


Foraging decisions of North American beaver (*Castor canadensis*) are shaped by energy constraints and predation risk

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Abstract Foraging herbivores have to trade-off between energy requirements and predator avoidance. We aimed to study the relative roles of these factors in beavers (*Castor canadensis*) when foraging on land. We hypothesized that beavers were able to assess the risk of predation by using two main cues: the distance from the water and the presence or absence of predator odors. First, we studied the food selection of beavers in relation to distance from the water in natural settings. The transects were made at beaver ponds, and the diameter, species, and distance from the shore of intact and beaver-cut trees were recorded. Secondly, we placed rows of aspen sticks (*Populus tremula*) perpendicular to the shore around beaver ponds, and treated each row with a neutral, alien, or wolf odor. We found that aspen, downy birch (*Betula pubescens*), and speckled alder (*Alnus incana*) were the preferred tree species. More of these species were cut close to the shore, and cut trees were smaller further away from the

shore, except in the case of aspen. In the experiment, most of the aspen sticks were taken close to the shore. As predicted, beavers took less aspen sticks in rows treated with wolf odor than water. As the predator odor did not affect the foraging distance from the shore, it is likely that our observation that foraging was the most intense close to shore is due to energetic constraints. However, predation risk probably affects the decision whether to forage on the land in the first place.

Keywords Anti-predator behavior · Food selection · Predator odors · Trade-offs

Introduction

Predation is one of the major factors affecting the fitness of the individuals of a prey species. The effect of predation in terms of fitness usually has two possible outcomes: the prey is killed or it escapes from the predator (Lima 1998; Curio 2012). Natural selection has favored prey with features that enhance the probability of survival in the face of predation, which explains the wide range of anti-predator defenses observed among prey species (Langerhans 2007). One of the most common anti-predator behaviors consists of avoiding places where the prey perceive a high risk of predation. To assess the risk of predation in a given area, prey species can rely on habitat characteristics (Ripple and Beschta 2004; Creel and Christianson 2008). For example, large ungulates which are preyed upon by wolves can reduce the risk of predation by avoiding habitats where wolves usually move, or choosing terrain in which it is difficult for the predators to hunt (Ripple and Beschta 2004; Salandre, own data). Prey that are able to recognize their predators can also assess the risk of predation by using different cues of predator presence. Those species employ activities to see, smell, hear, or

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chemically or electrically detect predators (Apfelbach et al. 2005; Langerhans 2007).

Many of these anti-predator tactics are costly in terms of reduced survival, growth, or reproduction (Lima 1998). For herbivores, the costs of anti-predation behaviors are particularly important in the context of foraging. Reducing the risk of predation often involves a decrease in the foraging rate due to an increased vigilance (Fortin et al. 2004; Kuijper et al. 2014) or the avoidance of more valuable, yet more risky foraging sites (Orrock et al. 2004). Thus, many herbivores have to trade-off between the benefits of anti-predator behaviors (reduced predation risk) and their costs (reduced energy intake, which can translate into reduced long-term survival or reproductive output; Lima 1998; Ripple and Beschta 2004). Numerous field and laboratory studies have shown that the trade-off between energy intake and predation avoidance is common in many taxa and often involves a reduction of foraging in high-risk habitats (Pitcher et al. 1988; Suhonen 1993; Scrimgeour and Culp 1994; Cowlshaw 1997; Thorson et al. 1998). For herbivores that make use of a refuge that the predators cannot access, the distance from the refuge is often seen as a surrogate for predation risk and individuals decrease their foraging with increasing distance from the refuge (Kotler et al. 1991; Basey and Jenkins 1995; Eccard et al. 2008).

Another important factor in shaping foraging decisions is energy constraints. According to optimal foraging theory, foragers should maximize their net rate of energy intake (e.g., Charnov 1976). For central place foragers, the distance from the central place, often a nest or refuge site, is crucial in affecting foraging decisions (Orians and Pearson 1979). When foraging, the animal has to deal with multiple constraints and options and these are not likely to be mutually exclusive, but can interact.

The beaver, *Castor* sp., is a semi-aquatic herbivore that occupies rivers or small lakes where the water is deep enough year round for it to swim and dive and for logs to float. From fall to early spring, when the herbaceous vegetation is not available, beavers feed on the bark and twigs of the trees that they fell (Jenkins 1975; Jenkins 1979; Svendsen 1980; Danilov et al. 2011). Beavers are central place foragers, i.e., they always forage from a same central place, the home pond. On land, beavers cut trees which they usually bring back next to the water, for immediate consumption or storage (Basey and Jenkins 1995; Gallant et al. 2004). Recent models of central place foraging (Olsson et al. 2008) predict that when the food items are larger than the forager, the cost of predation increases when foraging large items at greater distances from the central place. In this context, the foragers are expected to select smaller items at greater distances from the central place. On land, beavers are rather helpless when attacked by a large predator. Thus, they always attempt to escape to the water and are extremely careful when leaving it. The wolf (*Canis lupus*) is often cited as the main predator of beavers (Chavez and

Gese 2005; Collen and Gibson 2000; Baskin 2011; Müller-Schwarze 2011). For example, in Québec, beavers made up to 44% of the wolf diet and wolves took 15% of the beaver population (Potvin et al. 1992). In Europe, other predators of the beaver include brown bear (*Ursus arctos*), lynx (*Lynx lynx*), and wolverine (*Gulo gulo*) (Collen and Gibson 2000).

The aim of this study was to assess the effects of predation risk and energetic constraints on the foraging behavior of beavers. First, we studied the beavers' foraging behavior in a natural setting by investigating the foraging distance from the shoreline of different size categories and species of trees. Our expectation was that beavers cut more trees close to rather than far from the shore, and cut smaller trees at greater distances from the shore. To test whether this was because of predator avoidance or just energetic constraints, or both, we set up an experiment in which we placed aspen sticks (preferred food item) at different distances from the shore in sites treated with control or predator odors. If beavers assess the predation risk based on the presence or absence of a predator odor, we expected that the beavers take more aspen sticks in sites treated with the control odors than in sites with a predator scent. If they take more aspen sticks close to rather than far from the shore, this could be explained by either predator avoidance and/or energetic constraints. However, if they take aspen sticks further from the shore in sites treated with control odors than with predator scent, the foraging distance from the shoreline can be explained by predator avoidance. If this is not observed, the likely cause would be energetic constraints.

Materials and methods

Study area

All data were collected in the Evo area (61° 10' N, 25° 05' E), Kanta-Häme region, Southern Finland. This 85-km² forested area is situated in the southern boreal zone, has a mean annual temperature of +3.1 °C, and an average annual precipitation of 670 mm (Vanha-Majamaa et al. 2007). The vegetation is dominated by coniferous trees, mostly Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). Small stands of deciduous trees including quaking aspen (*Populus tremula*), downy (*Betula pubescens*), and silver birch (*Betula pendula*) are also found in the area, especially in moist sites. The Evo region also houses about a hundred lakes and ponds of different sizes which are interconnected via a network of natural streams and human-made ditches (Hyvönen and Nummi 2008).

A typical beaver habitat at the study area consists of a site that beavers had flooded by constructing dams on the outlets of a small lake or river. To find occupied beaver territories, we inspected most lakes and big rivers in the Evo area, looking for fresh signs of feeding.

Of the main predators of beavers, the lynx is currently common in the area but the brown bear and the wolf are rare and only passing individuals have been observed.

Study species

In the Evo region, as in many other parts of northern Europe, the native European beaver (*Castor fiber*) was hunted to extinction at the end of the nineteenth century. In 1935, two pairs of European beavers were introduced, and in 1955, the region was occupied by 15–18 individuals. In 1957, a pair of North American beavers (*C. canadensis*) were also introduced. This species thrived to such an extent that the Evo population now only consists of North American beavers (Hyvönen and Nummi 2008). Beavers are territorial animals which usually live in family units, consisting of two parental adults, the yearlings born the previous year, and the young of the year (Collen and Gibson 2000). North American beavers usually build lodges, but in the summertime, they can live in burrows in the shore banks (Lahti and Helminen 1974). Beaver families have to move when they have used up the food supply. In highly productive areas, a family of five–six members can stay on average 8 years at the same place (Danilov et al. 2011). Beavers are mostly active at night. An adult consumes about 1 kg of food every day, consisting of green vegetation when available or of the bark of deciduous trees (Aleksiuk 1970; Jenkins 1979; Danilov et al. 2011).

Observational study

Nine beaver ponds in the area had a sufficient number of tree cuts for the observational part of the study. In each of those sites, we established one to four transects, depending on the level of beaver activity around the pond, during July 2015. The transects were chosen for their relatively high number of tree cuts, and their great diversity of tree species and diameters. The transects were perpendicular to the shoreline and were 5-m wide and 20-m long, since most beaver activity was concentrated in the first 15 m from the water. In two transects, beaver cuts were found further than 20 m from the shore, so we extended the two transects until the last cut was included, 1 to 50 m and the other to 80 m from the shore. In the transects (20 in total), we recorded all the living trees and the stumps of trees cut by the beavers, their species, distance from the shore, and diameter at stump height (about 30 cm above ground). We did not record dead trees, trees smaller than 1 cm in diameter and those in very poor condition, mostly browsed by moose (*Alces alces*). Also, very old decayed stumps were not included in the analyses, as it was not possible to determine whether they were beaver-cut trees and often the tree species could also not be identified. However, these were rare in our study areas. In the Evo area, beavers occupy one site an average 3 years and return after ca. 10 years (Hyvönen and

Nummi 2008); therefore, observed cut trees were likely cut by present beaver families, while old omitted stumps might have been cut by beavers previously inhabiting the site.

Experimental study

Pieces of aspen were placed next to the shore in the sites with signs of recent beaver activity. Beavers were actively taking the aspen at six sites in the Evo area: three at lake sites, two at small river sites, and one at a site with a mixture of ditches and flooded lands. At each of these sites, three sets of three rows of aspen sticks (50 cm in length and 5–8 cm in diameter) were prepared around the lake or river (see Fig. 1). Each row of a set was perpendicular to the shore and parallel to the other rows. In a set, the rows were separated by 25 m, and the distance between two sets was at least 50 m. The rows were 30 m in length and were composed of ten aspen sticks placed 3 m apart in a row (the first stick being 3 m from the shore). The sticks were made out of the trunk of small aspen trees from the Evo area, and were kept in boxes filled with water for a few days, until used for the experiment. During the setup, the sticks were randomly assigned in the rows, laid on the ground, and wet *Sphagnum* sp. moss was placed around the base to keep them fresh as long as possible. Each row of a set was then treated randomly with a different odor: water (“no odor” control treatment), vinegar (“novel odor” control treatment), or wolf urine

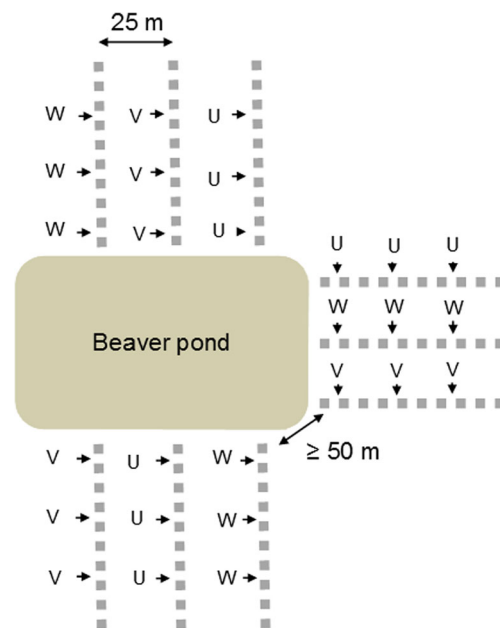


Fig. 1 Diagram of the experimental design of the study. Grey square: aspen stick; V: bottle with vinegar, W: bottle with water; U: bottle with urine. Three sets of three aspen rows (*Populus tremula*) are set up around each beaver pond. Rows are perpendicular to the shore, 30-m long, and composed of ten aspen sticks laying 3 m apart in a row. Two adjacent rows of a set are separated by 25 m, and each set is at least 50 m from the others. Each row of a set is treated with a different odor (water, vinegar, or wolf urine), presented in plastic bottles 5, 14, and 21 m away from the shore

(“predator scent” treatment). We used water directly from the sites, pure white vinegar, and commercial wolf urine (unknown sex and age, Pete Rickard’s, Galetton, PA, USA). To present the scents, we used 100-ml polyethylene bottles pierced with eight small holes made with a 1.5-mm nail, and filled with cotton balls to allow maximal odor diffusion. In each row, three bottles were attached to a tree, ca. 1 m from the ground, about 5, 14, and 22 m from the shore. They were then filled with 8 ml of water, vinegar, or wolf urine and closed with a cap.

For every 2 days during a period of 20 days, the sticks that had been taken by the beavers were recorded, and the moss was watered. The sticks that were taken by the beavers were not replaced. The bottles were not refilled during the experiment, as the vinegar and urine bottles still smelled strongly during the entire 20-day period.

Statistical analyses

Statistical analyses were conducted using R version 3.2.3 (R Development Core Team 2015).

For the observational part of the study, tree species for which less than 15 individual trunks were recorded (<1% of the total number) were excluded from the analyses. To test the

selectivity of beavers towards the different tree species, the method of Neu et al. (1974), further explained by Byers et al. (1984), was used. This procedure employs a χ^2 goodness-of-fit test to determine any significant difference between the expected and the observed utilization of the different tree species and uses Bonferroni confidence intervals to determine which species are preferred. The confidence interval is constructed using the following formula:

$$\bar{p}_i - Z_{\alpha/2k} \sqrt{\frac{\bar{p}_i(1-\bar{p}_i)}{n}} \leq p_i \leq \bar{p}_i + Z_{\alpha/2k} \sqrt{\frac{\bar{p}_i(1-\bar{p}_i)}{n}}$$

where p_i is the true proportion of utilization of the species i , n is the total number of cuts, \bar{p}_i is the number of cuts in the species i divided by n , and $Z_{\alpha/2k}$ is the standard normal table value corresponding to a probability tail area of $\alpha/2k$, k being the number of tree species tested. If the expected value of utilization of a species is below the interval, the species is preferred by the beavers; if it is above the interval, the species is avoided; if it is included in the interval, the species is used in proportion of its availability.

The effect of distance from the water on the proportion of tree cuts and the relationship distance-diameter of tree cuts were analyzed for the preferred species, using linear models.

Table 1 Selectivity index, expected utilization, and confidence interval for true utilization of tree species

Species	Number of trees (cuts included)	Number of cuts	Selectivity index (proportion of trees cut)	Expected utilization	Bonferroni confidence interval for p_i (95% family confidence coefficient)
Quaking aspen, <i>Populus tremula</i> ^a	84	56	0.67	0.054	$0.077 \leq p_i \leq 0.166$
Goat willow, <i>Salix caprea</i>	18	10	0.56	0.011	$0.002 \leq p_i \leq 0.041$
Speckled alder, <i>Alnus incana</i> ^a	102	55	0.54	0.066	$0.076 \leq p_i \leq 0.163$
Downy birch, <i>Betula pubescens</i> ^a	806	305	0.38	0.519	$0.599 \leq p_i \leq 0.727$
Black alder, <i>Alnus glutinosa</i>	17	6	0.35	0.011	$0 \leq p_i \leq 0.028$
Rowan, <i>Sorbus aucuparia</i>	61	13	0.21	0.039	$0.006 \leq p_i \leq 0.051$
Norway spruce, <i>Picea abies</i>	370	15	0.04	0.238	$0.009 \leq p_i \leq 0.057$
Scots pine, <i>Pinus sylvestris</i>	74	0	0	0.048	$0 \leq p_i \leq 0$
Honeysuckle, <i>Lonicera xylosteum</i>	22	0	0	0.014	$0 \leq p_i \leq 0$
Juniper, <i>Juniperus communis</i>	8	0	0	–	–
Silver fir, <i>Abies alba</i>	4	0	0	–	–
Bird cherry, <i>Prunus padus</i>	2	0	0	–	–

The confidence interval for the true utilization p_i informs on the preference of beavers for the species. If the expected value of utilization is below the interval of true utilization, the species is preferred by the beavers; if it is above the interval, the species is avoided; if it is included in the interval, the species is used in proportion of its availability

^a The species is preferred by the beavers

For the analysis, the data collected were divided into ten distance classes. In those models, only data from trees at most 20 m from the shore were used, except for quaking aspen, since it was the only species cut further than 20 m.

For the experimental part of the study, the effect of odor treatment (no odor, novel odor, predator scent) and the distance from the shore, as well as the interaction between these two factors on the binary dependent variable (aspen stick taken or not), were tested using logistic mixed models, with the study site given as a random factor (R package lme4, Bates et al. 2011).

Results

Observational study

A total of 1568 trees, including 460 beaver cuts, were recorded around the beaver ponds. Three of the 12 species recorded were excluded from the analyses, because they represented less than 15 individual trunks. Beavers did not select each species in proportion to its availability ($\chi^2 = 193.89$, $df = 8$, $p < 0.001$). The selectivity index (proportion of trees cut) and the confidence interval for the true utilization of each species are given in Table 1.

The expected values of utilization of quaking aspen, downy birch, and speckled alder (*Alnus incana*) were below the confidence interval of true utilization, which indicates that those species were highly selected by the beavers. Among those species, aspen seemed to be the most preferred one, as indicated by the highest selectivity index. In contrast, Norway spruce, Scots pine, and honeysuckle (*Lonicera xylosteum*) were determined to be avoided, with an expected value of utilization above the confidence interval. Despite a high selectivity index, goat willow (*Salix caprea*) was too rare in the transects to be considered as a preferred species. Thus, goat willow, as well as black alder (*Alnus glutinosa*) and rowan (*Sorbus aucuparia*), was considered to be used in proportion to its availability.

In the studied transects, the last tree cut of birch and speckled alder were found respectively 19 m and 14 m from the shore. Aspen was the only tree species cut further than 20 m from the water, with some cuts found as far as 80 m from the closest shoreline.

For the analysis of the effect of distance from the water on the proportion of cut trees within the preferred species, the data collected were divided into ten distance classes. For the preferred species, the proportion of trees cut by the beavers decreased with increasing distance from the water (Fig. 2, $t = -13.46$, $df = 8$, $p < 0.001$, $R^2 = 0.95$).

The diameter of birches, cut and uncut, recorded in the transects decreased with increasing distance from the shore ($t = -2.854$, $df = 772$, $p = 0.004$, $R^2 = 0.01$). The same effect of distance on diameter was observed for birches cut by the

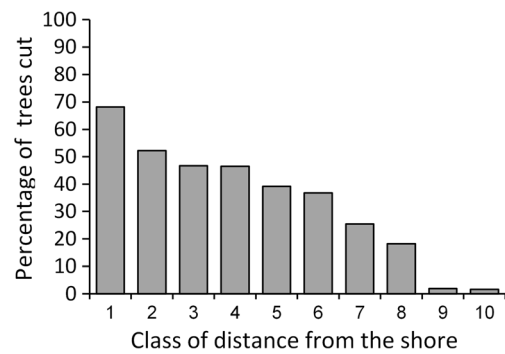


Fig. 2 Percentage of trees cut by the beavers (*Castor canadensis*) in relation to the class of distance from the water. Class 1: 0 to 2 m from the shore, class 2: 2.1 to 4 m from the shore, class 3: 4.1 to 6 m from the shore, etc. until 20 m. Only the preferred tree species were included, $n = 375$

beavers ($t = -6.362$, $df = 303$, $p < 0.001$, $R^2 = 0.12$, but a comparison of the slopes coefficients demonstrated that the decline was much steeper than for all birches taken together (Fig. 3, slope coefficients: -0.404 for cuts, -0.095 for all birches; $t = -3.874$, $df = 1075$, $p < 0.001$). For all speckled alders taken together, the diameter of the trees did not vary significantly with the distance from the shore ($t = -1.655$, $df = 100$, $p = 0.101$, $R^2 = 0.03$). On the other hand, the

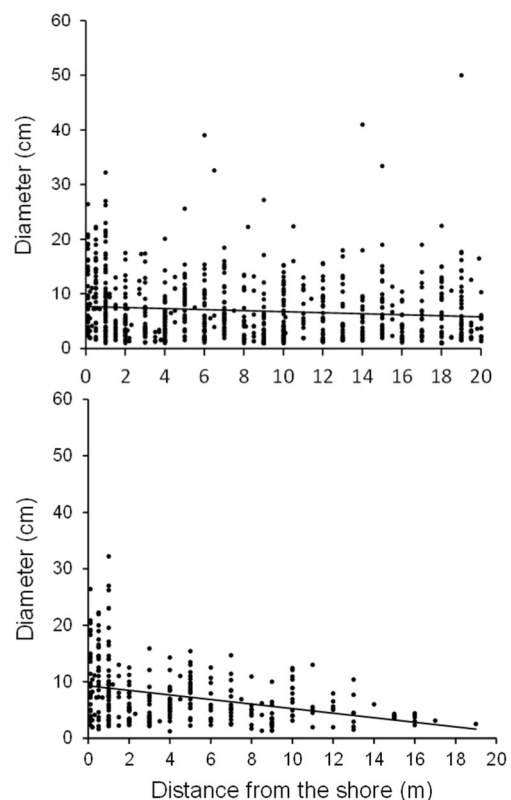


Fig. 3 Diameter of all birches (upper panel) recorded and birches cut (lower panel) by the beavers in relation to distance from the water, recorded in 20 transects around nine beaver ponds in Evo, Finland. Black lines: regression lines (upper panel: $R^2 = 0.01$; lower panel: $R^2 = 0.12$)

diameter of the speckled alders that were cut by the beavers was decreasing with increasing distance from the water (Fig. 4, $t = -2.865$, $df = 53$, $p = 0.006$, $R^2 = 0.13$). The diameter of aspens did not vary with distance from the shore, neither with cut and uncut trees taken together ($t = 1.429$, $df = 82$, $p = 0.157$, $R^2 = 0.024$) nor with cuts only ($t = 0.621$, $df = 54$, $p = 0.537$, $R^2 = 0.007$).

Experimental study

Owing to personal communications and to our own observations, we estimated the total number of beavers in the six study sites between 20 and 25 individuals. During the 20 days of the experiment, 47 aspen sticks (8.7%) were taken by the beavers. Three of the six studied sites accounted for 87% of the taken sticks, the other three sites having each only two sticks taken. Every site had at least one stick taken in a water-treated row, and five sites had at least one stick gone in a row with the vinegar treatment. However, the trend was opposite in urine-treated rows where a single site (Majajoki) accounted for all the sticks taken. The maximum distance from the shore where the beavers took a stick was 18 m.

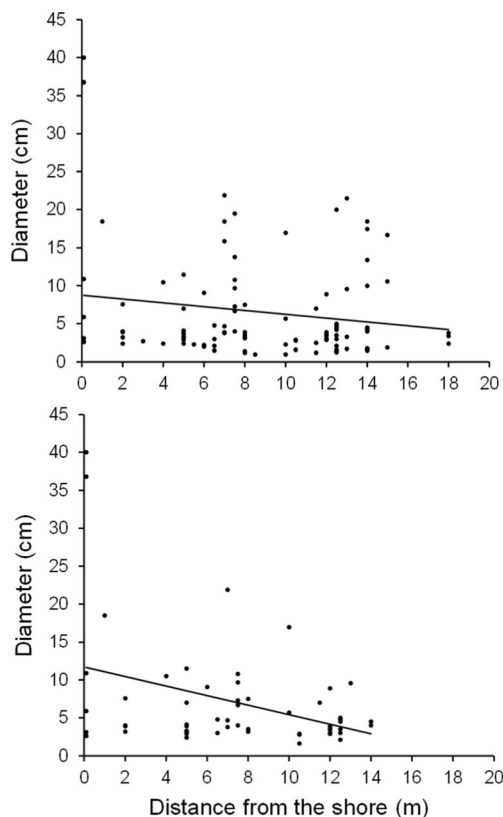


Fig. 4 Diameter of all speckled alders (*upper panel*) recorded and speckled alders cut (*lower panel*) by the beavers in relation to distance from the water, recorded in 20 transects at nine beaver ponds in Evo, Finland. Black lines: regression lines (*upper panel*: $R^2 = 0.03$; *lower panel*: $R^2 = 0.13$)

The scent treatment (Fig. 5, $\chi^2 = 7.318$, $df = 2$, $p = 0.026$) and the distance from the shore (Fig. 6, $\chi^2 = 40.801$, $df = 1$, $p < 0.001$) had a significant effect on the binary dependent variable (stick taken/not taken by the beavers). There was no significant interaction between treatment and distance ($\chi^2 = 2.268$, $df = 2$, $p = 0.322$), so the effects of the two variables were analyzed separately post hoc.

A stick located in a row treated with water had a higher probability to be taken by the beavers than a stick in a urine-treated row (two-sample z test, $z = 2.218$, $p = 0.027$). There was marginally non-significant difference between the water and the vinegar treatments ($z = 1.819$, $p = 0.069$), and no significant difference between the vinegar and the urine treatments ($z = 0.438$, $p = 0.661$).

The proportion of sticks taken by the beavers decreased sharply with increasing distance from the shore (Fig. 6, $z = -6.623$, $p < 0.001$, $R^2 = 0.92$). To help visualize behavioral preferences of beavers to forage closer or further from the shore, the sequential order of sticks taken was graphed (Fig. 7). Most sticks in the rows were taken in sequential order, i.e., a stick in a given row that was closer to the shore taken before a stick further from the shore.

Discussion

We found that beavers are selective in their choice of trees, so that certain species were clearly favored, namely quaking aspen, speckled alder, and downy birch. Most of these preferred tree species were also cut close to the shoreline, and size of the cut trees appeared to be smaller further away from the shore.

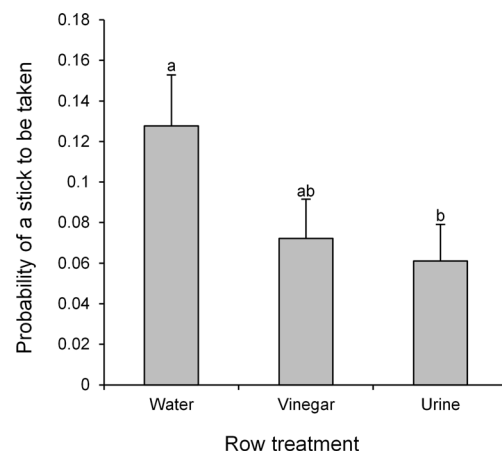


Fig. 5 Effect of scent treatment on the probability of an aspen stick (*Populus tremula*) being taken by beavers (*Castor canadensis*) at six different ponds in Evo, Finland. Bars represent the probability of a stick being taken from rows of sticks extending perpendicular to the shoreline that had three different scent treatments: water, vinegar, and wolf urine. Error bars indicate uncertainty of the probability to one standard error. No common letter between the two treatments indicates a significant difference

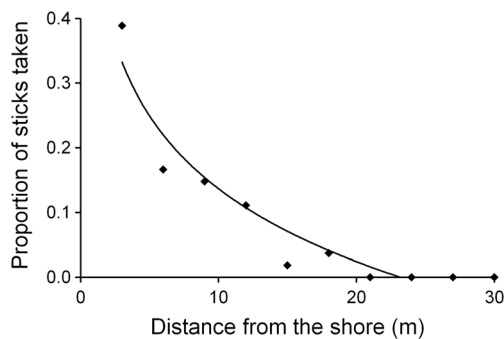


Fig. 6 Effect of distance from the shore on the proportion of aspen sticks (*Populus tremula*) taken by beavers (*Castor canadensis*) at six different ponds in Evo, Finland. Dots represent the proportion of sticks taken at each distance from the shore in 30-m rows perpendicular to the shore, in which each stick was 3 m further away from the water than the previous one

This observation was the most obvious for the speckled alder and non-existing for the most preferred species, the quaking aspen. The aspen was also the tree species which were cut by beavers at the longest distance from the shoreline. In line with these observations, we found that of the experimentally placed aspen sticks, most were taken close to shoreline. Results of our experiment also show that beavers used odors when assessing the predation risk as they took less aspen sticks in sites treated with wolf odor than those without odor (water treatment). However, beavers seem to be wary in foraging also in locations where the novel control smell (vinegar) was applied as the proportion of taken aspen sticks was intermediate in those sites.

We failed to demonstrate that the distance from the refuge, the shoreline of the pond, per se, is used by the beavers when assessing the predation risk while foraging on land. Even though beavers foraged closer to the shore in general, the applied predation odor did not affect the distance from shore that sticks were taken and therefore it seems that energetics play a larger role than predation risk in foraging decisions on land. This conclusion was also partly supported by the

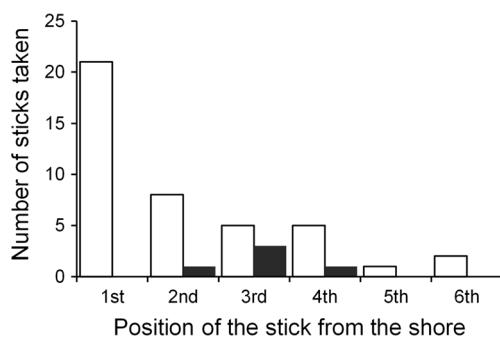


Fig. 7 Order in which the aspen sticks (*Populus tremula*) were taken by the beavers (*Castor canadensis*). White bars represent sticks that were taken in a sequential order from the closest to furthest from the shore. Black bars represent sticks that were taken out of a sequential order (e.g., a stick in a given row that was closer to the shore was taken after a stick further from the shore). Two adjacent sticks taken the same night were considered to be taken in a sequential order

observation that the most preferred and probably the most rewarding food tree species, the aspen, were taken further away from shore than other tree species and that their size was not related to distance as was observed in some less preferred species.

Beavers' food preferences

All coniferous species were rigorously avoided by beavers, with only a few cuts of Norway spruce recorded. This avoidance of coniferous trees is a common result in studies focusing on the food selection of beavers (e.g., Northcott 1971; Busher 1996; Gallant et al. 2004). From the species positively selected by the beavers, quaking aspen was the most preferred one. Aspen is frequently cited as the beavers' most preferred woody species (e.g., Lahti and Helminen 1974; Beier and Barrett 1987; Gorshkov and Gorshkov 2011). The relative food value of tree species depends on their palatability, nutritional value, and digestibility. Aspen has relatively high energy content compared to other woody species (Doucet and Fryxell 1993). For example, the consumption of 1 kg of aspen bark results in the production of three times as many calories as birch (Danilov et al. 2011). Fryxell et al. (1994) also showed that aspen was particularly valuable because of its short retention time, which is almost three times shorter than that of speckled alder. The digestion is thus faster, and this allows a higher rate of food intake. After aspen, willow is also cited as a preferred species (Erome 1983; Danilov et al. 2011; Gorshkov and Gorshkov 2011; Müller-Schwarze 2011). In this study, goat willow had a high selectivity index, but was too sparsely represented to be detected as a preferred food source. When aspens and willows are rare, beavers make great use of other species like birch and alder (Lahti and Helminen 1974; Johnston and Naiman 1990; Collen and Gibson 2000; Danilov et al. 2011), which is consistent with the results of this study.

Foraging activity and distance from the water

In this study, we found that the proportion of trees cut by the beavers decreased with increasing distance from the shore. This observation is consistent with the results of the experimental part of the study. Indeed, the aspen sticks were less likely to be taken by the beavers when moving further away from the pond. This decrease in foraging activity with increasing distance from the water has been observed in many beaver settlements. Baskin (2011) found that in southern Russian taiga, 99% of the beaver cuts were situated not further than 20 m from the shore and that 90% were situated less than 13 m from the shore. Erome (1983) showed that in the Rhône region of France, most beaver cuts were located in the first 4 m from the rivers. Hall (1960) in California, Jenkins (1980) in Massachusetts, Belovsky (1984) in Michigan, Gallant et al.

(2004) in New Brunswick, Haarberg and Rosell (2006) in Norway, and Raffel et al. (2009) in Ohio also found that in their study area, more trees (mostly aspen, willow, birch, alder, maple, and oak) were cut by the beavers next to the shore than further away.

The decrease of foraging activity with increasing distance from the shore could be explained by energetic considerations. Indeed, models of optimal foraging (Orians and Pearson 1979; Schoener 1979) state that foragers should maximize their net rate of energy intake. Movements on land are likely to be costly for the beavers in terms of energy and time loss. Thus, they are expected to forage close to the pond to minimize those costs. As their foraging activity depletes the food source next to the water, beavers have to move further inland to find new trees of good quality. As a result, there is a decreasing “gradient” in the proportion of cut trees with increasing distance from the shore. Most sticks were taken in the “right” order (stick closest to the shore taken first, following stick taken second, etc.), which means that the beavers took the sticks next to the shore before going further inland as the food source depleted. Thus, energy maximization by the beavers could explain the decrease in the proportion of trees cut with increasing distance from the water.

Beavers are central place foragers (Basey and Jenkins 1995) which move from a central place, the pond, to collect food that is usually transported back to the pond for consumption or storage. Classic models of central place foraging (Orians and Pearson 1979; Schoener 1979) predict a selection towards larger food items at greater distances from the central place, as the net benefit of a given item size decreases with the distance that the forager has to travel. Some authors studying the foraging behavior of beavers found results consistent with this theory (McGinley and Whitham 1985; Fryxell and Doucet 1991; Gallant et al. 2004; Haarberg and Rosell 2006). However, those studies mostly focused on small trees or branches. In the present study, a negative relationship between diameter and distance from the water was found for the birches and speckled alders cut by the beavers. Other authors, considering a large range of sizes of tree cuts, found similar results, with a decrease in the diameter of cut trees with increasing distance from the shore (Jenkins 1980; Pinkowski 1983; Belovsky 1984). Recent models of foraging (Olsson et al. 2008) include in their calculations the costs of transporting the food back to the central place. If those costs increase with increasing load size, foragers should be expected to select smaller items when foraging far from the central place. For the beavers, cutting trees with a large diameter far from the pond can have high costs in terms of time and energy expenditure. Indeed, large trees need to be cut into pieces and several trips are necessary to bring back all the pieces to the pond (Jenkins 1980). Furthermore, carrying pieces of large trees on land probably takes more time and is more energy consuming than carrying the pieces of smaller trees. When considering a wide range of tree diameters, cutting large trees far from the shore

should therefore be less advantageous than cutting smaller ones, and this could explain why the beavers seem to select smaller trees when far from the water.

No relationship between distance and diameter was found for aspen in this study. Baskin (2011) also found no difference in the width of cut aspens at different distances from shore. Perhaps aspen is so valuable in terms of energy intake that the benefits of cutting aspens exceed the costs, including predation risk, even for large trees far from the shore.

Another hypothesis, which is not mutually exclusive to energetic hypothesis, is that beavers forage close to the pond in order to minimize the risk of predation.

Effect of a predator scent on beavers' foraging behavior

During the 20 days of the experiment, less aspen sticks were taken in the rows treated with wolf urine than in the water control rows. In five of the six studied sites, not a single stick was taken in a urine-treated row. Thus, except at the Majajoki site, beavers seemed to totally stop foraging in sites where the predator odor was present. At the Majajoki site, we were not able to determine if only one beaver took the sticks in the urine-treated rows or if it was the work of the whole family. The only apparent response to the predator scent was that they brought the sticks of urine-treated rows on the other side of the river to eat the bark while the sticks of water- and vinegar-treated rows were consumed on the same side where they were taken. Why beavers in this colony foraged intensively in the rows with the predator odor was difficult to explain, since the urine-treated rows did not seem easier to access than the others. One hypothesis may come from the landscape characteristics of the Majajoki site. The part of the river where the experiment was performed is bordered by a wide forest road 50 m from the river on one side and by a clear-cut 40 m from the river on the other side. Thus, unlike at the other sites, Majajoki was surrounded by very narrow strips of forest. This characteristic may have made the beavers feel safer, since an approaching predator would have to cross an open space where it would be easily detected. Another hypothesis is that the difference between the Majajoki and the other sites may simply arise from personality differences in the fear response of beavers, like it has been shown in other rodents, with some individuals more willing to take risks than others (Kabbaj et al. 2000).

Beavers possess an acute sense of smell (Müller-Schwarze and Sun 2003), which they use especially for their territorial behavior (Sun and Müller-Schwarze 1998) and to choose their food (Doucet et al. 1994). The results of the present study suggest that beavers may use their sense of smell to assess the risk of predation when going on land to forage. Previous studies have shown that predator scents were reducing the beavers' scent marking activity (Rosell and Sanda 2006) and their use of foraging trails (Severud et al. 2011). Engelhart and Müller-Schwarze (1995) with *C. canadensis*, and Rosell and Czech (2000) with *C. fiber*, found that beavers fed more on

control aspen sticks than on sticks treated with predator scents. Other species of rodents have already been shown to adjust their foraging behavior when predator odors were present (Sullivan et al. 1988a; Sullivan et al. 1988b; Herman and Valone 2000; Rosell 2001).

The fact that beavers also decreased their foraging in vinegar-treated rows, and that we found no strong statistical difference between the effect of wolf urine and the effect of vinegar, comes to mitigate our conclusions. Three main hypotheses can be advanced to explain these results. First, it is possible that the beavers do react strongest to wolf urine, but that we did not have enough replicates to see a significant difference between all treatments; the difference between vinegar and wolf urine was only marginally non-significant and there was a clear trend between high consumption of water-treated sticks and low consumption of wolf urine-treated sticks, vinegar-treated sticks being intermediate. Second, it may be that the vinegar smell was so strong that it would mask all other odors, including scents of potential predators. In that case, beavers would be less likely to forage in the vinegar-treated rows because they could not use their sense of smell to assess the risk of predation. This also could explain marginally non-significant statistical difference between vinegar and urine treatments. Finally, beavers may perceive any novel odor as potentially threatening, which would explain the decrease of foraging in both urine- and vinegar-treated rows, compared to water-treated ones. In that case, beavers could react to the wolf urine only because it is a new scent and not necessarily because it indicates the presence of a predator. In this part of Finland, wolves were extirpated in the late nineteenth century prior to the introduction of *C. canadensis* to the Evo area in 1957. Wolves have remained very rare in the region during the past five decades with just occasional visitors. Thus, it is likely that most beavers in Evo do not have any experience with wolves. The innate response of prey to predator odors has been demonstrated in rodents which have been reared in captivity for many generations, and thus, never had any contact with predators (Fendt 2006; also see Apfelbach et al. 2005 for a review). Also, Chamaillé-Jammes et al. (2013) showed that wolf urine elicited anti-predator responses in the black-tailed deer, even though the top predator has been absent in their study area for a hundred years. It is hard to determine how long a trait will be maintained under “relaxed selection.” In any case, we cannot rule out that the originally innate response of Evo beavers to the wolf odor cues may have been weakened during apparent absence wolves. This may explain that no clear difference between the wolf and the novel control odor was detected.

Predation risk and energetic constraints modify beaver foraging behavior

A number of studies have shown that prey species perceive an increase in the risk of predation with increasing distance from a refuge (Holmes 1984; Lima et al. 1985; Newman and

Caraco 1987; Cooper 2000; Eccard et al. 2008). In their review of risk assessment in prey species, Stankowich and Blumstein (2005) showed that the perceived risk of predation increased by 43% on average when prey were far from rather than near a refuge. Water acts as a refuge for beavers (Baskin 2011; Müller-Schwarze 2011), because their main predators are terrestrial mammals which cannot follow them in deep water. Beavers should perceive a rising predation risk when they move further away from the pond, as the probability that they escape a predator when attacked depends mainly on the distance they have to travel to get back to the safety of water. Thus, beavers are expected to forage close to the shore, to lower the risk of predation. Smith et al. (1994) studied the foraging behavior of beavers on islands differing in the level of the black bears' predation on beavers, and found that on the island where the level of predation was more important, beavers foraged closer to the shore. Thus, predator avoidance could also explain the pattern of decreasing foraging activity with increasing distance from the water.

The hypothesis that beavers use the presence or absence of a predator scent *and* the distance from shore to assess the risk of predation leads to the prediction that beavers should take sticks closer to the shore in the urine-treated rows than in control rows. However, no interaction was found between the effect of odor treatment and the effect of distance. This can be explained by the fact that no stick was taken in the urine-treated rows, except at the site (Majajoki) where the beavers did not react to the predator scent. Thus, the conclusion about the interaction comes from only one beaver family, which may not be representative of the general population of beavers in the study area. Given that we found no interaction between the effect of odor treatment and the effect of distance, we were not able to demonstrate that predation risk had an effect on the foraging distance from the shore in beavers. Instead, the first hypothesis on energetic considerations in determining the beavers' foraging decisions related to the distance from the shoreline is a more likely explanation for the observed patterns. On the other hand, we noticed that not a single aspen stick was consumed on the spot but that they were brought next to the water. They were then stripped of their bark and left on the ground, but were not used as building materials in lodges or dams. Given that carrying the sticks all the way to the pond is energy and time consuming, and has no apparent benefit other than reducing the time spent far from the water, this observation suggests that beavers feel safer next to the pond. Although in this study we were not able to prove that predation risk is related to foraging distance from the shore, it is likely that it plays a role in foraging decisions, to go on the land or not, but when on the land, the energetic constraints are the most important factor in decision-making.

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