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Selection of bed-sites by roe deer *Capreolus capreolus* fawns in a boreal forest landscape

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Bed-site selection by 19 radio-collared roe deer Capreolus capreolus fawns from seven family groups was studied during June-July 1998 in southeastern Norway. The habitat consisted of small agricultural fields surrounded by industrially exploited boreal forest. Within the forest, fawns selected bed-sites that offered greater concealment, higher vegetation and more canopy cover than random sites. No such selection was evident within the homogenous pasture on the fields. Bed-sites in fields offered greater concealment than those in the forest, where there were no detectable differences between stand age classes. Compositional analysis revealed a significant preference for bed-sites to be located in forest, although fields and bogs were often used. Within the forest, stands of all age classes were used. The broad use of habitats may either reflect that habitats were equally good, or it may be a strategy to increase the area a predator has to search in order to find a fawn.

Key words: anti-predator behaviour, bed-sites, Capreolus capreolus, habitat selection, hiding behaviour, roe deer

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Neonatal ungulates are often exposed to high rates of mortality due to predation, starvation, or exposure in the first weeks following birth, with losses in many cases being over 50% (Linnell, Aanes & Andersen 1995, Byers 1997). Roe deer *Capreolus capreolus* are no exception to this pattern, with various studies reporting neonatal mortality rates of 17-50% (Aanes & Andersen 1996, Gaillard, Boutin, Delorme, van Laere, Duncan & Lebreton 1997, Gaillard, Liberg, Andersen, Hewison & Cederlund 1998, Andersen & Linnell 1998, Linnell, Wahlström & Gaillard 1998) depending on density and predator presence. As for other hider-type species, a secluded bed-site is the main protection against searching predators and in-

clement weather available to roe deer fawns (Lent 1974, Barrett 1981, Alldredge, Deblinger & Peterson 1991, Canon & Bryant 1997, Bowyer, Kie & van Ballenberghe 1998). During the first four weeks of life, roe deer fawns spend up to 80% of their time lying passive in their bed-sites, while the mother forages within 50-1,000 m (Linnell 1994, Linnell et al. 1998).

Given the reliance on bed-sites as a means to protect fawns, it might be expected that bed-sites should be carefully selected to provide good cover. If roe deer fawns are very selective for specific habitat characteristics, ensuring their availability should be an important aspect of habitat management, and

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would need to be taken into account when planning forestry or grazing activities (e.g. Loft, Menke, Kie & Bertram 1987). Although bed-site selection by adult roe deer has been studied (Mysterud & Østbye 1995, Mysterud 1996), very little data exist concerning bed-site selection by roe deer fawns (Gaillard & Delorme 1989, Linnell et al. 1998). In this study, we examine bed-site selection by roe deer fawns, living in boreal forest habitats, at two levels, i.e. selection of micro-sites and selection of main habitat types. In contrast to earlier studies (Gaillard & Delorme 1989, Linnell 1994) which were conducted at sites where predation on neonates was virtually non-existent, the major predators (Aanes, Linnell, Perzanowski, Karlsen & Odden 1998) of roe deer fawns like red fox Vulpes vulpes and Eurasian lynx Lynx lynx were present in our study site.

Study sites

Our study was conducted in the municipalities of Åmot and Trysil, in the county of Hedmark (61°10'N, 11°40'E), southeastern Norway. The area is almost entirely covered with coniferous forests of Scots pine Pinus sylvestris and Norway spruce Picea abies below 900 m a.s.l. Because the forest is intensively exploited, the landscape consists of a fine-grained mosaic of discrete stands of different ages. The climate is continental with cold, snowy winters (January average = -11°C) and warm summers (July average = 19°C). The predator community is relatively intact within the area. Red foxes were regaining their former abundance at the time of the study, following the sarcoptic mange epidemic of the 1980s (Lindström, Andrén, Angelstam, Cederlund, Hörnfeldt, Jäderberg, Lemnell, Martinsson, Sköld & Swenson 1994). Resident lynx were found throughout the area, and a few transient wolves Canis lupus were occasionally present. Although most domestic dogs are kept under control during summer, a few dogs are always running free close to houses.

Roe deer exist at very low densities (<1/km²) within the study area (Linnell, Støen, Odden, Ness, Gangås, Karlsen, Eide & Andersen 1996). During winter they concentrate along valley bottoms and around artificial feeding sites. In summer some remain at their winter sites or else make short migrations (Holand, Mysterud, Wannag & Linnell 1998). Our study concentrated on three different sites, Stener, Nordre Odden and Åsbygda where roe deer are fed

during winter. Each site consisted of a small enclave of human settlement and agricultural land (mainly small fields given over to grass production for hay and silage) within the surrounding boreal forest.

Methods

Capture and radio-collaring of animals

Adult female roe deer were caught in box-traps at winter feeding sites from 1995 through 1998. Animals were restrained manually and fitted with radio-collars. During the birth season (June in Hedmark see Linnell & Andersen 1998), the adult females were checked several times a week for signs of udder development. When it was apparent that a female had given birth, searches were made for her fawns. When found, each fawn was fitted with a small radio-transmitter (30 g) on an elastic collar. This was exchanged for a larger (100 g) transmitter on an expanding collar when the fawns reached 10 days of age. All radio-collars were manufactured by Televilt International AB.

The results presented here are based on 19 radio-collared fawns, born during June 1998 to seven radio-collared adult females (one each at Stener and Nordre Odden, five at Åsbygda). Data on bed-site and habitat use were collected from 3 June to 10 July. Three of the fawns died during the study period; two were killed by red foxes and one by a domestic dog. In earlier years of study in the same area, fawn mortality caused by red fox and lynx predation has also been observed, along with cases of starvation/ hypothermia (Linnell et al. 1996).

Radio-tracking and habitat sampling

After capture the roe deer fawns were located approximately each day. Each fawn was approached until visual contact was made, up until 2-3 weeks of age when they began to flush (Linnell et al. 1998). The bed-sites were marked and examined the next day, after the fawn had moved to a new location. For each bed-site and a random site located 50 m to the north, the following parameters were recorded, most of which were adapted from Mysterud (1996). The habitat type at the bed-site was categorised as either bog, field, forest or other (usually gardens). The forest sites were further categorised into age classes following the standard Norwegian system (I = clearcuts, II = young plantations, III = pole sized stands, IV = medium aged stands, V = mature stands). The height

of the tallest vegetation at each bed-site was measured with a tape measure. A 'model' fawn was placed on the exact bed-site. The distance at which the model was completely hidden at fox height (30 cm) was recorded from each of the four cardinal directions. The average of these values was used as a measure of visibility to predators. The distance to the nearest tree, the diameter of this tree, and the height of the first overhanging branch were all recorded. Canopy cover was measured using a flat mirror with lined grid angled so as to reflect the view from directly above the bed-site. The plant group covering most of the ground was recorded within each 10×10 cm square of a 50×50 cm quadrat centred on the bedsite. Six categories were recognised; herbs, grasses, wood (fallen branches and tree trunks), bushes (less than 130 cm), dwarf shrubs (mainly heather Calluna sp. and bilberry Vaccinium sp.), and low ground cover (lichens, moss, leaf litter, soil). After fawns became old enough to flush, we stopped locating their exact bed-site. These individuals were only approached to a distance where the habitat type in which they were lying could be identified.

Habitat availability

Within the home range of each sibling group, the availability of main habitat types was estimated by reading the habitat type at each of at least 100 systematic points in a grid superimposed on a forest map (1:5000) of the area. It was not possible to determine the relative availability of forest age classes within individual home ranges from these maps. However, a rough estimate of their overall availability was estimated by walking transects and recording the age class at 50 m intervals at two of the study sites (100 points each at Nordre Odden and Åsbygda).

Statistics and analysis

Each bed-site was regarded as an independent point for analysis of micro-site selection. However, because of a high degree of dependency between the movements of siblings, we calculated all home range data for family groups rather than individual fawns. Home ranges were analysed using the minimum convex polygon method and the RANGESV program (Robert Kenward, ITE, United Kingdom). Bed-sites were compared to random sites using the non-parametric Wilcoxon pair-test. Non-parametric tests, Kruskal-Wallis ANOVA and Mann-Whitney U-test,

were used throughout. Results are presented as means with standard deviation. Habitat selection within home ranges was analysed using compositional analysis (Aebischer, Robertson & Kenward 1993). Three habitat types were included in the compositional analysis, forest, fields and other (bogs and gardens combined). Due to a low sample size, and lack of detailed availability data, forest age-classes could not be incorporated into the compositional analysis. Varying availability of different age-classes within different family group home ranges may thus have biased the estimates of use of forest habitat. However, the fact that the use of different age classes of coniferous forest was approximately equal to their availability (see Results) indicates that this may not be a serious problem. Compositional analysis requires that there should be no missing values for either habitat use or availability. Following recommendations in Aebischer et al. (1993), missing values on habitat use were replaced by an estimated value using the formula (0.5/number of habitat types)/ (number of locations + 0.5). The first option in Appendix 2 of Aebischer et al. (1993) was chosen to treat missing values on habitat availability, since this method does not cause biases when only few habitats are missing (only the 'other' habitat was missing from within two home ranges).

Results

Selection of micro-sites

Within forest habitats, roe deer fawns demonstrated a clear selection for bed-sites that offered taller vegetation, lower visibility and greater canopy cover than that which was available at nearby random sites. However, they showed no selection for sites that were closer to trees (Table 1). Because fields offer a very homogenous distribution of cover, it was not surprising to find no significant difference between bed-sites and random sites in fields (see Table 1).

Bed-sites in the fields offered better cover than those in the forest, with significantly higher vegetation (76 \pm 25 vs 57 \pm 32 cm, U = 2824, P < 0.001) and lower visibility (35 \pm 79 vs 164 \pm 98 cm, U = 516, P < 0.001). By definition, bed-sites in the fields had no canopy cover, and were not close to trees. Within the forest, the degree of canopy cover increased significantly with increasing age class (from 32 \pm 34% in age class I to 86 \pm 16.2% in age class V, ($\chi^2 = 24.6$, df = 4, P < 0.001). However, there were

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Table 1. Hiding cover at bed-sites of roe deer fawns as compared to paired random sites. P-value refers to result of Wilcoxon pair-test,

| | N | Bed-site | | | Random site | | | |
|---|-----|----------|------|-----|-------------|------|-----|-------|
| | | Median | Mean | SD | Median | Mean | SD | P |
| Hiding cover: | | | | | | | | |
| Height of vegetation (cm) in forest | 133 | 60 | 58 | 32 | 38 | 43 | 31 | 0.000 |
| Height of vegetation (cm) in field | 47 | 80 | 76 | 25 | 80 | 70 | 24 | 0.052 |
| Visibility at fox height (cm) in forest | 103 | 145 | 156 | 87 | 250 | 298 | 184 | 0.000 |
| Visibility at fox height (cm) in field | 31 | 0 | 28 | 79 | 0 | 76 | 190 | 0.345 |
| Canopy cover (%) in forest | 104 | 78 | 65 | 39 | 58 | 54 | 39 | 0.013 |
| Nearest tree: | | | | | | | | |
| Distance to trunk (cm) in forest | 100 | 100 | 191 | 248 | 140 | 230 | 316 | 0.106 |
| Diameter of trunk (cm) in forest | 98 | 8 | 11 | 12 | 8 | 11 | 11 | 0.470 |
| Height to lowest branch (cm) in forest | 100 | 110 | 190 | 200 | 150 | 216 | 213 | 0.495 |

no significant differences between forest age classes for either the height of vegetation at the bed-site $(\chi^2 = 7.4, df = 4, P = 0.117)$ or the degree of visibility $(\chi^2 = 4.9, df = 4, P = 0.3)$.

A diverse range of plants species were found at both bed-sites and random sites within the forested habitats. No selection was demonstrated for bushes and herbs within either the early, or late halves, of the season (Table 2). However, some selection and avoidance was observed for the other categories. Fallen branches and tree trunks were selected for during the early period when other vegetation may not have developed sufficiently. As herbs developed and provided more ground cover (increase from 11 to 37% at random sites), the selection for wood vanished, and grasses and low shrubs were actually avoided. The 'ground' category was always abundant, and was actually selected for in the latter period.

Selection of main habitat types within the home range

Almost all available habitats within their home range were used by the roe deer fawns for bed-sites, including forests, fields (pasture and grain) and bogs (Table 3). Unsurprisingly, only gardens and roads were not used. Habitat use was significantly different from availability at the within home range scale (χ^2 = 17.305, df = 2, P < 0.005), with the habitats ranked -Forest > Field = Other. In other words, only forest was significantly more preferred than any of the other categories, which were preferred to the same degree. All forest age classes were used, from recent clear-cuts to over-mature stands in approximately the same percentage as they were available. The percentage use of age classes I, II, III, and IV-V (combined) was 31%, 24%, 25% and 20%, respectively. Lack of detailed availability data precluded statistical analysis, but from our transects the overall availability within the forests typical of the area was 27%, 19%, 29% and 26%, respectively.

Table 2. Vegetation composition of a 50×50 cm area surrounding the bed-sites of roe deer fawns and paired random sites within forest habitats only. P-value refers to result of Wilcoxon pair-test.

| Vegetation | Time | N | Bed-site | | | Random site | | | |
|------------|-------|----|----------|------|----|-------------|------|--------------------------------|-------|
| | | | Median | Mean | SD | Median | Mean | SD | P |
| Bushes | Early | 55 | 0 | 2 | 9 | 0 | 0 | 0 | 0.109 |
| | Late | 49 | 0 | 2 | 14 | 0 | 1 | | 0.655 |
| Herbs | Early | 55 | 0 | 15 | 25 | 0 | 11 | 22 | 0.201 |
| | Late | 49 | 36 | 39 | 31 | 32 | 37 | 33 | 0.751 |
| Low shrubs | Early | 55 | 0 | 15 | 23 | 12 | 21 | 26 | 0.175 |
| | Late | 49 | 0 | 3 | 10 | 0 | 9 | SD 0 5 22 33 26 21 31 28 26 20 | 0.088 |
| Ground | Early | 55 | 52 | 54 | 30 | 48 | 51 | 31 | 0.478 |
| | Late | 49 | 44 | 51 | 29 | 28 | 35 | SD 0 5 22 33 26 21 31 28 26 20 | 0.003 |
| Grass | Early | 55 | 0 | 7 | 14 | 0 | 13 | 26 | 0.078 |
| | Late | 49 | 0 | 4 | 11 | 0 | 15 | 20 | 0.003 |
| Wood | Early | 55 | 0 | 8 | 14 | 0 | 4 | 11 | 0.047 |
| | Late | 49 | 0 | 1 | 5 | 0 | 3 | 11 | 0.249 |

Table 3. Use and availability (%) of main habitat types for bed-sites within the home ranges (in ha) of roe deer fawn family groups in Hedmark, SE Norway, during summer 1998.

| Family | Area (ha) | Forest | | Field | | Bog | | Other | |
|--------|-----------|--------|--------|-------|--------|-----|--------|-------|--------|
| | | Use | Avail. | Use | Avail. | Use | Avail. | Use | Avail. |
| #32 | 103 | 82 | 66 | 0 | 17 | 18 | 17 | 0 | 0 |
| #49 | 67 | 100 | 90 | 0 | 8 | 0 | 2 | 0 | 0 |
| #52 | 92 | 100 | 96 | 0 | 4 | 0 | 0 | 0 | 0 |
| #53 | 44 | 57 | 35 | 43 | 42 | 0 | 0 | 0 | 23 |
| #54 | 107 | 78 | 75 | 22 | 21 | 0 | 0 | 0 | 4 |
| #56 | 60 | 89 | 77 | 11 | 23 | 0 | 0 | 0 | 0 |
| #58 | 56 | 22 | 14 | 78 | 71 | 0 | 0 | 0 | 15 |

Discussion

When compared to most other study sites where roe deer have been studied in Europe, the complete range of factors, most notably the predators, that could affect fawn survival are present in our Hedmark study site. We therefore expected strong selection pressure for effective hiding behaviour to be operating in this population. Not surprisingly, roe deer fawns in Hedmark selected bed-sites which offered better hiding cover than that which was available at random sites within forested habitats. Height of vegetation, and canopy cover were greater than expected, which led to a reduced visibility to searching predators. Such results have also been reported for other hider-type species like white-tailed deer Odocoileus virginianus, mule deer O. hemionus and pronghorn Antilocapra americana in North America (Tucker & Garner 1983, Huegel, Dahlgren & Gladfelter 1986, Alldredge et al. 1991, Gerlach & Vaughan 1991, Canon & Bryant 1997). On the homogenous fields, bed-sites did not differ from random sites. However, fields were not used until the grass had reached a sufficient height to provide effective cover.

Although there was some slight selection for and avoidance of specific vegetation components at bedsites within forests, the most striking feature was the large amount of low ground covering types (lichens, moss, litter) at the actual bed-site. This substrate type probably provides a greater degree of 'comfort' for lying fawns and allows them to lie closer to the ground which maximises the benefit from the surrounding provided by the other vegetation types (Canon & Bryant 1997). The main degree of cover was provided by low shrubs during the early period and by herbs in the later period, a pattern consistent with the successional development of vegetation during early summer. From the point of view of Bowyer et al.'s (1998) study of cover/food trade-offs, this presence of roe deer summer food (herbs) at fawn

bed-sites indicate that probably there is no trade-off between fawn hiding cover and adult food availability. However, when the distance between adult does and their hidden fawns is considered (Linnell et al. 1998), it seems unlikely that adult doe habitat selection is conditional on fawn habitat selection in these fine-scaled, mosaic habitats.

As in other studies (Riley & Dood 1984, Wallace & Krausman 1992, Linnell 1994) forests were preferred to other habitats at the within family group home range level in our study area. Even though forest habitats were preferred (relative to their availability) there was still extensive use of the field and bog habitats for bed-sites, to the extent that family group #58 had the majority of their bed-sites on the field. Although fields offered better concealment for bedded fawns when viewed from fox height, fields do not offer any concealment for adult females (Tufto, Andersen & Linnell 1996). Therefore, fields may not be favoured because of the risk of predators being able to watch the mother approach her fawns and use her cues to locate the fawn (Byers & Byers 1983, Fitzgibbon 1993). This argument was used by Aanes & Andersen (1996) to explain higher predation on roe deer fawns that used bed-sites on fields in another Norwegian study site. Within the forests, the broad use of stands of different age classes by the fawns, contrasts with the results of Gaillard & Delorme (1989) in France, who found a strong selection for forest openings. As the bed-sites in different age classes did not differ in the height of vegetation or the concealment offered in our study site, the consequences of this lack of selection are likely to be small. Such contrasting results highlight the different structures of the understory in Scandinavian coniferous and European deciduous forests. In the latter, the understory is often poor due to a combination of ungulate browsing and shading by the canopy.

The overall picture is one of roe deer fawns selecting micro-sites which offer better than expected concealment, due to dense ground vegetation rather than trees and bushes. Although forest was preferred, all habitat types were utilised, and stands of all age classes were used. Because the roe deer fawns were able to achieve effective concealment in virtually all situations this broad use of habitats may simply imply that all habitats were equally good in our study area. An alternative, and not mutually exclusive, hypothesis could be that broad patterns of habitat use is an adaptive strategy. Using only one preferred habitat would greatly reduce the area that a predator would have to search. Therefore, because fawns use all possible habitats, a predator is forced to search all available habitats, greatly increasing the energetic costs of hunting fawns, and thereby increasing the effectiveness of the hider strategy (Linnell 1994, Linnell et al. 1998).

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