

Bed-site selection by adult roe deer *Capreolus capreolus* in southern Norway during summer

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Bed-sites of radio-collared adult roe deer *Capreolus capreolus* were identified during summer 1994 in the Lier valley, southern Norway. Site characteristics were measured at the bed-site and at a randomly chosen site 50 m away. Roe deer preferred to bed down below dense canopy cover, but showed no preference for bedding close to tree trunks. The availability of herbs was higher at bed-sites than at random sites, and higher at bed-sites used by females than at bed-sites used by males. On warm days the abundance of herbs at bed-sites was lower than on cold days, indicating movement away from feeding sites. During warm days roe deer selected bed-sites with humid substrates, probably to increase heat loss by conduction. Bed-sites were well concealed.

Key words: bed-site selection, *Capreolus capreolus*, cover, habitat, roe deer, substrate, temperature, thermal strategies

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Habitat selection is usually evaluated by comparing utilisation of a habitat relative to its availability (Neu et al. 1974, Johnson 1980, Aebischer et al. 1993, Manly et al. 1993, Arthur et al. 1996). Habitat selection studies on roe deer *Capreolus capreolus* have estimated utilisation based on number of radio-telemetry fixes (Cederlund 1983, Cibien & Sempere 1989, Selås et al. 1991), pellet groups (Henry 1981, Aulak & Babinska-Werka 1990a,b) or direct sightings of individuals (Aulak & Babinska-Werka 1990a). These studies, however, fail to recognise that cervids have a feeding-resting-feeding rhythm (e.g. Cederlund 1981, 1989, Jeppesen 1989), and that choice of habitats may differ between feeding sites and resting sites.

Stüwe & Hendrichs (1984) found that roe deer only sought bed-site cover when feeding sites were within 400 metres of forest edges. This suggests that choice of feeding site is most important for habitat selection by roe deer on a large scale, and is related to both plant quantity and quality (e.g. Hanley et al. 1987, Hjeljord et al. 1990). However, when microhabitat selection is considered, the choice of bed-sites may differ from the choice of feeding sites (e.g. Huot 1974, Armstrong et al. 1983, Lang &

Gates 1985, Smith et al. 1986, Sargeant et al. 1994, Mysterud & Østbye 1995a). Thus, we may gain valuable new insight into habitat selection by differentiating these two activities. But so far, no studies of bed-site selection have been conducted in forested habitats in Scandinavia during summer.

When ambient temperatures exceed an animal's upper critical temperature (UCT), the animal per definition experiences additional thermoregulation costs (Bakken 1980, Parker & Robbins 1985). Two reported strategies by which ungulates may relieve heat stress (and thus lower energy expenditure) through bed-site selection are: 1) to bed under a dense canopy cover for shade (Belovsky 1981, Schwab & Pitt 1991, Sargeant et al. 1994, Demarshi & Bunnell 1995) and/or 2) to use a wet bed-site substrate which leads to greater heat-loss through conduction (Gatenby 1977, Jacobsen 1980, Merrill 1991, Sargeant et al. 1994).

This paper presents data from 80 bed-sites of radio-collared roe deer in southern Norway, and tests the predictions that roe deer use denser canopy cover and/or a more humid bed substrate when selecting a bed-site during hot weather.

Methods

Study area

The study area is located in the hilly terrain of the Lier valley in southern Norway (between 59°52'-59°58'N and 10°10'-10°20'E). Most of the area is forested, but vegetation varies on local as well as regional scales with both coniferous and deciduous tree species (see Mysterud & Østbye 1995a,b for a detailed description of the study area).

Sampling procedure

Roe deer were captured with box-traps during March 1994 and fitted with radio-collars (Televilt transmitters). The radio-collars were equipped with activity switches that, by changing the number of signals per time unit, indicated whether deer were active or inactive. Three territorial males and two females were followed. One female had at least two calves, while the other assumably lost its calf/calves during the summer.

The general location of the deer was determined by short distance triangulation. When transmitters indicated that they were inactive, the deer were stalked and their position located more accurately from the noise made by the fleeing deer. The exact bed-site was identified by flattened vegetation or substrate, often while the bed was still warm. Usually, it was possible to hear the fleeing deer. If two or more deer were flushed, it was usually easy to distinguish them from each other as they often were more than 10 metres apart.

Individual roe deer were located and registered randomly. Having located the bed-site of a deer, this deer was not located until all the other deer had been checked: all animals were located and recorded an equal number of times. The same deer was never recorded more than once a day. Since roe deer daily moved over most of their home range (A. Mysterud unpubl. data), the location of each bed-site was regarded as independent of the location of all other sites. Due to transmitter failure, one doe was located and registered only eight times, while each of the other four animals were recorded 18 times. After being disturbed, the roe deer often bedded a few hundred metres away. The disturbance is unlikely to have affected their behaviour, since deer in this area are prone to disturbances by humans.

The sampling procedure may, however, cause a bias in the duration of the bedding period towards beds used for longer periods, as it takes a few minutes to get an accurate triangulation of the animal after it has bedded down. Activity studies on roe deer have excluded activity/inactivity bouts of less than five minutes (Cederlund 1981), and therefore, in the present study only bed-sites in which the duration of bedding period was longer than five min-

utes were recorded. The study was conducted during the daytime (0800-2000) from mid-May to mid-July 1994.

Food characteristics

The availability of herbs, grasses, bilberry *Vaccinium myrtillus*, bracken and mosses was estimated within a 2 × 2 m square centered in the bed. The number of 10 × 10 cm squares covered by each of the different plant species/groups was then divided by the total number to give relative percentages in the entire 2 × 2 m square. A separate category included other vegetation, litter and bare soil.

Cover characteristics

- The distance to and diameter at breast height (dbh) of the nearest tree were measured. When the distance was less than five metres, the type of tree was noted as either a coniferous or deciduous tree.
- Canopy cover was measured (and given in %) using Lemmon's densiometer (Lemmon 1956, 1957) 30 cm above ground to simulate the height of the bedded animal (Mysterud & Østbye 1995a).
- Hiding cover, defined as potential for concealment, was measured using a 30 × 40 cm coverboard (Nudds 1977) with 40 gridcells (5 × 6 cm) each representing 2.5% cover. In a random direction, the minimum distance required for the board to be completely hidden at eye level was determined (hc1). The number of grid cells covered at five (hc2) and 30 metres (hc3) from the bed-site in a random direction was also counted. It was noted whether vegetation or topography obstructed visibility.

Thermal factors

Air temperature, windspeed and total incoming solar radiation (solarimeter, Thermo-Schneider) were measured ca 5-10 cm above ground at bed-sites, random sites (see below) and in open habitat (canopy cover = 0%). Ground humidity was measured (in %, Lambrecht hygrometer) in the upper layer of the substrate (0.5-1 cm below the surface) in order to estimate the potential for heat loss by conduction. It was also recorded whether deer had scraped the substrate at the bed-site before bedding down.

Statistical analysis

All parameters were measured at both the bed-site and at a site 50 metres away in a random direction (random site). To establish differences in local habitat parameters, pairwise comparisons were made. Continuous data were analysed using the Wilcoxon pair-test, and categorical data (e.g. coniferous or deciduous trees) using a sign test (Wilkinson et al. 1992a).

I tested 1) whether visibility at bed-sites was obstructed by vegetation more frequently than by topography (Sign test); 2) whether bed-sites where vegetation obstructed visibility were better concealed than bed-sites where topography obstructed visibility (hc1), 3) and whether females were better hidden than males. Spearman's correlation coefficients were calculated to examine the relationship between the various cover variables, and between the cover variables and the availability of herbs.

The relationship between temperature and bed-site characteristics (availability of herbs, canopy cover, humidity in bed substrate) was investigated using ANCOVA models with sex as a categorical variable and temperature as a covariate. In testing, humidity was entered as difference in humidity in substrate between bed-sites and corresponding random sites, since average humidity will decrease at high temperatures. To control for the possible confounding effect of differences in canopy cover between bed-sites and random sites, I also entered difference in canopy cover closure between bed-sites and random sites in this test. The upper critical temperature limit is not reported for roe deer, making the described approach the best option, though this may lower the power of the test. I transformed both availability of herbs and canopy cover ($\arcsin[\sqrt{\text{availability of herbs or canopy cover}/100}]$), since they were measured as percentages. Using logistic regression (Steinberg & Colla 1992), I also tested whether bed scraping (scraped or unscraped)

was more often performed by males than by females and if it increased on hot days.

Results

Food characteristics

There was a higher availability of herbs (mean 21%) at bed-sites than at the random sites (mean 13%), but random sites had a higher availability of grasses (mean 10%; bed-site mean 5%, Table 1). The availability of bilberry, bracken, mosses and others was not significantly different between bed-sites and random sites (see Table 1). At 13.8% of the bed-sites, no potential forage plants (herbs, grasses, bilberry) were found. At 37.5% of the bed-sites (N = 80) forage plants constituted less than 10% of the total ground cover.

Cover characteristics

Roe deer showed no preference for: a) bedding below coniferous trees as compared to deciduous trees (N = 65, P = 0.170), b) bedding closer to a tree than would be expected by chance, and random trees 50 metres away from the bed-site were no larger (dbh) than the trees closest to the bed (see Table 1).

Canopy cover above bed-sites was denser than above random sites, but with a large overlap in the distribution (Fig. 1).

Table 1. Bed characteristics and test results of Wilcoxon pair test between bed-sites and corresponding random sites (see text).

| | N | Bed-sites | | Random sites | | P |
|-------------------------------|----|-----------|--------|--------------|--------|-------|
| | | Mean | Median | Mean | Median | |
| Closest tree: | | | | | | |
| Distance to trunk (cm) | 64 | 112 | 100 | 127 | 100 | 0.291 |
| Dbh (cm) | 64 | 11 | 9 | 12 | 10 | 0.489 |
| Canopy cover (%) | 80 | 61 | 66 | 46 | 52 | 0.001 |
| Hiding cover: | | | | | | |
| hc1: total (m) | 80 | 12 | 10 | 20 | 15 | 0.000 |
| hc2: 5 m (%) | 80 | 47 | 38 | 29 | 18 | 0.000 |
| hc3: 30 m (%) | 80 | 98 | 100 | 90 | 100 | 0.003 |
| Availability (%) of: | | | | | | |
| Herbs | 80 | 21 | 10 | 13 | 5 | 0.004 |
| Grasses | 80 | 5 | 0 | 10 | 0 | 0.035 |
| Bilberry | 80 | 4 | 0 | 7 | 0 | 0.137 |
| Bracken | 80 | 9 | 0 | 5 | 0 | 0.118 |
| Mosses | 80 | 7 | 0 | 3 | 0 | 0.068 |
| Others | 80 | 54 | 55 | 62 | 67 | 0.105 |
| Air temp. (°C) | 80 | 18 | 18 | 19 | 18 | 0.510 |
| Radiation (W/m ²) | 80 | 124 | 178 | 279 | 424 | 0.012 |
| Windspeed (m/s) | 80 | 0.06 | 0 | 0.12 | 0 | 0.040 |
| Ground humidity (%) | 80 | 85 | 89 | 78 | 82 | 0.000 |

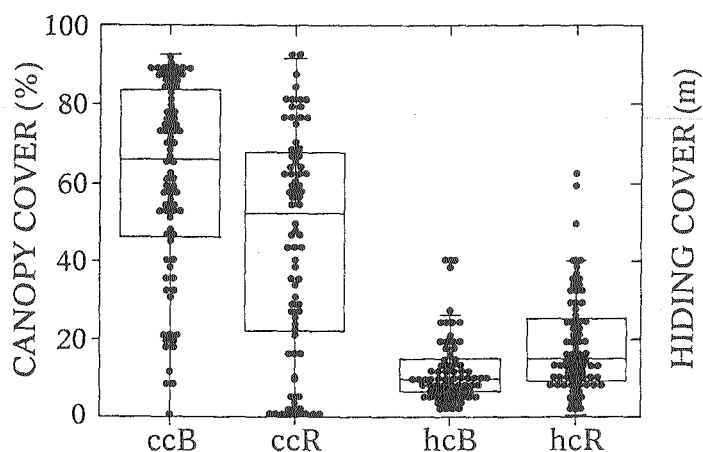


Figure 1. Canopy cover (in %) and hiding cover (in metres) for bed-sites (B) and random sites (R) showing plots of individual data and boxplots. Bed-sites had a denser canopy cover (ccB) and better hiding cover (hcB) than did random sites (ccR and hcR, respectively). One outlier is excluded from the figure for hcR. In the boxplots - the inside line gives the median, the upper boxline the upper quartile, the lower boxline the lower quartile. The horizontal lines above and below the box show the upper and lower fences, i.e. 1.5 times the distance between the median and the upper and lower quartiles (Wilkinson et al. 1992b).

All concealment indices showed more cover at bed-sites than at random sites, but hiding cover was relatively abundant also at random sites (see Table 1 and Fig. 1). Vegetation made up 73.8% ($N = 80$) of hiding cover (hc1) at bed-sites while constituting only 56.3% ($N = 80$) at random sites (Sign test, $P = 0.027$, $N = 80$). This was not due to a lower cover value at sites where vegetation obstructed visibility (Mann Whitney U-test, $P = 0.185$, $N = 80$). Males and females were equally well hidden (Mann Whitney U-test, $P = 0.992$, $N = 80$). The Spearman correlation coefficient between canopy cover and hiding cover (hc1) was -0.370 ($N = 80$, $P < 0.05$). This was the same whether vegetation (-0.368 , $N = 59$) or topography (-0.370 , $N = 21$) made up the cover. There was no correlation between canopy cover and availability of herbs (-0.177 , $N = 80$, $P > 0.05$) or between hiding cover (hc1) and availability of herbs at bed-sites (0.125 , $N = 80$, $P > 0.05$).

Influence of thermal factors

Mean air temperature in open habitat was 20°C (range 11 – 30°C), mean solar radiation was 837 W/m^2 (range 0 – 1874 W/m^2), and mean windspeed was 0.36 m/s (range 0 – 2 m/s). Roe deer bed-sites had the same air temperature as random sites, but solar radiation and windspeed were lower, though differences in windspeed were small (see Table 1).

The availability of herbs at the bed-sites of males was lower than at the bed-sites of females (ANCOVA, F-ratio 5.084 , $P = 0.027$), and the availability of herbs at bed-

sites decreased during warm weather (F-ratio 8.170 , $P = 0.005$) from 36.3% at 11°C to 7.8% at 30°C . There were no differences in the canopy cover over bed-sites of males compared to bed-sites of females (ANCOVA, F-ratio 2.423 , $P = 0.124$) and the canopy cover did not vary with air temperature (F-ratio 1.144 , $P = 0.288$). Neither were there any differences in the relative humidity in the substrate of male bed-sites compared to female bed-sites (multiple ANCOVA, F-ratio 0.742 , $P = 0.392$), but the difference in humidity between bed-sites and corresponding random sites increased with increasing temperature (F-ratio 4.975 , $P = 0.029$) from 0% at 11°C to 15% at 30°C . I simultaneously controlled for the possible confounding effect of differences in canopy cover (F-ratio 0.158 , $P = 0.692$). In total, 23.8% ($N = 80$) of the beds were scraped but there was no significant difference in the

frequency of scraping between males and females (logistic regression, $P = 0.904$), and the behaviour was not related to temperature ($P = 0.883$). Including the interaction term, $\text{sex} \times \text{temperature}$, did not change the results ($P = 0.855$).

Discussion

The higher availability of herbs at bed-sites than at random sites in my study indicated that roe deer often bedded at feeding sites. The roe deer, being a concentrate selector (Hofmann 1989), mostly eat herbs during summer, though bilberry and some grasses make up smaller proportions of their diet in Sweden and Norway (Cederlund et al. 1980, Selås et al. 1991). The availability of herbs was higher at female than at male bed-sites. This concurs with studies of rumen analyses showing higher quality food in the rumen of females (Ellenberg 1978), and that home ranges of females contain more herbs, shrubs and young trees (Thor 1990).

Both food and cover are reported to be important for habitat selection by roe deer during summer (Henry 1981, Selås et al. 1991). No correlation between either hiding cover or canopy cover and availability of herbs was found in my study. Patches with combinations of high/high, high/low, low/high and low/low availability of herbs and cover, respectively, were present. Therefore, it was not surprising that roe deer preferred patches which offered both a high availability of herbs and good cover. Never-

theless, there were no forage plants available at several bed-sites and there was a lower availability of herbs at bed-sites during warm weather. This indicates some local movement between feeding areas and bedding areas.

Thermal cover strategies

Seeking dense canopy cover for bedding purposes has been reported to be an important thermal strategy in moose *Alces alces* (Belovsky 1981, Schwab & Pitt 1991, Demarchi & Bunnell 1995) and mule deer *Odocoileus hemionus* (Sargeant et al. 1994) during summer to avoid heat stress. Merrill (1991), however, found no such relationship for elk *Cervus elaphus canadensis*. Temperature did not influence selection of canopy cover in my study, perhaps because roe deer often bedded below dense canopy cover even at low temperatures. Upper critical temperature limits of roe deer have not been reported, but are known to be above 25°C for roe deer in central Europe (Weiner 1977). The thermal environment experienced by an animal depends on the combined effects of air temperature, windspeed and radiation and will vary with the animal's specific shape, dimensions and thermal properties of pelage (e.g. Bakken 1980, Parker & Robbins 1985). No beds exposed to direct sunlight were recorded in this study, nor were any recorded in another study of diurnal bed-sites of adult white-tailed deer *Odocoileus virginianus* (Ockenfels & Brooks 1994). However, even though air temperatures in the shade reached 30°C, which probably is above the roe deer's upper critical temperature limit, no differences in air temperature between bed-sites and random sites were found. Therefore, shade may not be adequate for avoiding heat stress during hot summer days, not even in forested areas.

Thermal substrate strategies

Bedded deer may lose the most significant amount of heat through conduction, i.e. through direct transfer between deer and substrate (Moen 1973). Such losses have been reported to approach 30% of a sheep's *Ovis aries* minimum heat production on cold, poorly-insulated ground (Gatenby 1977). A wet bed will dissipate more heat (Jacobsen 1980), and this may explain why roe deer chose humid bed-sites, and included the use of wet bog mosses *Sphagnum* spp., when temperatures were high. Merrill (1991) observed elk in the blast-zone of Mount St. Helens move short distances between bed-sites without intermittent feeding, suggesting that conductive heat loss declined as animals had warmed up the bed-site, and that elk successively sought new and cooler bed-substrates.

Scraping the bed-sites before bedding exposes more humid substrate (Jacobsen 1980). Sargeant et al. (1994) showed that scraping activity for mule deer in an arid ar-

ea increased from 10% on overcast days to 63% on clear days. However, in my study, scraping activity did not increase at high temperatures. Scraping may also act as a communication signal during summer (Johansson et al. 1995). Bed-site scraping occurs throughout the year (Mysterud & Østbye 1995a, this study), but the reasons for bed scraping still remain unknown.

Antipredator strategies

There were no differences in hiding cover at the bed-sites of males and females, and hence it indicates that females not only hide in order not to reveal the location of their bedded fawns (Byers & Byers 1983, Linnell 1994). That adult deer also choose concealed bed-sites supports findings in a study on adult mule deer (Smith et al. 1986). Bed-sites of roe deer were more often concealed by vegetation than by topography; maybe because vegetation breaks up the profile of a bedded deer (Smith et al. 1986). In general, abundant hiding cover during summer may reduce the value of, or need for, alternative antipredator strategies in forested areas.

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