Ann. Zool. Fennici 37: 251–263 ISSN 0003-455X
Helsinki 29 December 2000

Disturbance by large herbivores in boreal forests with special reference to moose

Inga-Lill Persson[1], Kjell Danell[1] & Roger Bergström[2]

[1] *Department of Animal Ecology, Swedish University of Agricultural Sciences, SE-90183 Umeå, Sweden*
[2] *Research Division, Swedish Association for Hunting and Wildlife Management, Bäcklösavägen 8, SE-756 51 Uppsala, Sweden*

Received 14 April 2000, accepted 26 October 2000

Persson, I.-L., Danell, K. & Bergström, R. 2000: Disturbance by large herbivores in boreal forests with special reference to moose. — *Ann. Zool. Fennici*. 37: 251–263.

Moose and reindeer occur in large populations in the Fennoscandian boreal forests, and also roe deer occurs in dense populations in Sweden and Norway. These large herbivores affect the structure and function of the forest ecosystems. During periods of high densities discussions arise about the impact of these herbivores on e.g. economic forest trees and preservation of biodiversity. The aim of this study is to review the present knowledge of the disturbance caused by moose in the boreal forest. First, we give a quantitative estimate of the different disturbance factors (feeding, trampling, defecation and urination). Second, we discuss the ecological impact of the different disturbances.

Introduction

Large herbivores are suggested to affect both abiotic and biotic factors and, thus, ecosystem processes (Hobbs 1996). They may change the conditions for other organisms above and below ground in addition to directly affecting the plants they eat. These direct and indirect effects can affect ecosystem processes from the small to the large spatial scale and be long lasting (Pastor & Naiman 1992).

Disturbance in community ecology has been defined as any relative discrete event in time that removes organisms and opens up space which can be colonised by individuals of the same or different species. Agents of disturbance that create gaps include teeth, feet, faeces and urine of herbivores (Begon *et al.* 1990). The large herbivores can thus be considered as disturbance factors which may affect ecosystem processes by e.g. their feeding (Pastor & Naiman 1992, Pastor & Cohen 1997), trampling, defecation, urination, and leaving carcasses (McKendrick *et al.* 1980, Suominen *et al.* 1999b). The most important impact is suggested to be their food plant selection. Selective feeding can alter the competition between plant species, modify the structure and composition of the plant community (Pastor & Naiman 1992, Pastor & Cohen 1997) and affect the succession rate (Pastor & Naiman 1992, Davidson 1993, Bergquist 1997).

The direction and degree of responses in ecosystem processes to herbivory may to a large degree depend on herbivore species present, their population densities, habitat type and whether the herbivores have been present in the ecosystem for extended (evolutionary) time (Milchunas & Lauenroth 1993, Hobbs 1996).

The availability of plant nutrients in boreal forests is generally low (Vitousek 1982), and it is important to identify factors affecting availability and cycling of nutrients (Pastor & Naiman 1992). It is especially important to estimate effects on nitrogen cycling, because nitrogen frequently limits the productivity of boreal forests (Vitousek 1982). Studies from North America suggest that moose browsing can depress soil nitrogen availability (Pastor *et al.* 1998).

During recent decades, the Fennoscandian populations of moose (*Alces alces*) and roe deer (*Capreolus capreolus*) have increased to densities most likely not experienced in post-glacial time (e.g. Bergström & Willebrand 1992, Cederlund & Liberg 1995). The populations of semidomestic reindeer (*Rangifer tarandus*) have also increased considerably in some areas (e.g. Väre *et al.* 1996). Consequently, it is important to estimate the significance of disturbance caused by moose, roe deer and reindeer on ecosystem processes in boreal forests, not least in relation to short- and long-term management of wildlife and forests in the Nordic countries.

Due to the population increases of large herbivores in Fennoscandia during the last decades, there have been increasing demands for research into questions involving the food resources and damages to e.g. forestry and preservation of biodiversity (Bergström & Willebrand 1992). Theoretical, broad-scope assessments of the effects of large herbivores on ecosystems have generally been qualitative. However, quantitative assessments may provide a basis for evaluating and modifying theoretical models, and provide insight and perspective into the results of empirical studies (Milchunas & Lauenroth 1993). It is thus important to actually quantify the disturbance caused by large herbivores to be able to evaluate their impact on the ecosystem.

Quantitative estimation of disturbance caused by moose

We reviewed literature from Fennoscandia, North America and the former Soviet Union. Moose was chosen as a study species because its natural history is well known, even in quantitative perspectives. Further, moose is quite abundant in many boreal forest ecosystems. Because of its large size (about 300–370 kg for cows and 390–470 kg for bulls in Sweden, Sand *et al.* 1995) and high densities (at present up to about 2 moose per km^2 in Sweden) we can expect a significant impact on the forest ecosystems.

Food intake

The mean daily food intake of moose (dry and fresh mass) varies between seasons, and is considerably higher in summer than in winter (Novikov 1959, Schwarz *et al.* 1984, 1987, Renecker & Schwartz 1998, Schwartz & Renecker 1998). Two-three times higher intake rates of dry matter in summer than in winter have been reported (Schwarz *et al.* 1984, 1987, Renecker & Hudson 1985).

The quality and availability of food is higher in summer, resulting in increased activity levels and food intake (VanBallenberghe & Miquelle 1990, Schwartz & Renecker 1998). Intake rates are also affected by seasonal cycles in metabolic rate (Regelin *et al.* 1985), physiological demands of reproduction, age, diseases and parasites, condition, (likely) photoperiodism (Schwartz & Renecker 1998) and the snow cover in winter (Hjeljord 1987).

The quality and quantity of browse vary considerably between regions, but there seem to be no significant differences in the daily intake rates of gross dry matter between regions (Saether & Andersen 1989). There are some differences in the quantity of consumed food between moose of different age and sex (Novikov 1959, Schwarz *et al.* 1984), but the major difference in food intake over the year is still the difference in intake rates between summer and winter.

It thus seems reasonable to estimate an average intake rate of 5 kg dry matter per moose and day in winter (Table 1) and for summer 10 kg as estimated by Renecker & Hudson (1985).

For further calculations we have divided the year into summer and winter only. Assuming 180 days of winter and 180 days of summer, the average consumption per moose in one year is 2 700 kg of dry mass. In terms of fresh mass (10 kg per moose and day in winter and 30–40 kg per moose and day in summer), the average consumption per moose in one year is 7 200–9 000 kg.

Trampling

The activity patterns of moose vary considerably over the year (Risenhoover 1986, Cederlund 1989, VanBallenberghe & Miquelle 1990). Activity levels reach a minimum in late winter (Risenhoover 1986, Cederlund 1989), and a maximum in spring and early summer (Risenhoover 1986, Cederlund 1989, Cederlund *et al.* 1989, VanBallenberghe & Miquelle 1990). Some studies also report a second peak during the moose rut in autumn (Cederlund 1989), but the most pronounced transition in activity levels occurs in the shift between summer and winter diet (Cederlund 1989). The variation in activity levels over the year is probably mainly explained by temporal changes in the quality and distribution of food (Risenhoover 1986, Cederlund 1989, Cederlund *et al.* 1989, VanBallenberghe & Miquelle 1990).

The quality of food (and thus time needed for rumination) seems to be the most limiting factor on activity levels (Risenhoover 1986, Cederlund *et al.* 1989), and food quality is generally lower in winter than in summer. Low temperature, moderate snow levels or forage quantity in winter do not seem to limit activity levels significantly (Risenhoover 1986, Cederlund *et al.* 1989).

The differences in activity levels between regions are probably caused by differences in the quality of food, although differences in snow depths may contribute to this difference in winter (Saether & Andersen 1989). In addition to the variation on larger scales, the activity levels of individual moose are observed to vary from day to day. This variation is partly due to occasional long distance movements (Risenhoover 1986).

However, the major activity patterns seem to be rather similar in adult moose (Cederlund 1989, VanBallenberghe & Miquelle 1990) on larger scales in time and space (Table 2), and there seem to be no significant differences among years either (VanBallenberghe & Miquelle 1990). Differences in activity levels documented be-

Table 1. The average daily food intake of adult moose.

Area	Season	Intake (kg)	Range (kg)
Troms, Norway1)	Winter	5.5 (dry weight)	
Gausdal, Norway1)	Winter	4.3 (dry weight)	
Nordic Countries2)	Winter		8–15 (fresh weight)
Montreal, Canada3)	Winter	4.2 (dry weight)	
St. Petersburg, Russia4)	Winter	10 (fresh weight)	5–21 (fresh weight)
Moscow, Russia5)	Winter	13 (fresh weight)	
Soviet Union7)	Winter		6–12 (fresh weight)
Mean	**Winter**	**4.7 (dry weight)**	
Moscow, Russia4)	Autumn	20 (fresh weight)	
Pechora, Russia4)	Summer		30–40 (fresh weight)
Soviet Union5)	Summer		30–40 (fresh weight)
Soviet Union5)	Autumn		15–20 (fresh weight)
North America6)	Summer	10.0 (dry weight)	
Isle Royale, USA7)	Summer	6.5 (dry weight)	
Mean	**Summer**	**8.3 (dry weight)**	

1)Saether & Andersen 1989, 2)Hjeljord 1987, captive moose, 3)Joyal & Ricard 1986, 4)L. Baskin pers. comm., 5)Novikov 1959, 6)Renecker & Hudson 1985, 7)Miquelle 1983.

tween moose of different sex and reproductive status (Ericsson & Wallin 1996), and the occasional individual long distance movements are probably of smaller importance than the daily activities associated with feeding. Most of the active time of moose is spent on foraging, including searching for food (Risenhoover 1986). The difference in activity levels between summer and winter seems to be the most important source of variation, and to estimate a mean daily travelling distance of 1 km per moose and day in winter and 2 km per moose and day in summer seems reasonable (Table 2).

Most studies on moose movement are based on radio-telemetry. The estimates of distance moved per day are thus conservative estimates of the actual distance covered by moose, because this distance must have exceeded the distances between consecutive radio locations (Ericsson & Wallin 1996). However, because more precise data on the actual distance moved per moose and day were not available, we chose to use the estimates based on data obtained by radio-telemetry.

On average, a moose makes about 1.5 tracks per m (I.-L. Persson pers. obs.), giving an estimated mean of 1 500 tracks per moose per day in winter (1 000 m per moose and day × 1.5 tracks per m) and 3 000 tracks per moose per day in summer (2 000 m per moose and day × 1.5 tracks per m) The track area of moose in Canada has been estimated to be 443.7 cm^2 (range 370.5–515.4) for male moose, 3.5 years old, and 498.5 cm^2 (range 387.6–605.0) for older males, giving a mean area of about 110–125 cm^2 (range 96.9–151.3) per hoof (Kelsall 1969). Unfortunately, no data were available for female moose, but the sexual dimorphism concerning foot loading has been estimated to be 4.6% for moose in favour of females (Telfer & Kelsall 1984). This means that females, compared to males, have larger track area relative to their body weight, making the difference in hoof area smaller than expected from sex differences in size. The track area of moose does not seem to be significantly different between provinces although weights differ (Kelsall 1969), indicating that the track area is relatively constant.

For adult moose in Sweden it seems reasonable that the mean area of one track is about 115 cm^2. With this estimate, the actual area affected by trampling is on average 17.3 m^2 per moose per day in winter (1 500 tracks per moose and day 0.0115 m^2 per track), and 34.5 m^2 per moose per day in summer (3 000 tracks per moose and day 0.0115 m^2 per track).

Assuming 180 days of winter and 180 days of summer, the area affected by trampling of one moose is 9324 m^2 ≈ 0.9 ha in one year (17.3 m^2 per moose and day × 180 days) + (34.5 m^2 per moose and day × 180 days). Using an estimate of 350 000 moose in Sweden before the hunting season, the area affected by trampling in one year can be estimated to be 3 255 km^2, an area comparable to Vänern, the largest lake in Sweden

Table 2. The average time spent in activity and distance moved per moose and day (24 h).

Study area	Season	Active time (min)	Time moving (min)	Distance moved (m)
Grimsö, Sweden[1)]	Winter	445		
Furudal, Sweden[1)]	Winter	420		
Denali, Alaska, USA[2)]	Winter	390	85	950
Grimsö, Sweden[3)]	Winter	450		
Gausdal, Norway[4)]	Winter	390		1000
Troms, Norway[4)]	Winter	500		1250
Mean	**Winter**	**430**		**1070**
Grimsö, Sweden[3)]	Summer	580		
Västerbotten, Sweden[5)]	Autumn (pre hunt)			1740
Denali, Alaska, USA[6)]	Summer	605	60	
Mean	**Summer**	**590**		

[1)]Cederlund *et al.* 1989, [2)]Risenhoover 1986, [3)]Cederlund 1989, [4)]Saether & Andersen 1989, [5)]Ericsson & Wallin 1996, [6)]VanBallenberghe & Miquelle 1990.

(5 585 km^2). These are, however, underestimates because telemetry distances are shorter than moved distances, and also because moose makes tracks while standing still feeding. Quantitative data on the number of tracks made during feeding were not available. The effects of lying down on the ground might also be comparable to the effects of trampling, further contributing to the underestimate.

Defecation

Several studies report large variations in the defecation rates of moose (Joyal & Ricard 1986, Andersen *et al.* 1992, Timmermann & Buss 1998). The number of pellet groups deposited per moose and day varies between regions (Andersen *et al.* 1992, Timmermann & Buss 1998), with season (Andersen *et al.* 1992), with age and sex (Baskin & Lebedeva 1987, Timmermann & Buss 1998) and within and between individuals (Joyal & Ricard 1986, Andersen *et al.* 1992).

The variation in defecation rate may be explained by variations in the quality (digestibility) and availability of consumed food and intake rate (Lavsund 1975, Joyal & Ricard 1986, Saether & Andersen 1989, Andersen *et al.* 1992, Timmermann & Buss 1998). Intake rates are also scaled to body size. Larger moose will normally have higher defecation rates than smaller (Timmermann & Buss 1998), and males are observed to have significantly higher defecation rates than females (Franzmann & Arneson 1976). However, defecation rates do not always increase with body size, because some studies have reported defecation rates of moose calves as high (Joyal & Ricard 1986) or even higher than the rates of adults (Lavsund 1975, Andersen *et al.* 1992).

In spite of the large variations reported in defecation rates, the average number of pellet groups deposited per moose and day is rather constant (Table 3). The average defecation rate seems to be 14 pellet groups per moose and day. Few data on defecation rates in summer were available. Miquelle (1983) suggested that defecation rates for moose were higher in summer than in winter, but their estimate of 11.2 pellet groups per moose and day in summer does not support this suggestion when compared with other studies of defecation rates (Table 3).

Using the estimate of 14 pellet groups per moose and day both in summer and winter, we assessed that one moose on average produces 5 040 pellet groups in one year.

The wet and dry weights of pellet groups seem to be generally stable (Andersen *et al.* 1992). There is no significant effect of age and sex (Joyal & Ricard 1986), and the weight also seems to be rather similar in different regions (Andersen *et al.* 1992) and between seasons (Belovsky & Jordan 1981). The differences in daily total fecal output are thus mainly a result of variations in defecation rate (Andersen *et al.* 1992). Using an estimate of 170 g dry mass per pellet group (Table 4) and 14 pellet groups per moose and day, we calculated that one moose on average deposits 860 kg dry mass in one year, and the entire Swedish moose population 300 000 tonnes.

The amount of nitrogen (N) excreted is a function of dietary levels of nitrogen, digestible energy, tannins and body size (Hobbs 1996). There are few estimates of the nitrogen concentration in moose pellets. To estimate the contribution of N from moose pellets, pellet groups from free ranging and fenced moose in Västerbotten County

Table 3. The average number of pellet groups deposited per moose and day for adult moose.

Study area	Pellet groups	Range	Season
Garpenberg, Sweden¹⁾	13.0		Winter
Norway²⁾	18.6	7–31	Winter
Montreal, Canada³⁾	12.7	6.9–19	Winter
British Columbia, Canada⁴⁾	13.0		?
Soviet Union⁵⁾	14.0		Winter
Isle Royale, Michigan, USA⁶⁾	11.2		Summer
Ontario, USA⁶⁾	10.9		Summer
Alaska, USA⁷⁾	17.6	10–25	Winter
Alaska, USA⁸⁾	16.7		Winter
Mean	**14.2**		

¹⁾Lavsund 1975, ²⁾Andersen *et al.* 1992, ³⁾Joyal & Ricard 1986, ⁴⁾Edwards 1963, cited in Lavsund 1975, ⁵⁾Baskin & Lebedeva 1987, ⁶⁾Miquelle 1983, captive moose in Ontario, ⁷⁾Franzmann & Arneson 1976, ⁸⁾Oldemeyer & Franzmann 1981, mean of 2 winters (defecation rates of 16.2 and 17.2).

were collected (Table 5). The fenced moose were fed an approximately "natural" diet.

The content of N in summer pellets was significantly higher than in winter pellets (*F*-test, $p = 0.0001$, Table 5). There was no significant difference in the content of N in moose pellets from free ranging and fenced moose in winter (*t*-test, $p = 0.0761$).

Using the estimates that each moose on average produces 170 g dry mass per pellet group (Table 4) and 14 pellet groups per moose and day (2.38 kg dry mass per day) and our own unpublished estimates of 1.33% N in winter pellets and 2.44% in summer pellets on average (Table 5), we estimated the contribution of N to be: [(2.38 kg dry mass per day × 0.0133 kg N per kg dry mass × 180 days of winter) + (2.38 kg dry mass per day × 0.0244 kg N per kg dry mass × 180 days of summer)], for a total of 5.7 kg N per moose in winter and 10.5 kg N per moose in summer. Thus, the contribution of nitrogen from pellets was estimated to be on average 16 kg N per moose in one year, and 5 600 tonnes for the entire Swedish moose population.

Urination

The quantity of urine produced per moose and day differs between seasons; much less urine is produced in winter than in summer (Novikov 1959, Belovsky & Jordan 1981). The number of urinations per day is around 11.2 for free-ranging adult moose (Miquelle 1983) (Table 6).

Using the data of Belovsky & Jordan (1981) of 13.1 litres of urine per moose and day in summer and 11 urination events, we estimated each urination to be on average 1.2 litres. During the summer (180 days), one moose produces a total of about 2 360 litres of urine, distributed on almost 2 000 spots.

Data on moose urination in winter is scarce. Using the estimate of Novikov (1959) of 2–3 litres of urine per moose and day in winter and assuming 180 days of winter, we assumed that each moose produces, on average, 360–540 litres of urine per winter. Using the higher estimate of Belovsky & Jordan (1981) of 7.3 litres of urine per moose and day, we calculated that each moose produces, on average, 1315 litres of urine per winter, and the whole Swedish moose population 1.26 million m^3 in one year.

Because nitrogen is the most important limiting nutrient in boreal forests (Vitousek 1982), the compounds in urine containing nitrogen (i.e. urea, creatinine and uric acid) are probably most important concerning the contribution of plant nutrients.

The content of nitrogen in moose urine in summer was estimated to be 4.38 g N from urea, 0.28 g N from creatinine and 0.49 g N from uric acid per one litre of urine, adding up to a total of 5.15 g N per litre. This corresponds to a nitrogen concentration of about 0.5% N in moose urine (John Pastor pers. comm.). Using the estimate of 13 litres of urine per moose and day in summer and 180 days of summer, we found the total contribution of N from moose urine to be 12.1 kg

Table 4. The average output of faeces (dry mass) per moose and day for adult moose.

Study area	Daily output of faeces (kg)	Weight per pellet group (g)	Season
Gausdal, Norway[1)]	2.6		Winter
Troms, Norway[1)]	2.9		Winter
Norway[2)]		195	Winter
Montreal, Canada[3)]	2.3	181	Winter
Isle Royale, Michigan, USA[4)]	3.0	178	Winter
Isle Royale, Michigan, USA[5)]	1.4	126	Summer
Ontario, USA[5)]	2.2	179	Summer
Isle Royale, Michigan, USA[4)]	1.1	178	Summer
Mean	**2.2**	**173**	

1) Saether & Andersen 1989, 2) Andersen *et al.* 1992, 3) Joyal & Ricard 1986, 4) Belovsky & Jordan 1981, 5) Miquelle 1983, captive moose in Ontario.

N in one summer (13 litres of urine per moose and day × 5.15 g N per one litre of urine × 180 days) = 12.1 kg N. No data were available on the composition of moose urine in winter.

Effects of disturbance caused by large herbivores in boreal forests

Effects of feeding

Selective feeding by moose in boreal forests has been documented to affect tree canopy composition and structure, field and bottom layers, mycorrhizae and forest succession rate. Feeding has been suggested to have larger impact on ecosystem processes than trampling, faeces and urine, at least on larger scales in time and space (Pastor & Naiman 1992, Pastor *et al.* 1993, Suominen *et al.* 1999a) (Table 7).

The canopy structure

The main effect of browsing on the canopy structure is reduced twig density, resulting in a more open canopy (McInnes *et al.* 1992, Kielland & Bryant 1998, Suominen *et al.* 1999a, 1999b). An opening of the canopy has been associated with increased decomposition rates (Pastor *et al.* 1993, Augustine & McNaughton 1998) due to higher light intensity (Risenhoover & Maass 1987, McInnes *et al.* 1992, Kielland & Bryant 1998) and higher soil temperature (Kielland & Bryant 1998). Cold wet sites appear to have forest floors with low mineralization rates (Flanagan & Van Cleve 1983), and the lower soil moisture and lower relative humidity associated with a more open canopy (Kielland & Bryant 1998) may also contribute to increased decomposition rates. Another change that has been associated with a more open canopy is the tendency to increased cation and anion concentrations (Kielland & Bryant 1998).

The production of shrubs and herbs also often increases because more light reaches the forest floor (McInnes *et al.* 1992). These changes in habitat structure and microclimate in the shrub, field and bottom layers also affect invertebrate communities (Suominen *et al.* 1999a, 1999b).

Tree species composition

Selective browsing on trees by moose often results in a shift in the canopy composition towards increased dominance of unbrowsed species, and thus altered composition and quality of the litterfall (Pastor *et al.* 1988, McInnes *et al.* 1992, Pastor & Naiman 1992, Hobbs 1996, Kielland & Bryant 1998).

The quality of the substrate is a major factor governing microbial population sizes and litter decomposition rates, and is actually suggested to be more important than within- and between site microclimate differences (Flanagan & Van Cleve 1983). An altered composition of the litterfall is

Table 5. The content of N (estimated as % of dry weight) for 30 groups of moose pellets. The content of N for free ranging moose in winter is set as the basic level with which the other samples are compared in the statistical tests.

	Samples	%N	SE	*p*-value
Fenced moose, summer	10	2.44	0.053	0.0001
Fenced moose, winter	10	1.28	0.053	0.0761
Free ranging moose, winter	10	1.38	0.037	–

Table 6. The average volume of urine (l) produced per moose and day for adult moose.

Study area	Volume	Urinations	Season
Isle Royale, Michigan, USA[2)]	13.1		Summer
Isle Royale, Michigan, USA[3)]		11.2	Summer
Isle Royale, Michigan, USA[3)]	11.8	6.4	Summer
Soviet Union[1)]	15–17		Summer
Isle Royale, Michigan, USA[2)]	7.32		Winter
Soviet Union[1)]	2–3		Winter

[1)]Novikov 1959, [2)]Belovsky & Jordan 1981, [3)]Miquelle 1983 (the volume estimated for captive moose, the number of urinations of 6.4 is for one captive male yearling and 11.2 is for at least 10 free ranging female moose).

observed to affect soil carbon:nitrogen (C:N) ratios, pools of mineralizable carbon, fine root production, soil pH and soil moisture (Flanagan & Van Cleve 1983, Holland & Detling 1990, Kielland *et al.* 1997, Kielland & Bryant 1998).

Moose browsing in boreal forests in North America has been documented to result in a decrease in soil carbon and nitrogen content, cation exchange capacity, field nitrogen availability, potentially mineralizable nitrogen and microbial respiration rates (Pastor *et al.* 1988). The effect of the litterfall on the microbial N immobilization-mineralization dynamics is probably important in this context (Holland & Detling 1990). Microbial soil organisms in boreal forests seem to be limited by the supply of energy (C) rather than by the supply of nutrients (Flanagan & Van Cleve 1983). If the carbon availability (C:N ratio) decreases, the result may be reduced microbial growth and nitrogen immobilization, increased nitrogen mineralization and increased nitrogen availability for plants. Less allocation of carbon to root growth, resulting in a decrease in the total root biomass and C:N ratio in the presence of herbivores is also suggested to be part of the explanation (Holland & Detling 1990). Significant changes in the C:N ratios in the presence of herbivores are documented for young forest stands in boreal forests (Kielland *et al.* 1997, Kielland & Bryant 1998).

As browse species, deciduous trees are generally preferred over conifers, and the litterfall from deciduous trees also decomposes more easily than that from conifers (Flanagan & Van Cleve 1983, Pastor & Naiman 1992). In early successional stages with alder (*Alnus* sp.), selective browsing of moose has been suggested to increase the litter quality and decomposition rates, accelerating the soil organic matter turnover and increasing habitat productivity (Kielland *et al.* 1997).

In later successional stages, however, selective browsing on deciduous trees seems to increase the proportion of conifers and thus the

Table 7. Suggested and documented effects of selective browsing by moose in the tree layer. See text for references.

Affects	Suggested and documented effects
Canopy structure	More open canopy Higher light intensity Higher soil temperature Lower soil and air moisture Higher decomposition rates Changes in plant and animal communities
Tree species composition	Lower quantity of litter-fall Lower quality of litter-fall due to increased proportion of coniferous and decreased proportion of deciduous litter Lower soil N content Lower field N availability Lower potentially mineralizable N Lower soil C content Lower cation exchange capacity Decreased microbial respiration rates and decomposition Lower habitat productivity Higher quality of litter-fall in young successional stages with alder Higher decomposition rates in young successional stages with alder Higher habitat productivity in young successional stages with alder Changes in plant and animal communities
Mycorrhizae	Lower mycorrhizal infections of preferred browse species
Rate of forest succession	Retard succession rate in early seres Hasten succession rate in later seres

proportion of slowly decomposing coniferous litter, which is associated with slower carbon turnover and decreased decomposition rates (Pastor & Naiman 1992, Kielland *et al.* 1997, Suominen *et al.* 1999a).

The direction and strength of responses in ecosystem processes like nutrient availability and cycling to altered composition of the litterfall are not easy to predict. There are strong and complex interactions among the different factors (Flanagan & Van Cleve 1983), and existing results are opposing (Kielland *et al.* 1997). The effects on decomposition and mineralization rates depend more on quality of the litterfall than on its quantity. However, if the quantity of the litterfall (and thus C available for microbes) changes dramatically, decomposition rates and plant nutrient availability may be affected (Flanagan & Van Cleve 1983). Moose browsing has been documented to result in decreased quantity of litterfall (Pastor *et al.* 1988, Suominen *et al.* 1999a).

The mycorrhizae

Browsing and grazing by large herbivores seem to affect the mycorrhizal fungi (Helle & Aspi 1983, Rossow *et al.* 1997). Moose browsing is suggested to have a negative effect on mycorrhizal infections of fine roots of preferred browse species. Decreased allocation of carbohydrates to roots and thereby reduced availability of carbohydrates to ectomycorrhizae might be the explanation (Rossow *et al.* 1997). Opposing to this, reindeer grazing on lichens seems to have a positive effect on the mycorrhiza infecting Scots pine (*Pinus sylvestris*) and dwarf shrubs. Lichens produce toxins, which inhibit the development of mychorrizae fungi, and reduced lichen cover due to grazing may increase the extent of mycorrhizal infection (Helle & Aspi 1983).

The rate of forest succession

The rate of early forest succession seems to be under significant control of large herbivores (Pastor *et al.* 1998, Kielland & Bryant 1998), which usually prefer to feed on intermediate seral species like grasses, shrubs and pioneer trees. The general outcome of this food preference is that large herbivores retard the succession from early seres dominated of annuals and shorter perennials (if such seres are present), and hasten the succession from grasses, shrubs and pioneer trees to persistent trees (often including conifers, Davidson 1993). Moose and roe deer browsing on deciduous trees seems to prolong the stage dominated by grasses in early seres and to hasten succession to dominance of conifers in later seres (Bergquist 1997). Reindeer grazing on lichens (which are dominating forest floor species in late successional stages) can retard the succession rate (Helle & Aspi 1983).

Effects of trampling

Trampling is suggested to have substantial effects on the ground vegetation at high ungulate densities (Helle & Aspi 1983, Väre *et al.* 1996). Trampling by reindeer herds has been found to have a large impact on the vegetation cover in oligotrophic pine heaths, resulting in more barren ground and altered vegetation composition. Trampling also seems to damage fine roots (Väre *et al.* 1996) (Table 8).

The production of nitrate often increases rapidly after disturbance of the forest floor (Vitousek 1982). Trampling certainly is a disturbance factor and may result in higher mineralization rates of nitrogen inside compared to outside of the tracks.

Table 8. Suggested and documented effects of trampling and defecation. See text for references.

Disturbance factor	Suggested and documented effects
Trampling	Altered composition of ground vegetation More barren ground Negative effect on fine roots Higher N mineralization rates
Defecation and urination	Higher availability of plant nutrients Higher soil microbial processes Higher habitat productivity Impact on fungi, mosses and invertebrates

The effects of trampling are probably most pronounced at low productivity soils at northern latitudes with high ungulate densities.

Effects of defecation and urination

The contribution of plant nutrients from faeces and urine has been suggested to be trivial, assuming uniform deposition across the home range of an animal. However, herbivores in general do not use their habitats uniformly, and faeces and urine become concentrated in space at several scales. The contribution of nutrients may thus be significant in areas preferentially selected (Hobbs 1996). Faeces and urine offer plant nutrients easily available for plants and microbes (Hobbs 1996), and plant growth and soil microbial processes may thus be enhanced (Ruess & McNaughton 1987, Pastor *et al.* 1993). In boreal forests, the content of plant nutrients has been found to be higher under faeces and carcasses (McKendrick *et al.* 1980). Further, the contribution to the soil nitrogen from moose urine and faeces has been shown to constitute a considerable proportion of the total aboveground nitrogen input in early successional stages. The high proportion of faecal nitrogen was probably due to low litterfall in these habitats rather than especially high rates of faecal input, however (Kielland *et al.* 1997, Kielland & Bryant 1998).

The most interesting biological effect of defecation and urination might be the impact on species richness of fungi and invertebrates connected to faeces and patches of urine, but few data are available on moose. Studies have documented that there exists a whole community of coprophilous fungi on the faeces and urine patches of large herbivores, e.g. *Octospora aggregata* and *Nanfeldtiella aggregata* (Lundqvist 1972, Dix & Webster 1995, Petersen 1998, Petterson 1998), and also a large number of invertebrates, including *Atomaria peltataeformes* and *Aphodius nemoralis* (Kronblad 1971, Petterson 1998). Preliminary results indicate that some species of beetles (Coleoptera) connected to faeces and urine of moose have increased their distribution and abundance in Scandinavia due to the increase in the moose population (Petterson 1998).

Synthesis

The study of the direct and indirect effects of disturbance caused by large herbivores in boreal forests is a relatively new area of research. Herbivores are suggested to have a large impact on forest habitats (Tables 7 and 8), but there is considerable scarcity of data and the documentation of long-term effects is especially poor (Risenhoover & Maass 1987). Most of the studies are from North America and may thus not be directly applicable to boreal forests in Fennoscandia. Population densities of large herbivores in boreal forests are typically far higher in Fennoscandia than in North America (Karns 1998), and the food preferences may also differ (Suominen *et al.* 1999a).

Most studies of selective feeding by large herbivores have dealt with the direct effects on the tree layer (Table 7) or the lichen cover, and we have fairly good knowledge about how the large herbivores affect the canopy structure, the tree species composition and the lichen cover. However, except from reindeer grazing on lichens in winter, few studies have focused on how large herbivores affect the plant communities in the field and ground layers. The limited data suggest that the effects are significant, but it is not possible to make any general conclusions. Little attention has been paid internationally to the effects of large herbivores on the different animal assemblages (Suominen *et al.* 1999a). Significant changes in the communities of ground living invertebrates both in areas browsed by moose and areas grazed by reindeer have been documented in Fennoscandia (Suominen 1999, Suominen *et al.* 1999a, 1999b) and there are also indications that tree-living invertebrates are affected (Danell & Huss-Danell 1985). A change in the invertebrate fauna may affect other groups of invertebrates and vertebrates feeding upon them. Thus, disturbance caused by large herbivores has the potential to affect several trophic levels.

If, and to what extent, large herbivores affect fundamental ecosystem processes like decomposition rates, soil nutrient availability and habitat productivity are even less known than how they affect plant- and animal assemblages. Documentation of how below-ground systems like fine roots and mycorrhizal fungi may be affected are also insufficient. Studies from North America indicate that large herbivores have a large impact on different ecosystem processes (Pastor & Naiman 1992, Pastor *et al.* 1998). The interactions are complex (Pastor & Naiman 1992, Hobbs 1996) and (especially the abiotic) mechanisms underlying observed responses are poorly known and thus important to reveal.

Large herbivores may not only affect different groups of organisms and ecosystem processes by their feeding, but also by trampling, defecation and urination. The impact of the latter disturbance factors is poorly known, and may act in opposite ways to the effects of selective feeding. There are also suggestions that they are less important than the effects of selective feeding, at least on larger temporal and spatial scales (Pastor *et al.* 1993), but quantitative data are not available. On the other hand there are many species of fungi and invertebrates that are more or less specialized to substrates that the herbivores produce, e.g. pellets, urine patches and carcasses. These groups should be considered when the impact of herbivores on biodiversity is discussed.

As a conclusion, there is considerable scarcity of data concerning the impact of large herbivores in boreal forests, except for the direct effects of selective feeding on the tree layer and the lichen cover. Also, we do not know the relative impact of the different disturbance factors on different scales in time and space, the effects of different population densities, the effects on different productive soils, or if possible responses are linear or not. Further research of how large herbivores affect plant- and animal assemblages and also fundamental ecosystem processes in boreal forests is needed, and will probably reveal several complex (and unexpected) effects and interactions.

Acknowledgments

We thank Leonid Baskin and John Pastor for letting us use their unpublished observations. This work was financially supported by the Swedish Environment Protection Agency and the Swedish Council for Forestry and Agricultural Research.

References

Andersen, R., Hjeljord, O. & Saether, B. E. 1992: Moose defecation rates in relation to habitat quality. — *Alces* 28: 95–100.

Augustine, D. J. & McNaughton, S. J. 1998: Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. — *J. Wildl. Manage*. 62: 1165–1183.

Baskin, L. M. & Lebedeva, N. L. 1987: Moose management in USSR. — In: Göransson, G. & Lavsund, S. (eds.), *Swedish Wildlife Research*, Proceedings: 519–634. Second International Moose Symposium, Uppsala 1984:

Begon, M., Harper, J. L. & Townsend, C. R. 1990: *Ecology: individuals, populations and communities*, 2. ed. — Blackwell Scientific Publications, Boston.

Belovsky, G. E. & Jordan, P. A. 1981: Sodium dynamics and adaptations of a moose population. — *J. Mammal*. 62: 613–521.

Bergquist, J. 1997: *Influence by ungulates on early plant succession and forest regeneration in South Swedish spruce forests*. — Ph.D. thesis, Department of Animal Ecology, Swedish University of Agricultural Sciences, Umeå.

Bergström, R. & Willebrand, T. 1992: Research and statistics, tools in game management. — In: Bergström, R., Huldt, H. & Nilsson, U. (eds.), *Swedish game, biology and management*: 96–109. Almquist & Wiksell Tryckeri**,** Uppsala.

Cederlund, G. 1989: Activity patterns in moose and roe deer in a northern boreal forest. — *Holarct. Ecol.* 12: 39–45.

Cederlund, G., Bergström, R. & Sandegren, F. 1989: Winter activity patterns of females in two moose populations. — *Can. J. Zool.* 67: 1516–1522.

Cederlund, G. & Liberg, O. 1995: *Rådjuret. Viltet, ekologin och jakten.* — Almquist & Wiksell Tryckeri, Uppsala.

Danell, K. & Huss-Danell, K. 1985: Feeding by insects and hares on birches earlier affected by moose browsing. — *Oikos* 44: 75–81.

Davidson, D. W. 1993: The effects of herbivory and granivory on terrestrial plant succession. — *Oikos* 68: 23–35.

Dix, N. J & Webster, J. 1995: Coprophilous fungi. — In: Dix, N. J & Webster, J. (eds.), *Fungal ecology*: 203–224. Chapman & Hall, London.

Ericsson, G. & Wallin, K. 1996: The impact of hunting on moose movements. — *Alces* 32: 31–40.

Flanagan, P. W. & Van Cleve, K. 1983: Nutrient cycling in relation to decomposition and organic-matter quality in taiga ecosystems. — *Can. J. For. Res*. 13: 795–817.

Franzmann, A. W. & Arneson, P. D. 1976: Daily pellet groups and beds of Alaskan moose. — *J. Wildl. Manage*. 40: 375–376.

Helle, T. & Aspi, J. 1983: Effects of winter grazing by reindeer on vegetation. — *Oikos* 40: 337–343.

Hjeljord, O. 1987: Research on moose nutrition in the nordic countries. — In: Göransson, G. & Lavsund, S. (eds.), *Swedish Wildlife Research*, Proceedings, Second International Moose Symposium, Uppsala 1984: 389–397.

Hobbs, N. T. 1996: Modification of ecosystems by ungulates. — *J. Wildl. Manage*. 60: 695–713.

Holland, E. A. & Detling, J. K. 1990: Plant response to herbivory and belowground nitrogen cycling. — *Ecology* 71: 1040–1049.

Joyal, R. & Ricard, J. G. 1986: Winter defecation output and bedding frequency of wild, free-ranging moose. — *J. Wildl. Manage.* 50: 734–736.

Karns, P. D. 1998: Population distribution, density and trends. — In: Franzmann, A. W. & Schwartz, C. C. (eds.), *Ecology and managenent of the North American moose*: 125–140. Smithsonian Institution Press, Washington.

Kelsall, J. P. 1969: Structural adaptations of moose and deer for snow. — *J. Mammal.* 50: 302–310.

Kielland, K. & Bryant, J. P. 1998: Moose herbivory in taiga: effects on biogeochemistry and vegetation dynamics in primary succession. — *Oikos* 82: 377–383.

Kielland, K., Bryant, J. P. & Ruess, R. W. 1997: Moose herbivory and carbon turnover of early successional stands in interior Alaska. — *Oikos* 80: 25–30.

Kronblad, W. 1971: *Aphodius*-arter i älgspillning (*Col. Scarab*.). Några interessanta fynd från Vetlanda-trakten på Småländska höglandet. — *Entomol. Tidskr*. 92: 281–282.

Lavsund, S. 1975: *Investigations on pellet groups*. — Research Notes 23. Department of Vertebrate Ecology, Royal College of Forestry, Stockholm, Sweden. 47 pp.

Lundqvist, N. 1972: *Nordic Sordariaceae s.lat*. — Symbolae Botanicae Upsaliensis 20. Almqvist & Wiksell Tryckeri, Uppsala, Sweden. 374 pp.

McInnes, P., Naiman, R. J., Pastor, J. & Cohen, Y. 1992: Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. — *Ecology* 73: 2059–2075.

McKendrick, J. D., Batzli, G. O., Everett, K. R. & Swanson, J. C. 1980: Some effects of mammalian herbivores and fertilization on tundra soils and vegetation. — *Arctic and Alpine Res.* 12: 565–578.

Milchunas, D. G. & Lauenroth, W. K. 1993: Quantitative effects of grazing on vegetation and soils over a global range of environments. — *Ecol. Monogr.* 63: 327–366.

Miquelle, D. 1983: Summer defecation — urination rates and volumes of moose. — *J. Wildl. Manage*. 47: 1230–1233.

Novikov, C. A. (ed.) 1959: *Transactions of the Pechora-Ilych State Game Preserve*. [Translated from Russian into English, Canadian Wildlife Service, TR-RUS-85].

Oldemayer, J. L. & Franzmann, A. W. 1981: Estimating winter defecation rates for moose, *Alces alces*. — *Can. Field-Naturalist* 95: 208–209.

Pastor, J. & Cohen, Y. 1997: Herbivores, the functional diversity of plants species, and the cycling of nutrients in ecosystems. — *Theor. Pop. Biol.* 51: 165–179.

Pastor, J., Dewey, B., Moen, R., Mladenoff, D. J., White, M. & Cohen, Y. 1998: Spatial patterns in the moose-forest-soil ecosystem on Isle Royale, Michigan, USA. — *Ecol. Appl.* 8: 411–424.

Pastor, J., Dewey, B., Naiman, R. J., McInnes, P. F. & Cohen, Y. 1993: Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. — *Ecology* 74: 467–480.

Pastor, J. & Naiman, R. 1992: Selective foraging and ecosystem processes in boreal forests. — *Am. Nat*. 139: 690–705.

Pastor, J., Naiman, R. J., Dewey, B. & McInnes, P. 1988: Moose, microbes and the boreal forest. — *BioScience* 38: 770–777.

Petersen, J. H. (ed.) 1998: *Svamperiget*. — Gads Forlag, Köbenhavn.

Petterson, R. 1998: Skalbaggar i älgspillning. — *Natur i Norr, Umeå* 2: 91–102.

Regelin, W. L., Schwartz, C. C. & Franzmann, A. W. 1985: Seasonal energy metabolism of adult moose. — *J. Wildl. Mana*ge. 49: 388–393.

Renecker, L. A. & Hudson, R. J. 1985: Estimation of dry matter intake of free-ranging moose. — *J. Wildl. Manage*. 49: 785–792.

Renecker, L. A. & Schwartz, C. C. 1998: Food habits and feeding behavior. — In: Franzmann, A. W. & Schwartz, C. C. (eds.), *Ecology and managenent of the North American moose*: 403–439. Smithsonian Institution Press, Washington.

Risenhoover, K. L. 1986: Winter activity patterns of moose in Interior Alaska. — *J. Wildl. Manage*. 50: 727–734.

Risenhoover, K. L. & Maass, S. A. 1987: The influence of moose on the composition and structure of Isle Royale forests. — *Can. J. For. Res.* 17: 357–364.

Rossow, L. J., Bryant, J. P. & Kielland, K. 1997: Effects of above-ground browsing by mammals on mycorrhizal infection in a early successional taiga ecosystem. — *Oecologia* 110: 94–98.

Ruess, R. W. & McNaughton, S. J. 1987: Grazing and the dynamics of nutrient and energy regulated microbial processes in the Serengeti grasslands. — *Oikos* 49: 101–110.

Saether, B. E. & Andersen, R. 1989: Resource limitation in a generalist herbivore, the moose *Alces alces*: ecological constraints on behavioural decisions. — *Can. J. Zool*. 68: 993–999.

Sand, H., Cederlund, G. & Danell, K. 1995: Geographical and latitudinal variation in growth patterns and adult body size of Swedish moose (*Alces alces*). — *Oecologia* 102: 433–442.

Schwartz, C. C., Regelin, W. L. & Franzmann, A. W. 1984: Seasonal dynamics of food intake in moose. — Alces 20: 223–244.

Schwartz, C. C., Regelin, W. L., Franzmann, A. W. & Hubbert, M. 1987: Nutritional energetics of moose. — In: Göransson, G. & Lavsund, S. (eds.), *Swedish Wildlife Research*, Proceedings, Second International Moose Symposium, Uppsala: 265-280.

Schwartz, C. C. & Renecker, L. A. 1998: Nutrition and energetics. — In: Franzmann, A. W. & Schwartz, C. C. (eds.), *Ecology and managenent of the North American moose*: 441–478. Smithsonian Institution Press, Washington.

Suominen, O. 1999: *Mammalian herbivores, vegetation and invertebrate assemblages in boreal forests: feeding selectivity, ecosystem engineering and trophic effects*. — Ph.D. thesis, Section of Ecology, Department of Biology, University of Turku.

Suominen, O., Danell, K. & Bergström, R. 1999a: Moose, trees, and ground-living invertebrates: indirect interactions in Swedish pine forests. — *Oikos* 84: 215–226.

Suominen, O., Danell, K. & Bryant, J. P. 1999b: Indirect effects of mammalian browsers on ground-dwelling insects in an Alaskan floodplain. — *EcoScience* 6: 505–510.

Telfer, E. S. & Kelsall, J. P. 1984: Adaptations of some large North American mammals for survival in snow. — *Ecology* 65: 1828–1834.

Timmermann, H. R. & Buss, M. E. 1998: Population and harvest management. — In: Franzmann, A. W. & Schwartz, C. C. (eds.), *Ecology and managenent of the North American moose*: 559–615. Smithsonian Institution Press, Washington, USA.

VanBallenberghe, V. & Miquelle, D. G. 1990: Activity of moose during spring and summer in interior Alaska. — *J. Wildl. Manage.* 54: 391–396.

Väre, H., Ohtonen, R. & Mikkola, K. 1996: The effect and extent of heavy grazing by reindeer in oligotrophic pine heaths in northeastern Fennoscandia. — *Ecography* 19: 245–253.

Vitousek, P. 1982: Nutrient cycling and nutrient use efficiency. — *Am. Nat.* 119: 553–572.