Habitat selection by roe deer and sheep: does habitat ranking reflect resource availability?

Atle Mysterud, Per Kristian Larsen, Rolf Anker Ims, and Eivind Østbye

Abstract: Habitat ranking is often assumed to reflect food availability, but habitat selection may involve trade-offs, for example, between selecting for food or cover. We tested whether the habitat selection of 27 radio-collared European roe deer (*Capreolus capreolus*) and 10 free-ranging domestic sheep (*Ovis aries*) on a forest range in southern Norway reflected resource availability. We predicted that ruminants of different feeding types would use habitats according to the main forage class, but that antipredator behavior might remove the correlation between habitat selection and food availability, thus making temporal and spatial scaling crucial. As predicted, habitat selection by sheep was highly correlated with grass availability on both the home-range and study-area scales. The habitat ranking of roe deer habitat selection did not correlate with the availability of herbs on either scale, but rather was correlated with the availability of canopy cover. We found a clear effect of temporal scale on habitat selection by roe deer. During summer, roe deer used forest habitats with more forage to a greater extent when they were active than when they were inactive, and tended to use habitats with greater availability of herbs at night. We conclude that scale-dependent trade-offs in habitat selection may cause inconsistent habitat rankings when pooled across temporal and spatial scales.

Résumé : On assume généralement que le rang de préférence d’un habitat reflète la disponibilité de la nourriture qui s’y trouve, alors que la sélection d’un habitat suppose sans doute souvent des compromis, par exemple entre le choix de nourriture et la couverture. Nous avons suivi 27 Chevreuils (*Capreolus capreolus*) munis d’un collier émetteur et 10 moutons domestiques (*Ovis aries*) en liberté dans un habitat forestier du sud de la Norvège afin de déterminer si leurs habitats respectifs reflètent la disponibilité des ressources. Nous avons supposé au départ que des ruminants d’habitudes alimentaires différentes utilisent probablement leur habitat en fonction de la principale classe de brout, mais que le comportement antiprédateurs risque de rompre la corrélation entre le choix de l’habitat et la disponibilité de la nourriture, rendant de ce fait cruciales les échelles spatiale et temporelle. Tel que prédit, le choix de l’habitat du mouton était en forte corrélation avec la disponibilité des herbacées, aussi bien à l’échelle du domaine de l’animal qu’à l’échelle de la zone d’étude. Le choix de l’habitat chez le chevreuil, en revanche, n’était pas relié à la disponibilité des herbacées, ni à l’une ni à l’autre échelles, mais était en corrélation avec la disponibilité d’une couverture. Nous avons constaté l’existence d’un effet évident de l’échelle temporelle sur la sélection de l’habitat chez le chevreuil. En été, le chevreuil utilise les habitats boisés contenant plus de brout plus souvent au cours de ses périodes d’activité qu’au cours de ses périodes d’inactivité, et il a tendance à utiliser les habitats qui contiennent plus d’herbacées davantage pendant la nuit. Nous concluons que les compromis en fonction de l’échelle peuvent entraîner des choix d’habitat qui ne sont pas toujours cohérents par rapport aux échelles temporelle et spatiale.

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Introduction

Ruminants can be classified according to morphophysiological feeding types as concentrate selectors (browsers) that prefer browse, herbs, and fruits; grass–roughage eaters (grazers) that predominantly eat grass; and an intermediate type between these two (Hofmann 1989). The availability of forage in general is regarded by some as the most important determinant of habitat selection for all ruminants (e.g., Langvatn and Hanley 1993). According to classical theories of foraging (Charnov 1976) and habitat selection (Rosenzweig 1981), a forager should continue to exploit a patch until its harvest rate in the patch drops to its average over all patches (including foraging time in patches and travel time between patches). Under these conditions, the animal will spend most time in those habitats richest in food, and habitat selection is likely to reflect food availability. However, it is implicitly assumed that foragers have no alternative activities (they only forage) (Kotler 1997) and that there are no trade-offs between selecting different resources. Such trade-offs, for example, between foraging and predator avoidance, have been described in a number of habitat situations (e.g., Cowlishaw 1997*a*, 1997*b*; Kotler 1997; Turner 1997; review in Lima and Dill 1990). It is thus likely that an animal’s habitat selection may reflect a multitude of requirements that an individual must fulfil to successfully complete its life cycle, and not just the availability of forage (McFarland 1977; Orians and Wittenberger 1991).

Most methods used to evaluate habitat selection from animal space-use observations (e.g., radio fixes) infer habitat

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preference as the disproportional use of some habitats over others, without directly considering that trade-offs may be important (Neu et al. 1974; Johnson 1980; Aebischer et al. 1993; Manly et al. 1993; Arthur et al. 1996; Otis 1997; see also Alldredge and Ratti 1986, 1992; Thomas and Taylor 1990; Cherry 1996). The currently preferred option from a statistical point of view, compositional analysis, does not establish absolute preferences, but rather ranks habitats relative to each other from least to most preferred (Aebischer et al. 1993; see Tufto et al. 1996 for a recent application to cervids). However, Mysterud and Ims (1998) showed that preference for a habitat may be conditional on availability if, for example, an animal always forages in open habitat (forage-rich) and seeks cover habitat (less forage) when resting or uses an open habitat with abundant forage during the night and another habitat with more cover but less forage during the day. Habitat selection is thus often a scale-dependent process (Johnson 1980; Levin 1992), that is, different mechanisms and trade-offs that determine an animal's resource use may come into play on different spatial and temporal scales. Spatial and temporal scales are naturally linked (Wiens 1989). Patch selection within the home range may depend on shifting phases in the daily activity cycle of an animal, while the more infrequently occurring home-range shifts on a landscape scale may result from seasonal migrations (Morris 1987, 1992). Even though habitat-evaluation procedures (Bart et al. 1984) and multivariate approaches (Clark et al. 1993) take several habitat factors into consideration, these often fail to account for varying habitat availability and (or) spatial scale and may also run into problems of pseudoreplication (Aebischer et al. 1993).

In this study, we used radiotelemetry data to determine habitat selection by 27 European roe deer (*Capreolus capreolus*) and 10 free-ranging domestic sheep (*Ovis aries*) on a sympatric forest range with a mix of 12 habitat types that differ in their amounts of food and cover. We predicted that ruminants of different morphophysiological feeding type (Hofmann 1989) would use habitats according to main-forage class but that antipredator behavior might remove correlation between habitat selection and food availability. Thus, (*i*) we tested whether habitat ranking based on sheep habitat selection, as established from the compositional analysis of Aebischer et al. (1993), was correlated with the availability of grass, since no effect of cover availability was expected (Warren and Mysterud 1991; Warren et al. 1993); and further, (*ii*) we tested whether habitat ranking based on roe deer habitat selection was correlated with the availability of (*a*) herbs (due to feeding type; Cederlund et al. 1980; Selås et al. 1991; Tixier and Duncan 1996) or (*b*) cover (antipredator behavior; Henry 1981; Chapman et al. 1993; Mysterud and Østbye 1995; Mysterud 1996; Tufto et al. 1996). At the within-species level, we predicted that the habitat-selection pattern would vary with the spatial and temporal scales of observation, if the selection pattern was also influenced by antipredator behavior. For roe deer, (*iii*) we tested whether the availability of herbs was greater (*a*) at locations where they were active rather than inactive (Gill 1966; Huot 1974) and (*b*) at locations used at night or at those used during the day (Chapman et al. 1993); and (*iv*) we tested if they used more open habitats (*a*) when active rather than when inactive (e.g., Armstrong et al. 1983*a*; Mysterud and Østbye 1995) and (*b*) at night or during the day (e.g., Beier and McCullough 1990; Selås et al. 1991).

Methods

Study area

The study area is about 25 000 ha in size and is located in the Lier valley in southern Norway (between 59°45′ and 60°00′N and 10°05′ and 10°20′E). Most of the area is forested and is situated within the boreonemoral region (Abrahamsen et al. 1977). Vegetation is varied but is dominated by Norway spruce (*Picea abies*), which, on drier sites, is mixed with Scots pine (*Pinus sylvestris*). The forest has been commercially managed and there are several clearcuts of various sizes within the study area. Along the valley bottom, on richer soil, deciduous forest is dominant, fragmented by small cultivated fields (Kjøstvedt et al. 1998). In the deciduous forest, species such as hoary alder (*Alnus incana*) and bird cherry (*Prunus padus*) are common, and these are mixed with elm (*Ulmus glabra*) and linden (*Tilia cordata*) on the richest sites. The topography is hilly: on a coarse scale, it rises from lake Holsfjorden, at 63 m asl, to over 600 m asl and it is also variable on a more local scale (Mysterud 1999). The winter density of roe deer is about 3–5 deer/100 ha (Mysterud 1993), whereas for sheep, the density is 5–6 animals/100 ha but locally is much higher (Larsen 1997). Red fox (*Vulpes vulpes*) and, occasionally, lynx (*Felis lynx*) inhabit the study area.

Data collection

Roe deer were captured in box traps or drop nets during February and March 1994–1997 and fitted with radio collars (TXE-3, Televilt Int. AB transmitters). These radio collars were motion-sensitive, that is, they had a variable signal that indicated whether or not the deer was active. All fixes were obtained by standard triangulation using at least two bearings, usually from within 300 m of the animal. If the signal was weak, at least three bearings were used. These directions were plotted manually on forest-evaluation maps (see below). On average, individual deer were located every 18 h (starting at 10:00) in March (winter) and July (summer) during the first season following capture (one male and one female were followed in June 1995, but habitat selection was determined equally between June and July 1995; Lodgaard and Nergård 1997). The starting point of the triangulation route (1–8 h in length) was chosen at random so that each deer was triangulated at all hours to avoid biases. For the summer season (1994–1997), a total of 26 roe deer (9 adult females, 13 adult males, 2 yearling females, and 2 yearling males) were followed, whereas 27 (10 adult females, 13 adult males, 2 yearling females, and 2 yearling males) were followed for the winter season (1995–1997). In both March and July of each year, 33 fixes were obtained for each individual per month. Ten ewes from two herds (Dala breed) were also fitted with radio collars and followed from release on June 5th through July 1995 (one individual somewhat later), with the same 18 h between triangulations. The radio collars fitted to sheep were not motion-sensitive. All individuals were treated as independent, since none of the sheep stayed together after release and they seemed to move independently of each other.

Definition of habitat types

We identified habitat categories based on cutting classes, following the standard national forest evaluation of Norway (Landsskogstakseringen 1971; available on maps, scale 1:5000). Four categories of spruce stands were identified: class 1, clear cuts; class 2, young plantations; class 3, pole-sized stands; and class 4, medium-aged stands and older mature stands combined (corresponding to classes IV and V in Landsskogstakseringen (1971)). The information contained in the forest-evaluation maps about site

Table 1. Data on habitat availability and overall use by roe deer and sheep in the Lier valley, Norway.

		Summer							Winter			
		Roe deer		Sheep					Roe deer			
Habitat type	Quality	Overall use (%)	Availability (%)	Overall use (%)	Availability (%)	Herbs (%)	Grass (%)	Cover (%)	Overall use (%)	Availability (%)	Cover (%)	Availability in study area (%)
Spruce stands												
Class 1	L	0.9	1.9	2.5	1.9	2.0±1.2	1.2±0.3	6.5±2.7	2.4	5.0	4.6±1.9	4.7
	H	1.7	1.9	0	0.2				0.4	0.9		2.4
Class 2	L	5.0	4.6	54.2	42.5	10.8±2.6	24.2±6.1	29.8±7.5	5.3	4.0	14.6±5.9	12.5
	H	13.6	12.7	6.9	3.9	23.2±6.4	12.8±3.9	43.8±9.3	7.6	5.8	30.4±8.0	6.9
Class 3	L	2.8	1.9	13.5	15.0				4.5	2.7		2.9
	H	13.7	11.6	0.9	0.6	0.1±0.1	0±0	84.9±1.5	6.6	8.1	83.0±1.2	7.3
Class 4	L	8.2	9.3	17.8	25.9	1.2±0.5	8.3±1.7	69.7±2.3	7.4	6.7	48.8±12.3	17.5
	H	16.5	13.3	4.2	7.7	0.2±0.1	7.6±6.2	72.4±4.8	14.5	10.5	64.6±5.7	8.1
Deciduous forest		16.5	12.8	0	0	29.6±8.3	2.7±2.2	86.4±1.7	25.5	21.4	15.8±2.3	4.5
Pine forest		6.1	4.8	0	0	0.7±0.4	0±0	27.5±4.4	7.9	6.2	28.4±5.9	9.9
Agricultural fields		14.1	18.9	0	0				16.4	21.6		16.1
Other habitats		0.9	6.3	0	2.2				1.5	7.0		7.1

Note: Compositional analysis does not consider overall use against availability. Values for availability of herbs grass and cover are given as the mean ± SE. L, low site quality; H, high site quality.

quality (H, high; L, low) and the site's ability to produce spruce forest (in rankings, referred to, for example, as 4H or 2L) was also used. In addition, the habitat categories deciduous forest (DEC), pine forest (PINE), agricultural land (AGRIC), and other (OTHER) were identified. OTHER includes mostly human development, such as roads and buildings. The availability of habitats was calculated by using a grid to estimate the area of each habitat within the study area (landscape scale) and within individual home ranges (home-range scale). The home-range boundaries were demarcated using the 95% minimum convex polygon method, thus excluding 5% of the most distant fixes from the home-range centre (e.g., Andreassen et al. 1993).

Estimation of food and cover availability

In each of the major habitat types, the availability of herbs and grasses was estimated within 2 × 2 m squares along transects. For each such square, the number of 10 × 10 cm squares covered by each of the different plant groups was divided by the total number of 10 × 10 squares, to give the respective percentages in the 2 × 2 m square (Mysterud 1996). Broad groupings of plants were used, since roe deer can feed on up to 100 species during summer (Selås et al. 1991). Canopy cover (hereinafter referred to as cover) was estimated in the same squares, using Lemmon's densiometer (Lemmon 1956, 1957). There were three transects per habitat and three plots per transect, the mean of which constituted the estimate for a specific habitat. Plots were distributed randomly, 50–70 m apart, along each transect. Edge habitat was avoided (always more than 50 m from edge). Transects representing summer conditions were undertaken during July 1995 and those representing winter conditions during November 1996, just before snowfall but after leaves had fallen.

Compositional analysis of habitat selection

Habitat selection was analysed using the compositional analysis of log ratios described by Aebischer et al. (1993). Mature forest on rich soil (cutting class 4H) was chosen as the denominator in the log ratios, since this habitat category was present in most home ranges. During winter, this habitat was not present within the home ranges of two roe deer and, hence, they were omitted from the analysis. Missing values of use on the study-area scale were assigned values of 0.01% and, on the home-range scale, were estimated with the formula (0.5/number of habitat types) / (number of locations + 0.5) (Aebischer et al. 1993). Missing values of availability were treated according to the first option described in Appendix 2 in Aebischer et al. (1993). Effects of scale, sex, and age on habitat selection of roe deer were tested using multivariate ANOVA models (MANOVA) (SYSTAT Inc. 1992).

Habitat rankings and resource availability

We used Spearman's rank correlation (test of independence; Bhattacharyya and Johnson 1977, p. 531) to test the hypotheses regarding possible correlation of the habitat rankings of sheep and roe deer habitat selection (calculated with compositional analysis) with the habitat rankings based on food and cover availability. The correlation with food availability for roe deer was only done during the summer, when the main food of roe deer was herbs (Cederlund et al. 1980; Selås et al. 1991; Tixier and Duncan 1996). Food resources in the area during winter were unpredictable (Mysterud 1998).

Effects of temporal scale

For roe deer, average food and cover values were assigned to the habitat (as estimated above) of each radiotelemetry fix. The effects of activity (active–inactive) and period (night–day) on average food and cover value were then calculated. To avoid pseudoreplication, we used individual averages for food and cover

Table 2. Habitat rankings.

(A) Habitat rankings for roe deer and sheep measured with compositional analysis on different spatial scales and for different seasons.

	Season	Scale	*n*	Habitat ranking
Roe deer	Summer	Study area	26	4H > 3H > 2H ≥ AGRIC ≥ OTHER ≥ DEC ≥ 1H ≥ 4L ≥ 3L ≥ PINE ≥ 2L ≥ 1L
		Home range	26	4L ≥ DEC ≥ 4H ≥ 2H ≥ 3H ≥ 1H ≥ PINE ≥ 2L ≥ 3L ≥ AGRIC ≥ 1L ≥ OTHER
	Winter	Study area	27	4H ≥ AGRIC ≥ OTHER ≥ 3H ≥ 2H ≥ DEC ≥ PINE ≥ 3L ≥ 4L ≥ 1L ≥ 2L ≥ 1H
		Home range	27	4H ≥ PINE ≥ 2H ≥ AGRIC ≥ 4L > 3H ≥ 2L > 1L ≥ 3L ≥ DEC ≥ 1H ≥ OTHER
Sheep	Summer	Study area	10	3L ≥ 2L > 4L > 4H > 2H > OTHER > 3H > 1H > 1L > DEC > PINE/AGRIC
		Home range	10	2H ≥ 2L > 4L > 3L ≥ 4H ≥ 3H > OTHER

(B) Rankings of herb, grass, and cover habitats based on direct estimates within the most common habitat types.

	Season	*n*	Habitat ranking
Herbs	Summer	9	2H ≥ DEC ≥ 2L ≥ 1L ≥ 4L ≥ PINE ≥ 4H ≥ 3H
Grass	Summer	9	2L ≥ 2H ≥ 4L ≥ 4H ≥ DEC ≥ 1L ≥ PINE ≥ 3H
Cover	Summer	9	DEC ≥ 3H ≥ 4H ≥ 4L ≥ 2H ≥ 2L ≥ PINE ≥ 1L
	Winter	9	3H ≥ 4H ≥ 4L ≥ 2H ≥ PINE ≥ DEC ≥ 2L ≥ 1L

Note: See the text for habitat abbreviations.

availability for each activity (active–inactive) and period (night–day) in a way similar to compositional analysis (Aebischer et al. 1993) rather than using each fix separately. Habitat selection on both home-range and landscape scales (e.g., Morris 1987, 1992) may lead to individual differences in the average availability of food and cover. When analysing the effect of activity–nonactivity and day–night on habitat use within the home range, we therefore adjusted each individual's food and cover estimate by the mean for its own home range (subtracted the mean from the estimate). Note that this inflates any effect of sex or age on habitat selection; sex and age were incorporated nevertheless, to test for sex–age and period–activity interactions, with only second-order interactions being included. Some of the radio collars did not switch between active and inactive mode as planned, and these animals were therefore omitted from this analysis. Because the estimates of herb and cover availability were measured as percentages, these values were transformed:

$$\text{arcsine}\sqrt{\frac{\text{availability of herbs or cover}}{100}}$$

We used ANOVA models for testing for effects of activity and period of the day on average food and cover values in habitats. All statistical tests of effects of temporal scale were done in S-Plus (Venables and Ripley 1994). Models were checked for assumptions of linearity, homogeneity of variance, and influence values (Cook's *D*; Venables and Ripley 1994).

Results

Compositional analysis of habitat selection

Sheep

Quantitatively, the most important category of habitat to sheep (ewes) was the young plantation of low site quality; 54.2% of all locations fell within this category and mean availability of this habitat was 42.5% (Table 1). Habitat selection of 10 sheep was nonrandom during summer on both home-range ($\chi^2 = 40.35$, df = 6, $p < 0.005$) and study-area ($\chi^2 = 150.24$, df = 10, $p < 0.005$) scales. Rankings differed significantly between these two spatial scales (Table 2; MANOVA, Hotelling Lawley trace = 66.33, $F = 121.60$, $p = 0.000$). The most preferred habitats on the home-range scale were young plantations of high and low site quality, whereas on the study-area scale, pole-sized stands and young plantations of low site quality were preferred (Table 2).

Compositional analysis of habitat selection

Roe deer

Compared with sheep, roe deer used a wider range of habitats and used them more equally (Table 1). Roe deer habitat selection was nonrandom during both summer and winter and on both home-range (summer: $n = 26$, $\chi^2 = 51.04$, df = 11, $p < 0.005$; winter: $n = 27$, $\chi^2 = 71.88$, df = 11, $p < 0.005$) and study-area (summer: $n = 26$, $\chi^2 = 45.68$, df = 11, $p < 0.005$; winter: $n = 25$, $\chi^2 = 35.55$, df = 11, $p < 0.005$) scales. Owing to a high number of missing values (missing habitats) when using a large number of habitat types, certain habitats ranked equally on the home-range scale. If two habitats ranked equally, then the ranking between these two habitats was determined by paired comparison in the ranking matrices. Although we established habitat rankings for both summer and winter a priori (Table 2), ranking of habitat selection by roe deer during winter and summer was significantly different only on the home-range scale (MANOVA, Hotelling Lawley trace = 1.13, $F = 4.45$, $p = 0.000$) and not on the study-area scale (MANOVA, Hotelling Lawley trace = 0.20, $F = 0.76$, $p = 0.677$). Habitat rankings differed between the study-area and the home-range scales in both seasons (summer: MANOVA, Hotelling Lawley trace = 0.51, $F = 2.58$, $p = 0.022$; winter: MANOVA, Hotelling Lawley trace = 0.66, $F = 7.24$, $p = 0.000$). There were no effects of sex, age, or interaction between sex and age on habitat selection of roe deer on the study-area (summer–winter: MANOVA, all $p > 0.5$) or home-range (summer–winter: MANOVA, all $p > 0.1$) scale. The most preferred habitat was mature forest of high site quality, except during summer on the home-range scale, when mature forest of low site quality was the most preferred habitat (Table 2).

Habitat ranking and resource availability

Rankings of sheep habitat selection were correlated with grass availability on both spatial scales (home-range scale: $n = 5$, $r_{\text{sp}} = 0.900$, $p = 0.042$; study-area scale: $n = 8$, $r_{\text{sp}} =$

Table 3. Predictions of habitat selection considering different temporal scales relative to the spatial distribution of food and cover based on studies of some forest-dwelling cervids.

Prediction	Species	Sex	Method of data collection	Statistical method	Food[a]	Cover[a]	Season	Reference
Use open habitat more at night than during the day	*Alces alces*	M, F	Radiotelemetry	None	No	No	Summer	Hjeljord et al. 1990
		F	Radiotelemetry	None	No	No	Summer	Histøl 1992
	Capreolus capreolus	M, F	Radiotelemetry	χ^2 test	No	No	Summer	Selås et al. 1991
		M, F	Radiotelemetry	None	No	No	Summer, winter	Chapman et al. 1993
	Cervus elaphus	M, F	Direct observation	*t* test	No	No	Summer	Thirgood and Staines 1989
	Odocoileus virginianus	M, F	Direct observation	None	No	No	Winter	Montgomery 1963
		M, F	Radiotelemetry	ANOVA	No	No	Summer, winter	Beier and McCullough 1990
Use open habitat more when active than when inactive	*Capreolus capreolus*	M, F	Direct observation	None	No	No	Summer, winter	Stüwe and Hendrichs 1984
		M, F	Snow-tracking	ANOVA	No	Yes	Winter	Mysterud and Østbye 1995
	Cervus elaphus	M, F	Direct observation	None	No	No	Winter	Staines 1976
	Odocoileus hemionus	M, F	Direct observation	χ^2 test	No	No	Winter	Wood 1988
	Odocoileus virginianus	M, F	Direct observation	None	No	No	Winter	Gill 1966
		M, F	Snow-tracking	None	Yes	Yes	Winter	Huot 1974
		M, F	Snow-tracking	PCA[b]	No	Yes	Winter	Armstrong et al. 1983*a*
More forage available at night than at day locations	*Capreolus capreolus*	M, F	Radiotelemetry	None	No	No	Summer, winter	Chapman et al. 1993
More forage available at feeding than at bedding sites	*Odocoileus virginianus*	M, F	Direct observation	None	No	No	Winter	Gill 1966
		M, F	Direct observation	None	Yes	Yes	Winter	Hout 1974
More cover at day-bedding sites than at night-bedding sites	*Odocoileus virginianus*	M, F	Snow-tracking	PCA[b]	No	Yes	Winter	Armstrong et al. 1983*a*, 1983*b*

[a] Was or was not quantified.
[b] Principal component analysis.

0.762, $p = 0.018$). In contrast, habitat-selection rankings of roe deer were not correlated with herb availability on either scale (home-range scale: $n = 8$, $r_{sp} = 0.024$, $p > 0.1$; study-area scale: $n = 8$, $r_{sp} = -0.333$, $p > 0.1$); however, they were correlated with the availability of cover on both the study-area (summer: $n = 8$, $r_{sp} = 0.762$, $p = 0.018$; winter: $n = 8$, $r_{sp} = 0.786$, $p = 0.014$) and home-range (summer: $n = 8$, $r_{sp} = 0.738$, $p = 0.023$) scales, although not quite significantly on the home-range scale during winter ($n = 8$, $r_{sp} = 0.595$, $p = 0.066$).

Effects of temporal scale

In forested areas in the summer, roe deer used habitats with a higher average availability of herbs (adjusted to mean home-range levels) when they were active than when they were inactive (Fig. 1; ANOVA: 20 individuals, $n = 80$, $F = 5.26$, $p = 0.025$), and herb availability tended to be lower in habitats used during the day than in those used at night ($F = 2.81$, $p = 0.093$). Removing one statistically defined outlier that had a high Cook's D value strengthened this result ($F = 3.95$, $p = 0.051$). None of the interactions were significant (all $p > 0.2$).

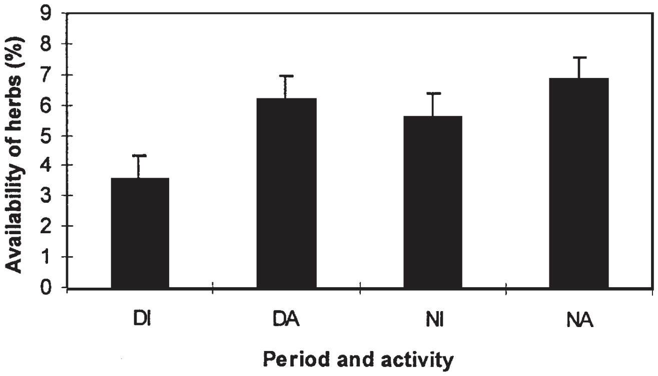
There was no clear effect of activity (ANOVA: 20 individuals, $n = 80$, $F = 0.99$, $p = 0.324$) or diurnal period ($F = 2.75$, $p = 0.101$) on the use of habitats with different mean amounts of cover (adjusted to mean home-range levels). However, there tended to be an interaction between age and period ($F = 3.24$, $p = 0.076$), that is, there was a tendency for younger deer to use more open habitats during the night. However, this result was dependent on one outlying value (a high Cook's D value; after excluding this value, all $p > 0.1$). The other interactions were not significant (all $p > 0.5$).

During winter, there was no effect of period or activity on choice of habitats with different mean availability of cover (adjusted to mean home-range levels; ANOVA: 20 individuals, $n = 80$, $p > 0.4$). There was, however, an interaction between age and period ($F = 6.01$, $p = 0.017$), that is, juveniles chose more open habitats during the night.

Discussion

As predicted, habitat rankings based on habitat selection of free-ranging sheep were successfully predicted by the availability of the food resource (grass) on both spatial scales. In contrast, herb availability was not associated with the habitat rankings established from roe deer habitat selection on any scale. Even though, theoretically, this lack of correlation between roe deer habitat selection and food availability may also arise from inaccuracy in telemetry fixes or failure to quantify the food resource properly, we do not think that this was the case, because sheep habitat rankings were predicted by food availability and there were clear effects of temporal scale on the selection of habitats with different amounts of herbs for roe deer (see below). Although canopy cover availability successfully predicted habitat selection by roe deer in most cases, we argue that habitat selection by roe deer is best viewed as a trade-off between selection of cover and selection of food. This implies that incorporating relevant spatial and temporal scales becomes crucial (Johnson 1980).

Fig. 1. Effect of temporal scale (D, day; N, night; I, inactive; A, active) on the use (mean ± SE) of forest habitats with different average availability of herbs by roe deer in Lier, Norway.



This study supports the hypothesis that temporal and spatial scales are important for the observed pattern of habitat selection in the roe deer, as has been observed for other cervids (reviewed in Table 3). As predicted, roe deer used habitats with a higher average availability of herbs when foraging and, presumably, also at night (Fig. 1). This indicates that the selection of food is traded for some other resource. However, the predictions that roe deer would use more open habitat when active and at night were not clearly supported. Although the trend was in the predicted direction, the lack of a pronounced effect may reflect that resources other than food and cover, such as substrate for bedding (Mysterud 1996), also influence habitat selection by roe deer.

Habitat selection by roe deer on the landscape scale did not differ significantly between winter and summer. This was especially surprising, considering that 70% of the females and 39% of the males in the population were migratory (Mysterud 1999). Although the cause of this migration was probably, in part, the result of social factors (Wahlström and Liberg 1995), there were clear movements along the altitudinal gradient in the study area. This migration is most likely a strategy for finding areas of shallow snow (e.g., Mysterud et al. 1997). Areas at low elevation were preferred year-round; however, although all roe deer in the Lier valley congregated at low altitudes during winter, during summer, 10–15% migrated to higher elevations (Mysterud 1999). This preference for low elevation year-round (Mysterud 1999) may explain the rather high ranking of the habitat category OTHER on the coarse scale, even though it contained mostly paved roads and housings, that is, it contained neither food nor cover and was ranked last at the home-range level in both seasons (Table 1). All housing in the area is situated at low elevation, and this high ranking is probably only a by-product of preference for low-elevation areas.

We conclude that habitat rankings established from compositional analysis may not clearly reflect resource availability when trade-offs, such as those that exist between selecting for food and selecting for cover, are involved. Taking into account relevant spatial and temporal scales for habitat selection in the analysis may help to detect existing patterns of habitat selection and facilitate more biologically relevant interpretations of the mechanisms involved, although trade-offs involved in habitat selection may obscure any pattern when the availabilities of more than one crucial habitat type varies among home ranges (Mysterud and Ims 1998).

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