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Life history patterns in female moose (*Alces alces*): the relationship between age, body size, fecundity and environmental conditions

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Abstract I examined the relationship between age, body size and fecundity in 833 female moose *(Alces alces)*from 14 populations in Sweden sampled during 1989–1992. Data on population density, food availability and climatic conditions were also collected for each population. Age and body mass were both significantly positively related to fecundity, measured as ovulation rate, among female moose. The relationship between the probability of ovulation and body mass was dependent on age with (1) a higher body mass needed in younger females for attaining a given fecundity, and (2) body mass having a stronger effect on fecundity in yearling (1.5 year) than in older (≥2.5 year) females. Thus, a 40 kg increase in yearling body mass resulted in a 42% increase in the probability of ovulation as compared to a 6% increase in older females. The lower reproductive effort per unit body mass, and the relatively stronger association between fecundity and body mass in young female moose compared to older ones, is likely to primarily represent a mechanism that trades off early maturation against further growth, indicating a higher cost of reproduction in young animals. In addition to age and body mass, population identity explained a significant amount of the individual variation in fecundity, showing that the relationship between body mass and fecundity was variable among populations. This variation was in turn related to the environment, in terms of climatic conditions forcing female moose living in relatively harsh/more seasonal climatic conditions to attain a 22% higher body mass to achive the same probability of multiple ovulation (twinning) as females living in climatically milder/less seasonal environments. The results suggests that the lower fecundity per unit body mass in female moose living in climatically harsh/more seasonal environments may be an adaptive response to lower rates of juvenile survival, compared to females experiencing relatively milder/less seasonal climatic conditions.

Key words Fecundity · Body size · Climate · Survival · Adaptation

Introduction

Reproductive patterns are known to exhibit large variation among species, populations, and individuals (Roff 1992; Stearns 1992). Early theoretical analyses predicted that mortality patterns, caused by environmental conditions, were important mechanisms for shaping age- and size-specific reproductive patterns. For example, an increase in adult mortality will select for a decrease in the age at maturity while an increase in juvenile mortality will favour delayed maturity (Gadgil and Bossert 1970; Michod 1970; Law 1979). Delayed reproduction may also be selectively advantageous in a varying and/or unpredictable environment (Schaffer 1974).

More recently it has been suggested that, in addition to age-specific mortality, rates of body growth, and size-dependent reproduction, are also crucial components for the evolution of reproductive patterns among organisms (Stearns and Koella 1986). Thus, one reason for delayed maturity may be that because in many organisms, reproductive rate increases with body size, an increase in fitness will result from a greater size at maturation. Accordingly, because conditions affecting growth and survival are variable between habitats and may change rapidly over time within habitats, to maximize fitness most organisms should mature neither at a fixed size nor at fixed age, but along an age-size trajectory (Stearns and Koella 1986).

For most organisms in general, and among large herbivores in particular, size-dependent reproduction is the rule rather than the exception (Sadleir 1969; White 1983; Caswell 1989). Therefore, any factor that affects variation in growth rates, and thus body size, will indirectly affect the age at maturity and adult fecundity rates among individuals. However, the relationship between body size and

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reproduction may differ among individuals within a population, among populations, and among species (Stearns 1992). As a consequence, variation in reproductive rates may not only depend on patterns of body growth, but also on the relationship between body size and reproductive rate among individuals (Bernardo 1993).

Variation in reproductive strategies may in turn be related to the type of environment, including factors such as predation (Michod 1970; Law 1979), climate and/or seasonality (Boyce 1978, 1979, 1988; Roff 1992) and food resource levels (Gadgil and Bossert 1970; Kozlowski and Uchmanski 1987). For example, the size-fecundity relationship within and among populations of female red deer was related to population density, with an increasing body mass threshold at high population densities (Albon et al. 1983), while a comparison between subspecies of Rangifer revealed large variation in reproductive effort, and was suggested to result from differential predation pressures (Skogland 1989).

In this study, I use data on age and size-related fecundity from 833 female moose from 14 geographically separated populations, distributed over 8° in latitude and with different population densities, availability of browse and climatic conditions. First, I test the predictions that age and body mass are both strongly independent predictors of fecundity and that older females make a larger reproductive effort, in terms of higher fecundity per unit body mass, compared to younger females. Second, I include population identity of females in the analyses, and predict that the size-fecundity relationship is variable among populations with increased body mass threshold, associated with low availability of food and/or relatively harsh/more seasonal climatic conditions. Possible mechanisms to the observed patterns are suggested and discussed in terms of life history theory.

Material and methods

Study sites

Data for moose and environmental variables were collected from 14 areas from 57.5° N to 66.0° N latitude, a distance of about 1000 km (Fig. 1). All sampling areas were located within the boreal vegetation zone (Ahti et al. 1968), and are dominated by forests. The forests are mainly composed of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), mixed with deciduous trees such as birch (*Betula pendula and B. pubescens*), aspen (*Populus tremula*) and willow (*Salix* spp.). The composition of the forest changes from more spruce dominated in the south to a larger proportion of pine in the north. The south-north gradient also includes a decreasing proportion of agricultural land and decreased productivity of the forest (Svensk Nationalatlas 1992a,b). Climatic conditions change from south to north, with increasing winter snow depth and decreasing temperatures causing a reduction in the duration of plant growing season, while summer precipitation is variable among areas but not related to latitude. See also Sand et al. (1995) for a more thorough description.

Collection and measurements of animals

Data on moose were collected from 833 females shot during the regular hunting season, October to December, in 1989–1992. For each moose shot, hunters recorded date, population identity, carcass mass, and collected the lower jaw for age determination. For females the uterus were collected together with information on presence of calf at heel and/or milk in the udder.

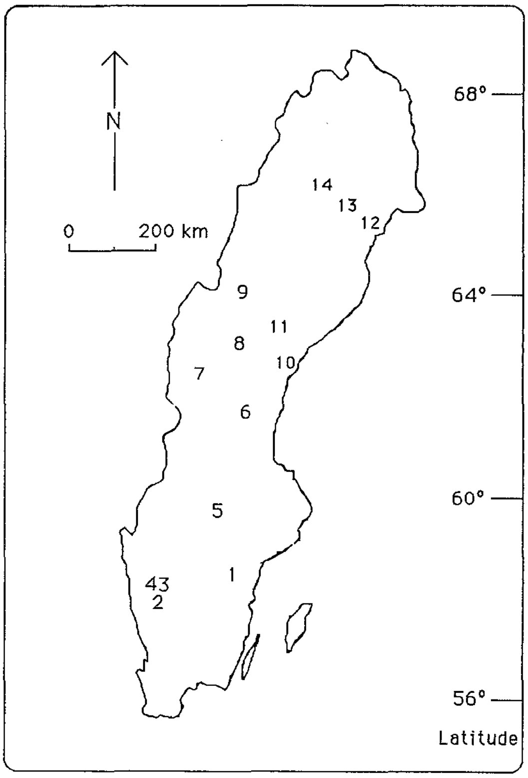

Fig. 1 Location of the 14 populations from where moose were sampled during the study period 1989–1992 in Sweden

Age determination was performed by a combination of ontogenetic development, tooth wear (Skunke 1949) and counting of the number of annual cementum layers in the first molar (M1) (Markgren 1969). Accordingly, juveniles were aged 0.5 years, yearlings 1.5 years, 2-year-olds 2.5 years, and so on.

Carcass mass (measured as total body mass minus head, skin, lower legs, blood and viscera) was measured to nearest kilogram, and throughout the paper carcass mass is referred to as body mass.

Fecundity was estimated by the number of large corpora lutea present in the ovaries (Markgren 1969). The ovaries were removed from the uterus and fixed in 70% alcohol for a minimum of 2 weeks, and were cut with a razor blade into 2-mm-thick slices for occular examination of large corpora lutea.

Population and environmental characteristics

Winter population densities of adult moose were estimated by a computerized simulation program (CERSIM) based on annual records of the number of moose observations made by the hunters during the first week of the hunting season (Lanestedt et al. 1988). Additional demographical information [fecundity rates, age and sex distribution, juvenile sex ratios among killed moose, and non-hunting (natural) mortality rates] were also incorporated into the model. Evaluation of the accuracy of this method by comparison of adult moose densities estimated from simulations versus aerial counts for a number of areas (n=13) in Sweden revealed fairly small deviations among the two methods (r^2=0.96, P=0.0001), ranging between 0 and 0.18 moose/km^2 (0–21%) and averaged 0.08 moose/km^2 (10.2%) (F. Karlsson, unpublished report). There was no systematic bias in the number of moose estimated by simulations irrespective of the size of an area used. The simulations were performed by personnel at the Research Unit of the Swedish

Table 1 Principal component (*PC*) analyses including the seven climatic variables as reduced to two principal components (*CLIMATE 1* and *CLIMATE 2*) for the 14 study sites of moose in Sweden. Correlation coefficient (r) for each variable to the principal component and the percentage variation explained by each principal component are given

Principal component (variable)	Correlation coefficient (loading) r	
	PC 1 (CLIMATE 1)	PC 2 (CLIMATE 2)
Duration of growing season	0.994	0.021
Mean winter temp.	0.976	0.153
Mean snow depth	−0.967	−0.204
Seasonality of temp.	−0.960	−0.159
Mean summer temp.	0.940	−0.253
Seasonality of precip.	−0.892	0.184
Mean summer precip.	0.580	0.808
Variance explained	83.0%	12.0%

Hunter's Association in Uppsala, Sweden. Among populations, moose densities ranged between 0.31 and 1.32 moose/km^2 and averaged 0.87 moose/km^2.

Climatological data were obtained from meteorological stations of the Swedish Meteorological and Hydrological Institute (SMHI) situated close to the study sites. The data included mean monthly values of temperature, precipitation and snow depth for the last 30 years. Mean summer temperature was calculated as the mean from May to August, while mean winter temperature and snow depth was equal to the average of December to March. The length of the plant growing season was calculated for each area by fitting a four degree polynomial curve [arbitrarily chosen to achieve a good statistical fit (r^2>0.99)] between date and the mean monthly temperatures and calculating the number of days with ≥6°C (Langvatn and Albon 1986). The coefficient of variation (CV) of mean monthly values of temperature and precipitation were calculated to give a measure of seasonality (Boyce 1978) for each area of sampling.

Data on the amount of browse available to moose in each study area were provided by the Swedish National Forest Survey at Umeå and based on samples from a regular survey of Swedish forests during 1986–1991 and pooled over the years to yield an average measure. Data were sampled by using circular plots (radius=10 m) which were systematically distributed throughout the country. The number of sample plots within each study area averaged 627 and ranged between 75 and 1305 depending on the size of the study area and density of plots laid out. In each sampling plot the amount of available browse was measured as the percentage cover of small shrubs and trees available to moose (0.5–3.0 m). The browse was classified in three groups: (1) PINE *(Pinus sylvestris and P. contorta)*, (2) BIRCH (*Betula pendula and B. pubeshens*) and (3) OTHER browse, including rowan *(Sorbus aucuparia)*, aspen *(Populus tremula)*, willow *(Salix* spp.*)*, juniper *(Juniperus communis)*, oak *(Quercus robur)*, and ash *(Fraxinus excelsior)*.

Data analyses

To examine the relationship betweeen age, body mass and fecundity among populations we used the logistic regression model:

$$Y=e^{(a+bx)}/(1+e^{(a+bx)})$$

where: Y=is the probability of ovulation, a and b are constants and x represents dependent variables.

The contribution of independent variables was tested using the likelihood ratio test and the chi-square distribution with significance level 0.05, and the model building strategy of stepwise forward inclusion or alternate exclusion of independent variables (Hosmer and Lemenshow 1989).

In the statistical model the number of corpora lutea per female constituted the dependent variable. In female moose, the number of corpora lutea per female usually ranged between 0 and 2, but might also on rare occasions reach 3 or 4. To estimate association between independent variables and both 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. Y1, where recoding was performed to test whether ovulation had occured or not. Thus, absence of corpora lutea was scored 0 (n=206) and presence was scored 1 (n=627).
2. Y2 where recoding was performed to test whether multiple ovulation (two or more) had occured versus no or single ovulations. Thus, females having zero or one corpora lutea were scored 0 (n=574), while those having two or more were scored 1 (n=259).

Inspection of linearity in age and body mass in relation to the dependent variables revealed that for the probability of ovulation (Y1) females could be classified into two age groups (1.5 and ≥2.5). For multiple ovulation (Y2) four age classes (1.5, 2.5, 3.5 and ≥4.5) was a more appropriate classification because production of multiple ovas is more common among older females (≥4.5) than in the younger age classes. No tranformation or classification was needed for body mass.

Because of strong intercorrelations among climatological variables a principal component analyses based on a correlation matrix with orthogonal transformation and quartimax rotation was performed. This reduced the original seven climatological variables to two new principal components which together explained 95% of the overall variation in climatic conditions among areas (Table 1). The two principal components explained 83.0% and 12.0%, respectively. The first one (CLIMATE 1) was strongly associated with the length of growing season, mean winter temperature, mean snow depth, seasonality of temperature, mean summer temperature and seasonality of precipitation, and could thus be equated with climatic harshness and/or seasonality. The second principal component (CLIMATE 2) was strongly correlated only with mean summer precipitation.

Confounding effects among variables

Since age class was used in the analyses as a covariate and was thus controlled for, possible variation in age distribution among populations was assumed to be irrelevant except in ≥2.5- and ≥4.5-year-old females. However, no significant variation in mean age was found between areas within either ≥2.5-year-old (df=13, H=13.38, P>0.4) nor ≥4.5-year-old females (df=13, H=13.44, P>0.4: Kruskal-Wallis test). Because the breeding period in moose occurs shortly before the hunting season, late breeding females may not yet have reached oestrus and thus lack visible corpora lueta when shot. However, inclusion of shooting date in addition to age class and body mass in the logistic regression model was not significant for either of the dependent variables (Y1: X^2=0.4, P>0.25, df=1; Y2: X^2=0.6, P>0.25) indicating that the rate of ovulation among females did not increase throughout the season. However, the date of the breeding period may differ among geographically distant populations and, thus, act as a potential confounding factor when analysing for covariation between fecundity and environmental conditions. There was no significant effect of shooting date when the only significant environmental variable (CLIMATE 1) was included in the model (Y1: X^2=1.8, P>0.10, df=1; Y2: X^2=0.05, P>0.25, df=1). Inclusion of the interaction term between shooting date and the climatic conditions was also non-significant (Y1: X^2=0.8, P>0.25, df=1; Y2: X^2=0.6, P>0.25, df=1) suggesting that shooting date was not an important factor af-

Table 2 The effect of the individual traits age (*AGE*) and body mass (*MASS*) on the probability of ovulation (*Y1*) and multiple ovulation (*Y2*) for 833 female moose in Sweden. The two univariate models including only age (step 1) or body mass (step 2) are tested against the model including the constant only (step 0), while the model including both age and body mass are tested against the model including only age (step 3). The effect of interaction between age and body mass are tested against the model including both age and body mass (step 4)

Step	Variable(s) included	Variable(s) entered	Log-likelihood	*G*	*df*	*P*
Dependent variable=Y1						
0	Null (constant only)	–	465.9			
1	Null	AGE	349.1	233.6	1	***
2	Null	MASS	377.4	177.0	1	***
3	AGE	MASS	332.5	33.2	1	***
4	AGE+MASS	AGE*MASS	325.1	14.8	1	***
	Dependent variable=Y2					
0	Null (constant only)	–	516.3			
1	Null	AGE	432.5	167.6	1	***
2	Null	MASS	437.0	158.6	1	***
3	AGE	MASS	400.4	64.2	1	***
4	AGE+MASS	AGE*MASS	400.3	0.2	1	n.s.

* P=0.05, ** P=0.01, *** P=0.001

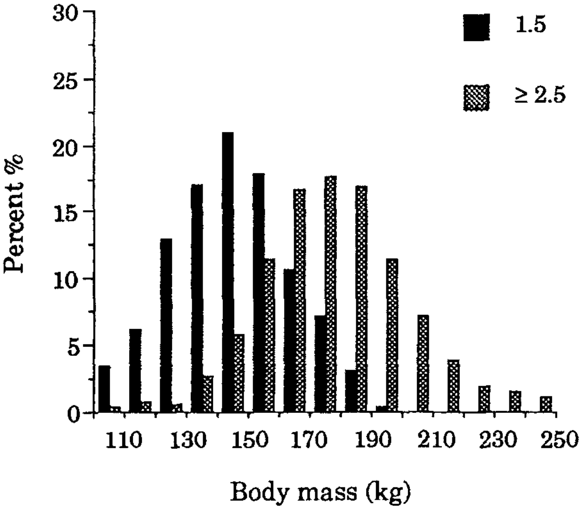

Fig. 2 Body mass distribution in 224 yearling (1.5-year-old) and 609 older (≥2.5-year-old) female moose in Sweden

fecting the relationship between climatic conditions and fecundity found in this data set. Moreover, it has also been suggested that young females, breeding for the first time, would come into oestrus later in the breeding season than older females. To test whether this could have a confounding effect on the results I examined whether shooting date was associated with fecundity in some age classes but not in others by including the interaction term between age class and shooting date in the model. This did not significantly improve the model (Y1: X^2=0.2, P>0.25, df=1; Y2: X^2=2.0, P>0.10, df=1) indicating that the variation in fecundity found among age classes was not associated with shooting date. Finally, I included the year of sampling as a categorical variable, in addition to age, body mass and population identity, in a new model to test for between-year variation in fecundity among populations. This showed that between-year variation was not a significant factor explaining variation in fecundity among populations in this dataset (Y1: X^2=2.0, P>0.25, df=3; Y2: X^2=0.2, P>0.25, df=3).

Results

Relation between age, body mass and fecundity

The relationship between age (AGE), body mass (MASS) and the two estimates of fecundity (Y1,Y2) was examined by including the two individual traits, first as single variables, and then simultaneously in a model. Age and body mass were significantly positively related to the probability of ovulation (Y1) and multiple ovulation (Y2), both as single variables and in the multi-variable model, indicating that both traits had an independent effect on fecundity in female moose (Table 2).

To test whether the significant association between the two individual traits and fecundity was dependent on each other, the interaction term between age and body mass was included into the model. This contributed further to explaining variation in the probability of ovulation but not multiple ovulation (Table 2). However, significant interaction may occur as a statistical artefact if there is little or no overlap in body mass among the age classes used in the analyses. Plotting the body mass distributions for the two age classes showed relatively large overlap (Fig. 2). Consequently, the effect of body mass on ovulation was dependent on age with a relatively stronger effect in yearling (1.5-year-old) females as compared to older (≥2.5-year-old) ones (Fig. 3). Thus, a 40 kg increase in body mass from 120 to 160 kg increases the probability of ovulation from 12% to 54% among yearling females while the same increase in body mass in older females results in an increase in the probability of ovulation from 82% to 88%. In contrast, the effect of body mass on the probability of multiple ovulation was equally strong in all age classes, with a 30% higher probability of multiple ovulation for a 40 kg increase in body mass from 150 to 190 kg (Fig. 4).

Variation among populations

Inclusion of population identity of females (POP) showed that, while controlling for the effect of age and body mass, female fecundity differed significantly among populations (Table 3). Although variation was small, alternate exclusion of the three independent variables from the full model showed that age was the most important variable, followed by body mass and population identity, for both estimates of fecundity. The significant effect of population identity on fecundity shows that the relationship between body mass and fecundity differs

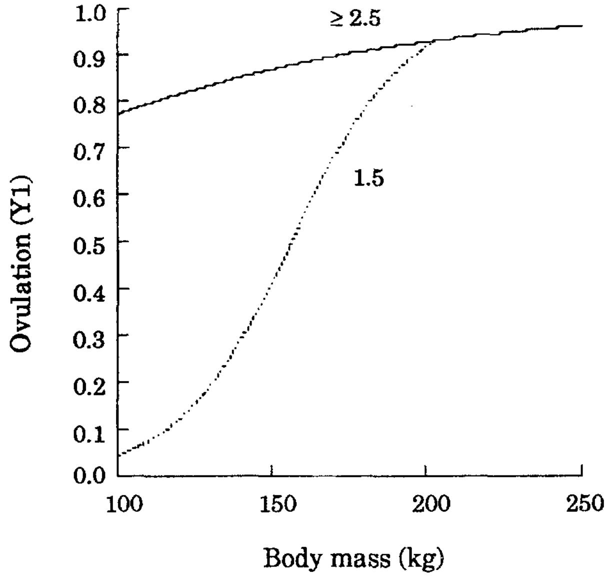

Fig. 3 The relationship between body mass and the probability of ovulation (*Y1*) in two age classes (1.5- and ≥2.5-year-old) of female moose in Sweden

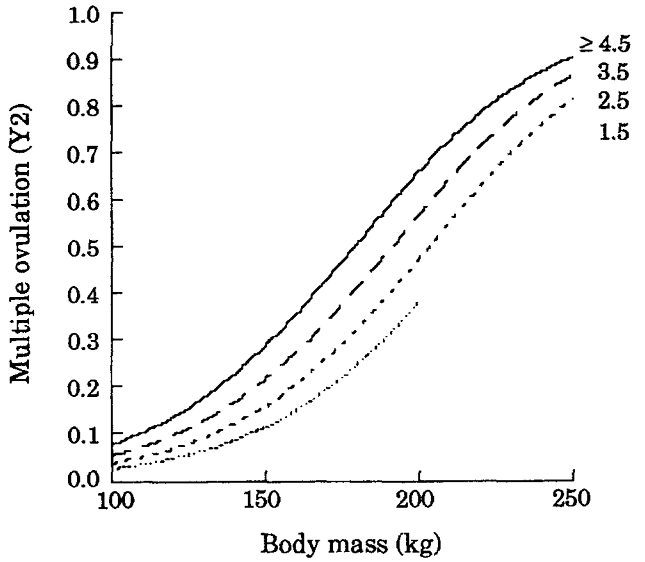

Fig. 4 The relationship between body mass and the probability of multiple ovulation (*Y2*) in four age classes (1.5-, 2.5-, 3.5- and ≥4.5-year-old) of female moose in Sweden

among populations. To quantify variation among populations in the size-fecundity relationship I calculated the body mass needed for ≥2.5- and ≥4.5-year-old females to have a 50% probability of ovulation and multiple ovulation. This body mass threshold showed large variation among populations and ranged from 93 kg to 209 kg and from 153 kg to 227 kg, respectively (Table 4). Consequently, to achieve the same probability of fecundity, females from some populations must attain a considerably greater body mass than females from other populations.

Relation to the environment

Association between the variable size-fecundity relationship and characteristics of the environment and population density was analysed by stepwise forward inclusion of the six independent variables in addition to age and body mass. Two variables, population density (DENSITY) and climatic harshness/seasonality (CLIMATE 1), were significantly related to the two estimates of fecundity (Table 5). Larger body size was needed for a given probability of fecundity at lower population densities and with increased climatic harshness/seasonality.

For both estimates of fecundity, CLIMATE 1 was the most important variable explaining variation among populations. After the inclusion of this variable no other variable could further significantly explain variation among populations in either of the two fecundity estimates. However, although CLIMATE 1 significantly improved the predictability of the model, it was not as good a predictor as the categorical variable of population identity (POP), suggesting that CLIMATE 1 only partly could explain variation in the size-fecundity relationship found among populations (Tables 3, 5).

Plotting the effect of climatic conditions on the size-fecundity relationship showed that adult (≥ 4.5-year-old) female moose living in populations exposed to a relatively mild/less seasonal climate had a 50% probability of multiple ovulation at 170 kg body mass, while female moose living in relatively harsh/more seasonal climatic conditions must attain a body mass of 207 kg (Fig. 5). Thus, in relatively harsh/more seasonal climatic conditions in Sweden female moose must attain on average 20–30% higher body mass than those living in a relative-

Table 3 Analyses of the relative contribution of age (*AGE*), body mass (*MASS*) and population identity (*POP*) (n=14) in explaining individual variation in fecundity, measured as the probability of ovulation (*Y1*) and multiple ovulation (*Y2*), among 833 female moose in Sweden. The relative contribution of each independent variable are estimated by alternate exclusion of each variable from the full model (0) including all three variables

Step	Variables included	Variable excluded	Log-likelihood	*G*	*df*	*P*
Dependent variable=Y1						
0	AGE+MASS+POP	–	311.6			
1	AGE+MASS	POP	332.5	41.8	13	***
2	AGE+POP	MASS	334.3	45.4	1	***
3	MASS+POP	AGE	354.5	85.8	1	***
Dependent variable=Y2						
0	AGE+MASS+POP	–	382.2			
1	AGE+MASS	POP	400.4	36.4	13	***
2	AGE+POP	MASS	413.2	62.0	1	***
3	MASS+POP	AGE	424.7	85.0	1	***

* P=0.05, ** P=0.01, *** P=0.001

Table 4 Body mass needed for having a 50% probability of ovulation (*Y1*) and multiple ovulation (*Y2*) in ≥2.5- and ≥4.5-year-old female moose among 14 populations in Sweden

Population	Body mass (kg) Y1	Body mass (kg) Y2	*n*
1	92.7	161.4	139
2	99.7	184.7	143
3	105.8	160.8	114
4	96.9	152.6	107
5	94.2	184.6	113
6	100.8	159.6	65
7	167.9	197.3	15
8	117.5	176.8	36
9	97.8	183.8	37
10	157.8	213.3	13
11	117.8	209.2	11
12	148.3	212.2	13
13	137.1	214.3	19
14	208.3	227.3	8

ly milder/less seasonal climate to have the same probability of fecundity.

Discussion

This study shows that female moose do not mature or attain a certain fecundity at a fixed size or age. For a given body size young females are less fecund and make a lower reproductive investment than do older females. Moreover, the strength (slope) of the relationship between body size and probability of ovulation was dependent on age, with body size being relatively more important in young (1.5-year-old) than in older (≥2.5-year-old)

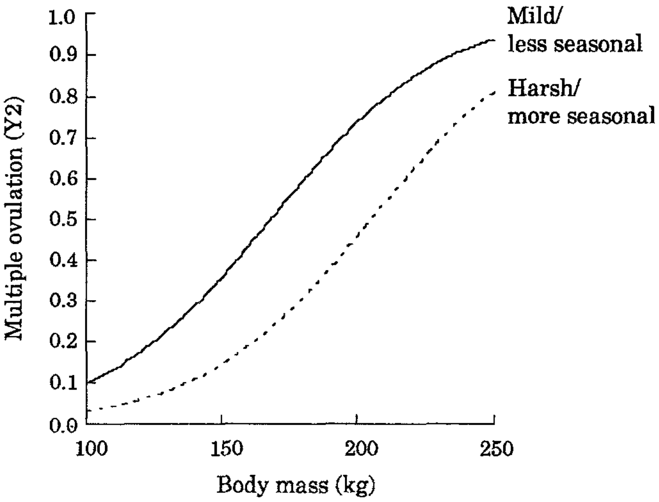

Fig. 5 The relationship between body mass and the probability of multiple ovulation (*Y2*) in ≥4.5-year-old female moose at two extreme values of climatic conditions (mild/less seasonal and harsh/more seasonal) found among 14 populations of moose in Sweden

Table 5 Multivariate analyses examining the effects of climatic conditions (*CLIMATE1*, *CLIMATE2*), availability of browse and population density (*DENSITY*) on the probability of ovulation (*Y1*) and multiple ovulation (*Y2*) while controlling for the effects of age (*AGE*) and body mass (*MASS*) for 833 female moose in 14 populations in Sweden (refer to the text for fuller definitions of variables). The model building strategy of stepwise forward inclusion is applied

Step	Variables included	Variable entered	Log-likelihood	*G*	Sign	*df*	*P*
Dependent variable=Y1							
0	AGE+MASS	–	332.5				
1		DENSITY	326.6	11.8	(+)	1	***
2		CLIMATE1	325.0	15.0	(–)	1	***
3		CLIMATE2	332.5	0	(–)	1	n.s.
4		BIRCH	331.0	3.0	(–)	1	n.s.
5		PINE	332.4	0.1	(–)	1	n.s.
6		OTHER	332.5	0	(–)	1	n.s.
0	AGE+MASS+CLIMATE1	–	325.0				
1		DENSITY	323.4	3.2	(+)	1	n.s.
2		CLIMATE2	325.0	0	(–)	1	n.s.
3		BIRCH	324.7	0.6	(–)	1	n.s.
4		PINE	324.5	1.0	(+)	1	n.s.
5		OTHER	324.9	0.2	(–)	1	n.s.
Dependent variable=Y2							
0	AGE+MASS	–	400.4				
1		DENSITY	396.4	8.0	(+)	1	**
2		CLIMATE1	393.9	13.0	(–)	1	***
3		CLIMATE2	400.4	0	(+)	1	n.s.
4		BIRCH	400.0	0.8	(–)	1	n.s.
5		PINE	400.1	0.6	(–)	1	n.s.
6		OTHER	400.1	0.6	(+)	1	n.s.
0	AGE+MASS+CLIMATE1	–	393.9				
1		DENSITY	393.4	1.0	(+)	1	n.s.
2		CLIMATE2	393.9	0	(+)	1	n.s.
3		BIRCH	393.9	0	(+)	1	n.s.
4		PINE	393.7	0.4	(+)	1	n.s.
5		OTHER	392.2	3.4	(+)	1	n.s.

**P*=0.05, ***P*=0.01, ****P*=0.001

females. In fact, body size had almost no effect on the probability of ovulation in older females, suggesting that the majority (80–90%) of females will produce at least one offspring irrespective of body size.

The cost of reproduction are generally believed to be higher in younger animals than in older ones (Clutton-Brock 1991) and theoretical models predict that allocation of energy to reproduction should be an increasing function of age (Williams 1966; Gadgil and Bossert 1970; Engen and Saether 1994). In female moose two factors are likely to be important in affecting the cost of early maturity, and thus the allocation of energy to reproduction, among age classes: (1) body growth continues after the attainment of sexual maturity, but is known to be strongly impaired by early maturity (Saether and Haagenrud 1985; Sand and Cederlund, in press; H. Sand, unpublished), and (2) there exists a strong positive association between body size and fecundity (multiple ovulation) among adult females (this study). This suggests that the relatively stronger association between fecundity and body mass in young female moose compared to older ones is likely to primarily represent a mechanism that trades off early maturation against further growth. Thus, for young female moose, reproducing at a small body size is likely to impose a relatively larger risk on future fecundity and ultimately lifetime reproductive success compared to older females, where production of at least one offspring will nearly always be possible irrespective of body size.

In addition to age and body mass, population identity also explained a significant amount of the individual variation in fecundity among females indicating that the size-fecundity relationship differed markedly among populations, forcing females in some populations to attain an approximately 25–30% greater body size to have the same probability of fecundity as in other populations (Table 4). Although a large number of studies on ungulates have presented data on age- and size-related fecundity (Sadleir 1969; Reimers 1983; White 1983; Saether and Haagenrud 1983, 1985; Albon et al. 1986; Gaillard et al. 1992), few have focused on variation in the size-fecundity relationship among populations. In red deer, this relationship was variable both within and between populations and was strongly related to population density (Albon et al. 1983). The authors explained the increased size-fecundity threshold in high density populations as an adaptive strategy whereby reproducing females increase the viability of offspring while reducing their own risk of dying in late winter. The proximate cause suggested was increased resource competition at high densities leading to a lowered nutritional level among females prior to and during the rut. Skogland (1989) compared Canadian caribou and Norwegian reindeer and found variable growth rates, size dimorphism and size-specific fecundity rates which could be attributed to variation in reproductive effort. In contrast to red deer (Albon et al. 1983), these patterns were ascribed to differences in age and size-specific mortality among the two subspecies caused by predation by wolves on young caribou as opposed to heavy hunting pressure by man on adult reindeer. The net result suggested was a genetic differentiation through selection for delayed maturity and a higher size-fecundity threshold in caribou as compared to wild reindeer.

Contrary to red deer, the size-fecundity thresholds among populations in the current study were negatively related to variation in population density, and were not significantly associated with the availability of browse. However, variation in the size-fecundity relationship was strongly related to climatic conditions in terms of climatic harshness and/or seasonality, and when climatic variation was accounted for there was no effect of either population density or the availability of any type of browse on the size-fecundity relationship. This suggests that although population density showed a four fold variation among populations, density dependent effects on fecundity and/or body growth was not pronounced, possibly because (1) the ecological carrying capacity differs among areas, and (2) all populations are annually harvested with approximately 30% of the summer population being taken. Thus, variation in climatic conditions may be a more important factor causing variation in the size-fecundity relationship than resource competition among populations of Swedish female moose. However, females living in populations exposed to relatively adverse and seasonal climatic conditions (low temperatures, short growing season, large snowdepth in winter) expressed a higher size-fecundity threshold as compared to females living in relatively milder and less seasonal climatic conditions. Climatic regime has been suggested as an important factor affecting life history patterns in animals in general, mainly through the effect on food resources (Boyce 1978, 1979, 1988; Porter and McClure 1984; Cameron and McClure 1988; Simpson and Boutin 1993). For Swedish female moose, climate may be important in at least two ways. First, in northern populations, relatively more snow during winter in combination with lower temperatures over a longer time throughout the year lead to increased energetic costs of mobility and thermoregulation compared to moose in southern populations, but may also affect the accessibility of browse to moose. Winter conditions, in terms of duration of snow cover, were shown to strongly affect growth patterns of juvenile moose in one population in southern Sweden (Cederlund et al. 1991). Increased energetic costs during winter may ultimately lead to a lower rate of survival which is more likely to affect juveniles than adult animals (Clutton-Brock and Albon 1989).

Second, climatic conditions may have an indirect effect on herbivores by modifying the nutritional quality of plants (Klein 1965, 1970; Albon and Langvatn 1992; Langvatn et al. 1994) and the duration of the period when food of high quality is available (Klein 1985). In general, nutritional quality (in terms of digestibility) of plants during summer is believed to increase with latitude, e.g. towards cooler climates (Van Soest 1983; Riley and Skjelvåg 1984; Albon and Langvatn 1992), and has been suggested as the proximate mechanism responsible for the positive correlation between body size and latitude found in ungulates (Geist 1987; Langvatn and Albon 1986). Elsewhere we have shown that adult body size in Swedish moose are also strongly positively correlated to latitude and climatic conditions (Sand et al. 1995). Thus, female moose in northern populations grow for a longer time in life, reach a larger final adult body size, but do not increase fecundity at the same rate, leading to an increased body size threshold for a given fecundity compared to female moose in southern populations.

A number of environmental characteristics have been suggested as being important factors affecting the evolution of life histories, including variability and unpredictability of the environment (Pianha 1970; Schaffer 1974), resource abundance and competition (Southwood 1988), climatic adversity and seasonality (Boyce 1979, 1988; Roff 1988) and predation (Michod 1970; Law 1979). However, the approach of relating the type of living environment (or habitat) to life history patterns among organisms has been cautioned by Stearns (1992), because the mechanisms that link the type of environment to life histories are not specified. Moreover, classification of environments may differ according the organism under study, indicating the importance to incorporate a mechanism when life histories are discussed in terms of the type of living environment. Theoretical models of life history variation suggest that two mechanisms are generally important influencing the age-/size-fecundity relationship (Stearns and Koella 1986; Stearns 1992). First, if fecundity is positively related to body size, and growth continues after sexual maturation, it should be advantageous to delay maturity until a certain size have been attained in order to increase the overall lifetime fecundity. Second, if survival among juveniles is dependent on the age or size of their mothers it should pay to refrain from reproduction until a sufficient age/size has been attained in order to increase the probability of survival of the juveniles. The latter may occur either because older animals are better parents due to having more experience, or just because larger animals will be able to put more resources into each offspring (Roff 1988).

Recent investigations into reproductive patterns of individual female moose show that there is a large variation in juvenile mortality rates among populations in Sweden. Thus, juvenile mortality rates during summer in one northern population were nearly twice as high compared to two southern populations (K. Wallin and G. Cederlund, unpublished data), suggesting that the reproductive value of producing a calf in southern populations is higher than in northern populations. Furthermore, the fact that the relatively higher juvenile mortality in the northern population occured mainly in early summer during the first two month of life, and was not caused by predation, implies that the nutritional status of the female may be the responsible cause of variable juvenile mortality rates among populations. Thus, although moose in northern populations probably experience more favourable nutritional conditions during summer compared to moose in southern populations, the relatively longer and more severe winter conditions may constrain females by decreasing the period when food of high quality is available. This is likely to increase depletion of body reserves during winter in female moose to the extent that it will seriously affect the nutritional status of females during late pregnancy and early weaning, and thus the viability of newborn offspring, as compared to females living in relatively milder climatic environments. Several studies have shown that among ungulate species, maternal body condition strongly affects juvenile body size (Lenvik et al. 1982; Clutton-Brock et al. 1988; Mech et al. 1991; Skogland 1984) and survival (Clutton-Brock et al. 1988).

I conclude that the lower fecundity per unit body mass in female moose living in climatically harsh/more seasonal environments may be an adaptive response to lower rates of juvenile survival as compared to females experiencing relatively milder/less seasonal climatic conditions. Thus, in climatically harsh/more seasonal environments, with a relatively short vegetative season allowing for somatic growth, reproduction may constitute a higher risk of wasting resources among females unless a relatively large body size is achieved to ensure that sufficient body reserves are available for the increased costs of pregnancy in late winter, ultimately to minimize the risk of juvenile mortality the following summer.

This study confirms earlier research in life history evolution showing that age and body size are both strong predictors of fecundity and that animals exposed to variable conditions should not mature at either a fixed age nor at a fixed size (Stearns 1992) but along an age-size trajectory. The results also supports the view that climatic conditions may be one important component for shaping reproductive strategies within animals species (e.g. Boyce 1988).

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