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ORIGINAL ARTICLES

Density-dependent variation in reproduction and body mass in female moose *Alces alces*

Håkan Sand, Roger Bergström, Göran Cederlund, Marina Östergren & Finn Stålfelt

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Female body mass and reproduction from harvested moose *Alces alces* were compared in four populations of moose at different stages (densities) of population development, i.e. pre-peak, peak and post-peak, in Sweden during 1961-1991. In two (1 and 2) of the four populations, age-related body mass and reproduction was significantly lower in the post-peak (intermediate density) stage than in the pre-peak stage; whereas for the other two populations (3 and 4), no differences, or higher growth and reproduction at post-peak density, were found. In one population (2) data from all three stages (densities) of population development were available. Age-specific mean body mass was 12.8% lower, and fecundity 46.0% lower (average among age classes), during the peak density stage, than during the pre-peak stage, but did not differ significantly between the peak and post-peak stages, except for fecundity in 1.5-year-old females. In the two populations showing a negative density-dependent response (1 and 2), fecundity decreased more from pre-peak to post-peak density than could be predicted from the reduction in body mass. This suggested a lower reproductive investment per unit body mass at high and intermediate densities, compared to the low density stage. Similar to age-related body growth and fecundity, the proportion of lactating and/or calf-rearing females was significantly lower at post-peak population density in populations 1 and 2 compared to pre-peak densities, but only in the youngest reproducing age class (2.5 years). It is concluded that: i) the large increase in population density has resulted in density-dependent resource limitation, which is expressed as lowered body growth and reproduction in two of the four populations studied; ii) the lower reproductive investment per unit body mass at higher densities may constitute an adaptive strategy to maximise juvenile survival as conditions deteriorate; iii) density-dependent effects in moose may occur at densities which are lower than close to the ecological carrying capacity; and iiii) the variable density-dependent pattern among populations may be due to differential harvest regimes, causing variable post-peak densities, and thus different levels of resource competition among populations.

Key words: density-dependence, reproduction, body growth, carrying capacity, Alces alces

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Ungulates, like other large mammals, experience various kinds of density-dependence (Fowler 1981b, 1987), such as altered physical condition of individuals in terms of body growth and fat deposition, and demographic vigour such as fecundity and survival (Klein 1968, McCullough 1979, Hanks 1981, Albon et al. 1983, Skogland 1985, Clutton-Brock et al. 1987). It is a general assumption that the primary mechanism behind density-dependence in ungulates is food competition (Klein 1970, Clutton-Brock et al. 1983, 1985, 1987, Skogland 1983, 1985, 1990). However, despite its vital importance for the understanding of population regulation, only a few studies have actually verified food limitation as the mechanism behind density-dependence (but see Skogland 1985, Choquenot 1991). For large mammals, it has been suggested that most density-dependence occurs close to the ecological carrying capacity (K), thereby showing a non-linear relationship between fitness traits and population density (McCullough 1979, Fowler 1981a, 1987).

Recent theoretical development of density-dependence has focused on the importance of life-history traits, both in the context of population dynamics and evolution (Boyce 1984, Stearns 1992). In the context of life-history theory, optimisation processes involving allocation of resources to body growth and reproduction are fundamental (Stearns 1992). For example, growth rate is important in determining the optimal body size and age at maturity, and animals may mature along an age/size trajectory instead of at a fixed age and/or size (Stearns & Koella 1986). Consequently, although several studies indicate a close relationship between fecundity and body size in ungulates (e.g. Reimers 1983, White 1983, Sæther & Haagenrud 1983, Albon et al. 1986), this relationship may vary with population density, leading to a change in reproductive investment per unit body mass (Albon et al. 1983, Skogland 1990).

In moose *Alces alces*, density-dependent reproduction has been suggested in both European (Nygrén 1983, Wallin et al. 1995) and in North American populations (Pimlott 1959, Blood 1974, Peterson 1977, Messier 1991). However, evidence for density-dependent effects on body growth and reproduction over time within free-living populations of moose is scarce. Few free-living game species have experienced such an eruptive population development on a country-wide scale as the Swedish moose during the 1970s and early 1980s. In this period (pre-peak), the moose population increased threefold, and thereafter declined (post-peak), mainly due to sharply increased harvest rates (Cederlund & Markgren 1987, Lavsund & Sandegren 1989, Hörnberg 1995, Cederlund & Bergström 1996). In the early 1980s (peak), the moose population exceeded 300,000 animals after harvest, and the maximum annual harvest was 175,000 animals in 1982. The increase was considered to be a combined effect of several major factors such as: 1) increased food supply due to changes in modern forestry practices (Lavsund 1980, 1987, Lavsund & Sandegren 1989); 2) low non-hunting mortality because of few or no natural predators (wolf *Canis lupus* and brown bear *Ursus arctos*); and 3) major changes in harvest strategies, promoting a higher proportion of juveniles in the harvest, resulting in a higher mean age among the surviving females, and thus higher reproductive rates in the population (Cederlund & Bergström 1996). During the years of peak population density, over-exploitation of food resources and considerable damage to young forest plantations in several areas occurred (Bergström & Hjeljord 1987, Lavsund 1987, Hörnberg 1995), and managers reported lowered body mass, reduced number of juveniles per female, and local die-offs, particularly among juveniles (Lönnroth 1982).

In this paper, we test the hypothesis that the strong increase, and subsequent reduction, in the Swedish moose population has resulted in density-dependent effects on body growth and reproduction, by using data from four geographically distant populations of moose at different population densities. We predict that females at peak population density would attain lower body mass and reproduction compared to females in the pre-peak stage. In the post-peak stage with intermediate density, the moose population is expected to have recovered partially in body mass and reproduction. Evidence of density-dependence is tested by comparison of age-related body mass and reproductive data from female moose harvested at different stages of population development, i.e. population densities. We define the pre-peak stage as 1961-73, the peak stage as 1982-84, and the post-peak stage as 1989-91 (Table 1). In this paper density-dependence is defined as a negative relationship between population parameters and population density (Fowler 1987, McCullough 1990).

Methods

Study areas and populations

The study was based on data from moose harvested from four populations in Sweden, located between 56.5°N and 62.5°N (Fig. 1). The four study populations were geographically separated and differed in climatic conditions, composition and type of vegetation, and levels of population density (see Table 1). However, data for population 1 were collected from two different areas but were combined and treated as one southern moose population.

Climatic conditions change from south to north with decreasing temperatures, shorter growing season, and increasing snow depth in winter. Mean winter (December-March) snow depth ranged from 15-20 cm in the south-

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Table 1. Population density estimates, type, and year of sampling among four populations of moose at different stages of population development during 1961-91 in Sweden. For part of population 2 (2*) aerial counts were available for all three stages of population development.

	Population				
	1	2	3	4	2*
Stage	Population density (moose/km^2)				
Pre-peak (1961-1973)	0.45 (70,72)[a]	0.54 (69)[a]	0.50 (70)[b]	0.30 (70)[b]	1.04 (70)[a]
Peak (1982-1984)	-	-	-	-	2.36 (82-84)[c]
Post-peak (1989-1991)	1.25 (92)[d]	1.55 (89-91)[c]	0.62 (90)[e]	0.47 (88)[e]	1.57 (89-91)[c]

Type and sources of density estimation:

[a] Aerial counts (Stålfelt & Norling 1974)

[b] Aerial counts + estimations by managers (Markgren 1982)

[c] Aerial counts (G. Cederlund & H. Sand, unpubl. data)

[d] Pellet counts (Bergström et al. 1995)

[e] Aerial counts (Gävleborgs and Jämtlands läns Jaktvårdsförening, unpubl. data)

ernmost study area (pop. 1) to 40-45 cm in the northernmost study area (pop. 4); mean monthly summer (May-August) temperatures ranged between 14.0°C and 11.8°C. In contrast, mean monthly summer precipitation is not related to latitude, and ranged between 63.9 mm (pop. 3) and 75.0 mm (pop. 1). Population 1 was situated within the boreo-nemoral vegetation zone, whereas populations 2-4 belonged to the boreal vegetation zone (Ahti et al. 1968). All areas were dominated by forests composed of Norway spruce *Picea abies* and Scots pine *Pinus sylvestris* mixed with birches *Betula pendula, B. pubescens*, aspen *Populus tremula* and willows *Salix* spp. The south-north gradient also includes a change from more spruce-dominated forest in the southern part of the country to a larger proportion of pine in the north. Forest productivity and the proportion of agricultural land also decreases towards the north (Svensk Nationalatlas 1992). Altitudes range between 0 and 400 m a.s.l. in the southernmost study areas (pop. 1 and 2), whereas the two northernmost study areas (pop. 3 and 4) show considerably larger altitudinal variation ranging between 0 and 1,200 m a.s.l. Forests were generally composed of 5-50 ha stands of different age. Forest generation time is shorter in the south, 70-120 years between final cuttings compared to 90-150 years in the north.

Data collection

In total, data from more than 5,000 female moose killed during 1961-1991 were collected. In populations 1-3, all animals were killed after the rut which takes place in October-November; in population 4, kills mainly took place before the rut in September. For all the moose killed, hunters recorded date, locality, sex, and carcass mass and collected the lower jaw. For the majority of females, the uteri were collected as was information on the state of lactation and the number of calves present.

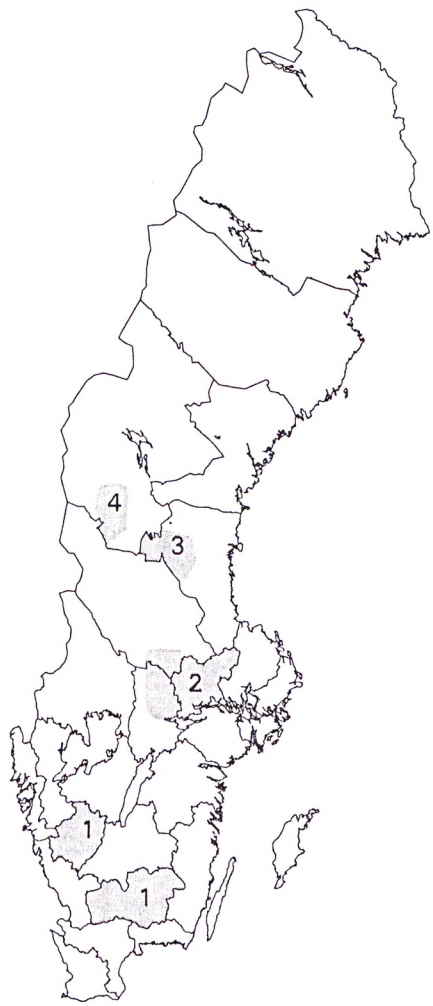


Figure 1. Locations of the four study populations (1-4) in Sweden from which data on moose were sampled during 1961-91. Data from population 1 was sampled from two areas and combined to represent one southern study population.

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Measurements of moose

Age was determined by a combination of ontogenetic development, tooth wear (Skuncke 1949) and counts of the number of annual cementum layers in the first molar (M1) (Markgren 1969). In the analyses, female moose were grouped in five age classes: juveniles (0.5-year-olds), yearlings (1.5-year-olds), and older moose (2.5-year-olds, 3.5-year-olds, and ≥4.5-year-olds).

Carcass mass was total body mass minus head, skin, lower legs, blood and viscera, weighed to the nearest kilogram. In this paper, carcass mass is equivalent to body mass. Estimated body mass or partially weighed moose were excluded from the analyses.

Fecundity was measured as the number of *corpora lutea* present in the ovaries (Markgren 1969). The ovaries were removed from the uterus and fixed in 70-80% alcohol or 10% formaldehyde for a minimum of two weeks. Ovaries were then sectioned longitudinally with a scalpel in 1-2 mm thick slices and were macroscopically examined for *corpora lutea*.

Recruitment rates were based on the proportion of females showing signs of lactation and/or having a juvenile present when killed. State of lactation was recorded from visual inspection of the udder of the female. Because milk production ceases within a few weeks after weaning, and a large proportion of the juveniles were killed early in the hunting season, only females killed during the first 10 days of the hunting season were included in the analysis.

Population density

In the early pre-peak stage of population development (1961-73), aerial counts in winter were made in populations 1 and 2 (Stålfelt 1974) (see Table 1). In populations 3 and 4, aerial counts were made locally, and together with information from field experience by managers and data on annual harvest quotas, average winter population densities in 1970 were estimated (Markgren 1969, 1982).

In the late post-peak stage of population development (1989-91) winter population densities were estimated either by aerial counts (pops. 2, 3 and 4) or by pellet counts (pop. 1) made from a regional survey of moose*forest interactions performed in 1992 (Bergström et al. 1995).

For a part of study population 2 (see 2* in Table 1), data from aerial counts were available from all three stages of population growth. Data showed that population density, in the early pre-peak stage of population development in 1970, was 44% of the density found during the peak in 1982-84. In the late post-peak stage in 1989-91, population density had declined to approximately 67% of the level found during the peak stage of population development. All estimates of population density from aerial surveys were corrected for bias in visibility (Tärnhuvud 1988).

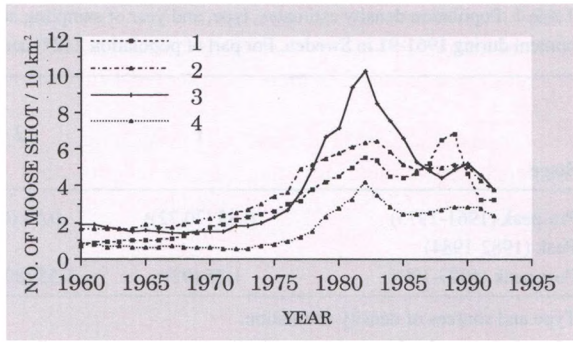


Figure 2. Annual harvest figures, measured as the number of moose killed per 10 km², during 1960-1992 for each of the four study populations in Sweden.

Although we used different methods to estimate population density, errors of estimation were probably small in relation to the large variation found between stages of population development. In the four study populations, winter population density during the early pre-peak stage of population development was 36%, 35%, 81%, and 63%, respectively, of the density found during the late post-peak stage (see Table 1). However, the true development of population densities may be best reflected in the annual harvest statistics, although these figures probably reflect the population size as it was 2-3 years earlier (Fig. 2). Thus, all populations in this study probably experienced an even larger variation in population density during the study period than is presented in Table 1.

Data analyses

Variations in age-specific body mass, fecundity and recruitment rates between stages of population growth within each population were tested with a one-tailed t-test. Logistic regression with maximum likelihood estimation computed by SYSTAT (SYSTAT 1992) and the Logit Module (Steinberg 1988) was used to examine variation in size-specific fecundity rates between stages of population development. In the model, the number of *corpora lutea* per female constituted the dependent variable. In female moose, the number of *corpora lutea* per female usually ranges between 0 and 2, but may reach 3 or 4 on rare occasions. To estimate association between age, body mass, and the probability of ovulation (potentially reproducing females) and multiple ovulation (potentially twinning females), the outcomes of the dependent variable were recoded to yield two binary variables:

1) FECUND = recoding was performed in respect to whether ovulation had occurred or not. Thus, absence of *corpora lutea* was scored 0 (n = 298), and presence was scored 1 (n = 1,317).
2) TWIN = recoding was performed to test whether multi-

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ple ovulation had occurred versus single ovulation. Thus, females having 1 *corpus luteum* were scored 0 (n = 701), whereas those having 2 or more were scored 1 (n = 616).

Inspection of linearity in age and body mass in relation to the dependent variables revealed that, for the probability of ovulation (FECUND), females could be classified into two age groups (1.5 and ≥2.5); whereas for multiple ovulation (TWIN), four age classes (1.5, 2.5, 3.5 and ≥ 4.5) were a more appropriate classification.

Variation in age and size-related fecundity between stages of population development among populations was examined by including stage of population development (pre-peak, peak, and post-peak), and population identity of females (1-4), as categorical variables in the model. Significant contribution of independent variables to the model was tested by the likelihood ratio-test with the chi-square (χ^2) distribution, and the model building strategy of stepwise forward inclusion of independent variables (Hosmer & Lemenshow 1989). For all analyses the significance level of 0.05 was accepted.

Results

Body mass

Juvenile body mass data were available from populations 1 and 2 and showed significant variation among stages of population growth. Juvenile body mass was lower in the post-peak stage than in the pre-peak stage for both populations (pop. 1: t = 3.66, df = 808, P < 0.001; pop. 2: t = 6.66, df = 744, P < 0.001). In population 2, mean juvenile body mass was also significantly lower during the peak stage than during the pre-peak stage (t = 4.93, df = 729, P < 0.001), but not between the peak and post-peak stages (t = 0.78, df = 105, P = 0.44). Among older females (≥1.5 years) in population 1, significantly lower mean body mass in the post-peak stage than in the pre-peak stage was also found for 1.5-year-old (t = 7.69, df = 448, P < 0.001) and ≥4.5-year-old females (t = 3.09, df = 354, P = 0.0011), but not for 2.5-year-old (t = 1.40, df = 163, P = 0.08) and 3.5-year-old females (t = 1.02, df = 93, P = 0.15). In population 2, older females showed the same pattern as in population 1, with lower mean female body mass during the post-peak stage than during the pre-peak stage (1.5 years: t = 7.52, df = 418, P < 0.001; 2.5 years: t = 1.54, df = 177, P = 0.06; 3.5 years: t = 3.20, df = 102, P < 0.001; ≥4.5 years: t = 5.68, df = 337, P < 0.001, Fig. 3). As for juveniles, older females killed during the peak stage in population 2 had significantly lower mean body mass than females killed during the pre-peak stage (1.5 years: t = 7.89, df = 405, P < 0.001; 2.5 years: t = 3.05, df = 169, P = 0.0014; 3.5 years: t = 3.32, df = 102, P < 0.001; ≥4.5 years: t = 5.61, df = 345, P < 0.001), but not compared to females killed during the post-peak stage (1.5 years: t = 1.46, df = 51, P = 0.07; 2.5 years: t = 1.65, df = 38, P = 0.054; 3.5 years: t = 0.16, df = 24, P = 0.44; ≥4.5 years: t = 0.24, df = 112, P = 0.40, see Fig. 3). In contrast, there was no significant difference in age-related body mass between the pre-peak and post-peak stages of population development in population 3 (1.5 years: t = 0.87, df = 66, P = 0.19; 2.5 years: t = 1.50, df = 39, P = 0.072; 3.5 years: t = 1.0, df = 21, P = 0.16; ≥4.5 years: t = 0.08, df = 85, P = 0.47). In population 4, two of three age classes showed a reversed pattern, with females in the post-peak stage having a higher mean body mass than females in the pre-peak stage (1.5 years: t = 3.0, df = 51, P = 0.002; 2.5 years: t = 2.17, df = 30, P = 0.019; 3.5 years: insufficient sample size; ≥4.5 years: t = 0.15, df = 85, P = 0.44). The difference in age-related body mass between pre- and post-peak stages averaged 4.6% in population 1, 12.7% in population 2, 3.6% in population 3 (differences were not uniform among age classes), and 7.1% in population 4 (opposite direction compared to population 1 and 2).

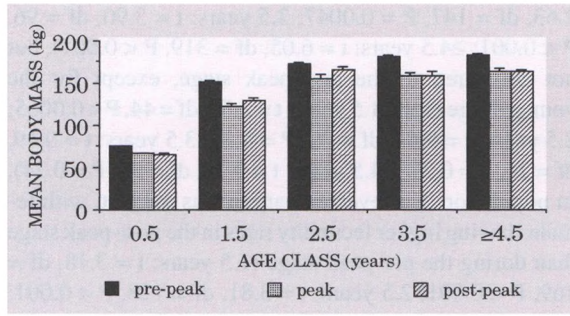


Figure 3. Mean age-specific body mass (kg) among females at low (pre-peak), high (peak) and intermediate (post-peak) population densities in population 2 in Sweden.

Fecundity rates: age-specific

As for body mass, age-specific fecundity rates were significantly different between stages of population development in three of the four study populations, and followed the same pattern as body mass. In populations 1 and 2, all age classes showed lower fecundity rates during the post-peak stage than during the pre-peak stage (pop. 1: 1.5 years: t = 8.99, df = 360, P < 0.001; 2.5 years: t = 5.69, df = 131, P < 0.001; 3.5 years: t = 4.16, df = 66, P < 0.001; ≥4.5 years: t = 4.95, df = 287, P < 0.001; pop. 2: 1.5 years: t = 3.57, df = 393, P < 0.001; 2.5 years: t = 2.22, df = 151, P = 0.014; 3.5 years: t = 3.84, df = 90, P < 0.001; ≥4.5 years: t = 4.25, df = 303, P < 0.001). Females in population 2 showed a significantly lower fecundity during the peak stage than during the pre-peak stage (1.5 years: t = 6.31, df = 397, P < 0.001; 2.5 years: t =

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2.63, df = 147, P = 0.0047; 3.5 years: t = 3.90, df = 96, P < 0.001; ≥4.5 years: t = 6.05, df = 319, P < 0.001), but not compared to the post-peak stage, except for the youngest age class (1.5 years: t = 2.59, df = 44, P < 0.0065; 2.5 years: t = 0.64, df = 32, P = 0.26; 3.5 years: t = 0.49, df = 26, P = 0.32; ≥4.5 years: t = 0.72, df = 96, P = 0.24). In population 3, a reversed pattern was evident, with females having higher fecundity rates in the post-peak stage than during the pre-peak stage (1.5 years: t = 3.18, df = 169, P < 0.001; 2.5 years: t = 3.81, df = 128, P < 0.001; 3.5 years: t = 1.81, df = 67, P = 0.038; ≥4.5 years: t = 4.01, df = 318, P < 0.001). In population 4, adequate sample size (n > 10) from both stages of population growth was available only for the oldest age class (≥4.5 years) and suggested, similar to population 3, a higher post-peak fecundity, although this was not statistically significant (t = 1.01, df = 23, P = 0.16, Fig. 4).

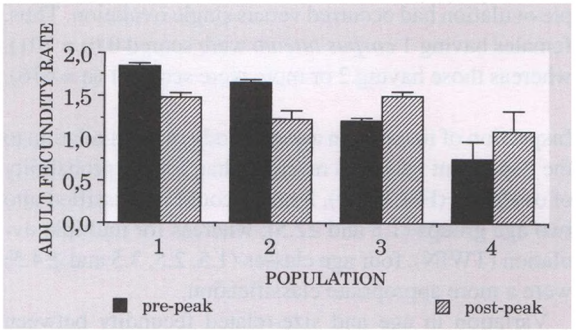


Figure 4. Mean fecundity rates among ≥4.5-year-old female moose in the four study populations at low (pre-peak) and intermediate (post-peak) population density in Sweden.

Fecundity rates: size-specific

We examined if the variation in age-related fecundity between stages of population development among the four study populations could be explained solely by the variation in body mass, by analysing data on age, body mass, stage of population development and population identity in relation to fecundity in a logistic regression model. Both age and body mass were strongly and independently related to fecundity in female moose (Table 2, Model 1 and 2). However, when controlling for the effect of age and body mass on fecundity, inclusion of stage of population development also was highly significant (Model 3), suggesting that the variation in age-related fecundity found between stages could not be solely attributed to variation in body mass. Thus, age-related fecundity differed more between stages of population development than could be predicted from the variation in female body mass alone.

However, the analyses of age-related fecundity and age-related body mass indicated that the effect of population stage differed between populations (see Fig. 4). To examine if the effect of stage of population development on the size/fecundity relationship was dependent on the population under study, we first included population identity as a separate categorical variable (Model 4), and then the interaction term between stage of population development and population identity in addition to age and body mass (Model 5). Inclusion of the interaction term contributed significantly to the model including all four variables, suggesting that, although the level of relationship between body mass and fecundity was dependent on the stage of population development, this effect differed between populations.

By plotting the probability of multiple ovulation on

Table 2. Logistic regression analyses with χ^2-tests for the effect of stage of population development (STAGE), and population identity (POP) on age and body mass-related fecundity among 1,615 female moose from four populations in Sweden.

Model	Variable(s) included	Variable entered	Log-likelihood	G	df	P
Probability of ovulation (FECUND)						
0	Null (constant only)	-	772.3			
1	Null	AGE	665.2	214.2	1	***
2	AGE	MASS	588.6	153.2	1	***
3	AGE+MASS	STAGE	567.9	41.4	2	***
4	AGE+MASS+STAGE	POP	542.2	51.4	3	***
5	AGE+MASS+STAGE+POP	STAGE*POP	535.3	13.8	5	*
Probability of multiple ovulation (TWIN)						
0	Null (constant only)	-	910.1			
1	Null	AGE	841.3	137.6	1	***
2	AGE	MASS	781.8	119.0	1	***
3	AGE+MASS	STAGE	756.8	50.0	2	***
4	AGE+MASS+STAGE	POP	749.0	15.6	3	**
5	AGE+MASS+STAGE+POP	STAGE*POP	735.7	26.6	5	***

P: *<0.05, **<0.01, ***<0.001

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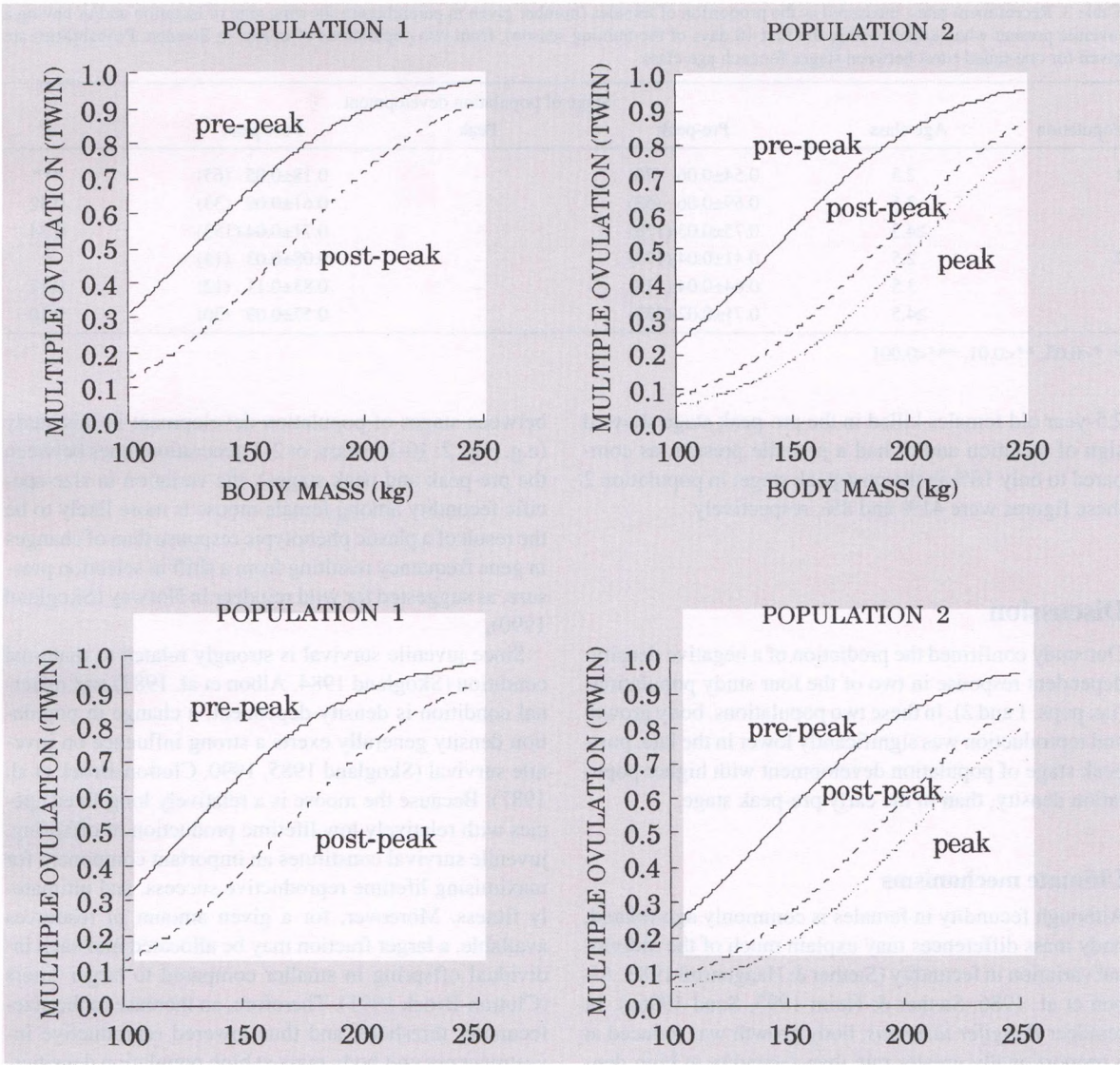


Figure 5. Relationship between fecundity, measured as the probability of multiple ovulation (TWIN), and body mass (kg) among ≥4.5-year-old female moose in the four study populations and at different stages of population development during 1961-91 in Sweden.

body mass for adult females (≥4.5 year) (Fig. 5), we found that during the post-peak stage of population development females in populations 1 and 2 had to attain a 40-50 kg higher body mass to have the same probability of multiple ovulation as in the pre-peak stage. In contrast, adult females in the post-peak stage in population 3 needed a 25 kg lower body mass, and a 60 kg lower body mass in population 4 was sufficient for the same probability of multiple ovulation, compared to the pre-peak stage. Thus, the relationship between body mass and fecundity was not constant but changed between stages of population development. As a consequence, to have a 50% probability of multiple ovulation, 25-30% higher body mass was needed in the post-peak stage than during the pre-peak stage in study populations 1 and 2; whereas for females in populations 3 and 4, a 15-30% lower body mass was sufficient.

Proportion of recruiting females

Furthermore, we examined if the apparent variation in female fecundity between stages of population development also was expressed in recruitment rates in populations 1 and 2 (data on recruitment was not available from populations 3 and 4). Recruitment rates differed significantly in both populations between stages of population development, but only for the youngest reproducing age class (2.5-year-olds, Table 3). In population 1, 54% of the

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Table 3. Recruitment rates, measured as the proportion of females (number given in parentheses) showing sign of lactation and/or having a juvenile present when killed (within the first 10 days of the hunting season), from two populations of moose in Sweden. Probabilities are given for one-tailed t-test between stages for each age class.

Population	Age class	Stage of population development			P
		Pre-peak	Peak	Post-peak	
1	2.5	0.54±0.06 (70)	-	0.18±0.05 (65)	***
	3.5	0.69±0.06 (52)	-	0.61±0.09 (33)	0.42
	≥4.5	0.75±0.03 (178)	-	0.71±0.04 (153)	0.34
2	2.5	0.41±0.04 (177)	-	0.08±0.03 (13)	*
	3.5	0.64±0.04 (118)	-	0.83±0.11 (12)	0.17
	≥4.5	0.71±0.02 (333)	-	0.57±0.09 (30)	0.10

P: *<0.05, **<0.01, ***<0.001

2.5-year old females killed in the pre-peak stage showed sign of lactation and/or had a juvenile present, as compared to only 18% in the post-peak stage; in population 2 these figures were 41% and 8%, respectively.

Discussion

Our study confirmed the prediction of a negative density-dependent response in two of the four study populations (i.e. pops. 1 and 2). In these two populations, body growth and reproduction was significantly lower in the late, post-peak stage of population development with higher population density, than in the early pre-peak stage.

Ultimate mechanisms

Although fecundity in females is commonly age-related, body mass differences may explain much of the individual variation in fecundity (Sæther & Haagenrud 1983, Albon et al. 1986, Sæther & Heim 1993, Sand 1996a). In reindeer *Rangifer tarandus*, body growth was reduced at a proportionally greater rate than fecundity at high densities (Skogland 1990), whereas in red deer *Cervus elaphus*, fertility was more sensitive to changes in population density than was body mass (Albon et al. 1983). Although both body mass and fecundity changed with variation in population density in the present study, age-specific fecundity showed larger variation among stages of population development than did age-specific body mass. Thus, in populations 1 and 2 female moose made a lower reproductive investment (defined as the mean number of *corpora lutea* produced per unit body mass) at high population densities, whereas in populations 3 and 4 a higher reproductive investment per unit body mass was made at high density. This suggests that although body size and fecundity are strongly interrelated this relationship may not be constant, but show variation over time within populations due to changes in living conditions for moose. Considering the relatively short time period that elapsed between stages of population development in this study (e.g. pop. 2: 10-15 years, or 2-3 generation times between the pre-peak and peak stages), the variation in size-specific fecundity among female moose is more likely to be the result of a plastic phenotypic response than of changes in gene frequency resulting from a shift in selection pressure, as suggested for wild reindeer in Norway (Skogland 1990).

Since juvenile survival is strongly related to maternal condition (Skogland 1984, Albon et al. 1987) and maternal condition is density-dependent, a change in population density generally exerts a strong influence on juvenile survival (Skogland 1985, 1990, Clutton-Brock et al. 1987). Because the moose is a relatively long-lived species with relatively low lifetime production of offspring, juvenile survival constitutes an important component for maximising lifetime reproductive success, and ultimately fitness. Moreover, for a given amount of resources available, a larger fraction may be allocated into each individual offspring in smaller compared to larger litters (Clutton-Brock 1991). Therefore, an increase in the size-fecundity threshold, and thus lowered reproductive investment per unit body mass at high population densities, ensures that only females in relatively good condition may reproduce; this is likely to constitute an adaptive strategy to maximise fitness by promoting a high juvenile, and possibly also adult female, survival as environmental conditions deteriorate (Stearns 1992). But see also Sæther et al. (1996) and Sand (1996a) for a discussion on geographical variation in reproductive strategies in female moose.

In addition to fecundity, a reduction in recruitment rate was also found at high population densities, although this was significantly detectable only for the youngest reproducing age class (2.5-year-old females). However, because moose is a species where twinning rarely occurs in the youngest reproducing age class, but is rather common among older females, we may expect that regulation in the older age classes occurs mainly through a reduction in the number of females giving multiple births. Conse-

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quently, differences in recruitment rates, based on the proportion of calf-rearing females, between stages of population development are therefore likely to be detected only in the youngest reproducing age classes.

Proximate mechanisms

Although stress, or limitation of access to space, is sometimes put forward as a likely explanation for density-dependence in ungulates, empirical evidence is still scarce. More often, evidence is presented for food limitation as being the operating mechanism of density-dependence among ungulates (Bobek 1977, Sinclair 1977, 1989, Messier & Crête 1984, Skogland 1984, 1985, Sæther 1987, Choquenot 1991). However, the type and effect of density-dependent food limitation may differ depending on the type of environment in which the species has evolved.

The moose has evolved in a rapidly changing and unpredictable environment, created by wind storms, insect outbreaks, flooding, and especially forest fires. The moose has responded to this type of environment by redistribution (Geist 1974, 1981) and by evolving an inherent flexibility in reproductive parameters, such as age at maturity and twinning rates among adult females (Geist 1974, Franzman & Schwartz 1985, Liberg & Wahlström 1995). In Fennoscandia, modern forest practices during the last 40-50 years have almost completely replaced the role of wild-fires (Zachrisson 1977). In turn, this has resulted in a high abundance of moose browse (Bergström & Hjeljord 1987, Cederlund & Bergström 1996) and thus increased the ecological carrying capacity (K) for moose. A major change in moose harvest strategy and almost no natural predators contributed to nearly optimal conditions for a rapid population growth during the 1970s in Sweden, resulting in at least a three-fold increase in population density in 10-15 years (Cederlund & Markgren 1987, Lavsund & Sandegren 1989, Cederlund & Sand 1991, Hörnberg 1995, Cederlund & Bergström 1996). However, in most populations densities were reduced in the early 1980s, due to heavily increased harvest quotas, to a level approximately 60-80% of that prevailing during the peak years.

Considering the reduction in moose population density in the years following peak density in the early 1980s (Hörnberg 1995), we should expect population condition to have improved 6-8 years after the reduction in population density (post-peak). However, no major improvement in population parameters from the peak to the lower post-peak density was found in population 2, the only population with data from all three stages of population growth. We suggest three possible explanations to this pattern: 1) the existence of a cohort effect on adult females produced and reared during peak population densities; 2) an extensive time-lag in the recovery rate of the vegetation that precluded a significant improvement in foraging conditions for moose; and/or 3) a 40% reduction in population density was not sufficient to remove the effects of food limitation in the population.

Cohort effect

Cervids produced and reared under unfavourable conditions may not obtain maximum adult body mass, and such effects may be transferred to future generations (i.e. cohort effects; Mech et al. 1987, Clutton-Brock et al. 1988, Albon et al. 1992). However, the mean life expectancy of moose in Sweden is short due to high annual harvest rates (30-40% of the previous winter population). For males, the risk of being shot before five years of age is >90% and for females about 70% (population 2*; Cederlund & Sand 1991). Short life expectancy among individual moose results in a relatively high turnover rate in the population, and implies that the majority of the younger females in this study were produced and reared by females that had grown up after the peak in population density. Furthermore, Solberg & Sæther (1994) showed that cohort effects on growth in Norwegian moose only persisted for 1-2 years, and that most of the individuals that had experienced poor initial conditions, were able to compensate by prolonged growth later in life. Thus, we conclude that the lack of improvement in population parameters in population 2 is unlikely to be caused by persistent density-dependent effects on cohorts born during or shortly after the peak density stage.

Food recovery rate or continued high population density

Surveys of the winter food situation for moose in Sweden have shown a heavy use of preferred species (e.g. aspen, willows, and mountain ash *Sorbus aucuparia*), especially during the stage of peak population density in the early 1980s (Hörnberg 1995, Ball et al., unpubl. data). The abundance of preferred deciduous species may at least for some time have been kept in a 'predator pit' by moose, i.e. lower densities of moose were able to regulate the abundance of these species once they had been severely reduced. However, the browsing pressure on trees and shrubs has decreased during the last 10-15 years (Hörnberg 1995), i.e. parallel to the population decrease, and this reduction may have triggered an improvement in the abundance of high-quality food. A fairly quick recovery of birch *Betula* spp. after several years of heavy browsing has been recorded in exclosure experiments (R. Bergström, unpubl. data). A considerable and rapid recovery of *Epilobium angustifolium*, considered an important summer food species for moose, appeared shortly after exclusion (by fences) of large herbivores in southern Sweden (Nilsson et al. 1994). Furthermore, in a long-term

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study of density-dependent effects in an enclosed moose population, Wallin et al. (1995) found no support for a more permanent depletion of the food resource at high population density. In their study, the reproductive rate of females showed an immediate response to a reduction in population density and returned (increased) along the same level during the reduction-phase of the population as in the phase of population increase. Thus, we conclude that, although high population densities during the early 1980s caused reduced abundance of high-quality food for some years, persistent effects of food limitation on population condition is not likely unless it occurred in combination with a continued high browsing pressure (density) by moose. This conclusion is also supported by an investigation of the present winter browsing pressure and abundance of browse in population 1 in 1992 (Pehrson & Faber 1993), which revealed relatively heavy use of the preferred browse species by moose. Moreover, dense populations of moose may cause short-term carry-over effects, e.g. from heavy summer browsing to both the following winter food resources and the next summer food situation (Bergström & Danell 1995).

Although the ecological carrying capacity (K) is likely to differ among populations of moose, post-peak moose densities in our study populations (0.47 - 1.55 moose/km^2) are assumed to be well below moose carrying capacity both for Swedish moose (Cederlund & Sand 1991), and some populations of North American moose (Crête 1989). Despite this, our results showed considerable variation in population parameters between stages of population development, suggesting that moose in two of the four study populations are still constrained by food limitation. However, density-dependent responses in large mammals are believed to occur mainly close to carrying capacity (McCullough 1979, Fowler 1981a, 1987). Our results contradict this conclusion because, although we found evidence for density-dependent effects on body growth and reproduction between stages of population development in populations 1 and 2, post-peak populations still expressed relatively high recruitment rates (0.7 - 0.8 calves per female in autumn from moose observations), and low juvenile mortality (<10%, among radio-collared females (K. Wallin & G. Cederlund, unpubl. data)). This allowed an annual sustainable harvest of approximately 30-40% of winter population. We conclude that density-dependent effects on body growth and reproduction in moose may occur at lower densities than will seriously affect juvenile mortality, i.e. close to carrying capacity.

Contrasting patterns between areas

At least three, not mutually exclusive, explanations may be invoked as a cause of the contrasting density-dependent pattern found among populations: 1) a difference in recovery rate of the vegetation between study areas; 2) seasonal migration in the two northernmost populations (i.e. populations 3 and 4) may act as a buffering mechanism against density-dependent effects; and 3) variable post-peak moose densities in relation to carrying capacity between populations.

First, we believe it is unlikely that the differences in response pattern are due to differences in vegetation recovery rate, as this rate is expected to be more rapid in the more productive areas in the south (i.e. populations 1 and 2). Secondly, if interactions between browsing on summer and winter food resources are of any significance, the migratory behaviour of moose in areas with relatively large altitudinal variation (Sweanor & Sandegren 1986) may act as a buffering mechanism (Geist 1981, Skogland 1990), i.e. it decreases the risk of feeding on the same food resource during both summer and winter. At present, this explanation cannot be further evaluated. Thirdly, harvest data, and data on population development based on experience by local managers (Sandewall 1988, Lavsund & Sandegren 1989), suggest that harvest rates in populations 3 and 4 increased at a far greater rate between the pre-peak and peak stages, compared to populations 1 and 2 (Figs. 2 and 6). This is likely to have resulted in a less pronounced peak in population density in populations 3 and 4 in the early 1980s, but also in lower post-peak densities, compared to populations 1 and 2. This explanation is also supported by a country-wide survey of browsing pressure and abundance of browse for moose performed in 1992 (R. Bergström, unpubl. data). Results showed a more pronounced current browsing pressure on the preferred browse species in populations 1 and 2 than in populations 3 and 4. Thus, density-dependent food limitation may have persisted in populations 1 and 2 due to a prolonged period of high or relatively high population densities, whereas in populations 3 and 4 density-dependent food limitation in the post-peak stage was precluded by more intensive harvest regimes.

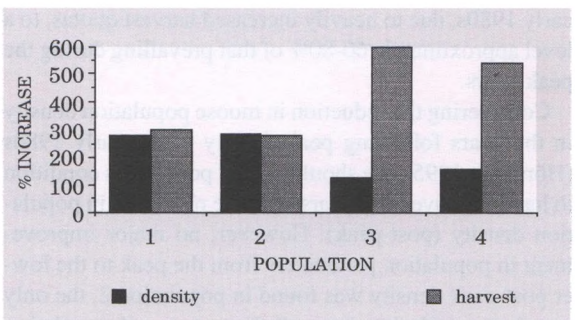


Figure 6. Increase in percent, in population density between the pre-peak and post-peak stages, and in harvest rates between the pre-peak and peak stages of population development among the four study populations of moose in Sweden.

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However, this does not explain why we found higher fecundity rates in the post-peak stage than in the pre-peak stage in populations 3 and 4. In another study we showed that there was significant annual variation in body growth and reproduction in a part of population 2, and that conditions for body growth and fecundity in the post-peak years (1989-91) were better than average during the sampling period (1982-94, Sand 1996b). Thus, if this pattern was consistent over a larger geographical scale (i.e. over a major part of the Swedish moose population), it is likely that inter-annual variation in climatic conditions provided better conditions for growth and reproduction in the post-peak stage than in the pre-peak stage. If this is true, density-dependent effects in populations 1 and 2 in the present study may have been even more pronounced than found in this data set.

This study shows the existence of density-dependent effects on body growth and reproduction in female moose where food limitation is the most probable operating mechanism, and evidence is presented for density-dependent responses to occur at lower densities relative to the ecological carrying capacity than has been suggested for large mammals in general (McCullough 1979, Fowler 1981a, 1987).

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