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Effects of snow depth on food and habitat selection by roe deer *Capreolus capreolus* along an altitudinal gradient in south-central Norway

Atle Mysterud, Bjørn Helge Bjørnsen & Eivind Østbye

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Roe deer *Capreolus capreolus* food and feeding habitat selection was studied by snow tracking on transects along an altitudinal gradient in Flatdal, the county of Telemark, south-central Norway, during winter 1979/80. The main food was bilberry *Vaccinium myrtillus* (36.8%), rowan *Sorbus aucuparia* (24.4%) and arboreal lichens *Alectoria sarmentosa*, *Bryonia* spp., *Hypogymnia physodes, Usnea* spp. (17.4%), which were also the only preferred food plants. The amount of food removed from the field layer was stable through the winter. Roe deer used the lower part of the study area most heavily. At lower altitudes, older mature stands and edges between medium-aged stands and clear-cuts/plantations were preferred, pole-sized stands and edges between older mature stands and clear-cuts/plantations were used as expected from their availabilities, whereas medium-aged stands, clear-cuts and young plantations were avoided. That snow depth was an important factor determining habitat use by roe deer was evident in three ways: 1) use of areas at higher elevations decreased as winter progressed, 2) use of mature forest stands increased from early to late winter relative to open habitats, and 3) use of mature forest stands was more extensive at higher than at lower elevations compared to open habitats.

Key words: altitude, boreal forest, Capreolus capreolus, food selection, habitat selection, roe deer, snow

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Snow conditions are regarded as an important component of the habitat at northern latitudes for cervids (e.g. Formozov 1946, Coady 1974, Telfer & Kelsall 1984). Snow reduces the availability of forage to deer, and increases the cost of locomotion profoundly, especially when layers exceed breast height (Parker, Robbins & Hanley 1984). Several studies of North-American cervids have concluded that snow depth is a major factor determining habitat selection (Huot 1974, Kucera 1976, Armstrong, Euler & Racey 1983, Beier & McCullough 1990, Pauley, Peek & Zager 1993, Armleder, Waterhouse, Keisker & Dawson 1994), and that older mature forest is often preferred winter habitat due to its ability to intercept snow (Huot 1974, Armstrong et al. 1983, Weber, Mautz, Lanier & Wiley 1983, Pauley et al. 1993, Armleder et al. 1994).

Data on roe deer *Capreolus capreolus* habitat selection during winter in Fennoscandia are few, but spruce forest was reported as an important winter

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habitat in Finland by Helle (1980), whereas Cederlund (1983) found no consistent pattern of habitat selection in central Sweden, although bogs and clear-cuts were typically avoided. No studies on roe deer have tested the effects of snow depth on habitat selection. Critical snow depth for roe deer is regarded to be only 50 cm (Cederlund & Liberg 1995), and as snow depth is higher during most winters in Norway, snow may be an important factor in food and habitat selection.

Here, we present data on food and feeding habitat selection along an altitudinal gradient in a boreal habitat in south-central Norway. We test the hypothesis that roe deer prefer low elevation areas and mature forest stands due to consistently shallower snow depths and that use of higher elevation areas will be more restricted to mature forest stands than at lower elevations. The relative strength of selection between high/low elevation and open/mature forest is expected to change with increasing snow depth for two reasons: 1) snow depth increases proportionally between habitats (e.g. a snow depth of 20 cm in dense and 40 cm in open habitat increase to 40 and 80 cm, respectively) and 2) energetic costs of movement increase exponentially when snow depth exceeds breast height (Parker et al. 1984). We therefore test whether use of higher elevations decreases and use of mature forest stands increases from early to late winter in accordance with changes in snow depth.

Study area

The study area, Flatdal, is situated in the community of Seljord in the county of Telemark, south-central Norway (between 59°32'-59°34'N and 8°32'-8°36'E) and the altitude ranges from 170 m a.s.l. to 1,000 m a.s.l., the area sloping between 15° and 30° (Bjørnsen 1985). The terrain is hilly also on a smaller scale, with many large boulders and small cliffs. The area is forested and situated within the northern boreal zone, though it is close to the boreo-nemoral border-zone (Abrahamsen, Jacobsen, Kalliola, Dahl, Wilborg & Påhlsson 1977). Plant species representative of both vegetation zones are found within the study area. Norway spruce *Picea abies* is the dominant tree species, but scattered stands of Scots pine *Pinus sylvestris* occur on poor and dry sites. At the highest altitudes, birch *Betula* spp. predominates. The forest is commercially managed. There are no farms or houses within the study area, which is rather undisturbed, even though some hunting occurs during autumn. Roe deer density was about 2-4 deer/km^2.

Material and methods

Tracking procedure

Data were collected by snow tracking along seven transects traversing all major habitat types in the study area, covering the height gradient from 170 to 1,000 m a.s.l. Transects were laid at least a few hundred metres apart. Data were collected within subunits of each transect in intervals 50 metres long and 15 metres wide. There were 789 such intervals. Tracking was performed during the period November 1979 to April 1980. Each transect was covered by one day of tracking. Every interval was checked with approximately two weeks interim when tracking conditions were good. Only new tracks were registered, i.e. tracks not recorded during the last visit to the transect.

Feeding signs on all species were recorded as frequencies, i.e. number of intervals with recorded feeding on a particular plant species. Coverage of the different plant species (availability) was estimated using the Hult-Sernander coverage scale. The relationship between the horizontal projection of all plants of a species within an interval and the area of the interval gives the plant coverage (Rønning 1972). We distinguished between feeding in the field and bush layers. Graminoids *Poaceae* spp., *Cyperaceae* spp. and *Juncaceae* spp. and arboreal lichens *Alectoria sarmentosa*, *Bryonia* spp., *Hypogymnia physodes*, and *Usnea* spp. were pooled.

All intervals with registered feeding activity were recorded as habitat use. We differentiated between nine elevation classes (100-metre intervals) and five cutting classes following the standard national forest evaluation of Norway (Landskogstakseringen 1971); clear cuts (class I), young plantations (class II), pole sized stands (class III), medium-aged stands (class IV) and older mature stands (class V). Intervals containing both class IV and class I/II were termed edge 1, and edge 2 if both class V and class I/II were present. Classes IV and V combined are referred to as mature forest stands, and classes I and II as open habitat.

Snow depth and structure were measured at six altitudes from 180 to 720 m a.s.l. and in open (Class I) and mature forest (Class V) habitat at each altitude.

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Snow hardness was measured with ramm-penetrometer (e.g. Coady 1974, Skogland 1978, Perla & Glenn 1981). We also measured depth of tracks and cratering depth from January to April.

Statistical procedures

Since we get pooled data on habitat use for all animals in the area (Design 1, *sensu* Thomas & Taylor 1990), we used Bonferroni z-statistics (Neu, Byers & Peek 1974, Byers, Steinhorst & Krausman 1984) when testing habitat use against availability. Even though this method does not consider habitat selection as a two-step process, as more recent methods do (Johnsen 1980, Aebischer, Robertson & Kenward 1993), it is reported to perform well in simulation tests compared to other methods (Alldredge & Ratti 1986, 1992). This test is thus sensitive to how availability is defined, and hence, we first considered choice of elevation class in the area, and then studied choice of cutting classes within the preferred area (see below) to limit this problem of spatial scale in a way similar to considering choice of home range and then choice within a home range (Johnsen 1980, Aebischer et al. 1993). Overall difference from availability was tested using Chi-square Goodness of fit tests (Bhattacharyya & Johnson 1977).

Autocorrelation plots (Wilkinson, Hill, Welna & Birkenbeuel 1992) showed that there were autocorrelation between adjacent intervals, but never between three consecutive intervals. Autocorrelation does not bias estimates, but will bias P-values (Ims & Yoccoz 1995). We therefore adjusted P-values appropriately, equivalent to using every other interval and hence removed the autocorrelation (Ims & Yoccoz 1995). This adjustment was only done for habitat selection, since food choice and track/cratering depth were regarded as choices on a more local scale.

Table 1. Food choice of roe deer in Flatdal, Norway, winter 1979/80 (N = 634). Use exceeding availability is marked +, use as expected from availability is marked 0, whereas use less than expected is marked -.

Species	Obs. use (%) ± c.i.		Expected use (%)
Field layer (total)	46.4		
Vaccinium myrtillus	36.8 ± 5.4	+	16.3
Graminoids	4.7 ± 2.4	-	18.0
Calluna vulgaris	2.7 ± 1.8	0	1.8
Dryopteris austriaca	1.9 ± 1.5	-	8.9
Oxalis acetosella	0.2 ± 0.5	-	6.4
Browse (total)	53.6		
Sorbus aucuparia	24.4 ± 4.8	+	14.4
Arboreal lichens	17.4 ± 4.2	+	13.1
Rubus idaeus	2.5 ± 1.7	-	5.5
Populus tremula	2.1 ± 1.6	0	2.9
Fraxinus excelsior	2.1 ± 1.6	0	1.4
Juniperus communis	1.9 ± 1.5	0	1.0
Salix caprea	1.4 ± 1.3	0	2.5
Rosa spp.	0.5 ± 0.8	0	0.2
Corylaceae avellana	0.5 ± 0.8	-	2.7
Tilia cordata	0.3 ± 0.6	0	0.3
Prunus padus	0.3 ± 0.6	0	0.1
Alnus incana	0.2 ± 0.5	-	3.3
Viburnum opulus	0.2 ± 0.5	0	0.3

Results

The only plants preferred and also the ones most used by roe deer in the study area were bilberry *Vaccinium myrtillus* (36.8%), rowan *Sorbus aucuparia* (34.4%) and arboreal lichens (17.4%), whereas other plants each constituted only minor amounts of the food (Table 1). There was a similar frequency of feeding (N = 634) recorded in the field layer (46.4%) and on browse (53.6%) including arboreal lichens in the last category, and no significant difference in the amount

Table 2. Habitat selection of roe deer in Flatdal, Norway during the winter 1979/80 (N = 496). Only data collected below 469 m a.s.l. is included in the comparison of use and availability of cutting classes (N = 480). Use higher than availability is marked +, use as expected from availability is marked 0, whereas use less than expected is marked -.

Habitat	Obs. use (%) ± c.i.		Expected use (%)
Altitude (m a.s.l.)			
170 - 269	32.7 ± 5.4	+	18.3
	± 5.9*	+	
270 - 369	54.2 ± 5.7	+	27.0
	± 6.2*	+	
370 - 469	10.1 ± 3.4	-	18.0
	± 3.8*	-	
470 - 569	1.6 ± 1.4	-	10.3
	± 1.6*	-	
570 - 669	1.4 ± 1.4	-	7.5
	± 1.5*	-	
670 - 769	0		4.5
770 - 869	0		4.9
870 - 969	0		7.8
970 - 1069	0		1.6
Cutting classes			
Class I	6.7 ± 2.8	-	11.8
	± 3.1*	-	
Class II	3.8 ± 2.2	-	8.6
	± 2.4*	-	
Class III	1.7 ± 1.5	0	3.0
	± 1.6*	0	
Class IV	21.9 ± 4.6	-	28.3
	± 5.1*	-	
Class V	53.3 ± 5.6	+	40.6
	± 6.2*	+	
Edge 1	8.8 ± 3.2	+	2.5
	± 3.5*	+	
Edge 2	4.0 ± 2.2	0	5.3
	± 2.4*	0	

* adjusted autocorrelation

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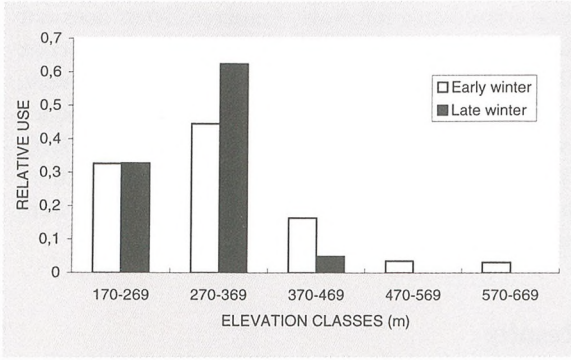


Figure 1. Roe deer proportional use of elevation classes (170-669 m a.s.l.) during early (November-January) and late winter (February-March) 1979/80 in Flatdal, Norway.

removed from the field layer from early (51.4%, November-January) to late winter (48.6%, February-March, $\chi^2 = 1.7$, df = 1, $P > 0.05$).

Selection of feeding habitat by roe deer in the study area showed an overall difference from random use when elevation class above sea level was considered ($\chi^2 = 354.6$, df = 8, $P < 0.001$; adjusted autocorrelation (marked with * below) $\chi^2 = 177.3$, $P < 0.001$). Roe deer preferred the lower part of the study area (Table 2), and use of the higher elevations declined from early (November-January) to late (February-March) winter ($\chi^2 = 59.0$, df = 4, $P < 0.001$; $*\chi^2 = 29.5$, $P < 0.001$; Fig. 1). Areas above 469 m a.s.l. were therefore excluded from the analysis of choice of cutting classes. Overall choice of cutting classes was different from that expected from availability ($\chi^2 = 132.1$, df = 6, $P < 0.001$, $*\chi^2 = 66.0$, $P < 0.001$). Class I, II and IV were used less than expected, class III and edge 2 as expected and class V and edge 1

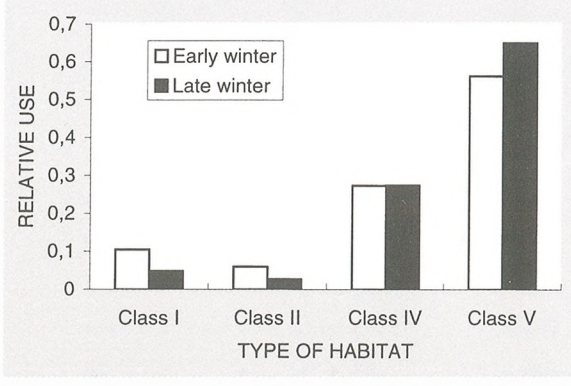


Figure 2. Roe deer proportional use of open habitat (Class I and II) and mature forest stands (Class IV and V) during early (November-January) and late winter (February-March) 1979/80 in Flatdal, Norway.

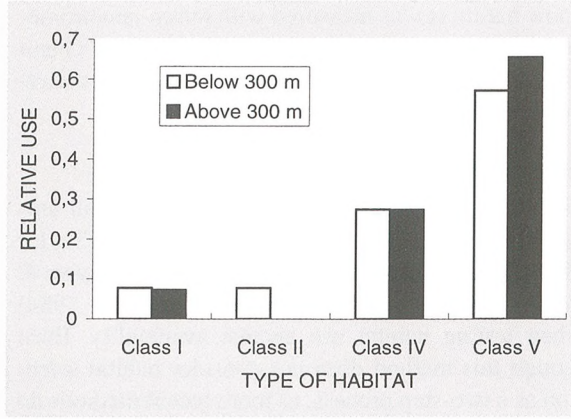


Figure 3. Roe deer proportional use of open habitat (Class I and II) and mature forest stands (Class IV and V) at high (above 300 m a.s.l.) and low (below 300 m a.s.l.) elevations during winter 1979/80 in Flatdal, Norway.

more than expected (see Table 2). The use of (dense) mature forest stands (class IV and V) relative to open habitats (class I and II) increased as the winter progressed ($\chi^2 = 14.0$, df = 3, $P < 0.005$, $*\chi^2 = 7.0$, $P < 0.1$; Fig. 2) and were higher at higher than at lower (<300 m) altitudes ($\chi^2 = 17.4$, df = 3, $P < 0.001$, $*\chi^2 = 8.7$, $P < 0.05$; Fig. 3).

Snow depth increased through the winter and was on average deeper in February-March than in November-January (Fig. 4). The snow was very soft through the entire winter, with low penetrometer-values. Only one measurement gave a higher value than 30 kg, and even this was regarded as rather soft snow. A multiple ANCOVA model (N = 406, $r^2 = 0.101$) showed that track depth (range 5-35 cm) did not differ from early to late winter (F-ratio = 0.121, P = 0.729), differed only slightly between cutting classes (F-ratio = 2.507, P = 0.030), with no interaction between effect of period and cutting classes (F = 0.949, P = 0.449). Track depth increased only marginally with altitude (mean = 19.2 cm for 170-269 m a.s.l., mean = 20.3 cm for 370-469 m a.s.l.; F-ratio = 27.325, P = 0.001). Also very little of the variation in cratering depth (range 1-40 cm) was explained by the same factors (multiple ANCOVA, N = 281, $r^2 = 0.091$), with no increase from early to late winter (F-ratio = 0.608, P = 0.436), no difference between cutting classes (F-ratio = 1.478, P = 0.197), and no interaction between the effect of period and cutting classes (F-ratio = 1.832, P = 0.107). Cratering depth increased marginally with altitude (mean = 9.4 cm for 170-269 m a.s.l., mean = 13.3 cm for 370-469 m a.s.l.; F-ratio = 8.734, P = 0.003).

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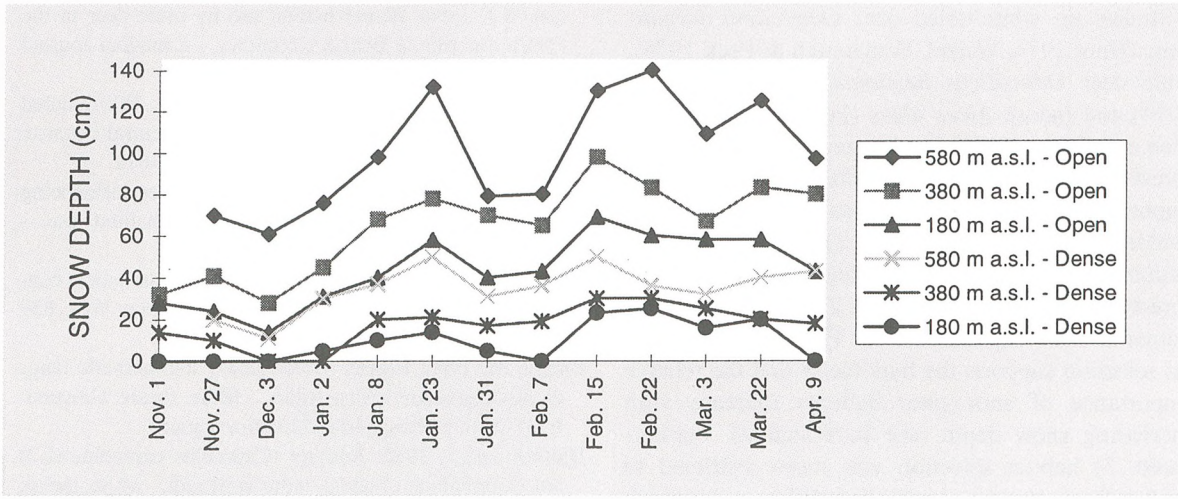


Figure 4. Snow depth (in cm) at different altitudes in Flatdal, Norway, during winter 1979/80 in open habitat (Class I) and in mature forest stand (dense; Class V).

Discussion

Food plant selection

The roe deer generally occurs in a wide variety of habitats; the food supply and thus the food selection therefore vary much from one locality to another (Helle 1980, Petersen & Strandgaard 1994, Tixier & Duncan 1996). Bilberry seem to be the main bulk food source for roe deer during winter in Fennoscandia (Hagen 1958, Cederlund, Ljungqvist, Markgren & Stålfelt 1980, this study), although it was only the sixth most important food plant at Muhos in Finland (Helle 1980). Differences between areas are more evident when other food plants are considered. Rowan was important in our study and also in a study in the county of Østfold further southeast in Norway (Hagen 1958), but made up only a small proportion of the diet at Grimsö in Sweden (Cederlund et al. 1980), and were not even present in the diet of roe deer at Muhos in Finland (Helle 1980). In addition to plants, arboreal lichens were found in roe deer diet in rather large amounts during winter in coniferous areas in both Fennoscandia (Helle 1980) and in the Alps (Wotschikowsky & Schwab 1994). The amount of feeding in the field layer was constant through the winter, whereas earlier studies have found a decreasing amount of field layer species in the roe deer diet with increasing snow depth (Cederlund et al. 1980, Helle 1980, Mysterud & Østbye 1995b). The stable amount of feeding in the field layer may be due to the increase in use of mature forest stands as winter progressed and snow depth increased. Snow structure was soft throughout this winter, and the deer were therefore able to dig through the snow the entire winter. It was surprising, however, that cratering depth did not increase through the winter or with altitude in accordance with increasing snow depth. This implies that there may be some threshold level of snow depth, above which costs of cratering are high. A similar threshold, between cratering behaviour of reindeer Rangifer tarandus and snow hardness, was found to be remarkably similar in Alaska (Lent & Knutson 1971) and Norway (Skogland 1978). However, also track depth was rather stable, and this suggests that roe deer selectively used habitats with shallow snow depth.

Habitat selection and snow depth

Roe deer in the study area preferred the lower elevations of the altitudinal gradient that consistently provided a shallower snow depth. This fits the general pattern for cervids with migration to lower elevations during winter (Brazda 1953, Dalke, Beeman, Kindel, Robel & Williams 1965, LeResche 1974, Albon & Langvatn 1992, Bjerga 1996), and snow is regarded as the most important factor causing such migration (e.g. Nelson 1995). This study further supports studies that have shown that mature forest is the preferred winter habitat for cervids at northern latitudes (Huot 1974, Kucera 1976, Armstrong et al. 1983, Beier & McCullough 1990, Pauley et al. 1993, Armleder et al. 1994).

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Studies on white-tailed deer *Odocoileus virginianus* (Huot 1974, Wetzel, Wambaugh & Peek 1975), mule deer *Odocoileus hemionus* (Armleder et al. 1994) and moose *Alces alces* (Peek, Scott, Nelson, Pierce & Irwin 1982) show increased use of mature forest with increasing snow depth. That snow was an important factor for habitat selection by roe deer was evident in three different ways: 1) use of higher elevations decreased (see Fig. 1) and 2) use of mature forest stands increased (see Fig. 2) from early to late winter as snow depth increased. This change in habitat selection supports the hypothesis that the relative importance of snow-poor habitats increase with increasing snow depth (see Introduction). Furthermore, 3) habitat selection was more restricted to mature forest stands at higher than at lower elevations (see Fig. 2).

A problem often faced when trying to dissolve the factors affecting ranging behaviour and habitat choice during winter, is that snow depth and low temperature are often correlated (Cederlund 1982). Mysterud & Østbye (1995a) showed that during a winter with low snow depth thermal factors affected choice of bed-site by roe deer, but not choice of feeding site. In our study, only the feeding habitat was investigated. Thus, the changes in habitat use were more likely to have been caused by increasing snow depth than by decreasing temperature.

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