614.64	8.96	0.01
7	1	1	1	1	1	1	1	1	0	0	10	616.73	11.05	0.00
8	1	1	1	1	1	1	1	1	1	0	11	619.64	13.96	0.00
9	1	1	1	1	1	1	1	1	1	1	12	622.83	17.15	0.00

Table 8. AIC-table showing all interactions used for mean antler length comparing between Koberg and Bogesund populations. Model with lowest AIC/AIC-weight in bold.

Antlers (Koberg vs Bogesund)														
Model no.	**Study area (K/B)**	**Age class**	**Body mass**	**Metatarsus**	**Study area*Age class**	**Study area*Body mass**	**Study area*Metatarsus**	**Age class*Body mass**	**Age class*Metatarsus**	**Body mass*Metatarsus**	**K**	**AIC**	**ΔAIC**	**AIC-wt**
1	1	1	0	0	0	0	0	0	0	0	4	2844.66	17.07	0.00
2	**1**	**1**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**5**	**2827.59**	**0.00**	**0.56**
3	1	1	1	1	0	0	0	0	0	0	6	2829.29	1.70	0.24
4	1	1	1	1	1	0	0	0	0	0	7	2830.86	3.27	0.11
5	1	1	1	1	1	1	0	0	0	0	8	2832.97	5.39	0.04
6	1	1	1	1	1	1	1	0	0	0	9	2835.10	7.52	0.01
7	1	1	1	1	1	1	1	1	0	0	10	2834.28	6.69	0.02
8	1	1	1	1	1	1	1	1	1	0	11	2834.47	6.88	0.02
9	1	1	1	1	1	1	1	1	1	1	12	2836.65	9.06	0.01

Publishing and archiving

Approved students' theses at SLU are published electronically. As a student, you have the copyright to your own work and need to approve the electronic publishing. If you check the box for **YES**, the full text (pdf file) and metadata will be visible and searchable online. If you check the box for **NO**, only the metadata and the abstract will be visible and searchable online. Nevertheless, when the document is uploaded it will still be archived as a digital file. If you are more than one author, the checked box will be applied to all authors. Read about SLU's publishing agreement here:

- https://www.slu.se/en/subweb/library/publish-and-analyse/register-and-publish/agreement-for-publishing/.

☒ YES, I/we hereby give permission to publish the present thesis in accordance with the SLU agreement regarding the transfer of the right to publish a work.

☐ NO, I/we do not give permission to publish the present work. The work will still be archived and its metadata and abstract will be visible and searchable.