Habitat use, bed-site selection and mortality rate in neonate fallow deer Dama dama

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Petter Kjellander, Ida Svartholm, Ulrika A. Bergvall & Anders Jarnemo

An understanding of mortality patterns, and especially the variation in juvenile mortality, is an important component in vertebrate population dynamics. Our study investigates, for the first time, neonate mortality and two levels of spatial behaviour, in a free-ranging fallow deer *Dama dama* population in southwestern Sweden. In the summers of 2008 and 2009, 36 fawns were marked with radio-collars. Neonate mortality calculated by the Kaplan-Meier method was 23.6%. Mortality caused by predation was low, since only one of eight non-surviving fawns died from predation, probably by red fox *Vulpes vulpes*. The spatial behaviour of the neonates was examined by habitat selection at home-range level, which in fact is a selection made by the mother, and at bed-site level within that habitat. Compositional analysis revealed a significant preference for arable land, pasture and coniferous forest between 5-15 m high, compared to young forest. Selected bed sites showed significantly lower visibility and higher amount of canopy cover than random sites. Surprisingly, we did not find any relationship between canopy cover and visibility in selected bed sites while it showed a significant and negative relationship at random bed sites. We interpret this finding as while high canopy cover and low visibility covary at the habitat level, fawns seem to select these two bed-site variables independently, perhaps for thermoregulatory reasons. Since there are few predators in our study area and predation pressure is low, this behaviour is not connected to actual survival rates in this area, but would rather be in support of the hypothesis of 'pleiotropy' as thermoregulatory reasons for bed-site selection in neonate fawns might be the most important contemporary selection force in the absence of large predators.

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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% (Lin-

nell 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 categorised as either a 'hider'- or a 'follower'-type (Lent 1974). In species categorised as hiders, 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 even though the hider phase can vary in time from 2-3 days in some species (e.g. Siberian ibex *Capra ibex*, mouflon *Ovis orientalis* and red deer *Cervus elaphus*), to 2-4 months in others (e.g. Uganda kob *Kobus kob* and reedbuck *Redunca redunca*; Lent 1974). In follower species, newborns actively follow the mother and 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 *Rangifer tarandus* and the muskox *Ovibos moschatus*; Lent 1974, 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 behaviour 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 during the first two weeks of their life (San José & Braza 1992, Ciuti et al. 2006). The mother typically stays within hearing distance of her fawn and visits several times per day to feed and groom it (Chapman & Chapman 1997) and fallow deer females rarely move further away than 400 m from the fawn (U.A. Bergvall, unpubl. data). 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. Although 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 *Capreolus capreolus* (Linnell et al. 1999) and white-tailed deer *Odocolius virginianus* (Heugel et al. 1986)) has been examined previously. However, this behaviour has not yet been studied in fallow deer.

As well as serving as 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, Mysterud & Østbye 1999). Ungulate neonates are vulnerable to cold and wet weather, and hypothermia is often mentioned as the main cause of non-predator mortality in the review of Linnell et al. (1995; see also Olson et al. 2005). The high neonate mortality recorded for fallow deer kept in open paddock conditions on deer farms is thought to be a result of the lack of shelter from high rainfalls (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. Selection is therefore expected to also act towards fawns choosing the most beneficial bed site also for thermoregulatory reasons, for a given weather condition (Van Moorter et al. 2009). Beside selection for cover against predators, bed-site selection in neonate fallow deer might, therefore, also be an example of Byers (1997a) 'pleiotropy', i.e. an anti-predatory behaviour that remains because it also has an alternative function (see also Stearns 2010).

There are obviously many factors affecting habitat selection among herbivores, such as food quality and abundance, availability of shelter and cover from predators or unfavourable weather conditions, but also social structure and population densities (Putman 1988, Sinclair et al. 2006). Furthermore, the presence of fawns leads to changes in social behaviour and space-use of calving females (Shackleton & Haywood 1985, Schwede et al. 1993, Bon et al. 1995, Kohlmann et al. 1995, Tufto et al. 1996, Ciuti et al. 2006, Bongi et al. 2008). Ciuti et al. (2006) showed that female fallow deer in Italy adopt an anti-predator behaviour in their habitat selection, since calving females to a higher extent used suboptimal 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).

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 Northern Europe and Scandinavia (Chapman & Chapman 1997, Carlström & Nyman 2005). The species was first introduced to Sweden in the 1570s, and it is now well-distributed in the form of scattered occurrences over the southern part of the country (Carlström &

Nyman 2005). The reported annual harvest of fallow deer in the wild has increased from 1,000 animals in 1955 to almost 17,000 in 2005 (Bergström & Danell 2009). 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, indicate that approximately 30% of neonate fallow deer in a population at Koberg in southwestern Sweden do not survive their first summer (P. Kjellander, unpubl. data). Our study is the first trying to verify these indicative findings and to investigate causes of neonate mortality.

The aims of our study were therefore to investigate 1) the level of neonate mortality in a free-ranging fallow deer population in Sweden, 2) the habitat selection, made by the mother, and 3) the environmental factors affecting bed-site selection by the fawn that may influence neonate survival. Because of the anti-predatory origin of the hider strategy and the sensitivity to thermal conditions seen in ungulate neonates, we expected the fallow deer fawns to select bed sites that provided more cover and better concealment than random sites (Lent 1974, Putman et al. 1996, Linnell et al. 1999). As a consequence, we also predicted bed-site selection to affect fawn survival, e.g. we expected the surviving fallow deer fawns to have chosen bed sites with better cover and concealment compared to the non-surviving fawns.

Material and methods

Study area
Our study was performed at the Koberg estate (58°N, 12°E) in southwestern Sweden (Västra Götaland County). Our study area (54.35 km²) is mostly covered with different types of forest (79%), and the remaining area consists 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, consisting of arable land and pastures, are today, to a large extent, cultivated in order to improve wildlife habitats, and supplementary food is also given during wintertime. 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 1920s (N. Silfverschiöld, unpubl. data). The fallow deer population in our study area was estimated in April each

year by a Distance Sampling procedure (Buckland et al. 2001) to 17.7 and 19.9 animals/km² in 2008 and 2009, respectively (P. Kjellander, unpubl. data.). Other ungulates occurring in the area regularly are roe deer, moose *Alces alces* and wild boar *Sus scrofa* and occasionally red deer. Controlled hunting is performed each fall (September-February, with a pause during the rut), and potential predators beside wild boar present in the area are the red fox *Vulpes vulpes* and occasional visits of lynx *Lynx lynx* and wolf *Canis lupus*.

Temperature and precipitation in our study area was recorded by the Swedish Meteorological and Hydrological Institute (SMHI) at the Gendalen meteorological station, situated 12 km from our study area. Mean monthly temperatures in our study area during summer (June-August) usually range between 15 and 17°C, with the highest temperatures during July (SMHI 2009). Mean monthly precipitation (June-August) range between 86 and 130 mm with June and July normally being equally dry whereas August has the highest rainfall (SMHI 2009). The two summers included in our study (2008 and 2009) did not diverge substantially from the monthly mean weather conditions reported here, as mean temperature ranged between 15.6 and 15.8°C in the two years, while there was slightly less rain fall than average in June and July 2008 (60-64 mm) as well as June 2009 (65 mm), while August 2008 and July 2009 was unusually wet with 50-100% more rain than the monthly average (197 and 162 mm, respectively).

Data collection
Data was collected during the summers of 2008 and 2009. Fallow deer fawns were found, by either searching the near surroundings of solitary females observed standing by their own outside a group, or by waiting for them to visit their hidden fawns. Fawns could also be detected by chance when searching probable fawning areas. The fawns were caught during the first days in life, when they still adopt a prone position, either 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. The fawns were ear-tagged with coloured plastic tags and equipped with a radio-transmitter attached to an expandable collar with a drop-off function. In 2008, 15 fawns were caught; 12 were fitted with VHF transmitters (Televilt, Lindesberg, Sweden) and only three were ear-tagged. In

2009, 24 fawns were caught, and this year, we marked them 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). All possible sorts of concern to prevent negative effects of the first capture was taken (e.g. keeping silent and calm during handling, minimising disturbance time (< 10 minutes) and number of people at capture sites (≤ 2) and by rubbing grass on hands and tools).

Fawn survival was normally checked daily for up to four weeks of age, until mid July, then once a week until mid September. Fawns marked with VHF transmitters were located using three element yagi antennas and receivers. The exact locations of the fawns were estimated with a script built on the R platform (R version 2.10.0, R development core team (2006-2009)) by using bearings from three or four reference points. If a fawn was observed during radio tracking (N = 5 locations), the observed position was used. In order to establish and categorise the cause of death, the location of the found collar or the dead fawn was investigated for markings or other signs of predation, and the dead fawns were necropsied and investigated for bite marks and signs of diseases.

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, by the same person throughout the whole study. We started measuring from a maximum distance of 50 m, and then we recorded the distance from which the ball was first detected at a height of 50 cm above the ground. 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 sites. In order to make a correct comparison between the selected and the randomly chosen bed sites, 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

As the weather conditions and population density estimates were rather constant between years and annual sample sizes fairly small, we pooled data over the two years. Following that, we estimated fawn mortality 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. We tested differences in survival rates between male and female fawns with the G-test of goodness of fit.

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. We analysed the data on fawn positions in Arc GIS 9.3 and used a satellite generated digitalised map to define each habitat. The map was derived and developed from the Swedish CORINE Land Cover map to 'Svensk marktäckedata' (SMD) with a 25 × 25 m pixel resolution (Lantmäteriet 2004). We randomly moved fawn positions that ended up between two habitats into one of the two neighbouring habitats (five out of 726 positions). The habitat type 'lakes and ponds, open water surface' was not considered available habitat and therefore removed from further analysis.

We accordingly based data on home ranges and habitat use on locations collected during the estimated first month of each fawn's life, starting with the first marked fawn 21 June and ending 15 August with the latest marked fawn (marked 14 July). We calculated home ranges 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. We analysed the habitat use within the MCP home range with compositional analysis (CA; 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 CA, we combined similar and

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rare habitat categories as follows: land in active agricultural management as arable land (ARABLE), open grasslands never ploughed but previously or currently grazed by live stock as pastures (PASTU), new or recently replanted clear-felled forests with sprouts up to 2 m height (CLEAR), younger forest with a tree height between 2-5 m (YOUNG), mixed conifer-deciduous forest > 5 m (MIXED), pure coniferous forest of 5-15 m height (CON 5), pure coniferous forest > 15 m (CON 15) and finally wet areas as various types of mires and over-grown water ponds (WETLAND). Since CAs require no missing values for either habitat use or habitat availability, we replaced missing values with 0.001. Considering the small sample sizes (number of fawns) and the eight habitat classes, we arbitrarily discarded fawns with < 15 positions in order to balance the data set somewhat for the CA (Aebisher et al. 1993). Hence, only data from 14 fawns from both years could be used, since many of the fawns died or lost their collars too early resulting in a mean of 43 ± 6.47 SE locations per fawn (range: 15-81 locations). When we corrected for the number of fixes as a covariate in a resource selection function model (RSF) with a logistic approach, it did not change our conclusions. We therefore decided to only account for the result from the CA. Because of the fact that fawns died before we acquired enough positions, we were unable to calculate home ranges and test for differences in habitat choices between surviving and dead fawns. Even though we are referring to the positions and habitat use of the fawns, this selection, as discussed earlier, is in fact made by the fallow deer female.

We used the mean distance (of the four cardinal distance measures), at which the model fawn was detected, as a measure of visibility. Firstly, we tested for differences in visibility between the selected bed sites and random bed sites, between individual fawns, fate (dead or alive) and the interaction between site (selected and random) and fate (dead or alive) with an analysis of variance (repeated ANOVA). Secondly, we analysed the data for possible differences in visibility between the different habitats. 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-squareroot transformation $(y = \sqrt{\sin^{-1} x})$ 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. We tested differences in bed-site selection between surviving and non-surviving fawns with repeated ANOVAs. All statistical tests, beside the CA, were performed in StatView 5.0.1.

Ethical approval for our study was granted by the Gothenburg Board for Laboratory Animals (Dnr: 187-08 & 405-08).

Results

A total of 39 fawns (18 males, 21 females) were captured and marked during our study; 15 fawns in 2008 and 24 fawns in 2009 (Table 1). In 2008, three 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 males, 19 females) eight fawns died, of which five were males and three females. The death of one fawn could likely be assigned to red fox predation, since the collar was found with fox bite marks, traces of blood and scent of red fox urine. Six fawns died from starvation and one of unknown causes. All of those six starved fawns had no traces of milk in the gastro-intestinal tract, implying that they had never been fed by their mothers. The cumulative mortality according to the Kaplan-Meier analysis was 23.6% ($\pm$ 0.07 SE) for all fawns. Even though not significantly different, the mortality was 16.4% ($\pm$ 0.08 SE) in females and 32.1% ($\pm$ 0.1 SE) in males (G = 0.27, df = 1, P = 0.6; Fig. 1). The mean date of birth was 23 June ($\pm$ 5.0 days) for the marked fawns.

Habitat use
According to the CA, the habitat use of the fawns, selected by their mothers at the home-range scale differed significantly from a random choice (χ^2 = 14.65, df = 7, P < 0.05). The habitat classes arable

Table 1. Numbers, sex and mortality of neonate fallow deer fawns marked at Koberg in southwestern Sweden in 2008 and 2009. In 2008, three of the 15 marked fawns were only ear-tagged (one male and two females).

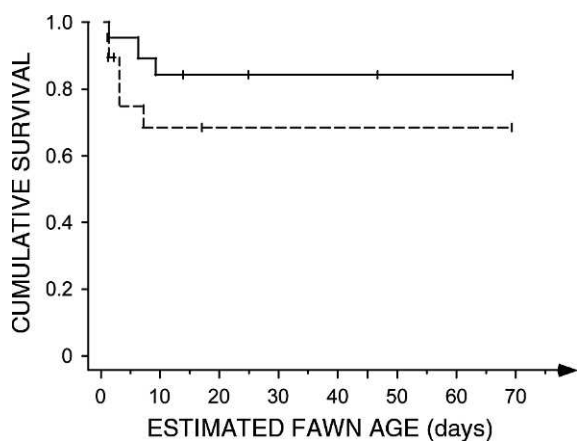|	2008	2009	Both years
Number marked	15	24	39
Males	6	12	18
Females	9	12	21
Number dead	3	5	8
Males	1	4	5
Females	2	1	3

Figure 1. The cumulative survival of fallow deer neonate females (N = 19, black line) and males (N = 17, dashed line) at Koberg, Sweden, during their first summer of life. Censored animals are indicated by |, i.e. individuals lost to our study due to dropped collars. Data from 2008 and 2009. The gender specific survival rate indicated in the figure did not differ significantly from each other (see the result section for more details).

Figure 2. Habitat selection by fallow deer fawns ($\pm$ SD) at Koberg in southwestern Sweden. 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 >15 m, WETLAND = wet areas, MIXED = mixed forest > 5 m, CLEAR = clear felled areas, forest up to 2 m, YOUNG = young forest 2-5 m.

land (ARABLE), pasture (PASTU) and coniferous forest between 5-15 m (CON 5) were significantly more preferred (t > 2.282, df = 13, P ≤ 0.040 in all cases) than young forest (YOUNG; Fig. 2), while no significant differences in use of the remaining habitat classes were found (CLEAR, MIXED, CON 15 and WETLAND; t < 1.843, df = 13, P > 0.088 in all cases).

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 our study (one fawn lost its collar during the first 24 hours).

Out of 77 bed sites, 25 (32.5%) were situated in the habitat class ARABLE, 19 (24.7%) in CON 15 and 12 (15.6%) in MIXED. YOUNG, CON 5 and PASTU had the least number of bed sites (6.5% in each habitat type). Six bed sites (7.8%) were situated on CLEAR and no bed sites were found in WETLAND. 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. Three bed sites on ARABLE were situated within the edge of some kind of forest. Eight bed sites in forest were situated within the edge of ARABLE (four of the bed sites in CON 5, one in CON 15 and three in MIXED). One bed site on CLEAR was situated in the edge zone of ARABLE.

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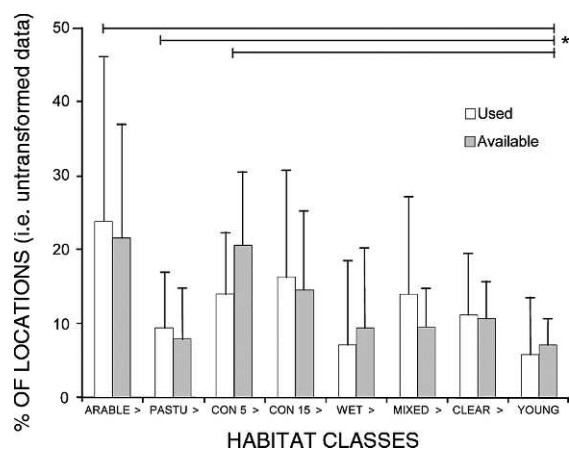
that did not survive (45.5%). This habitat had the lowest canopy cover (4.8% at the selected bed sites), but also a low visibility (3.1 m).

Visibility

There was a significant difference in visibility between bed sites of the individual fawns (minimum: 1.4 ± 0.5 m; maximum: 41.6 ± 0 m; $F_{22, 54} = 4.15$, 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; $F_{1, 22} = 31.8$, P < 0.0001). Visibility between bed sites of surviving and non-surviving fawns did not differ ($F_{1, 21} = 2.45$, P < 0.133; Fig. 3A).

The visibility of the bed sites differed significantly between habitat types ($F_{6, 70} = 3.28$, P = 0.007). Even though CON 15 was the second most chosen habitat category 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 (Fig. 4 and Table 2). 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).

Canopy cover

There was a large difference in canopy cover, ranging from 0 to 100%, between bed sites of the individual

Figure 3. Mean bed-site visibility (A) and cover (B) of the selected (white) and random bed sites (light grey) of 18 surviving and five non-surviving fallow deer fawns ($\pm$ SD) at Koberg in southwestern Sweden, in the summer of 2009.
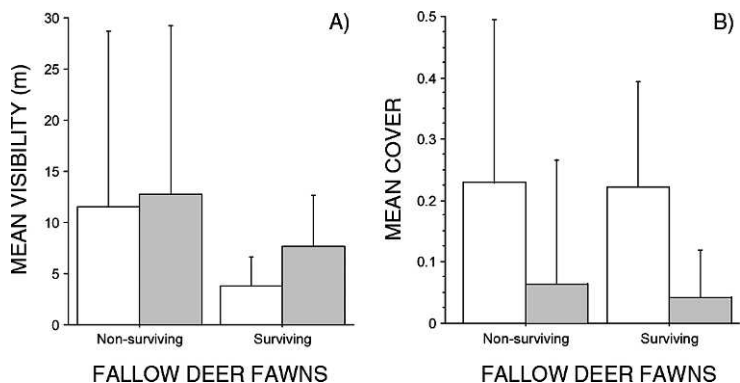
fawns, and the selected bed sites had a significantly better mean canopy cover (24.8 $\pm$ 32.3%) than the random bed sites (5.3 $\pm$ 17.3%; $F_{1,\ 22} = 36.2$, P < 0.0001; see Fig. 3B), but canopy cover between bed sites of surviving and non-surviving fawns did not differ ($F_{1,\ 21} = 0.06$, P = 0.8; see Fig. 3B). The amount of canopy cover differed significantly between habitats ($F_{6,\ 70} = 4.03$, P = 0.002; Fig. 5), and ARABLE, PASTU and CLEAR had almost no canopy cover at all at the random sites, with a mean cover < 1% (ARABLE: 0.6 $\pm$ 0.5%, PASTU: 0.6 $\pm$ 0.5%, CLEAR: 0.2 $\pm$ 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 $\pm$ 7.8%, PASTU: 24.6 $\pm$ 38.7%, CLEAR: 34.5 $\pm$ 40.5%). The best cover at the random sites was found in YOUNG (23.4 $\pm$ 47.8%) and CON 5 (24.2 $\pm$ 58%), but at the selected bed sites the amount of canopy cover exceeded 24% in all habitats, except ARABLE.

The relationship between visibility and canopy cover

We found a significant and negative relationship between canopy cover and visibility at the random bed sites ($R^2 = 0.059$, df = 76, P = 0.034) while no such relationship appeared in the selected sites ($R^2 = 0.012$, df = 76, P = 0.172). This means that high canopy cover and low visibility covary at the habitat level. However, fawns seem to select the two bed-site variables (canopy cover and visibility) independently from each other, but always better than random bed sites.

Discussion

Neonate mortality of fallow deer was 23.6% and the mortality caused by predation was low, since only one of eight non-surviving fawns died from what we defined as predation. As expected, fawns selected bed sites that offered better concealment (lower visibility)

Table 2. Bed-site selection of fallow deer fans at Koberg in southwestern Sweden, during the summer of 2009. Based on a total number of 77 selected bed sites from 23 marked fawns (+ 77 random bed sites). Surviving fawns: N=18 and non-surviving fawns: N=5. Relative (%) habitat use is indicated within brackets. On arable land, three bed sites were situated in the edge zone (within 5 m) of forest. On clear cut, one bed site was situated in the edge zone (within 5 m) of arable land. In forest, eight bed sites were situated in the edge zone (within 5 m) of arable land.

| | | | | | Environmental variables | | | |
| | Selection of bed sites | | | | Mean visibility (m) | | Mean canopy cover (%) | |
Habitat	Total number	%	Surviving fawns	Non-surviving fawns	Selected bed sites	Random bed sites	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	58.0	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
WETLAND	0	0	0	0	NA	NA	NA	NA
Total	77	100	66 (100)	11 (100)				
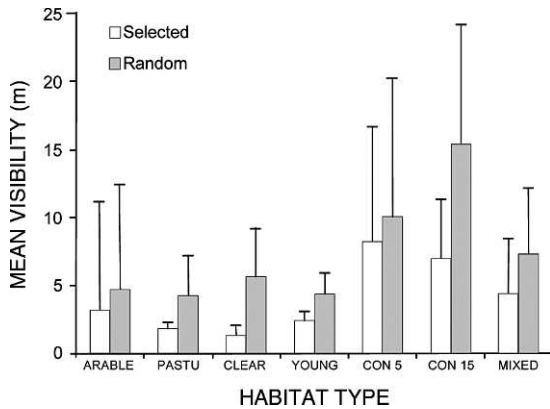
Figure 4. Mean visibility of selected bed sites compared to mean visibility of random bed sites (± SD) of each main habitat type for fallow deer fawns in southwestern Sweden, during summer 2009.

Figure 5. Mean canopy cover of selected bed sites compared to random bed sites (± SD) of each main habitat type for fallow deer fawns in southwestern Sweden, during summer 2009.

and more canopy cover than available at random sites. As predation was low, we did not find support for difference in bed-site selection between surviving and non-surviving fawns. The high level of selectiveness when choosing a bed site, with no apparent effect on fawn survival, does not entirely rule out neither of the two bed-site selection hypotheses, i.e. the 'ghost of predators past' (Byers 1997a) or for thermoregulation (Linnell et al. 1995). We interpret our results to be in line with Byers (1997a) hypothesis of 'pleiotropy', i.e. an anti-predatory behaviour that remains because it also has an alternative function (Stearns 2010). Being in an environment with few predators, it seems as the anti-predator behaviour in our study area is an adaption to a higher predation pressure that have persisted under relaxed selection with thermoregulation as the most likely alternative function maintaining the behaviour.

Preliminary data indicating 30% neonate mortality in our study area is 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). This suggests that the mortality rate of 23.6% in our study is not an overestimation of the actual rates caused by capture induced mortality. Six of the fawns died from starvation. In all these cases, the necropsy showed that none of these fawns had suckled for some time as no signs of milk were found in the intestinal tracts. We cannot exclude the possibility that the handling and marking of the fawns had an effect on this, i.e. causing the abandonment and subsequently starvation. However, studies of marking induced neonate mortality in fallow deer (Galli et al. 2008) and other ungulate species in enclosures (e.g. pronghorn
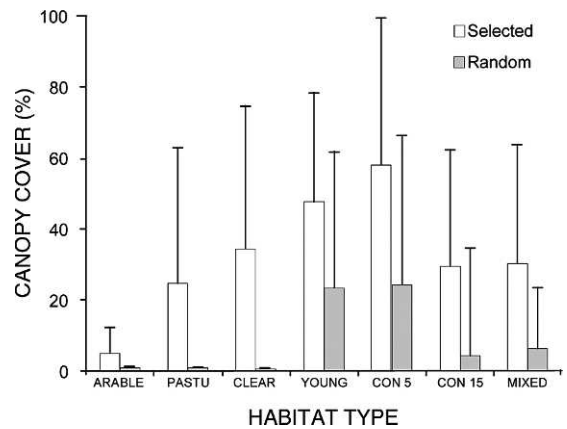
Antilocapra americana (Byers 1997b) and white-tailed deer (Ozoga & Clute 1988)) has shown no evidence of increased mortality due to handling. Furthermore, suckling usually occurs within the first hour after birth (Chapman & Chapman 1997), and since most of the fawns were estimated to be at least 24 hours or older at capture, they should have had time to feed at least once before the possible disturbance by the handling, suggesting that something was not right prior to the capture.

To our knowledge there are unfortunately no previous studies on mortality rates in wild neonate fallow deer. However, our estimated mortality rate of < 24% is not particularly high in comparison to studies of other species in predator-free environments but rather low for an area with predators (Andersen & Linnell 1998). Gill (1994) found a mean mortality rate of 26% for roe deer fawns, in a 23-year data set from England in a predator-free area, and in studies of other free-ranging ungulates in predator-free environments, neonate mortality has been reported to range between 10 and 20% (red deer (Guinness et al. 1978), white-tailed deer (Ozoga & Verme 1986, McGinnes & Downing 1977), moose (Stubsjoen et al. 2000)). In contrast, a mortality rate of > 40% is repeatedly reported for roe deer fawns in areas were mainly red fox function as a predator of fawns (Aanes & Andersen 1996). Our estimated predation rate therefore seems very low in the light of those reported on roe deer. It is likely that even during the short period a fallow deer fawn is likely to be killed by a red fox, the fox is too small a predator to be as successful in killing fallow deer fawns of more than double the size of a roe deer fawn, particularly as it seems as fallow deer females actively and collec-

tively successful defend their fawns. Roe deer females, which are smaller than fallow deer females, have 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 the fox away (Jarnemo 2004). This suggests that female fallow deer would have a good chance of defending their fawns as well. In fact, repeated observations of females running towards the field worker was done, and if the fawn screamed during the handling, several females sometimes came running from different directions as an obvious effect of the alarming fawn. This behaviour indicates a strong willingness to defend fawns against predators. In line with that, we once actually observed a group of females aggressively chase away a fox from a fawn.

If the mortality rate reported in our study in large is not an effect of handling or predation, why do the fawns die? Veterinary autopsies, did not reveal any acute diseases or high parasite loads. Even if no extreme weather occurred during the two years, the fawns did experience some heavy summer rains and hypothermia can not be ruled out as the ultimate death cause. Considering that the mean birth date of fallow deer is 3-6 weeks later in our study area than reported for the native deer species (moose (Sæther & Heim 1993), red deer (Meisingset 2003) and roe deer (Nordström et al. 2009)), this might indicate sensitiveness in fallow deer fawns to bad weather conditions.

On the other hand, 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, attributed to the improved maternal skills of older, more experienced females, has also been recorded for pronghorn (Byers 1997a) and white tailed deer (Ozoga & Verme 1986). 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 our study might be inexperience and possibly a higher sensitivity to disturbance of young females. The high population density in our study area could further increase the losses in at least two different ways. First, it is likely that this population is severely food limited, and it is well established that females in poor body condition give birth to fawns with low birth weights which results in low survival (Guinness

et al. 1978). Secondly, disturbance of human origin and interactions of intra- or interspecific origin might disturb the female to fawn imprinting process and negatively affect the willingness of particularly young inexperienced females to continue to invest in a fawn also after a short separation, as observed in sheep *Ovis aries* (Otal et al. 2009).

Albeit mortality biased towards males is often seen in sexually dimorphic species (Owen-Smith 1993), and more male fawns than female fawns actually died during our study in both absolute (five males and three females) and relative numbers (32% mortality in males and 16% in females), the small sample size could not with any significance confirm this as a general pattern. To reach significant differences in gender specific survival of that magnitude would have required more than three times as many marked fawns as marked in our study.

The spatial behaviour of fallow deer neonates was examined at two different levels, i.e. the habitat selection within their home range, which in fact is a selection made by the mother, and the bed-site selection within that habitat. Open habitats, including arable land and pastures, were selected over forest habitats by fallow deer mothers at Koberg and arable land was most used according to the CA. This habitat also 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 fawn's (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 intermediate mixed feeders (Hofmann 1989), fallow deer are 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 supports the findings in our study, as female fallow deer in our study area did not make any trade-offs in their habitat selection, but in fact used the habitat that gained themselves in terms of energy intake, contrary to fallow deer females in Italy that moved to poorer but safer habitats when rearing offspring (Ciuti et al. 2006). However, even though canopy cover were low in the selected habitat (arable land), fawns that bedded in this habitat still seemed to have a good concealment since the visibility was 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. Since fallow deer females seem quite capable of defending their fawns from red fox predation, they may also 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 be able to detect other larger predators.

Since most of the fawns in our 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 our 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 habitat types were to some extent utilised by fallow deer mothers and their neonates. This could imply that all habitats were suitable for the fawns to find satisfying cover. 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.

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 were the visibility of the fawns are low when they are bedded, but when they are standing up and moving to another location they might be spotted from long distances. All habitat types except wet lands were utilised for bed sites.

Despite predation pressure at our study site being low, which was probably partly due to a high level of predator control, the results of our study show that there is still a risk for predation on fallow deer neonates since one fawn most likely was killed by a red fox. Furthermore, regardless of the fact that we did not find any differences in the bed-site selection of surviving compared to non-surviving fawns in our study, 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 gives her fawn a higher probability of survival.

Even though the low occurrence of predators might explain the lack of importance of bed-site visibility for the fawn survival, this does not explain the fact that we 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, we found that fallow deer fawns selected bed sites that offered better canopy cover than available at random sites. We did not, however, find any evidence of the presumed relationship between canopy cover and survival. On the other hand, we found a significant and negative relationship between canopy cover and visibility at the random bed sites while no such relationship appeared in the selected sites. We interpret this as, while not surprisingly, high canopy cover and low visibility covary at the habitat level, fawns seem to select the two bed-site variables (canopy cover and visibility) independently of each other. 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. More importantly, 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, thus fawns might search for exposure to sun on sunny days (Van Moorter et al. 2009), perhaps to dry up after rainfall or cold and humid nights to reduce hypothermia. Thus, it makes us interpret the role of canopy cover for fawn survival to be partly in support of Byers (1997a) hypothesis of 'pleiotropy'. Following that, the significance of thermoregulation will perhaps be the most important contemporary selection force in the absence of large predators, since this behaviour could also depend on weather conditions not investigated in our study.

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