INTERACTIONS BETWEEN A GENERALIST HERBIVORE, THE MOOSE, AND ITS WINTER FOOD RESOURCES: A STUDY OF BEHAVIOURAL VARIATION

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ABSTRACT: Based on studies of radio-collared female moose (*Alces alces*) in three different winter areas in Norway, this paper describes variations in resource utilization and diet selection, and how these variations are associated with range use and activity. Moose on good winter ranges allocated more time to foraging activities and used larger areas in search for browse than moose on poor ranges. Although geographic and individual variation in foraging behaviour are caused by variation in forage quality, quantity and accessibility, a large proportion of the individual variations within a single area was explained by differences in body weight, probably related to variation in competitive ability. Thus, heavier animals have access to browse of higher quality than lighter animals, which reduces the time needed for rumination. A multidimensional concept to explain the relationship between intake, quality and quantity of browse is suggested.

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One major concern of wildlife biologists and managers is to predict the population responses to variation in food resources. As a part of this relationship, we have to understand the foraging behaviour of the animals in relation to the food availability. MacArthur and Pianka (1966) sought an evolutionary explanation for observed patterns in foraging behaviour. They assumed that an animal would promote its fitness by maximizing the rate of energy intake. However, energy maximization is not the only contributor to fitness. Animals must derive specific nutrients, react to competitors, avoid predators and allocate time to other essential functions (Hughes 1990). In this paper we ask whether application of optimal foraging theory can explain patterns recorded at the population level. We will argue that a proper understanding of the relationship between consumption of browse and browse availability depends on an understanding of the behaviour of the animal. The study was carried out in three different winter areas in Norway; a northern area with medium availability of high quality browse, a central area with low availability of low quality browse and a southern area with high availability of medium quality browse. We will briefly (1) present variations in resource utilization and diet selection, (2) discuss on the relationship between activity patterns and resource utilization, (3) present some data relating body weight to consumption rates, and finally (4) discuss the effects of environmental conditions and how these factors affect the functional response of moose during winter.

Resources Utilization and Diet Selection

Comparisons between the moose population in northern and central Norway, showed that for a single browse species birch (*Betula pubescens*), the average clip diameter differed in relation to the availability of browse. The largest clip diameters were taken in the area with lowest food availability (Saether and Andersen 1990). Also the amount of browse which was removed per unit area by a browsing individual was highest in the area with low resource availability (Saether and Andersen 1990).

Comparing the diet composition of moose in all three areas, we found strong preference for *Sorbus aucuparia*, *Prunus padus* and *Salix* spp., all characterized by medium and high digestibility. the consumption of these species were only to a lesser degree influenced by

the presence of other, less preferred species (Saether and Andersen, in prep). Geographic variation in the selection of scots pine (*Pinus silvestris*) and birch was proposed to be caused by higher availability of high quality tree species (Saether and Andersen, in prep.). Consequently the diet choice of moose does not become a fixed function of the characteristics of the plant itself, but depend on the relative and absolute abundance of the available browse species. The differences in diet choice were further associated with differences in range use.

Activity Pattern and Consumption of Food

According to Holling (1965), the functional response consists of two components: (1) the amount of resources removed per unit time while foraging and (2) the time available for foraging. Consequently, a detailed understanding of the factors affecting the available foraging time are a prerequisite for a proper understanding of the interactions between a herbivore and its resources.

Referring to the northern and central study area, great differences in the activity level was found. In the northern area adult moose allocated ca. 2 hr more per day to foraging activities as compared with adult moose in the central area (Saether and Andersen 1990). Due to the fact that dry matter intake (DMI) did not differ between the areas, while net digestible intake did, we suggested that moose in the northern area used their increased foraging time to increase their selectivity for high quality forage. On the contrary, moose in the central area utilized a greater proportion of the available food, causing an intake of food of low digestibility which greatly extended the time needed for rumination. Consequently, moose on good quality ranges allocated more time to foraging than moose on poorer ranges.

The Effect of Environmental Conditions on DMI

Earlier we have argued that rate of forage intake in large herbivores is determined by the interaction of three components: quantity, quality and accessibility of the food (Saether *et al.* 1989). In contrast to snow depth and temperature, variation in the quantity of the browse was able to explain a significant proportion of the variance in the forage intake of both calves and cows. There was a positive correlation both in calves and cows between the mean digestibility of the twigs selected and available biomass (Andersen and Saether, 1992). This indicates that the moose included a higher proportion of twigs in the diet of species of high digestibility when the food supply was rich. The twigs of those species is generally larger than the twigs of species of less digestibility (Bergström and Danell 1987, Saether 1990). Thus, a correlation will then appear between bite size and available biomass, as demonstrated by Spalinger *et al.* (1988).

Functional Response of Moose

The linear relationship between dry matter intake and food availability leads to the suggestion that the intake rate while foraging is the principal component determining the functional response curve of moose in winter. A similar argument has been made by Åström *et al.* (1990). We were not able to demonstrate a relationship between quality of the browse and total foraging time, although an inverse relationship between diet quality and rumination time is generally known for large herbivores (Robbins 1983). In fact, we have already shown that a larger proportion of the day was used for foraging at winter ranges with a rich supply of high quality browse (Saether and Andersen 1990).

Body weight is another factor which may influence the total foraging time. In the northern area a close negative relationship between body size and total foraging time exists (Andersen *et al.*, in prep.). Thus, the lightest cows were found to allocate a greater proportion of the day to foraging activities

than heavier cows in the same area. We also found an inverse relationship between the amount of selected browse species within the habitat and total foraging time. In fact, the amount of preferred species were able to explain 86% of the variation in total foraging time. This strengthens our suggestions that the lightest cows are excluded from the high quality patches by heavier competing animals. Consequently, we will suggest that the higher activity level associated with the lightest cows was caused by an increased searching time. Although a correlation between DMI and body size for adult cows was missing ($P > 0.1$), cows with large body size will not be exposed to an increased energy cost related to searching for food, as would lighter cows in the same area, which can be allocated to other fitness-enhancing activities (Abrams 1982). Thus, "the time available for foraging" - component of the functional rate may depend on body weight.

We suggest on the basis of this reasoning on the relative importance of the different components of the functional response, a multidimensional approach to the relationship between intake, quality and quantity of food in large herbivores (Fig. 1). This study has demonstrated a positive relationship between intake and browse availability. Whether this is a Holling curve of Type 1 or Type 2 (Holling 1959) does not matter for the sake of argument. For a given abundance of browse, we assume that the intake will also depend on the quality of the browse, because a larger proportion of the time can be used foraging when the browse is of high quality. Consequently, the intake may be described by a three-dimensional function of those two variables. An essential similar argument has previously been made by Abrams (1982). The figure shows a hypothetical relationship between dry matter intake per 24-h (DMI) of a large generalist herbivore, quality (expressed as digestibility) and quantity of browse.

Simulations of plant-herbivore interactions have shown that the dynamics is sensitive to the variation in the functional response

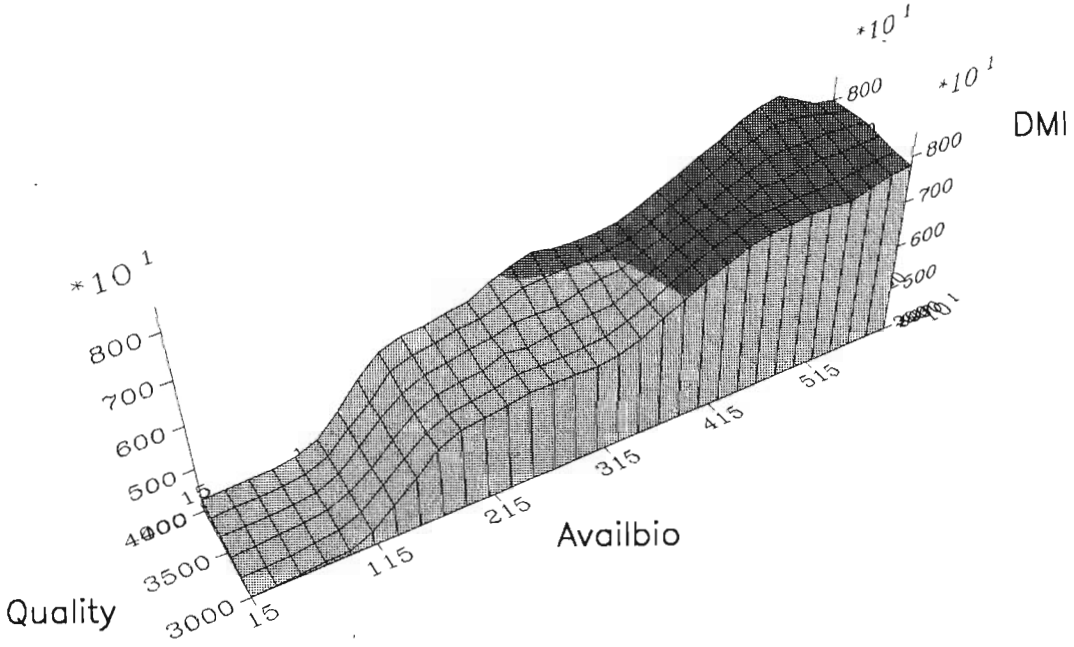

Fig.1. A hypothetical relationship between dry matter intake per 24-h (DMI), quality (expressed as digestibility) and available biomass (Availbio), of a large generalist herbivore.

(Crawley 1983). The present study may provide a link between behaviour of individuals and population dynamics. The impact of this type of functional response on the dynamics between herbivores and their resources should therefore be examined (cf. Lundberg and Åström 1990).

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REFERENCES

ABRAMS, P.A. 1982. Functional response of optimal foragers. Am. Nat.120: 382-390

ANDERSEN, R., and B-E. SAETHER. 1992. Functional response during winter of a herbivore, the moose, in relation to age and size. Ecology 73:542-550.

BERGSTRÖM, R., and K. DANELL 1987. Effects of simulated winter browsing by moose on morphology and biomass of two birch species. J. Ecol. 75: 533-544.

CRAWLEY, M.J. 1983. Herbivory. The dynamics of animal-plant interactions. Blackwell Scientific publication, Oxford.

HOLLING, C.S. 1959. Some characteristics of simple types of predation an parasitism. Can. Entomol. 91: 385-398.

_____. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. Mem.Ent. Soc. Canad. 45: 1-60.

HUGHES, R.N., editor. 1990. Behavioural mechanisms of food selection. NATO ASI series, Vol. G 20. Springer Verlag.

LUNDBERG, P. and ÅSTRÖM, M. 1990. Low nutritive quality as defence against optimally foraging herbivores. Am. Nat. 135: 547-562.

MACARTHUR, R.H. and E.R. PIANKA 1966. On optimal use os patchy environment. Am. Nat. 100: 603-609.

ROBBINS, C.T. 1983. Wildlife feeding and nutrition. Academic press, New York.

SPALINGER, D.E., T.E. HANLEY, and C.T. ROBBINS 1988. Analysis of the functional response in foraging in the sitka black-tailed deer. Ecology 69: 1166-1175.

SAETHER, B-E. 1990. The impact of different growth pattern on the utilization of tree species by a generalist herbivore, the moose Alces alces: implication of optimal foraging theory. Pages 323-340 in R.N. Hughes, ed. Behavioural mechanisms of food selection. NATO ASI Series, Vol G 20, springer Verlag.

_____, and R. ANDERSEN 1990. Resource limitation in a generalist herbivore, the moose *Alces alces*: ecological constraints on behavioural decisions. Can. J. Zool. 68: 993-999.

_____, S.ENGEN, and R. ANDERSEN 1989. Resource utilization of moose *Alces alces* during winter: constraints and options. Finnish Game Res. 46: 79-86.

ÅSTRÖM, M., P. LUNDBERG and K. DANELL 1990. Partial prey consumption by browsers: Trees as patches. J. Anim. Ecol. 59: 287-300.