

Bed-site selection by European roe deer (*Capreolus capreolus*) in southern Norway during winter

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Abstract: Roe deer (*Capreolus capreolus*) beds were located by tracking in snow in the Lier valley in southern Norway during the winter of 1992–1993. Roe deer preferred to bed down below heavy canopy cover in order to derive thermal and possibly other benefits, whereas they fed in areas with little or no canopy cover. This led to the use of "forage beds" with little cover close to feeding areas and "cover beds" with heavy canopy cover farther away. The duration of the bedding period and temperature influenced the decision of the roe deer as to whether to leave the feeding area before bedding down. Bedding down in open habitat required more ground cover for protection against the wind, so wind was probably a significant factor in the operative temperature. Roe deer preferred to bed on microtopographic "tops," and animals in groups bedded down 2–4 m apart. This was interpreted as an antipredator strategy.

Résumé : Les aires de repos des chevreuils *Capreolus capreolus* ont été repérées par dépistage dans la neige à Lier, dans le sud de la Norvège, au cours de l'hiver 1992–1993. Les chevreuils avaient tendance à se coucher dans les zones bien protégées par la couverture d'arbres à cause de leurs avantages thermiques et peut-être pour d'autres raisons, alors qu'ils se nourrissaient dans les zones découvertes ou clairsemées. Ces choix donnaient lieu à deux types d'aires de repos, les « lits de broutement », à couverture clairsemée, au voisinage des zones de broutement, et les « lits à couverture », à couverture épaisse, situés plus loin des zones de broutement. La durée des périodes de repos « au lit » et la température étaient les facteurs déterminants du choix des chevreuils, à savoir s'ils devaient ou non quitter la zone de broutement avant de se coucher. Les chevreuils qui se couchaient dans les zones ouvertes avaient besoin d'une couverture au sol plus épaisse contre le vent, ce qui semble indiquer que le vent modifie probablement la température réelle. Les chevreuils préféraient s'étendre sur des élévations microtopographiques et les animaux en groupe se couchaient à 2–4 m les uns des autres. Il s'agit sans doute là de stratégies contre les prédateurs.

[Traduit par la Rédaction]

Introduction

In temperate regions, winter is considered to be a critical period for deer because low temperatures may increase the amount of energy needed for survival and to avoid hypothermia (Moen 1973, 1976; Mautz 1978; Schmitz 1991). This coincides with a period of low availability and quality of forage (Mautz 1978; Parker and Robbins 1984), which increases the need for thermoregulatory behaviour (Parker and Robbins 1985).

Bedding in conifer stands has long been known to be an energy-conserving strategy among cervids (Robinson 1960; Gill 1966; Armstrong et al. 1983; Gilbert and Bateman 1983; Lang and Gates 1985). To rest under conifer shelter during a cold, clear night may reduce energy requirements by 20% compared with resting in open habitat (Moen and Gustafson, unpublished data in Weber et al. 1983). Areas with dense

canopy cover often contain little forage (Peek et al. 1982), therefore deer must balance two opposite requirements: foraging in exposed habitats and seeking thermal shelter in coniferous forest areas (Moen 1976; Gates and Hudson 1979; Peek et al. 1982; Parker and Robbins 1984; Schmitz 1991).

Bed-site selection may also be used as an antipredator strategy (Smith et al. 1986), and winter aggregations of white-tailed deer (*Odocoileus virginianus*) in coniferous forest areas are considered to be an important means of lowering predation pressure (Messier and Barrette 1985).

Although roe deer rest for 60–65% of the time, divided into about 8 intervals of different lengths, during winter (Cederlund 1981; Jeppesen 1989), no one has thoroughly studied their winter bed-site selection. Our data were obtained from bed sites located by tracking roe deer in snow and from random plots close to the bed sites. The aim of this study is to describe roe deer winter bed sites, particularly with regard to cover characteristics and position in relation to topography. We test the prediction that if roe deer forage in open areas and seek thermal shelter in coniferous forest areas only when this confers an energy advantage, the amount of canopy cover closure over roe deer winter beds will be correlated with temperature and the duration of the bedding period.

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Study area

The study area is located in the Lier valley in southern Norway (between 59°52' and 59°58'N and 10°14' and 10°20'E). Most of the area is forested and situated within the boreonemoral region (Abrahamsen et al. 1977). Vegetation is varied and dominated by Norwegian spruce (*Picea abies*) mixed with Scots pine (*Pinus sylvestris*) in the drier and poorer locations. The forest has been commercially managed and there are several clearcuts of various sizes within the study area. Along the bottom of the valley, on richer soil, deciduous forest predominates, fragmented by cultivated fields. In the deciduous forest, species such as hoary alder (*Alnus incana*) and bird cherry (*Prunus padus*) predominate, mixed with elm (*Ulmus glabra*) and linden (*Tilia cordata*) on the richest sites. On sites with soil profiles rich in calcium there is a large amount of yew (*Taxus baccata*), an important winter browse plant for roe deer in parts of the area (E. Østbye, unpublished data). The roe deer population in the cultivated area feeds on agricultural crops as well as on wild plants.

The terrain is hilly, rising from Lake Holsfjorden at 63 m asl to over 400 m asl 1.5–2.5 km from the lake. Some parts of the area are largely flat, but on a smaller scale, severe erosion of the clay sediments has resulted in undulating and hilly terrain with many ravines (10–100 m between top and bottom).

The area hosts a large population of roe deer, which is heavily hunted (August–December). Within the study area, which covers 740 ha, the population was estimated to be between 25 and 40 roe deer.

Material and methods

Tracking procedure

Beds were located from November to January by using the following sampling technique. The area was divided into three main regions based on vegetation. These were subdivided into easily recognizable geographical units (size 22–110 ha). Usually we checked several of these units each day. To decide which one to start at, a random block design was used, with the three large areas as the blocks. One or two areas from each block were chosen at random until we had 5 selected areas. These were checked in random order. Then we drew 5 more areas at random until all areas had been checked once. Then all areas were put back in the pool before we started again.

To locate roe deer tracks within the local areas, lines approximately 150 m apart were walked. When a track was found, we followed it both backwards and forwards until the border of another area was reached. The areas were checked as soon as there was snow cover, but never on snow more than 3 days old. All the beds were marked and numbered so that we could measure the parameters later. We assumed every bed within a radius of 30 m of another to be within the same bed site. This could be due either to reuse of a site, or to its use by a group of animals. In most cases these two possibilities could be distinguished by means of tracks. Within a bed site we chose one at random as being representative. Of a total of 294 beds located, there were only 118 bed sites. There is a risk of underestimating preferences if, for instance, reused beds have specific habitat characteristics. To check this,

we categorized bedsites as reused or not, and checked whether important parameters such as percentage of canopy cover and location in relation to topography differed (Mann–Whitney *U* test). This was done for bed reuse within 5 m (see Huot 1974) and 30 m. If a group of animals had used the site, we counted how many had been there, and measured the distance between beds within the site.

Local bed choice

All parameters (see below) were measured both in the bed and at a point 50 m away in a random direction. This provided an opportunity to use paired comparisons, each bed "with its own random point." For continuous data we used Wilcoxon's pair test, whereas when we had a category (i.e., coniferous or deciduous trees), we used the sign test (see Wilkinson et al. 1992b). For tree species closest to the bed (see below), we also checked preferences against a random point only 10 m away, to ensure that we were within the site habitat. Spearman's correlation coefficient between canopy cover and ground cover was calculated (see below).

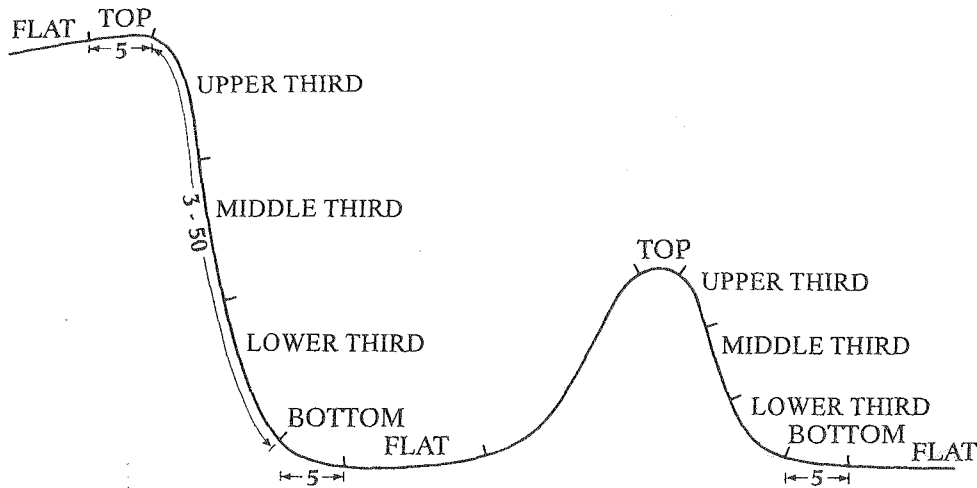
Cover characteristics

(1) The tree species closest to the bed were characterized as either a coniferous (mostly Norwegian spruce) or deciduous. If a tree was a conifer, we measured the distance to it, the diameter at breast height (dbh), and the height to the closest live branch (if the distance from the trunk was <3 m) hanging over the bed. Tests for differences in distances and dbh were only made when both beds and random points were closest to a conifer. (2) Canopy cover was measured using a Lemmon (1956, 1957) spherical densiometer (model C); canopy closure was measured as percent coverage and measurements were taken 30 cm above ground to simulate a bedded roe deer's perception of the cover. (3) Ground cover was measured using a revised version of the cover index from Mysterud (1983). We placed a 30 cm diameter cylinder in the centre of the bed and marked it 40 cm above ground. We then moved away from the spot and measured the distance to the point where the cylinder was first totally hidden (sighting distance) from a person standing to the north, south, east, and west. The mean distance was our ground cover index. (4) To check whether the roe deer had a better view in the direction from which it had walked into the bed (called the incoming track), perhaps watching for predators following its track, we compared the sighting distance in that direction with the sighting distance in the opposite direction using Wilcoxon's pair test.

Topographic characteristics

(1) Location relative to topography was categorized as "top," "upper third," "middle third," "lower third," or "bottom" (Fig. 1). We wanted to study the positions of the beds in relation to "microtopography," defined as a difference of 3–50 m between top and bottom (Fig. 1). We measured the exact distance. If a spot was more than 5 m away from such a slope, it was characterized as flat (although it could have a "macrotopographic" slope). The topography was distinct in the area, with slopes changing from 0° to 20–50° within 2–5 m. We also tested preferences when both the bed and the random point could not be characterized as flat. We

Fig. 1. Bed categorization in terms of microtopography (see the text). Distances are given in metres.



tested preference for tops against all other categories combined except for flat areas. Preference was only tested when both bed and random point were not flat. (2) Slope was measured (400° Ranger compass) as the tangent of a 3- to 5-m line centred in the bed.

Other behavioural characteristics

Roe deer often scrape away loose material and snow with their front hooves before bedding down. We quantified this behaviour in order to test whether scraping could be related to the substrate or bedding time. We tested substrate indirectly by using the tree species closest to the bed as an indicator (Mann-Whitney *U* test). We used bedding time to test whether the deer scraped beds they used for a long time more often than beds used for a short time (Mann-Whitney *U* test).

Influence of feeding

We followed tracks in the direction in which the animal had entered the bed site. The first sign of feeding located during this backtracking was used to represent the feeding area, and the distance between bed and feeding site was measured. We measured canopy cover at the feeding site by the same method as for bed sites. Sometimes it was impossible to follow a single track that far because of high roe deer density and the presence of many tracks. Long distances between bed and feeding sites may therefore be underrepresented. We categorized beds as being situated far from or close to feeding sites, based on whether they were more or less than 30 m from the feeding area. We also checked local choices for these two bed categories, using pairwise comparison with random points as described above.

Influence of temperature and duration of the bedding period

If roe deer have to feed in open areas and they spend less energy while resting under cover, their energy-conservation strategy should take into account (i) the energy costs of travelling (distance, elevation, snow depth, etc.), (ii) the difference in energy expenditure during bedding, and (iii) the duration of the bedding period.

We did not measure the distance to cover because of the difficulty of defining "enough cover." Snow depth was

measured at several stations at different altitudes and in different habitats. During the study period snow depth never exceeded 16 cm; we therefore considered snow to have had practically no effect on movement. During a "normal" winter, snow depth usually exceeds 1 m. The bedding period was characterized as short or long according to the amount of snow melting in the bed. There are several uncertainties in this evaluation. We do not know the extent to which snow depth affects melting, and scraped beds contain less snow (see below). We do know from activity studies (Cederlund 1981; Jeppesen 1989), however, that there is great variation in the duration of the bedding period. Despite these uncertainties, our method should indicate trends. We were extremely cautious, and evaluated this parameter only when there was little doubt, and only when there was no snow melting because the ambient temperature was high ($n = 67$ out of 118 beds). We assume that either there is a greater difference in temperature between open and covered sites during cold periods and (or) the difference is of greater importance to deer in cold weather (i.e., because the temperature is further outside the thermoneutral region). The use of thermal cover is related to temperature, radiation, and wind speed (the concept of operative temperature; Schwab and Pitt 1991). We used data from a nearby meteorological station (DNMI 1868 Tryvasshøgda II). Because we could not know at what time of the day or night the deer had bedded at a given site, we only categorized the air temperature as either low or high, based on whether the minimum temperature had been below -5°C . Minimum temperature varied between -0.5 and -11.0°C .

Canopy closure was therefore used as a dependent variable and temperature and the duration of the bedding period as independent variables in an ANOVA. Because canopy closure is a percentage, the data were transformed (arcsine [square root (canopy closure/100)]). Differences between cold and mild periods could mean that either the deer fed under denser canopy at low temperatures or they travelled longer distances between feeding sites and bedding sites. We therefore used distance from bed to feeding area as a dependent variable and the same independent variables in another ANOVA to distinguish between those two possibilities.

Wind speed did not vary much during the study period (from 3 to 7 m/s, but mostly 5 m/s), so it could not be used

Table 1. Bed characteristics and data from Wilcoxon's pair test.

	Total number of beds			Random points (median)	Bed close to feeding site			Bed far from feeding site		
	Median	<i>n</i>	<i>p</i>		Median	<i>n</i>	<i>p</i>	Median	<i>n</i>	<i>p</i>
Conifer closest to bed										
Distance to trunk (cm)	85	37	0.000	180						
			0.003	150						
Dbh (cm)	21	37	0.008	13						
			0.110	17						
Height to lowest live branch (cm)	205	40	0.840	120						
Canopy cover (%)	48	117	0.000	21	10	47	0.812	59	56	0.000
Ground cover index	27	118	0.000	22	34	47	0.006	24	56	0.180
Sighting distance to incoming track (m)	27	91	0.018	23 ^a	37	35	0.013	19	50	0.571
Sighting distance incoming wind direction (m)	17	13	0.039	55 ^a						
Slope (°)	17	118	0.000	25	12	47	0.001	22	56	0.005

Note: For the conifer closest to the bed, the first line is for a random point 50 m away and the second for a random point 10 m away.

^aMeasured in the opposite direction (see the text).

Table 2. Bed characteristics and data from the sign test.

	Total number of beds			Random points (count)	Bed close to feeding site			Bed far from feeding site		
	Count	<i>n</i>	<i>p</i>		Count	<i>n</i>	<i>p</i>	Count	<i>n</i>	<i>p</i>
Tree species (coniferous/deciduous)	77/36	105	0.000	46/59	22/21	40	0.248	45/11	51	0.000
		107	0.000	50/57		40	0.102		53	0.000
Topographic placement (top/other – flat)	64/16	118	0.000	13/65	22/8	28	0.000	36/6	35	0.000

Note: For tree species, the first line is for a random point 50 m away and the second for a random point 10 m away. Topographic placement is divided into only two categories in this test: "top" and "upper third / middle third / lower third / bottom," excluding "flat" (Fig. 1).

in the ANOVA. To check if wind was a factor in bed choice, we tested whether beds with canopy cover of less than 10% had more ground cover in the direction from which the wind blew than in the opposite direction (Wilcoxon's pair test). However, this was only done when the wind direction had been stable (i.e., within the quadrant that defined the wind direction) between snowfall and the time when tracking was performed.

Results

A total of 22.9% ($n = 118$) of the bed sites were reused within the 30-m radius. As much as 77.8% of reuse was within the 5-m radius. There was no difference in canopy cover characteristics between beds that were reused and not reused (Mann-Whitney U test, $n = 117$, $p = 0.065$ for the 30-m radius and $p = 0.477$ for the 5-m radius or topographic position ($n = 85$, $p = 0.884$ for the 30-m radius and $p = 0.506$ for the 5-m radius), regardless of whether the 5- or 30-m radius was employed during reuse categorization.

At 61% ($n = 118$) of locations, more than one roe deer had been present. Of these sites, 41.6% had been used by 2 deer, 30.6% by 3 deer, 13.9% by 4 deer, and 13.9% by an unknown number of deer. The average median minimum distance between beds was 4.3 m for 2 deer ($n = 28$), 2.2 m for 3 ($n = 22$), and 2.0 m for 4 ($n = 9$).

Cover characteristics

Data for cover and topographic characteristics are presented in Tables 1 and 2. (1) Roe deer preferred bedding below coniferous species, and closer to a conifer trunk than expected by chance. These trees did not differ (dbh, height to the

lowest live branch) from randomly selected trees 10 m away. However, randomly selected trees 50 m away had a smaller dbh. Beds far from feeding sites were more often situated under conifers than expected, whereas beds close to feeding sites were not. (2) Both the total number of beds and the number of beds far from feeding sites were associated with a higher percentage of canopy closure than randomly selected points, whereas beds close to feeding sites did not differ from randomly selected points. (3) Both the total number of beds and the number of beds close to feeding sites were related to less ground cover (a higher ground cover index) and (4) to a better view of the deer's own incoming track than expected. Beds far from feeding sites did not differ from random points in terms of these characteristics. Spearman's correlation coefficient between canopy cover and ground cover was -0.491 ($n = 117$, $p < 0.05$).

Topographic characteristics

Beds in all categories were more frequently located on (i) microtopographic tops (Table 3) and (ii) more level slopes than expected by chance. The median elevation of the microtopographic tops (distance from top to bottom) was 10 m ($n = 76$).

Other characteristics

In total, 48.3% ($n = 118$) of the beds were scraped. Scraped beds were located below conifers more often (81.5%, $n = 54$) than unscraped beds (55.9%, $n = 59$) (Mann-Whitney U test, $n = 113$, $p = 0.004$). Scraped beds were used for a long time (82.8%, $n = 29$) more often than unscraped beds (28.9%, $n = 38$) (Mann-Whitney U test, $n = 67$, $p = 0.000$).

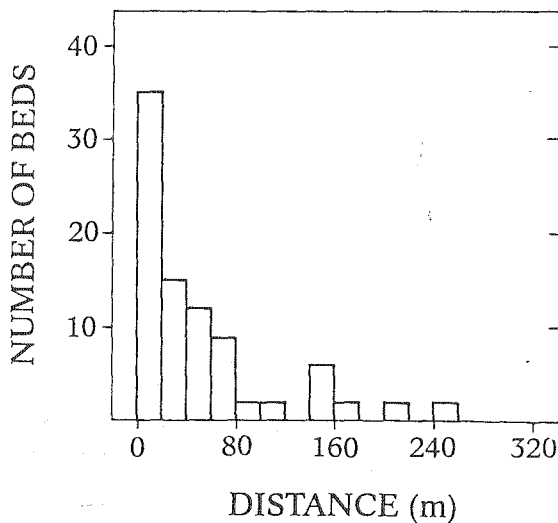
Table 3. Locations of roe deer beds in relation to microtopography and their distance (near or far) from feeding sites during the winter of 1992–1993 in the Lier valley, southern Norway.

	Location relative to topography ^a						Sum
	Top	Upper third	Middle third	Lower third	Bottom	Flat	
Total no. of beds	64	6	3	0	7	38	118
No. of beds near	22	2	2	0	4	17	47
No. of beds far	36	3	1	0	2	14	56
No. of random points	13	13	18	14	20	40	118

Note: Some beds were not classified as near or far.

^aSee Fig. 1.

Fig. 2. Distances from feeding areas to roe deer beds ($n = 87$) during the winter of 1992–1993 in the Lier valley, southern Norway.



Influence of feeding

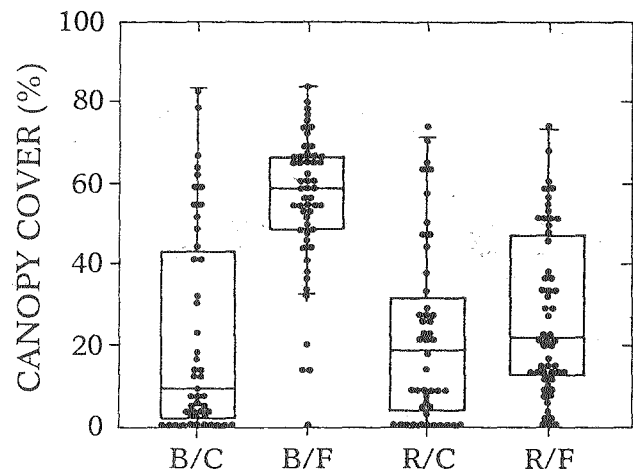
The roe deer bedded down at various distances from the feeding area (Fig. 2). Feeding occurred in open areas (median canopy cover 1%; $n = 84$). The beds close to and far away from feeding sites could easily be divided into two categories according to the percentage of canopy cover above the bed (Fig. 3). There were also differences in ground cover index (Fig. 4).

Influence of temperature and the duration of the bedding period

The percentage of canopy cover was higher above beds used for a long time than above those used for a short time and over beds made during cold periods than in those made during mild periods (Fig. 5, Table 4). This was a result of the animals moving farther away from feeding areas when they bedded down for a longer time and when they bedded down during colder periods (Table 5).

In open habitat the ground cover index was lower (more cover) in the direction of the prevailing wind than in the opposite direction (Table 1).

Fig. 3. Differences in canopy cover for beds situated near to (B/C) and far from (B/F) from feeding sites. Canopy closure was significantly higher for B/F than for the random points (R/F), whereas B/C did not have a significantly different canopy closure from the random points (R/C). Plots of individual data and box plots, where the middle line is the median, the upper line the upper quartile, and the lower line the lower quartile, are shown. 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. 1992a).



Discussion

It would have been advantageous in this study to radio-track animals, so that each animal's movements and rest periods could be recorded and more closely correlated with real-time weather conditions. To avoid drawing conclusions based on many beds belonging to few roe deer, we considered all beds within 30 m of one another to be within the same bed site. In terms of important characteristics such as canopy cover and topographic placement, there were no differences between bed sites that were reused and not reused. Our procedure thus seems to have worked properly.

Comfort as a constraint

"Comfort" behaviour, for anatomical or physiological reasons, can always limit an animal's opportunities to make other

Table 4. ANOVA results where canopy cover (transformed) was the dependent variable, with bedding time and temperature as independent variables ($n = 67$).

	Sum of squares	df	Mean square	F ratio	p
Bedding time	1.541	1	1.541	15.006	0.000
Temperature	0.722	1	0.722	7.035	0.010
Bedding time \times temperature	0.037	1	0.037	0.360	0.551
Error	6.469	63	0.103		

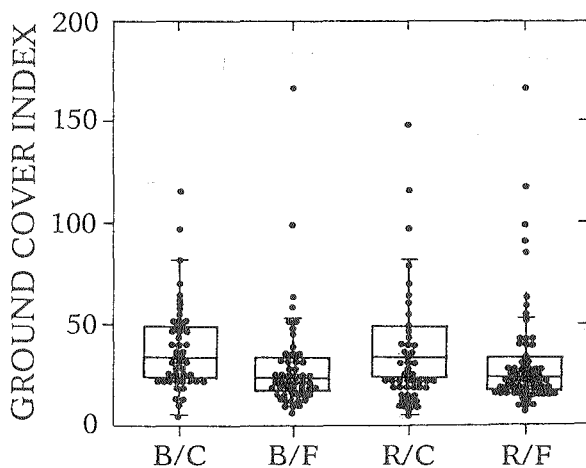
Note: Multiple $R = 0.507$; squared multiple $R = 0.257$.

Table 5. ANOVA results where distance between the feeding area and bed site was the dependent variable, with bedding time and temperature as independent variables ($n = 56$).

Source	Sum of squares	df	Mean square	F ratio	p
Bedding time	25 619.811	1	25 619.811	7.961	0.007
Temperature	23 867.834	1	23 867.834	7.417	0.009
Bedding time \times temperature	1 400.463	1	1 400.463	0.435	0.512
Error	167 335.036	52	3 217.981		

Note: Multiple $R = 0.478$; squared multiple $R = 0.229$.

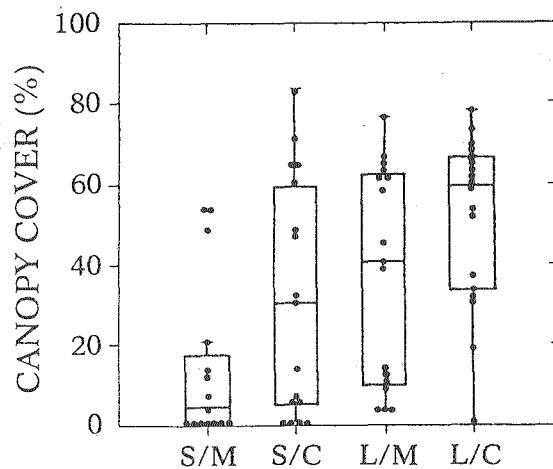
Fig. 4. Differences in ground cover among bed types (see Fig. 3 for details).



choices. For instance, deer need a flat spot so that they do not slide off the bed (Beall 1974; Huot 1974; Smith et al. 1986). In part of the clay-eroded ravine landscape in our study area, this is an important constraint because of the locally steep terrain, and could partially explain why deer preferred to bed down on spots that, on a larger scale, were level.

About half of the beds were scraped. This is a special characteristic of roe deer bedding behaviour that is seldom exhibited by other deer species. Scraping the beds could be interpreted as comfort behaviour; branches and other material are removed and the bed itself becomes more concave. Scraping might also be an energy-saving strategy. A bedded animal loses most of its heat to the ground (conduction) and a wet bed will be more heat conductive (Moen 1968). Scrap-

Fig. 5. The relationship of both bedding time and temperature to canopy cover over beds was significant. S, short time; L, long time; M, mild period; C, cold period (see Fig. 3 for details).



ing of roe deer beds removes snow and rime and might thereby reduce heat loss by conduction.

Thermal cover

In studies of winter bed-site selection by white-tailed deer (Gill 1966; Huot 1974; Armstrong et al. 1983; Lang and Gates 1985) and elk (*Cervus canadensis*) (Beall 1974), all showed a preference for bedding below coniferous species in winter, and roe deer are no different. Selection of cover seems to occur on two scales. First, the animal moves into an area with a high percentage of canopy closure that also provides good ground cover. Then it seeks a bed site below

a specific conifer that adds more canopy cover but not more ground cover (Mysterud 1993). If reduction of radiation is the objective, it is of little importance whether a single tree or a stand of trees is chosen (Euler and Thurston 1980). That roe deer sought a higher percentage of canopy closure during colder periods could indicate that it was the climate within a stand of trees that was preferred, which would mean that wind speed was important. Within a mature conifer stand there is also a higher mean minimum daily temperature but a lower maximum temperature than in open areas (Ozoga 1968).

When roe deer bed down under a cover of conifers, they do not bed close to the trunk: getting under the branches seems to be enough. The same pattern is found in white-tailed deer (Gill 1966; Armstrong et al. 1983), whereas Beall (1974) reported that elk prefer bedding as close to the trunk as possible. A preference for bedding under trees with a larger dbh than expected by chance was shown for white-tailed deer (Huot 1974) and elk (Beall 1974), whereas only a tendency in this direction was apparent for roe deer. The height to live branches was found to be less than expected for white-tailed deer by Armstrong et al. (1983) and Lang and Gates (1985), whereas Euler and Thurston (1980) did not find such a relation, and not even a tendency towards this was seen in roe deer in this study. Moen (1973) mentioned finding beds under conifers where snow bends the branches down to form a hollow room. Only one such bed was located during this study, possibly because of the shallow snow during the winter of 1992–1993. Such beds have been reported for roe deer by Markgren (1966).

Balancing forage and cover

Bed-site selection for canopy cover and topography could be considered non-interactive factors in an optimal foraging theory framework (sensu Senft et al. 1987), where feeding is of course the ultimate factor. Huot (1974) distinguished white-tailed deer habitats as being either combined or separate depending on whether or not food and cover occurred in the same habitat. It is important, however, to distinguish canopy cover from ground cover. Canopy cover is the most important thermal cover (Black et al. 1976; Peek and Scott 1985), while ground cover characteristics cannot be described as being either combined with or separate from food in our study.

Because the roe deer were feeding in habitats with little or no canopy cover and sought thermal shelter in areas with dense canopy cover, we could classify two different bed types, "forage beds" and "cover beds"; their main distinction was whether the animals had travelled long or short distances from feeding areas to bed down. The duration of the bedding period and temperature influenced the decision of the roe deer whether to leave the feeding area before bedding down. Our model did not explain much of this variation (26%). This was expected, because we only used very rough estimates of both bedding time and temperature and lacked appropriate methods to quantify the costs of getting to cover. However, the simple model shows the validity of thinking in terms of energy requirements when examining bed-site selection.

We did show that wind was a factor in bed-site selection in open habitats, so wind was probably an important influence on the operative temperature. Radiation may lower or eliminate the thermal advantages of resting under dense canopy

cover rather than in open habitat on clear days. The situation described, where a thermal benefit is derived from dense canopy cover, will apply in most cases, since at this time of year in Norway the days are short, with little incoming radiation.

Although the exact critical temperatures for roe deer on their winter range are unknown, the upper critical temperature limit for white-tailed deer is around 0°C and the lower limit around -8°C (Schmitz 1991). Our study was carried out within a temperature range in which the upper critical limit was of little importance. Schmitz (1991) explained the use of open habitats by white-tailed deer as resulting from overheating in conifer habitats. This is probably of little importance for winter activities of roe deer in Scandinavia.

Antipredator strategies

All antipredator strategies must operate within a realistic energy budget. Strategies may vary in terms of energy cost, but they do not have to be expensive (Messier and Barrette 1985). Antipredator strategies will probably vary according to several factors, such as predation pressure and the severity of winter weather. We consider bed-site selection to be an antipredator strategy if it (i) lowers the probability of the predator discovering the bedded deer, (ii) improves the deer's chances of discovering the predator, (iii) improves the deer's chances of escaping, or (iv) reduces the predator's opportunities to attack.

We found no signs of predation on roe deer, but there was intense human hunting (with dogs) prior to the study. Therefore the bedding behaviour observed in the study could be a general strategy against predators rather than a short-term response.

Choice of a bed with maximum ground cover is a well-known strategy used for ungulate calves for defence against visually searching predators (Barrett 1981; Huegel et al. 1986; Gerlach and Vaughan 1991). Most roe deer beds had good ground cover, although several forage beds had little. These could be night beds, for which visibility is less important. Species like roe deer and moose (*Alces alces*) use open habitat more often at night (Hjeljord et al. 1990; Selås et al. 1991; Histøl 1992). A high percentage of canopy closure could also be an antipredator strategy; in a forest, the contrast is broken up by logs, etc., and there is less light (Smith et al. 1986). Possibly scent does not spread as much because of a less active wind regime. That the roe deer had a slightly better view of their own incoming tracks to the beds could be interpreted as a defence against tracking predators sneaking into the site. However, it might also be due to the animals moving energy-efficiently in the terrain, following ridges, etc., and needs closer study.

The use of microtopographic tops during bedding is most likely an antipredator strategy. A deer bedded on a top will have a better auditive regime and can escape downhill, while a predator must attack uphill. The fleeing roe deer will be hidden from one side as soon as it leaves the top. A predator like the lynx (*Lynx lynx*) is less successful when attacking roe deer if it has to follow the deer for a long distance (Haglund 1967). Thermal factors could be favourable on small tops because of higher temperatures (Geiger 1965), but forage beds situated on tops are at more risk of being exposed to wind. Although it might be favourable from a thermal view,

the greatest benefit of placing beds on tops is defence against predation. The same preference for tops has been found for both white-tailed deer (Huot 1974; Stocker and Gilbert 1977; Armstrong et al. 1983) and mule deer (*Odocoileus hemionus*) (Smith et al. 1986). Whereas cover is often a vague term, few authors seem even to try to define topography. This makes comparative behavioural work difficult. The size of the topographical features is probably a major concern. If the distance to the top is 100 m, the predation pressure or thermal difference has to be large to compensate for the energy costs of getting there. The use of small tops could be an energy-efficient but still effective antipredator strategy.

Roe deer in groups are usually spaced 2–4 m apart, so they are denied opportunities for social thermoregulation. However, bedding down some distance apart can make it more difficult for an approaching predator to sneak in unseen. The same strategy was reported for white-tailed deer, and Gilbert and Bateman (1983) considered bedding in groups to be more important than thermal factors when bed sites are chosen.

Conclusions

During winter, roe deer prefer to bed in areas with dense canopy closure that provides thermal and possibly other benefits. Because they have to feed in areas with little or no canopy cover, they must balance the need for feeding in open areas with seeking shelter in conifer stands. Part of this dynamic pattern can be explained in terms of bedding time and ambient temperature. Bed placement on microtopographic tops is probably an antipredator strategy. Studies carried out under different predation pressures are needed to verify bed choice as an antipredator strategy. There is still a need for more stringent criteria to quantify cover and especially topography.

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