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Abstract

The level of neonate mortality in a free ranging fallow deer (*Dama dama*) population at the Koberg estate in south western Sweden was investigated using radio-tracking techniques. During this study a total of 36 fawns (17 ♂, 19 ♀) were captured and marked with vhf or gps radio collars; 12 fawns in 2008 and 24 fawns in 2009. The neonate mortality calculated by the Kaplan-Meier method was 23.6 % and the mortality caused by predation was low, since only 1 of 8 non-surviving fawns died from predation by red fox (*Vulpes vulpes*). The spatial behavior of the fallow deer neonates were examined at two different levels i.e. the habitat selection within their home-range, which would in fact be a selection made by the mother, and the bed-site selection within that habitat. Compositional analysis revealed a significant preference for the habitat classes arable land, pasture and coniferous forest between 5 - 15 m compared to the habitat class young forest. Visibility and canopy cover were estimated for selected and random bed-sites for fawns marked in 2009, and as expected the selected bed-sites showed significantly lower visibility and higher amount of canopy cover than the random sites. However, since there are few predators in this study area and predation pressure is low, this behavior is not connected to actual survival rates in this area, but would rather be an adaption to a previous history of higher predation pressure. This persistence of anti-predator behavior under relaxed selection is referred to as the “ghost of predators past” hypothesis.

Key words: anti-predatory behavior, bed-sites, *Dama dama*, fallow deer, habitat selection, neonate mortality, predation, red fox

Sammanfattning

Dödligheten hos frilevande dovhjortskalvar (*Dama dama*) studerades genom att förse dagsgamla kalvar på Koberg i Västergötland (64° N, 13° E) med radiosändare. Indirekta och preliminära uppgifter, bland annat baserat på material från skjutna djur, tyder på att ca 30 % av de nyfödda dovkalvarna i populationen på Koberg inte överlever sommaren. Inga tidigare studier har gjorts för att säkerställa dessa uppgifter och för att utreda orsaken till denna dödlighet. Syftet med denna studie var därför att undersöka hur många kalvar som dör och varför. Dessutom undersöktes kalvarnas rörelser i landskapet på två skalnivåer; dels habitatvalet inom dess hemområde, dels valet av lega inom det valda habitatet.

Dovhjorten är ett flockdjur och är starkt knuten till öppna marker. Arten är med människans hjälp spridd över hela världen och anses ha kommit till Sverige på 1570-talet. Brunsten infaller i oktober-november, och kalvningen sker i mitten av juni till mitten av juli. Innan kalvning drar sig hinden undan från kärnflocken och föder oftast endast en kalv. Den nyfödda kalven ligger den första tiden still i sin lega och besöks bara av hinden under digivningen. Eftersom de nyfödda kalvarna är känsliga för fukt och kyla samt utsatta för predation, anses valet av habitat samt val av lega vara viktigt för överlevnaden.

Totalt 36 kalvar (17 ♂, 19 ♀) märktes med radiosändarhalsband i den här studien; 12 kalvar under sommaren 2008 och 24 kalvar under sommaren 2009. Dödligheten för dessa kalvar uppgick till 23,6 %. En av de 8 kalvar som dog under studien blev dödad av rödräv (*Vulpes vulpes*), 6 dog av svält och för en kalv är dödsorsaken okänd. Kalvarnas habitatval analyserades genom att jämföra de erhållna positionerna med mängden tillgängligt habitat inom dess hemområde. Resultatet visade att habitatklasserna 'odlad mark', 'betesmark' och 'barrskog 5 – 15 m' föredrogs framför 'ungskog'. På grund av att få kalvar dog samt dog relativt tidigt i studien kunde dock inte överlevande och döda kalvars habitatval jämföras med någon statistisk säkerhet. Att hindarna till stor del väljer att "lägga" kalvarna på öppna marker kan bero på att de vill ha en bra överblick för att tidigt kunna upptäcka potentiella predatorer.

Under sommaren 2009 undersöktes även kalvarnas val av lega. Kalvarnas skydd från sidan och uppifrån uppskattades för de verkligt valda legorna samt för parvis slumpade legor inom samma habitat. Resultaten visar att kalvarna valde legor med bättre skydd både från sidan och uppifrån än de slumpvis valda legorna. Däremot hittades inga statistiskt säkerställda skillnader i val av lega mellan de döda och de överlevande kalvarna. Då valet av lega inte påverkade överlevnaden i den här studien samt eftersom antalet rovdjur i studieområdet är lågt kan detta beteende att välja bra skydd, tolkas som en tidigare (evolutionär) anpassning till en miljö med fler och delvis andra rovdjursarter.

Denna studie ingår i ett större forskningsprojekt vid Grimsö forskningsstation (SLU) med syfte att studera konkurrenssituationen mellan dovhjort och rådjur samt ta fram ny kunskap om dovhjortens ekologi.

Nyckelord: *Dama dama*, dovhjort, habitatval, legor, neonatal dödlighet, predation, rödräv

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Introduction

An understanding of mortality patterns, and especially the variation in juvenile mortality, is an important component in vertebrate population dynamics (Gaillard et al. 1993, Aanes & Andersen 1996; Van Moorter et al. 2009). Ungulate species generally show a U-shaped mortality curve with the highest mortality occurring at early and late periods of life (Caughley 1966) and the rate of neonate mortality in temperate ungulates sometimes exceeds 50 % (Linnell et al. 1995, Aanes & Andersen 1996, Jarnemo et al. 2004). This first summer mortality can be caused by disease, starvation, hypothermia, parasites and accidents, but in areas where predators are present, the number one mortality factor for neonate ungulates is predation (Linnell et al. 1995).

Due to the high risk of predation, neonate ungulates and their mothers have evolved a range of anti-predator strategies (Lent 1974, Ciuti et al. 2006, Bongi et al. 2008). Based on the type of mother-infant relationship, most ungulate species can be categorized as either a “hider-” or a “follower”-type (Lent 1974). In species categorized as hidiers, the mother and the infant stay separated and out of contact for long periods of time, during which the infant stays hidden in the vegetation. Most species of cervids fall into this category, as well as gazelles and many antelope species, even though the hiding phase can vary in time from 2-3 days in some species e.g. Siberian ibex, Mouflon and Red deer, to 2-4 months in others e.g. Uganda kob and Reedbuck (Lent 1974). In follower type species, the newborn actively follow their mother and they maintain a close and frequent contact from the start. Many of the follower species are seasonal movers, associated to grassland or tundra habitats e.g. the caribou and the muskox (Lent 1974, Lent 1991). This strategy provides protection against predators by allowing the mother and fawn to remain in a group, relying on group defense and permitting extensive movements (Lent 1991). In case of relaxed selection because of the loss of one or more predator species, anti-predator behavior like these can still persist, which is referred to as “the ghost of predators past” hypothesis (Byers 1997a, Blumstein et al. 2006).

The fallow deer (*Dama dama*) is classified as a hider-species, since the fawns lie hidden for their first few days in life (San José & Braza 1992, Ciuti et al. 2006). The mother stays within hearing distance of her fawn and visits several times per day to feed and groom it (Chapman & Chapman 1997). Since a secluded bed-site is the main protection for these fawns, bed-sites could be expected to be selected thoroughly in order to provide good cover. Even though the change of hiding place is typically initiated by the female, the exact position of the actual bed-site is chosen by the fawn (Lent 1974, Heugel et al. 1986). Bed-site selection by fawns of other hider-type species e.g. roe deer (Linnell et al. 1999, Bergman 2006) and white-tailed deer (Heugel et al. 1986) has been examined in earlier studies, however, this behavior has not yet been studied in fallow deer.

As well as being a protection against predators, the use of cover and the importance of bed-site selection can also be expected to be affected by climatic factors (Heugel et al. 1986, Myrsterud & Østbye 1999). Ungulate neonates are known to be vulnerable to cold and wet weather, and the main cause of non-predator mortality in the review of Linnell et al. (1995) was starvation/hypothermia. The lack of shelter from high rainfall is thought to be the reason for the high neonate mortality recorded for fallow deer kept in open paddock conditions on deer farms (Putman et al. 1996). Thus, at a higher level, the selection of main habitat types might be very

important since different habitats may provide different opportunities for the fawns to choose a protected bed-site.

There are many factors affecting habitat selection among herbivores, such as food quality and abundance of forage, availability of shelter and cover from predators, but also social structure and population densities (Putman 1988, Sinclair et al. 2006). Furthermore, the presence of fawns may lead to changes in social behavior and space-use of calving females (Ciuti et al. 2006, Bongi et al. 2008). Ciuti et al. (2006) showed that female fallow deer in Italy adopt an anti-predator behavior in their habitat selection, since calving females to a higher extent used sub-optimal habitats that offered the best cover and thereby reducing the predation risk for their fawns, compromising their own energy intake. In order to be close to their fawns, calving females also reduced the size of their home ranges, using areas between two or three times smaller than the areas used by non-calving females (Ciuti et al. 2006).

The fallow deer is, due to human activities, widely distributed all over the world and can be found in many different types of habitats (Chapman & Chapman 1997). They commonly browse trees and shrubs and seek shelter in woodlands, even though they are predominantly grazing animals feeding in fields and pastures. Fallow deer are gregarious and form herds, which can vary in size and composition with the time of year and between different localities (Chapman & Chapman 1997). The adult males live most of the year in bachelor groups, while female herds include adult females, yearlings and fawns (Chapman & Chapman 1997). The rut occurs in October - November and in mid June to mid July female fallow deer usually give birth to a single fawn, after isolating herself from the core group a few days earlier (Carlström & Nyman 2005). Although the degree and duration of isolation before parturition varies, maternal isolation is considered essential for mother-infant bonding in many ungulate species (Lent 1974, Ozoga et al. 1982).

Despite the fact that the fallow deer is one of the most widely distributed species of deer in the world (Chapman & Chapman 1997), relatively little research has been done regarding the ecology of the species (Borkowski & Pudelko 2007), and especially on free ranging fallow deer in Sweden (Carlström & Nyman 2005). The species was first introduced to Sweden in the 1570s and is now well-distributed in the form of scattered occurrences over the southern part of the country (Carlström & Nyman 2005). With an increasing population, the need of good management plans increases, and an important part of population dynamics is the understanding of mortality patterns. Preliminary and indirect data, based on harvested females and the difference in the proportion of females with fetuses in the spring and the proportion of lactating females next fall, indicates that approximately 30 % of neonate fallow deer in a population at Koberg in south western Sweden does not survive their first summer (P. Kjellander unpubl. data). No previous studies have been made to verify this information and to investigate the cause of this neonate mortality.

The aims of this study were therefore to investigate (i) the level of neonate mortality in a free ranging fallow deer population in Sweden; (ii) the habitat selection, made by the mother, and (iii) the bed-site selection of the fawn and the importance of these factors for the survival of the neonates.

In the context of these aims I made the following predictions;

Prediction 1 – as a consequence of the hiding strategy adopted by the fallow deer fawns and in accordance with other studies of bed-site selection in hider type species (Linnell et al. 1999,

Huegel et al. 1986), I expected the fallow deer fawns to select bed-sites that provided more cover and better concealment than random sites.

Prediction 2 - because of the anti-predatory origin of the hider strategy and the sensitivity to thermal conditions seen in ungulate neonates (Lent 1974, Linnell et al. 1999, Putman et al. 1996), I also predicted bed-site selection to affect fawn survival e.g. I expected the surviving fallow deer fawns to have chosen bed-sites with better cover and concealment compared to the non-surviving fawns. However, since the predation pressure at the current study site is not expected to be very high, I discuss my results in the context of the “ghost of predators past” hypothesis (Byers 1997a) stating that anti-predator behavior can be retained after the loss of predators, if it is not too costly (Blumstein et al. 2006).

Material and Methods

Study area

This study was performed at the Koberg estate (64° N, 13° E) in south-western Sweden (Västra Götaland County). The study area (54.35 km²) is mostly covered of different types of forest (79 %), and the remaining area constitutes of arable land and pastures (16 %), mires and marshes (2 %), lakes, ponds, parks and properties around houses (3 %). The two most common habitat types are coniferous forest > 15 m (29 %) and coniferous forest 5 - 15 m (15 %)(Winsa 2008). The open landscape at Koberg, arable land and pastures, are today to large extent cultivated in order to improve wildlife habitats, and supplementary food are also given during wintertime to ensure large and viable populations of deer in the management area. Free ranging fallow deer has been present in the area since the release of a few animals (approximately 20) from an enclosure in the end of the 1920's (Count Niclas Silfverschiöld unpubl. data). In 2006, the fallow deer population in the study area was estimated to 327 animals/10 km² (Rydholm 2007). Other ungulates occurring in the area are roe deer (*Capreolus capreolus*), moose (*Alces alces*) and wild boar (*Sus scrofa*) and occasional observations of red deer (*Cervus elaphus*). Controlled hunting is performed each fall and potential predators present in the area are the red fox (*Vulpes vulpes*) and occasional visits of lynx (*Lynx lynx*).

Data collection (Deer capture and tracking)

Data used in this study was collected during the summers of 2008 and 2009. Fallow deer fawns were caught, mostly by searching the near surroundings of females that were observed standing by themselves, or waiting for females to visit their hidden fawns and move in after the mother had left and the fawn bedded again. Alternatively, when a female and her fawn were seen moving together and there was a risk of losing sight of the fawn, they could be approached, causing the mother to run away and the fawn to adopt a prone position. The fawns were caught by hand or with landing nets. Sex and body mass of the fawns were determined at capture together with other measurements such as length of metatarsus, heart girth and body temperature (Appendix 1). The fawns were ear-tagged with coloured plastic tags and equipped with a radio-transmitter attached to an expandable collar with drop-off function. In 2008, 15 fawns were caught; 12 were fitted with VHF transmitters (Televilt, Lindesberg Sweden) and 3 only ear-tagged. In 2009, 24 fawns were caught and this year marked with either a traditional VHF (n = 21) or a VHF/GPS transmitter (n = 3; Telemetry solutions, Concord, California USA). GPS transmitters were programmed to take one position every hour. All transmitters were equipped with a mortality function (motion-sensitive). Fawn age at capture was estimated

based on a number of characteristics, such as the texture of the fur, the status of the umbilical cord, hoof abrasion and the behavioural reactions of the fawn during capture, handling and release (Galli et al. 2008).

Fawn survival was normally checked daily for up to 4 weeks of age, until mid July, then once a week until mid September. Fawns were located using three element yagi antennas and receivers. The locations of the fawns were calculated by triangulation using bearings from three or four reference points. If a fawn was observed during radio tracking the observed position was used, however, if marked fawns were accidentally seen in the study area, the position was not included in the analysis in order to avoid bias towards open areas where the fawns obviously are more easily observed than in closed forests. In order to establish and categorise the cause of death a procedure was followed where location of the found collar or the dead fawn was investigated for markings or other signs of predation and finally the dead fawns were necropsied and investigated for bite marks, signs of diseases etc.

Bed site selection

Data on bed-site selection was collected from 21 June to 14 July 2009, for fawns marked during the same period. Each fawn was radio-tracked and carefully approached in order to localise their exact bed-site. The location of the bed-site was noted with a hand held GPS, marked with a plastic strip and examined the following day(s) when the fawn had moved to another location. For each bed-site a random bed-site was selected using a random table where direction and distance from the actual bed-site was given. An inflated basket ball representing the fawn was placed in the bed-site and approached from each of the four cardinal directions. Starting from a maximum distance of 50 m, the distance from which the “fawn” was first detected at a height of 50 cm from the ground was recorded. Canopy cover above the bed-site was estimated in percent from a height of approximately 1.5 m and a short description of the bed-site was made. The same procedure was repeated for the randomly selected bed-site.

The habitat type around the bed-site was categorized as: arable land, pasture, overgrown land, mire/bog, forest, grove or clear cut (Appendix 2). Forest was further categorized into age/height classes: plantation: less than 1 m; young forest: 1.1 to 2 m; young forest: 2.1 to 5 m; thinned out forest: 5.1 to 15 m and older forest: higher than 15 m and the most common tree species were noted. The area within 5 m in both directions from the edge between two habitat types was also classified as edge zone. These categories were later combined and modified depending on utilisation to match the categories obtained from a satellite generated map (SMD; see the section on data analysis of habitat use). In order to do a correct comparison between the selected and the randomly chosen bed-site, they had to be situated in the same habitat type or forest stand. In case the random distance reached out of the current habitat the remaining distance were measured back from the border of the habitat towards the selected bed-site.

Data analysis

Mortality

Fawn mortality was estimated by the Kaplan-Meier method (Pollock et al. 1989) for the first 70 days of age, on data from both years. This method allows for animals to enter the study at different times, since the estimated birth date is set as day 1 for all fawns. Differences in survival rates between male fawns and female fawns were tested for with logrank (Mantel-Cox) test.

Habitat use

The marking positions of each fawn were not included in the habitat-use analysis, since most of the fawns were found in open areas, due to a higher level of visibility in such habitats. The data on fawn positions were analysed in Arc GIS 9.3. A satellite generated digitalized map, "Svensk marktäckedata" (SMD), with a 25×25 m pixel resolution was used to define each habitat. Fawn-positions that ended up between two habitats were randomly moved into one of the two neighbouring habitats. The habitat type "lakes and ponds, open surface" was not considered available habitat and therefore removed from further analysis.

Home ranges were calculated with the minimum convex polygon method (MCP) using the extension Hawth's Tools. Random points were then generated within each home range in order to estimate the habitat availability for each fawn. The habitat use within the MCP home range was analysed with compositional analysis (Aebisher et al. 1993) in the software Resource selection (Resource selection for Windows, version 1.00 Beta 8.1, 1999 Fred Laban). To reduce the number of habitat types for the compositional analysis, similar and rare habitat categories were combined as follows (referring to the numbers of the original habitat category according to SMD): arable land (ARABLE)(30), pasture (PASTU)(5 and 32), clear-felled area: forest up to 2 m (CLEAR)(54), younger forest: between 2-5 m (YOUNG)(55) mixed forest higher than 5 m (MIXED)(40 and 48), coniferous forest 5-15 m (CON 5)(43, 44 and 47), coniferous forest higher than 15 m (CON 15)(45) and wet areas (WET)(46, 49 and 72). Since compositional analysis require no missing values for either habitat use or habitat availability, missing values were replaced with 0.001. Fawns with less than 15 positions were not included in the habitat-use analysis. Hence, only data from 14 fawns from both years could be used, since many of the fawns died or lost their collars too early. Because of the fact that fawns died before I acquired enough positions I was unable to calculate home ranges and test for differences in habitat choices between surviving and dead fawns. Even though I am referring to the positions and habitat use of the fawns, this selection, as discussed earlier, is in fact made by the fallow deer female.

Bed-site selection

The mean distance (of the four cardinal distance measures) at which the model fawn was detected was used as a measure of visibility. Differences in visibility between the selected bed-sites and random bed-sites, between individual fawns, fate (dead or alive) and between different habitats were tested for with a repeated measure analysis of variance (repeated ANOVA). Results are presented as means with standard deviation, if not otherwise specified. In order to analyse data on canopy cover which were recorded in percent, an arcsine-sqrt ($y = \sqrt{\sin^{-1} x}$) transformation was required (Krebs 1999). The transformed values on canopy cover were then tested in the same way as the data on visibility. The presented means (with sd) are nevertheless based on the original, non transformed data. Differences in bed-site selection between surviving and non surviving fawns were tested for with repeated ANOVAs and logistic regressions.

Results

A total of 39 fawns (18 ♂, 21 ♀) were captured and marked during this study; 15 fawns in 2008 and 24 fawns in 2009 (Table 1). In 2008, 3 fawns were only ear-tagged and they could therefore not be included in the mortality calculations. Thus, out of a total of 36 fawns (17 ♂, 19 ♀) 8 fawns died, of which 5 were males and 3 females. The cumulative mortality according to the Kaplan-Meier analysis was 23.6 % (± 0.07 SE) for all fawns. Even though not significantly different, the mortality was 16.4 % (± 0.08 SE) in females and 32.1 % (± 0.1 SE) in males ($\chi^2 = 1.2$, $df = 1$, $P = 0.27$), (Figure 1). The 23rd of June (± 5.0 days) was the mean birth date for the marked fawns. During this study, the death of 1 fawn could be assigned to red fox predation, since the collar was found with bite marks and traces of blood, smelling of red fox urine. Six fawns died from starvation and 1 of unknown causes.

Table 1. Numbers, sex and mortality of neonate fallow deer fawns marked at Koberg in south western Sweden in 2008 and 2009.

	2008	2009	both years
No. marked	*15	24	39
Males	6	12	18
Females	9	12	21
No. dead	3	5	8
Males	1	4	5
Females	2	1	3

* 3 fawns in 2008 only ear-tagged; 1 male and 2 females.

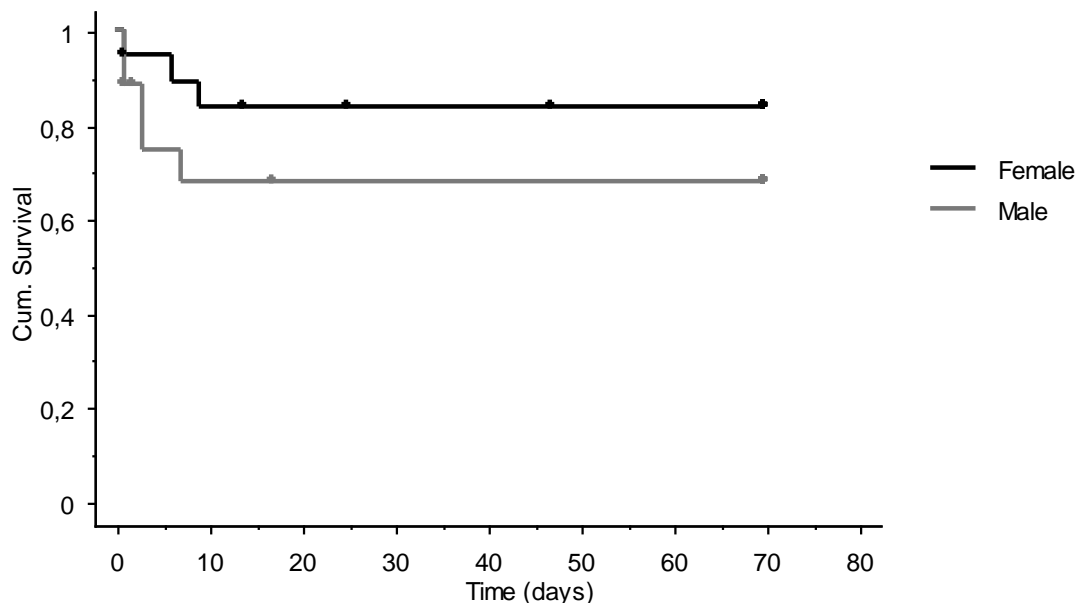


Figure 1. The cumulative survival of fallow deer neonate females (n = 19, black line) and males (n = 17, grey line) at Koberg, Sweden, during their first summer in life. + indicates censored animals, i.e. individuals lost to the study due to dropped collars. Data from neonates marked in 2008 and 2009.

Habitat use

According to the compositional analysis, the habitat use of the fawns at the home range scale differed significantly from random ($\chi^2 = 14.65$, $df = 7$, $P < 0.05$). The habitat classes arable land (ARABLE), pasture (PASTU) and coniferous forest between 5 - 15 m (CON 5) were significantly more preferred ($t > 2.28$; $P \leq 0.04$; $df = 13$ in all cases) than young forest (YOUNG) (Figure 2).

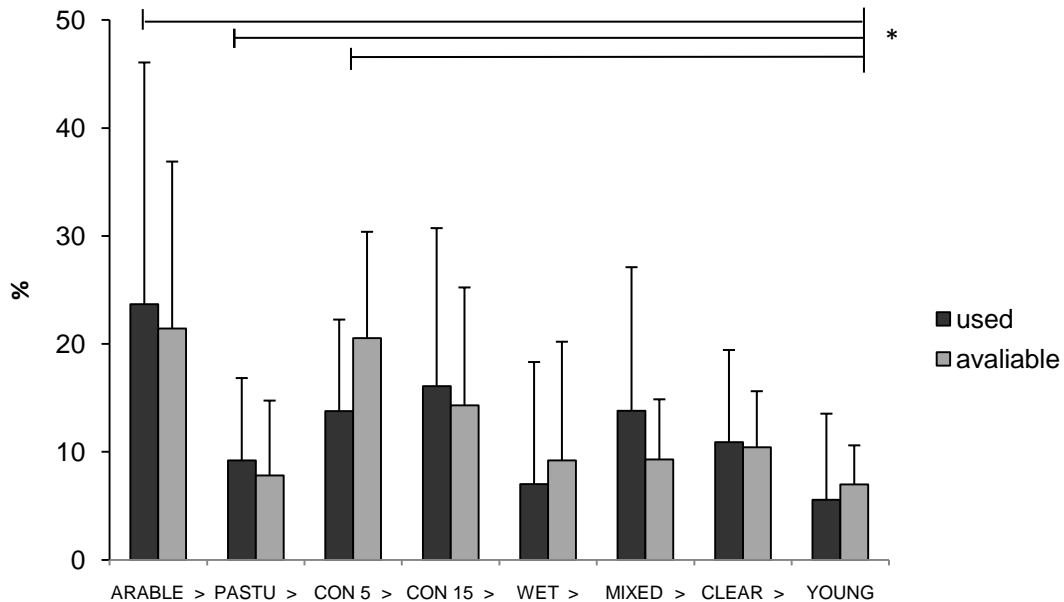


Figure 2. Habitat selection by fallow deer fawns (*Dama dama*) (\pm sd). Habitat classes to the left of the symbol > are selected over those to the right. * = $P < 0,05$ (compositional analysis) indicate significant differences between those habitat classes connected by a line. ARABLE = arable land; PASTU = pasture; CON 5 = coniferous forest 5 – 15 m; CON 15 = coniferous forest higher than 15 m; WET = wet areas; MIXED = mixed forest higher than 5 m; CLEAR = clear felled areas, forest up to 2 m; YOUNG = young forest, 2- 5 m.

The differences in habitat selection by surviving and non surviving fawns were not testable due to the low sample size. However, based on the few obtained positions from the non surviving fawns it seems like these fawns over-utilize ARABLE, YOUNG and CON 15, compared to the amount of available habitat (Table 2). According to the measurements of visibility and canopy cover at random bed-sites in the different habitat types, ARABLE has low visibility (4.6 ± 7.8 m), but also low amount of canopy cover (0.6 ± 0.5 %). The habitat type YOUNG has low visibility (4.3 ± 1.6 m) and a high amount of canopy cover (23.4 ± 47.8 %) and CON 15 has a high visibility (15.4 ± 9.0 m) and a low amount of canopy cover (4.1 ± 10 %). Since these habitats are also used by the surviving fawns, I did not find any results indicating that the non surviving fawns differed in their habitat use from the surviving.

Table 2. Habitat use of fallow deer fawns within their home range (MCP), based on radio-tracking positions during the summers of 2008 and 2009 at Koberg in south western Sweden. Overall use based on positions from 14 surviving fawns with a minimum of 15 positions. “Use by non-surv. fawns” based on 16 available positions obtained from the 8 fawns that died in both years. The “environmental variables” presented (mean visibility and mean canopy cover) for each main habitat type gained from measurements of randomly selected bed-sites in 2009. Since no bed-sites were situated in habitat type “wet areas”, these values are missing (NA).

Habitat	Habitat use within home range			Environmental variables	
	Available (%)	Surv. fawns (%)	Non-surv. fawns (%)	Mean habitat visibility (m)	Mean canopy cover (%)
ARABLE	21.4	23.7	31.3	4.6	0.6
PASTU	7.8	9.2	0.0	4.2	0.6
CLEAR	10.4	10.9	0.0	5.6	0.2
YOUNG	7.0	5.6	18.8	4.3	23.4
CON 5	20.5	13.8	0.0	10.0	24.2
CON 15	14.3	16.1	25.0	15.4	4.1
MIXED	9.3	13.8	12.5	7.3	6.3
WET	9.2	7.0	0.0	NA	NA

Bed-site selection

A total of 77 bed-sites from 23 marked fawns in 2009, 1-5 bed-sites for each fawn, was visited and measured during this study (1 fawn lost its collar during the first 24 hours).

Out of 77 bed-sites, 25 (32.5 %) was situated in the habitat class ARABLE, 19 (24.7 %) in CON 15 and 12 (15.6 %) in MIXED (Table 3). YOUNG, CON 5 and PASTU had the least number of bed-sites (6.5 % in each habitat type). 6 bed-sites (7.8 %) were situated on CLEAR and no bed-sites were found in WET. Of all bed-sites, 12 (15.6 %) were also situated in an edge zone, i.e. within 5 m of another habitat type, mostly between forest and open field. 3 bed-sites on ARABLE were situated within the edge of some kind of forest. 8 bed-sites in forest were situated within the edge of ARABLE; 4 of the bed-sites in CON 5, 1 in CON 15, 3 in MIXED. One bed-site on CLEAR was situated in the edge zone of ARABLE.

The habitat ARABLE was most used for bed-sites by surviving fawns (30.3 %), as well as for the fawns that did not survive (45.5 %)(Table 3). This habitat had the lowest canopy cover (4.8 % at the selected bed-sites), but also a low visibility (3.1 m).

Table 3. Bed-site selection of fallow deer fawns at Koberg in south western Sweden, during the summer of 2009. Based on a total number of 77 selected bed-sites from 23 marked fawns (+ 77 random bed-sites). Alive fawns: n = 18; dead fawns: n = 5. Relative (%) habitat use is indicated within brackets.

Habitat	Selection of bed-sites				Environmental variables			
	Total number	%	Surv. fawns	Non-surv. fawns	Mean visibility (m)		Mean canopy cover (%)	
					Selected bedsites	Random bedsites	Selected bed-sites	Random bed-sites
ARABLE	^{*)} 25	32.5	20 (30.3)	5 (45.5)	3.1	4.6	4.8	0.6
PASTU	5	6.5	4 (6.1)	1 (9.1)	1.7	4.2	24.6	0.6
CLEAR	^{*)} 6	7.8	6 (9.1)	0	1.3	5.6	34.5	0.2
YOUNG	5	6.5	5 (7.6)	0	2.4	4.3	47.8	23.4
CON 5	^{†)} 5	6.5	2 (3.0)	3 (27.3)	8.2	10.0	58	24.2
CON 15	^{†)} 19	24.7	18 (27.3)	1 (9.1)	6.9	15.4	29.8	4.1
MIXED	^{†)} 12	15.6	11 (16.7)	1 (9.1)	4.3	7.3	30.2	6.3
WET	0	0	0	0	NA	NA	NA	NA
Total	77	100	66 (100%)	11 (100%)				

^{*)} 3 bed-sites on arable land were situated in the edge zone (within 5 m) of forest

^{†)} 1 bed-site on clear cut was situated in the edge zone (within 5 m) of arable land

^{†)} 8 bed-sites in forest were situated in the edge zone (within 5 m) of arable land

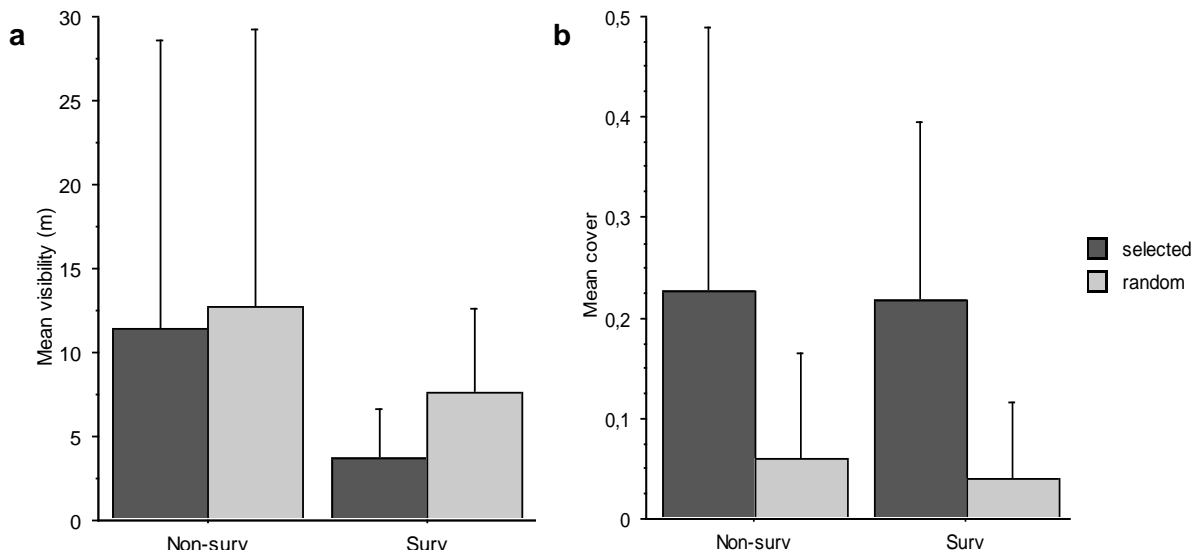


Figure 3. Mean bed-site visibility (a) and cover (b) of the selected (dark grey) and random bed-sites (light grey) of 18 surviving (Surv) and 5 non-surviving (Non-surv) fallow deer fawns (\pm sd) at Koberg in south western Sweden, in the summer of 2009.

Visibility

There was a significant difference in visibility between bed-sites of the individual fawns (min: 1.4 ± 0.5 m; max: 41.6 ± 0 ; $F = 4.15$, $df = 22; 54$, $P < 0.0001$) and the selected bed-sites showed significantly lower visibility (4.29 ± 6.0 m) than the random bed-sites (8.07 ± 8.3 m; $F = 31.8$, $df = 1; 22$, $P < 0.0001$).

I did not find any significant difference in visibility between bed-sites of surviving and non surviving fawns ($F = 2.45$, $df = 1; 21$, $P = 0.13$; Figure 3a). However, the logistic regression indicates a negative effect of visibility on fawn survival, for both selected (LL = 10.65; $R^2 = 0.12$; $n = 23$; $\beta: -1.92 \pm 0.71$ (SE); $\chi^2 = 7.2$; $P = 0.007$; 0.11 ± 0.09 (SE); $\chi^2 = 1.42$; $P = 0.23$) and random bed-sites (LL = 11.52; $R^2 = 0.05$; $n = 23$; $\beta: -1.87 \pm 0.77$ (SE); $\chi^2 = 5.88$; $P = 0.01$; 0.06 ± 0.06 (SE); $\chi^2 = 1.18$; $P = 0.28$). Even though low explanation rate, a low visibility seems to increase the chance of survival for the fawns (Figure 4).

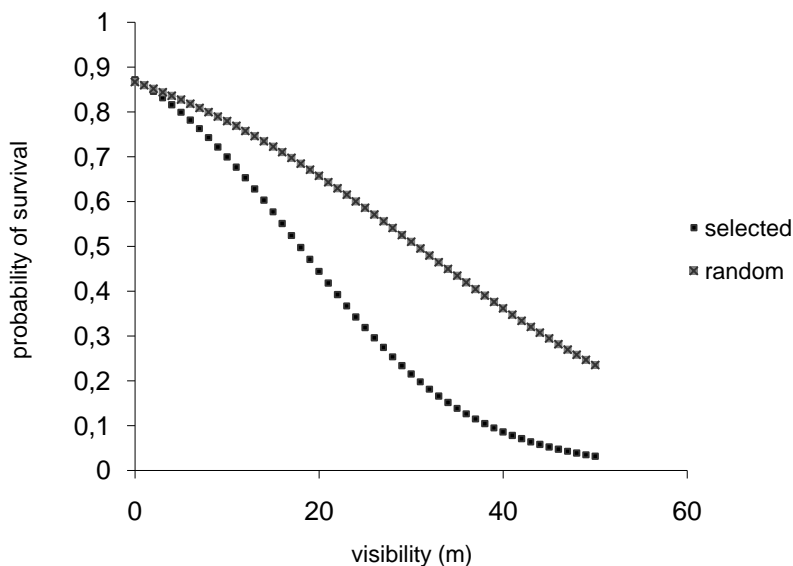


Figure 4. Probability of survival for fallow deer neonates depending on visibility in selected and random bed-sites. The predicted values are calculated from a logistic regression model with data from Koberg, Sweden, 2009.

The visibility of the bed-sites differed significantly between habitat types ($F = 3.28$, $df = 6; 70$, $P = 0.007$). Even though the habitat category CON 15 was the second most chosen for bed-sites, the visibility in this habitat, based on random bed-sites, were the highest with a mean of 15.4 ± 9.0 m (Figure 6; Table 3). However, the selected bed-sites in CON 15 had a mean visibility of 6.9 ± 4.5 m, which was lower than the mean visibility for the selected bed-sites in CON 5 (8.2 ± 8.5 m). The habitat classes with the lowest visibility were ARABLE (4.6 ± 7.8 m), PASTU (4.2 ± 3.0 m) and YOUNG (4.3 ± 1.6 m).

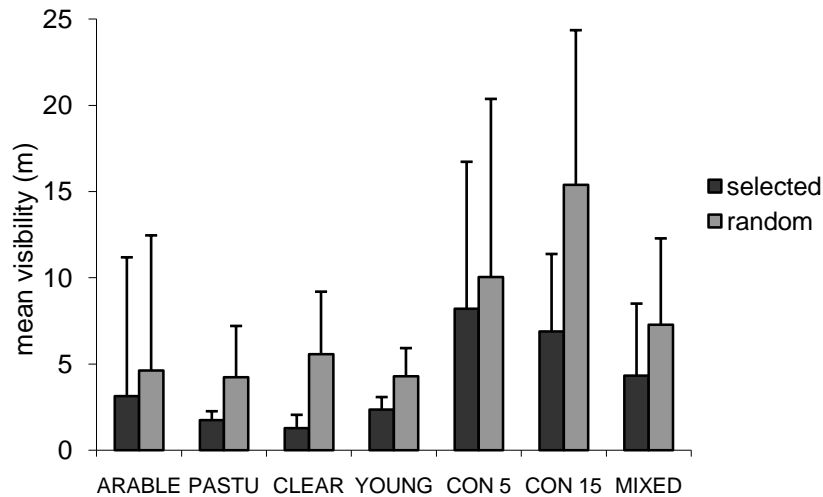


Figure 6. Mean visibility of selected bed-sites compared to mean visibility of random bed-sites (\pm sd) of each main habitat type for fallow deer fawns (*Dama dama*) in south western Sweden, during summer 2009.

Canopy cover

I did not find any difference in canopy cover between bed-sites of surviving and non surviving fawns ($F = 0.06$, $df = 1$; 21, $P = 0.8$; Figure 3b) but the selected bed-sites had a significantly better cover (24.8 ± 32.3 %) than the random bed-sites (5.3 ± 17.3 %; $F = 36.2$, $df = 1$; 22, $P < 0.0001$; Figure 3b). The amount of canopy cover differed significantly between habitats ($F = 4.03$, $df = 6$; 70, $P = 0.002$; Figure 7) and ARABLE, PASTU and CLEAR had almost no canopy cover at all at the random sites, with a mean cover of below 1 % (ARABLE: 0.6 ± 0.5 %; PASTU: 0.6 ± 0.5 %; CLEAR: 0.2 ± 0.4 %). However, the measurements from the selected bed-sites revealed that the fawns still managed to find some cover in those habitats as well (ARABLE: 4.8 ± 7.8 %; PASTU: 24.6 ± 38.7 %; CLEAR: 34.5 ± 40.5 %). The best cover at the random sites was found in YOUNG (23.4 ± 47.8 %) and CON 5 (24.2 ± 58 %), but at the selected bed-sites the amount of canopy cover exceeded 24 % in all habitats, except ARABLE.

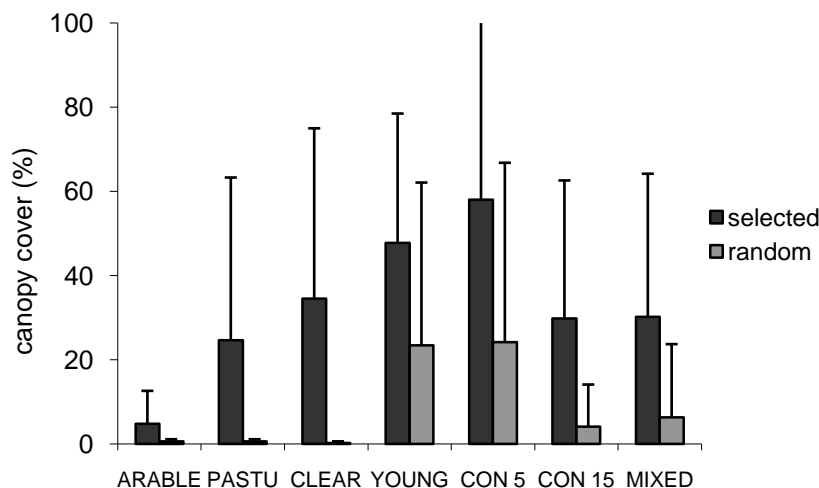


Figure 7. Mean canopy cover of selected bed-sites compared to random bed-sites (\pm sd) of each main habitat type for fallow deer fawns in south western Sweden, during summer 2009.

Discussion

The neonate mortality of fallow deer in this study was 23.6 % and the mortality caused by predation is low, since only 1 of 8 non-surviving fawns died from predation. As expected, fallow deer fawns at Koberg selected bed-sites that offered better concealment (lower visibility) and more canopy cover than available at random and thus I found support for Prediction 1. However, I did not find any support for Prediction 2 as no difference in bed-site selection between surviving and non surviving fawns was found. The high level of selectiveness when choosing a bed-site, even though not affecting fawn survival in this study site, supports a 'ghost of predators past' interpretation (Byers 1997). Being an environment with few predators, it seems as though the anti-predator behavior seen in fallow deer fawns in this area is an adaption to a higher predation pressure that have persisted under relaxed selection.

Many of the non-surviving fawns (6) died from starvation. In all these cases, the necropsy showed that neither of these fawns had suckled as no signs of milk were found in the intestinal tracts. I can not exclude the possibility that the handling and marking of the fawns had an effect on this i.e. causing the abandonment. However, studies of marking induced neonate mortality in other ungulate species (e.g. pronghorn: Byers 1997b, white-tailed deer: Ozoga & Clute 1988) in enclosures has shown no evidence of increased mortality due to handling. Furthermore, suckling usually occurs within the first hour after birth (Chapman & Chapman 1997) and since most of the fawns were estimated to be at least 24 h or older, they should have had time to feed at least once before the possible disturbance by us, suggesting that something was not right prior to the capture.

Studies of the relationship between longevity and reproductive success in roe deer (Kjellander et al. 2004) and reindeer (Weladji et al. 2006) have demonstrated that females that live the longest have the highest fitness. An age effect on successful reproduction has also been recorded for pronghorn (Byers 1997a) and White tailed deer (Ozoga & Verme 1986), attributed to the improved maternal skills of older, more experienced females. Furthermore, maternally inexperienced females are suggested to be more likely to abandon their fawns than older females (Ozoga & Verme 1986). Thus, a reason for some of the recorded abandonments in this study might be inexperience and a higher sensitivity to disturbance of young females. In the summer of 2009, one fawn was found bedded out on a cut field where it could be spotted from more than hundred meters away. This field, in the middle of the study area, is close to a frequently used road and must therefore be regarded as an unexpected place to leave a fawn. This fawn was most likely abandoned by its mother. After marking by us, this fawn was seen wandering around alone in the same area and was later found dead.

Previous preliminary data indicating 30 % neonate mortality in the study area based on the difference in the proportion of females with fetuses in the spring and the proportion of lactating females next fall (P. Kjellander unpubl. data) further suggests that the mortality rate of 23.6 % in this study is not an overestimation of the actual rates caused by capture induced mortality.

More male fawns than female fawns died during this study, but there were no significant difference in mortality rates between the sexes. A higher predation rate in male roe deer fawns compared to female fawns have been reported from a Norwegian study (Aanes & Andersen 1996), although other studies have revealed no such differences (Jarnemo et al. 2004). Mortality biased towards males is often seen in sexually dimorphic species (Owen-Smith, 1993), and the explanation for this is usually differences in activity patterns between the sexes (Aanes &

Andersen 1996). However, a larger sample size would be needed in order to draw any conclusions about differences in mortality rates between male and female fallow deer fawns in this study area.

In this study, I have examined the spatial behavior of fallow deer neonates at two different levels i.e. the habitat selection within their home-range, which would in fact be a selection made by the mother, and the bed-site selection within that habitat.

Habitat use

Open habitats; ARABLE and PASTU were selected over forest habitats by fallow deer mothers and their fawns at Koberg. ARABLE was the habitat most used by all fawns according to the compositional analysis. Because of the low sample size, I was not able to test differences in habitat selection between surviving and dead fawns, however, it does not seem to be any big differences in habitat use between the two groups since data indicates that ARABLE were most used by both groups respectively. ARABLE were also most selected for bed-sites by all fawns. This habitat had the lowest canopy cover compared to the other habitat types, even though the measured visibility to predators was quite low at these sites.

Since the habitat selection is made by the mother within her home range, she has to consider her own needs as well as the fawns (Ciuti et al. 2006), and one of the most important factors generally affecting habitat use is the availability and quality of forage (Putman 1988). Being grazers, fallow deer is known to spend most of their time feeding in open grasslands (Chapman & Chapman 1997, Borkowski & Pudelko 2007) and a previous study at Koberg (Winsa 2008) confirmed that arable land was the preferred habitat by fallow deer also in this study area. This is in support of my results as female fallow deer in this area do not make any trade-offs in their habitat selection but in fact use the habitat that gain themselves in terms of energy intake, contrary to fallow deer females in Italy that moved to poorer but safer habitats when rearing for offspring (Ciuti et al. 2006). However, even though canopy cover were low in the selected habitat ARABLE, fawns bedded in this habitat still seemed to have a good concealment since the visibility were quite low at the selected bed-sites.

Apart from the measured environmental variables, there could also be other factors explaining habitat choice made by the mothers. Roe deer females, which are smaller than fallow deer females, has been shown to be quite capable of defending their fawns from red fox predation, either by deterring the fox from areas were fawns are bedded or by attacking and chasing away the fox (Jarnemo 2004), suggesting that female fallow deer would have a good chance of defending their fawns as well. This agrees with one observation made during this study of a female fallow deer chasing away a red fox moving towards her fawn. Fallow deer females may therefore choose to keep their fawns in open habitats in order to be able to discover potential predators in time, suggesting that fallow deer females do make habitat choices to reduce predation risk to their neonates. Furthermore, the female also needs to consider her own safety and being able to detect other larger predators.

Since most of the fawns in this study were found and marked in open habitats, this could be causing a bias towards fawns using open habitats, giving the possibility that the results of this study does not reflect the true spatial distribution of the population. However, even though habitats within the home-range were not used by random, all habitats types were to some extent utilised by fallow deer mothers and their neonates. This could imply that all habitats were good enough for the fawns to find satisfying cover in. Additionally, as suggested by Linnell et al.

(1999), this could also be an anti-predator strategy by not having a strong preference towards a single habitat type but instead utilising all habitat types and therefore forcing a potential predator to search all available habitats, making the hiding strategy even more effective. Furthermore, since I did not find any results indicating that the surviving and non-surviving fawns differed in their habitat use or that the non-surviving fawns to a higher extent used a habitat type that could be regarded as a “bad choice”, I can not say that any habitat in this area would be safer for the fawns than another.

Many bed-sites of surviving fawns were located in forest habitats, with relatively high visibility. While these habitats do not seem to provide protected bed-sites, the vegetation in the forest might still provide a good concealment for the fawns when moving with their mothers. This is in contrast with the open habitats where the visibility of the fawns is low when they are bedded, but when they are standing up and moving to another location they might be spotted from long distances.

Bed-site selection

Visibility

All habitat types except WET were utilised for bed-sites and, as expected, fallow deer fawns at Koberg selected bed-sites that offered better concealment (lower visibility) than available at random. This selection did not seem to affect survival since I did not find any difference in bed-site selection between surviving and non-surviving fawns. Together with the low mortality caused by predation in this study, this suggests that the anti-predator behavior of fallow deer neonates and their mothers is an adaptation to a previous history of higher predation pressure and other predators than present today in Sweden.

Even though the evolution of fallow deer is not perfectly known, its history exceeds back several million years (Chapman & Chapman 1997). The greatest evolution of deer occurred during the Pliocene; about ten to three million years ago (Chapman & Chapman 1997) and today the deer family consists of a wide variety of species adapted to different environments (Putman 1988). Things they share with each other are adaptations for avoiding predation, such as acute senses and long limbs with strong muscles, modified for fast running (Putman 1988). During the late Pleistocene (3 million – 100 000 yrs ago) extinctions of large carnivores such as lions and sabertooths in Eurasia and North America resulted in a relaxation in predator imposed selection on many ungulates (Byers 1997, Owen-Smith 1993). In the same way as pronghorns in North America are adapted to and fully capable of dealing with predators such as North American lions and cheetahs which are now extinct (Byers 1997), fallow deer have also during millions of years coevolved with predators, suggesting that behavior and reproductive traits seen in modern fallow deer reflect previous selection more than it reflects the current selection.

Despite predation pressure at the study site being low, probably partly due to a high level of predator regulation by the estate, the results of this study show that there is still a risk for predation on fallow deer neonates, since one fawn was killed by red fox. Furthermore, regardless of the fact that I did not find any differences in the bed-site selection of surviving compared to non-surviving fawns in this study, the logistic regression indicates that visibility in bed-sites has an effect on survival both for random and selected bed-sites. The random bed-sites could be thought of as reflecting the habitat choice made by the female, suggesting that females which choose a habitat with low visibility give their fawn a higher probability of

survival. For the bed-sites selected by the fawns, the logistic model suggests that visibility is even more important, where a high visibility at the selected bed-site means that the probability of survival is very low.

Canopy cover

Even though the absence of predators might explain the lack of importance of bed-site visibility for the fawn survival, this does not explain the fact that I did not find canopy cover to be of any importance for the survival. In accordance with the study of Linnell et al. (1999) on roe deer fawns, I found that fallow deer fawns selected bed-sites that offered better canopy cover than available at random. I did not, however, find any evidence of the presumed relationship between canopy cover and survival. In a study from France, Van Moorter et al. (2009) found that survival of young roe deer fawns was positively related to the selection of bed-sites with more canopy cover, but older fawns were rather selecting bed-sites with more light penetration, i.e. less canopy cover. They also report a connection to weather conditions where bed-sites with denser cover were used on days with low temperature and bed-sites with more light penetration on warm days. As speculated by Van Moorter et al. (2009) fawns might search for exposure to sun on sunny days, making the interpretation of the importance of canopy cover for fawn survival less clear, since this could be depending on weather conditions. The weather during the time of this study was generally hot and sunny, but with some colder rainy days and it would have been interesting to relate the bed-site choice and survival of the fawns in this study to the weather conditions during this time.

In this study, I measured canopy cover only by estimating the amount of cover at the height of 1.5 m, not taking in to account the cover that could have been present at a higher level which can be crucial for e.g. rain protection. Estimating canopy cover in another way may have resulted in a better understanding of the effect of canopy cover on survival rates for the fawns.

In conclusion, fallow deer females keep their fawns mostly in open habitats; arable land and pastures. This suggests that they do not make trade-offs in their habitat choice between their need for high quality forage and protection for the fawns, although further studies would be needed in order to test this, preferably by comparing the habitat use of calving and non-calving females. A reason for keeping fawns in open habitats is suggested to be the higher ability for the females to see and drive away predators. Although the measured visibility is low for bed-sites in arable land, canopy cover is also low, which could imply that habitat selection by the mother and bed-site selection by the fawn is more focused towards anti-predator behavior than thermal regulation effects. Since there are few predators in this study area and predation pressure is low, this behavior is not connected to actual survival rates in this area, but would rather be an adaption to a previous higher predation pressure.

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MARKINGS OF FAWNS, Koberg

Date: 200 - -

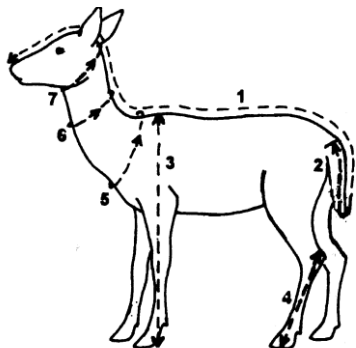
Marked by: _____.

Time(start:) _____ (stop:) _____

Place: _____.

ID number	
Mother	
Sex	
Fur colour	
Temperature	
Weight with collar (g)	
Weight without collar (g)	
Metatarsus (mm) (4)	
Heart girth (cm)	
DNA	YES / NO
Age at marking	

COLLAR/MARKING	
Type	
Frequency	
Colour	
EAR TAGS	
Left	
Right	
Umb. cord	
Faeces	
Fur (wet/dry)	
Hoof abrasion	



Disturbance (mother/fawn behaviour):.....

.....

.....

.....

.....

.....

.....

Location:

Mother GPS	X:	Y:	Habitat:
Fawn GPS	X:	Y:	

Bed-sites fallow deer

Observer: _____ Date: _____

ID: _____

	Actual	Randomised	
N			Direction:
S			Distance:
E			
W			
X-coord			
Y-coord			
Standing visibility (%)			

General description		
------------------------	--	--

Habitat

Forest <input type="checkbox"/>	Grove <input type="checkbox"/>	Mire/bog <input type="checkbox"/>	
Clear cut <input type="checkbox"/>	<input type="checkbox"/>	3 most common tree species (%):	_____
Plantation <1m <input type="checkbox"/>	<input type="checkbox"/>		_____
Young forest 1,1 - 2m <input type="checkbox"/>	<input type="checkbox"/>		_____
Young forest 2,1 - 5m <input type="checkbox"/>	<input type="checkbox"/>	Overgrown land <input type="checkbox"/>	
Thinned out forest 5,1 - 15m <input type="checkbox"/>	<input type="checkbox"/>	Pasture <input type="checkbox"/>	
Older forest >15m <input type="checkbox"/>	<input type="checkbox"/>	Arable land (+ high) _____	