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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 achieve the same probability of multiple ovulation (twinning) as females living in climatically milder/less seasonal environments. The results suggest 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
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.

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 ocular 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/km² (0–21%) and averaged 0.08 moose/km² (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