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Diet overlap among ruminants in Fennoscandia

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Abstract Information on overlap in resource use is central to understanding of interspecific exploitation competition and resource partitioning. Despite this, measures of diet overlap among northern ruminants in Fennoscandia is limited to one earlier study (reindeer and sheep). Diet overlap between sympatric moose and roe deer calculated with Schoener's index was 20.7% and 33.6% during summer (data from one area) and winter (data from two areas), respectively, whereas average diet overlap between moose and red deer was 32.0% during winter (data from four areas). Diet overlap between a coastal island population of red deer and sheep was 59.3% during summer and 63.9% during winter. Summer diet overlap between a sheep and a goat population and a sheep and a reindeer population calculated with data on main types of forage plants was 77.0% and 55.1%, respectively. However, overlap calculated with main plant groups was sometimes considerably higher than when calculated for individual forage species. Neither difference in feeding type nor body mass successfully predicted diet overlap between species pairs ($n=9$), although there tended to be negative correlation ($r_p=-0.586$, $P=0.098$) between diet overlap of main plant groups (calculated across studies) and difference in feeding type.

Key words Competition · Diet breadth · Diet overlap · Interaction · Ruminants

Introduction

A central mechanism of interaction among large herbivores is exploitation competition (e.g. Sinclair and Northon-Griffiths 1982; Sinclair 1985; Putman 1986, 1996; Illius and Gordon 1987; Gordon and Illius 1989).

Usually three conditions must be fulfilled in order to get interspecific exploitation competition. There must be overlap (1) in habitat use and (2) in diet consumed, and (3) the shared resources must be limited (de Boer and Prins 1990; Tokeshi 1999). Information on overlap in resource use is thus central for the understanding of interspecific competition (Schoener 1974; Abrams 1980). Gordon and Illius (1989) have presented data on resource overlap among red deer (*Cervus elaphus*), cattle, goats and ponies on the Isle of Rhum in Scotland; Putman (1996) on cattle, ponies, fallow deer (*Dama dama*), sika deer (*Cervus nippon*), roe deer (*Capreolus capreolus*) and red deer from the New Forest in England; Ludewig and Bowyer (1985) for moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*) during winter in Maine, United States; Hansen and Reid (1975) for mule deer (*O. hemionus*), elk (*Cervus elaphus canadensis*) and cattle in Southern Colorado, United States; and Schröder and Schröder (1984) for roe deer, red deer and chamois (*Rupicapra rupicapra*) in Germany. However, although there are numerous studies of food selection of individual large herbivore species in Fennoscandia (Table 1), diet overlap has only been calculated between domestic sheep and reindeer (*Rangifer tarandus*) in Norway (Skogland 1984). Thus, data on overlap among ungulate species pairs in northern extreme climates is lacking, and no study has tried to test how differences in overlap among species pair relate to niche theory for ungulates.

I here calculate diet overlap among ungulates in Fennoscandia. The main determinants of niche separation in ruminants are body size (Bell 1971; Jarman 1974; Demment and Van Soest 1985; Illius and Gordon 1987) and morpho-physiological feeding type (Hofmann 1973, 1989). I therefore tested the hypotheses that diet overlap between species pairs was correlated with (1) differences in body size or (2) morpho-physiological feeding type.

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Material and methods

Study area

Fennoscandia (Finland, Norway and Sweden) is usually divided into six main vegetation zones (Fig. 1; Abrahamsen et al. 1977): (1) the nemoral zone (Nz) is dominated by deciduous forest on fertile soil, (2) the boreonemoral zone (BN) is between Nz and the boreal zone (Bz) which is dominated by Norway spruce (*Picea abies*) with Scots pine (*Pinus sylvestris*) on dry and poorer sites. Bz is subdivided into the (3) southern (BzS), (4) middle (BzM) and (5) northern boreal zone (BzN). In mountainous regions is (6) the alpine zone (Alp) dominated by birch (*Betula* spp.), shrubs, ground cover or bare rock.

During the last century, the population size and range of cervids in Fennoscandia have increased dramatically (Gill 1990), as is evident from the harvest records from Norway (Statistics Norway

1998). This is most marked for moose in BN and Bz, roe deer and red deer in all zones except Alp, while the population of reindeer living in Alp has been more stable. Harvests of roe deer, red deer and moose have increased from, respectively, 7,261, 2,484 and 7,864 individuals in 1965 to, respectively, 34,300, 21,226 and 36,059 in 1997 (Statistics Norway 1998). Red deer are expanding eastward from the coastal western habitats into continental areas with moose and roe deer, and vice versa. The number of municipalities harvesting red deer and moose increased from 120 and 274 in 1965 to 204 and 317 in 1997, respectively (Statistics Norway 1998). All of the cervids except reindeer are reported to winter at low elevation (red deer: Albon and Langvatn 1992; roe deer: Mysterud et al. 1997; moose: Pulliainen 1974). Sweden also hosts some populations of fallow deer, and there are white-tailed deer in Finland.

Free-ranging domestic animals are not common in Finland and Sweden, but semidomestic reindeer are common in northern parts

Fig. 1 Vegetation zones in the Nordic countries (adapted from Abrahamsen et al. 1977) with the approximate position of the different study areas indicated by numbers (see Table 1)

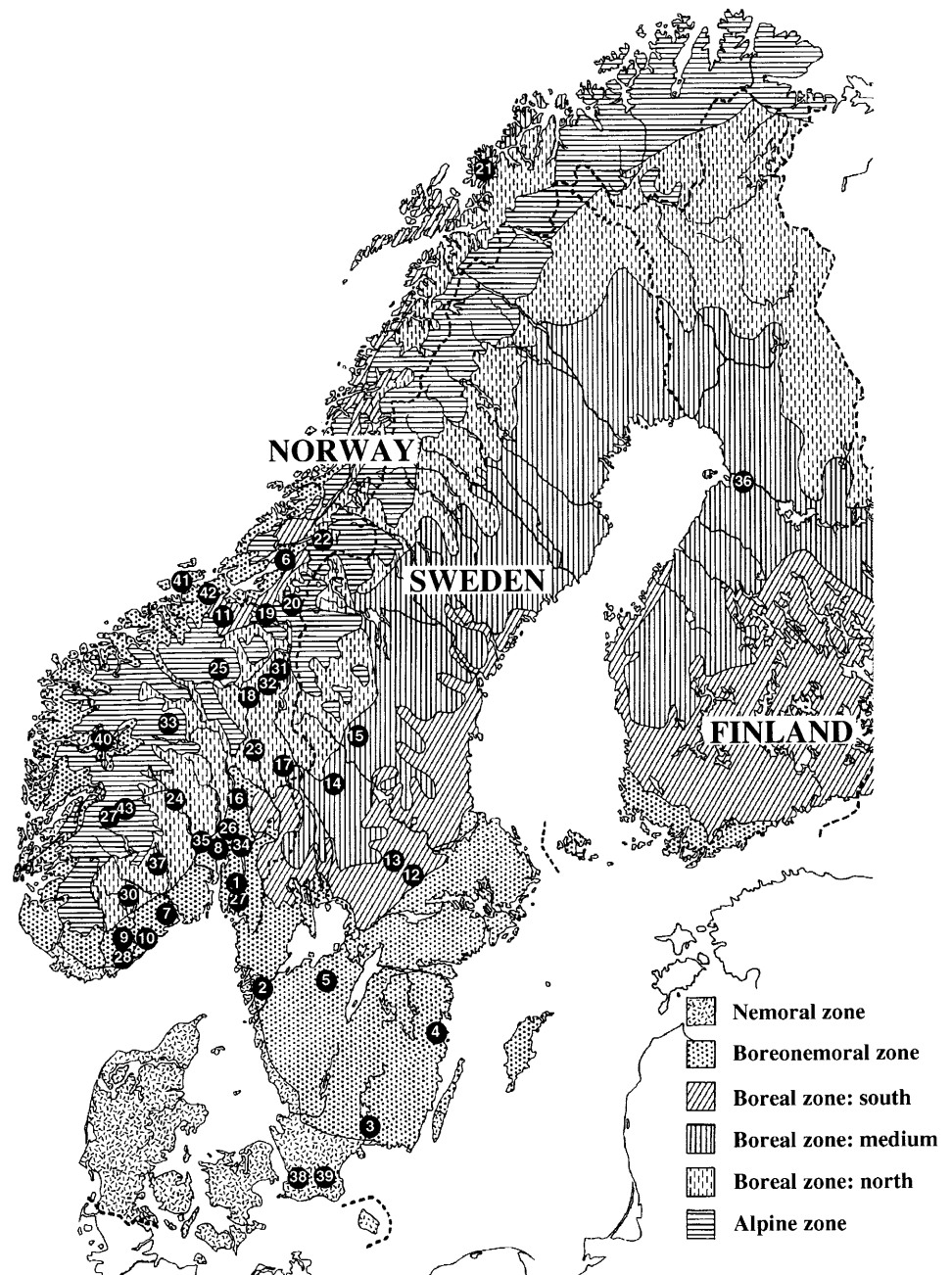


Table 1 Diet composition (*Gra* graminoids, *Her* herbs, *Shr* low shrubs, *FLH* fems/lyco-pods/horsetails, *Dec* deciduous browse, *Con* coniferous trees, *Lic* lichens, *Mos* mosses, *Oth* other) of ruminants in different seasons of the year (W winter, S summer) in different study areas in Fennoscandia (F Finland, N Norway, S Sweden) that lies in different vegetation zones (Nz nemoral zone, BN boreonemoral zone, BzS southern boreal zone, BzM Fig. 1 indicating the study areas location

Species	No.	Study area	Vegetation zone	Method	Season (year)	Diet composition											
						Gra	Her	Shr	FLH	Dec	Con	Lic	Mos	Oth	Reference		
<i>Alces alces</i>	1	Vestby (N)	BN	SnT	W (1957)			0.5	60.0	39.5							Hagen 1958
	2	Hunneberg (S)	BN	SnT	W (1958)			1.1	36.4	62.4							Hagen 1958
	3	Älmeboda (S)	BN	SnT	W (1962/63)			2.2	46.3	51.6							Ahlén 1965
	4	Misterhult (S)	BN	SnT	W (1963/64)			6.8	19.9	73.4							Ahlén 1965
	5	Timmersdala (S)	BN	SnT	W (1968/69)				68.6	32.0							Ahlén 1975
	6	Verdal (N)	BN	SnT	W (1967/68)			0.1	78.5	21.6							Ahlén 1975
					W (1970)				82.0	17.8							Ahlén 1975
					W (1965/66)				53.6	46.5							Ahlén 1975
					W (1966/67)				60.3	39.7							Ahlén 1975
					W (1967/68)			2.6	80.7	19.2							Ahlén 1975
					W (1968/69)				78.0	19.5							Ahlén 1975
	7	Vegårshei (N)	BN	SnT	W				42.2	43.7							Hagen 1983
	8	Bærum (N)	BN	SnT	W				81.4	13.0		14.0					Hagen 1983
	9	Aust-Agder (N)	BN	SnT	W (1994)			28.5	26.5	45.0		5.7					Fjeld et al. 1997
	10	Grimstad (N)	BN	SnT	W (1992)				18.4	80.8		0.8					Fjeld et al. 1997
	11	Storås (N)	BzS	SnT	W (1963/64)			34.1	10.8	55.0	0.3						Ahlén 1965
	12	Skinnskatteberg (S)	BzS	SnT	W (1969)				27.3	72.4	0.4						Ahlén 1975
	13	Grimså (S)	BzS	Rum (48)	W (1973-77)	0.9	0.1	9.1	20.2	58.0							Cederlund et al. 1980
	14	Lima (S)	BzM	SnT	W (1966/67)				81.0	18.7		11.9					
					W (1968/69)			0.3	58.4	40.4	1.1						Ahlén 1975
					W (1969/70)				80.4	18.9	0.6						Ahlén 1975
	15	Älvdalen (S)	BzM	SnT	W (1968/69)				76.6	23.4							Hagen 1958
	16	Hurdal (N)	BzN	SnT	W (1957)			12.4	52.6	47.5							Hagen 1958
	17	Åmot-Trysil (N)	BzN	SnT	W (1957-58)				53.8	34.3							Hagen 1958
	18	Tynset (N)	BzN	SnT	W (1963/64)				55.0	45.0							Ahlén 1965
	19	Selbu (N)	BzN	SnT	W (1965/66)				23.2	76.8							Ahlén 1975
					W (1968/69)			0.1	52.3	47.6							Ahlén 1975
	20	Meråker (N)	BzN	SnT	W (1965/66)				65.9	34.1							Ahlén 1975
					W (1966/67)				85.1	15.0							Ahlén 1975
					W (1967/68)			7.6	63.0	29.5							Ahlén 1975
					W (1968/69)			2.6	74.0	23.4							Ahlén 1975
					W (1969/70)			0.9	42.7	56.4							Ahlén 1975
	21	Tranøy (N)	BzN	SnT	W			7.3	83.1	16.9							Hagen 1983
	22	Snåsa (N)	BzN	SnT	W				81.0	11.4					0.2		Hagen 1983
	23	Stor-Elvdal (N)	BzN	SnT	W				36.9	63.1							Hagen 1983
	24	Nes i Hallingdal (N)	BzN	SnT	W				43.8	56.1	0.1						Hagen 1983
	25	Oppdal (N)	Alp	SnT	W (1963/64)		0.1		44.1	55.5	0.8						Ahlén 1965
	9	Aust-Agder (N)	BN	RT(10)/DO	S(1994)	4.0		18.0	75.0								Fjeld et al. 1997
	16	Hurdal (N)	BN	RT(8)/DO	S		14.0	32.0	45.0								Hjeljord and Histøl 1999
	26	Nannestad (N)	BN	RT(8)/DO	S		23.0	24.0	48.0								Hjeljord and Histøl 1999
	27	Østfold (N)	BN	RT(26)/DO	S	2.0	7.0	18.0	72.0								Hjeljord and Histøl 1999
	28	Lillesand (N)	BN	RT(4)/DO	S(1993)	1.3		28.7	70.0								Damelsen and Olsén 1994

Table 1 (continued)

Species	No.	Study area	Vegetation zone	Method	Season (year)	Diet composition										Reference		
						Gra	Her	Shr	FLH	Dec	Con	Lic	Mos	Oth				
	29	Hedmark (N)	BzS	RT(6)/DO	S	77.0	1.0	21.0								1.0	Hjeljord and Histøl 1999	
	13	Grimstø (S)	BzS	Rum (27)	S(1973-77)	2.7	10.1	39.7	3.1	8.1	8.1					21.9	Cederlund et al. 1980	
	30	Bygland (N)	BzN	RT(4)/DO	S(1995)	19.2	19.3	56.6	2.4	2.4	2.4						Bjerga	
<i>Capra hircus</i>	31	Nord-Østerdal (N)	BzN	RT(25)/DO	S	0.9	33.0	41.0								23.1	Hjeljord and Histøl 1999	
	32	Nord-Østerdal (N)	BzN	RT(14)/DO	S(1993)	11.7	47.3	40.1	0.4	40.1							Gunneng 1997	
<i>Capreolus capreolus</i>	33	Jotunheimen (N)	Alp	OeF (2)	W(1986)	35.0	19.0	37.0	4.5	4.5	4.5					5.9	Garmo et al. 1990	
	1	Vestby (N)	BN	SnT	W(1956)			37.7	4.4	4.4	4.4					4.0	Hagen 1958	
					W(1957)		0.8	48.8	41.3	5.4	5.4						Hagen 1958	
					W(1958)		0.4	11.3	45.8	42.4	42.4						Hagen 1958	
	34	Romerike (N)	BN	RT(12)/DO	W(1995)		35.1	63.6	1.6	1.6	1.6						Christiansen and Kvarme 1997	
	35	Lier (N)	BN	RT(10)/SnT	W(1996)		10.7	80.5								9.0	Mysterud et al. 1999b	
	13	Grimstø (S)	BzS	Rum (48)	W(1973-77)	19.8	4.9	10.7	0.1	19.1	19.1					12.1	Cederlund et al. 1980	
	36	Muhos (F)	BzM	SnT	W(1975/76)	3.2	1.5	34.3	34.3	23.3	23.3					5.2	Helle 1980	
	37	Flatdal (N)	BzN	SnT	W(1976n7)	2.0	1.5	53.6		18.7	18.7					7.1	Helle 1980	
	34	Romerike (N)	BN	RT(8)/DO	W(1979/80)	4.7	0.2	34.5	1.9	1.9	1.9						Mysterud et al. 1997	
<i>Cervus elaphus</i>					S(1994)	0.8	75.5	23.3	0.2	23.3							Gjerlaugsen and Haug 1995	
	13	Grimstø (S)	BzS	Rum (34)	S(1973-77)	11.5	60.2	13.5	5.4	1.9	0.1					7.5	Cederlund et al. 1980	
	38	Böringe (S)	Nz	SnT	W(1962/63)	7.3	0.4	82.1		10.2							Ahlén 1965	
					W(1963/64)	19.7	0.9	75.7										Ahlén 1965
	39	Vomb (S)	Nz	SnT	W(1962/63)	69.7	9.9				20.2						0.1	Ahlén 1965
					W(1963/64)	79.5					2.5						0.1	Ahlén 1965
	2	Hunneberg (S)	BN	SnT	W(1962/63)	5.2	80.9	4.5	0.7	3.8	5.2	0.4						Ahlén 1965
					W(1963/64)	4.9	75.8	0.2		17.4	1.0							Ahlén 1965
	40	Leikanger (N)	BN	SnT	W(1963/64)		69.3	1.4		29.5								Ahlén 1965
	41	Hitra (N)	BN	Rum (6)	W(1979)	14.5	55.1	4.6		23.9	1.7	1.0						Vaag 1980
				Rum (4)	W(1980)	73.1	1.1	2.9		5.5							Vaag 1980	
11	Storås (N)	BzM	SnT	W(1963/64)		30.2	8.7		60.2	0.7	0.1						Ahlén 1965	
18	Tynset (N)	BzN	SnT	W(1963/64)	1.0	56.8	24.0	0.2	15.7	1.7							Ahlén 1965	
25	Oppdal (N)	Alp	SnT	W(1963/64)	1.7	0.2	10.6		36.2	17.8	0.1						Ahlén 1965	
41	Hitra (N)	BN	Rum (3)	S(1979)	69.6	7.1	1.0		0.5								Vaag 1980	
42	Åstfjorden (N)	BN	Rum (19)	S(1986?)	55.5	29.9	14.6										Albon and Langvatn 1992	
<i>Ovis aries</i>	41	Hitra (N)	BN	Rum (5)	S(1979)	77.3	7.1	10.4		4.9	0.2						Vaag 1980	
	43	Hardangervidda (N)	Alp	DO (3) ^a	S(1969-72)	42.6	49.0	6.8		6.8							Wielgolaski 1975, 1976	
				DO (3)	S(1969-71)	35.3	45.9	8.4	10.4	21.0	1.0					2.0	Wielgolaski 1975, 1976	
33	Jotunheimen (N)	Alp	OeF (2)	S(1986)	37.0	38.0	1.0		1.0	1.0							Garmo et al. 1990	
41	Hitra (N)	BN	Rum (4)	W(1979)	13.2	0.1	63.9		18.2	0.7	0.4						Vaag 1980	
				Rum (4)	W(1980)	66.7	1.6	4.1		2.2							Vaag 1980	
43	Hardangervidda (N)	Alp	Rum (12)	S(1970)	50.7	7.6	12.6		24.3	2.7							Gaare and Skogland 1975	
				Rum (9)	W(1970)	28.3	9.0		56.8	2.5	3.4						Gaare and Skogland 1975	

^a Study of sheep in enclosure at high stocking density (3 sheep ha⁻¹). First line from dry meadow, second line from wet meadow

of all countries. In Norway, the number of free-ranging domestic sheep during summer has increased from 1.7 million in 1939 to 2.2 million in 1995 (Drabløs 1997). Winter grazing of sheep occurs occasionally only in a few coastal areas. Numbers of free-ranging goats and cattle have declined from, respectively, 162,000 and 899,000 in 1939 to, respectively, 87,000 and 215,000 in 1995 (Drabløs 1997). The majority of free-ranging domestic herbivores are grazing in the Alpine zone sympatric with reindeer or coastal habitats sympatric with red deer, but in several areas domestic animals are sympatric with roe deer and moose (e.g. Mysterud et al. 1999a).

Methods

The international and national literature was reviewed for studies on food selection by ungulates in Fennoscandia during winter (November to March) and summer (May to August) period (Table 1). Diet overlap was when possible calculated at both the plant species and main plant group level in cases when a study provided data on more than one ungulate species in the same area. When comparing allopatric populations, it was only possible to calculate overlap for main plant groups (Table 1), due to inter-author variability in classification of vegetation. Any lumping of plant species into main plant groups will lead to higher (or equal) estimates of overlap (Abrams 1980). Further, differing food availabilities between areas may influence the overlap measures if not accounted for (Colwell and Futuyma 1971; Hanski 1978; Hurlbert 1978; Abrams 1980; Lawlor 1980). Diet overlap was therefore calculated only between studies that were conducted within the same main vegetation zones of the Nordic countries (Fig. 1, see also description of study area). I also calculated diet overlap within species between studies so that the effect of between-source variation could be estimated.

The overlap in diet were calculated using Schoener's index (Renkonen 1938; Schoener 1968):

$$O_{jk} = 1 - 1/2 \sum |P_{ij} - P_{ik}| \quad (1)$$

where O_{jk} is the overlap between ungulate species j and k ; p_{ij} is the proportion of species j feeding on plant species/group i ; and p_{ik} is the proportion of species k feeding on plant species/group i . Overlap in diet between species j and k is complete when $O_{jk}=1$ and is absent when $O_{jk}=0$ (Gordon and Illius 1989). This index has been recommended by Abrams (1980) as the best overall index of niche overlap.

Niche breadth was calculated with the Shannon-Wiener information measure (Hanski 1978):

$$B_j = -\sum_j p_{ij} \ln(p_{ij}) \quad (2)$$

where B_j is the niche breadth of ungulate species j .

Correlations (Pearson's coefficient, r_p) were calculated between summer diet overlap (log-transformed) for species-pairs with difference in morpho-physiological feeding type (0, 1 or 2; data from Hofmann 1989), and the difference in body weight between species pairs (log-transformed; data from Mysterud 1998; except for goat: Mason 1981).

Results

Sympatric populations of moose and roe deer had diet overlaps of 20.7% and 33.6% during summer (data from one area) and winter (data from two areas), respectively, whereas average diet overlap between moose and red deer was 32.0% during winter (data from four areas) (Table 2). Diet overlap between a coastal island population of red deer and sheep was 59.3% during summer and 63.9% during winter. Summer diet overlap between a sheep and a goat population and a sheep and a reindeer population calculated with data on main type of forage plants was 77.0% and 55.1%, respectively. Note, however, that diet overlap calculated with main plant groups was between 11.7 and 31.1% higher than when calculated for individual forage species for species-pairs where both comparisons were available (Table 2). Intra-specific diet overlap between two winters or summers (different years) varied between 54.6% and 62.5% (Table 2).

The across-study comparison yielded data on species-pairs that not yet have been studied in sympatry, and with data on main forage groups only (Table 3). Intra-specific across-study diet overlap was high and variable between 60.8% and 83.4%. There was a tendency towards a negative correlation between diet overlap and difference in feeding type ($n=9$, $r_p=-0.586$, $P=0.098$). There was no significant negative correlation between diet overlap and difference in body size ($n=9$, $r_p=-0.323$, $P=0.397$).

Niche breadth for winter and summer, respectively, was 0.707 ± 0.038 ($n=25$) and 1.026 ± 0.097 ($n=10$) for moose, 0.914 ± 0.088 ($n=8$) and 0.908 ± 0.062 ($n=2$) for red deer, 1.118 ± 0.163 ($n=6$) and 0.937 ± 0.322 ($n=2$) for roe deer, 1.102 ($n=1$) and 1.315 ($n=1$) for reindeer, 0.972

Table 2 Mean overlap (\pm SE) in utilized plant species during summer (*italics*) and winter (*bold*) between sympatric ungulate populations in Fennoscandia calculated with the index of Schoener (1968). Number of populations compared in parentheses. Within-

species value of diet overlap is calculated from studies that have been conducted over several years in the same area. An *asterisk* indicates that overlap was calculated with main plant groups (see Table 1). ^a*Superscript numbers* refer to references

	<i>Alces alces</i>	<i>Cervus elaphus</i>	<i>Capreolus capreolus</i>	<i>Ovis aries</i>
<i>Alces alces</i>	0.625\pm0.044 (6) ^{1,2,3} *0.779\pm0.022		0.207 (2) ⁴ *0.518	
<i>Cervus elaphus</i>	0.320\pm0.112 (8) ¹ *0.437\pm0.185	0.546\pm0.078 (4) ^{1,5} *0.726\pm0.121		0.593 (2) ⁵ *0.881
<i>Capreolus capreolus</i>	0.336\pm0.071 (4) ^{1,4} *0.576\pm0.059		0.621\pm0.168 (2) ^{1,6} *0.739\pm0.051	
<i>Rangifer tarandus</i>				*0.551 (2) ⁷
<i>Capra hircus</i>				*0.770 (2) ⁸
<i>Ovis aries</i>		0.639 (2) ⁵ *0.894		0.436 (1) ³ *0.445

^aReferences: 1 Hagen 1958, 2 Ahlén 1965, 3 Ahlén 1975, 4 Cederlund et al. 1980, 5 Vaag 1980, 6 Helle 1980, 7 Gaare and Skogland 1975, Wielgolaski 1975, 8 Garmo et al. 1990

Table 3 Average diet overlap of ungulate populations in Fennoscandia calculated across different studies and based on data on use of plant groups during summer (*italics*) and winter (*bold*) (da-

ta, sample sizes and references in Table 1). Within-species value of diet overlap is calculated between studies to estimate inter-study variability

	<i>Alces alces</i>	<i>Cervus elaphus</i>	<i>Capreolus capreolus</i>	<i>Capra hircus</i>	<i>Ovis aries</i>
<i>Alces alces</i>	0.710 0.720	0.279	0.382		0.211
<i>Cervus elaphus</i>	0.217	0.771 0.608	0.200		0.806
<i>Capreolus capreolus</i>	0.515	0.382	0.692		0.131
<i>Rangifer tarandus</i>	0.006	0.284		0.572	0.567
<i>Capra hircus</i>					0.637
<i>Ovis aries</i>	0.174	0.666	0.296		0.834

($n=1$) and 0.988 ± 0.132 ($n=3$), and 1.330 ($n=1$) for goats during summer. Only for moose were there enough data to test for seasonal differences. Diet breadth of moose was higher during summer than during winter (t -test, $t=-4.184$, $df=34$, $P<0.001$).

Discussion

A high level of resource use overlap has often been used to infer that competition is occurring (e.g. Jenkins and Wright 1988; see Belovsky 1986 for a review). However, it is the density of individuals relative to the resource base (in space and time) that determines the strength of competitive interactions, and not resource use overlap per se (Abrams 1980). A high degree of overlap may equally well indicate an absence of competition permitting a sharing of common resources (Gordon and Illius 1989; Putman 1996). It has been argued that it is pertinent to describe resource overlap both at times of the year when resources are abundant and when they are scarce, and infer the existence of competition if and when overlap declines in the lean season (Smith et al. 1978; Gordon and Illius 1989). This is partly built on the presupposition that grazing ungulates start using lower-quality forage when outcompeted from mutually preferred swards (Illius and Gordon 1987). Data on diet from two seasons within the same area was only available for roe deer/moose (Cederlund et al. 1980) and red deer/sheep (Vaag 1980). In both cases, diet overlap was somewhat higher during winter than during summer. This may imply that no competition was occurring, which is likely since these studies were conducted prior to the recent large increase in cervid population sizes in Fennoscandia (Statistics Norway 1998). The same applies to most of the other studies, and thus small overlap most likely mean low level of potential competition (*sensu* Putman 1996).

Although differences in feeding type tended to predict degree of diet overlap, whereas body mass did not, the weak predictive power of both these niche axes may imply that several niche axes need to be taken into account to successfully predict ungulate diet (e.g. Hanley and Hanley 1982). Resource use overlap between the natural guild of large herbivores in Scandinavia (moose, red deer and roe deer) was generally low (<35%), which

may imply that interspecific competition play only a minor role in population dynamics even at high density. Earlier studies have also reported low diet overlap between red deer and roe deer (Schröder and Schröder 1984; Putman 1996). However, diet overlap between sympatric native cervids (red deer and reindeer) and an exotic species (sheep) was relatively high (>50%). Domestic sheep are only free-ranging during summer in Norway, except for a few southern areas along the coast. Generally, it is considered that winter forage determines the number of individuals an area can supply, whereas summer forage determines condition of the animals (Klein 1965). It is not known whether summer forage is in limited supply on these pastures with the present stocking rates, which on mountain pasture vary from 5 to about 50 sheep km⁻².

Intra-specific resource use overlap between two winters or summers varied between 54.6% and 62.5%, which suggest that temporal variation in inter-specific resource use overlap can occur. It is at present uncertain whether geographical differences in interspecific diet overlap are significant, but there may thus be both temporal and spatial variation in the potential for competition for a given pair of species (Belovsky 1984, 1986). Other sources of variation in resource use overlap, such as sex dependence (Gordon and Illius 1989), age dependence, and possible breed dependence for sheep, should be evaluated. Further, there are several other important mechanisms of interaction among ungulates apart from (interference and exploitation) competition:

1. Grazing and browsing may increase primary production and quality of forage and thus lead to facilitation (e.g. McNaughton 1976; Gordon 1988; Alpe et al. 1999). Cederlund et al. (1980) also noted that roe deer were using moose trails during a severe winter, which may be a mechanism of facilitation in a wide use of the term.
2. Herbivory may remove cover that is important for hiding neonates and thus lead to higher levels of predation (Loft et al. 1987). This may be especially important for roe deer fawns which remain in dense cover for the first weeks after birth (Linnell 1994), and which may experience high levels of predation from red fox (Aanes and Andersen 1996).

3. A generalist predator may respond numerically to increase in one species, and subsequently increase predation on another species (Holt and Lawton 1994).
4. Even if no numerical response of the predator occurs, switching may reduce or increase predation levels depending on the spatio-temporal distribution of herbivores.
5. Indirect interactions mediated by parasites may occur (Holt and Lawton 1994), though Bye (1987) found no evidence of nematode transfer between reindeer and sheep.

Clearly, the complex issues of interaction in ungulate assemblages need further research in order to be able to assess the relative roles of these mechanisms for population dynamics of the large herbivore guild in Fennoscandia.

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