Moose Population Density and Habitat Productivity as Drivers of Ecosystem Processes in Northern Boreal Forests

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Abstract

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Ungulates have traditionally been viewed as consumers of plants and prey for predators, but recent studies have revealed that they also can have a significant indirect impact on fundamental ecosystem processes and biodiversity.

In my thesis, I focus on how moose (*Alces alces*) can affect the boreal forests ecosystem in Sweden. Because of its wide distribution and at present high population densities we can expect moose to be important. The outcome depends on moose density as well as habitat productivity, and we chose an experimental approach where we simulated browsing, defecation and urination of different moose population densities in exclosures situated along a forest productivity gradient. The simulation was based on a review of available literature.

I found that moose can have a significant impact on the morphology and productivity of the main food plants in winter, Scots pine (*Pinus sylvestris*) and birch (*Betula pubescens* and *B. pendula*). The outcome was highly dependent on moose density. At "low" to "moderate" moose densities, small and non-significant effects were found, whereas the effects were large at higher moose densities. I concluded that both foraging efficiency and food availability can be affected at higher moose densities over extended time, and that food production may steadily decrease to a level where winter food is limiting. Habitat type also affected the results. At low productive sites both birch and pine had low productivity and thus compensatory ability to defoliation by moose. Birch and pine also seemed to respond differently to habitat productivity, and the explanation might have been that pines suffered from competition with deciduous trees at richer sites.

The quantity and quality (species mix) of litter from the tree and shrub layers were affected by the level of simulated moose population density and habitat. Richer sites produced more high quality litter (*i.e.* lower proportion of conifer needles). The quantity decreased and the proportion of conifer needles increased with simulated moose density. Despite the high browsing pressure on Scots pine, the general outcome of moose at high population densities over extended time seems to be decreased quantity and quality of litter, and thus reduced nutrient cycling and habitat productivity in the long run.

Decay rates of moose dung appeared to be rather low, suggesting that the fertilizing effect also was low. However, the dung disappeared fast at richer sites due to concealment by vegetation, and visibility was negatively correlated with litter production.

The coprophilous community colonizing moose dung appeared to be species rich and poorly known, and the abundance and species richness are affected by interactions with other organisms as well as habitat type.

In my thesis I show that moose can affect fundamental ecosystem processes and biodiversity in Swedish boreal forests, and act as an important ecosystem engineer. Productivity gradients are important to consider when studying effects on the ecosystem level. Based on my findings, I suggest that more studies should be done on other tree species, plants in the field and bottom layers, soil properties, microclimate, and organisms connected to faeces and urine.

Key words: Alces alces, biodiversity, birch, boreal forest, browsing, coprophilous organisms, food ecosystem processes, faeces, habitat, litterfall, moose, productivity, Scots pine, selective feeding, Sweden.

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Appendix

Papers I-VI

I base my thesis on the following papers, which will be referred to by the corresponding Roman numerals in the text.

I. Persson, I.-L., Danell, K. and Bergström, R. 2000. Disturbance by large herbivores in boreal forests with special reference to moose. *Annales Zoologici Fennici 37*, 251-263.

II. Persson, I.-L., Danell, K. and Bergström, R. Effects of moose on morphology and productivity of Scots pine and birch: importance for foraging efficiency and food availability. (Manuscript).

III. Persson, I.-L., Danell, K. and Bergström, R. How forest productivity affects growth responses of Scots pine and birch subjected to simulated browsing, defecation and urination of moose. (Manuscript).

IV. Persson, I.-L., Pastor, J., Danell, K. and Bergström, R. Impact of moose population density and forest productivity on the production and composition of litter in boreal forests. (Manuscript).

V. Persson, I.-L. Seasonal and habitat differences in visibility of moose pellets. (Manuscript submitted to *Alces*).

VI. Nyberg, Å. and Persson, I.-L. 2002. Habitat differences of coprophilous fungi on moose dung. *Mycological Research 106*, 1360-1366.

Introduction

The central theme in ecology is the understanding of how organisms interact with each other and the environment (Begon, Harper & Townsend 1990). The prevailing approach has been to study the direct trophic interactions between organisms, but recent research has revealed that indirect interactions can be even more important (Jones et al. 1994; Hobbs 1996).

Ungulates have traditionally been viewed as consumers of plants and prey for predators (Hobbs 1996). Less known is their role as important agents of changes in the environment, which can modify conditions for other organisms (Hobbs 1996). They are important regulators of ecosystem processes like primary production, nutrient cycling and abiotic disturbance, they regulate process rates, modify spatial mosaics and can control transitions between alternative ecosystem states (Naiman 1988; Crawley 1989; Hobbs 1996; Moen, Pastor & Cohen 1998). Some ungulates thus fulfil the criteria of being ecosystem engineers; organisms that directly or indirectly modulate the availability of resources to other species by causing physical state changes in biotic or abiotic materials, and in so doing modify, maintain and/or create habitats (Jones et al. 1994).

Ungulates affect ecosystem properties mainly through four mechanisms (Pastor, Moen & Cohen 1997): (1) Defoliation, resulting in immediate, short-term compensatory growth of the food plants; (2) deposition of faeces and urine; (3) long-term successional changes in plant species composition and (4) changes in the physical environment as a result of 1-3. The outcomes vary widely among ecosystem types (Bryant et al. 1991; Augustine & McNaughton 1998; Hester et al. 2000), and must thus be studied for each ecosystem specifically. In my thesis I focus on the impact of the ungulates inhabiting the northern boreal forests, with special emphasis on moose (*Alces alces*).

Regulation of ungulate populations

To understand the impact of ungulates, better knowledge about the relations between their population dynamics and ecosystem processes is necessary (Hobbs 1996; Augustine & McNaughton 1998). To reveal which factors limit and regulate the population growth is therefore essential (Crawley 1989; Sæther 1997). Limiting factors can be defined as any process which quantifiably affect population growth, and can thus be both density-dependent and density-independent factors (Messier 1991). Examples of limiting factors are weather conditions and when the proportion of the prey population killed by predators decreases with increasing prey density (inverse density-dependence). Regulatory factors are any density-dependent processes that ultimately keep populations within normal density ranges (Murray 1982; Sinclair 1991; Skogland 1991). Examples are when the proportion of the prey population killed by predators increases with prey density, or when mortality caused by starvation increases with population density. Regulating factors thus constitute a subset of limiting factors, and have the potential to depress population growth as animal abundance increases (Messier 1991). Limiting factors can explain changes in animal abundance (Messier 1991; Sinclair 1991; Skogland 1991), but only regulating factors can explain the upper limit on population density

(Messier 1991; Sinclair 1991). Which factors regulate populations is therefore especially important to reveal.

Competition for food and predation is considered to be the main factor which can regulate population growth of the ungulates inhabiting the northern boreal forests (Peek 1980), but there is no general agreement about which factor is most important (Peek 1980; Thompson & Peterson 1988; Messier 1994). Hairston, Smith & Slobodkin (1960) claimed that whether organisms are regulated by predators or resources depends on their position in the food chain. In terrestrial ecosystems, plants are resource limited, not herbivore limited, and obvious depletions of green plants are exceptions. Predators regulate herbivore populations, and thereby allow plant biomass to accumulate - "the world is green" concept. According to Hairston, Smith & Slobodkin (1960), ungulates should thus be regulated by their predators. The ungulates inhabiting the northern hemisphere have coevolved with efficient predators (Pimlott 1967), of which the grey wolf (*Canis lupus*) is the dominant non-human predator most likely to influence the populations (Mech 1970). Predation obviously inflicts losses in the prey population, and thus is a limiting factor by definition (Sinclair 1991; Boutin 1992). However, it is considerably more difficult to determine if it also regulates growth of the prey population (Sinclair 1991; Ballenberghe & Ballard 1994), but some studies have found the ungulate populations to be regulated by predation (Peek 1980; Messier & Crête 1985; Ballenberghe & Ballard 1994; Messier 1994).

The top-down view concerning the effect of predation on population dynamics of ungulates proposed by Hairston, Smith & Slobodkin (1960) has been topic for considerable debate (Crawley 1989; Boutin 1992; Ballard & Ballenberghe 1998; Ballenberghe & Ballard 1998). According to Crawley (1989) food more often than predation regulates vertebrate herbivores, and there are studies which have found that ungulates are regulated by food competition (Peek 1980; Peterson, Paige & Dodge 1984; Messier 1991; Skogland 1991). Some ungulates, red deer (*Cervus elaphus*) and moose in particular, seems to be entirely extrinsically regulated (*i.e.* regulated by resource availability, predators and/or diseases, Caughley & Crebs 1983), and can therefore increase to numbers beyond the sustaining level of their food supply (Pimlott 1967; Keith 1974).

However, if food competition or predation regulates the ungulate populations depends on the conditions; there is no general answer but rather a continuum of possible outcomes (Mech 1970; Peek 1980; Caughley 1981; Thompson & Peterson 1988; Messier 1991). Predation and food competition can act concomitantly to regulate ungulate populations (Caughley 1981), or neither of them may have a regulatory function. Environmental factors (*e.g.* climate) also seem to have a strong influence on the population dynamics of ungulates (Sæther 1997). Predation is most likely to be the main regulatory factor if the ungulate densities are low (Messier & Crête 1985; Sinclair 1991; Messier 1994), and/or if the predator(s) are very efficient (Messier 1994). It also seems to have a larger impact in systems with multiple predators than in systems with only one predator species present (Ballenberghe 1987; Bergerud & Snider 1988; Larsen, Gauthier & Markel 1989, Gasaway *et al.* 1991). Population regulation through food competition can be expected to occur at high ungulate densities, where the food plants no longer can compensate for the tissue loss, and is most likely to arise during winter when environmental stochasticity (*e.g.* weather) and density dependence in combination

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affect the resource base (Sæther 1997). The concept of carrying capacity is important (Sinclair 1991; Ballenberghe & Ballard 1998) and has been defined as the maximum density of animals that can be sustained indefinitely without inducing trends in vegetation, *e.g.* the ungulate - vegetation equilibrium (Caughley 1976). However, carrying capacity is no simple conception (Pastor, Moen & Cohen 1997; Sæther 1997), and a stable equilibrium between ungulate populations and the food resources has been claimed to be unlikely to exist in predator-free environments (Sæther 1997). Thus, ungulate populations are not characterized by a simple carrying capacity, and regulating factors rather act to keep population densities within certain limits (Caughley 1976; Begon, Harper & Townsend 1990; Pastor, Moen & Cohen 1997).

The moose in Sweden

The moose is abundant in the boreal forests of the northern hemisphere (Karns 1998), and invaded Sweden after the last glaciation, some 9,000 - 10,000 years ago (Cederlund & Bergström 1996). The population density and distribution has varied considerably since then, but has increased dramatically after the Second World War (Lykke 1974; Markgren 1974; Cederlund & Bergström 1996). Moose is now distributed over the whole country except from the island Gotland (Gustafsson & Ahlén 1996) and occur in densities higher than experienced in historic time, at present up to about 20 moose per 1000 ha in average winter density (Cederlund & Bergström 1996).

The main reasons for the increase in the moose population are predator control, regulated hunting and the large-scale introduction of the modern forestry with clear-cutting, resulting in a considerable increase in available food (Cederlund & Bergström 1996). At the Scandinavian Peninsula (Norway and Sweden), the native predators of moose, wolf and brown bear (*Ursus arctos*), were almost extirpated during the last decades of the 19th century (Haglund 1975; Swenson *et al.* 1994). The populations are now recovering (Swenson *et al.* 1994; Wabakken *et al.* 2001), but they are yet not numerous enough to regulate the moose population. Today the main mortality of moose in Sweden is human hunting, and approximately 100,000 moose are shot each year (http://www.jagareforbundet.se, 14 Feb. 2003). However, despite the high hunting pressure and increased food abundance, density-dependent effects of resource depletion on body growth and reproduction has been found in some areas in Sweden (Sand 1996). When the population density is at a level near carrying capacity, we can also expect the indirect impacts on ecosystem processes and biodiversity to be especially strong. Studies of the interactions between the moose and its food resources at high population densities, as well as effects on fundamental ecosystem processes and biodiversity are therefore necessary.

The moose - ecosystem interaction

The grazing and browsing (Hofmann 1989) by large ungulates can affect the morphology and productivity of their food plants (Jameson 1963; McNaughton 1979; Paige & Whitham 1987; Crawley 1989; Gordon & Lindsay 1990; Danell, Bergström & Edenius 1994). Morphological changes can affect the harvest rates (*i.e.* food intake per unit time) and thus foraging efficiency (Spalinger & Hobbs

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1992; Shipley *et al.* 1999), whereas changes in the productivity can affect the entire resource base (Gordon & Lindsay 1990). Studies of moose browsing have shown that both morphology and productivity of the food plants can be affected (Oldemeyer 1983; Bergström & Danell 1987; Danell, Bergström & Edenius 1994; Bergman 2001). Because winter food is considered a critical factor for moose (Thompson & Euler 1987; Andersen 1991; Shipley, Blomquist & Danell 1998), changes in the productivity of the main food plants in winter are especially important.

Ungulates can also affect fundamental ecosystem processes like nutrient cycling and habitat productivity (Holland *et al.* 1992; Pastor & Naiman 1992; Milchunas & Lauenroth 1993; Hobbs 1996; Augustine & McNaughton 1998). Their selective feeding, changing the structure and species composition of the plant community and thus the quantity as well as quality (species mix) of plant litter seems to be most important (McInnes *et al.* 1992; Pastor *et al.* 1993; Hobbs 1996; Kielland & Bryant 1998; Ryerson & Parmenter 2001). Ungulates generally prefer plants which are rapidly growing, rich in N and low in secondary compounds (Bryant *et al.* 1991; Jefferies, Klein & Shaver 1994). Studies from North America indicate that the general outcome of moose browsing in boreal forests is increased dominance of the less preferred conifers with slowly decomposing, nutrient-poor litter, and thus reduced nutrient cycling and habitat productivity (Pastor *et al.* 1988; Bryant *et al.* 1991; McInnes *et al.* 1992; Pastor *et al.* 1993). However, the effect of moose browsing might be different in Sweden than in North America, because Scots pine (*Pinus sylvestris*) is important in the winter diet of Swedish moose (Cederlund *et al.* 1980; Bergström & Hjeljord 1987; Heikkilä & Härkönen 1993).

Faeces and urine of large ungulates offer easily available plant nutrients which can increase plant productivity (Ruess & McNaughton 1987; Pastor *et al.* 1993). However, the fertilizing effect depends on decomposition rates, which have been found to vary over the year and among habitat types (Smith 1968; Lavsund 1975; Harestad & Bunnell 1987; Lehmkuhl, Hansen & Sloan 1994; Massei, Bacon & Genov 1998). To reveal such differences is also important concerning wildlife management. With the large moose population we have in Sweden, reliable and cheap methods to estimate population density and trends are important to develop, and count of pellet groups is a commonly used method (Wallmo *et al.* 1962; Neff 1968; Timmermann 1974; Harestad & Bunnell 1987). Different disappearance rates over the year and among habitat types can bias the estimates and are important to reveal.

Large ungulates can also affect other animal assemblages, and studies of moose have shown changes in the abundance and species diversity of ground and tree-living invertebrates (Danell & Huss-Danell 1985; Roininen, Price & Bryant 1997; Suominen, Danell & Bryant 1999; Suominen, Danell & Bergström 1999). Faeces and urine of moose are also interesting concerning biodiversity. Many species of fungi, mosses and invertebrates are specialised to live on these substrates (Marino 1988; Hanski & Cambefort 1991; Dix and Webster 1995), but data are scarce concerning wild, forest-living species. The community composition can also be expected to vary with habitat type, but there are little data.

In an ecosystem perspective, few studies have dealt with the impact of either moose or other ungulates (Naiman 1988; Pastor, Moen & Cohen 1997; Augustine & McNaughton 1998; Kienast *et al.* 1999). Many studies have been done as

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exclosure experiments, where ungulates have been excluded (Crawley 1989; Hester *et al.* 2000). The differences between inside the exclosure (representing the ecosystem without ungulates) and the outside subjected to a more or less known ungulate density, have then been estimated. There are several shortcomings with these studies, however. Ungulates are an integral part of many ecosystems, and the interactions cannot be assessed simply by removal of the ungulates (Hester *et al.* 2000). Plant - animal - ecosystem interactions are spatially and temporally dynamic systems, and responses are often not linear (McNaughton 1979; Hilbert *et al.* 1981; Pastor, Moen & Cohen 1997). There might also exist critical threshold values (Kuznetsov 1984; Kienast *et al.* 1999; Hester *et al.* 2000) which is important to reveal, but few data are available (Hester *et al*; 2000). Also, the outcome of the interactions differs among ecosystem types (Augustine & McNaughton 1998), as well as among habitat types within ecosystems (Thompson & Peterson 1988; Jefferies, Klein & Shaver 1994; Hester *et al.* 2000). Gradients of primary productivity have been shown to affect the outcome of the herbivore - plant - ecosystem interaction in grasslands (Milchunas & Lauenroth 1993), and there is clearly a need for more studies of the impact of productivity in forest ecosystems (Hester *et al.* 2000). To reveal the impact of moose and other ungulates on ecosystem processes and biodiversity in forest ecosystems, controlled, experimental studies where several known ungulate densities as well as productivity gradients are taken into account should be done (Hester *et al.* 2000).

Objectives

The intent with my thesis was to study the impact of moose on some important ecosystem processes and on biodiversity in Swedish boreal forests. I also conducted a study of the visibility of moose dung. More specifically, the following questions were asked in papers I - VI:

(I) How large is the disturbance by moose (*i.e.* biomass removal, trampling, defecation and urination) in quantitative terms?

(II) How will simulated browsing, defecation and urination of different levels of moose population density affect the morphology and productivity of Scots pine and birch (*Betula pubescens* and *B. pendula*)?

(III) How will the variation in forest productivity affect the response of Scots pine and birch to simulation of browsing, defecation and urination of different levels of moose population density?

(IV) How will simulated browsing, defecation and urination of different levels of moose population density affect the litter production and quality (species mix) in the tree and shrub layers along a forest productivity gradient?

(V) How do season and habitat affect the visibility of moose pellet groups?

(VI) Which fungal species colonize summer dung of moose in northern Sweden, and how large is the variation in fungal abundance and species richness between different habitat types?

Study Area

The study was performed in the middle boreal zone (Ahti, Hämet-Ahti & Jalas 1968), coastal northern Sweden (Figure 1). The length of the vegetation period (average day temperature > 5 °C) in the study area is 120 - 150 days with onset between 10 and 20 May, and precipitation during the vegetation period is 300 - 350 mm (Nilsson 1996). Snow covers the ground approximately from 20 - 25 October to 5 - 15 May (Raab & Vedin 1996). The climatic variation within the study area is thus rather small, and we could assume that climatic conditions were the same at the different study sites. Approximately 80 - 90% of the total land area is forested (Nilsson 1996), and the area is subjected to intensive forestry. Young forest stands cover approximately 15 - 25% of the total forested area (Statistical yearbook of forestry 1999). Scots pine, common birch (*Betula pubescens*) and silver birch (*B. pendula*) were the dominant tree species at the study sites, but also rowan (*Sorbus aucuparia*), aspen (*Populus tremula*) and willows (*Salix* spp.) occured (Table 1). Raspberry (*Rubus idaeus*) was common in the shrub layer at some sites (*i.e.* Åtmyrberget and Mörtsjöstavaren). Wavy hair grass (*Deschampsia flexuosa*), bilberry (*Vaccinium myrtillus*), lingonberry (*V. vitis-idaea*) and heather (*Calluna vulgaris*) were common in the field layer, and *Pleurozium schreberi*, *Polytrichum commune* and *Cladina* spp. were common in the bottom layer (Table 2).
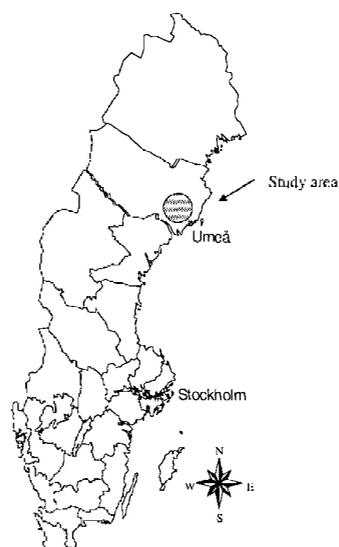
Fig. 1. Map over Sweden showing the study area.

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Table 1. *The study sites ranked after increasing site index (SI) for pine (i.e. mean height at 100 years). Further are the litter production in the control plots (g dry mass per m^2 and year), mean age of trees (years), geographic position (WGS84), altitude (m above sea level), browse biomass (g dry mass per m^2) estimated in 1999, pine density (trees per m^2) and major tree species presented. B = Betula spp., P = Pinus sylvestris, Po = Populus tremula, S = Sorbus aucuparia and Sa = Salix spp. Tree species occurring sparsely are in brackets. For all data, means and standard errors (in brackets) are presented*

Site	SI	Litter	Age[1]	Geogr. position	Altitude
Lögdåberget	12.9	3.17	16	64° 00' N, 18° 45' E	300
Skatan	14.7	4.55	9	64° 13' N, 19° 09' E	265
Djupsjöbrännan	24.3	4.59	9	64° 06' N, 19° 12' E	250
Åtmyrberget	24.8	17.47	9	64° 12' N, 19° 17' E	305
Selsberget	26.3	4.27	7	64° 15' N, 19° 16' E	175
Mörtsjöstavaren	26.4	12.03	7	64° 22' N, 20° 07' E	280
Ralberget	27.3	6.44	9	64° 13' N, 20° 42' E	250
Rönnäs	27.9	3.07	9	64° 02' N, 20° 40' E	62

Table 1. cont.

Site	Browse birch	Browse pine	Pine density	Tree species
Lögdåberget	0.7 (0.21)	51 (3.23)	0.56 (0.02)	B, P, Po, (S, Sa)
Skatan	4.7 (0.43)	37 (2.49)	0.62 (0.02)	B, P, (Po, Sa)
Djupsjöbrännan	5.3 (0.18)	28 (1.58)	0.27 (0.01)	B, P, Sa
Åtmyrberget	14.0 (0.46)	21 (1.35)	0.16 (0.01)	B, P, S, Sa, (Po)
Selsberget	1.5 (0.11)	15 (0.83)	0.21 (0.01)	B, P, S, (Po, Sa)
Mörtsjöstavaren	9.0 (0.59)	22 (1.55)	0.15 (0.01)	B, P, S, Sa
Ralberget	9.4 (0.37)	39 (2.53)	0.18 (0.01)	B, P, S, Sa, (Po)
Rönnäs	3.5 (0.47)	22 (1.01)	0.22 (0.01)	B, P, (Po)

[1]*The mean age was the same for birch and pine at all sites*

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Table 2. *The dominant plant species in the field and bottom layers at the different study sites. Particularly dominant species are in bold*

Site	Field layer	Bottom layer
Lögdåberget	**Calluna vulgaris**, *Vaccinium myrtillus, V. vitis-idaea*	*Pleurozium schreberi, Cladina rangiferina, Dicranum scoparium, C. arbuscula*
Skatan	*Calluna vulgaris, Vaccinium vitis-idaea, V. myrtillus, Empetrum* spp.	*Cladina rangiferina, Pleurozium schreberi, C. arbuscula, Dicranum scoparium, Polytrichum commune*
Djupsjöbrännan	***Deschampsia flexuosa***, *Vaccinium vitis-idaea, V. myrtillus*	***Polytrichum commune***, *Pleurozium schreberi, Dicranum scoparium*
Åtmyrberget	***Deschampsia flexuosa***, *Carex globularis, Gymnocarpium dryopteris, Dryopteris carthusians, C. canescens*	***Polytrichum commune**, Sphagnum* spp.
Selsberget	***Deschampsia flexuosa***, *Vaccinium myrtillus, V. vitis-idaea, Maianthemum bifolium, Luzula pilosa*	*Pleurozium schreberi, Polytrichum commune*
Mörtsjöstavaren	***Deschampsia flexuosa***, *Gymnocarpium dryopteris, Vaccinium myrtillus, Epilobium angustifolium*	***Polytrichum commune**, Dicranum scoparium, Pleurozium schreberi*
Ralberget	***Deschampsia flexuosa***, *Vaccinium myrtillus, V. vitis-idaea, Carex globularis, Gymnocarpium dryopteris*	*Polytrichum commune, Pleurozium schreberi, Dicranum scoparium*
Rönnäs	***Deschampsia flexuosa***, *Vaccinium vitis-idaea, Calluna vulgaris, V. myrtillus*	*Polytrichum commune, Dicranum scoparium, Pleurozium schreberi*

Material and Methods

We chose a controlled experimental study where we aimed at simulating browsing, defecation and urination of different levels of moose population density in exclosures situated along a forest productivity gradient. The exclosures were built in 1998, and the field work started in early spring 1999. A separate study was done to investigate the community of coprophilous organisms colonizing moose dung.

The exclosures

The simulation of moose was done in 8 exclosures, each of 4,900 m². The exclosures were situated in young forest stands with a mixture of Scots pine and deciduous trees (Table 1), the habitat type most preferred by moose (Cederlund & Bergström 1996). In treatment plots (25 × 25 m, Figure 2) inside each exclosure, we simulated browsing, defecation and urination corresponding to 0 (control), 10, 30 and 50 moose per 1000 ha on a landscape level. The simulated moose densities were allocated randomly among these subplots within each exclosure. The reasons

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for choosing the moose densities were that 10 moose per 1000 ha approximately corresponded to the average winter density of moose in the study area (Ball, Danell & Sunesson 2000), and was also common in many other areas in Sweden (Hörnberg 2001). Thirty moose per 1000 ha was slightly higher than the highest estimated winter density of moose on the County basis in Sweden (24 moose per 1000 ha, Värmland County 1980-81, Hörnberg 2001), and 50 moose per 1000 ha represented the extremely high moose density. However, as high and even considerably higher moose densities have been documented locally in Sweden, *e.g.* in winter concentration areas.

We did not obtain the estimated biomass removal in the 50 moose per 1000 ha plot at some sites, even after compensating among species (Table 3). In those cases, as much biomass as possible was clipped in the "50 moose" treatment plot, and 1/5 and 3/5 of that biomass was then clipped in the "10" and "30 moose" plots respectively in order to maintain the same proportional simulated population densities. Due to the complexity in the herbivore - food plant - ecosystem interaction, there hardly exists any simple asymptotic food carrying capacity (Pastor, Moen & Cohen 1997; Sæther 1997). In those cases where we did not gain the estimated biomass, the food base could not support a moose density of "50" at that specific site and would have been a limiting factor. The use of proportional clippings thus allowed us to estimate the impact of a moose density of 1/5 (20%) and 3/5 (60%) the size of the moose density a given site can support. Pooling all study sites, the biomass removed per m^2 and year corresponded to simulated moose population densities of 8, 24 and 40 per 1000 ha on average. However, because we could remove biomass corresponding to the intended population densities at most sites, I have used 10, 30 and 50 moose per 1000 ha as figure legends and in the discussion.

The study of how habitat differences affected the composition of the coprophilous community colonizing moose dung was done within the same study area, but outside the exclosures. Here we chose older forests; a mature pine forest (sunny and dry), a mature pine - spruce forest (shady and mesic) and a mire (sunny and wet).

Definition of the forest productivity gradient

The forest productivity gradient was a main factor in the study, and it was important to find useful quantitative measurements to rank the sites. We chose to estimate site index of pine (*i.e.* estimated top height at 100 years) using methods developed for young forest stands (Lindgren *et al.* 1994; Elfving & Kiviste 1997). Site index is a common measurement of habitat productivity in forestry in Sweden, and is developed for coniferous trees. However, conifers and deciduous trees seem to have fundamentally different soil - plant interactions (Ollinger *et al.* 2002). As complementary productivity measurements, we also used the estimated available browse biomass of birch and pine before the treatment started (Table 1, Figure 2) as well as litter production in the tree and shrub layers in the control plots (Table 1, Paper IV).
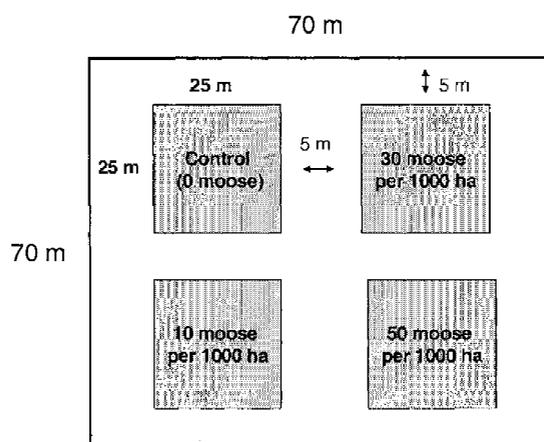
Fig. 1. The design of the exclosures. Treatment (level of simulated moose density) was allocated at random to plots (25 × 25 m) within each exclosure. The fence was 3 m, and there were buffer zones of at least 5 m between treatment plots and between treatment plots and the fence.

Table 3. *The real moose densities (per 1000 ha) simulated in the "50 moose" per 1000 ha plot at the different sites in winter and summer during 1999-2001, and average biomass (g dry mass) removed per m^2 and year. Reasons for the deviations from the intended moose densitiy: Winter clipping: Åtmyrberget had low pine biomass, and the pines were attacked by* Melampsora pinitorqua. *Selsberget had both low pine and birch biomass. At Rönnäs, the pines were rather small in 1999, and the birch biomass was low. However, the biomass corresponding to 50 moose per 1000 ha could be clipped in 2000 and 2001. Summer clipping: Lögdåberget and Skatan were lichen-rich pine heaths. The occurrence of deciduous trees was low, and raspberry and fireweed were missing. Aspen, rowan, willows as well as raspberry, blueberry and heather were scarce at Djupsjöbrännan; birch was therefore treated extremely hard to compensate. Rönnäs had low biomass of birch and other deciduous trees, fireweed and raspberry*

Site	Winter	Summer	Biomass removal
Lögdåberget	52	13	19.5
Skatan	53	23	24.8
Djupsjöbrännan	53	44	35.3
Åtmyrberget	46	48	35.5
Selsberget	22	48	29.5
Mörtsjöstavaren	51	49	37.3
Ralberget	54	48	37.5
Rönnäs	39	24	21.8
Mean	**46**	**37**	**30.2**

Simulation of moose browsing, defecation and urination

Inside the plots (25 × 25 m), we simulated browsing, defecation and urination of moose. Assuming that moose consumes 5 times more dry mass in young forest stands than in other habitats (based on pellet counts of moose in the study area, K. Danell, unpubl. data) and that young forest stands cover about 20 % of the forested area (Statistical yearbook of forestry 1999), the biomass removal, number of dung

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piles and urine spots deposited per month for the different moose densities were estimated (Persson, Danell & Bergström 2000, Paper I). The amount of clipping of different food plants was based on the diet composition of moose (Cederlund *et al.* 1980; Bergström & Hjeljord 1987; Shipley, Blomquist & Danell 1998, Table 4). If it was impossible to gain the estimated biomass of one food plant, the remaining biomass was clipped from another food plant(s) in the diet. As far as possible, biomass from plants in the tree and shrub layers was compensated with biomass from other species in those layers, and the same was done for field layer plants.

Each of the winter and summer season was set to 180 days. In winter when plants are dormant, we did the clipping for the whole winter in April, and in summer we clipped once a month (Figure 2). The dung for the winter was laid out in May, and the dung and urine for the summer was laid out in September - October (Figure 2). The dung was collected at a nearby moose farm. The animals were using mainly natural habitats and had free access to natural food (Nyberg & Persson 2002, Paper VI). The urine was done by solving urea in water (5.15 g per l, Persson, Danell & Bergström 2000, Paper I). Data on the composition of winter urine was not available.

The moose dung used in the study of coprophilous organisms (Nyberg & Persson 2002, Paper VI) was also collected at the moose farm. Here we emphasized to collect newly deposited dung, and no dung pile was older than 24 h when it was collected. To collect the dung at the moose farm also offered dung from moose with the same diet, and thus basically the same inoculum of fungal species.
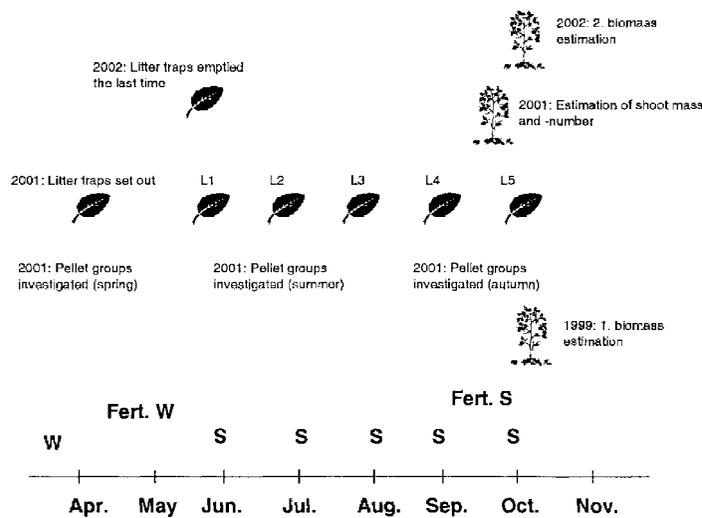

Fig. 2. The simulation of browsing, defecation and urination of moose and data sampling in the exclosures during 1999-2002. W = winter clipping, S = summer clipping (same procedure repeated each year). Fert. W = winter dung laid out, Fert. S = summer dung and - urine laid out (same procedure repeated each year). L = litter traps emptied (one annual production cycle, Paper IV). Data on shoot mass and number as well as biomass is presented are Papers II - III. The results of the pellet group investigation are presented in paper V.

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Table 4. *The estimated composition of the diet of moose, expressed as % of dry mass. The other deciduous trees; "other dec. trees" were* Populus tremula, Sorbus aucuparia *and* Salix spp. *The winter season was from November through April (180 days) and the summer season from May through October (180 days)*

Food plant	Winter	May	June	July	Aug.	Sept.	Oct.
Pinus sylvestris	60	30					30
Betula spp., twigs	30	20				10	20
Betula spp., leaves		10	50	50	50	50	
Rubus idaeus			10	10	10		
Vaccinium myrtillus		30	10	10	10	25	15
Calluna vulgaris						5	25
[1]E. angustifolium			20	20	20		
Other dec. trees, twigs	10						10
Other dec. trees, leaves		10	10	10	10	10	

[1]*Epilobium angustifolium*

Results and Discussion

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

Reviewing available literature on moose, the average daily food intake, area trampled as well as dung and urine deposited were estimated. All studies reported considerable variation in these variables, but the average values turned out to be remarkably similar in different parts of the world. The main differences were between summer and winter; the food intake, distance moved (and thus area trampled) and urine deposited were about twice as high in summer as in winter. No seasonal differences were found concerning dung deposition, however.

Using the estimates from the literature review and an estimate of a total population of 350,000 moose in Sweden before the hunting season, the total biomass removed during one year would roughly be 2.5 - 3.2 × 10^9 kg dry mass. The area trampled would be 3,255 km^2, which is comparable to Vänern, the largest lake in Sweden (5,585 km^2). Some 3 × 10^8 kg dung containing 5,6 × 10^6 kg N and 1.3 × 10^6 m^3 urine containing an unknown amount of N (data on the composition of winter urine was not available) would be deposited. Thus, we concluded that the large moose population we have in Sweden clearly has the potential to directly and indirectly affect the forest ecosystem, especially in preferred moose habitats.

Reviewing existing studies of the impact of moose on the ecosystem also revealed considerable scarcity of data except from the direct impact of browsing on economically valuable forest trees (*e.g.* Scots pine). The interactions are complex, and no general conclusions can be made based on existing studies. Also, many studies are from North America, and results from those studies may not be directly applicable to Sweden, because moose have different diet preferences in Sweden and generally occur at higher densities. We therefore concluded that more studies of how moose affects the boreal forest ecosystem in Sweden are necessary.

The morphology and productivity of Scots pine and birch (II - III)

In Paper II we investigated the impact of simulated browsing, defecation and urination of different levels of moose population density on the morphology and productivity of the quantitatively most important food plants in winter, birch and Scots pine (Ahlén 1973, Cederlund *et al.* 1980, Bergström & Hjeljord 1987) after 3 years of treatment. In Paper III we investigated how the growth responses varied along the productivity gradient and if birch and pine responded differently.

Morphology and productivity of both birch and pine were affected by the level of simulated moose population density. The mean yearly height development decreased, the number of annual long-shoots decreased, and the mass of individual long-shoots increased with increasing density. The total biomass of long-shoots per tree in the height interval 0.5 - 2.5 m and the yearly development in browse biomass per m^2 decreased with increasing density. We found small and non-significant effects at a population density of roughly 10 moose per 1000 ha, whereas the effects of both morphology and productivity were highly significant at "30" and "50 moose". We concluded that at high moose densities, harvest rates (*i.e.* food intake per unit time) and thus foraging efficiency as well as food production can be affected. Larger shoots might result in increased foraging efficiency, if not the increase in harvest rate is outweighed by associated decreases in food quality and/or energy expenditure. However, at high moose densities over extended time, the food availability might steadily decrease to a level where moose compete for food in winter and we can expect density-dependent effects on the population growth rate.

We also found considerable variation among sites in the growth responses of both birch and pine subjected to the same levels of simulated moose population density. The mass of individual long-shoots was positively correlated with site index for both birch and pine. The smallest shoots were found on lichen-pine heaths, which are dry and have nutrient-poor soils (Scholes & Nowicki 1998). Trees growing at such sites might thus have lower compensatory ability to herbivory. For birch, the total shoot mass per tree was positively correlated with litter production in the control plots (Paper IV). Litter is a main source of soil nutrients (Melillo, Aber & Muratore 1982; Flanagan & Van Cleve 1983), and the soil nutrient availability likely increased with litter production, explaining the correlation with productivity of birch. Birch (and other deciduous trees) might therefore have higher compensatory ability at richer sites. We found no correlations between the total shoot biomass of pine and site index or litter production. The explanation might have been competition between pine and birch (and other deciduous trees). At richer sites, deciduous trees have higher growth rate and are competitively dominant to conifers (Lundmark 1988; Keeley & Zedler 1998). Pines might have faced a trade-off between abiotic stress due to nutrient deficiency at the poorest soils, and biotic stress due to competition with deciduous trees for nutrients and light at richer sites. Pines might therefore have the highest compensatory ability at some medium-rich sites.

At the highest level of simulated moose population density we found pronounced decreases in food production also at rich sites suggesting that the impact of moose overrides other habitat differences at high moose densities. However, the

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productivity and thus compensatory ability of the food plants vary with habitat, and habitat differences in productivity might be more important at lower moose densities.

The production and composition of litter (IV)

We found significant effects of both level of simulated moose population density and habitat productivity (here defined as litter production in the control plots) on the quantity and quality (species mix) of litter from the tree and shrub-layers. The sites with high birch biomass produced large amounts of high quality litter (*i.e.* low proportion of conifer needles). The level of simulated moose population density had a large effect. The quantity of litter produced decreased considerably with increasing density, and was on average 53% lower in the "50 moose" plots than the control plots. The quality of litter also decreased with density, but the effect was only statistically significant at the "50 moose" per 1000 ha level, where the proportion of conifer needles had increased from on average 46% (g dry mass) in the control plots to 68%. Our results agree with Suominen, Danell & Bergström (1999), who suggested that the main effect of moose browsing at pine-dominated sites is a more open canopy and lower litter quantity, whereas the main effect in mixed conifer-deciduous sites is both reduced quantity and quality. Despite the high browsing pressure on pine in Sweden, the general outcome of moose browsing seems to be the same as in North America; decreased litter quality and thus reduced nutrient cycling and habitat quality. However, the moose density where we have a significant effect are likely higher in Sweden than North America. Studies at Isle Royale, Michigan, suggest that a biomass removal of 2 - 4 g per m^2 and year seems to cause decreased nutrient cycling (Pastor *et al.* 1988), whereas we had a significant effect only at a biomass removal of on average 30 g per m^2 and year. The forest methods with clear-cutting offering an abundance of moose food, as well as the high browsing on Scots pine in Sweden might explain the differences between our results and those at Isle Royale. However, more long-term studies are needed to conclude about which levels of moose population density that lead to increased dominance of conifers in Sweden. Also, more studies of the effects changes in the tree and shrub layers can have on the litter production and species mix in the field layer are necessary.

Seasonal and habitat differences in the visibility of moose pellets (Paper V)

In paper V, I investigated how fast moose dung disappeared along the forest productivity gradient (measured as site index and litter production). The study was done in the exclosures, and was thus an experimental study with pellet groups of equal size and origin. The visibility decreased at the fastest rate during the transition from spring to summer due to concealment with the new vegetation. I also found large habitat differences in how fast visibility decreased. No correlations were found between the visibility and site index, whereas visibility decreased with litter production. The vegetation in the field and ground layers were also important; pellet groups on dry, lichen-rich sites were visible considerably longer than those at sites with richer field vegetation. After one winter of exposure,

more than 95% of the pellet groups were visible *(i.e* visibility > 0) independent on habitat type, but thereafter visibility decreased fast in the richer sites. I therefore concluded that pellet group counts can be a precise and useful method to estimate habitat use and population trends for moose in winter. However, the correlation between visibility and litter production indicates that visibility can be estimated as a function of habitat productivity, and pellet counts could therefore also be used in the vegetation period and with longer periods between plot visits.

Habitat differences of coprophilous fungi on moose dung (Paper VI)

In paper IV, we investigated the abundance and species richness of coprophilous fungi developing in summer dung of moose, and if it was dependent on habitat type. Despite rather limited sampling in space and time, we found 26 different species of fungi, of which two species were not previously described. Our results thus strongly support the assumption that moose dung is a species rich community, which is interesting concerning biodiversity.

We also found significant habitat differences. Fungi are generally associated with moist habitats, and we expected to find the highest abundance and species richness in the shady and mesic pine - spruce forest. However, we had the lowest abundance and species richness here. We suggest that the explanation might be negative effects of coprophilous insects on the development of fungi. The insect load was largest in the pine - spruce forest, and invertebrate feeding on the substrate, mycelia and spores, as well as crumbling and disrupting the dung when moving around might have been negative for the growth and development of the fungi. Our findings thus demonstrate how abiotic and biotic interactions vary within the ecosystem and can result in highly unexpected outcomes.

Conclusions

In my thesis I found that moose significantly can affect fundamental ecosystem processes like structure and primary productivity of the tree and shrub layers, as well as production and composition of litter. These findings indicate that moose can act as an important ecosystem engineer in Swedish boreal forests.

Both the productivity of pine and birch and the production and composition of litter differed considerably among study sites, demonstrating the importance of taking productivity gradients into account when studying the effects of large ungulates on ecosystem processes. However, to rank sites after productivity turned out to be a challenge, and differences in stand history prior to treatment likely had a significant effect and complicated the interpretations. Site index, the productivity measurement for pine used in forestry in Sweden, could not explain differences between sites, but gaps in the productivity gradient (*i.e.* no sites had a site index between 14.7 at Skatan and 24.3 at Djupsjöbrännan) may have influenced the results of the analyses. However, production of litter might be as good or better measurement of habitat productivity in young forest stands. Another factor explaining the problems with the productivity ranking might have been that pine

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and birch (and likely other deciduous trees) appeared to respond differently to habitat productivity. Productivity of deciduous trees was likely positively correlated with nutrient availability, whereas pines might have faced a trade-off between nutrient deficiency at poor soils and competition with deciduous trees at richer, resulting in the highest productivity at some medium rich sites.

The effects on the structure and productivity of trees and shrubs as well as the production and composition of litter were strongly dependent on the level of simulated moose population density, and the impact of moose seemed to be more important than other habitat differences at high densities. The effects were small and non-significant at the lowest moose density which can be considered as "low" to "moderate" in Sweden, but large at densities of on average 25 per 1000 ha or more on the landscape level. In a study of life history strategies of Swedish moose, Sand (1996) concluded that moose densities of approximately 10 per 1000 ha can be considered to be well below food carrying capacity. However, he also concluded that density-dependent resource limitation had resulted in reduced body growth and fecundity in some moose populations during the population peak in the 80ies, at population densities of approximately 20 - 25 per 1000 ha. We studied effects of several levels of simulated moose population density on the availability of winter food, and the findings agree with Sand (1996). Food availability will not be a limiting factor at moose densities of approximately 10 per 1000 ha. However, at population densities of 25 - 30 per 1000 ha or more over extended time, the food plants can not longer compensate for tissue loss due to browsing, and the food availability will steadily decrease to a level where winter food is a limiting factor which can regulate population growth rate. Also, the decrease in litter production and increased dominance of coniferous material in the litter at high moose densities likely will result in decreased soil nutrient availability, nutrient cycling and habitat productivity, reinforcing the decrease in food production. The food carrying capacity can thus be set at a lower moose density in areas subjected to high browsing pressure over extended time.

I also conclude that the negative impact of selective browsing was more important than a fertilizing effect of faeces and urine on the productivity of trees and shrubs, otherwise we should have found higher biomass production and/or litter production in at least one level of simulated moose population density compared to the control plots. The slow decay rate of the pellet groups also suggests that the fertilizing effect might be rather small. There seems to be a negative correlation between disappearance rate of moose pellets and habitat productivity, and the relationship could be developed further to obtain more precise estimates which could be useful for moose managers. Faeces from moose are also interesting concerning biodiversity. The coprophilous community developing in moose dung seems to be species-rich and poorly known, and the community composition determined through complex interactions between abiotic and biotic factors.

Future Perspectives

I found large effects of the level of simulated moose population density on the tree and shrub layers. These changes probably also affects other components in the ecosystem. Based on my findings, I suggest the following topics for future research:

More studies on other plant species in the tree and shrub layers should be done. We focused on the effects on morphology and productivity of the quantitatively most important food plants in winter, birch and Scots pine. However, these species are of medium preference to moose (Bergström & Hjeljord 1987; Shipley, Blomquist & Danell 1998), and studies should also be done on the preferred species. Rowan has been found to rank highest in preference for moose (Shipley, Blomquist & Danell 1998), and does also seem to be tolerant to browsing (Miller, Kinnaird & Cummins 1982). During the field work I got the impression that rowan has a remarkable compensatory ability after clipping, and sites with high abundance of rowan likely have high production of high-quality food for moose and are interesting for moose managers. Studies have shown that growth responses in rowan depend on browsing as well as resource availability (Bergman 2001), but data on rowan are scarce. It would be interesting to estimate the impact of several levels of moose population density and habitat productivity on the morphology and productivity of rowan, and compare with the growth responses of birch and pine.

Moose mainly browse in the tree and shrub-layers (Cederlund *et al.* 1980; Belovsky 1981; Bergström & Hjeljord 1987), and effects might thus first be apparent here. Therefore I focused on these vegetation layers in my thesis. However, the indirect effects of changes in the tree and shrub-layers, as well as direct effects of the clipping, might have induced changes in the productivity and species composition in the field and bottom layers, and more studies of these vegetation layers should be done. The reduced height growth and number of shoots per tree (Paper II) imply a more open canopy, offering more sunlight down to the ground. The outcome might be increased productivity in the field and bottom layers (McInnes *et al.* 1992), but the outcome likely vary with habitat type as well as moose density.

The changes in the vegetation community might also have induced changes in abiotic factors. The more open canopy and increased irradiation might have affected temperature and moisture of soil and air, as well as daily and annual temperature variation. Effects on abiotic factors can feed back on both the plant community and other animal assemblages, and should be studied more.

Effects on soil properties are especially important to reveal. The significant effects on the litter production found in my thesis strongly suggest that the biochemical properties of soils can be affected. Because N availability generally limits productivity in boreal forests (Flanagan & Van Cleve 1983), I suggest that the main focus should be on how soil N availability, mineralization and decomposition rates are affected by moose density and habitat productivity. Studies of the soils would also reveal how soil properties are correlated with site index as well as biomass and litter production, and offer more precise estimates of habitat productivity.

More studies on how pellet group visibility is correlated with habitat productivity should be done. The coprophilous community on the faeces and urine should also be studied more. Special attention should be paid to reveal how abiotic and biotic factors interact to determine the abundance and species richness.

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