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Selective foraging on woody plant species by the Eurasian beaver (Castor fiber) in Telemark, Norway.

Selective foraging on woody plant species by the Eurasian beaver (*Castor fiber*) in Telemark, Norway

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Abstract

Beavers Castor spp. are generalist herbivores, feeding on the bark, shoots and leaves of woody plants, terrestrial herbs and forbs, ferns and aquatic vegetation. As central-place foragers, beavers move out from water to select and cut trees and vegetation, and then transport it back to their refuge. These terrestrial forays are energetically costly; therefore, beavers should concentrate their foraging activity near the central place and increase the degree of selectivity for specific sizes or species off ood with increasing distance from the water. The aim of this study was to test the predictions of the central place and the optimal foraging theories for the food selection of the Eurasian beaver Castor fiber, and show the foraging preferences of the focal species in the boreal conifer forest zone of Europe. Foraging intensity by beavers and the abundance of woody species were surveyed in transects positioned randomly at seven beaver territories. In compliance with the central-place foraging theory, the foraging intensity declined with increasing distance from the river. Beavers fed preferentially on willows (Salix), rowan (Sorbus) and birches (Betula), although alders (Alnus) dominated their diet. Size selectivity showed similar patterns to previous North American studies, which were also carried out in habitats with predominantly small saplings. The probability of selection of small saplings dropped as distance increased, which is consistent with the predictions of optimal foraging models that larger prey items are more likely to be favoured with increasing provisioning distance.

Introduction

A growing body ofl iterature deals with optimal prey selection in the aspect of both species and size selection (e.g. Pulliam, 1974; Schoener, 1979; Jenkins, 1980; Stephens & Krebs, 1986; Fryxell & Doucet, 1991). In the case of the central-place foraging theory several models have been proposed (Orians & Pearson, 1979; Schoener, 1979). These models dictate that prey selection by predators should maximize the net rate of energy intake per unit time. A variant for single-prey loaders further suggests that although the best prey close to the central place should still be those that have the highest energy per provisioning time ratio, the best prey far from the central place would be those that provide the most energy, considering that provisioning time is negligible compared with travelling time (Orians & Pearson, 1979; Gallant et al., 2004). Questions may arise on the location of the central place if the available foraging patches are given, or on foraging patch, prey and load size selection if the organism has a fixed central place (Orians & Pearson, 1979). In organisms showing territorial behaviour, both approaches are valid; firstly when the organism has several potential foraging patches and should locate a burrow, nest or a feeding station as a central place, and secondly when the animal selects prey within the foraging patch.

Both North American beaver Castor canadensis and Eurasian beaver Castor fiber are central-place forager herbivores, feeding on the bark, shoots and leaves of woody plants, terrestrial herbs and forbs, ferns and aquatic vegetation (Wilsson, 1971; Jenkins, 1975; Svendsen, 1980; Nolet et al., 1995; Donkor & Fryxell, 1999). During periods when the green vegetation is mostly unavailable, the bark of trees and shrubs is likely to become the dominant dietary component of the beavers. Foraging by beavers leaves unmistakable signs on these plants; hence many studies have assessed their woody diet selection. As central-place foragers, beavers move out from water to select and cut trees and vegetation, and then transport it back to the water to eat immediately, or to the lodge to feed dependent offspring or to store for later use (Orians & Pearson, 1979; Schoener, 1979; Jenkins, 1980; McGinley & Whitham, 1985; Basey, Jenkins & Busher, 1988; Fryxell & Doucet, 1991). These terrestrial forays are energetically costly, and it would be advantageous for the beavers to make efficient use of their foraging time on land (Fryxell & Doucet, 1991). The foraging choices of the beavers should be the result of a trade-off between the quality of the food and the distance from the

water at which they are located. Therefore, beavers should concentrate their foraging activity near the central place (Andersson, 1978; Fryxell, 1992), and increase the degree of selectivity for specific sizes or species off ood with increasing distance from the refuge in a manner that maximizes the net rate of energy intake per unit time (Orians & Pearson, 1979; Schoener, 1979).

Many studies have assessed the species and size selectivity of North American beavers (Jenkins, 1975, 1979, 1980; Belovsky, 1984; McGinley & Whitham, 1985; Barnes & Dibble, 1988; Basey et al., 1988; Johnston & Naiman, 1990; Doucet & Fryxell, 1993; Fryxell & Doucet, 1993; Donkor & Fryxell, 1999), whereas less information exists on the foraging behaviour of the Eurasian beaver (Erome & Broyer, 1984; Nolet, Hoekstra & Ottenheim, 1994; Recker, 1997), especially in boreal conifer forests. Therefore, our objectives were to (1) show foraging preferences of Eurasian beavers in the aspect of trees species selectivity and (2) test hypotheses of central-place foraging theory. Specifically, we predicted that the feeding intensity of beavers on trees would decrease with distance from the central place, and that beavers are more selective for tree species and size as the distance increases from water.

Methods

Study area and materials

The fieldwork was carried out on the Lunde and Gvarv rivers in the municipalities of Nome and Sauherad in Telemark County, south-eastern Norway. The study area is situated between 59 and 60l northern latitude, in the vegetation zone of southern taiga.

In terms of monoclimax, the climax vegetation type is Eu-Piceetum subass. myrtilletosum in areas with intermediate soil conditions, dominated by Norway spruce Picea abies and some Scots pine Pinus sylvestris. In addition, Vaccinio-Pinetum can be found on shallow soil and dry glacial deposits and Oxycocco-Pinetum in bogs and mires low in nutrients. On low-lying sandy or marine deposits, there are forms of Melico-Piceetum in relatively dry places, Pruno-Alnetum incanae on elevated terraces that may be flooded temporarily, and Lysimachio vulgaris-Alnetum glutinosae in stagnant wet places. Stable Salix shrubs of the alliance Salicion cinereae are found in old river basins and at riparian sites, which are influenced by periodic inundation. The shrubs in these areas mainly consist of grey sallow Salix cinerea and eared sallow Salix aurita, some bog-myrtle Myrica gale and alder buckthorn Frangula alnus (Kielland-Lund, 1981; O. Vevle, pers. comm.).

The rivers meander through mixed woodland and agricultural countryside. Both rivers flow slowly and have mostly clear water. The width of the rivers varies from 10 to 100 m. Both Lunde and Gvarv rivers are regulated along a part of their length, resulting in limited fluctuations in water temperature and reduced ice cover in winter. The Lunde river forms part of the Telemark Canal and the section used in this study was bound at each end by canal locks and weirs. The Gvarv river follows a more natural flow regime and empties into Lake Nordsjø. The section used in the study forms the lower reaches, including part of Lake Nordsjø. There are no beaver dams in the study area as both rivers are either too large for beavers to dam or are already deep enough to make damming unnecessary. Therefore, contrary to studies on the North American beaver that create ponds, linear stretches of rivers were considered as central places, because the distance measurements to the stems of woody species were made from the shoreline. In general, the beavers in the study area live in burrows, covering only the entrance of the burrow by branches, and yearly build food caches at the entrance of the winter den. The rivers have been occupied by beavers since the 1920s (Olstad, 1937). Presently, only c. 20 wolves Canis lupus and 250 lynxes Lynx lynx exist in Norway (Brøseth, Odden & Linnell, 2004). Hunting and trapping pressure are low to non-existent. The population density is high, with one colony/1.4 km on the Lunde- and one colony/1.2 km on the Gvarv river (Rosell & Hovde, 2001). In the study area, beavers use the entire riverbank apart from unreachable sites and areas without forest cover (Pinto, 2001).

Field sampling

Foraging intensity by Eurasian beaver and the abundance of woody species (trees and shrubs) were surveyed at seven beaver territories. Each territory was occupied by a colony consisting of adults, subadults and yearlings (family size mean ± SD = 4.4 ± 1.1). The study was carried out during a short period, between 22 May and 25 June 2001, when water levels were low and stable. Information on the location of territory borders was obtained from radio-tracking data collected in 2000 (see details in Sharpe & Rosell, 2003; Herr & Rosell, 2004; Campbell et al., 2005). A geographical information system (GIS) software program (Arc View version 3.2, ESRI) was used to determine the total length of wooded banks within the territories. Existing data on the habitat characterization of the study area (Campbell, 2000) were used to identify the wooded banks in each territory.

The use and the availability of woody vegetation was determined by collecting data in transects in each territory. Within each territory, the length of wooded riverbank was divided into 10 m wide sections, and 5% of these sections were chosen randomly for the survey. The species and diameter of both cut and uncut (standing) woody plants Z 1 cm in diameter were recorded along 10 × 40 m transects oriented perpendicular to the edge of rivers. The transects were divided into four plots, each 10 m wide (first distance category = 0–10 m, second distance category = 10–20 m, third distance category = 20–30 m, fourth distance category = 30–40 m). The cut-offpoint of 40 m was based on a study of an adjacent population of beavers in southern Norway where the average maximum distance of beaver-damaged woody plants from the river was found to be 36 m (Parker et al., 2001). The number of available trees within each species was defined as the sum of cut and standing trees.

Species identification of cut stems can generally be determined by the characteristics of the bark. Beaver cuttings are easily recognized by their conical shape, height above the ground, arrangement of tooth marks and other characteristics. All stems that had been completely severed from the trunk or were in the process of being severed, indicated by the fresh wood chips (e.g. Johnston & Naiman, 1990), were recorded. Felled trees and branches severed from standing trees were not treated separately. However, the latter category accounted for 2.5% of the cut stems. Furthermore, adult and juvenile growth forms were not treated separately, even though the content of secondary compounds may vary between sapling and adult trees, as herbivory can evoke negative feedback mechanisms, such as enhanced secretion of defensive chemicals (Basey et al., 1988; Martinsen, Driebe & Whitham, 1998).

Cut woody plants and branches severed from a standing tree were taken into consideration and the diameter of the stem was measured at the point of cutting. The diameter of uncut plants was measured at 20 cm above the ground, as this has been recorded as the mean height at which cutting occurs (e.g. Belovsky, 1984). Fallen and standing dead trees were rare, and were not measured.

Data analyses

In the data analyses, we included the five most common genera of deciduous trees in the beaver's diet (Alnus alder, Sorbus rowan, Salix willow, Betula birch, Prunus prunus); conifers (which included Norway spruce, Scots pine and common juniper Juniperus communis) and all other plant species (including alder-buckthorn, common ash Fraxinus excelsior, alpine elder Sambucus racemosa, guelder rose Viburnum opulus, pedunculate oak Quercus robur, aspen Populus tremula, hazel Corylus avellana, rose sp. Rosa sp., juneberry Amelanchier spicata, Norway maple Acer platanoides, bog-myrtle, crab apple Malus sylvestris, fly honeysuckle Lonicera xylosteum) were pooled into a seventh category, because their numbers were so low that not pooling them would have created statistical problems.

We tested whether the mean values of the proportion of cut trees (=number of cut trees/number of available trees) differed among territories, distance categories and species groups, with an analysis of variance (ANOVA). Because of the restricted randomization of the species groups within territory and distance, the data were analysed using a split-plot experiment (Kuehl, 1994; Hicks & Turner, 1999). Because most of the observations (proportions) are between 0.25 and 0.75, the binomial distribution approaches a normal distribution; therefore, transformation was not required. Also, the residuals were tested for normality and uniform variance assumptions, and they met the requirements. Although the variances were not found to be different for the four distance categories (Bartlett's w^2 test), the variances for the seven species groups indicated some differences, however not large enough to warrant transformations. Because of the unbalanced nature of the data, the general linear model (GLM) technique was used to calculate the ANOVA (Statistical Analysis System, 1985; Hicks & Turner, 1999), and the differences among the territories, distance categories and species groups were tested by Bonferroni's multiple comparison (a = 0.05).

The relationship between the proportion of stems cut and the distance from water was explored by regression analysis. The diameter selection within the distance categories and the species groups was also analysed by regression analysis. Nonlinear least-squares technique was used to derive the regression models. The curves were compared with approximate t-tests based on the approximate standard errors of the estimated parameters, which are calculated for nonlinear least-squares models by the statistical program we used (Statistical Analysis System, 1985).

Results

Species preference and foraging intensity

A total of 79 transects was surveyed at seven territories (transects/territory mean = 11.3; range = 7–20). Twenty-seven transects out of 79 (34%) were 40 m long; the length of the rest varied between 10 and 30 m because of adjoining agricultural fields and gardens. Grey alder Alnus incana, rowan Sorbus aucuparia, bird cherry Prunus padus, Norway spruce, alder-buckthorn, common ash, silver birch Betula pendula, downy birch Betula pubescens and alpine elder were the most available species at the study area, accounting for 83.5% of stem density. Norway spruce, grey alder, Scots pine, silver birch, bird cherry, rowan and downy birch had the highest basal area, accounting for 91.5% of basal area (Table 1).

In 97% (total = 6088) of the cases it was possible to identify trees cut by beavers from bark characteristics and/or regrowth from the trunk. Although 24 species of trees and shrubs were cut at least once in the transects surveyed, beavers' feeding activity was mainly concentrated on seven species, which contributed 82.6% of all cut stems. Grey alder, rowan, bird cherry, silver birch, downy birch, dark-leaved willow Salix myrsinifolia and eared sallow were browsed most frequently, with grey alder predominating. Although alpine elder had a high density in the study area because of human disturbances, it has never been browsed by beavers. Grey alder, rowan, downy birch, silver birch, bird cherry, eared sallow and grey sallow comprised 77.8% of the total basal area cut by beavers, with grey alder predominating (Table 1).

Six species groups – alder, rowan, willow, birch, prunus and conifers – comprised 90% of the beaver's diet (Table 2). Although alders were cut the most frequently, the proportional use of these species was the lowest among the plant generas, except for conifers. The ANOVA model indicated that the species of woody plants significantly affected the probability of beaver cutting (Table 3). The Bonferroni multiple comparisons suggest the following order of species preference: willow4 rowan4 birch4 prunus4 others4 alder4 conifers (Table 4). However, the preference values were not significantly different, neither between the first

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Table 1 Species composition of standing and cut woody plants $\geq$ 1 cm in diameter recorded in transects at seven Eurasian beaver *Castor fiber* territories in Telemark in 2001

Species	Available vegetation		Cut vegetation	
	% available stems [a]	% available basal area [b]	% cut stem [c]	% cut basal area [d]
Alder-buckthorn Frangula alnus	5.09	0.89	0.33	0.09
Alpine elder Sambucus racemosa	3.51	0.59	0.00	0.00
Aspen Populus tremula	0.90	0.61	0.59	1.04
Bay willow Salix pentandra	0.07	0.01	0.21	0.21
Bird cherry Prunus padus	6.77	2.88	7.06	6.02
Bog-myrtle Myrica gale	0.06	0.00	0.00	0.00
Common alder Alnus glutinosa	0.62	1.20	0.30	0.32
Common ash Fraxinus excelsior	5.04	1.66	2.41	3.28
Common juniper Juniperus communis	0.23	0.08	0.08	0.07
Crab apple Malus sylvestris	0.03	0.02	0.02	0.00
Crack willow Salix fragilis	0.05	0.00	0.10	0.04
Dark-leaved willow Salix myrsinifolia	2.18	0.18	5.80	2.54
Downy birch Betula pubescens	3.52	2.62	5.81	8.70
Downy willow Salix lapponum	0.01	0.00	0.00	0.00
Eared sallow Salix aurita	2.47	0.41	4.98	3.58
Fly honeysuckle Lonicera xylosteum	0.01	0.00	0.00	0.00
Goat willow Salix caprea	1.19	0.86	1.77	3.03
Grey alder Alnus incana	36.06	29.28	34.82	31.70
Grey sallow Salix cinerea	1.91	0.30	3.73	3.54
Guelder-rose Viburnum opulus	1.56	0.22	0.10	0.04
Hazel Corylus avellana	1.21	0.17	1.56	0.64
Juneberry Amelanchier spicata	0.21	0.01	0.13	0.02
Norway maple Acer platanoides	0.16	0.09	0.08	0.02
Norway spruce Picea abies	5.82	32.18	1.17	0.58
Pedunculate oak Quercus robur	1.54	0.67	1.59	1.76
Rose sp. Rosa sp.	0.26	0.01	0.00	0.00
Rowan Sorbus aucuparia	13.43	2.68	18.33	15.74
Scots pine Pinus sylvestris	0.77	15.14	0.07	0.58
Silver birch Betula pendula	4.28	6.69	5.81	8.57
Unidentified	1.06	0.53	3.14	7.87

[a] % available stems=percentage of stems of 17 958 total available stems.
[b] % basal area=percentage of basal area of 56 m^2 total available basal area cover.
[c] % cut stems=percentage of stems of 6088 total number of stems harvested by beavers.
[d] % cut basal=percentage of basal area of 3.7 m^2 total basal area browsed by beavers.

Table 2 Percentage of available (cut plus standing) and cut stems within the five most abundant plant genera, conifers and the category others used in the compositional analysis for seven Eurasian beaver *Castor fiber* territories in Telemark in 2001

	% available stems	% cut stems
Alder	36.7	35.1
Rowan	13.4	18.3
Willow	7.9	16.6
Birch	7.8	11.6
Prunus	6.8	7.1
Conifers	6.8	1.3
Others	20.6	10.0

three nor between the last four species groups. However, because of the significant distance×territory interaction, the differences as indicated here might not be the same between the territories within individual distance categories and/or between distance categories within individual territories. On the basis of the lack of interaction between distance and species groups (Table 3), beavers did not become more species selective with increasing distance from the water.

The relationship between the proportion of stems cut and the distance from the water could be significantly ($P < 0.05$) described by an exponential function [cut=0.471 $\times$ 0.718$^{-0.038x}$, I^2=0.193 (I^2 is an estimated R^2 (coefficient of determination) value used in nonlinear least squares)] (Fig. 1). This result was also confirmed by Bonferroni's test. It was clear that the proportion of tree cutting is much higher in the first distance category than in any of the other three, among which no difference could be shown (Table 4). However, as the territory $\times$ distance interaction was significant in the ANOVA model (Table 3), the differences may

Source	d.f.	Mean square	F value
Territory	6	0.59	15.41***
Distance	3	0.62	8.03**
Territory × distance (error 1)	18	0.08	2.04 *
Species group	6	0.62	16.26 ***
Distance × species group	18	0.05	1.26
Error 2	112	0.04	
Full model	163		

*Po 0.05; **Po 0.01; ***Po 0.0001.
ANOVA, analysis of variance.

Table 4 Least-square (LS) means of the proportion of cut trees compared by Bonferroni's multiple comparison (a=0.05) in seven Eurasian beaver Castor fiber territories, four distance categories and seven species groups in Telemark in 2001

Territory	LS mean for the territories	Distance category	LS mean for the distance categories	Species group	LS mean for the species groups
1	0.55 a	0−10	0.48 a	Alder	0.19 c
2	0.54 a	10−20	0.30 b	Rowan	0.49 a
3	0.18b c	20−30	0.25 b	Willow	0.53 ab
4	0.32 b	30−40	0.19 b	Birch	0.39 a
5	0.18b c			Prunus	0.24 bc
6	0.13 c			Conifers	0.09 c
7	0.23b c			Others	0.20 c

Means marked by the same subscript letter are not significantly different.

not be the same in each of the seven territories. Similarly, there were some differences among the territories, but because of the significant territory × distance interaction these differences may not be the same within each distance category.

Size selectivity

Ninety-five per cent of stems cut by beavers were $1 \, cm \leq d \leq 5 \, cm$ diameter; this comprised 47% of the total basal area (total=3.7 m^2) browsed. Most of these small-diameter saplings removed by beavers were grey alder, rowan and bird cherry. Only 5% of stems cut by beavers were 4 5 cm diameter, although this comprised 53% of the total basal area browsed. Most of these species removed by beavers were grey alder, rowan and silver birch. The diameter ofl arge trees (diameter4 5 cm) that were browsed averaged 8.1 ± 3.6 cm. The maximum stem diameter cut was 27 cm (downy birch) in the first, 25.5 cm (grey alder) in the second, 15 cm (silver birch) in the third, and 15 cm (rowan) in the fourth distance category.

The relationship between the diameter and the proportion of stems cut could be well described with an exponential
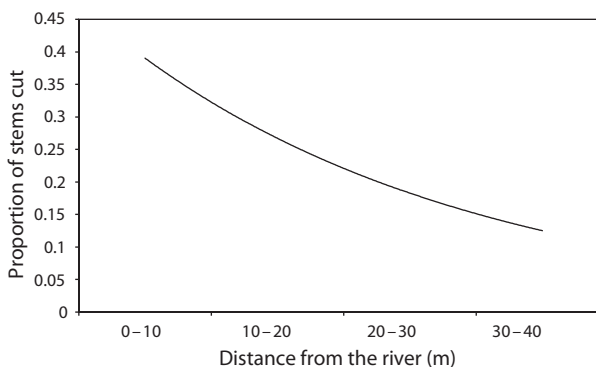

Figure 1 Proportion of stems cut by Eurasian beavers Castor fiber in relation to distance from the water's edge (cut=0.471 × 0.718$^{-0.038 x}$, I^2=0.193), at seven territories in Telemark in 2001.
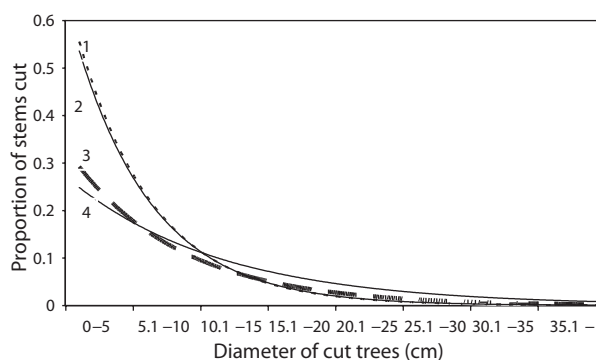

Figure 2 Diameter selection by Eurasian beavers Castor fiber in four distance categories measured from the edge of the river (1=0–10 m, 2=10–20 m, 3=20–30 m, 4=30–40 m) (cut$_1$=0.693 × 0.718$^{-0.180 x}$, I_1^2 ¼ 0:985, n_1=7500; cut$_2$=0.613 × 0.718$^{-0.171 x}$, I_2^2 ¼ 0:980, n_2=2015; cut$_3$=0.333 × 0.718$^{-0.125 x}$, I_3^2 ¼ 0:922, n_3=1292; cut$_4$=0.274 × 0.718$^{-0.089 x}$, I_4^2 ¼ 0:825, n_4=1007), at seven territories in Telemark in 2001. All equations presented are statistically significant at the 0.05 probability level.

function both within the distance categories (Fig. 2) and within species groups (Fig. 3), although no equations were fit for prunus, conifers and others because of the lack of information. After plotting the predicted values, the four curves for the four species groups were all different. According to the location and steepness of the curves, proportionally willows were the most used in the small-diameter classes. In the large-diameter classes, rowan had the highest values of proportional utilization. Alders were the least used compared with its availability in all diameter categories. This tendency was the most obvious in the diameter classes exceeding 10 cm, where – although alder was still the most available genera – it was cut in a very small amount.

In the case of the distance categories, the curves could be safely combined also for distance 1 and 2 as for distance 3 and 4. The proportion of small stems cut was considerably higher in the first two distance categories than in the last two.
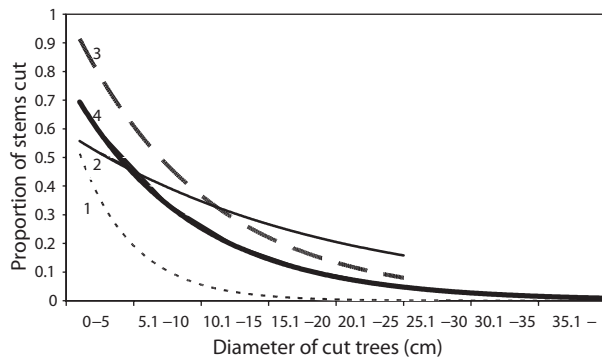
Figure 3   Diameter selection by beavers in alders and the three preferred plant generas (1 = alders, 2 = rowan, 3 = willows, 4 = birches) ($cut_1 = 0.755 \times 0.718^{-0.262x}$, I_1^2 ¼ 0:982, $n_1 = 6586$; $cut_2 = 0.587 \times 0.718^{-0.053x}$, I_2^2 ¼ 0:660, $n_2 = 2411$; $cut_3 = 1.013 \times 0.718^{-0.102x}$, I_3^2 ¼ 0:914, $n_3 = 1417$; $cut_4 = 0.777 \times 0.718^{-0.112x}$, I_4^2 ¼ 0:950, $n_4 = 1400$), at seven territories in Telemark in 2001. All equations presented are statistically significant at the 0.05 probability level.

Discussion

Species preference and foraging intensity

Beavers showed a strong preference for willows in Telemark, which is consistent with other food-selection studies of the Eurasian beaver in Europe (Erome & Broyer, 1984; Nolet et al., 1994; Schley, 2004). The leaves and bark of willows are the favourite food of beavers, probably because of the short retention time of these easily digestible plants (Fryxell et al., 1994).

Willows, which are the most common species besides alders in the riparian zone, were almost completely utilized in our study area. Therefore, less preferred but more available alders had become the bulk food of beavers. Fryxell & Doucet (1993) found that alders are less digestible and have lower energy content than aspens, and they suggested that beavers consume only a small proportion of alders because of digestive constraints. This could explain why alders were the most frequently but proportionally the least utilized. In North America, beavers use alders primarily for building purposes (Doucet, Adams & Fryxell, 1994; Barnes & Mallik, 1996). However, beavers in our study area do not build dams, and use only a small amount of wood to cover the entrance of their burrows. Furthermore, the food caches are nearly completely utilized year to year, and we frequently witnessed beavers consuming the leaves and bark of grey alder; hence we have to assume that grey alder was principally used as a food source rather than for other purposes in Telemark.

No species were prominently selected with increasing distance from the water, but the proportional utilization of alders was dropped sharply as diameter increased, compared with the preferred species groups. This shows that although alders constituted the bulk food of beavers, it was not profitable to devote longer cutting and provisioning time to utilize these species. In compliance with the central-place foraging theory (Orians & Pearson, 1979; Schoener, 1979), foraging intensity of Eurasian beavers declined with increasing distance from the refuge, which is, in our case, the edge of the river. Similarly, both previous (Jenkins, 1980; Belovsky, 1984; McGinley & Whitham, 1985; Basey et al., 1988; Donkor & Fryxell, 1999; Donkor & Fryxell, 2000) and recent studies (Gallant et al., 2004) showed that North American beavers select fewer trees with increasing distance from the water. It is predicted that beavers, as central-place foragers, would first deplete foraging patches close to the water before exploiting patches further away (Orians & Pearson, 1979; Schoener, 1979). Terrestrial foraging journeys are likely to be costly both energetically and in time, so beavers are expected to choose vegetation items in a manner that maximizes net energy intake by unit of time.

First of all, beavers prefer willows as the first rank, so they are expected to feed in close proximity to water, where riparian willow forests grow. Willows invest a civilian response rather than a defence response early in the regrowing phase, so after the heavy autumn and winter browsing the cut shrubs have a better food quality (more water and nitrogen content) and less phenolics (defence function) in the following spring (A. J. Veraart, B. A. Nolet, F. Rosell & P. P. de Vries, unpubl. data). Apparently, willows invest their carbon in regrowth rather than carbon-based defence (like phenolic glycosides; Veraart et al., unpubl. data), so increased plant secondary compounds are not affecting the beavers' foraging choices when feeding on their most preferred plant genera. This is different from the case of the North American beaver, whose favourite food items, the aspens (Populus spp.), produce increased quantities of secondary metabolites in the juvenile-form sprouts already after a year of occupation by beavers (Basey et al., 1988; Basey, Jenkins & Miller, 1990). Such a strong defensive response to browsing by beavers obviously has a large effect on both foraging patch and food size selection (Gallant et al., 2004).

Several other suggestions have been provided to explain why beavers forage close to water, for example thermal stress (Steen & Steen, 1965), asymmetric growth of riparian forests along the shoreline (Barnes & Mallik, 2001) and vulnerability to predators (Basey & Jenkins, 1995). Moving further away from the water imposes a higher predation risk, which may put an additional limit to the beaver's foraging range in some places. Wolf has been allopatric with the beaver for the last 100 years in our study area but wolves were the most important beaver predator until the end of the 19th century (Rosell, Parker & Kile, 1996; Nolet & Rosell, 1998). Lynx was common in the 19th century but was nearly extinct by 1930 (Anonymous, 1996; Kvam, 1997). However, beavers in our study area probably show an innate response to both lynx and wolf, although response to lynx may have been refined through learning (Rosell & Sanda, 2006).

The significant interaction between two factors affecting the probability of beaver cutting, territories and distance, can be explained by the varying areal extent of each plant community and the different scale of human use between the territories. Plant communities altered by people such as forest

plantations, gardens, meadows or agricultural fields certainly did affect the abundance of forage species in the last three distance categories (10–20, 20–30, 30–40 m), but the proportion of the impacted area was different between the territories. Nevertheless, the total impact of human use in the study area might have contributed to the exponential decrease of foraging intensity with increasing distance from the water.

Size selectivity

For the beaver, there are four important components of food handling time: time required to cut down prey, provisioning time (the time used to drag items back to the central place), time spent consuming the prey and time required for digestion. From the perspective of optimal foraging theory, the animal can travel further and select larger food sizes until travel costs exceed energy gain (Fryxell, 1999). Donkor & Fryxell (1999) found that beavers harvest a wide range of tree sizes close to the central place, whereas at greater distances from the water they show increasing preference for smaller food items. Similarly, Jenkins (1980) found a decreasing preference for larger food items with increasing provisioning distance in habitat dominated by large trees. In our study, the size selectivity of food items showed a slightly different pattern. Although beavers selected predominantly small stems in all distance categories, we found that they more likely selected small saplings close to the river, and the utilization of large stems was maintained as distance increased. This pattern is similar to the findings of McGinley & Whitham (1985), whose study of the North American beaver was also carried out in a habitat with predominantly small saplings (diameter $\leq 5\,cm$), where the size is in the range where provisioning time is independent of branch size. Both optimal foraging models of Schoener (1979) and Orians & Pearson (1979) predict that larger prey items are more likely to be favoured with increasing provisioning distance. Orians & Pearson (1979) suggested that larger energy intake is expected by multiple-prey loading of small prey for short travelling times, whereas single-prey loading of big prey is more profitable for longer travelling times, which can be explained by the greater amount of edible biomass offered by larger trees. The time spent for cutting a tree down and dragging it back to the water increases allometrically with stem diameter; therefore, if provisioning time increases with prey size (i.e. beavers fell large trees), the statement above might be inappropriate (Schoener, 1979).

Conclusion

In conclusion, the results of this study are consistent with the predictions of the central-place foraging theory. Better knowledge of Eurasian beavers' foraging behaviour, in aspects of both species and size selectivity, can help to understand their impact on forest community composition, structure and succession. Nevertheless, as beavers are living in managed forests and farmlands in our study area, their impact has to be considered in the light of the damages they might cause over their role in natural processes.

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