MOOSE FEEDING IN RELATION TO POSITION OF FOOD PLANTS

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ABSTRACT: Moose foraging on woody plants in winter was experimentally studied with respect to spatial browsing patterns. Within stands of low palatability trees located along the edges were browsed to a higher extent than trees in other positions. In stands of higher palatability no such pattern was found. The results are discussed with reference to optimal foraging theory.

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The position of food plants relative to others in a habitat can affect the foraging behaviour of herbivores. For example, it has been demonstrated that trees located along the edges are more utilized than trees from the interior parts of a stand (Drolet 1978; Hamilton *et al.* 1980). Such patterns can arise for various reasons, e.g. it may be advantageous for herbivores to forage close to cover as to avoid predation and physiologically stressfull environments (Moen 1973; Hamilton *et al.* 1980). However, intense utilization of food items located along edges may also be a consequence of how herbivores perceive food, i.e. how foraging decisions are taken. In this study we tested how foraging behaviour of moose was related to the position of food plants within small and isolated artificial habitats (stands). More specifically, we focused on the following two questions: 1) Are edge trees browsed more intensively than trees in other positions?, and 2) is the spatial browsing pattern by moose influenced by plant species composition in the stand?

MATERIAL AND METHODS

Study Area

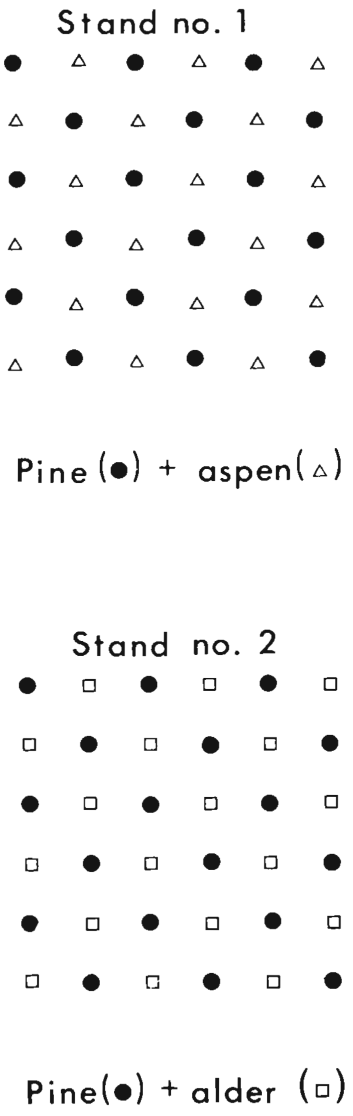
The experimental area was located in coastal northern Sweden, about 30 km SW of Umeå (63°39'N, 19°49'E). The area was dominated by mixed coniferous forests, with Norway spruce (*Picea abies*) on moist sites and Scots pine (*Pinus sylvestris*) on drier hills. Other important habitats included small open mires and farmlands. During winter the moose density is about 0.8 animals per km^2. The snow cover during winter (November-April) normally exceeds 30 cm.

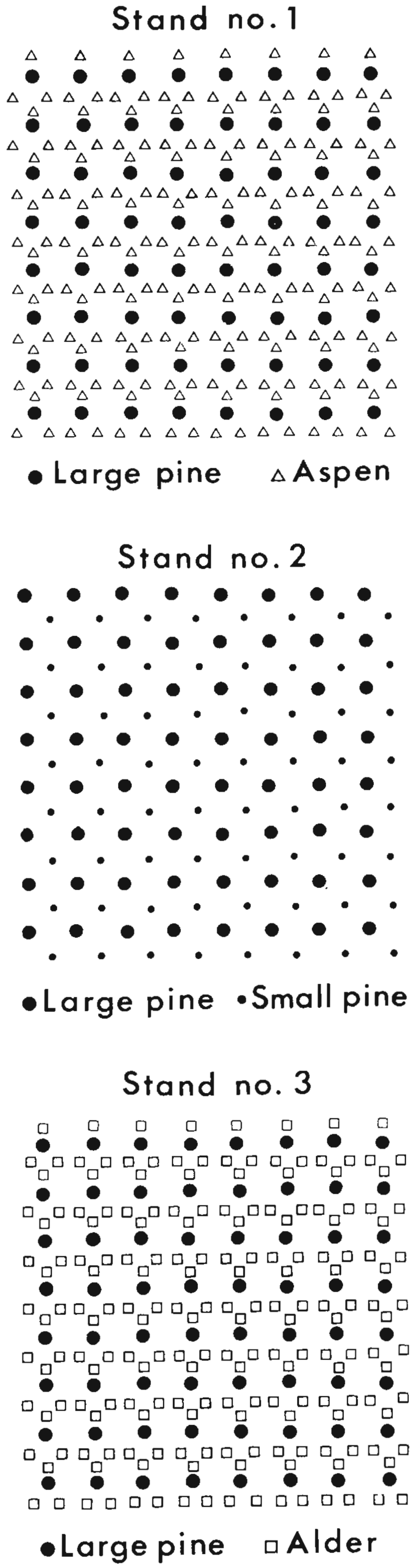
Experimental Design

Two experiments were performed, the first (experiment A) in winter 1986/87 and the second (exp. B) in winter 1988/89. In both experiments artificial stands were created by "planting" trees in the ground. Dormant and unbrowsed trees were cut and transported to the area where they were frozen solid to the ground in holes. Aspen (*Populus tremula*), Scots pine and grey alder (*Alnus incana*) were used. They represent a wide range of palatibilities to moose in Fennoscandia, with aspen being most preferred and alder least preferred (see e.g. Bergström and Hjeljord 1987 for review). Tree characters are given in Table 1.

Two types of stands were created: A highly attractive Scots pine + aspen mixture and a less palatable Scots pine + grey alder association. In exp. B a pure Scots pine stand was also used, representing an intermediate level of palatability (Figs. 1, 2). Stands were separated by 10-25 m, and the closest distance to a forest border was 10 m. Experimental setups were replicated 10 times. The mean distance between replicates was 0.6 km and 4.4 km in exp. A and B respectively.

Trees located in the outermost row and column were categorized as "edge trees", and trees in all other positions as "central" trees. Once all stand types had been browsed, but before the most preferred species (*aspen*) had been totally depleted, a survey was made. All





Figs. 1, 2. Design of experiments testing the effect of food plant position on moose foraging behaviour. Scots pine, a species moderately preferred by moose, occurred in all stand types. In exp. A (winter 1986/87; Fig. 1) every other tree was an aspen or alder (18 of each species placed 1 m apart). Aspen is highly preferred by moose, whereas grey alder is of low preference. In exp. B (winter 1988/89; Fig. 2), 64 pines were placed in a quadrat, 2 m apart. Aspen or alder were placed in between the pines in the relation 3:1. In a third stand type, one small pine was placed in between the larger pines. Stem numbers were adjusted to minimize between-stand differences in available twig biomass.

Table 1. Morphological characters and age of trees used for testing the effect of food plant position on moose foraging behaviour. Mean values and SE are given.

	Height (cm)	Stem diameter (mm)	Age (year)	N
Exp. A:				
Pine	256±3	46±1	14±0.8	50
Aspen	275±4	25±1	7±0.2	50
Alder	271±3	29±1	6±0.1	50
Exp. B:				
Large pine	273±3	38±1	17±0.3	40
Small pine	198±4	32±1	17±0.4	40
Aspen	286±4	24±1	10±0.3	40
Alder	283±3	23±0	4±0.1	40

twigs bitten by moose were counted, and the diameter at the browsing point was measured to nearest mm with a caliper. Twig biomass removed distal to the browsing point was estimated by establishing the relationship between twig diameter and weight (Table 2).

RESULTS

In exp. A all replicates were browsed by moose and nine out of ten in exp. B. Total number of trees browsed was 492 and 875 in each experiment. Within all stand types twig biomass consumption on Scots pine was, on average, higher on edge trees than on central trees. Similary, alders located at the edge were browsed more intensively than alders in other positions. By contrast, the use of aspen was not related to the spatial distribution (Fig. 3). Significant differences in browsing intensity between tree categories were only found within the pine + alder stands (Fig. 3).

When comparing categories in terms of the number of twigs bitten per tree a similar pattern was found. Thus more twigs were taken on edge trees than on other trees for Scots pine and grey alder, whereas no such pattern was apparent for aspen (Fig. 4).

Still, the only significant difference was

Table 2. Relationship between twig diameter (mm) and weight (g dry mass) for trees used in the experiments. The regressions had the form $\log_e(\text{weight}) = a + b\log_e(\text{diameter})$. Data were obtained by clipping twigs in mm-classes (N=40 in each class). Twigs were weighed after drying to constant mass at 70°.

	a	b	R^2	F^*
Exp. A:				
Pine	-2.21	2.55	0.94	5262
Aspen	-3.81	3.08	0.95	6672
Alder	-4.29	3.33	0.96	6240
Exp. B:				
Large pine	-2.27	2.59	0.93	4169
Small pine	-2.23	2.53	0.92	3379
Aspen	-4.21	3.26	0.96	9654
Alder	-4.11	3.30	0.94	4122

* P<0.001 in all cases

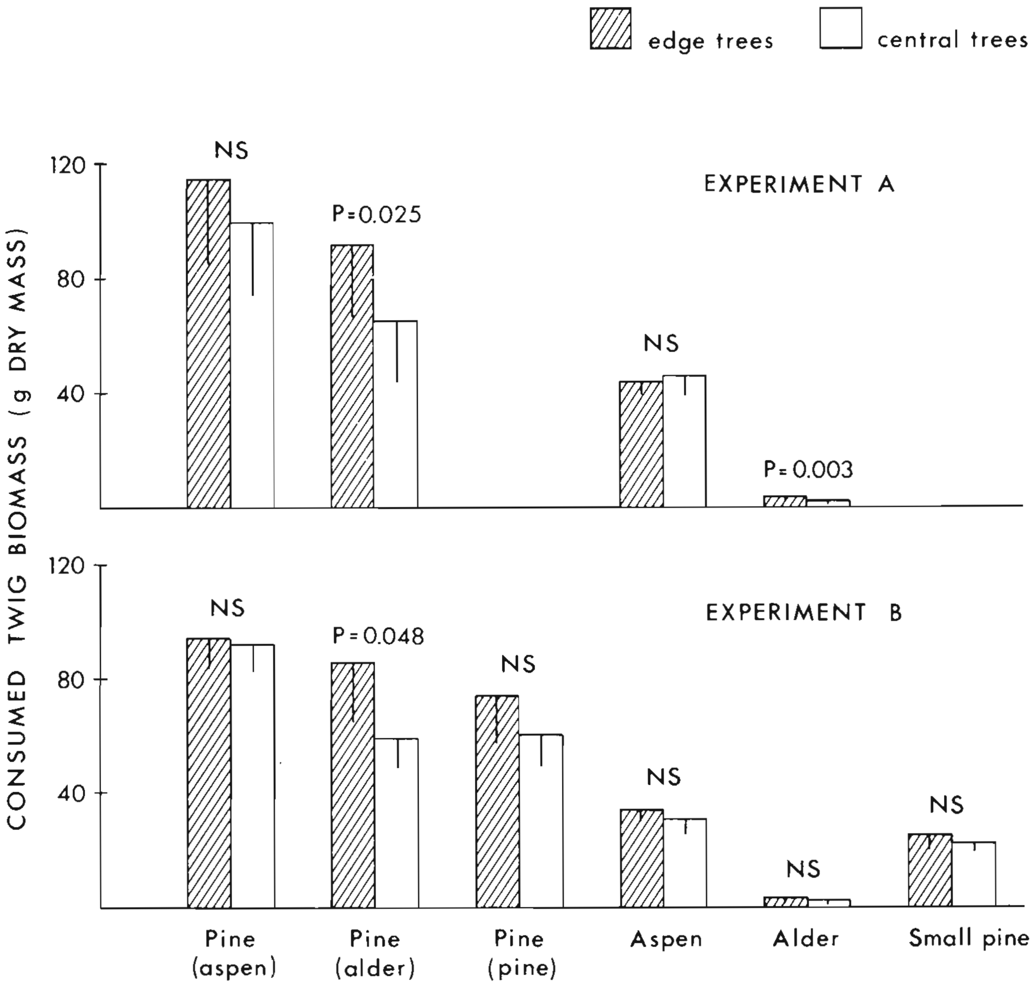


Fig. 3. Consumption of twigs per tree (g dry mass) by moose on "edge" and "central" trees in different stand types. Edge trees (hatched bars) were located in the outermost row or column in each stand type, whereas "central" (open bars) refers to all other positions. Differences were considered significant for P<0.05 (paired t-tests). N=10 and 9 in exp. A and B, respectively.

for Scots pine in the pine + alder association in exp. A (Fig. 4). There was no clear relationship between bite size and tree position in either experiment (Fig. 5).

DISCUSSION

The physical distribution of food plants per se apparently can affect moose foraging behaviour on a small scale basis. Available twig biomass per unit stand area was lower at the edge compared to the interior parts as the trees were evenly distributed within stands. Hence one might expect that moose should have spent less time on edge trees, since more profitable foraging conditions were to be found within the stand. No such browsing pattern was however found. This may be explained such that moose had to pass edge trees to get into the stand.

The preference for edge trees was negatively associated to the preference for stand types (Fig. 6), that is, the spatial browsing pattern was related to the quality of the stands. Optimal foraging theory (e.g. Stephens and Krebs 1986) might provide an explanation for this relation. As within patch residence time would be long in the good quality patches (pine + aspen) and comparably short in the poor quality ones (pine + alder), large differences in twig biomass consumption between stands would be expected. Such a relationship was indeed found: in exp. B for example, pine + aspen stands were harvested to a magnitude two times that of pine + alder stands (Danell, Edenius and Lundberg 1991). If moose assess quality of patches (stands) by "testing" the outermost trees, the good quality of pine +aspen stands discovered thereby would result in an intense exploitation of the trees occurring in the stand. Contradictory, the assessment of the low quality of pine + alder stands would result in shorter residence time and thereby a less intense use of trees. Test of these ideas by direct observation of foraging animals could provide new insight in the food selection process of moose.

Although the results presented here were obtained under manipulated conditions they indicate that the problem of edge-preference may be a many-sided phenomenon. A preference for edge trees under natural conditions could be due to "edge effects" on their intrin-

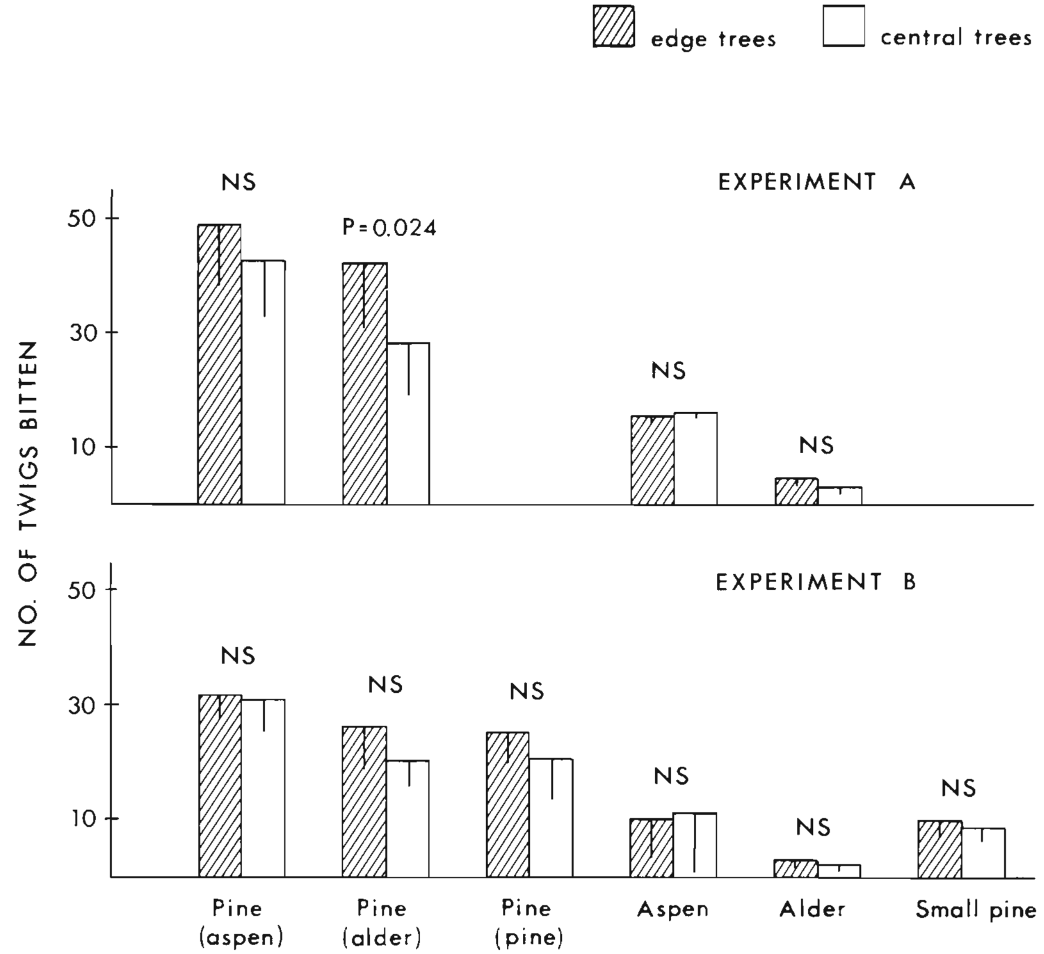


Fig. 4. Number of twigs bitten per tree by moose on edge trees (hatched bars) and central trees (open bars) in different stand types. N=10 and 9 in exp. A and B, respectively.

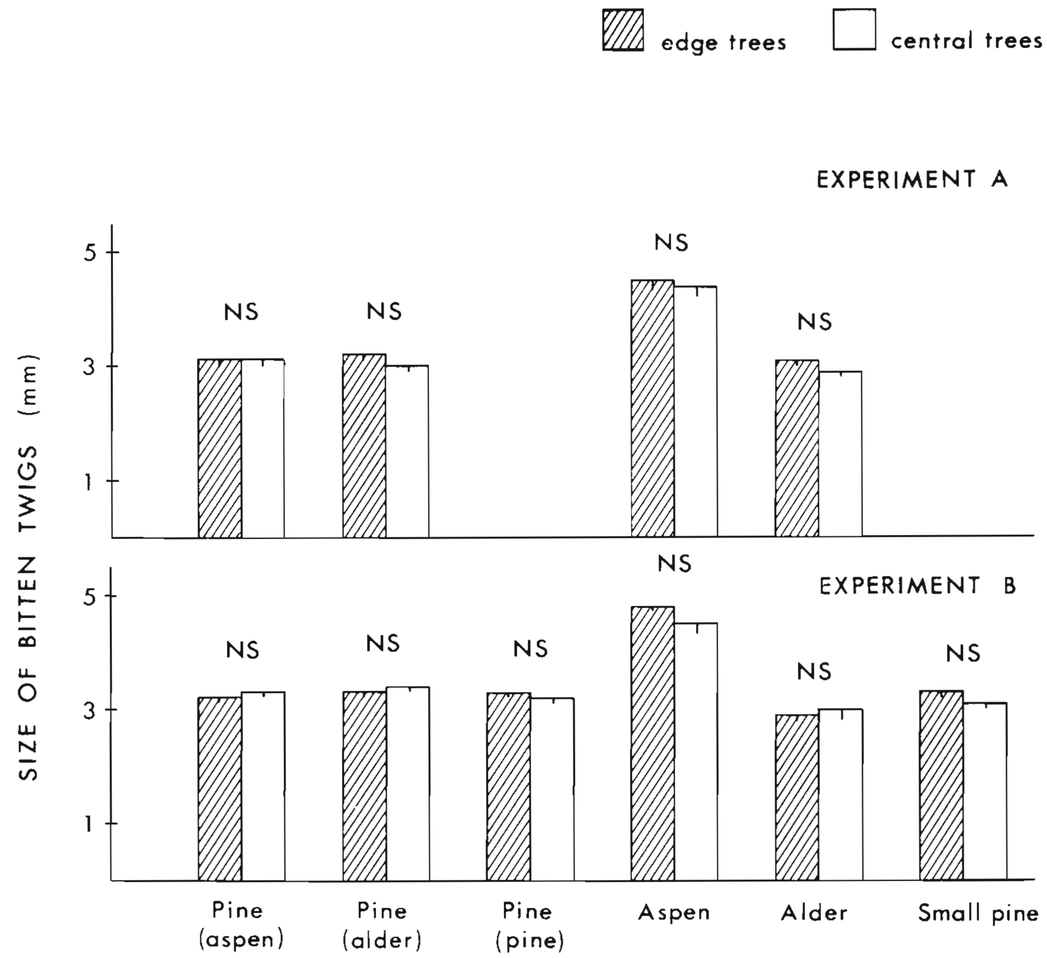


Fig. 5. Diameter of twigs (mm) bitten by moose on edge trees (hatched bars) and central trees (open bars) in different stand types. N=10 and 9 in exp. A and B, respectively.

sic properties; released intraspecific competition could modify palatability through nutrient and growth enhancement (Danell *et al.* 1985; Niemelå and Danell 1988; Thompson et al. 1989). I therefore suggest that preferences for edge trees by moose under natural conditions may be related both to specific qualities of the outermost trees and to the overall quality of the stand (species composition).

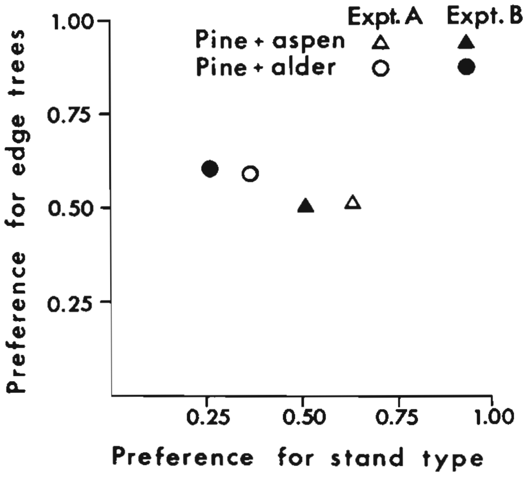


Fig. 6. Preference for edge trees as a function of preference for stand type (pine + aspen and pine + alder associations). A preference value above 0.5 denotes preference for, equal to 0.5 feeding proportionally to availability, and below 0.5: avoidance.

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