

Selection of bed-sites by roe deer *Capreolus capreolus* fawns in an agricultural landscape

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The vegetation characteristics and habitat selection associated with the bed-sites used by neonatal roe deer *Capreolus capreolus* (Linnaeus, 1758) fawns were studied in an agricultural environment in central Norway. Data were collected from 85 radio-collared fawns belonging to 38 families during 1992–1994. All bed-sites used provided effective cover, although this differed between habitats and increased during the summer as the herbaceous vegetation developed. Seasonal use of farmland increased and then decreased reflecting the growth, and cutting of the grass. Habitats were not used in relation to their availability. Early born fawns significantly avoided farmland, whereas later born fawns showed no significant selection or avoidance of any habitats. The data show how roe deer fawns are able to exploit small patches of non-cultivated habitats in an agricultural landscape.

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Introduction

In ungulates there are two main types of neonatal security strategies: followers and hidiers (Lent 1974). In hider species, neonatal security relies on their ability to remain undetected by predators while lying out at a distance from the mother and siblings. This means being inactive for long periods of time (Schwede *et al.* 1992), having cryptic coloration, and using vegetation and terrain features to obscure their visibility. With the high rates of neonatal predation typical of ungulates (Linnell *et al.* 1995), the efficiency of concealment should be under strong selection. One way of decreasing the visibility is to selectively choose bed-sites that offer a high level of concealment. The fact that several studies have found habitat specific differences in predation rates (roe deer *Capreolus capreolus*: Aanes and Andersen 1996; white-tailed deer *Odocoileus virginianus*: Nelson and Wolf 1987; pronghorn *Antilocapra americana*: Bodie 1979, Barrett 1981) indicates that bed-site selection does indeed have survival consequences. Furthermore, thermal stress (hypo- or hyperthermia) is a common cause of death in roe deer (Andersen and Linnell 1997).

Thus, being selective choice of favourable microclimates when choosing bed-sites could also reduce the possibility of being exposed to thermal extremes.

Roe deer *Capreolus capreolus* (Linnaeus, 1758) occupy many different habitats across Europe, including agricultural areas where their densities can on occasion reach very high levels (Andersen and Linnell 2000). While adult roe deer habitat requirements and usage in agricultural areas are well studied (Tufto *et al.* 1996, Mysterud *et al.* 1999, Hewison *et al.* 2001), the use of such areas by fawns is poorly understood. As roe deer are vulnerable to mortality from mechanised agriculture (Kałuziński 1982), an understanding of their habitat selection in agricultural environments may assist in producing recommendations to minimise losses. Red foxes *Vulpes vulpes* are the most significant predator of neonatal roe deer (Borg 1991, Liberg *et al.* 1992, Aanes and Andersen 1996), and can also live at high densities in agricultural environments. As roe deer are classic hiders (Espmark 1969), red foxes probably depend on sight to locate fawns, as the fawns have little scent and make little noise. From the predators point of view, the relative efficiency of searching for fawns versus alternative prey is determined by the distance from which a fawn can be visually detected (Byers and Byers 1983, Fitzgibbon 1993), or in other words how well obscured its bed-site is by vegetation and terrain features. Therefore, an understanding of the habitat selection and vegetation characteristics of neonate bed-sites is important for understanding the complex of traits that make up the hider strategy.

Here we present an analysis of bed-site vegetation characteristics and individual habitat selection of radio-collared roe deer fawns during the hiding phase in a low-intensity agricultural area in central Norway with the aim of identifying their relative preference for different habitats. As the vegetation undergoes a successional development during early summer, we put a special focus on the temporal aspects of the habitat use and selection.

Material and methods

Study area

The study area (7.8 km²) was located on Storfosna (10.8 km²), an island 2 km off the coast of west-central Norway (63°40'N, 09°30'E). The island is made up of a fine-scaled mosaic of heather-dominated moorland (33%), abandoned meadows (18%), cultivated farmland (35%), and mixed coniferous and deciduous woodland (12%). The climate is cold oceanic, with about 160–180 growing days each year. The mean precipitation is 1048 mm/year, and snow rarely settles for > 1 week at a time. The island provides good foraging conditions for the roe deer population (Tufto *et al.* 1996), with spring flush being coincidental with roe deer birth season (Linnell and Andersen 1998). During the study period, from 1992 to 1994, the population density increased from 19.2 deer/km² in spring 1992 to 30.4 and 40.6 deer/km² in spring 1993 and 1994, respectively (Andersen and Linnell 2000). The habitats on the island were surveyed in 1989, and a digital map created using ArcGIS Ver. 8.1 (ESRI 2000) geographical information systems (Austrheim 1995). For the purposes of this study five habitat types were recognised: (1) Moorland – dominated by heather (*Calluna* sp.) and grasses with scattered clumps of birch *Betulla pubescens* and willow (*Salix* sp.) scrub, and some small marshes; (2) Farmland – mainly used for cultivation of grass for hay and silage production, with some cattle grazing during

summer, but also with some small patches for growing cereal crops, vegetables and gardens; (3) Abandoned meadow – areas once grazed but now neglected, covered in rich herbaceous vegetation with some shrubs during summer, but providing little cover during the winter and spring; (4) Coniferous woodland – small patches of pine *Pinus sylvestris* wood having a mean area of 1.8 ha with well-developed herbaceous and shrub layers of blueberry (*Vaccinium* sp.), heather, birch and rowan; (5) Deciduous woodland – small strips and patches of birch woodland, with a mainly herbaceous layer. Red foxes were absent from this island, although they were present in the adjacent mainland from which the population of roe deer colonised the island within the last 20 years. We also observed fawn mortality due to domestic dogs and cats (Andersen and Linnell 1998), and human disturbance was a constant factor, leading us to believe that the fawns showed normal, or at best close to normal, anti-predator behaviour in this population.

Data collection

Fawns were captured and radio-collared during the birth period using methods that have been described elsewhere (Andersen and Linnell 1997, 1998). A total of 245 fawns were captured and marked during 1992–1994. Data from 39, 22 and 24 fawns representing 18, 9 and 11 families were available from 1992, 1993 and 1994, respectively. Only families with at least 20 locations in the first 40 days of life were utilised. The fawns were radio tracked at approximately 2–3 day intervals, but never more than once a day. Fawns were approached closely (to within 5 m) so that the precise habitat-type in which they were lying could be determined in all years. In 1992 only, we approached fawns even closer (until we could see them) so that bed-site characteristics could be quantified. This was only done for fawns that were so young that they would not flush when approached (Linnell *et al.* 1998) or in cases where the fawns were being recaptured for weighing (Andersen and Linnell 1997). At these bed-sites, the height of the combined herbaceous and shrub layers were recorded. Furthermore, the maximum distance from which a fawn could be seen from a height of 35 cm (approximate fox eye height) from each cardinal direction was measured. We used the mean of these values as a measure of visibility (VIEW). Unfortunately, we did not design our data collection to collect VIEW data from adjacent random sites, so that we can only analyse use and not selection for this parameter. Of the fawns radio-tagged in 1992, 53 were used in the bed-site study. The habitat type in which the fawns were bedded was determined in 1004 cases, the height of herbaceous and shrub layers in 722 cases and full visibility characteristics in 253 cases, from May 7th until July 15th. After this period fawns flushed at too great a distance for bed-sites to be located.

Statistical analysis

We used linear regression to evaluate the temporal change in herbaceous layer height, shrub height and VIEW, whereas differences between the habitat classes in the same parameters were analysed using Kruskal-Wallis ANOVA. In the bed-site analyses, each bed-site was regarded as an independent point. We analysed habitat selection using the compositional analysis technique, as proposed by Aebischer *et al.* (1993). Missing values in habitat use were replaced by 0.01% (Aebischer *et al.* 1993), and missing values on habitat availability were replaced by the mean of all non-missing values for that log-ratio (the third, and recommended, option in appendix 2, Aebischer *et al.* 1993). However, as the sibling's home ranges are highly dependent on each other (as they all depend upon the home range of the dam) we conducted all analysis of habitat selection for families (ie with siblings pooled) rather than for individual fawns (Linnell *et al.* 1999). Habitat availability was defined as that which was available within the composite family home range, and habitat use was based on the visual assessment from the close approach telemetry. The exact availability of habitat types within the home ranges was calculated using the ArcGIS program package. The home ranges were estimated with the minimum convex polygon method, using the RANGES V program (Kenward and Hodder 1996). In order to examine for changes in habitat selection during the summer, we separated the fawns born before the peak of the birth period (ie 23 May; Linnell and Andersen 1998) from those born afterwards (29 and 9 families, respectively). Habitat selection was analysed during the first 40 days of life in both groups.

Results

Bed-site usage

The mean herbaceous layer height, shrub layer height, and visibility (VIEW) varied significantly between habitats (Kruskal-Wallis ANOVA: $\chi^2 = 177.1$, $df = 4$, $p < 0.001$ for layer height; $\chi^2 = 219.3$, $df = 4$, $p < 0.001$ for shrub height; $\chi^2 = 57.5$, $df = 4$, $p < 0.001$, for VIEW; Table 1). During the course of the study period, habitat usage changed (Fig. 1), with the frequency of usage of coniferous wood declining, and that of deciduous wood and meadow increasing. Farmland was increasingly used in the middle of the period, but then declined. Moorland use had the opposite trend with a mid-period decrease followed by an increase to its former level. The

Table 1. Mean values (\pm SD) of herbaceous layer height, shrub layer height and VIEW (all values in m) at roe deer fawn bed-sites in the different habitat classes.

Habitat	Herbaceous layer	Shrub layer	VIEW
Coniferous	0.25 \pm 0.14	1.84 \pm 1.23	0.64 \pm 0.34
Deciduous	0.19 \pm 0.18	1.46 \pm 1.49	0.74 \pm 0.61
Moorland	0.28 \pm 0.26	1.24 \pm 1.07	0.65 \pm 0.47
Meadow	0.48 \pm 0.39	0.78 \pm 1.03	0.54 \pm 0.66
Farmland	0.50 \pm 0.18	0.06 \pm 0.24	0.29 \pm 0.56

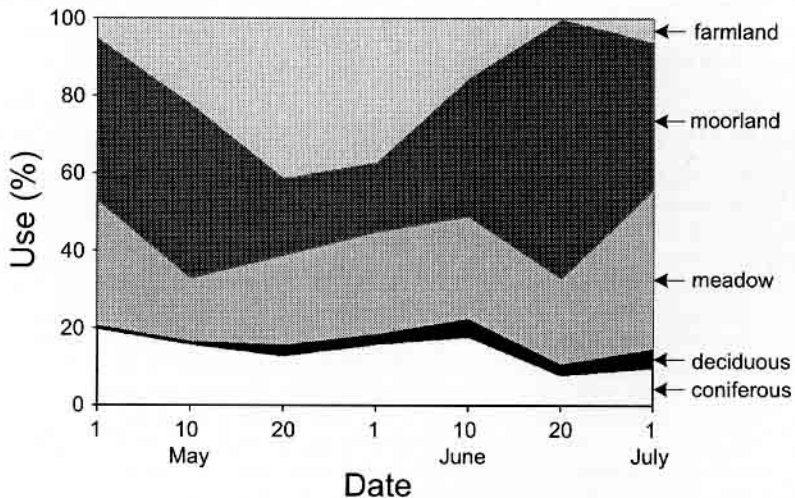


Fig. 1. Percentage use of the different habitat classes by roe deer fawns during the summer in central Norway.

effects of vegetation succession can be seen from changes in cover parameters at the bed-sites during the summer with herbaceous layer height increasing (ANCOVA: $F = 136.1$, $df = 1,694$, $p < 0.001$, $y = 0.05 + 0.01$ m/day) and shrub layer height decreasing ($F = 14.3$, $df = 1,667$, $p < 0.001$, $y = 1.48 - 0.01$ m/day), but with the resultant overall visibility decreasing significantly ($F = 21.66$, $df = 1,251$, $p < 0.001$, $y = 0.99 - 0.02$ m/day). The interaction between habitat class and time was significant ($F = 14.1$, $df = 2,250$, $p = 0.014$), indicating that the temporal change in VIEW differed between habitat classes. When analysing the relationship between VIEW and year day for the habitat classes separately, only meadow had a significant decrease in VIEW ($p = 0.005$). Comparison of bed-sites of fawns under 20 days of age in May and of similar age in June reveals the same trends (Mann-Whitney U -test: $U = 10037$, $n = 379$, $p < 0.001$ for herbaceous layer height; $U = 11811$, $n = 379$, $p < 0.001$ for shrub layer heights; $U = 2823.5$, $n = 210$, $p = 0.002$ for VIEW) indicating that the changes are primarily due to vegetational succession and not to fawn age effects.

Bed-site habitat selection

There was an overall significant difference between the habitat at bed-sites and its availability within the individual family home ranges (Wilk's lambda: $\lambda = 0.525$, $df = 4,28$, $p = 0.001$). Establishing a ranking matrix based on the log-ratios (Table 2) revealed the following rank: meadow > moorland > coniferous > deciduous > farmland (the underlining refers to habitats types that were not ranked significantly different from each other). However, there was a significant difference in habitat selection between fawns born before the peak of the birth season from the fawns born after (Wilk's lambda: $\lambda = 0.688$, $df = 4,27$, $p = 0.034$). When separating the two periods, the ranking for early summer was (Table 3): coniferous > deciduous > meadow > moorland > farmland. For the fawns born after the peak of the birth season, we found no evidence of habitat selection (Wilk's lambda: $\lambda = 0.523$, $df = 4,8$, $p = 0.217$).

Table 2. Ranking matrix of log-ratios derived from compositional analysis of roe deer fawn habitat selection (of bed-sites) during the whole study period. A negative value in the matrix indicates that the habitat class at the upper line is used more than expected by chance compared to the habitat in the left hand column (* - significant at 0.05, ** - significant at 0.005).

Habitat	Meadow	Moorland	Coniferous	Deciduous
Moorland	-0.14 (0.32)			
Coniferous	-0.39 (0.43)	-0.15 (0.45)		
Deciduous	-0.71 (0.72)*	-0.67 (0.67)	-0.27 (0.70)	
Farmland	-2.00 (0.47)**	-1.87 (0.44)*	-2.32 (0.56)*	-1.05 (0.70)

Table 3. Ranking matrix of log-ratios derived from compositional analysis of roe deer fawn habitat selection (of bed-sites) for fawns born before the mean birth date (May 23rd). A negative value in the matrix indicates that the habitat class at the upper line is used more than expected by chance compared to the habitat in the left hand column (* – significant at 0.05, ** – significant at 0.005).

Habitat	Coniferous	Deciduous	Meadow	Moorland
Deciduous	-0.49 (1.04)			
Meadow	-0.58 (0.44)	-0.03 (1.20)		
Moorland	-0.19 (0.47)	-0.05 (1.03)	-0.18 (0.47)	
Farmland	-3.53 (0.71)**	-0.71 (1.20)*	-1.53 (0.59)*	-1.41 (0.58)*

Discussion

When considering the adaptation and flexibility of roe deer to diverse habitats it is not surprising that fawn bed-sites were found in all available habitat types, including agricultural pastures and even vegetable gardens. The fine-scale mosaic of vegetation types in the study area provided most animals with a choice between most of the available habitat types. However, the results of this study show that these were not used in the same proportion as they occurred.

The temporal pattern of bed-site habitat usage reflected the succession of vegetation development at this latitude. During early-May the grass on pastures was only beginning to develop along with the herbs on the abandoned meadows and in the deciduous woodland. During this period most bed-sites were in coniferous woodland and moorland where heather and other evergreen or woody plants and shrubs provided the best cover. The open pasture was the first habitat to develop a rich herbaceous layer and by late May and early June was at its maximum height, and was used by the most fawns at this time. Unfortunately this was the period at which fawns are vulnerable to being killed in grass mowers as many had still not developed the flight response at this age (Kałuziński 1982, Linnell *et al.* 1998). Later in June after the first cuts of grass for silage the use of fields dropped again and remained low. By this time the herbaceous layers in the meadows and deciduous forests were well developed and their use increased. As the vegetation succession advanced the increasing height of the herbaceous layers in all habitats reduced the visibility of fawns and provided better cover. As the herbaceous layer increased at bed-sites the average height of shrubs at bed-sites decreased, indicating a decreased dependence on shrubs to provide cover. This pattern of decreasing dependence on shrubs and increase in use of herbs was also found for roe deer fawns in a Norwegian boreal forest study site (Linnell *et al.* 1999).

Regardless of habitat type used, all fawns bedded in sites that provided excellent cover. The area of the circle with the mean value of VIEW (ca 0.5 m) was 0.79 m². It was inside this area that a predator would be able to visually detect the fawn. In

many cases the VIEW was actually zero. This is much lower than the estimates of 4 m and 20 m reported for pronghorn (Byers and Byers 1983). Although we have no estimates of alternative cover availability (and cannot test for active selection), this ability to make good use of cover, as indicated by the constantly low visibility, is consistent for other studies on cervids where fawns select vegetation with better cover than the surrounding areas (Tucker and Garner 1983, Huegel *et al.* 1986, Alldredge *et al.* 1991, Gerlach and Vaughan 1991, Canon and Bryant 1997, Bowyer *et al.* 1998, Linnell *et al.* 1999).

Habitats were not used randomly. When considering the whole period farmland was avoided, and abandoned meadows were the most preferred habitat. However, this overall picture hides the temporal response to phenological development of the herbaceous vegetation. Fawns born before the peak birth season when herbaceous vegetation was poorly developed selected those habitats that had evergreen or shrub vegetation, and farmlands were avoided to a significant degree. However, for fawns born after the peak birth season there was no demonstrable preference or avoidance of habitats. In this period, the herbs, and grass on the fields, had developed to such an extent that good cover was available in all habitats so that selection was not necessary to gain access to concealed bed-sites.

In terms of the overall neonatal survival strategy of roe deer, it appears that there is an avoidance of the most open habitats (farmland) early in the season when the height of the grass is low. Although even short grass can provide cover for a fawn when it is crouched, it is likely that it is avoided because of the general lack of canopy cover to protect fawns from rain at a time of the year when temperatures can be cold (Barrett 1981, Gaillard and Delorme 1989), and because the short grass does not provide any cover for the fawn when walking beside the doe during movement or lactation. As predators may greatly increase the effectiveness of searching for neonates by taking cues from the mother (Byers and Byers 1983, Fitzgibbon 1993), we should expect roe deer does to avoid hiding their fawns in open habitats that will not conceal an active or standing fawn while giving it milk. Parallel studies have also shown that fawns in farmland are exposed to the greatest levels of red fox predation (Aanes and Andersen 1996), indicating that avoidance of farmland will have survival value. However, the overall picture is one of roe deer fawns finding effective hiding cover in all habitats within our study area. This general use of all habitats implies that a predator has to search in all habitats, greatly decreasing the search efficiency, and increasing the chances that alternative prey will be preferred (Byers and Byers 1983), however it is not possible to determine from our data if this is a deliberate strategy or a consequence of there being good cover in all habitats.

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