Timing of the Rut in Fallow Deer *Dama dama*

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Supervisors: Petter Kjellander, SLU, Department of Ecology
Geir Rune Rauset, SLU, Department of Ecology

Examiner: Henrik Andrén, SLU, Department of Ecology

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Abstract

The timing of the fallow deer *Dama dama* rut was determined by investigating the time of ovulation and rut excursions in a free ranging population at the Koberg estate, in south-western Sweden. Various factors (body mass, body condition, age and population density) that might determine the time of ovulation were included in the analyses. Ovulation data was collected from 1705 animals (adults, sub adults, senescent), shot in the years 2006 - 2015. GPS-positions from 21 collared females were also analysed. Half of the does ovulated before October 30 while the mean rut excursion date was October 21. Age class and population density were factors that significantly affected the yearly variation in ovulation date and individual body mass was only affecting sub adult ovulation. Bone marrow fat content showed no significant relationship with the probability to ovulate in any age class. The probability to ovulate was not affected by lactation. Probably because lactating females to a high extent consisted of prime aged females, who were able to buffer against the cost of repeated annual reproduction. Swedish law imply a break in the hunting season, with the purpose to avoid hunting related disturbance during the rut. It was found that the break was protecting close to 28% of the female population in Koberg from such disturbance during their ovulation.

Key words: fallow deer, *Dama dama*, ovulation, rut, hunting season

Populärvetenskaplig Sammanfattning

Tiden för dovhjortens *Dama dama* brunst i Sverige och vilka faktorer som kan ha en påverkan på den årliga variationen studerades. Data samlades in från 1705 stycken skjutna hindar (honor) från Koberg, Västra Götaland, samt 21 hindar försedda med GPS-halsband under åren 2006 - 2015. Faktorer som inkluderades i analysen var tidpunkt för ovulation (ägglossning), brunstexkursioner, kroppskondition, ålder och populationsstorlek. Resultatet av denna studie kan komma till nytta för myndigheter, markägare, viltvårdare och jägare som förvaltar dovhjortsstammar. Under hösten är det en paus i jakten (oktober 21 – november 15) för att djuren ska få brunsta ifred. Frågan är hur stor andel av populationen som täcks in av denna paus?

Dovhjorten är vida spridd över världen och brunstar sent i jämförelse med andra hjortdjur, detta oavsett var i världen de befinner sig. De har lagt om tiden för brunsten så att den är anpassad till årstiderna, men det generella intrycket är att kalvarna föds sent på våren. I Sverige föds de första dovhjortskalvarna i mitten av juni. Medan de inhemska arterna är tidigare där kronhjort föder redan i månadsskiftet april-maj, älg i mitten av maj och rådjur i slutet av maj, början av juni.

För hjortdjur i Norden har ålder och populationsstorlek visat sig vara faktorer som styr ovulationen. Vikten tycks avgöra vid vilken ålder en hind blir könsmogen och ovulerar för första gången, då det verkar som att de måste uppnå en tröskelvikt innan de blir könsmogna. Hos en del arter har även åldrande observerats då äldre djur inte föder kalvar lika frekvent längre.

Resultatet av denna studie visar att hälften av hindarna på Koberg har ovulerat innan den 30 oktober. Analyserna av brunstexkursionerna, vilka blev synliga genom GPS-positioner funna utanför hindens hemområde, indikerar att brunsten i genomsnitt äger rum runt den 21 oktober. Ålder och populationsstorlek visade sig, precis som hos andra hjortdjur, ha en betydande del i den årliga variationen av tiden för ovulation. Mängden benmärgsfett visade sig sakna betydelse för sannolikheten att ovulera för samtliga åldersgrupper. Lakterande hindar med kalv hade samma sannolikhet att ovulera som icke lakterande hindar, trots att det i termer av energi är kostsamt. Detta kan bero på att hindar som har kalv i hög grad är i sina mest produktiva år och då har råd med att föda kalv flera år i rad.

Ungefär 28 % av hindarna ovulerar under det tvingande jaktuppehållet. Om det finns etiska skäl för att uppehållet skall täcka in en större andel av hindpopulationen, skulle pausen behöva förlängas.

Nyckelord: Dovhjort, *Dama dama*, reproduktion, brunst, ovulation, jaktsäsong

Introduction

To produce and support offspring is a huge investment and postnatal energy cost for any female, especially in mammals, considering the milk production (Clutton-Brock et al. 1983, Moen et al. 1997). Therefore it is important to have access to high quality food during lactation. For ungulates in the northern hemisphere the solution is to time birth with vegetation spring flush and the peak of the plant growing season, so that females easily can access required energy (Linnell & Andersen 1998). There is a risk of giving birth too early in the spring, during May the temperatures can be so low that the fawn risk to die of hypothermia (Linnell & Andersen 1998, SMHI 2015). If the fawn is born too early there will not be any high nutritious food and the doe may have trouble producing quality milk (Linnell et al. 1995). Hypothermia and starvation has shown to be the main non-predator cause of death for young fawns (Linnell et al. 1995). The fawns of ungulates are not born with a lot of body fat and are therefore prone to hypothermia (Linnell et al. 1995). Climatic conditions, temperature and the lack of nutritious food in early spring are thought to be the main reason preventing deer to give birth early in the season (Bowyer et al. 1998, Linnell & Andersen 1998). Females also need to be in good condition to afford reproduction since, in the ungulates, they take the total cost for both prenatal and postnatal care (Birgersson & Ekvall 1997). If the female gives birth too late she might not have enough time to recover before winter and the following year's reproduction might be at risk (Clutton-Brock et al. 1983). Also, if the calf is born too late it might not gain enough weight before winter and the chances of survival decreases (Birgersson & Ekvall 1997, Gaillard et al. 1993, Hogg et al. 1992). A mismatch with the plant growing season leads to lost access to high quality nutrients when it is needed the most (Plard et al. 2014). The female should therefore ovulate during a time under the summer-autumn so that she gives birth to her calf neither too early, nor too late in the spring.

Ungulates timing of birth, and therefore also time of ovulation, varies between species, as do gestation length. In general and on species level, the heavier adult body mass the longer gestation period (Asher 2011). In Scandinavia red deer *Cervus elaphus* gives birth to one calf in the shift of April-May (The Swedish Association for Hunting and Wildlife Management 2012a); moose *Alces alces* gives birth to 1-3 calves in mid-May (Ericsson et al. 2001); roe deer *Capreolus capreolus* 1-4 fawns in late May – early June (Linnell & Andersen 1997, Andersen & Linnell 1998). Compared to these species the fallow deer *Dama dama* gives birth to a single calf, very late, in mid-late June (Birgersson & Ekvall 1997, Kjellander et al. 2012).

Female red deer usually mate for the first time during their second or third year and young females often ovulate 2 - 3 weeks after adults (Asher et al. 2011, Langvatn et al. 2004). At what age a red deer female ovulate for the first time is weight dependent, but body mass is less important in prime aged females (Langvatn et al. 2004). Senescence in older females is observed at an age of 13 in a study of Langvatn et al. (2004) and at an age of 20 in a study by Mysterud et al. (2001). A small weight loss during the rut is observed in female red deer, but not at all as pronounced as in males (Yoccoz et al. 2002). Females can re-cycle

several times if they are not successfully fertilized during the first ovulation cycle (Asher 2011). The ovulation is delayed in prime aged females when population density is high, but it also becomes more synchronized (Langvatn et al. 2004). The chance for a primiparous female to ovulate decreased with increased density (Langvatn et al. 2004). Langvatn et al. (2004) conclude that this density dependence shown for both prime aged and sub adult females might be related to the condition of the females or the abundance of males, both factors that may change with density.

At birth, the moose calves weigh about 15 kg and are therefore less likely to suffer from hypothermia compared to smaller calves of other species (Bowyer et al. 1998). In female moose, the age of first reproduction is highly correlated with the body mass. Usually this happens when they reach a threshold weight of 200 kg, which normally occurs during their second or third year (Belovski 1977, Sæther & Heim 1993, Sand 1996, Sand & Cederlund 1996). Females also have their first ovulation earlier in life if they weigh more as a calf and grows fast. Probability of multiple ovulations (twinning rate) is also positively correlated with weight (Sand 1996). Age has shown to be a good indicator of how much female moose invest in the reproduction. Younger females give more often birth to single calves, whereas older females more often have twins (Sæther & Haagenrud 1983). Moose females peak in their reproduction when they are 3 - 10 years old (Ball et al. 1999) and after 12 years of age signs of senescence is observed (Ericsson et al. 2001).

Roe deer has a delayed implantation and are mating already during the summer, (Hewison & Gaillard 2001). Age and body weight have shown to have an effect on fecundity (Hewison & Gaillard 2001). A French study demonstrated that early born females had a greater adult body size than late born females (Plard et al. 2015). Early born fawns also had a higher survival rate compared to late born fawns (Plard et al. 2015). Roe deer mate for the first time during their second summer, but do not give birth at the same rate as adults (>2years old) (Hewison 1996). Senescence is observed at an age of 8 (Hewison & Gaillard 2001). The fawns weigh about 1.5 kg at birth (Andersen & Linnell 1997).

For the species mentioned above, variation in age and population density seem to be the most common factors resulting in variation in ovulation in boreal ungulates. In young animals there seem to be strong effects of body mass, with thresholds for first ovulation. The declining importance of body mass for the probability of reproduction in prime aged females could be interpreted as that this age group afford the cost of reproduction several years in a row. Senescence is noted in all species. In Scandinavia with cold and snowy winters, body weight might play a more important role since harsh winter conditions potentially result in weight loss and thereby an additional cost during the gestation period.

Until this study, very little is known about factors affecting timing of rut and ovulation rate in free ranging fallow deer. Female fallow deer is expected to gain in weight until three years of age and then weigh 45 kg on average (Chapman & Chapman 1975, McElligott et al. 2002). Langbein & Putman (1992) found low variation in reproductive rates in adult females even with a high variation in

body mass, indicating that weight has a limited importance for the probability to ovulate in prime aged females. In theory, good body condition should increase the reproductive rate and ovulation but this relationship might be more important in younger females (Sand 1996) and maybe even more important in Scandinavia where the winters are harsher. Females might lose some weight during the rut since they eat less or nothing at all when they are at the lekking site (Appollonio et al. 1989), but it should not influence ovulation rate since they are at the lekking site for such a short period of time compared to the males (Clutton-Brock et al. 1988). With GPS-collared individuals eventual rut excursions should be possible to determine as outliers in the range of all locations of an individual. Heavy females have shown to give birth to larger offspring with a high growth rate (Birgersson & Ekvall 1997), which should increase fawns survival during first winter. Cost of previous reproduction might affect the condition of the doe and the probability to ovulate again. The gestation period in fallow deer is 231 days (Birgersson & Ekvall 1997). The earliest birth in Sweden is documented in a study by Kjellander et al. (2012) to be 21st of June and the last 14th of July. If the fawn is born too late, which might be in the cases were the doe have been fertilized in the second or third ovulation cycle, this might affect the reproduction in the following year (Clutton-Brock et al. 1983). A doe can re-cycle 3 - 6 times if she is not fertilized (Asher 1985). The female do rarely ovulate during her first year (Langbein & Putman 1992). Young females (<2 year old) have been observed to ovulate 7 - 8 days later than older does in a New Zeeland population (Asher & Kilgour 1985). Senescence in female fallow deer has not been reported to my knowledge, but it has been well documented in several other ungulate species (Bérubé et al. 1999, Ericsson et al. 2001, Mysterud et al. 2001).

Management
In Sweden, fallow deer is mainly found in the southern third of the country and the first animals were introduced during the sixteenth century (Chapman & Chapman 1980). Fallow deer has become a popular game species in Sweden with a total harvest of 20,000-30,000 animals, annually the last couple of years (The Swedish Association for Hunting and Wildlife Management 2015a). For ethical reasons a break in the legal hunting season has been established to prevent possible negative effects of hunting disturbance during the rut. The break is set to 26 days between October 21st and November 15th and protects the males (The Swedish Association for Hunting and Wildlife Management 2015b). Females and calves are still legal to hunt. It is not known if this break cover the whole rut and if the actual rut vary between years. A study by Komers et al. (1999) show that females ovulated earlier when exposed to mature males and later when only young, premature males were around. The abundance of mature male thus seems valuable for an early rut. If there are too few adult males, young males that would not have the chance to mate otherwise will now have an increased chance (Mysterud et al. 2008). Since population sex ratio and male age composition is mainly determined by the local hunters it is up to the landowners to make sure that the proportions of adult males vs. females is viable. The hunting season are supposed to be adjusted to each species' ecology, their different life strategies, and also according to different biogeographic gradients

along the country. The hunting seasons are updated approximately every third year by the Swedish government (The Swedish Association for Hunting and Wildlife Management 2012b). Still, every landowner and hunting team can choose to wait if they think the legal hunting season start too early in relations to the rut, and what is appropriate for their area (The Swedish Association for Hunting and Wildlife Management 2012b). A recent example is 120 hunting teams in southern Sweden that this year (2015) decided to postpone the start of the moose hunt with one week (Jaktjournalen 2015) since the moose rut in their area not seem to be over when the hunting starts (Malmsten et al. 2014).

Aims of study

The aim of this study is to a) determine the timing of the fallow deer rut (time of ovulation and rut excursions in females) and b) investigate various factors (body mass, body condition, age and population density) influencing the ovulation. I will do that by examining a data set based on 21 GPS-collared adult females together with data from > 1700 killed females at one estate in south western Sweden during 2006 – 2015.

Predictions

1. Changes in movements could indicate the rut and occurs if the lek area is not within the home range of the female. This change in movement would be observed as GPS-locations indicated as outliers in relation to the ordinary home range.
2. Females in high density populations will ovulate later and more synchronized than females in areas with lower population density due to decreased body condition related to higher density.
3. The probability to ovulate will depend on age. Prime aged animals will reproduce at a higher rate and more synchronized than other age groups. Sub adults should ovulate later in the season than the prime aged females and the oldest females (senescent) are expected to ovulate at the lowest rate.
4. Lactating females should show various degrees of decreased body condition compared to non-lactating females due to increased energy expenditure and cost of current reproduction (Clutton-Brock et al. 1983). Females in poor condition (low body mass and low bone marrow fat) will generally have a lower probability to ovulate.

Materials and Methods

Study area

The study was performed in Koberg estate (58°N, 12°E), situated in south west of Sweden in the county of Västra Götaland. The area is divided in two parts by a fenced road, limiting the movement of animals between the two sub areas. The northern area is 27.1 km^2 and the southern area is 54.0 km^2. The density of fallow deer differs between the northern and the southern area. Distance sampling surveys performed 2007 - 2015 gives an average of 114.3 fallow

deer/10 km^2 in the north and 307.7 fallow deer/10 km^2 in the south (Kjellander, unpublished data). Compared to each other, the northern area is the low density area and the southern the high density area. The first fallow deer, approximately 20 animals, were released from a small enclosure at the estate in the end of the 1920's (Silfverschiöld, unpublished data). Land is mainly covered by forest (79%). Arable land and pastures covers 16%, mires and marshes 2% and lakes, ponds, parks and properties represent 3% of the land (Kjellander et al. 2012). The most common habitat is coniferous forest (44%) (Winsa 2008). Supplementary food is given during the winter to support the large populations of deer (Garrido et al. 2014), and a large part of the arable land is cultivated to improve the habitat for wildlife (Grönberg 2011). During the autumn controlled hunting is performed in the management area.

Data collecting
Ovulation data used in this study was collected between 2006 - 2015, mainly from the ordinary harvest of fallow deer in Koberg (1st of September – 28th of February), complemented by some animals culled on special permits and from animals killed in vehicle incidents during other times of the year. For each individual, data was recorded in a specifically designed form (Appendix 1): e.g. area where the animal was shot, hunting method and date of the killing. In addition, body mass (total body mass, dressed weight or slaughter weight in kg) and metatarsus length (in cm, from the tip of the joint to the tip of the hooves, Appendix 2) were estimated, and ovaries, uterus and jaws were collected. It was also noted if the doe was lactating or followed by a calf. This was done in the slaughterhouse at Koberg by research project associates. The ovaries, uterus and jaws were then brought to the Grimsö research station where the uterus was checked for fetuses and the ovaries for *corpus luteum* to determine if the doe had ovulated or not (Langvatn et al. 2004, Mysterud et al. 2008). The length of the jaw was measured and from 2012 the bone marrow from the lower mandible was collected and weighed (dry and wet weight) to estimate fat content (Ratcliff 1980). Each individual was age determined by cutting the first molar (the 4th tooth) and counting the cementum layers (The Swedish Association for Hunting and Wildlife Management 1996).

Fallow deer density in this study area was estimated by using the Distance Sampling procedure, described by Buckland et al. (2001). In this case based on 85, one kilometre long permanent transects walked 2-3 times in the evening, in April each year.

A total of 24 females were marked with a GPS collar (Vectronic Aerospace GmbH, Berlin, Germany, model Pro-light) between the years 2006-2010. The collars were programmed to take one position every fourth hour. Female age was estimated during marking by investigating tooth eruption and wear (if >2 years old) (The Swedish for Hunting and Wildlife Management 1996). Later and if the deer was shot or found dead during the study the jaw was brought to the lab and the age was determined by cutting the first molar.

Data analysis

Dates for when the deer was shot as well as GPS dates were converted into relative date (1 – 365), where 1st of July was set to day 1.

The females were divided into 4 age groups (factor): juvenile (< 1 year old), sub adult (1 year old), adult (2 - 14 years old) and senescent (≥ 15 years old). The juveniles were excluded from the analysis since they are not expected to ovulate during their first autumn (Langbein & Putman1992). Sub adults are expected to have a lower success rate in reproduction then adults (Langbein & Putman 1992). An earlier study from the same area showed a drop in reproduction effort in ≥ 15-year-old fallow deer females (Molenaar unpublished).

Most animals (98.7 %) had the dressed weight noted in the protocol. For those who did not, whereas data on total weight or slaughter weight was taken, a conversion factor was calculated based on those animals that where weighed for both measures ("Slaughter weight" / 0.727 = "Dressed weight" (n = 15) and "Total weight" * 0.700 = "Dressed weight" (n = 8). The transformation coefficient was then used to convert the weight given for the individual to dressed weight. To correct for size - weight differences between individuals, relative weight (numerical) was calculated by dividing each individuals dressed weight with the length of the metatarsus. The length of metatarsus has proven to be correlated with body size for many ungulate species (McMahon 1975). To divide dressed weight by jaw length to get relative weight would give a more accurate index. The jaw was measured in millimetres in a lab under controlled conditions where there is a higher possibility to standardize measurements than in the slaughterhouse where the metatarsus was measured (in centimetres). However, several samples lacked information of jaw length due to damaged jaws and therefore to maximize sample size, I used the metatarsus length only.

To see if the doe had ovulated or not the ovaries were cut from the uterus and then put in 70% alcohol for 7 days. They were then cut in two places with a scalpel. If the doe has ovulated the corpus luteum is visible. This is the so-called "yellow body" – a remaining structure from the ovulated egg in the ovary.

A set of models were built and ranked according to their Akaike information criterion corrected for small sample sizes (AIC_c). The model with the lowest AIC_c value reflects the model with the best compromise between precision and complexity (Burnham and Anderson 2002). ΔAIC_c is the difference between the best fitted model and the given model. If two models differs with <2 units they can be considered as competitive (Burnham & Anderson 2002). The Akaike weights shows to which extent a model is supported by the data and also takes in the other models in the set (Burnham & Anderson 2002).

Probability of ovulation was fitted as a generalized linear model (glm) with binomial error distribution (i.e. logistic regression) in program R (R core team 2015), aided by software RStudio (Version 0.98.1049 – © 2009-2013 RStudio, Inc.). All candidate set of ovulation models included relative date as an explanatory variable, in various combinations with age group (sub adults, adults and senescent), density (high and low), and body condition (Table 2). To

investigate annual variation in the time of rut, year was added as a categorical variable to the best model. The peak of the rut was defined as the date where 50% of the females had ovulated.

A glm (binomial) was performed to investigate the impact of lactation on the probability of ovulation (Table 3) and another one to investigate the impact of lactation (binomial) on the condition of the doe and the resulting probability of ovulation (Table 4). Only individuals shot within the first three weeks of the hunting season (12th of October to 7th of November) were included in these analyses of cost of current reproduction i.e. lactating females (n = 377). This time limit was set since the lactation will cease within three to four weeks after loosing the calf (Langbein & Putman 1992, Röken unpublished). Juveniles and sub adults were obviously excluded since they are not expected to have a calf.

To investigate the effect of body condition on probability of ovulation, relative bone marrow fat content and relative weight were included in a sub-analysis (binomial glms), based only on individuals from 15 - 19 November (n = 83, Table 5). The short period is due to that the hunting starts again the 15th of November, but I did not want to stretch the period further, then the effect from lower food supply during the winter might interfere with the cost of reproduction.

Rutting excursions
Data from the GPS-collars was used to investigate potential rut excursions, which would be detected as spatial outliers relative to locations belonging to the individual ordinary home ranges. A net square displacement analysis (NSD; Börger & Fryxell 2012) was performed in R package AdehabitatLT (Calenge 2006) for all the radio-collared animals where the doe had worn the collar during at least one autumn (n = 21). Data was analysed individually and annually (1st July - 30th June). The outliers were then taken under a closer consideration in QGIS to confirm if it was a true rut excursion. The outliers were considered to be more interesting if they occurred in mid to late October or in the beginning of November. Excursions in late November could be interpreted as a second ovulation (re-rut). Excursions on dates outside the rutting season might be caused by hunting disturbance, if the animal was chased by a dog etc. To ensure that it was a true rut excursion I removed those coinciding with known hunting.

Results

A total of 1,705 females were used in the analyses of ovulation, divided into 362 sub adults, 1,296 adults and 47 senescent individuals. Analyses including bone marrow fat content were based on 14 sub adults, 67 adults and 2 senescent individuals.

Overall did 50% of the does ovulate before October 30, 75% of the does before November 23. Only 27.8% of the females ovulated during the break for the rut in the hunting season (October 21 – November 15) and 69% had ovulated before

the end of the break in the hunting period (Figure 1, Table 1). These results indicate an estimated mean birth date to be June 18.
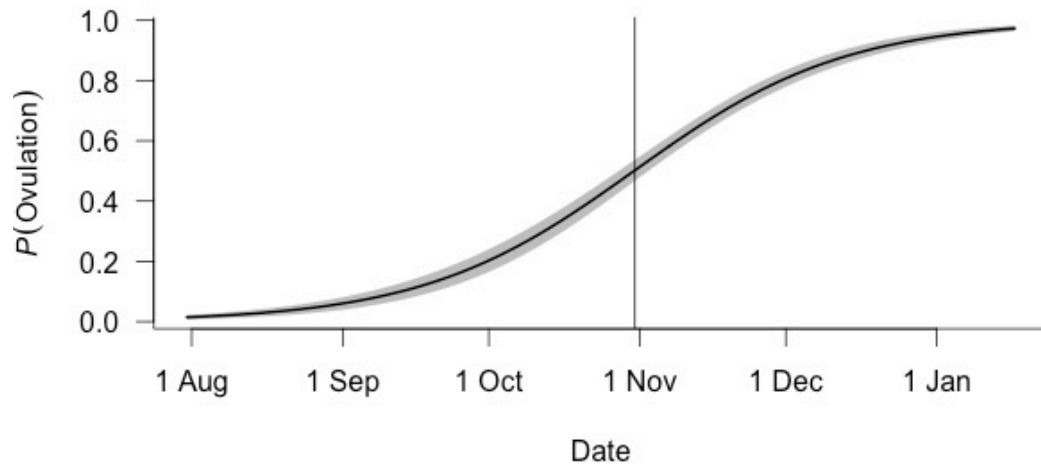

Figure 1. Probability of ovulation in female fallow deer (Logit (Y) = -5.60 (±0.34 SE) + 0.05 (± 0.003 SE) * relative date, p < 0.0001). Before October 30, 50% of the does have ovulated (vertical line). Grey shaded area indicates 95% CI. Data from >1700 killed females at Koberg, Sweden, 2006 - 2015.

Table 1. Yearly variation in ovulation of fallow deer at Koberg estate, Sweden. The date (Ovulation = 0.5) indicate when 50% of the does have ovulated according to modelled probability of ovulation (Appendix 3).

Mean ovulation date									
Year	2006	2007	2008	2009	2010	2011	2012	2013	Mean
Observations	203	315	277	233	137	176	149	136	203.25
Ovulations	161	258	198	165	77	73	101	88	140.13
Ovulating (%)	79.31	81.90	71.48	70.82	56.20	41.48	67.79	64.71	66.71
Ovulation =0.5	7 Nov	18 Oct	1 Nov	20 Oct	12 Nov	22 Nov	2 Nov	6 Nov	3 Nov

In a model that included age groups (sub adults, adults and senescent) as well as relative date, adults were found to be the first to ovulate (reference group, P(ovulation) = 0.5 at October 26), then sub adults (P(ovulation) = 0.5 at November 10) and last senescent (P(ovulation) = 0.5 at November 26; Figure 2).
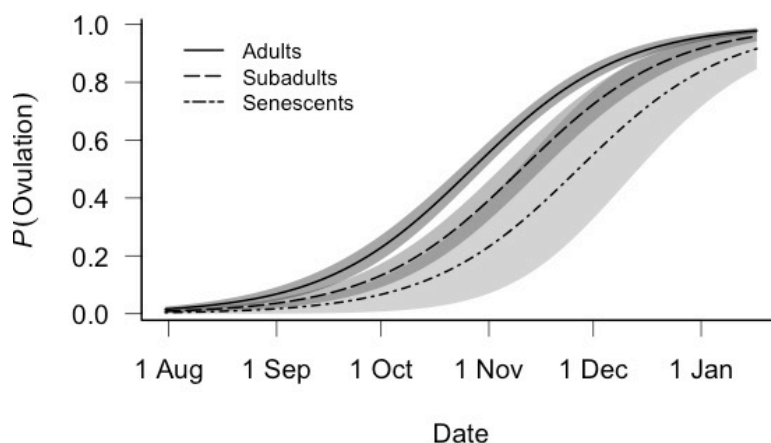

Figure 2. Probability to ovulate in three age classes of female fallow deer; sub adults (<1 year old; β = -0.66, ± 0.16 SE, P < 0.0001), adults (2 - 14 years old) and senescent (≥15 years old; β = - 1.35, ± 0.46 SE, P < 0.004). Shaded area display 95% CI. Data from >1700 killed animals during 2006 - 2015 in Koberg estate, Sweden.

The two different densities were included in the model, showing that the females in the high density area ovulated about two weeks earlier than the does in the low density area (reference area) (Figure 3). Still, females ovulate in the same order (adults first, then sub adults and last senescent). In adults, 50 % of the individuals in the high density area ovulated ≤October 24, compared to ≤November 9, in the area with lower density. In sub adults this date was ≤November 8 in the high density area and ≤November 22, in the area with lower density. In senescent females the dates were ≤November 22 and ≤December 7, for high and low density, respectively.
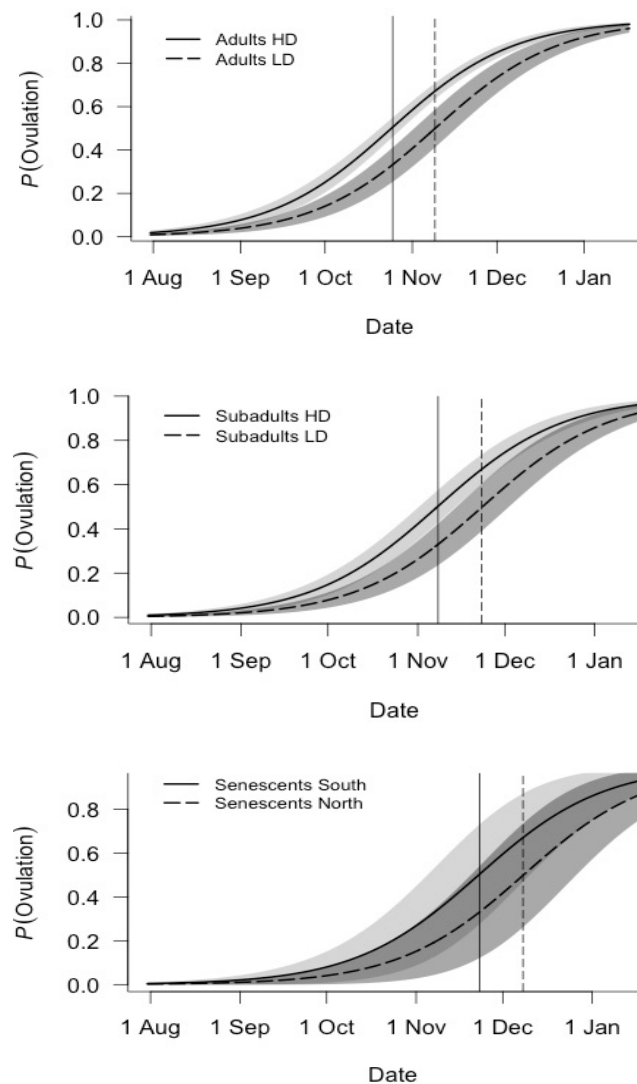

Figure 3. The probability to ovulate in three age classes of female fallow deer; sub adults (<1 year old), adults (2 - 14 years old) and senescent (≥15 years old) depending on density. Does in the high density area (HD) ovulate about two weeks earlier than the does in area with a lower density (LD, reference area) (β = 0.72, ±0.19 SE, P < 0.0002). Grey shaded area indicates 95% CI. The date where 50% of all females have ovulated is indicated by vertical lines. Data from animals shot 2006-2015, Koberg, Sweden.

Table 2. AIC_c selection summary of five models examining the contribution of age (age group), date, body mass/body size (relative weight) and population density for the probability to ovulate. K refers to the total number of parameters (including the intercept). W_i indicate model weight (summing up to 1). Models are ordered in terms of ΔAIC_c (of the best model). Data from 1705 killed female fallow deer collected in Koberg, Sweden, 2006 - 2015.

Model	K	AIC_c	ΔAIC_c	W_i
Date + age group + density	4	1326.23	0	0.999
Date + age group	3	1339.32	13.09	< 0.01
Date + relative weight	3	1349.38	23.15	<0.0001
date	2	1359.59	33.36	<0.0001
relative weight	2	2027.02	700.79	<0.0001
intercept only	1	2073.92	747.69	<0.0001

Table 3. AIC_c selection summary of one model examining the effect of lactation (that the doe has reared a calf during the summer) for the probability to ovulate. Only individuals killed within the first three weeks of the start of the hunting season (12th of October to 7th of November) was included in the analysis. K refers to the total number of estimable parameters (including intercept). W_i indicate model weight (summing up to 1). Models are ordered in terms of ΔAIC_c (of the best model). Data from 377 killed female fallow deer collected in Koberg, Sweden, 2006 - 2015.

Model	K	AICc	ΔAICc	W_i
intercept only	1	464.52	0	0.67
lactation	2	465.90	1.38	0.33

Table 4. AIC_c selection summary of three models examining the effect of age (age group), body mass/body size (relative weight) and population density for the probability to ovulate when the female has reared a calf during the summer. K refers to the total number of estimable parameters (including intercept). W_i indicate model weight (summing up to 1). Models are ordered in terms of ΔAIC_c (of the best model). Data from 377 killed female fallow deer collected in Koberg, Sweden, 2006 - 2015.

Model	K	AIC_c	ΔAIC_c	W_i
relative weight + age group	3	377.56	0	0.78
relative weight	2	380.24	2.68	0.20
intercept only	1	386.24	8.68	0.010
density	2	387.21	9.65	0.006

Body condition

Based on AIC_c, none of the candidate models performed substantially better than the model with intercept only (i.e. none of the explanatory variables had support, see table 5). Bone marrow fat content alone did not seem to significantly affect the probability of ovulation. When including relative body mass in the model, there was a significant relationship between body mass and probability of ovulation. When date was included, body mass lost its importance and the model became non-significant (see Appendix 4 for coefficients). When running a model on only sub adults (sampled from the whole hunting season, n=362) the body mass became more important and remained significant when including the relative date (β = 6.04, ±1.81 SE, P < 0.0001; see Appendix 5 for coefficients).

Table 5. AIC_c selection summary of five models examining the contribution of body condition (i.e. wet bone marrow/dried bone marrow = relative bone marrow), age (age group), body mass/body size (relative body mass) and date for the probability of ovulation. K refers to the total number of estimable parameters (including intercept). W_i indicate model weight (summing up to 1). Models are ordered in terms of ΔAIC_c (of the best model). Built on a subset of 83 killed females of the total data set, by only including individuals with measures of bone marrow fat content, between November 15 - 19. Data from Koberg, Sweden 2006 - 2015.

Model	K	AIC_c	ΔAIC_c	W_i
relative bone marrow	2	44.75	0	0.28
intercept only	1	44.78	0.031	0.28
relative bone marrow + relative weight	3	45.81	1.06	0.17
relative bone marrow + age group	3	46.53	1.77	0.12
relative bone marrow + date	3	46.88	2.14	0.098
relative bone marrow + age group + relative weight	4	48.02	3.28	0.055

Lactating females weigh less than non-lactating (β = -3.13, ±1.13 SE, P < 0.001). Senescent individuals were less likely to lactate, adults used as reference (β = -1.41, ±0.63 SE, P < 0.03). The probability to lactate was not density dependent (β = 0.37, ±0.35 SE, P < 0.30).

Movements

In total, 80 NSDs (net square displacement analysis) were performed and in 20 cases they occurred between October 14 and November 26, defined as an outlier that could be recognized as a possible rut excursion. The later occurring outliers could be a result of a second ovulation (re-rut) since one ovulation cycle is about 3 weeks (Asher 1985). The excursion lasted from 4 to 36 hours (mean= 12.9 ±11.9 SE). The longest excursion was estimated to be 6 km as the straight distance from the centre of the home range used the week prior to the excursion. Four of the NSDs were very typical, where the females were within the same area the whole year except from one movement during the period of October 27 to November 1. Based on NSD, the mean rut of the fallow deer occurs around 21 of October (n= 20 ±14.2 SE). In one case during an excursion in 2010 it was documented that the female (ID 9) likely was accompanying a mature and large GPS-marked trophy male (ID 15) since they were in the same area during the same time.

In 2011, ID 45 (4 yrs. old) had a clear outlier indicated by the NSD (Figure 6a) since two positions during October 31, ranged 2 km from the centre of the home range. The previous or consecutive locations were within the area of her ordinary home range where she is found from July to November. When comparing the NSD with a map (in QGIS) the same pattern of locations and a 2 km excursion directing SW from her ordinary home range occur in October 31 and she stays there for >4 hours, before she returns back to the same spot she started from (Figure 6b).
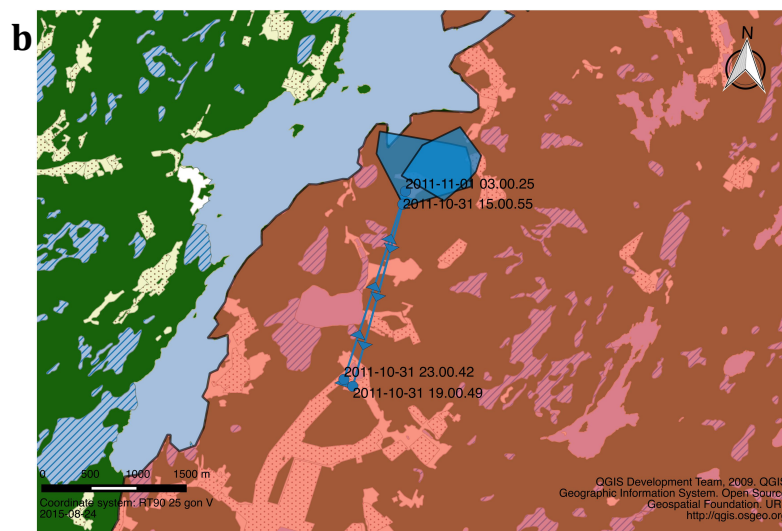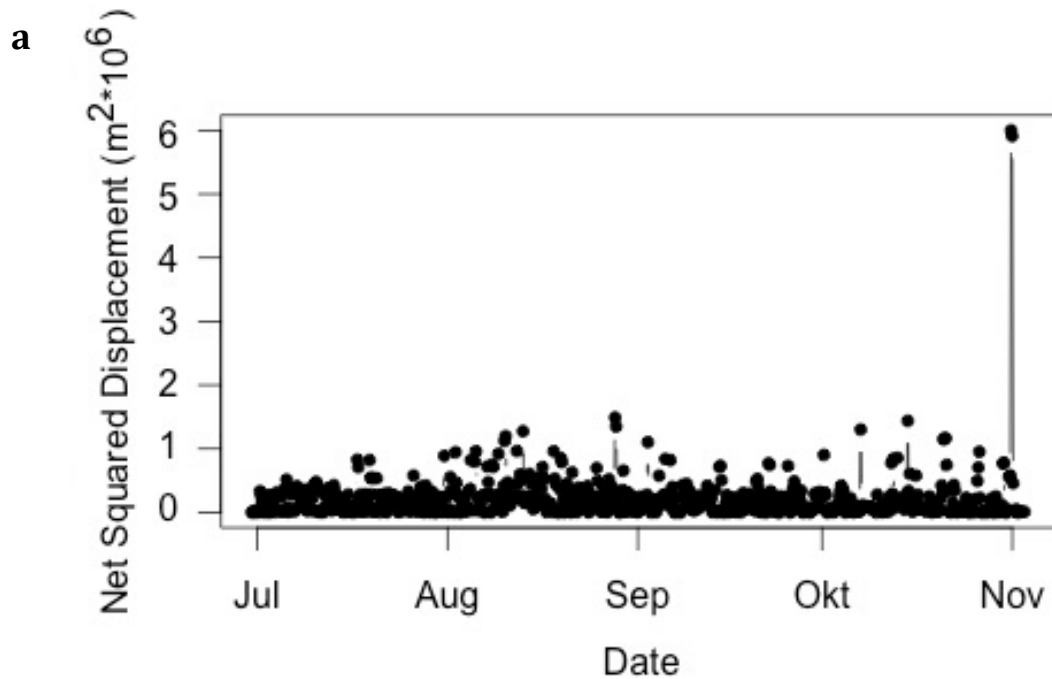
Figure 6. Rut excursion of the GPS-collared female ID45 in 2011: In the afternoon (15.00 hrs) of 2011-10-31, she walks 2 km south out of her home range (blue polygons) and stay there for >4 hours. Then she walks back to her home range and return in the night at 03.00 hrs November 1. Visualized with a NSD (a) performed in R and a map (b) exported from QGIS. Data from the research area (red) at Koberg estate, Sweden.

Discussion

In this study I show that half of the does ovulate before October 30 while the NSD-estimate indicate a mean rut excursion date of October 21. Clutton-Brock et al. (1988) reports about a peak between 24 - 29 of October for fallow deer in southern England. Age class and population density (high vs low) were factors that significantly affect variation in ovulation date and individual body mass was significantly affecting the probability for sub adults and first ovulation. However, body mass was less important in adults and senescent females. Bone marrow fat content showed no significant relationship with the probability to ovulate in either age classes. The probability to ovulate was not found to be affected by lactation. Probably because the females who were lactating during the time of the rut to a high extent consist of prime aged females, who can take the cost of a

yearly reproduction several years in a row. The break in the hunting season, with the purpose to avoid hunting related disturbance during the rut, is in fact protecting close to 28% of the female population in Koberg from such disturbance.

By forward calculating from mean ovulation date, and a gestation period of 231 days (Birgersson & Ekvall 1997), mean fawn birth date is June 18. That is accordance with Kjellander et al. (2012) that report a mean birth date at 23 June for radio collared neonate fawns from the same area. Since 2006, average monthly precipitation for June have varied between 50 - 150 mm and the lowest measured temperatures ranging between 3 - 8°C for Västergötland, Sweden (SMHI 2015). The observed and late mean birth date (compared to other Nordic ungulates) might be because females "buffer" against occasional cold springs, meaning it is more risky to be born too early (and die of hypothermia if it is a rainy and cold spring) (Kjellander et al. 2012) than too late (and not gain enough weight before the winter; Birgersson & Ekvall 1997, Gaillard et al. 1993, Hogg et al. 1992). A question to look into further is if the fallow deer fawns are more sensitive to cold weather compared to fawns of other ungulate species. For instance, roe deer give birth both to smaller fawns and about three weeks earlier than fallow deer, and roe deer fawns do not seem to be affected by cold weather to any large extent.

Why do fallow deer females give birth so late? The time for the fawn to gain in mass before the winter is then very restricted. Even worse if a fawn is conceived during a second, or third, estrus cycle. Fallow deer has been successfully introduced all over the world, to South and North America, Oceania, Asia, Europe and South Africa (Chapman & Chapman 1975), and has adjusted its rut and birth season to the new climatic conditions and seasons (Asher & Kilgour 1985). It is thus clear that the fallow deer is adaptable. The question is why is not the rutting season earlier? Are there possibly other factors working against an earlier birth date? It seems like the species would benefit from an earlier birthing time to access high quality food when the need of energy is at its peak for the females and fawn. One would think that if the small fawn of a roe deer that is born earlier, can survive without dying of hypothermia, should the larger fallow deer fawn, survive too. The males would also benefit from an earlier rut so that they would have a longer time to regain some of the lost weight during the rut, before the winter season. Today their energy reserves are depleted when winter arrives (Monteith et al. 2013).

Females in the southern high density area on average always seem to ovulate earlier than the females in the low density area in the north. This could be interpreted, as in contrast to what we predicted, that females living in areas with a higher population density of adult males stimulate and synchronize and advance ovulation time in the females (Chemineau 1987). Contrary to Langvatn et al. (2004) who showed delayed ovulation in high density red deer populations, probably due to limited resources and declining body conditions.

Adults had the highest probability to ovulate and ovulate earliest in the season. Sub adults ovulated approximately 14 days later, in contrast to Asher & Kilgour

(1985) that found a 7 - 8 day span between the adults and the sub adults. This is in accordance to general life history theory (Stearn 1992) and similar to what is found in other species (Asher et al. 2011, Langvatn et al. 2004). A doe in her prime age will have the highest probability to ovulate. The sample size for senescent females were smaller compared to the other groups (362 sub adults, 1,296 adults and 47 senescent females), and that in combination with high individual variability explains the larger CI. The probability to survive to high age is unfortunately not very high as approximately one third of the population is killed every year, explaining the small sample size in the senescent age class. Still, the trend in every investigated model output shows that senescent females ovulate last and at a lower rate than the two other age classes, just as predicted. This is also expected when comparing to other ungulates (Ericsson et al. 2001, Hewison & Gaillard 2001, Mysterud et al. 2001).

Females that were lactating in the autumn weighed less than females that did not. However, the probability to ovulate was not affected by lactation. This means that a doe that suffered the cost of reproduction from the previous year was equally expected to ovulate the following year as one who had not. Neither did the probability to ovulate depend on the body mass in adults or senescent females while body mass did significantly affect the probability to ovulate in sub adults. Indicating the same pattern as in moose that females needs to reach a certain body mass threshold before ovulating the first time (Sand 1996). This is in contrast to adults in their prime age that seem to be able to reproduce successfully year after year irrespective of body mass.

In this study bone marrow fat content varied between 14.8 and 93.9% with an average of 66.1 % (±13.2% SE). The bone marrow fat content showed no significant relationship with the probability to ovulate. Since body mass did not affect ovulation rate, the bone marrow fat content, should neither. Still, having in mind that it is a fairly small sample size of individuals measured for bone marrow fat compared to the other variables and samples from only a short period (15-19 of November). Bone marrow fat was only sampled the last three years of the study. For the data collected 2014/2015 was only about a third of the samples analysed before the start of this report. Bone marrow fat levels <50% is interpreted as the animals was in poor condition when shot (Ratcliffe 1980). Murray et al. (2006) reports about a starvation threshold at 30 %, if an animal has lower levels than the threshold it is expected to affect survival.

Management implications
The break in the hunting season seems to be well timed with the rut, but a bit too short to include a clear majority of the main rutting season. To cover an even larger part of the rut a prolonged break needs to be considered. To maximize the protective effect of a 25 day long break, it should be advanced four days to last between October 17 and November 11. Interestingly, the result support the observations, made by the game keeper in the area, that the rut seem to be earlier than in the past, when the hunting break was decided in the legislation (A. Friberg pers. comm. 2015). If the pattern is an ongoing process, we might need to advance the break even further in the future.

A bigger and more interesting question is first, how much the hunting is actually disturbing the animals during the rut and secondly, how big part of the population that is supposed to be covered by the hunting break for it to be considered as well adjusted? If the break would be prolonged with one week (to November 23) 75 % of the females would have ovulated before the end of the break. To include all females (100%) the break needs to be prolonged with several months. At what proportion the break should aim is however an ethical question and basically out of the scope of this work.

It is possible to have a productive population with a good harvest policy, resulting in a balanced population where you annually can harvest a large proportion and yet have a positive population growth (Solberg et al. 1999). The question is what eventual genetic variation that might be lost in the hunt that may slow down an eventual adaptation towards an earlier rut and birth season? In heavily harvested populations it is no longer the strongest or fittest that survives longest or necessarily have the highest fitness. Another aspect to consider is if the supplemental winter feeding decrease the selection pressure for earlier births due to effects on the survival for both does, males and calves.

These results can be used by legislators, county officials, hunters and landowners to manage fallow deer populations to a stable and viable resource. For example a higher density (possibly of adult males) will most likely result in earlier born fawns.

Conclusions

The aim of this study was to determine the timing of the fallow deer rut by looking at the time of ovulation and rut excursions in females. Factors that might influence the ovulation were also investigated. The time of ovulation suggest that in Sweden the fallow deer rut occurs around October 30. The rutting excursion gave a mean date of 21st of October. Female age, population density, and for sub adults, body mass, are the main factors identified in this study that determine the variation in timing of the rut. No continuous trend of an advanced mean date of the rut could be detected during the 10 years this study was ongoing.

Acknowledgements

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Fältblankett, Koberg

Skjuten art: **Dovhjort** ☐   **Rådjur** ☐

Djurnr: K -10	Skytt:
Datum:	**Område:**
Jaktsätt:	**Plats/Pass:**

Kön och ålder   **Uppgift om djuret**

Get/Hind

			Ja	Nej	Vet ej
Vuxen	☐	Mjölk i juvret	☐	☐	☐
Kid/Kalv	☐	Åtföljd av kid/kalv	☐	☐	☐
		Antal kid/kalv	☐		

Bock/Hjort

			Fällda	Kvar	Bast
Vuxen	☐	Horn	☐	☐	☐
Kid/Kalv	☐				

	Spets	Stång	Halvskovel	Helskovel
Typ och antal taggar	☐	☐	☐	☐

	Vänster	Höger
Hornlängd (cm)	☐	☐

Mått och vikter   **Insamlat mtrl.**

			Ja	Nej
Helvikt	(kg och hekto)	Livmoder	☐	☐
Passvikt		Äggstockar	☐	☐
Slaktvikt		Käke	☐	☐
Haslängd	(cm)	Vomprov	☐	☐
		DNA	☐	☐

Övrigt (mor/dotter/son till annat fällt djur, ev. märkning, abnormitet mm.)

Lab-data, Grimsö, SLU

Ålder: [ ]   **Käklängd:** [   ] **(mm)**

Metod: Snittning [ ]   Tandväxling [ ]   Slitage [ ]

Antal foster: [ ]

  Kön, foster1: [ ]   **Kön foster 2:** [ ]   **Kön foster 3:** [ ]

  Längd, foster1: [ ]   **Längd foster 2:** [ ]   **Längd foster 3:** [ ] **(mm)**

  Vikt, foster1: [ ]   **Vikt foster 2:** [ ]   **Vikt foster 3:** [ ] **(g)**

Antal ovarier: [ ]

Antal C.L.: [ ]

Appendix 2
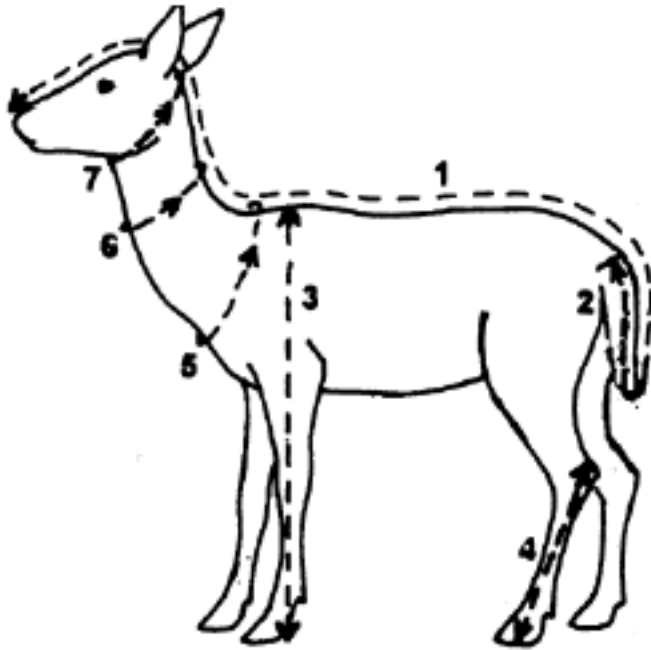
Picture showing how metatarsus (4) was measured (in cm).

Appendix 3

Parameters used for a generalized linear model with the aim to examine the yearly variation of when 50% of the does in Koberg estate, Sweden, have ovulated.

Parameter	B (± SE)	z	p
Intercept	- 6.35 (± 0.48)	-13.11	<0.0001
Relative date	0.046 (± 0.0027)	17.47	<0.0001
Age group – sub adult [1]	- 0.60 (± 0.17)	- 3.56	< 0.0005
Age group - senescence [1]	- 1.46 (± 0.49)	- 2.98	< 0.003
Density – high density[2]	0.60 (± 0.20)	3.04	< 0.003
Hunting.year – 2007/2008[3]	0.87 (± 0.30)	2.87	< 0.005
Hunting.year – 2008/2009[3]	0.35 ((± 0.30)	1.17	0.24
Hunting.year – 2009/2010[3]	0.82 (± 0.30)	2.77	< 0.006
Hunting.year – 2010/2011[3]	-0.14 (± 0.33)	-0.43	0.67
Hunting.year – 2011/2012[3]	-0.66(± 0.32)	-2.05	0.040
Hunting.year – 2012/2013[3]	0.28(± 0.33)	0.84	0.40
Hunting.year – 2013/2014[3]	-0.0054(± 0.33)	-0.016	0.99

1 – Age group "adult" is used as reference
2 – Low density area is used as reference
3 – Hunting year 2006/2007 is used as reference

Appendix 4

Parameters used in a generalized linear model to examine how body condition of the doe affect the probabilty of ovulation.

Parameter	B (± SE)	z	p
Intercept	- 25.73 (± 203.52)	- 0.13	0.90
Relative bone marrow	- 4.76 (± 3.77)	- 1.27	0.21
Relative body weight	3.89 (± 4.37)	0.89	0.37
Age group – sub adult [1]	0.075 (± 1.27)	0.059	0.95
Relative date	0.20 (± 1.47)	0.14	0.89

1 – Age group "adult" is used as reference

Appendix 5

Parameters used in a generalized linear model to examine how body condition
affect the probabilty of ovulation for sub adults.

Parameter	B (± SE)	z	p
Intercept	- 10.94 (± 1.8)	-6.07	<0.0001
Relative body weight	6.04 (± 1.81)	9.13	<0.0001
Relative date	0.046 (± 0.0051)	9.13	<0.0001