

Scale-dependent trade-offs in foraging by European roe deer (*Capreolus capreolus*) during winter

Atle Mysterud, Lise-Berith Lian, and Dag Øystein Hjermmann

Abstract: We studied food preferences of and patch and habitat selection by European roe deer (*Capreolus capreolus*) by snow-tracking radio-tagged individuals. To account for the possible biases caused by patch/habitat selection on measures of food preference, we adopted a new method in which diet choice is compared with availability within each forage patch successively rather than to some home-range or study-area average. There was no difference in food preference between males and females or between day and night. When compared with that in random sites 50 m from feeding sites (patch scale), selection was random with regard to cover; however, the food availability index was higher for feeding sites than for random sites. Roe deer selected feeding sites with more cover during cold weather, whereas the food availability index had no effect at this scale (habitat scale). Roe deer selected more open habitat and feeding sites closer to human settlement at night and as snow depth increased. Females tended to select foraging sites that were more hidden than those of males. There was direct evidence of a trade-off between selection of food availability and both canopy cover and distance to human settlement but not between food availability and concealment cover.

Résumé : Nous avons étudié les préférences alimentaires, de même que la sélection des zones alimentaires et des habitats chez le Chevreuil (*Capreolus capreolus*) par repérage d'individus porteurs d'émetteurs dans la neige. Pour contourner les effets que peuvent avoir la sélection de l'habitat et de la zone alimentaire sur les préférences alimentaires, nous avons adopté une nouvelle méthode qui compare le choix alimentaire et la disponibilité des aliments successivement dans chaque zone d'alimentation, plutôt que de le considérer par rapport à une moyenne reliée au domaine vital ou à la zone d'étude. Nous n'avons pas trouvé de différences de préférences alimentaires chez les mâles et les femelles, la nuit ou le jour. Comparativement à des sites aléatoires à 50 m des zones d'alimentation (à l'échelle de la zone d'alimentation) la sélection est aléatoire par rapport à la couverture végétale, mais les zones d'alimentation ont un coefficient de disponibilité de nourriture plus élevé que les sites aléatoires. Les chevreuils choisissent des sites d'alimentation à couverture plus abondante durant la saison froide, alors que le coefficient de disponibilité de nourriture n'a pas d'effet à cette échelle (échelle de l'habitat). Les chevreuils préfèrent les habitats plus ouverts et plus près des agglomérations humaines la nuit et lorsque la couche de neige est épaisse. Les femelles ont tendance à choisir des zones d'alimentation plus protégées que les mâles. Les chevreuils font donc un compromis entre la disponibilité de la nourriture et la couverture végétale/distance de la plus proche agglomération humaine, mais pas entre la disponibilité de la nourriture et la couverture protectrice.

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Introduction

An animal's diet can be viewed as the result of choices made at a hierarchy of spatial scales (e.g., Johnson 1980; Nudds 1980; Senft et al. 1987; Ward and Saltz 1994; Brown and Morgan 1995; Bailey et al. 1996). When an animal chooses which plants or plant parts to eat at a patch/feeding site, it has first chosen a home range and then a habitat within the home range before finally arriving at the patch. Important in this regard is that mechanisms affecting selection may be scale-specific. A herbivore may try to maximize

its energy intake when choosing a food plant from a patch, but such a strategy may be traded with other factors on broader scales (Senft et al. 1987; Bailey et al. 1996), such as predation risk (Lima and Dill 1990; Kotler and Blaustein 1995; Mysterud and Ims 1998).

Juvenile ungulates are often reported to experience very high levels of predation (reviewed in Linnell et al. 1995). It is therefore often reported that females with young use safe habitats even at the expense of forage quality, whereas males seek habitats where food is of high quantity and quality in order to maximize body growth (the reproductive-strategy hypothesis (RSH); Main and Coblenz 1990; Miquelle et al. 1992; Main et al. 1996; Bleich et al. 1997). For example, female moose (*Alces alces*) (Edwards 1983), caribou (*Rangifer tarandus*) (Bergerud et al. 1984; Bergerud and Page 1987; Heard et al. 1996), and bighorn sheep (*Ovis canadensis*) (Festa-Bianchet 1988) all selected home ranges with habitats that provided security from predators at the expense of forage quality, whereas males selected home ranges with habitats

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that provided an abundance of high-quality forage. Studies on sheep have also reported greater use of escape terrain by females than by males (bighorn sheep (Berger 1991) and mouflon (*Ovis gmelini*; Bon et al. 1995)), and female mule deer (*Odocoileus hemionus*) used areas of lower coyote (*Canis latrans*) activity than males (Main and Coblentz 1996).

Few data on patterns of sexual segregation in habitat use of small ungulates with low levels of sexual body-size dimorphism, such as the European roe deer (*Capreolus capreolus*), exist. According to the RSH, segregation will take place during periods of high predation pressure on calves, most commonly around parturition (Linnell et al. 1995). However, roe deer are also prone to severe predation in winters of deep snow, and calves are more prone to predation than adults during their first winter (Cederlund and Lindström 1983). Linnell (1994) also reported that females with young were more vigilant than males. Thus, a study of habitat use by roe deer during winter may advance our understanding of sexual segregation in ungulates.

The hierarchical nature of foraging decisions has received little attention when the foraging behaviour of cervids is studied (Hanley 1997). Despite the theoretical knowledge that predation risk may affect habitat selection in a scale-dependent way, current methods of evaluating food selection by large herbivores are unable to reveal whether the selected diet is preferred (sensu Johnson 1980; Thomas and Taylor 1990) or is eaten simply because it is available in safe habitats. We present an analysis of food selection using a statistical method that assesses use relative to availability of forage within successive feeding sites, rather than commonly used methodological designs that compare chosen diets (use) with their availability within the whole study area (Neu et al. 1974; Byers et al. 1984) or within individuals' home ranges (Johnson 1980; Aebischer et al. 1993). The new approach takes advantage of Arthur et al.'s (1996) method of examining habitat selection for autocorrelated data at the within-home-range scale, and allows availability to vary between observations.

We used data on feeding signs recorded while snow-tracking free-ranging radio-marked roe deer. We test the prediction that food preferences within a foraging site would be similar between males and females, but that sexual segregation will occur at the patch scale and (or) habitat scale, owing to trade-offs between foraging and predation risk (RSH). Trade-offs in selecting different resources were demonstrated (i) indirectly by temporal scale-dependence in selection of one resource at a time (a difference in selection between night and day), and (ii) directly by showing a negative relationship between the availability of one resource and that of another (only possible at a coarse scale). At a fine scale, we tested whether food choice was random and differed between night and day. At a coarser scale, we tested whether temporal scale (night/day) affected habitat use (cover, food, distance to human settlement) and for effects of temperature (e.g., Schmitz 1991; Mysterud and Østbye 1995) and snow depth (e.g., Armleder et al. 1994; Mysterud et al. 1997), because of earlier reports that these have an important influence on habitat selection by cervids during winter. We also assessed whether selection of foraging site is a process that occurs at the patch and (or) habitat scale.

Study area

The study area is located along the Lier valley in southern Norway (59°52'–59°58'N, 10°10'–10°20'E). Most of Lier is forested and situated within the boreonemoral region (Abrahamsen et al. 1977). The vegetation is varied and dominated by Norway 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 that vary in size within the study area, creating habitat heterogeneity. Along the bottom of the valley on richer soil, deciduous forest predominates, 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 dominant, mixed with elm (*Ulmus glabra*) and linden (*Tilia cordata*) on the richest sites. The terrain is very hilly, rising from Lake Holsfjorden at 63 m above sea level to over 600 m 1.5–2.5 km from the lake (Mysterud 1999). The bottom of the valley is undulating and hilly with many ravines on a fine scale (10–100 m between top and bottom), owing to erosion in clay sediments. The density of roe deer during winter is approximately 3–5/100 ha (Mysterud 1993). Deer are heavily hunted by humans using dogs (August–December), and a few deer are also shot during winter (January–March) to reduce damage to crops. Red foxes (*Vulpes vulpes*) are common in the area, and there are also occasional visits by lynx (*Felis lynx*), both of which are potential predators on roe deer.

Material and methods

The 5 adult male (mean body mass 25.8 kg) and 5 adult female (mean body mass 26.5 kg) roe deer included in this study were captured using box traps and drop nets during February and March 1995 and fitted with motion-sensitive radio collars (Televilt Int. AB, TXE-3). The deer were captured at different locations covering most of the study area in order to sample more widely with regard to habitat use (Mysterud 1998). They were followed from January 4 to March 7, 1996, when snow conditions allowed tracking. Usually, two feeding sites were recorded during daylight hours (09:00–16:00) and one site after dark (18:00–23:00). During this period, 4 does were accompanied by fawns. Most deer were occasionally in company of other deer, but groups in the study area were small (Mysterud 1998). A male and a female radio-collared deer were occasionally seen together, but not as a stable group.

Individual deer were observed in stratified order. Once data for a specific (random) deer had been recorded, that deer was not tracked again until data for all the other deer had been recorded, a period of 6 days on average. This sampling insured that the number of feeding sites (as defined below) was the same for all deer ($n = 11$). The general location of the chosen deer was determined by triangulation when the radio collar indicated that the deer was active. The animal was then stalked and its tracks were found in the snow. Because of low deer density, it was usually easy to separate fresh tracks from older ones. By back-tracking, we marked three consecutive feeding sites where fresh feeding signs were found. The spot at which the feeding signs were found, with all food and habitat measurements, is hereafter referred to as a feeding site. All site characteristics were collected also at a random location 50 m from the feeding site to allow a pairwise comparison (see below).

Food and habitat characteristics were determined randomly at one of the three sites. For feeding sites that were located at night, cover parameters were recorded later. The availability of each food plant species above the snow was estimated within a 2×2 m

square centered where the fresh feeding signs were found. The number of 10×10 cm squares covered by each plant species was divided by the total number to give the percentage in the entire 2×2 m square. Within the 2×2 m square, all fresh feeding signs were counted as instances of use for each species.

Feeding-site characteristics

(1) *Canopy cover* (%) was measured using Lemmon's densiometer (Lemmon 1956, 1957). (2) *Concealment cover* (sighting distance), defined as the potential for hiding the deer, was measured using a 30×80 cm cover board (Nudds 1977; Griffith and Youtie 1988). In a random direction, the minimum distance required for the board to be completely hidden at eye level was determined (Mysterud 1996). Since predators in the study area are known to search by sight (red foxes, humans), obtaining good concealment cover (i.e., a low value for sighting distance) is regarded as an antipredator strategy. (3) A *food-availability index* was calculated for each site. The coverage of each plant species at the site was multiplied by the average food-selection index (see below) for that species. The food-availability index is thus the summation of coverage multiplied by the average food-selection index for all forage species at the site. In this way both food quantity (coverage) and quality (measured indirectly as the food-selection index) are incorporated into the food-availability index. Because fruits were known, from feeding experiments, to be high-quality forage (Tixier and Duncan 1996), they were incorporated and given a high food-selection index (0.3). (4) *Distance to human settlement* was measured as the shortest distance from the site to houses on a map (scale 1:5000). Maintaining a long distance from human settlement is regarded as an antipredator strategy, since the chance of being shot by humans increases with proximity to houses. (5) The *temperature* (to the nearest degree Celsius) was recorded about 10 cm above ground in shade and the *snow depth* (to the nearest centimetre) was measured. Because there was rarely any wind, data on wind speed were excluded from the analysis. For the analysis of habitat selection, independent data on temperature (from a nearby meteorological station; DNMI 1868 Tryvasshøgda II) and snow depth (from a fixed location within the study area in open habitat) were chosen, rather than measuring climatic conditions at the feeding sites, to avoid any bias in measurements of temperature or snow depth due to the selection of preferred microhabitats. Snow depth averaged 27 cm (range 10–42 cm) in open habitat within the study area, and the average temperature during the study was -8°C (from $+2$ to -17°C).

Calculation of the food-selection index

We used Arthur et al.'s (1996) method, originally presented for assessing habitat selection when availability changes, to analyze our food-selection data. Arthur et al. (1996) defined o_{ik} as the proportional use of habitat k (in our case food item) on day i . Because the animal can only be in one habitat at a time, for habitat selection $o_{ik} = 0$ for all unused habitats and $o_{ik} = 1$ for the one habitat used (at one time). In our case, o_{ik} was calculated as the number of feeding signs on a particular food item divided by the total number of signs found within a particular feeding site (i.e., $o \in [0,1]$, all o values sum to 1). We only included the most common forage plants, defined as those that were available on at least 10% of the feeding sites. Sites containing only one of these forage species were also deleted from the analysis because they precluded any within-site choice by the deer. However, these sites were included in the analysis of feeding-site selection (coarser scale).

Statistical analyses

Differences between the characteristics of feeding sites and those of random locations were tested with Wilcoxon's pair tests (SYSTAT 1992). We used linear regression when testing directly for a trade-off in selection between food and cover or distance to

human settlement at the coarse spatial scale. Relationships among feeding-site characteristics and sex, time period (night/day), snow depth, and temperature were tested with general linear models. Because the RSH predicts differences between females with young and males or females without young, we included the female without young in tests of both sex groups. We did not include higher than second-order interactions in the models. We checked models for assumptions of linearity, homogeneity of variance, and statistical influential values (measured with Cook's D ; Venables and Ripley 1994). To obtain normality we transformed percent canopy cover closure using an arcsine square root transformation, and log-transformed concealment cover, the food-selection index, and distance to human settlement. Because we were interested mainly in the within-home-range scale, we also used a model with the same parameters, but adjusted response variables by individual averages so that any possible effect of higher than third-order selection (sensu Johnson 1980) was removed; these are referred to as *adjusted values*:

$$[1] \quad y_{\text{adjusted}} = y_{\text{feeding site}} - \left(\sum_{i=1}^{n_i} y_{\text{feeding site}} \right) / n_i$$

where $y_{\text{feeding site}}$ is the response variable (canopy cover, concealment cover, food-availability index, distance to human settlement) at a site and n_i is the total number of feeding sites for the individual deer recorded at this site. This also inflates any effects of sex on the response variable. Sex was nevertheless incorporated into these models to test for interactions with the other factors. To test whether this was the result of habitat or patch selection, we calculated a *contrasted value*:

$$[2] \quad y_{\text{contrasted}} = y_{\text{feeding site}} - y_{\text{random site}}$$

where $y_{\text{feeding site}}$ is the response variable (canopy cover, concealment cover, food-availability index) at each feeding site and $y_{\text{random site}}$ is the response variable at the adjacent random site. For example, if $y_{\text{feeding site}}$ correlates with temperature, this may be due to the animal selecting either a different patch or a different habitat when the temperature changed. If selection is at the habitat scale, $y_{\text{contrasted}}$ will not correlate with temperature (since the value in the random location only 50 m away is equal if it is within same habitat). But if selection is at the patch scale, $y_{\text{contrasted}}$ will correlate with temperature (since the value in the random location is in a different patch). We only calculated contrasted values when normal or adjusted values gave a significant effect, since otherwise the pattern represents random use.

Results

Food-plant selection

We recorded feeding on 22 of the 36 different plant species/groups available (Table 1). The most frequently eaten plants were bilberry (*Vaccinium myrtillus*), ash (*Fraxinus excelsior*), and hazel (*Corylus avellane*), which made up 25.7, 22.2, and 20.1% of the diet, respectively, when calculated as total number of signs on a forage plant divided by the total number of signs on all plants.

Selection among the 11 most common plant species was nonrandom ($\chi^2 = 50.43$, $n = 79$, $df = 10$, $p = 0.00$). We therefore calculated food-selection indexes (Table 1). The highest food-selection indexes were for aspen (*Populus tremula*) (0.25), ash (0.24), and rowan (*Sorbus aucuparia*) (0.19). There was no difference in food selection between the sexes ($\chi^2 = 3.43$, $df = 10$, $p = 0.97$) or between night and day ($\chi^2 = 2.32$, $df = 10$, $p = 0.99$), i.e., no trade-off between food selection and risk factors (which varied between the

Table 1. Food selection by 5 female and 5 male roe deer in the Lier valley, Norway, in winter 1996, based on data from 110 patches.

Plant species	Forage type ^a	UF (%)	AF (%)	U (%)	AC (%)	Q (%)	Food-selection index ^b
<i>Sorbus aucuparia</i>	B	31.2	43.1	23.0	5.8	11.7	0.19 (0.09, 0.33)
<i>Fraxinus excelsior</i>	B	29.4	40.4	21.7	11.0	22.2	0.24 (0.13, 0.47)
<i>Corylus avellana</i>	B	15.6	22.9	11.5	13.3	20.1	0.09 (0.02, 0.21)
<i>Populus tremula</i>	B	10.1	15.6	7.4	2.9	4.2	0.25 (0.11, 0.90)
<i>Vaccinium myrtillus</i>	S	10.1	12.8	7.4	11.0	25.7	0.08 (0.02, 0.34)
<i>Prunus padus</i>	B	9.2	18.3	6.8	5.2	3.8	0.14 (0.05, 0.31)
<i>Salix caprea</i>	B	4.6	9.2	3.4	1.7	4.8	
<i>Acer platanoides</i>	B	4.6	5.5	3.4	0.6	2.3	
<i>Malus sylvestris</i>	A	2.8	2.8	2.1	1.2	—	
<i>Sorbus aucuparia</i>	F	2.8	2.8	2.1	1.7	—	
<i>Rhamnus frangula</i>	B	1.8	2.8	1.3	0.6	0.3	
<i>Tilia cordata</i>	B	1.8	1.8	1.3	2.3	0.5	
<i>Lonicera xylosteum</i>	L	1.8	2.8	1.3	0.6	0.9	
<i>Vaccinium vitis-idea</i>	S	1.8	10.1	1.3	1.7	0.8	0 (0, 0.02)
<i>Rosa</i> spp.	F	1.8	1.8	1.3	0.6	2.3	
<i>Alnus incana</i>	B	0.9	10.1	0.7	2.3	0.1	0 (0, 0.02)
<i>Daphne mezereum</i>	L	0.9	1.8	0.7	0.1	0.1	
<i>Fraxinus excelsior</i>	F	0.9	0.9	0.7	1.2	—	
<i>Daucus carota</i>	A	0.9	0.9	0.7	0.6	—	
<i>Brassica oleracea</i>	A	0.9	0.9	0.7	0.6	—	
“Salt lick”	A	0.9	0.9	0.7	0.6	—	
<i>Avena sativa</i>	A	0.9	0.9	0.7	1.2	—	
<i>Betula</i> spp.	B	0	10.1	0	1.7		0 (0, 0.05)
<i>Salix</i> spp.	B	0	0.9	0	0.0		
<i>Ulmus glabra</i>	B	0	0.9	0	0.2		
<i>Picea abies</i>	C	0	33.0	0	24.4		0 (0, 0.00)
<i>Juniperus communis</i>	C	0	3.7	0	0.6		
<i>Rubus idaeus</i>	L	0	10.1	0	1.7		0 (0, 0.08)
<i>Rosa</i> spp.	B	0	3.7	0	0.6		
<i>Deschampsia flexuosa</i>	G	0	6.4	0	1.7		
<i>Luzula pilosa</i>	H	0	3.7	0	0.1		
<i>Urtica dioica</i>	H	0	1.8	0	0.1		
<i>Poa</i> spp.	G	0	1.8	0	0.1		
<i>Juncus alpinus</i>	G	0	0.9	0	0.0		
<i>Anemone hepatica</i>	H	0	0.9	0	0.2		
<i>Limnosa borealis</i>	H	0	0.9	0	0.0		

Note: UF, number of patches at which a plant species was recorded eaten divided by the total number of patches; AF, number of patches in which a plant species was recorded available divided by the total number of patches; U, same as UF but adjusted to 100%; AC, availability of the different forages averaged over all patches; Q, quantity calculated as the total number of signs on a forage plant divided by the total number of signs on all plants. A dash indicates that it was not possible to calculate this for that particular forage. Values in parentheses show the 95% confidence interval.

^aC, conifer; B, browse (deciduous trees); S, shrubs; G, grass; L, low “bush”; F, fruits/berries; A, agricultural forage or mostly from artificial forage sites.

^bCalculated as within-feeding-site choice using Arthur et al.’s (1996) method for forages, where AF > 10%.

sexes and temporal scales) could be found at the within-site scale.

Feeding sites versus random locations

The food-availability index was significantly higher at feeding sites than at random locations nearby, whereas the amount of cover, temperature, and snow depth did not differ (Table 2). Results were similar when the analysis was partitioned by sex and time period (Table 2).

Variation in feeding-site selection

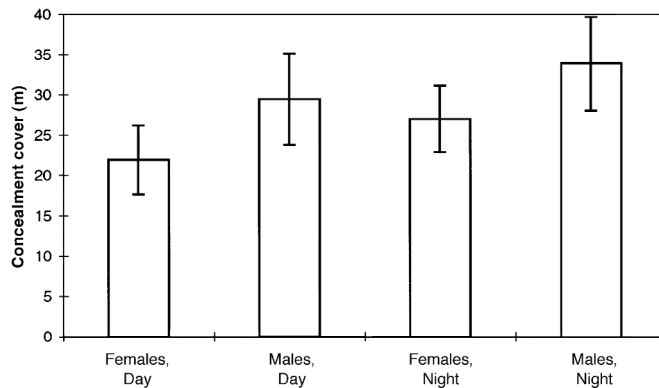
(1) Deer used areas of greater canopy cover during cold than warm weather (ANCOVA, $r^2 = 0.09$, $n = 109$, $F_{[1]} = 6.14$, $p = 0.02$), but there was no effect of sex, time period,

or snow depth. Nor were any of the interactions significant (all $p > 0.1$). This result was robust when adjusted values were used, and also when the female without young was treated as a male. There was no effect of temperature when contrasted values were used ($F = 0.57$, $p = 0.45$), i.e., the effect of temperature on selection of canopy cover was due to a choice made at the habitat scale rather than the patch scale. There was a significant trade-off in selection between canopy cover and food availability (regression, $r^2 = 0.19$, $p = 0.00$).

(2) There was denser concealment cover at roe deer feeding sites in cold weather (ANCOVA, $r^2 = 0.16$, $n = 109$, $F_{[1]} = 4.55$, $p = 0.04$) and more cover at daytime sites than at nighttime sites ($F = 4.21$, $p = 0.04$). Females tended to

Table 2. Descriptive statistics for roe deer feeding sites compared with random locations in the Lier valley during winter 1996.

	<i>n</i>	Roe deer feeding sites			Random locations			<i>p</i> (Wilcoxon's pair test)				
		Mean	SE	Median	Mean	SE	Median	All data	Females	Males	Night	Day
Canopy cover (%)	108	41.0	2.3	39.8	40.0	2.9	39.0	0.36	0.25	0.81	0.26	0.72
Concealment cover (m)	105	27.0	2.9	20.0	33.5	5.1	20.0	0.65	0.16	0.86	0.70	0.49
Food-availability index	109	1.5	0.2	0.9	0.3	0.1	0.0	0.00	0.00	0.00	0.00	0.00
Temperature (°C)	108	-5.5	0.6	-6.0	-5.5	0.6	-5.5	0.24	0.45	0.36	0.25	0.43
Snow depth (cm)	110	22.7	1.0	22.0	22.4	1.1	22.0	0.91	0.29	0.35	0.29	0.57

Fig. 1. Concealment cover (values are given as the mean; bars indicate SE) at feeding sites of female and male roe deer during the day and at night in the Lier valley, Norway, in winter 1996. Concealment cover was measured as the sighting distance, so a high value indicates little cover.

choose sites with more concealment cover than those chosen by males ($F = 3.48$, $p = 0.07$). There was no effect of snow depth on selection of concealment cover ($F = 0.68$, $p = 0.41$). There was an interaction between time period and temperature ($F = 4.50$, $p = 0.04$), i.e., the effect of temperature on cover selection was only evident during the day. No other interactions were significant (all $p > 0.5$). Treating the female without young as a male slightly strengthened the effect of sex ($F = 3.68$, $p = 0.06$), which suggests that females with young tended to select better hidden sites than deer without young. All results were robust when adjusted values were used. There was no effect of time period ($F = 1.43$, $p = 0.24$) or temperature ($F = 0.87$, $p = 0.35$) when contrasted values were used, i.e., the effect of time period and temperature on selection of concealment cover was the result of a choice made at the habitat scale rather than at the patch scale. There was no trade-off in selection between concealment cover and food availability (regression, $r^2 = 0.08$, $p = 0.84$).

(3) The *food-availability indexes* (which combine plant quantity and quality) at roe deer feeding sites were equal for the sexes and time periods and did not vary with temperature or snow depth, and there were no significant interactions (ANCOVA, $r^2 = 0.09$, $n = 103$, all $p > 0.08$). These results were robust when adjusted values were used and when the female without young was treated as a male (all $p > 0.05$).

(4) *Distance to human settlement* was less at night than during the day (Fig. 1; ANCOVA, $r^2 = 0.10$, $n = 110$, $F_{(1)} = 5.15$, $p = 0.03$), but there was no effect of sex, temperature, or snow depth (all $p > 0.1$). However, the use of adjusted

values strengthened the effect of time period ($r^2 = 0.14$, $F = 7.38$, $p = 0.01$) and distance to human settlement, which decreased with increasing snow depth ($F = 4.21$, $p = 0.04$). When we treated the female without young as a male, females with young foraged somewhat closer to human settlement ($F = 4.04$, $p = 0.05$). However, this result was totally dependent on two highly outlying values for this female (after exclusion, $p = 0.10$), which there were biological grounds to exclude, since they were recorded immediately before she migrated to a lower elevation. There was a trade-off in selection between distance to human settlement and food availability (regression, $r^2 = 0.12$, $p = 0.05$).

Discussion

An animal's food selection can be viewed as the outcome of (at least) two processes: choosing of where to eat and choosing what to eat once there (Brown and Morgan 1995). We have described the use of a statistical method (Arthur et al. 1996) that compares food eaten with availability of forage plants within each patch in succession rather than comparing total use with some average measure of availability in the study area or home range (Neu et al. 1974; Aebischer et al. 1993), which should give food-selection indexes that are closer to food preferences. "Preference," as opposed to "selection," is usually reserved for situations in which all components are offered on an equal basis, preferably in an experimental setting at a low animal density (Johnson 1980; Thomas and Taylor 1990). Although the described method avoids the problem of patch- or habitat-selection effects, a forager has, by definition, a lower probability of encountering cryptic foods than conspicuous foods (Brown and Morgan 1995). Even if a food item is present at a site, it may not stand an equal chance of being detected by a foraging deer. This may be especially important during winter, when there is snow. However, we only estimated the amount of forage that extended above the snow, which should minimize this potential problem. We did not observe cratering behaviour during this study, but such behaviour (see Cederlund et al. 1980; Myrsetrud et al. 1997) would clearly exacerbate the problem. Further, we do not know, therefore, whether the result would be the same in more severe winters, when depletion of fat reserves may also influence foraging behaviour.

Bowyer et al. (1996) convincingly demonstrated the importance of considering spatio-temporal scales when studying sexual segregation in space use. However, the problem of the size of sampling unit can be avoided by regarding the habitat itself as the sampling unit when studying sexual segregation in habitat use, but scaling then becomes more important from the perspective of hierarchical decision making.

Even though earlier studies on sexual segregation reported both a higher (Shank 1982; Bleich et al. 1997) and a lower (Staines et al. 1982; Perez-Barberia et al. 1997) quality of diet for male than female ungulates, this was likely an effect of foraging location, not of food preference. As predicted from the hypothesis of a spatial-scale-dependent trade-off between forage intake and predation risk (Senft et al. 1987), there was no difference in food selection at the within-site scale among male and female roe deer, nor did food selection at the within-site scale vary on a diurnal basis. At a coarser scale, female roe deer tended to select more hidden foraging sites than did males, which is the first reported case from the winter season that supports the RSH. However, we found no direct evidence for a trade-off in selection between food availability and concealment cover. There was more convincing evidence for a general trade-off between foraging and predation risk, as both sexes selected more open habitat and feeding sites closer to human settlement at night (when the chance of detection was low) and as snow depth increased (when less food was available). There was also direct evidence for a trade-off in selection between food availability and distance to human settlement. Use of cover also increased with decreasing temperature, which was reported earlier for selection of bedding sites by roe deer (Mysterud and Østbye 1995) as well as other deer species (elk (*Cervus elaphus*), Beall 1974; white-tailed deer (*Odocoileus virginianus*), Armstrong et al. 1983; Lang and Gates 1985).

Selection of where to eat may be the outcome of home-range, habitat, and patch selection (e.g., Johnson 1980). When adjusting for individual differences among home ranges (V_{adjusted}), we removed the effect of home-range selection. Compared with random sites 50 m from the feeding site (patch scale), selection was random with regard to cover, but feeding sites had a higher food-availability index than random sites. Roe deer selected feeding sites with more cover during cold weather, whereas the food-availability index had no effect at this scale (habitat scale). In contrast, in selection of bedding sites by roe deer in the same area, cover was important also at the patch scale (Mysterud and Østbye 1995). Schaefer and Messier (1995) found a similar pattern of habitat selection by muskoxen (*Ovibos moschatus*) using a nested hierarchy of spatial scales. This was due to the fact that muskoxen selected one particular forage species at all scales. Temporal and spatial scaling becomes more important when there is a trade-off between selection of different resources (see also Mysterud et al. 1999).

Future studies on the foraging behaviour of deer may thus involve testing the predictions of different scale-specific foraging theories such as habitat selection (Fretwell and Lucas 1970; Sutherland 1996), patch use (Charnov 1976; Brown 1988, 1992), and diet choice (Pulliam 1974). Further, the trade-off between selection of food and safety has not been quantified in terms of energy at any scale, although the current study demonstrates that the trade-off is scale-specific and, at the habitat scale, varies with time period and sex. Possible approaches include measuring "giving-up-densities" on artificially planted depletable food trays (Brown 1988, 1992; Kotler 1997; Morgan et al. 1997) or by "tritating" food and safety by controlling the energy content of forage presented in different habitats (Kotler and Blaustein 1995). Until now these methods have been used mainly for

rodents (but see Kotler et al. (1994) for the Nubian ibex (*Capra ibex*)). However, research on individually marked individuals will obviously occupy a central place in the future, especially in the study of sex- or age-dependent patterns of foraging.

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