

Diet shift of a facultative scavenger, the wolverine, following recolonization of wolves

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Summary

1. Wolves *Canis lupus* L. recolonized the boreal forests in the southern part of the Scandinavian peninsula during the late 1990s, but so far there has been little attention to its effect on ecosystem functioning. Wolf predation increases the availability of carcasses of large prey, especially moose *Alces alces* L., which may lead in turn to a diet switch in facultative scavengers such as the wolverine *Gulo gulo* L.

2. Using 459 wolverine scats collected during winter–spring 2001–04 for DNA identity and dietary contents, we compared diet inside and outside wolf territories while controlling for potential confounding factors, such as prey density. We tested the hypothesis that wolverine diet shifted towards moose in the presence of wolves, while taking into account possible sexual segregation between the sexes. Occurrence of reindeer, moose and small prey was modelled against explanatory covariates using logistic mixed-effects models. Furthermore, we compared diet composition and breadth among habitats and sexes.

3. Occurrence of reindeer, moose and small prey in the diet varied with prey availability and habitat. As expected, diet contained more moose and less reindeer and small prey in the presence of wolves. Their diet in tundra consisted of 40% reindeer *Rangifer tarandus* L., 39% moose and 9% rodents. In forest with wolf, their diet shifted to 76% moose, 18% reindeer and 5% rodents; compared to 42% moose, 32% reindeer and 15% rodents in forest without wolf. This diet switch could not be explained by higher moose density in wolf territories. Female diet consisted of more small prey than for males, but there was a tendency for females to use the highly available moose carrion opportunistically and to hunt less on small prey within wolf territories.

4. Our study highlights how wolves increase scavenging opportunities for wolverines, and how sexual differences in diet may also apply to large scavengers. Due to their more restricted home range, female wolverines are forced to rely more on hunting small prey. The relatively high occurrence of wolf kills, however, forms an important food source to wolverines in this area. The recolonization of wolves may therefore have contributed to the consequent recolonization of wolverines into the same area.

Key-words: hunting, intraguild interactions, large carnivores, scavenging, sexual segregation

Introduction

The recent recolonization of large carnivores such as the wolf *Canis lupus* L. to their former range in both Europe and North America seems to be linked to legal protection, reduced hunting and to increased ungulate populations (e.g. Massolo & Meriggi 1998; Oakleaf *et al.* 2006). This has sparked great interest in

how ecosystem function has changed after the return of these top predators. Attention has focused mainly on the effect of wolves on deer populations, and how this in turn affects vegetative cover (e.g. Ripple *et al.* 2001; Vucetich & Peterson 2004; Fortin *et al.* 2005). Surprisingly little attention has been paid to the influence of top predators on scavengers, with a few exceptions in North America and Poland (Berger 1999; Wilmers *et al.* 2003; Wilmers & Post 2006; Selva & Fortuna 2007).

In 1966 the wolf was regarded as functionally extinct in Norway and Sweden, but recovered slowly after 1978 when

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the first reproduction was confirmed in the northernmost part of Sweden (Wabakken *et al.* 2001b). In southern Norway, wolverines were hunted to functional extinction and received protection in 1973. However, few wolverines remained in the mountain areas along the Swedish–Norwegian border, which received protection in Sweden from 1969. During the late 1970s they recolonized the Snøhetta plateau in south-central Norway (Landa, Lindén & Kojola 2000) and during the late 1990s their range extended from these western mountainous areas to the eastern boreal forest (Flagstad *et al.* 2004) after wolves had recolonized the same region a few years earlier (Wabakken *et al.* 2001b). Wolverines can both hunt and scavenge for food (Haglund 1966; Krott 1982; Magoun 1987). In Scandinavia the wolverine has been regarded mainly as a scavenger on large ungulates (Haglund 1966; Myhre & Myrberget 1975; Landa *et al.* 1997), with the ability to switch between different food sources if one prey species is becoming rare (Landa *et al.* 1997). The high degree of utilization by wolverines on wolf-killed moose *Alces alces* L. in the boreal forests in southern Norway (J. van Dijk *et al.*, unpublished data) suggests that wolf presence may be important to the wolverine diet. However, quantitative information is lacking.

Populations of large mammals are generally structured strongly according to age and sex, so it is vital to understand if and how the ecology of the two sexes differ. Many studies of large herbivores focus upon sexual segregation (review in Ruckstuhl & Neuhaus 2005), but few studies of sexual segregation exist for large predators (see Wielgus & Bunnell 1994; Rode, Farley & Robbins 2006) and none on scavengers. Adult male wolverines have larger home range sizes than females (Landa *et al.* 1998); especially compared to the restricted range use in reproducing females (Landa *et al.* 1998; Magoun & Copeland 1998). We therefore expected that scavenging opportunities may be more important for male than female wolverines. The more restricted female would be expected to compensate for having less opportunity to find carrion by hunting on small prey.

In this study we examined the winter–spring diet of wolverines throughout their range in southern Norway between 2001 and 2004. The presence of wolves was expected to increase scavenging opportunities for wolverines, leading to a diet switch to scavenging, and increasing the occurrence of moose in their diet. We controlled for potential confounding factors, such as the local availability of prey species that could either be hunted or scavenged upon. Furthermore, we predicted this diet switch to differ between male and female wolverines because females have relatively smaller home ranges compared to male wolverines and are therefore more restricted in their search for wolf-kills.

Methods

STUDY AREA

In southern Norway the range of wolverines encloses many different ecological conditions, from remote mountainous areas in the west and centre with peaks up to 2000 m to more accessible forest areas and low mountain ranges in the east. The treeline can be found around 900–1000 m above sea level. In southern Norway, snow is present from October/November until May/June, depending upon elevation.

Throughout the study area, free-ranging sheep graze unattended on summer pastures from June to September. The largest European population of wild reindeer *Rangifer tarandus* L. is found in the mountainous areas in the west and centre. In the north-eastern, north-western and south-eastern part, herding of semi-domestic reindeer is practised. Moose, roe deer *Capreolus capreolus* L., hare *Lepus timidus* L., ptarmigan *Lagopus muta* M., lemming *Lemmus lemmus* L., various rodents (*Microtus* spp. and *Clethrionomys* spp.) and insectivores *Insectivora* spp. (lemming, rodents and insectivores are hereafter called rodents) form possible food sources for the wolverine in southern Norway, either as hunted prey or through scavenging.

The estimated wolverine population in southern Norway increased from 83 to 130 adult individuals (≥ 1 year old) between 2001 and 2004 (Brøseth & Andersen 2003; Brøseth & Andersen 2004). They share the boreal forests in the east with wolves, bears *Ursus arctos* L. and lynx *Lynx lynx* L., but live alone in the higher alpine habitat in the west. The general location of the wolf area, where two to three wolf packs with 2–11 members per pack lived between 2001 and 2004, is shown in Fig. 1 (Wabakken *et al.* 2001a, 2002, 2004a, 2004b, 2005). Low numbers of bears were found in the eastern part of the study area, but no bear reproductions have been documented officially in the study area between 2001 and 2004 (Swenson *et al.* 2003; State of the Environment Norway 2005). Lynx are found at lower elevations within the study area, and the number of registered family groups ranged from 43 to 39 for 2001 and 2004, respectively (Brøseth, Odden & Linnell 2004). Red foxes *Vulpes vulpes* L. are also common in the study area, but no population estimates exist.

SCAT COLLECTION AND DIET ANALYSIS

As part of the National Large Carnivore Monitoring programme, wolverine scats are collected yearly in southern Norway by the Norwegian State Nature Inspectorate during late winter–early spring (i.e. April–May, depending on snow conditions). A small portion of each scat sample is used within the DNA-based monitoring programme (Flagstad *et al.* 2004), resulting in individual identification (ID) and sex when DNA is extracted successfully. Scat samples collected in 2001–04 for which DNA was extracted successfully ($n = 459$; 86 in 2001, 104 in 2002, 144 in 2003 and 125 in 2004) were analysed for dietary contents (Fig. 1). The DNA analysis identified 162 different individuals (72 males and 90 females).

Each scat sample was washed in a 0.5 mm-diameter sieve until the water was clear. Hairs and feathers were separated from other dietary remains (e.g. bones, plant material, nonfood items) and were oven-dried at 70 °C for 24 h. The relative contribution of the hairs and feathers was estimated visually with use of a superimposed grid (van Dijk *et al.* 2007). Hairs and feathers were identified to species level using macroscopic and microscopic characteristics (see Williamson 1951; Teerink 1991) and reference collections.

ECOLOGICAL CONDITIONS AND PREY AVAILABILITY

For each scat sample's location, habitat type (i.e. tundra, forest and shrubland) was derived from a 1 × 1 km land cover map (classified AVHRR image, United States Geological Survey: <http://edcdaac.usgs.gov/glcc/background.html>), using Geographic Information System software package ArcView 3.3 (ESRI, Environmental Systems Research Institute, Redlands, CA, USA).

As an index for prey density, hunting statistics from Statistics Norway (<http://www.ssb.no>) were used, as carried out and validated in earlier studies on cervids from Norway (for moose, see Herfindal

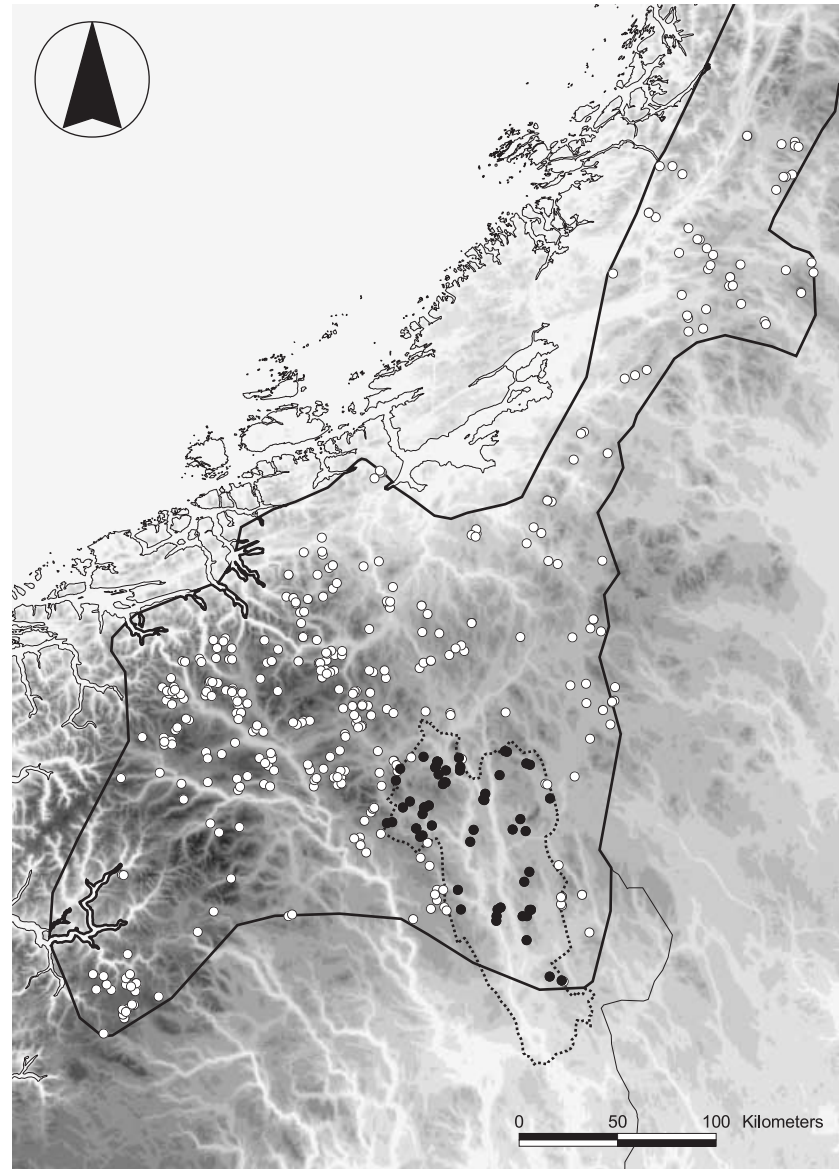


Fig. 1. Overview of the wolverine scat samples analysed within the dietary study in southern Norway. Black circles represent scat samples collected within the area with wolf presence, and white circles represent scat samples collected outside the area with wolf presence. The wolverine range in southern Norway is indicated with a solid line, and the wolf area is indicated with a dotted line.

et al. 2006). Numbers of wild reindeer and moose shot during the hunting season (i.e. autumn) before the scat sample was collected (i.e. late winter following the hunting season) were divided by the municipality surface area in which the scat sample was collected. Statistics for semi-domestic reindeer were obtained from data available from the Directorate of Reindeer Husbandry (2000–03; <http://www.reindrift.no>). Numbers of semi-domestic reindeer for the different herds were divided by municipality surface area of where the scat sample was collected to obtain a relative measure for semi-domestic reindeer density. Average annual densities for wild and semi-domestic reindeer and moose are given in the Supplementary material, Fig. S1. Because hunting statistics on small game (i.e. Galliform spp., Passeriform spp., Columbiform spp., mustelids, beaver *Castor fiber* L., mountain hare and red squirrel *Sciurus vulgaris* L.) were available only at county level, numbers of small game were divided by the county surface area. Because small game hunting statistics were available only from 2001 to 2004 (thus not from the hunting season in 2000, representing small prey density for the scat samples collected in 2001), we used the statistics of 2002 to represent

small prey density in 2001. To include possible annual fluctuations in rodent densities, monitoring data (2000–03) from the Directorate for Nature Management's programme for terrestrial nature monitoring on rodents (hereafter called TOV) at a study site in the west, Åmotsdalen (latitude 62°27', longitude 9°30'), and at a study site in the east, Gutulia (latitude 62°00', longitude 12°13') (<http://tov.dirnat.no>) were included for comparison.

STATISTICAL ANALYSES

Based on the geographical position of the scat samples and sex of the wolverine the percentage of occurrence for the prey species was calculated (Table 1, after van Dijk *et al.* 2007). Diet breadth per habitat and sex was calculated using the standardized Levin's measure of niche breadth B_j following equation 1.

$$B_j = \frac{(\sum p_{ij}^2)^{-1} - 1}{i - 1}, \quad \text{eqn 1}$$

where p_{ij} represents the proportion of occurrence for prey species i in subset j (e.g. subset 'tundra' containing all scats collected in tundra) (Hurlbert 1978). We checked for possible dietary differences among the habitats and between the sexes by comparing percentage of occurrence with the overall percentage of occurrence using χ^2 tests.

Occurrence of reindeer, moose and small prey species (i.e. hare, birds and rodents taken together) in the diet were assessed using logistic mixed-effects regression models with presence/absence of prey species as a binary categorical response variable and ID as random factor to control for repeated observations of the same individuals. Explanatory variables included were year (categorical), wolf presence (i.e. the scat was found inside or outside the wolf area, Fig. 1), sex, habitat type and the density index for wild reindeer, semi-domestic reindeer, moose and small prey. The variable year was included in the models to capture annual fluctuations in rodent densities, because no spatially explicit data on rodents were available. Also, other factors varying among years will be captured by this variable, such as snow conditions. Model selection was conducted using a backward stepwise procedure, where the most parsimonious model corresponded to the model with the lowest corrected Akaike Information Criterion (AIC_c) (Anderson, Burnham & Thompson 2000; Burnham & Anderson 2002). Models with ΔAIC_c scores lower than 2, compared to the most parsimonious model, were included as possible alternative models (Burnham & Anderson 2002).

Statistics were performed using the statistical software program R version 2.4.0 (R Development Core Team 2006) using the lmer function with a binomial distribution of the lme4 library (Bates & Sarkar 2005). Model fit was calculated using the Laplace approximation of the maximum likelihood. All other statistical analyses were performed with SPSS version 14 (SPSS Inc., 2005) and Microsoft Excel, version 2003.

Results

WOLVERINE DIET AND NICHE BREADTH

Of the analysed scat samples, 135 were collected in tundra, 189 in shrubland and 135 in forest habitat. Number of yearly collected scat samples did not vary significantly by habitat in which the scats were found [analysis of variance (ANOVA), $F_{2,9} = 1.733$, $P = 0.231$].

Dietary contents expressed as percentage of occurrence (PO) showed that moose was the most important prey species for wolverines in southern Norway in late winter–early spring, followed by reindeer and rodents (Table 1). In tundra,

however, reindeer was more important than moose in the diet of wolverines. The diet of wolverines in tundra was significantly different from the overall diet in southern Norway [$\chi^2 = 19.149$, degrees of freedom (d.f.) = 6, $P = 0.004$], while the diet in shrubland and forest was not ($\chi^2 = 4.757$, d.f. = 6, $P = 0.575$ and $\chi^2 = 4.461$, d.f. = 6, $P = 0.615$ for shrubland and forest, respectively). Niche breadth in tundra was broadest, while niche breadth in forested areas was narrowest ($B_{\text{tundra}} = 0.341$, $B_{\text{shrubland}} = 0.307$ and $B_{\text{forest}} = 0.291$; Table 1). In forest, we found a significant difference in the diet with wolf presence vs. without wolf presence ($\chi^2 = 31.154$, d.f. = 6, $P < 0.001$). Niche breadth of wolverines in forested areas with wolf presence was narrower than without wolf presence (respectively, $B = 0.103$ and $B = 0.382$; Table 1).

A significant difference in the diet of male and female wolverines was found in forest habitat ($\chi^2 = 12.905$, d.f. = 6, $P = 0.045$). This effect was similar both in forested areas with wolf presence and without wolf presence ($\chi^2 = 9.218$, d.f. = 2, $P = 0.010$ and $\chi^2 = 13.570$, d.f. = 6, $P = 0.035$ for wolf presence and wolf absence, respectively), with females having a higher percentage of occurrence of small prey and moose in their diet, but a lower occurrence of reindeer. No tendency for a sex effect was found in shrub habitat ($\chi^2 = 10.420$, d.f. = 6, $P = 0.108$) and in tundra ($\chi^2 = 5.554$, d.f. = 6, $P = 0.475$).

EXPLAINING PREY SPECIES IN WOLVERINE DIET

The best model explaining reindeer occurrence in the scat samples showed that reindeer occurrence was lower in the area with wolf presence and higher in areas with higher wild reindeer densities. The next best model also indicated that reindeer occurrence was higher in tundra (Table 2).

The best model for moose occurrence in the scat samples varied per year and wolf presence had a positive effect on moose occurrence. The next best model for moose occurrence indicated that moose density also had a positive effect on moose occurrence in the diet. According to the third model, shrubland and forest had a positive effect on moose occurrence.

The best model explaining small prey occurrence in the scat samples showed that small prey occurrence was lower in scat samples from male wolverines. Furthermore, small prey occurrence varied per year and increased with small prey

Table 1. Percentage of occurrence for the different prey species found within different subsets of wolverine scat samples. The final row gives the standardized Levin's niche breadth for the different subsets. The three main prey species are shown in bold type

	Southern Norway						Forest wolf absent			Forest wolf present		
	All	Male	Female	Tundra	Shrubland	Forest	All	Male	Female	All	Male	Female
Number of scats	459	202	257	135	189	135	93	44	49	42	31	11
Reindeer	31.4	34.2	29.3	40.2	27.8	27.9	31.9	36.4	27.7	18.4	22.2	9.1
Moose	47.5	49.5	45.9	38.6	50.6	51.9	41.8	43.2	40.4	76.3	74.1	81.8
Roe deer	1.1	2.1	0.4	0.8	1.1	1.6	2.2	2.3	2.1	0.0	0.0	0.0
Sheep	2.8	2.1	3.3	0.8	5.0	1.6	2.2	4.5	0.0	0.0	0.0	0.0
Hare	3.2	2.1	4.1	9.4	0.6	0.8	1.1	0.0	2.1	0.0	0.0	0.0
Birds	2.3	1.1	3.3	0.8	2.2	3.9	5.5	2.3	8.5	0.0	0.0	0.0
Rodents	11.7	8.9	13.8	9.4	12.8	12.4	15.4	11.4	19.1	5.3	3.7	9.1
Niche breadth	0.323	0.282	0.355	0.341	0.307	0.290	0.382	0.331	0.419	0.103	0.111	0.076

Table 2. Results of the logistic regression models used within the dietary analyses of wolverine scat samples in southern Norway. The models represent the variables explaining the diet of wolverines based on all scats for which DNA was extracted successfully (459 scat samples, 162 individuals). Each first model corresponds to the most parsimonious model with the lowest corrected Akaike information criteria (AIC_c). The next models, with $\Delta\text{AIC}_c < 2$ compared to the most parsimonious model, are included as possible alternative models. One, two or three asterisks indicate significance at $P < 0.05$, $P < 0.01$ or $P < 0.001$, respectively

Models	Variables	Coef.	SE	Z-value	P	AIC _c	ΔAIC_c
Reindeer occurrence, model I	Intercept	-1.144	0.197	-5.801	0.000***	541.234	0.000
	Wolf presence	-1.240	0.464	-2.674	0.008**		
	Wild reindeer density	3.479	1.804	1.928	0.054		
Reindeer occurrence, model II	Intercept	-0.906	0.274	-3.308	0.001***	542.656	1.422
	Wolf presence	-1.206	0.484	-2.492	0.013*		
	Wild reindeer density	3.676	1.846	1.991	0.047*		
	Shrubland ^b	-0.482	0.297	-1.624	0.104		
	Forest ^b	-0.196	0.347	-0.566	0.571		
Moose occurrence, model I	Intercept	-0.636	0.243	-2.619	0.009**	614.164	0.000
	Year 2002 ^a	-0.149	0.320	-0.466	0.641		
	Year 2003 ^a	0.855	0.296	2.890	0.004**		
	Year 2004 ^a	0.166	0.306	0.541	0.589		
	Wolf presence	1.165	0.319	3.648	0.000***		
Moose occurrence, model II	Intercept	-0.716	0.250	-2.866	0.004**	614.671	0.507
	Year 2002 ^a	-0.200	0.321	-0.622	0.534		
	Year 2003 ^a	0.792	0.299	2.653	0.008**		
	Year 2004 ^a	0.131	0.307	0.428	0.669		
	Wolf presence	1.001	0.340	2.947	0.003**		
	Moose density	1.470	1.148	1.280	0.201		
Moose occurrence, model III	Intercept	-0.989	0.301	-3.285	0.001**	615.456	1.292
	Year 2002 ^a	-0.112	0.323	-0.348	0.728		
	Year 2003 ^a	0.857	0.302	2.843	0.004**		
	Year 2004 ^a	0.171	0.307	0.557	0.577		
	Wolf presence	0.969	0.344	2.819	0.005**		
	Moose density	1.532	1.273	1.203	0.229		
	Shrubland ^b	0.441	0.253	1.747	0.081		
	Forest ^b	0.132	0.317	0.417	0.677		
Small prey occurrence, model I	Intercept	-3.167	0.720	-4.400	0.000***	378.804	0.000
	Year 2002 ^a	2.083	0.541	3.853	0.000***		
	Year 2003 ^a	0.487	0.574	0.848	0.396		
	Year 2004 ^a	0.889	0.560	1.590	0.112		
	Male ^c	-0.737	0.347	-2.127	0.033*		
	Moose density	-2.696	1.784	-1.511	0.131		
	Small prey density	0.373	0.234	1.595	0.111		
Small prey occurrence, model II	Intercept	-2.961	0.756	-3.914	0.000***	379.936	1.132
	Year 2002 ^a	2.042	0.556	3.671	0.000***		
	Year 2003 ^a	0.436	0.589	0.740	0.459		
	Year 2004 ^a	0.868	0.576	1.506	0.132		
	Male ^c	-0.777	0.361	-2.154	0.031*		
	Moose density	-2.896	2.059	-1.406	0.160		
	Small prey density	0.425	0.244	1.747	0.081		
	Shrubland ^b	-0.632	0.382	-1.654	0.098		
	Forest ^b	-0.153	0.467	-0.327	0.744		

^aYear effect is given relative to year 2001; ^bhabitat effect is given relative to tundra; ^csex effect is given relative to female.

densities, but was affected negatively by moose density. In the next best model small prey occurrence was also found to be higher in tundra, relative to shrubland and forest (Table 2).

PREY DENSITIES AND ANNUAL VARIATION

The study was not sufficiently long-term to test explicitly for factors causing annual variation in the wolverine diet. However, as rodents constituted 69% of small prey occurrence in the faeces, the yearly density index for rodents derived from TOV was plotted against the average percent-

ages of rodents, moose and reindeer found within the scat samples collected in the areas with or without wolf presence (Fig. 2). In areas without wolf presence the average percentage of rodents occurrence in the scat samples qualitatively followed the yearly density index of rodents, showing an increase in the percentage of moose occurrence when the yearly density index of rodents was low (Fig. 2a). In the area with wolf presence the average percentage of rodent occurrence in the scat samples did not follow the yearly density index of rodents, and moose occurrence was relatively high regardless of the fluctuating density index of rodents (Fig. 2b).

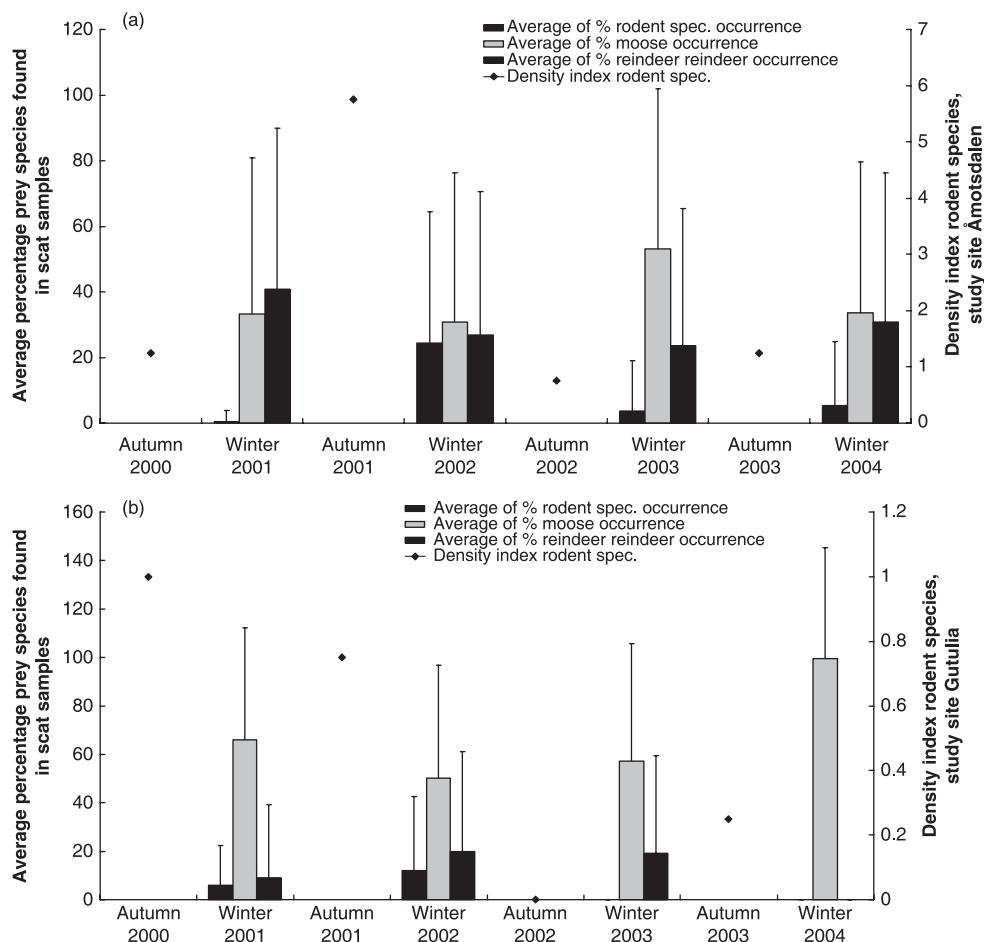


Fig. 2. The average percentage of rodent species (black columns), moose (grey columns) and reindeer (white columns) occurrence found in the scat samples in the area outside wolf territories (a) and inside wolf territories (b) per winter plotted against the yearly density index for rodents in that area (♦) during the previous autumn. The error bars indicate the standard deviations of the average percentages.

Discussion

THE WOLVERINE IN THE FOOTSTEPS OF WOLVES

Our study revealed that during the winter–spring period wolverines ate more moose within than outside wolf territories, suggesting that wolf recolonization have induced a diet shift in a facultative scavenger, the wolverine. Wolverines both scavenge and predate, and switch between the two strategies depending on what is most profitable (Haglund 1966; Stephens & Krebs 1986). Carrion has proved to be an important winter and spring food resource for the wolverine, both in North America (Houston 1978; Magoun 1987; Wilmers *et al.* 2003) and Scandinavia (this study, Landa *et al.* 1997) when carrion supply is more abundant (Selva *et al.* 2005). The availability of carcasses due to natural mortality is seasonally pulsed, while wolf kills form a more constant resource for scavengers (Wilmers *et al.* 2003; Selva & Fortuna 2007). Moose is assumed to be available to the wolverine as carcasses, and although high moose densities imply a high availability of carcasses due to natural mortality and traffic kills (Solberg *et al.* 2006), in wolf areas the number of available carcasses increases enormously (Wilmers *et al.* 2003; Smith *et al.* 2004;

Sand *et al.* 2005). Indeed, wolf presence had a strong effect on moose occurrence in the wolverine's diet in our study. Both reindeer occurrence and small prey occurrence in the wolverine's diet were lower in scats found in the area where wolves were present. Apparently the increase of available scavenging opportunities provided by wolves enables the wolverine to shift from a broad diet with reindeer, mountain hare, birds and rodents to a narrower diet with almost exclusively moose, as niche breadth for wolverines coexisting with wolves was remarkably narrower (Table 1). Both rodents and wild reindeer as traditional wolverine diet species (Landa *et al.* 1997) are, however, also more abundant in the mountainous areas in the western region of southern Norway (see also Fig. 2 with rodent index from study site Åmotsdalen in the west and Gutulia in the east). Whether the increase in scavenging opportunities provided by wolves have actually triggered wolverines to recolonize previously occupied areas clearly merits further research. We also have to keep in mind that, although the effect size was strong (i.e. a significant increase in carrion provision by wolves; Sand *et al.* 2005), the observed diet shift may not be ascribed to wolves *per se* as the study enabled us to compare only one wolf area with one non-wolf area. Nor did the study enable us to highlight the potential

role of other large carnivores, such as bears (low numbers) or lynx (widely distributed). The lynx in Norway is a roe deer specialist (Odden, Linnell & Andersen 2006), and as we found very little roe deer in wolverine diet, lynx presence might not be important for the wolverine's diet, also confirmed by snow tracking studies (J. van Dijk *et al.*, unpublished data).

THE ROLE OF PREY AVAILABILITY

It is also clear that prey availability is important for wolverine diet, because local availability of reindeer, moose and small prey were all part of the best models explaining occurrence in the diet. Although data were available only for a limited number of years, the occurrence of rodents in wolverine diet outside wolf territories seemed to follow the yearly fluctuations in small rodent availability (Fig. 2a). In autumn 2002, when the yearly rodent index was low, wolverines switched to scavenging on moose carcasses during winter 2002–03. Such a switch was not apparent within the wolf territories (Fig. 2b). Landa *et al.* (1997) showed that the reproductive success in wolverines was correlated with the density cycle of rodents, but this may thus not be the case in areas where wolves exist.

The two previous studies conducted on wolverine winter diet in Norway reported that reindeer was their most important prey species (Myhre & Myrberget 1975; Landa *et al.* 1997), whereas this study revealed moose as being the most important prey species for the wolverine. During the last decades, in particular, moose densities have increased enormously (Lavsund *et al.* 2003), which might explain the diet shift from reindeer to moose in a historical perspective. Also, the studies from Landa *et al.* (1997) and Myhre & Myrberget (1975) were conducted in the high mountainous areas in south-central Norway and northern Norway, respectively, where moose densities are relatively low (Lavsund *et al.* 2003) and reindeer more abundant. Our study, however, included both the south-central mountain region and the eastern forest region. When considering wolverine diet only in tundra, reindeer was in fact the most important prey species, consistent with the two earlier studies. Wild reindeer densities in our study area have been more or less constant over the years, due to a hunting management regime that aims to keep the population stable (Punsvik & Jaren 2006; Solberg *et al.* 2006).

SEXUAL SEGREGATION IN DIET

Our study revealed that more small prey species were found in the diet of female wolverines relative to males. To what extent the differences in diet are the result of sexual segregation due to differences in body sizes or resource use (Ruckstuhl & Neuhaus 2002) is difficult to assess, especially because dimorphism in body size, differing diet and foraging behaviour between individuals of different sex in the wild have rendered varying results (e.g. Holmes & Powell 1994; Begg *et al.* 2003; Rode *et al.* 2006). The fact that male wolverines have two to three times larger home range sizes compared to females (Landa *et al.* 1998) might increase their chances for encountering large prey to scavenge upon compared to the more restricted

female. The observed differences in diet are therefore probably the result of sexual segregation due to different space use between the sexes.

Although only 11 scat samples from female wolverines were found in wolf territories (vs. 31 scat samples from male wolverines), there was a tendency for females to use the highly available moose carrion opportunistically and to hunt less on rodents. The two to three times larger home ranges of male wolverines probably enables them to come into contact with reindeer either as carrion or as hunted prey more than females. The more restricted home ranges of females force them to rely more upon small prey that is available locally. Because scavenging on moose carrion will have a relatively low energetic cost, the female wolverine may switch to this food resource when abundant, despite the fact that females with dependent cubs may face an increased risk of intraguild predation by wolves (cf. R. May *et al.*, unpublished data).

Acknowledgements

We thank personnel of the Norwegian State Nature Inspectorate for collecting the wolverine scats. We also thank the Evolutionary Biology Centre in Uppsala, Sweden, for the possibility to use the scat sample for our diet analysis. This study was part of the project 'Wolverines in a Changing World', which was financed by the Norwegian Research Council, the Directorate of Nature Management, Sparebank-1 Midt-Norge, the Norwegian Institute for Nature research and Alertis, Fund for Bear and Nature Conservation from the Netherlands.

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Received 14 October 2007; accepted 25 May 2008

Handling Editor: Piran White

Supplementary material

The following supplementary material is available for this article.

Fig. S1. Average densities of moose, wild reindeer and semi-domestic reindeer for the different study years. Based on the hunting statistics, moose was hunted in 56 of the 56 communities in which scat samples were collected, whereas wild reindeer was hunted in 31 and semi-domestic reindeer was herded in 29 of the 56 communities.

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