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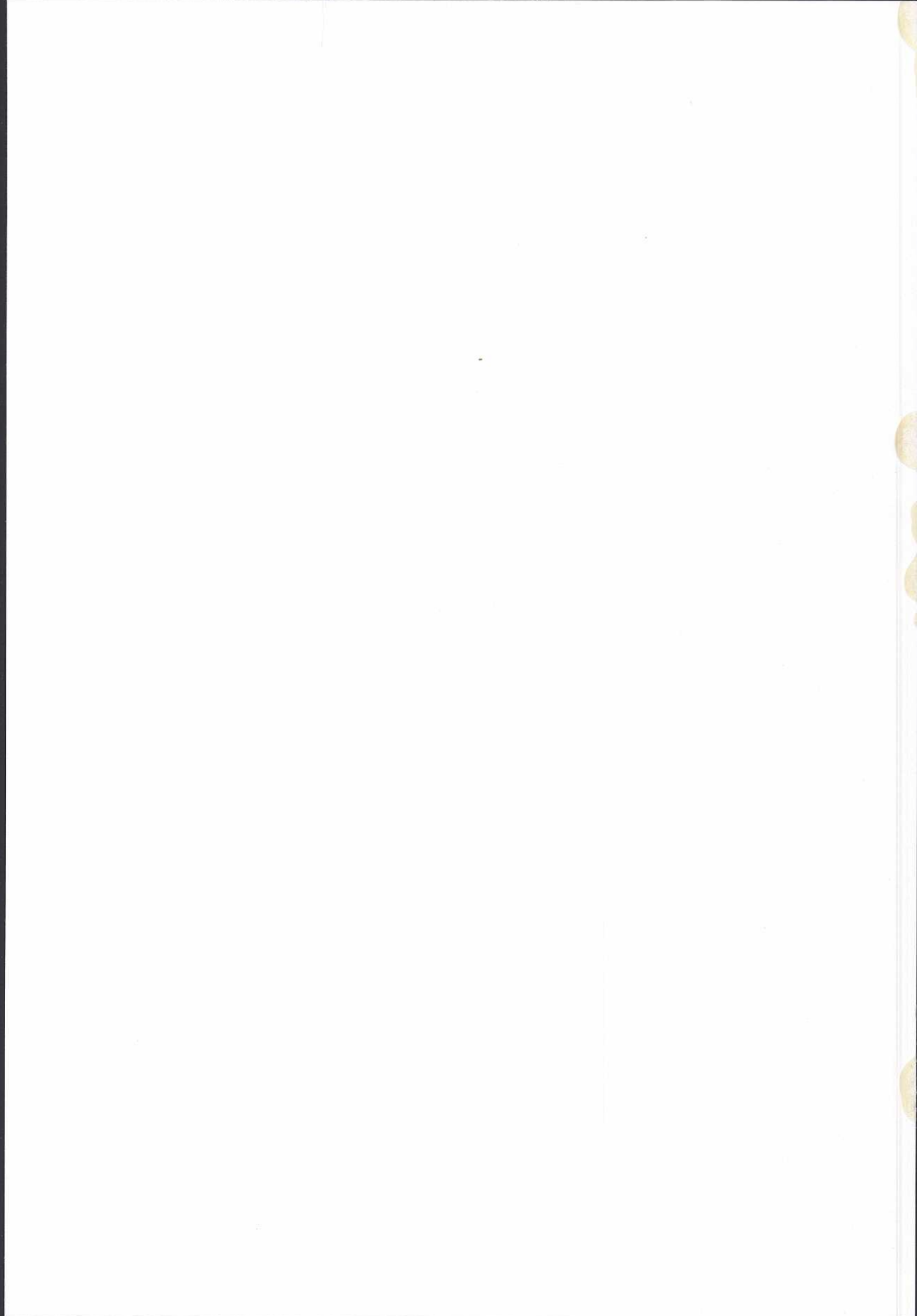
Environment and Moose Population Dynamics



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GÖTEBORGS UNIVERSITET

Environment and Moose Population Dynamics

Emil Broman

Akademisk avhandling som för avläggande av filosofie doktorsexamen vid Göteborgs Universitet försvaras vid offentlig disputation den 31 januari 2003, klockan 10.00 i Stora Föreläsningssalen, Institutionen för miljövetenskap och kulturvård, Carl Skottbergs gata 22 B, Göteborg.

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ABSTRACT

This thesis deals with the moose and its environment, with emphasis on matters that affect moose foraging and population dynamics. I have examined death risks in moose adults, tested for density dependence in body size, fecundity and antler size, and examined diet selection with emphasis on the hierarchical selection process, frequency dependent selection, and reproductive response. I also have examined shortcomings and successes of local moose management.

The wasting syndrome observed in moose (MWS) since the mid 1980s in Sweden have affected senescent individuals more than other adult age classes; males have been at least as vulnerable as females; there has not been any locality in Sweden with an obviously higher death risk; the death risk seems to have been uniform over the four seasons. There is as yet no definitive knowledge of the underlying cause(s) of MWS. Reconsidering MWS in light of this new demographic description might give important clues to understanding observations at the individual level.

Population density can affect early-life body growth, resulting in a lower probability of ovulation and smaller antler size as yearlings. Adults appear less sensitive to density. Slow growth and late age at maturity imply time-delayed population dynamics.

Birch (*Betula* sp.) is the quantitatively most important forage species in the early summer diet of moose. It also seems to be a highly preferred species, both in comparison with availability at feeding patches and availability in the environment overall. The selection of each food types declines with availability. In early summer, thus, moose seem to balance intake from different food sources instead of maximising the intake of a single food type. High fecundity was associated with high dietary diversity. The negative frequency-dependent selection and the reproductive response together suggest that moose is a 'clever ungulate'.

In winter the relative risk to be browsed increased for top ranked forage species but decreased for bottom ranked species when moose density was experimentally reduced. This is in agreement with an energy maximising strategy. Thus moose may adopt different foraging strategies in winter and summer; nutrient mixing in early summer but energy maximising in winter.

I believe local management can be both important and successful. Because it involves those who have a direct interest in a particular biological resource, they are likely to be willing to act. However, difficulties arise when attempting to apply scientific concepts and methods where non-scientifically trained people are involved. Therefore, for local natural resource management to succeed, I suggest that local involvement should mainly focus on goal *formulation*, and less on how specifically to *manage* the resources so as to achieve these goals.

Key words: Alces alces, antler size, carcass mass, death risk, density dependence, diet selection, food limitation, frequency dependent selection, local management, moose, Moose Wasting Syndrome, ovulation rate, population dynamics, ungulate

Doctoral thesis for degree of Doctor of Philosophy

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SAMMANFATTNING

Denna avhandling tar upp olika aspekter av miljöns inflytande på älgens födoval och populationsdynamik: dödsrisker hos vuxna älgar, älgtäthets betydelse för kroppstillväxt, fruktsamhet och hornutveckling, älgens sommardiet, födopreferenser och olika födovalsstrategier. Brister och framgångar inom svensk älgförvaltning diskuteras också.

Den älgssjukdom som upptäcktes under 1980-talet och som benämns Älvsborgssjukan har främst drabbat vuxna älgkor. I motsats till antal döda älgar där flertalet fynd härstammar från södra Älvsborg så har dödsrisken inte någon tydlig koppling till kön eller geografiskt område. Tydligt är dock att sjukdomen uppvisar ett starkt åldersberoende där den årliga dödsrisken stiger med stigande ålder. Skillnaden mellan antal döda älgar och dödsrisk förklaras av en stor andel gamla djur, främst hondjur, i populationen samt lokalt ett stort intresse att rapportera sjukdomsfynd. Älvsborgssjukans direkta orsaker är inte klarlagda men virus, älgtäthet, markkemi och organiska gifter har diskuterats som tänkbara orsaker.

Vid experimentell sänkning av populationstätheten i södra Älvsborg påvisades större kroppstillväxt, tidigare könsmognad och ökad hornstorlek hos unga djur. Inga påvisbara effekter på vuxna djur eller skillnader mellan kön kunde observeras. Dessa effekter på unga men inte gamla djur leder till tidsfördröjd reglering av populationen och en stabil jämvikt utan jakt är därmed inte trolig. Minskad täthet följdes av för älgan förbättrade födoresurser. Med sänkt älgtäthet observerade vi större förekomst av hallon och mjölkört, ett förändrat betesmönster, samt en benägenhet att inte utnyttja ytor med liten födomängd. Trots en effekt av populationstäthet på kroppstillväxt så är kalvar i början av 2000-talet mindre än för tjugo år sedan. Tänkbara orsaker kan vara konkurrens från rådjur och att älgkors förvärvade storlek påverkar storleken hos sina kalvar.

Älgar har under tidig sommartid en likartad diet var de än befinner sig i Sverige. Björklöv och blåbärsris utgör stapelfödan. Födovalen är beroende av den relativa förekomsten av olika födoslag. Sommartid tycks älgarna försöka balansera dieten och älgar med bredare dietsammansättning verkar vara mer reproduktiva d.v.s. föder fler kalvar. Vintertid tycks enskilda födoslag som vide och rönn exploateras hårdare om födotillgången ökar medan älgarna i samma situation undviker gran och glasbjörk. Älgar verkar därmed ha olika födovalsstrategier under olika tider på året; älgarna ser ut att vara "näringmixare" på sommaren och "energimaximerare" på vintern.

Det finns både mer och mindre lyckade exempel på älgförvaltning med starkt lokalt inflytande från jägare och markägare. Lokal förvaltning har fördelen att de som är mest berörda har störst vilja att vidta åtgärder. Svårigheter uppstår när vetenskapliga metoder och idéer praktiseras där vetenskapligt otränade personer är involverade. För att effektivt kunna förvalta en förnyelsebar naturresurs som älgarna behövs därför personer som kan hantera information samt en övergripande organisation som håller samman de olika delarna. Det lokala inflytandet bör vara inriktat på *målformuleringen* och mindre på *själva förvaltningen* att nå dessa mål.

Tack till alla som har gjort denna avhandling möjlig. Tack till anslagsgivare, myndigheter, handledare, kollegor, studenter, jägare, vänner och familj. Tack till alla som inte föraktar ärlighet och logik.

The present thesis is based on following papers, which will be referred to by their Roman numerals:

- I. Broman, E, K. Wallin, M. Steen, G. Cederlund. 2002. A wasting syndrome in Swedish moose (*Alces alces*): background and current hypotheses. *Ambio* 31(5): 409-416.
- II. Broman, E, K. Wallin, M. Steen, G. Cederlund. 2002. "Mass" deaths of moose *Alces alces* in southern Sweden: population level characterisation. *Wildlife Biology* 8(3): 219-228.
- III. Broman, E, K. Wallin. Density dependent effects in moose (*Alces alces*) – an experimental test. Manuscript.
- IV. Broman, E, K. Wallin, G. Cederlund, G. Ericsson. Summer diet selection in free-ranging moose (*Alces alces*) in Sweden: ranking, frequency dependence and reproductive response. Manuscript.
- V. Wallin, K. M. Broberg, E. Broman. Shortcomings and successes of the Malawi principles in Swedish moose management. Manuscript.

'Would you tell me, please, which way I ought to go from here?'

'That depends a good deal on where you want to go,' said the Cat.

'I don't much care where...' said Alice.

'Then it doesn't matter which way you go,' said the Cat.

'...so long as I get somewhere,' Alice added as an explanation.

'Oh, you're sure to do that,' said the Cat, 'if you only walk long enough.'

From Alice in Wonderland by Lewis Carroll

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INTRODUCTION

There is only one way to solve a problem – do the right thing(s) – but there are two ways of get rid of it, solve it or redefine it. Though this statement is tautological and trivial, the matter as to what significantly contributes to solving a given problem is not. To that, determine the most efficient solution to a problem given particular objective is an even harder task. Probably it offends no one to say that science deals with problems, but otherwise there is much controversy as to what science is, or rather should be (Chalmers, 1982; Molander, 1983).

My thesis deals with the moose – a large herbivorous mammal that inhabits the northern taiga (Karns, 1997) – and its environment, with emphasis on matters that affect moose population dynamics. Humans are a significant aspect of the moose environment – an aspect of the environment for many large mammals today. Studying the moose is thus not simply a matter of learning more about the moose; it is also an attempt to understand more about the world that all living beings and we depend on. My thesis may thus be categorised as environmental science, though it is of no concern to me whether it is or not. Instead my concern is about what view it represents.

Environmental science is a new scientific discipline, and as Bowler (1992) notes on page 2 of *The Fontana History of the Environmental Sciences*, it is ‘...not created by the sciences themselves; it is imposed by the public’s growing awareness of the threat posed to the environment by our own activities.’ Worthy origins, but the consequence can be that norms are not clearly separated from universal descriptions. For example, Cunningham and Saigo (2001) express this view on page 17 of their widely used textbook, *Environmental Science – A Global Concern*: ‘In contrast to more theoretical disciplines, environmental science is mission-oriented. That is, it seeks new, valid contextual knowledge about the natural world and our impacts on it, but obtaining this information creates a responsibility to get involved in trying to do something about the problems that we have created.’ This is a rather naïve attitude in cases where there is no political consensus as to the objectives to be achieved. For example, if some people value high moose populations and there is high moose mortality due to human activities such as hunting, polluting, or forestry, is it my responsibility to do what I can to allow the moose population to increase? But what if there are also people who value low moose populations, as damage to crops and commercial tree saplings increases with moose density? What’s my responsibility now? These conflicts are not matters of science, but of politics, and I feel it is my responsibility not to take sides.

MATERIAL AND METHODS

Study areas

The data upon which this thesis is based was sampled from populations in various parts of Sweden. For various purposes (II, IV, and V), I used data obtained from radio-tagged, individual moose from six areas, ranging from the boreonemoral biogeographic region in the south to the boreal region in the north (Fig. 1). An extension of the study area called Mark, or southern Älvsborg, was used for the experiment presented in paper III. Parts of the data presented in paper II were sampled from all over Sweden. For more detailed descriptions of the study areas, please refer to the attached papers.

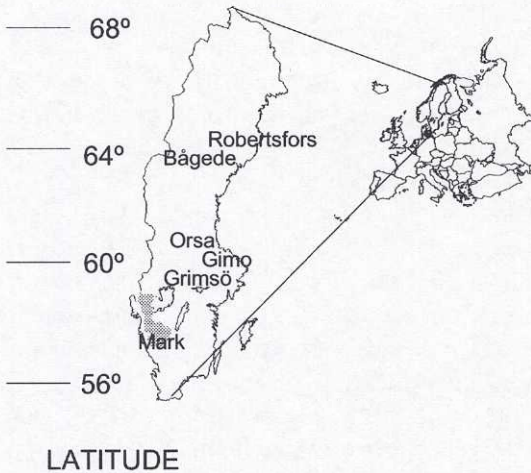


Figure 1. The locations of the study areas where most of the data for this thesis was sampled. The grey background colour near the Mark area indicates the former County of Älvsborg.

Measurements

To discuss a problem or answer any question one ultimately needs definitions and a way of quantifying the issue. If one fails in this, disorder reigns. As far as possible this research uses definitions suggested by others. When the literature suggests several conflicting definitions, I have arbitrarily selected one or formulated a new one. My choice of methods is primarily based on the experience of others, but some non-validated methods have also been applied. The data was collected by measuring various qualities of individual moose, including by directly and indirectly observing moose foraging behaviour, quantifying habitat qualities, and directly and indirectly counting moose populations. I will briefly present, in alphabetical order, the variables considered. For the specific contexts, sampling techniques and estimation methods, please view into the attached papers.

Age (II, IV, V) – Moose age in years: if dead, this is considered to be the number of *cementum annuli* in the first molar of the jawbone (Sergeant and Pimlott, 1959); if alive, preliminarily estimated from tooth wear and eruption (Skunke, 1949).

Antler spread (III) – Distance between the two most distant antler points of the moose antlers: post rut measures of culled moose (Gasaway et al., 1987).

Antler points (V) – Number of antler points of the moose antlers: post rut measures of culled moose (Gasaway et al., 1987).

Birth rate (IV, V) – Measure of per capita fecundity: number of observed neonates per radio-collared female per year.

Carcass mass (III) – Measure of body size: body mass after removal of skin, viscera, head, and lower legs (Langvatn, 1977).

Death risk (II, V) – Probability any moose individual face to die within a specified period, e.g., month or year (Carey, 1989; Pollock et al., 1989): estimates of risk from a single death source is corrected for competing risk sources and is thus always higher than the observed proportions of deaths in any single death category. Synonyms for death risk are death rate and mortality.

Degree of coverage (III, IV) – Measure of forage amounts: coverage of fresh biomass projected from a height of 3 metres in circular plots of 20 m² or 100 m² (Ahlén, 1975; Hörnberg, 2001).

Diet (IV) – Composition of defined food types consumed by members of a species over times ranging from one feeding period to periods over which fluctuations in the relative abundance of foods average out (Westoby, 1978): estimated by direct observation of radio-collared females. Each observation is assigned a value of 0 or 1.

Discovery rate (II) – Measure of hidden statistics: proportion of dead radio-collared moose left *in situ* reported by the public.

Moose density (III, V) – Number of moose per given area, e.g., km², estimated using three different counting techniques: aerial survey (Skalski and Robson, 1992), pellet group counts (e.g. Bennett et al., 1940; Neff, 1968; Rowland et al., 1984), and ‘Sight moose’ (Engen et al., 1998). Both winter and summer estimates were used.

Ovulation probability (III) – Probability that any female in the population will ovulate 0, 1, or 2 eggs: number of ovulated eggs measured by number of visible *corpora lutea* (Markgren, 1969).

Ovulation rate (III) – Number of visible *corpora lutea* per every two ovaries: i.e., average number of ovulated eggs per culled female (Markgren, 1969).

Proportion of browsed ramets (III) – Measure of browsing intensity: proportion of ramets browsed since start of the latest growing season.

Proportion of deaths (II, V) – Proportions of deaths in each of three cause-of-death categories: hunting, vehicles, or non-trauma. Non-trauma refers to diseases, starvation, and other causes not directly dependent on humans.

Proportion of plots (III) – Proportion of stationary survey plots displaying any specific characteristic, e.g., occurrence of a specific plant species.

Relative risk (III, IV) – Selection ratios (Manly et al., 1993), adding up to one: interpreted as the proportion of the used resources that each resource type would comprise if all resource types were present in equal amounts in the environment (Gendron, 1987). Synonyms to relative risk are standardised selection ratio (Manly et al., 1993) and Chesson's index (Chesson, 1983).

Selection ratio (III, IV) – Proportion of used units in one resource category divided by the proportion of available units in the same category. Defined as the value of the selection ratio proportional to the probability of that unit being utilised, given that the selecting organism has unrestricted access to the entire distribution of available units (Manly et al., 1993). Synonyms are forage ratio or preference index.

Deductions

The works on which this thesis is based include a review (I), observational studies (II, IV), 'true' experimental studies (III) (Manly, 2001), and case studies (V). For the inferential statistics I have chosen tests that I believe are appropriate.

RESULTS AND DISCUSSION

Moose population dynamics

A fairly simple model can illustrate population dynamics, i.e., the temporal and spatial changes in the number of individuals (Fig. 2). Population size is determined by rates of survival, reproduction, and dispersal. The limits depend on the life history and current environment or intrinsic and extrinsic factors (Stearns, 1992). Today we know that many species are age or stage structured (Fig. 3); there is variation in vital rates among individuals depending on age or size (see Gaillard et al., 2000 for a review of how this pertains to large herbivores).

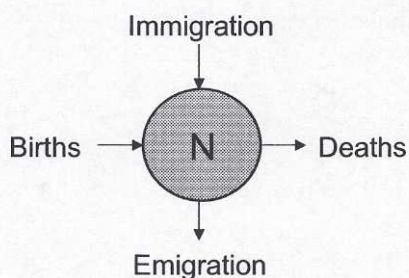


Figure 2. Principal components of population dynamics. N indicates population size.

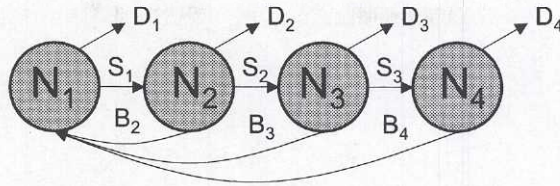


Figure 3. Principal components of age-structured population dynamics. D, S, and B indicate death rate, survival rate, and birth rate respectively. Numbers indicate age category.

One important implication of age-structured populations is that the consequences of extrinsic factors that affect only some (st)ages can be foreseen or exaggerated if one does not have accurate demographic information (Gaillard et al., 2001). In recent times a wasting syndrome (MWS, Stéen et al., 1993, I) has been regarded as a serious threat to moose in one Swedish region (Frank, 1994; Merza et al., 1994). Large numbers of diseased adult female moose indicated age- and sex-specific disease (Sand and Cederlund, 1992), but closer examination found that a positive age-dependent mortality schedule (Fig. 4) and a large segment of senescent females could together explain the observations (II).

Slow body growth can be a consequence of high population density (Bonenfant et al., 2002; Hjeljord and Histol, 1999; Leblanc et al., 2001; Pettorelli et al., 2002, III). Since body mass is critical for the onset of reproduction (Albon et al., 1983; Jorgenson et al., 1993; Saether and Haagenrud, 1983; Skogland, 1985, III), population density can, thus, have time-delaying consequences for the average reproductive rate (Saether, 1997). As fecundity in prime-aged individuals is less sensitive to population density (Gaillard et al., 1998; Saether, 1997, III), one might foresee density effects until age at maturity significantly increase, and thus a decline in average reproductive rate.

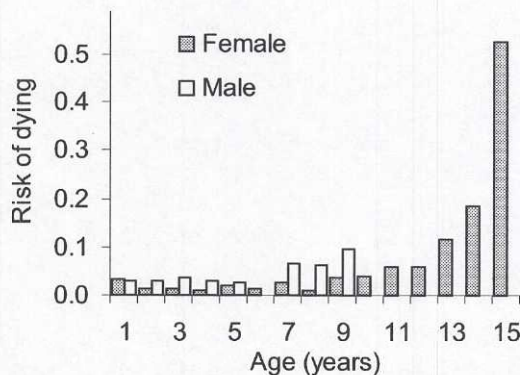


Figure 4. Age-specific risk of death from non-traumatic causes, including MWS, estimated from data on dead moose reported by the public between 1991 and 1998.

From a wasting syndrome to small calves

A wasting syndrome, of as yet unknown etiology, was discovered (Stéen et al., 1993, I) after the dramatic increase – synonymous to the terms ‘irruption’ used by Leopold (1943) and ‘eruption’ used by Caughley (1970) – in the moose number in Sweden in the 1970s and 1980s (Cederlund and Markgren, 1987). Also, high numbers of moose dead from no obvious cause were reported in the Älvsborg region (Fig. 1, II). There was concern about moose health status, and also about the potential local extinction of moose in Älvsborg (Frank, 1994; Merza et al., 1994). At the time the syndrome appeared in the late 1980s, calf mass in Älvsborg had been declining for almost ten years (Fig. 5). However, reproduction and body growth and condition were said to be as good as in other populations in southern Sweden (Sand and Cederlund, 1992). The number of moose harvested also decreased in Älvsborg in the early 1990s (Johansson, 1998). The reason for the decrease is unknown, but it might have created or strengthened some perhaps already existing, density-dependent effects as, after a small recovery, a second trend of decreasing carcass mass was observed in the mid 1990s (Fig. 5). Low fecundity (unpubl. data) and small-antlered bulls were also observed (Wallin et al., 1996). However, compared to an area with almost no reports of MWS, Robertsfors in northern Sweden (Fig. 1), the adult mortality risk was not higher in Älvsborg (II).

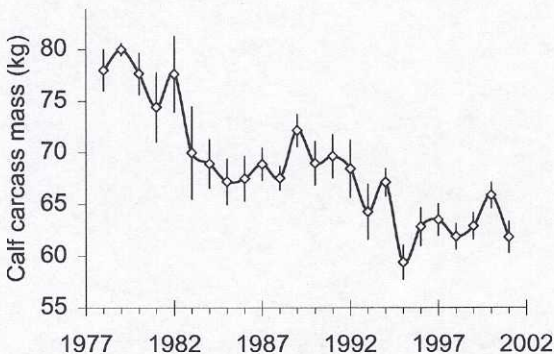


Figure 5. Carcass mass of moose calves shot during hunting season (October to December). Total number of calves is 755. Bars indicate standard error.

Reproductive performance and small-sized calves were not the only observations indicating that moose were food limited in the mid 1990s. Simultaneously with the appearance of MWS, browsing and bark stripping of Norway spruce (Faber and Pehrson, 2000) were recorded in Älvsborg. As moose do not normally browse that species (Cederlund et al., 1980), moose browsing of spruce may indicate some kind of food shortage. Roe deer population density increased considerably in the late 1980s (Bergström and Wahlström, 1997). The interaction between roe deer and moose is not well

understood, but since they forage on many of the same species (Cederlund et al., 1980; Myrnerud, 2000), increased roe deer population density should increase the incidence of inter-specific competition. Competition would also increase from the reduced production of moose food. Young forest stages, which provide more moose food than older stages (Bergström and Hjeljord, 1987), have decreased in southern Älvsborg since 1984 (Riksskogstaxeringens databas 2001). Also, the availability of the highly preferred fireweed (*Epilobium angustifolium*) has decreased in southern Sweden since the mid 1980s (Odell and Ståhl, 1998).

Density-dependent growth and reproduction

Density dependence can be defined as the regulation of the size of a population by mechanisms themselves controlled by the size of that population (Allaby, 1994).

When most of the concerns regarding the local extinction of moose due to the high adult death rate were set aside, several indications of high population density emerged. The result was that Älvsborg was suggested for full-scale testing of density-dependent effects (K. Wallin, pers. comm.). The study area located in southern Älvsborg was divided into eight parts, four of which were randomly chosen to have decreased moose density (treatment areas), while the other four were chosen to be controls. The experiment was carried out between 1996 and 2001, and population reductions were made through increased regular harvest quotas starting in 1997. We tested for density-dependent effects on body mass, ovulation rate, and antler size (III).

We observed density dependence in body size, ovulation probability, and antler size in juveniles, but not in adults (Fig. 6 and 7, III). However, body mass explained most of the variation in ovulation probability and antler size (III), and there was no significant additional effect from population density when body size was controlled for. That suggests that density dependence works mainly through body growth (III). The results are in accordance with the general pattern observed in large ungulates (Gaillard et al., 1998; Saether, 1997). Increased body growth rate and earlier onset of first reproduction can profoundly affect population dynamics (Stearns, 1992), but the dynamic consequences of time-lagged effects are not fully understood (Beckerman et al., 2002). Saether (1997) suggested that stable equilibrium without predation is unlikely as the regulatory mechanisms are very slow-acting.

Food limitation

Density dependence can be mediated through food limitation (Fryxell, 1987; Sinclair et al., 1985; Skogland, 1986). However, besides food competition, population may also be regulated by parasite burdens (Albon et al., 2002), predation (Messier, 1994), and harvesting (Solberg et al., 1999). Also, density dependence may occur without depletion of resources (Goss-Custard

et al., 2001), defined as interference competition as opposed to exploitation competition where an increasing population is associated with decreasing amounts of resources.

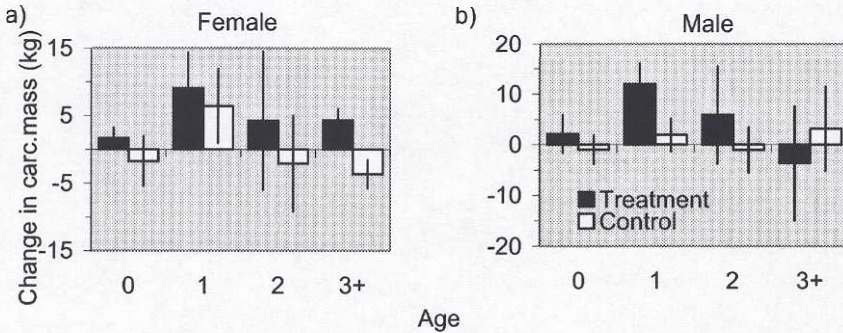


Figure 6. Age-specific change in (a) female carcass mass, and (b) male carcass mass before and after the start of density reduction, in treatment areas ($n = 4$, black bars) and control areas ($n = 4$, white bars). Thin bars indicate standard error.

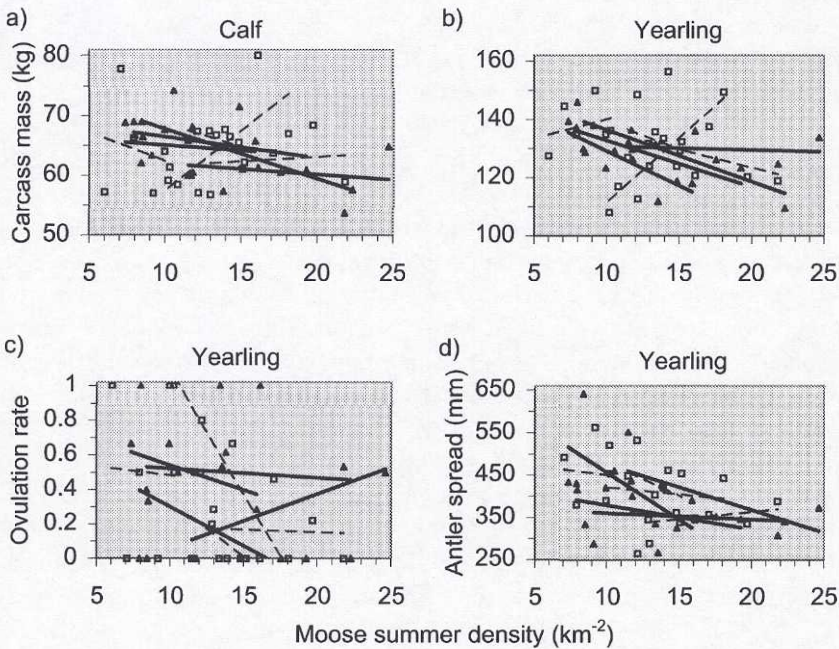


Figure 7. (a) Calf carcass mass, (b) yearling carcass mass (c) yearling ovulation rate, and (d) yearling antler spread in relation to moose summer density in treatment areas ($n = 4$, filled squares, solid lines) and control areas ($n = 4$ open squares, broken lines).

Many studies of herbivore population dynamics treat interactions between the herbivore and their resources only implicitly (Choquenot and McLeod, 1997). As density dependence effects on body growth, reproductive output, and survival are not only mediated through limited resources, but can be

caused by other factors such as parasite burdens (Albon et al., 2002), our objective was, besides studying moose growth and fecundity, to explore the browsing patterns associated with moose density.

The proportion of browsed ramets declined during the early and late portions of the study period, and correlated positively with moose density (Fig. 8, III). Also, the occurrence of raspberry and fireweed – commonly observed components of the moose diet (Cederlund et al., 1980) – was found to correlate positively with moose density (III). Thus, food resources have evidently improved in recent years. And a possible increase in per capita consumption rate, due to improved forage quality and faster rumen turnover (Schwartz and Renecker, 1997), has apparently not matched the effect of the population decrease. These results do not really prove whether the density-dependent effects observed in moose are mediated through food limitation. However three other observations make it reasonable to assume that the observed density dependence in body size, ovulation probability, and antler size are associated with available forage. First, we observed a continuously lower proportion of browsed ramets in treatment areas (III), suggesting that intra-specific competition was lower in treatment than in control areas. Second, the relative risk decreased and increased in preferred and non-preferred species respectively, i.e., the browsing pattern changed when moose density decreased (Fig. 9, III). The way of diet change, a switch, is to be expected when moose try to maximise energy or a single nutrient (Fryxell and Lundberg, 1998). It is not fully understood, however, whether moose apply a diet-mixing strategy (Edenius et al., 2002) instead of maximising energy or a single nutrient (Lundberg et al., 1990; Shipley et al., 1998). If the latter is true, we see no obvious reason why moose should change their diet if they are not food limited. Finally, from optimal patch use theory (e.g. Charnov, 1976), it is expected that moose should leave alone small patches of browsing land if resources become more abundant. As we observed a significant interaction between moose density and browse coverage (Fig. 10, III), moose might have been food limited in the observed density interval.

Inter-specific competition and cohort effects

Despite significant density dependence in moose growth and vital rates, moose calves in Älvsborg are still small compared to their size before the eruption in moose numbers in the 1980s (Fig. 5). We have no data on population densities, but harvest size, which could reflect density fairly well (Solberg and Saether, 1999), indicates that moose density is at least at the same levels as before the population eruption. There is reason to believe that the fairly small density effects observed have to do with impaired moose habitat. If Älvsborg follows the trend of southern Sweden (2001), there is a negative trend in the extent of young forest area. Also, the roe deer population is at historically high levels, several times higher than in the 1970s (Bergström and Wahlström, 1997), and roe deer to some extent share

the same niche as moose (Myrsterud, 2000). Thus, it is possible that not only intra-specific but also inter-specific competition has affected moose growth and vital rates. Small moose calves might also be explained by a profound maternal effect (Albon et al., 1987; Lummaa and Clutton-Brock, 2002).

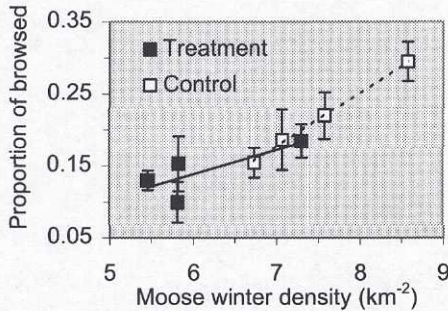


Figure 8. Proportion of browsed ramets in relation to winter moose density. The average proportions for treatment areas are indicated by filled squares while the averages for control areas are indicated by open squares. Handles indicate standard error.

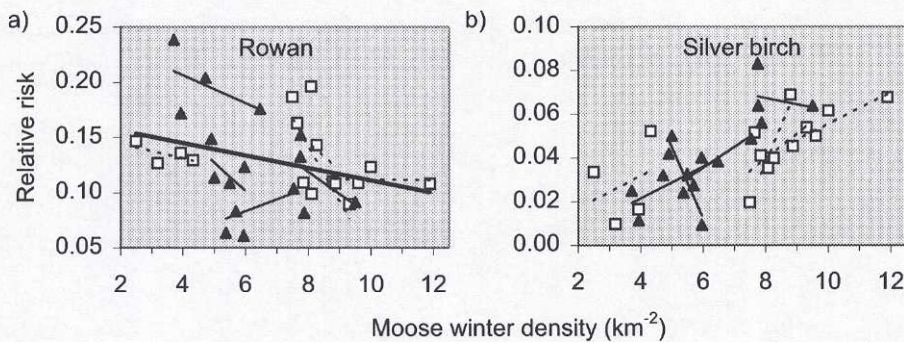


Figure 9. (a) Relative risk (proportion of browsed ramets, adding up to one) of rowan (a preferred species), and (b) silver birch (a non-preferred species) in relation to winter moose density for treatment areas (filled squares, solid lines) and control areas (open squares, broken lines).

Adult death risks and environmental influence

The most significant external factor that limits moose populations in Sweden is sport hunting (Ericsson and Wallin, 2001). Next come a number of environmental factors that potentially affect individual growth, maintenance, and reproduction of moose, e.g., plant species (III, IV), parasites (Stéen et al., 1998), and pollutants (Örberg, 1999). However, many effects that are significant at the individual level, e.g., collisions with cars usually kill moose (unpubl. results), may be small or negligible at the population level. Both in Mark (II) and Robertsfors (Ericsson and Wallin, 2001), fewer than 10% of the adults die from vehicle collisions.

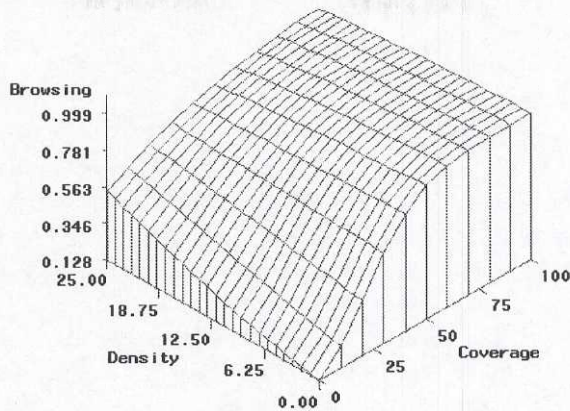


Figure 10. Logistic model fitted to demonstrate change in browsing probability with moose density and degree of forage coverage. At low density thin patches are more likely to be rejected.

Much effort has been spent attempting to understand what causes the MWS (I) first seen in 1985 in Dalarna County (Feinstein et al., 1987). The results published so far give no coherent picture as to what causes the syndrome, but two rough sets of hypotheses have been suggested (I): food-related and host-parasite related. In turn the food-related hypotheses are postulated to have any of following ultimate causes: acidification/liming, browser density/food production, or pollution. Most of the hypotheses are supported by observations, which is to be expected because these are *post-hoc* attempts to explain these very observations.

Until recently little was really known about the demographic pattern of MWS. Any clues to understanding the underlying cause(s) as related to age, sex, seasonality, and locality have thus been unavailable or inaccurate. I have noted that MWS has mostly affected senescent individuals (Fig. 4), males are at least as vulnerable as females (Fig. 4), no Swedish locality has an obviously higher mortality risk, and death risk is the same for all four seasons (II). Bearing this demographic pattern in mind, earlier results can be reconsidered. First, all hypotheses dependent on environmental conditions in the Älvsborg region are unlikely to be true. The rationale for polybrominated diphenyl ethers (PBDE) and dioxin-like compounds (Sellström et al., 1993) being potential causes was that the density of textile factories might be more than coincidentally associated with the high frequency of diseased moose found in the same area (Örberg, 1999). Second, the mortality pattern is in line with that observed in mammals in general: the shape of the death rate curve is exponential (Caughley, 1966), and age-specific death rates are often higher for males than females (Loison et al., 1999; Owen-Smith, 1993; Peterson, 1977). Thus, as MWS is associated with senescent stages, MWS

might be a consequence of physiological, hormonal, and metabolic changes with age (Stearns, 1992).

Resource selection

The moose is a generalist browser. Moose consume parts of a variety of plant species and forage types, though they mainly browse on woody plants (Renecker and Schwartz, 1997). Thus the staple food consists of twigs in winter and leaves stripped from deciduous species in the summer. The summer diet generally includes many plant species, but only a few of them in any considerable quantity (Bergström and Hjeljord, 1987; Cederlund et al., 1980; Hjeljord and Histol, 1999; Hjeljord et al., 1990; Renecker and Schwartz, 1997). The results found by my co-workers and myself were in line with this. We observed over 33 species in the early summer diet, with two genera, birch (*Betula* sp.) and bilberry/cowberry (*Vaccinium* sp.), comprising over 60% (63–88%) of the diet in all six studied areas.

In relation to the number of food types available, birch, willow (*Salix* sp.), and rowan (*Sorbus aucuparia*) tended to be selected (Fig. 11, IV). This indicates that these food types are preferred (defined as what animals would like to eat if offered at equal amounts with other food types, Manly et al., 1993) and might be more profitable (defined as the nutrient or energy content of a single typical food item divided by the time it takes for a consumer to handle that item, Fryxell and Lundberg, 1998) than other food types. However, drawing conclusions as to preferences from studying diet selection in free-ranging animals includes several practical as well as theoretical pit-falls.

To start with, in free-ranging animals, a smorgasbord scenario is utopia. Animals are constrained by several factors such as predation risks, habitat structure, and perceptive ability (Fryxell and Lundberg, 1998). For example, a highly preferred food type may be observed as non-preferred if it occurs in patches where there is high predation risk for the consumer. Quantifying what is available to a selecting animal from the abundance in the environment is thus critical, as has been recognised by several authors (e.g. Boitani and Fuller, 1993; Johnson, 1980; Wiens, 1981). Johnson (1980) introduced the concept of selection order in recognition of the hierarchical nature of selection. One selection process is of higher order than another if it is conditional upon the latter. For example, selection of food items within foraging patches is of a higher order than selection of patches within a home range. The selection process could be divided into a number of orders, but up to four are most common in the ecological literature (Johnson, 1980).

We compared diets with amounts of forage at two spatial levels: the local environment (L, average coverage of food type in the study area), and the feeding site (F, average coverage of food type in patches where we observed animals feeding) (Fig. 12). Selection ratios were generally closer to one when comparing consumption with the amount of forage at the feeding site

than with availability in the local environment. However, the ranking orders of the selection ratios were highly correlated (IV). Availability at the two usage levels, L and F, was also correlated, but not at levels L and D (IV). It seems that moose are selective, and that a significant part of the total selection process occurs at the feeding patches. Thus, the concern with how to define availability in light of problems of scale seems to be only a minor problem.

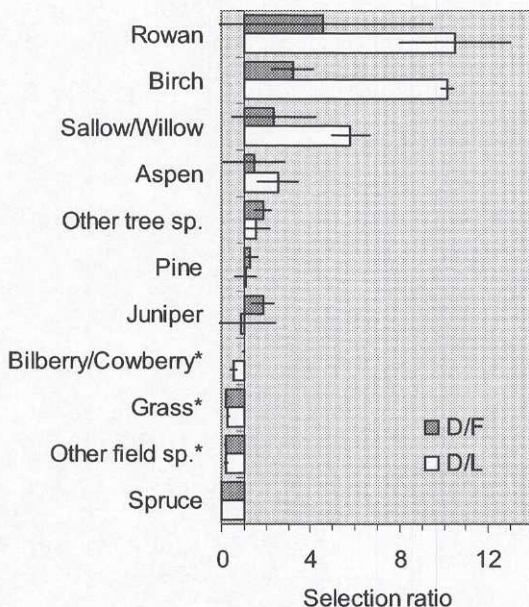


Figure 11. Diet selection ratios. Diet proportions in relation to forage proportions at feeding sites (D/F, dark bars) and in relation to forage proportions in the local environment (D/L, light bars). Asterisks indicate categories in the field layer. Thin black bars indicate standard error. Data from Mark area.

Preferences might also be dependent on the condition of the animal. How hungry the animal is (Krebs and Kacelnik, 1993; Mangel and Clark, 1988), or what foods types have recently been consumed (Belovsky, 1978) can influence preferences. In one of our analyses we classified females according to whether they had given birth or were barren during the observation year (see foraging strategy below). Otherwise we did not explicitly consider variation stemming from the condition of the animals, but instead let it be part of the unexplained variance.

Though methods for quantifying moose browsing are not well developed, much has nevertheless been accomplished (K.Wallin pers. comm.). We estimated consumption by directly observing moose (see methods in paper IV), and quantified availability by measuring coverage of forage biomass (Ahlén, 1975). None of these methods have been validated to date. As far as I know, no thorough evaluation has been conducted to test whether one

observation, or one degree of coverage, for one species is comparable with that of another species, and whether relationships between species are consistent over the total number of observations, or total degree of coverage. Conclusions as to the importance of various food types, both quantitatively and qualitatively, must therefore be treated with some reservations.

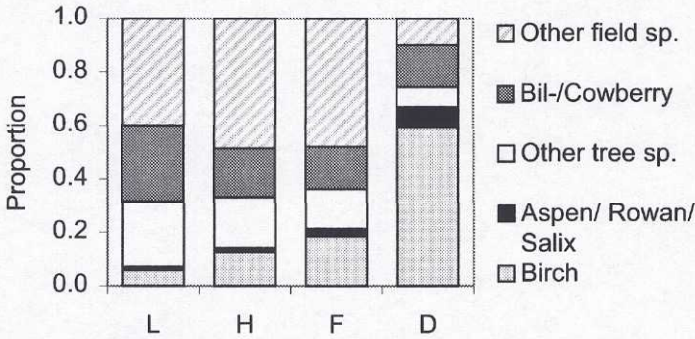


Figure 12. Resource usage levels. Forage proportions in local environment (L), in habitat (H), in forage habitat (F), and in diet (D). Data from Mark area.

Foraging strategy

It is widely believed that natural selection favours animals that maximise nutrient or energy intake (Fryxell and Lundberg, 1998), however several factors such as risk of predation could constrain diet selection (Edwards, 1983; Kie, 1999). In the standard model of optimal diet selection (see for example Charnov, 1976; MacArthur and Pianka, 1966; Schoener, 1971) prey types should always be included or always rejected. In most studies, however, partial preferences are the rule (Stephens and Krebs, 1986), suggesting that animals are generally neither energy nor nutrient maximisers. Still, animals may behave optimally within certain broader frameworks, so the standard model may be simplistic or its underlying assumptions invalid. McNamara and Houston (1987) have reviewed various ways in which partial preferences can be optimal. Some statistical variations in diet choice are also to be expected when deviations from optimal behaviour are not too costly (McNamara and Houston, 1987). Depending on the optimality criteria, different patterns of usage in relation to availability are to be expected. If energy or a single nutrient is to be maximised, the most profitable prey type should be over-represented in the diet if the availability is above a critical threshold (positive frequency dependent selection, switching or sigmoid functional response, see Gendron, 1987 for a review). Besides an energy-maximising diet-selection strategy, several other mechanisms, such as predator search image, spatial segregation of various prey in the environment, risk avoidance by foragers, or optimal patterns of foraging effort, could cause positive frequency-dependent selection (Fryxell and Lundberg, 1998). If a mixed diet is needed to satisfy all the nutritional requirements, relative food consumption should not depend on its relative

availability, at least above a threshold where total prey biomass does not constrain intake (Westoby, 1974). The result is decreased relative prey risk when relative availability increases (negative frequency dependent selection, see e.g. Pulliam, 1975).

Fryxell and Lundberg (p.46, 1998) offer three observations that are pertinent in discriminating between the balanced nutrient and the energy-maximising hypotheses: 'First, the proportion of each prey type in a balanced diet should remain roughly constant as resource availability changes.... In contrast, energy-maximising models suggest that the proportion of each prey in the diet should reflect its ratio in the environment when densities fall below a critical threshold, but become highly skewed when the density of preferred prey is high. Second, the fitness of animals fed a mixed diet should be greater than that of experimental animals fed a monospecific diet. Third, the model for balanced nutrient intake predicts that rates of consumption of each prey type should be enhanced by increased density of alternate prey, whereas the contingency model of diet selection predicts that adding alternate prey would either have no effect or negative impact on consumption of preferred prey, depending on the optimal diet.' I suggest, from testing the first two of the three critical observations, that the balanced nutrient hypothesis best explains the moose browsing strategy in early summer (IV).

Negative frequency-dependent food utilisation was observed both at the small-scale, individual level (Fig. 13, IV) and at the large-scale, population level (IV). Some cautions must, however, be emphasised. According to the literature, a mixed strategy seems to be the rule in herbivores (Fryxell and Lundberg, 1998); however, a lack of quantitative a priori statements could be the reason for such a reported bias (Fryxell and Lundberg, 1998). Food types might be misleading as a measure of food quality if profitability varies more between plant individuals of the same species than among different species, i.e., if there is large overlap in energy, digestibility, or nutrient values between species. My co-workers and I have no data on either the nutrient content or handling time for the selected food types, so an energy-maximizing strategy might still be possible, though it seems less likely.

Individual birth rate was positively associated with diet diversity (Fig. 14a, IV) and negatively associated with the proportions of birch in the diet (IV). Thus it seems as female fitness varies with food quality. As the effects of various diet compositions have not been experimentally tested, it could be argued that the association between diet composition and fecundity might represent a coincidental rather than a causal relationship. A female's habitat usage might be different when she is taking care of a newborn compared to when she is barren. When predators are present such response has been observed (Edwards, 1983; Kie, 1999). We did not, however, observe such behavioural differences (Fig. 14b, IV), which make a causal relationship between diet quality and fitness more likely.

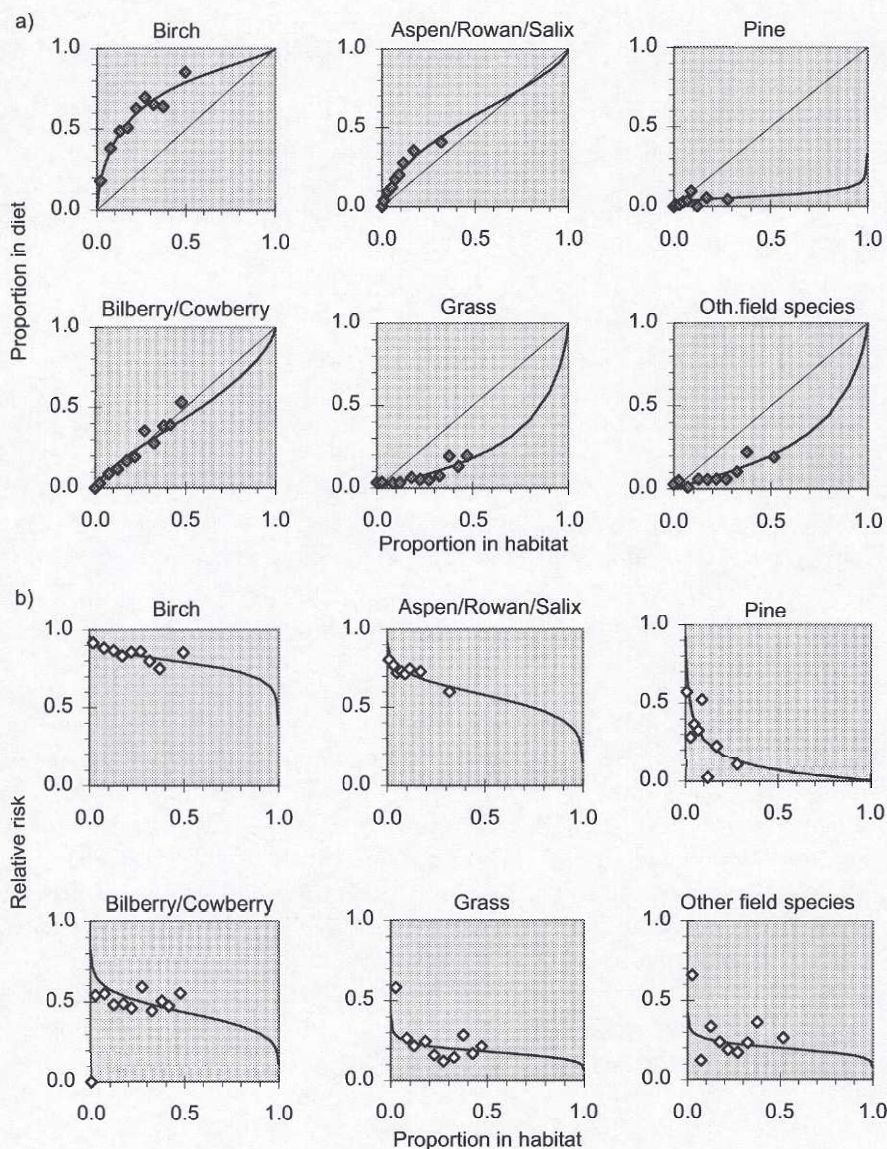


Figure 13. Frequency-dependent browsing expressed as, (a) proportion of one food type in the diet, or (b) the relative risk of one food type, as a function of its relative density at feeding patches.

Do moose apply different browsing strategies in the summer and winter? The browsing patterns observed after experimentally reducing moose density indicated that moose were more likely to select highly preferred species when population density decreased. That is directly contrary to the mixed feeding strategy that seems to be applied in the summer. In winter, when

ambient temperature is low and moose loose weight despite the food offered, i.e., in periods when they rely on deposited fat reserves for maintenance and survival (Schwartz and Renecker, 1997), it might be more important to maximise energy rather than meet diverse nutritional needs – possibly most important during periods of growth and lactation.

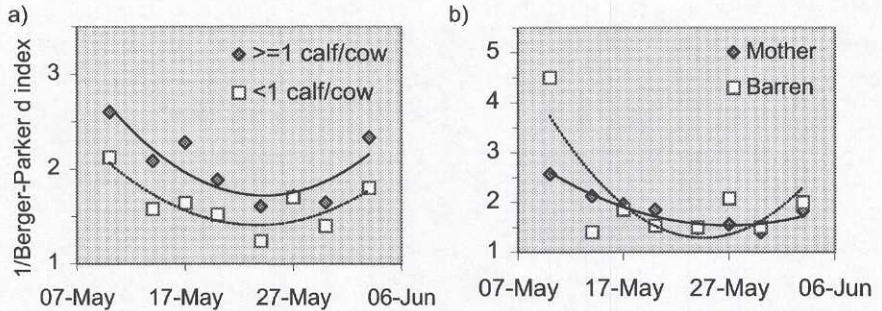


Figure 14. (a) Diet diversity for highly fecund females (filled diamonds) and less fecund females (open squares); and (b) diet diversity for females nursing offspring (called 'mother', filled diamonds) and not nursing offspring (called 'barren', open squares) in a given year. Curves are second order polynomials fitted to the data. Data from Mark area.

Moose management

The moose are a resource. Humans, predators, scavengers, and parasites all use moose for their own purposes. Humans may have three interests in a natural resource, and thus three overall problem areas must be dealt with, namely, conservation, harvesting, and control (Shea and NCEAS Working Group On Population Management, 1998). Where the focus lies depends on the objectives; in Sweden today, all three are aspects of moose population management. *Conservation*: The impact of moose browsing on the recruitment rate of large deciduous trees may negatively influence species dependent on mature forest stages (Andrén and Angelstam, 1993). Thus, naturalists are concerned about how heavy browsing by large ungulates might affect biodiversity. *Harvesting*: In economic terms, the moose is the most important game species (Ekman et al., 1993). Thus, how to optimise harvest rate or any moose quality is a central theme when discussing harvest quotas. *Control*: Moose damage to forestry has been documented since the end of the 19th century (Lavsund, 1987), and the forest industry is still concerned about the problem (Anon, 1990; Hamilton, 2000).

Differing objectives pertaining to natural resources means conflicting interests, as the objectives are not always mutually compatible (Anon. 2000). An increasingly popular view (Danielsen, 2001; Pearse and Wilson, 1999) is that natural resources should be locally and democratically managed, i.e., local people should manage and take responsibility for local resources. This was also emphasised in a workshop held in Malawi in January 1998 (Anon. 1998). One of the twelve principles proclaimed in Malawi (Malawi principles, MP) was that natural resource management should be

decentralised to the lowest appropriate level (MP no. 2). The twelve MPs together comprise an ecosystem approach that is defined thus: 'The ecosystem approach is based on the application of appropriate scientific methodologies focused on levels of biological organization, which encompass the essential processes and interactions amongst organism and their environment. The ecosystem approach recognizes that humans are an integral component of ecosystems' (Anon. 1998, p. 3). The limitations of classical nature-conservation approaches as sole management tools are what motivate the MP or the ecosystem approach (Anon. 1998). Besides helping to define appropriate management levels, the ecosystem approach should consider all forms of relevant information, including scientific, indigenous, and local knowledge, innovations, and practices (MP no.11).

My experience and that of my co-workers in dealing with local moose management leads us to suspect that there might be some difficulties with local management, and thus with applying some of the MPs (V). Many of these problems arise when attempting to apply scientific concepts and methods where non-scientifically trained people are involved. In paper five (V) I present, together with my colleagues, four case studies and their consequences for the moose population. These case studies should be viewed only as illustrations of what may happen, as we know nothing about their general applicability. Starting from what we determined were the management objectives, these studies examine both management successes and failures. To say something is a success or not is, otherwise, a subjective matter. As neither my co-authors nor myself have, as scientists, any objection to what the management objective should be, our presentation should be viewed as a description and not a value judgement as to what is good or bad work.

After completing the research for paper V, I have come to the conclusion that local management can be important and successful. This is because it involves those who have a direct interest in a particular biological resource, and will thus be willing to act. Since they have a direct interest in what happens to the resource, and may even be dependent on it, it seems reasonable that they should be involved in determining the management objectives. However, this does not preclude other parts of society from also having opinions on these local goals. For instance, rare species, such as large predators, have local impacts but their existence is also of national interest. The most important task for local management might be to find ways to determine the management goals and how the natural resources can be used. However, the *formulation* of human goals for natural resource management should not be confused with the specific ways by which these goals are to be achieved. I agree with what Brown says in his paper, *Ngongas and ecology: on having a worldview* (2001), that one can be hardworking, bright, and dedicated, and still be ineffective. To be effective in managing resources I believe one has to distinguish between the objectives, how the system ought

to work, and the way the system can be managed. The reason for this is that formulating the objectives often involves several interests, so there is considerable potential for conflict. The solution to such disagreement cannot be arrived at objectively, but by negotiation. To facilitate such negotiation, local interests need to have indisputable information on the condition of the resource and its dynamics. For that reason, an independent organisation trusted by all local interests is needed. However, if that organisation gets involved in any way in determining the goals, it will sooner or later be called to task for taking sides.

CONCLUSIONS AND PROSPECTS

- The wasting syndrome observed in moose (MWS) since the mid 1980s in Sweden affects senescent individuals more than other adult age classes; males are at least as vulnerable as females; there has not been any locality in Sweden with an obviously higher death risk; and the death risk seems to be uniform over the four seasons. There is as yet no definitive knowledge of the underlying cause(s) of MWS. Reconsidering MWS in light of the new demographic description might give important clues to understanding observations at the individual level.
- Population density can affect early-life body growth, resulting in a lower probability of ovulation or smaller antler size as yearlings. Adults appear less sensitive to density. Slow growth and late age at maturity implies time-delayed population dynamics.
- Population density is critical for calf size but explained little of the total variance in my colleague's and my large-scale experiment. Also, calves are smaller today than they were in late 1970s in our study area, despite an over 50% reduction in population size during the experiment. Besides density-independent factors such as weather and range quality, I suggest intra-specific competition with roe deer and maternal effects might have considerable effects on body growth.
- Birch is the quantitatively most important forage species in the early summer diet of moose. It also seems to be a highly preferred species, but the selection of birch declines with availability. Thus moose seem to balance intake from different food sources instead of maximising the intake of a single food type. Avoiding an overload of secondary compounds and balancing the intake of beneficial constituents are two possible mechanisms.
- Negative frequency-dependent selection suggests that moose are a clever ungulate, as moose with a more rather than less diverse diet have greater reproductive success. Apart from that a mixed feeding strategy seems to be independent of reproductive state – the diet of

pregnant/nursing females does not differ from that of barren females – little can be said about the mechanism.

- The results presented in this thesis suggest that moose are nutrient mixers in early summer but energy maximisers in winter. Thus, moose may adopt different foraging strategies in winter and summer.
- Diet selection indices depend critically on estimates of available proportions of various food types. To date, no thorough evaluation has been conducted to test whether one degree of coverage for one species is comparable with that of another species, and whether the relationships between species are consistent over all degrees of coverage. Thus, there is a need for improved methods for quantifying moose food resources.
- I believe local management can be both important and successful. Because it involves those who have a direct interest in a particular biological resource, they are likely to be willing to act. However, difficulties arise when attempting to apply scientific concepts and methods where non-scientifically trained people are involved. Thus, for local natural resource management to succeed, I suggest that local involvement should mainly focus on goal *formulation*, and less on how specifically to *manage* the resources so as to achieve these goals.

ACKNOWLEDGEMENTS

Understanding our world is based on experience, yours and mine, which in turn is based on the experience of our forerunners and so forth. Thus, first of all, I must dedicate all people that in history have racked their brains giving me the pleasure to all aha experience. Some of you I know by names. Some of you a bit more. Some of you just a bit more. When trying to summarise whom of you that I have appreciated most during my PhD period I will probably miss someone that have been, and perhaps also is, significant to me. If you cannot find your name below, do not blame yourself, do not blame your childhood and do not blame printer's gremlin but blame me!

I have had luck. From childhood until now I have had caretakers, friends and models. People that have believed in me and supported me. Without you I would have been nobody. At least someone very different from whom I am now. It was in January 1995 I first met Kjell, my future supervisor. I was a biology student interesting in animals that one didn't need instruments to view at. Someone told me about a "mooser", Mr. Wallin. I contacted him asking for supervising my master thesis work. Soon I recognised he was not a "mooser". He was something much more important to me. He was a scientist. And he believed in me. And he arranged financial support for doing PhD studies. I still wonder why? But thanks Kjell, thanks also to your nice family.

My first two published papers took an awful long time to finish. It was not my co-authors fault. They have always been willing to discuss problems whenever I have asked for help. Thanks for being persons with great social endowments. Thanks Margareta "Maggan" Stéen and Göran Cederlund.

Many of my PhD colleagues at sister departments have complained about how their superior treat them. Few have told me – "starved wolfs are best at hunting" – at my department. An otherwise not uncommon attitude among academics. I am very impressed of my department head Åke Larsson who persistently butt with the big bulls and care for his staff. I am pleased to have had my office at Åke's research and education hotel.

Moose research at the department of applied environmental science started some years before I entered the arena. Besides Kjell it was "the man who never cries" Petter Lind. When I was an inexperienced moose catcher in summer of 1995, Petter was my biggest support. The awful cow 245 or the freaky hand-receiver, nothing could break my confidence when having Petter as back up. In all years, in rain and snow, there have never been any complaints but a hell of more data to work on. Thanks Petter for being devoted and indefatigable.

For two years I was the only male PhD student at the department. As a representative for gender equality I succeeded a bit when Martin Broberg was accepted for studies. Soon after that was also Johan Truvé one of us. Together we have, among many others things, witnessed drinking habits of

our Finnish brothers and learned how to immobilise a tame moose cow at Kolmården Zoo. Without you, my studies would have been a lot more boring. Thanks Martin. Thanks Johan.

One of my main tasks as PhD student has been to conduct a large-scale experiment but also some other fieldwork. Ambitious and reliable men and women have been needed for success. Because research seldom offers moons and stars, I have been a bit surprised that it has never been hard to find them. We have Bo-Martin "Bosse" Bjelkenberg, who besides Petter, has been my right hand. And the greatest moose hunter among us. Thanks Bosse for being skilful and straightforward. Then we have the Håkansson brothers, Conny and Bengt with families, which deserve mentioning first of all for letting their cottage at Basterås available as head quarter whenever we needed it. Together with Gunnemar Abrahamsson, Bertil Axelsson, Börje Axelsson, Gunnar Byhlin, Björn Larsson, Tomas Pihlman they have also helped Bosse and Petter with collecting specimens. To all of you, thanks a lot. We have all the persistent counters of moose droppings and browsing inspectors. Besides Petter, Bosse and Martin it have been Dan Andersson, Lars Andersson, Nils-Bruno "Nicke" Bengtsson, Fredrik Bergman, Gilbert Brännhult, Bengt-Erik Eriksson, Sören Eriksson, Angelica Hammarström, Helena Karlsson, Anna Nilsson, John Norgren, Ingvar Norrby, Jörgen Rydholm, Inger Toompea and Jan Werner. Also Gunnemar have made inventories. Together with Gilbert and Petter every spring and autumn since we started. Impressive. From another parish we have Lars-Anders Ågren, Per "Grängen" Grängstedt, Kent Sköld and Eric Andersson. All experts in catching full-grown moose. And we have Eric Carlsson and Bengt-Erik that have helped Petter, Bosse, Martin, Kjell and me to run down baby moose. Also Helena, Angelica and Emma Lind know how to do that. I hope that you have had as fun as me. Thanks also Anders Håkansson and Niklas Egriell for, besides Petter and Bosse, doing radio tracking. We have all the thousands local sports hunters and their representatives. Thanks for voluntarily supported my research all those years. Especially I would say thanks to Alf Johansson, Lars Plahn, Tommy Berglund, Ingvar Gabrielsson, Jörgen Johansson and Bo-Erik Persson. In this connection also Lisbeth Johansson and Ingela Gjers at the County Administrative Board of Västra Götaland for every year provided me with hunting statistics. At last I would mention Jonas Wallin and Emma for being excellent data punchers. Thank you.

I have also run through some money. The one and only financier of my research have been the Swedish Environmental Protection Agency. Thanks Anders Lundvall with colleagues for all support and confidence. I hope from now on I am able to pay back.

In everyday work a lot of people have supported me. Colleagues, students and others. I know that I sometimes can get on people's nerves. Being too eager and devoted. Thanks for putting up with me. I owe you all greatest

gratitude. Of you that have been at the department during my PhD studies but today run business elsewhere I have to mention Linda Nilsson and Magnus Jofjord. Linda, it was a pleasure to supervise you during your exam course. Hope you soon will have your study published. Magnus, you taught me how to get muscles and you often freed me from my "oxygen free chamber". Thanks for that and for many nice lunch breaks.

Dear family and dear friends I have really missed you during my thesis spurt. Latest two months I have been working, working and to say it again working. I have spent most time at my office. Most time means both day *and* night. Workaholic or not, it is time for curing I think. So I am glad for having you. Or have had. If you forgotten me please give me a second chance and I shall try to make up for my social absence. Thanks mum and dad for always being there. Thanks sister Susanna and sister Maria and my brother in laws Torgny and Keith for taking care of "the little brother".

So which of you shall I choose for being lonely with at an uninhabited island? That's a simple question. My next-door neighbour, alias my fiancée, Victoria. No one makes me smile as you do.

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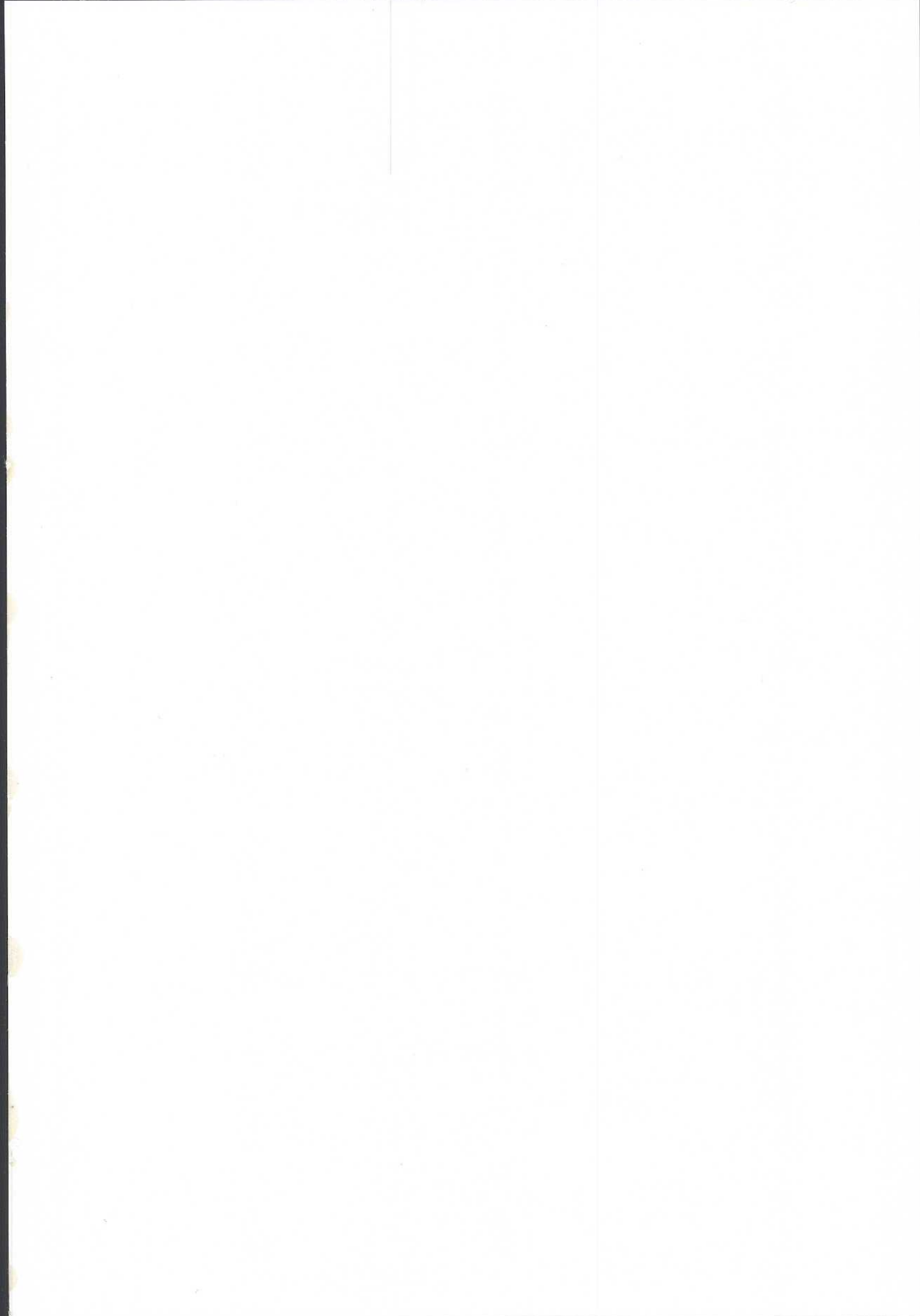
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