ARE MOOSE ONLY A LARGE DEER?: SOME LIFE HISTORY CONSIDERATIONS

Jean-Michel Gaillard

Unité Mixte de Recherche N°5558 “Biométrie et Biologie Evolutive”, Université Claude Bernard Lyon 1, Bâtiment 711, 43 Boulevard du 11 novembre 1918, 69622 Villeurbanne Cedex, France

ABSTRACT: Body mass generally accounts for a large part of variation in life history traits of ungulates. However, phylogeny and ecological features such as habitat or diet have been shown to cause differences in life history patterns among species of similar size. To assess the factors that shape life history traits of moose (*Alces alces*), the largest deer (Cervidae) species, I fitted allometric relationships among ungulate species for a set of life history traits. I compared moose life history traits first with both traits expected from allometric equations and traits of similar-sized bovids. Both kinds of analyses led to the same results. While moose calves grow as expected from the size of their mothers, they start life at only about half the expected size. Moose populations have higher growth rates and shorter generation times as compared to similar-sized ungulates. Females reproduce earlier and have larger litters relative to their body size. The resulting faster than expected life cycle for moose cannot be accounted for by changes in survival patterns: moose closely fit the general pattern of ungulate population dynamics characterized by a low and variable juvenile survival as opposed to a high and constant survival of prime-age females. High reproductive output accounts for the fast life cycle of moose populations compared to other similar-sized ungulates. I propose that the high reproductive output has evolved in response to the unpredictable environmental conditions of early successional habitats preferred by moose. The evolutionary strategy of moose appears more similar to that of a very large roe deer (*Capreolus capreolus*) than that associated with larger deer in general.

ALCES VOL. 43: 1-11 (2007)

Key words: allometry, birth mass, evolution, fitness, generation time, maternal care, reproductive output, survival patterns, ungulates

---

Since the pioneering work by Stearns (1976), the study of variation in life history traits has become a popular task among evolutionary ecologists. The analyses of variation in life history traits can be performed at two different scales. First, the variation at the interspecific level is generally studied using species-specific data collected from the literature by using comparative analyses (sensu Harvey and Pagel 1991). Second, the existence of evolutionary trade-offs between fitness components or the assessment of life history variation generated by differences in phenotypic quality are usually performed at the intraspecific level by analyses of population- or individual-specific data (see Roff 1992, Stearns 1992 for reviews). At the interspecific level, the variation in life history traits of vertebrates is mostly accounted for by three major structuring factors. Variation in body size generally accounts for more than half of the variation in most life history traits (Peters 1983, Calder 1984, Brown and West 2000 for reviews). In mammals, for instance, it is well-established that large mammals live longer, reproduce later, and produce fewer offspring per year than small ones (Stearns 1983, Gaillard et al. 1989). However, for a given size, taxa often show marked differences in life history traits. For example, it is well known that bats outlive similar-sized rodents. Thus, ecological correlates of life history traits also occur. Differences in diet and differences in habitat quality have been shown to generate differences in life history traits (Sæther and Gordon 1994 for ungulates, Fisher et al. 2001 for marsupials).

Moose (*Alces alces*) are the largest members of the Cervidae family (from 200 to 825 kg, Novak 1993). Therefore, I expect that its large body size may have markedly shaped life history traits currently observed in moose populations. From comparative analyses of maternal care and demographic patterns reported in populations of moose and related ungulate species, I assessed whether moose life history can simply be accounted for by large size (i.e., moose are only large deer), or whether moose have specific life history traits independent of their size relative to other deer (i.e., moose are different than a large deer).

METHODS

To assess whether moose are simply large deer, I performed two types of analyses on life history traits related to maternal care (birth mass and early growth rate) and population dynamics (population growth rate, generation time, and fitness components such as age-specific survival and reproduction). First, I used allometric analyses in a three-step procedure. I first fitted allometric relationships without including moose for studied life history traits among ungulate species for which published information was available. Although species do not represent independent data points, I performed the analyses by fitting usual linear models without accounting for phylogenetic relationships among species. My approach was based upon: (1) the similar results obtained from analyses on raw data (as performed here) and analyses including corrections for phylogenetic dependence (such as independent contrasts, see Garland et al. 1992) often reported (e.g., Fisher and Owens 2000); and (2) criticisms of the usefulness of phylogenetic methods such as independent contrasts (Ricklefs and Starck 1996, Björklund 1997, Price 1997), mainly based on the strong assumptions made by such methods on evolutionary changes of traits (Harvey and Rambaut 2001). Then I used the allometric equation to obtain the predicted value of the traits for a cervid with the same size as moose. Lastly, I compared predicted trait values with those reported in literature for moose populations. The second type of analyses consisted of comparing life history traits observed in moose with those observed in similar-sized bovids.

I fitted 4 allometric relationships according to the life history traits (birth mass and early growth rate) and to the species-specific litter size (polytocous and monotocous species). Indeed, individual offspring of polytocous ungulates that produce 2 offspring per breeding attempt might be lighter at birth than single offspring of monotocous ungulates (Roff 1992). Moreover, birth mass of singletons is often higher than birth mass of twins in polytocous species (e.g., moose, Schwartz and Hundertmark 1993). I found data for 38 (birth mass) and 22 (growth rate) monotocous ungulates and for 8 (birth mass) and 6 (growth rate) polytocous ungulates.

To assess demographic patterns of moose as well as of other ungulate populations, I estimated population-specific generation time (i.e., the mean age of mothers at the time of birth, TB, in a given population, Leslie 1966) and population growth rate, r (i.e., the Malthusian parameter, Fisher 1930) from demographic data collected from the literature. To do that, I considered the following female fitness components for describing the life cycle of ungulate populations: the juvenile survival from birth to 1 year of age, the yearling survival between 1 and 2 years of age, the annual survival of prime-age females between 2 and 7 years of age (or 10 depending on the size, Gaillard et al. 2000), the annual survival of females from 7 (or 10) years of age onwards, the age-specific proportion of females that give birth from the age at first parturition onwards, and the age-specific litter size. For a given population, I entered these fitness components into Leslie matrix models and estimated both r and TB (see Caswell 2000 for further details). For species in which I obtained data from several populations, I used the median to define the species-specific estimate. I found data for 42 populations belonging to 22 species including 6 moose populations (in South-Central Alaska, Ballard et al. 1991; in South Coast Barrens of Newfoundland, Albright and Keith 1987; in Northwest Territories (Canada), Stenhouse et al. 1995; and 3 populations in Northern Norway, Stubsjoen et al. 2000).

To assess whether observed survival patterns account for the relatively rapid life cycle observed in moose populations, I used published estimates of both adult and juvenile survival in ungulate species. From a previous literature review (Gaillard et al. 2000), I found data on adult survival in 61 populations belonging to 25 species (including 9 populations of moose) and on juvenile survival in 53 populations belonging to 25 species (including 7 populations of moose). Because very low between-year variation in survival could also contribute to the higher than expected population growth rate of moose (see Tuljapurkar 1989 for a discussion of the changes in population growth generated by environmental variation), I also compared the magnitude of annual variation of both juvenile and adult survival (measured as the coefficient of variation (CV) of annual estimates) in moose populations with the variation reported in other ungulate species. To account for the expected increase in survival with increasing body size (see Peters 1983, Calder 1984 for reviews), I regressed both mean survival and CV of survival for juveniles and adult females (measured as the median of population-specific values found in a given species) on adult body mass.

To assess whether observed reproductive patterns account for the relatively rapid life cycle observed in moose populations, I collected data for ungulate species on two reproductive traits (age at first parturition and litter size), as well as on body mass and generation time (see above). I found data for 21 species excluding moose. I first looked for differences in reproductive traits according to adult body mass with 1-way ANOVAs using reproductive traits as factors (i.e., three classes of age at first parturition: 1, 2, or > 2 years of age; and two classes of litter size: 1 or 2) and the log-transformed adult body mass as the dependent variable. I then compared the adult body mass of moose with the mean mass expected from species with similar reproductive traits. In a second step, I performed the same kind of analysis by using the log-transformed generation time instead of adult body mass. I assumed that once variation in adult body mass is taken into account, differences in reproductive traits between moose and other ungulates account for the relatively faster life cycle of moose compared to other ungulates, and moose should reproduce earlier and more frequently relative to their size but perform as expected from their generation time.

RESULTS AND DISCUSSION

Patterns of Maternal Care in Moose: Birth Mass and Early Growth Rate

As expected, a strong positive relationship occurred between birth mass (BW) and adult body mass (ABW) in both monotocous ($\mathrm{Ln}\ (BW) = -1.366 + 0.902\ \mathrm{Ln}\ (ABW)$; $r = 0.977$, $P < 0.0001$) and polytocous ($\mathrm{Ln}\ (BW) = -3.274 + 1.059\ \mathrm{Ln}\ (ABW)$; $r = 0.892$, $P = 0.0029$) species. There was no difference between slopes according to litter size ($F = 0.903$; df = 1, 42; $P = 0.347$). However, for a given adult body mass, birth mass was larger in monotocous than in polytocous species (difference in intercepts of 0.295 (SE = 0.107); $F = 7.630$; df = 1, 43; $P = 0.008$). Similarly, early growth rate (GR) was allometrically related to adult body mass (ABW) in both monotocous ($\mathrm{Ln}\ (GR) = -2.689 + 0.733\ \mathrm{Ln}\ (ABW)$; $r = 0.968$, $P < 0.0001$) and polytocous ($\mathrm{Ln}\ (GR) = -0.691 + 0.561\ \mathrm{Ln}\ (ABW)$; $r = 0.744$, $P = 0.0090$) species. However, litter size did not influence the allometric relation-

Table 1. Comparison of life history traits (LHT) among moose to similar-sized bovids as related to maternal care.

LHT	Wildebeest (*Connachaetes taurinus*)	Cattle (*Bos taurus*)	Eland (*Taurotragus derbianus*)	Moose (*Alces alces*)	Buffalo (*Syncerus caffer*)
Adult mass (kg)	165	309	363	340-450	536
Birth mass (kg)	16.5	24	31.5	13-16	37.2
Growth rate (kg/d)	0.29	0.64	1.11	0.79	1.47
Litter size	1	1	1	1-2	1

ship between early growth rate and adult body mass (differences in slope: $F = 0.574$; df = 1, 24; $P = 0.456$; differences in intercept: $F = 2.770$; df = 1, 25; $P = 0.109$). Using such allometric relationships to estimate expected values for moose, I obtained birth mass of 30.12 kg and 34.99 kg and early growth rates of 777.11 g/d and 639.61 g/d from the equations of monotocous and polytocous species, respectively. Observed birth mass was only about half the expected values: 16.2 kg for monotocous moose and 13.5 kg for polytocous moose (Schwartz and Hundertmark 1993). On the other hand, an observed early growth rate of 785 g/d (Reese and Robbins 1994) was very similar to the expected values from allometric equations.

Comparison of moose to similar-sized bovids led to the same conclusions. Moose had a much lighter birth mass than similar-sized species (Table 1). Birth mass in moose was similar to the birth mass of wildebeest (*Connochaetes taurinus*) whose adult body size is only half that of moose. On the other hand, early growth rates in moose were mid-range to those measured in similar-sized bovids.

Comparative analyses of maternal care show that moose produce small newborns in relation to their size (about half the newborn size expected from other cervid species and similar-sized bovids). On the other hand, relative to their size, newborn moose grow at the same rate as other cervids and similar-sized bovids. I can thus also conclude that moose allocate energy to maternal care as a monotocous species during the gestation period but as a polytocous species during the lactation period.

Demographic Patterns of Moose Populations

As expected, a marked positive allometric relationship occurred between TB and adult body mass (ABW) among the 21 ungulate species other than moose ($\mathrm{Ln\,(TB)} = 0.967 + 0.247\,\mathrm{Ln\,(ABW)}; r = 0.646, P = 0.0016$; Fig. 1). The allometric exponent was very close to that expected for a measure of biological time such as generation time (0.25; Calder 1984), indicating that populations of large ungulate species have relatively slower life cycles than populations of small ungulate species. From such a relationship, TB of moose would be expected to be 11.76 years. From the 6 moose populations for which I found published information, the estimated TB was consistently shorter (from 4.57 to 10.66 years) than the expected value (Table

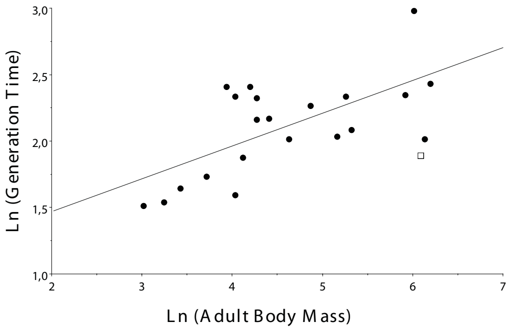

Fig. 1. Allometric relationship between generation time and adult body mass fitted from data collected from 21 ungulate species (filled circles). Observed generation time of moose (as measured by the median value from 6 populations) corresponds to the open square.

Table 2. Population growth rate (r) and generation time (TB) estimated for 6 moose populations from fitness components published in the literature.

r	TB	Reference
0.10	8.89	Ballard et al. 1991
0.26	6.14	Stubsjoen et al. 2000
0.34	4.57	Stubsjoen et al. 2000
0.27	6.02	Stubsjoen et al. 2000
-0.03	10.66	Albright and Keith 1987
0.08	6.91	Stenhouse et al. 1995

2), meaning that moose have a relatively short TB for their size. The median values observed for moose in the allometric relationship linking TB and adult body mass led to the largest negative residual.

Likewise, according to previous work on a large range of taxa (e.g., Blueweiss et al. 1978) and work on mammals specifically (e.g., Sinclair 1996, 1997), a negative allometric relationship tended to occur between r and adult body mass (ABW) among 17 ungulate species other than moose that showed a positive r (i.e., increasing populations: Ln (r) = -1.402 - 0.303 Ln (ABW); $r = 0.395$, $P = 0.117$; Fig. 2). The slope was close to the theoretical expectation of -0.25 (Calder 1984), meaning that the product between r and TB is a dimensionless number (life history invariant sensu Charnov 1993). From such a relationship, r would be expected to be 0.039 for increasing populations of moose. From the 5 increasing moose populations for which I found published information, the estimated r was consistently higher (from 0.077 to 0.344; Table 2) than the expected value, meaning that moose populations have a high growth rate relative to female body size. The median value observed for moose on the allometric relationship between r and adult body mass led to one of the two largest positive residuals with a colonizing population of bison (*Bison bison*) (Van Vuren and Bray 1986).

Such allometric analyses suggest that overall demographic patterns of moose populations are more similar to those of small- or medium-sized ungulates than to those of similar-sized species. From expectations based on their body size alone, moose populations increase faster and the turnover of individuals is faster. Such overall demographic features can have three explanations: (1) survival of juveniles and/or adult female moose is much lower than that of similar-sized ungulates; (2) reproductive output of moose is much higher than that of similar-sized ungulates; or (3) both lower survival and higher reproductive output occur simultaneously in moose populations relative to similar-sized ungulates.

Do Observed Survival Patterns Account for the Relatively Rapid Life Cycle Observed in Moose Populations?

Contrary to expectation, the logit of female adult survival (LAS, which corresponds to the log-transformed adult life expectancy) did not increase with increasing adult body mass among ungulate species (LAS = 2.205 + 0.040 Ln (ABW); $r = 0.054$, $P = 0.801$; Fig. 3). Female adult survival was high irrespective of body mass (from 0.710 in topi (*Damaliscus lunatus*) to 0.978 in pronghorn (*Antilocapra americana*); mean of 0.903, SE = 0.012). Female survival varied

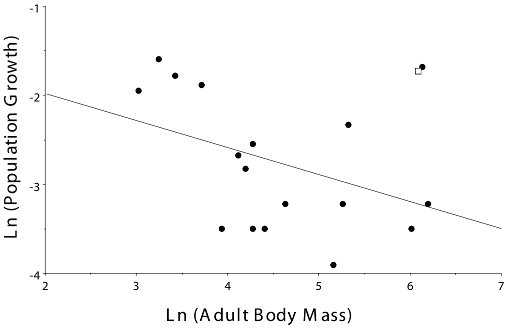

Fig. 2. Allometric relationship between population growth rate and adult body mass fitted from data collected from 17 ungulate species with increasing populations (filled circles). Observed population growth rate of moose (as measured by the median value from 5 increasing populations) corresponds to the open square.

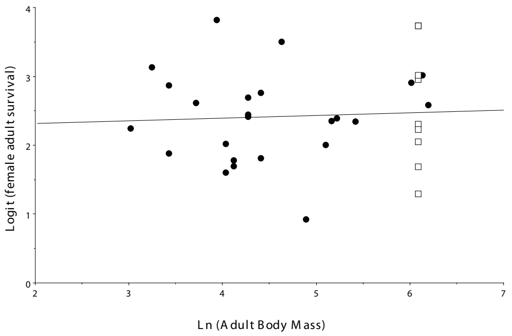

Fig. 3. Allometric relationship between adult survival of females (after logistic transformation) and adult body mass fitted from data collected from 24 ungulate species (filled circles). Observed female adult survival of moose in 9 populations corresponds to the open squares.

from 0.780 to 0.976 and averaged 0.907 (± 0.022) among the 9 moose populations for which data were available. Therefore, we can conclude that female adult survival of moose is similar to adult survival reported for other female ungulates. Likewise, there was no effect of adult body mass on CV of adult survival in female ungulates (CV = 0.069 + 0.001 Ln (ABW); *r* = 0.021, *P* = 0.927; Fig. 4). CV of female adult survival was low, irrespective of body mass (from 0.017 in reindeer (*Rangifer tarandus*) to 0.130 in mouflon (*Ovis gmelini*); mean of 0.073, SE = 0.007). CV of adult survival of females varied from 0.009 to 0.051 and averaged 0.035 (± 0.005) among the 7 populations of moose for which data were available. Such between-year variation appears to be a little lower than that observed in other ungulates.

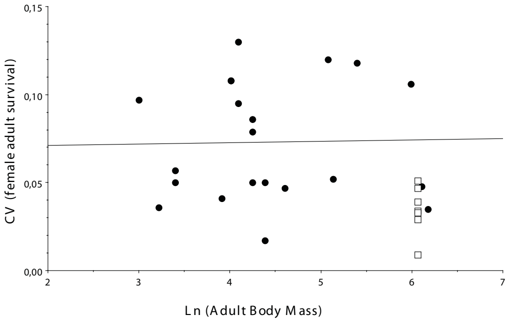

Fig. 4. Allometric relationship between temporal variation in adult survival of females (as measured by the coefficient of variation (CV)) and adult body mass fitted from data collected from 21 ungulate species (filled circles). Observed temporal variation in female adult survival of moose in 7 populations corresponds to the open squares.

As expected, the logit of juvenile survival (LSJ) tended to increase with increasing adult body mass among ungulate species (LSJ = -1.648 + 0.409 Ln (ABW); *r* = 0.314, *P* = 0.135; Fig. 5). Expected juvenile survival indeed increased from 0.40 for an ungulate weighing 20 kg to 0.69 for an ungulate weighing 400 kg. Juvenile survival varied from 0.235 to 0.835 and averaged 0.640 (± 0.088) among the 7 moose populations from which I found data. Therefore, I can conclude that juvenile survival of moose is similar to juvenile survival reported for similar-sized ungulates. Likewise, there was a trend in the CV of juvenile survival to decrease with increasing adult body mass among ungulates (CV = 0.648 – 0.072 Ln (ABW); *r* = 0.353, *P* = 0.099; Fig. 6). Expected CV in juvenile survival decreased from 0.430 for an ungulate weighing 20 kg to 0.220 for an ungulate weighing 400 kg. CV of juvenile survival of moose varied from 0.126 to 0.710 (average of 0.332 (± 0.130), median of 0.245) among the

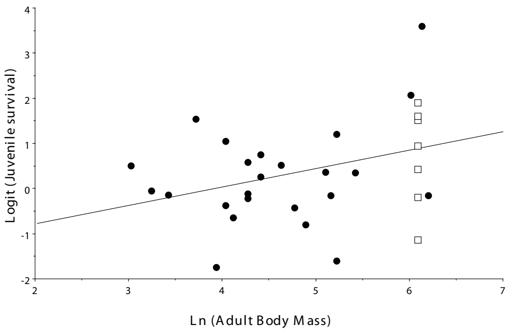

Fig. 5. Allometric relationship between juvenile survival (after logistic transformation) and adult body mass fitted from data collected from 24 ungulate species (filled circles). Observed juvenile survival of moose in 7 populations corresponds to the open squares.

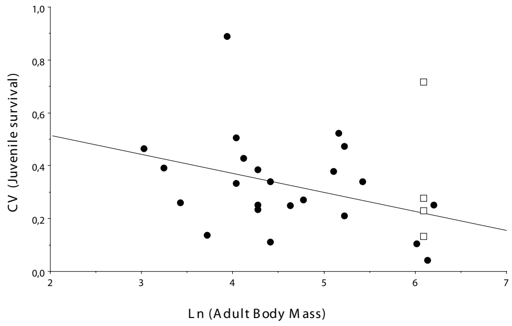

Fig. 6. Allometric relationship between temporal variation in juvenile survival (as measured by the coefficient of variation (CV)) and adult body mass fitted from data collected from 23 ungulate species (filled circles). Observed temporal variation in juvenile survival of moose in 4 populations corresponds to the open squares.

4 populations of moose with available data. Such between-year variation was similar to that observed in other similar-sized ungulates.

Comparison of moose survival to survival in similar-sized bovids led to the same conclusions (Table 3). Both survival estimates and temporal variation in survival of juvenile and adult female moose were very close to the values for similar-sized bovids. My analyses showed that moose fit the general survival pattern of ungulates, especially among smaller species, characterized by both a high and constant survival of adult females, irrespective of the species considered, and a low juvenile survival with high variability among years (see Gaillard et al. 1998, 2000 for similar conclusions). Because survival patterns reported in moose closely fit those found in other ungulate species, survival patterns cannot be an explanation for the relatively rapid life cycle in moose.

Do Observed Reproductive Patterns Account for the Relatively Rapid Life Cycle Observed in Moose Populations?

As expected, the mean body mass of ungulates differed according to the observed age at first parturition ($F = 4.808$; df = 2, 18; $P = 0.021$), increasing from species that give birth at 1 year of age (20 kg; $n = 1$) to species that give birth at > 2 years of age (159 kg; $n = 10$). Ungulates that usually start to give birth at 2 years of age had an intermediate mean body mass (67 kg) that differed significantly from that of ungulates starting to give birth at 3 years of age or older (Fisher's LSD test, $P = 0.028$). Moose often give birth at 2 years of age when they are faced with favorable environmental conditions (Schwartz 1992). With a female adult body mass usually between 350 and 450 kg, moose do not belong to the size distribution of ungulates that normally start to reproduce at 2 years of age but belong to the size distribution of ungulates that normally do not start to reproduce before 3 years of age.

Likewise, the mean body mass of ungulates differed according to the observed litter size ($F = 13.57$; df = 1, 19; $P = 0.002$), decreasing from species that give birth to

Table 3. Comparison of traits related to survival patterns among moose and similar-sized bovids.

Traits	Wildebeest	Kudu	Moose	Bison	Buffalo
Adult mass (kg)	165	170	340-450	450	536
JS[1]	0.58	0.45	0.71	0.97	0.45
CV (JS)[2]	0.37	0.52	0.25	0.04	0.24
AS[3]	0.88	0.91	0.91	0.95	0.93
CV (AS)[4]	0.12	0.05	0.03	0.05	0.04

[1] Juvenile survival.

[2] Coefficient of variation in juvenile survival.

[3] Adult survival.

[4] Coefficient of variation in adult survival.

single offspring (139; $n = 10$) to species that give birth to twins (37 kg; $n = 6$). Moose often give birth to twins when they are faced with favorable environmental conditions (Boer 1992). With a female adult body mass usually between 350 and 450 kg, moose do not belong to the size distribution of ungulates that are expected to produce twins but belong to the size distribution of ungulates that normally produce single offspring.

Looking now at the relationship between age at first parturition and generation time, I found that as expected, generation time increased with increasing age at first parturition ($F = 5.89$; df = 2, 18; $P = 0.011$) from 4.5 years for ungulates that give birth first as yearlings to 10 years for those giving birth for the first time at > 2 years old. Ungulates that usually give birth for the first time at 2 years of age had an intermediate generation time (6.9 years) that differed significantly from that of ungulates giving birth at > 2 years of age (Fisher's LSD test, $P = 0.013$). The generation times observed in moose populations (from 4.57 to 10.66 years) match the distribution of generation times of ungulates that reproduce for the first time at 2 years of age. Likewise, generation time decreased as expected with increasing litter size ($F = 11.27$; df = 1, 19; $P = 0.003$) from 9.3 years for ungulates that normally produce single offspring to 5.7 years for those that can produce twins. The generation times observed in moose populations (from 4.57 to 10.66 years) match the distribution of generation times of ungulates that can produce twins.

Comparison of moose reproductive patterns with those of similar-sized bovids led to the same conclusions (Table 4). The age at first parturition for moose was closer to that of smaller wildebeest and kudu (*Tragelaphus strepsiceros*) than that of larger bison and buffalo (*Syncerus caffer*). Moreover, both the proportion of 2 year-old females that give birth and the litter size were greater in moose than in smaller wildebeest and kudu.

I can therefore conclude that female moose reproduce earlier (often giving birth at 2 years of age instead of 3 years of age for similar-sized ungulates) and have larger litters (often producing twins instead of single offspring as in similar-sized ungulates) than expected from their size. High reproductive output accounts for the rapid life cycle of moose populations compared to populations of other, similar-sized ungulates. Indeed, the distribution of generation times reported in moose populations fits the distribution of generation times expected for ungulate populations that give birth for the first time at 2 years of age and often produce twins.

Conclusions: Are Moose a Large Roe Deer or a Very Large Deer?

Although only a few comparative analyses have reported clear ecological correlates of life history strategy, there is general agreement among evolutionary ecologists that

Table 4. Comparison of reproductive traits among moose to similar-sized bovids.

Traits	Wildebeest	Kudu	Moose	Bison	Buffalo
Adult mass (kg)	165	170	340-450	450	536
Age of primiparity	2	2	2	3	3
% 2[1]	0.27	0.1	0.4	0	0
% M[2]	0.9	0.9	0.81	0.62	0.7
Mean litter size	1	1	1.32	1	1

[1] Proportion of 2 year-old females giving birth in a given year in a population.

[2] Proportion of multiparous females giving birth in a given year in a population.

among-species differences in habitat and diet should lead to differences in life history traits (Stearns 1992), especially in mammals (Saether and Gordon 1994 for ungulates, Geffen et al. 1996 for fissipeds, Fisher et al. 2001 for marsupials). I therefore may ask whether moose-specific diet and habitat might account for the relatively high reproductive output of moose? Contrary to other large cervids such as red deer (*Cervus elaphus*), moose appear to select early successional vegetation stages as a preferred habitat and are concentrate selectors (browsers) rather than grazers or mixed-feeders (Hofmann 1989). From these features, moose are much closer to roe deer (*Capreolus capreolus*), with which they occur often in sympatry, than to larger deer.

Like all cervids, roe deer and moose both fit the body growth patterns and survival patterns of other ungulates. Strong selective pressures might have been operating during the evolutionary history of ungulates in response to predation (see Byers 1997). The canalization of adult survival (Gaillard and Yoccoz 2003) and the production of large and fast growing offspring within allometic constraints might have been selected for in the first stages of ungulate evolution, leading these life history traits to vary little among ungulate species as ecological conditions vary. On the other hand, both moose and roe deer have a relatively high reproductive output, maybe in response to unpredictable environmental conditions in early successional habitats (as proposed by Liberg and Wahlström 1995). Female moose (weighing about 400 kg) cannot produce offspring as fast and as often as roe deer (weighing about 25 kg) because of allometric constraints (Peters 1983, Calder 1984, Brown and West 2000). Thus, most female roe deer give birth for the first time at 2 years of age under a large range of environmental conditions, while only about half of female moose in the most productive populations (e.g., Vega Island in Norway where most females produce twins, Solberg, personal communication) do the same (Schwartz and Hundertmark 1993). Litter size of roe deer can be 3 offspring in very good conditions, while moose litter size is commonly 2 in the same situation. Lastly, because of their large size, moose cannot be a true polytocous species. To reach their high reproductive output, moose have to trade quality of offspring (moose offspring are half the size of other ungulates' offspring) for a higher quantity of offspring (female moose produce twins as soon as environmental conditions allow).

This comparative analysis of moose life history traits suggests that moose are large roe deer rather than simply large deer, and supports current theory on life history evolution that species occupying unpredictable habitats live at a faster rate than species living in more predictable habitats (Yodzis 1989).

ACKNOWLEDGEMENTS

This paper was prepared for the 5th International Moose Symposium held at Lillehammer, Norway, August 2002. I thank Erling Solberg and Bernt-Erik Saether for inviting me to the Symposium.

REFERENCES

ALBRIGHT, C. A., and L. B. KEITH. 1987. Population dynamics of moose, *Alces alces*, on the south-coast barrens of Newfoundland. The Canadian Field-Naturalist 101:373-387.

BALLARD, W. B., J. S. WHITMAN, and D. J. REED. 1991. Population dynamics of moose in South-central Alaska. Wildlife Monographs 114.

BJÖRKLUND, M. 1997. Are 'comparative methods' always necessary? Oikos 80:607-612.

BLUEWEISS, L., H. FOX, V. KUDZMA, D. NAKASHIMA, R. PETERS, and S. SAMS. 1978. Relationship between body size and some life history parameters. Oecologia 37:257-272.

BOER, A. H. 1992. Fecundity of North American moose (*Alces alces*): a review. Alces Supplement 1:1-10.

BROWN, J. H., and G. B. WEST. 2000. Scaling In Biology. Oxford University Press, New York, New York, USA.

BYERS, J. A. 1997. American Pronghorn: Social Adaptations and the Ghosts of Predators Past. The University of Chicago Press, Chicago, Illinois, USA.

CALDER, W. A. III. 1984. Size, Function and Life History. Harvard University Press, Harvard, Cambridge, Massachusetts, USA.

CASWELL, H. 2000. Matrix Population Models. Construction, Analysis and Interpretation. Sinauer Associates, Sunderland, Massachuetts, USA.

CHARNOV, E. L. 1993. Life History Invariants. Some Explorations of Symmetry in Evolutionary Ecology. Oxford University Press, Oxford, U.K.

FISHER, D. A., and I. F. P. OWENS. 2000. Female home range size and the evolution of social organization in macropod marsupials. Journal of Animal Ecology 69:1083-1098.

_____, _____, and C. N. JOHNSON. 2001. The ecological basis of life history variation in marsupials. Ecology 82:3531-3540.

FISHER, R. A. 1930. The Genetical Theory of Natural Selection. Oxford University Press, Oxford, U.K.

GAILLARD, J.-M., M. FESTA-BIANCHET, and N. G. YOCCOZ. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13:58-63.

_____, _____, _____, A. LOISON, and C. TOIGO. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367-393.

_____, D. PONTIER, D. ALLAINE, J. D. LEBRETON, J. TROUVILLIEZ, and J. CLOBERT. 1989. An analysis of demographic tactics in birds and mammals. Oikos 56:59-76.

_____, and N. G. YOCCOZ. 2003. Temporal variation in survival of mammals: a case of environmental canalization?. Ecology 84:3294–3306.

GARLAND, T., P. H. HARVEY, and A. R. IVES. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. Systematic Biology 41:18-32.

GEFFEN, E., M. E. GOMPPER, J. L. GITTLEMAN, H. K. KUH, D. MACDONALD, and R. K. WAYNE. 1996. Size, life history traits, and social organization in the Canidae: a reevaluation. American Naturalist 147:140-160.

HARVEY, P. H., and M. D. PAGEL. 1991. The Comparative Method in Evolutionary Biology. Oxford University Press, Oxford, U.K.

_____, and A. RAMBAUT. 2001. Comparative analyses for adaptive radiations. Philosophical Transactions of the Royal Society of London Series B 355:1599-1605.

HOFMANN, R. R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia 78:449-457.

LESLIE, P. H. 1966. The intrinsic rate of increase and the overlap of successive generations in a population of guillemot (*Uria aalge* Pont). Journal of Animal Ecology 35:291-301.

LIBERG, O., and K. WAHLSTROM. 1995. Habitat stability and litter size in the Cervidae; a comparative analysis. Pages 1-60 *in* K. Wahlström. Natal Dispersal in Roe Deer. An Evolutionary Perspective. Unpublished Ph.D. Thesis, University of Stockholm, Sweden.

NOVAK, R. M. 1993. Walker's Mammals of the World. Fifth Edition, Volume II. The John Hopkins University Press, Baltimore and London, U.K.

PETERS, R. H. 1983. The Ecological Implication of Body Size. Cambridge University

Press, Cambridge, U.K.

Price, T. 1997. Correlated evolution and independent contrasts. Philosophical Transactions of the Royal Society of London Series B 352:519-529.

Reese, E. O., and C. T. Robbins. 1994. Characteristics of moose lactation and neonatal growth. Canadian Journal of Zoology 72:953-957.

Ricklefs, R. E., and J. M. Starck. 1996. Applications of phylogenetically independent contrasts: a mixed progress report. Oikos 77:167-172.

Roff, D. A. 1992. The Evolution of Life Histories. Chapman and Hall, London, U.K.

Saether, B. E., and I. J. Gordon. 1994. The adaptive significance of reproductive strategies in ungulates. Proceedings of the Royal Society of London Series B 256:263-268.

Schwartz, C. C. 1992. Reproductive biology of North American moose. Alces 28:165-173.

_____, and K. J. Hundertmark. 1993. Reproductive characteristics of Alaskan moose. Journal of Wildlife Management 57:454-468.

Sinclair, A. R. E. 1996. Mammal populations: fluctuation, regulation, life history theory and their implications for conservation. Pages 127-154 *in* R. B. Floyd, A. W. Sheppard, and P. J. De Barro, editors. Frontiers of Population Ecology. CSIRO Publishing, Melbourne, Australia.

_____, 1997. Fertility control of mammal pests and the conservation of endangered marsupials. Reproduction, Fertility and Development 9:1-16.

Stearns, S. C. 1976. Life-history tactics: a review of the ideas. Quarterly Review of Biology 51:3-47.

_____, 1983. The influence of size and phylogeny on patterns of covariation among life history traits in the mammals. Oikos 41:173-187.

_____, 1992. The Evolution of Life Histories. Oxford University Press, Oxford, U.K.

Stenhouse, G. B., P. B. Latour, L. Kutny, N. MacLean, and G. Glover. 1995. Productivity, survival, and movements of female moose in a low-density population, Northwest Territories, Canada. Arctic 48:57-62.

Stubsjoen, T., B. E. Saether, E. J. Solberg, M. Heim, and C. M. Rolandsen. 2000. Moose (*Alces alces*) survival in three populations in northern Norway. Canadian Journal of Zoology 78:1822-1830.

Tuljapurkar, S. D. 1989. An uncertain life: demography in random environment. Theoretical Population Biology 21:141-165.

Van Vuren, D., and M. P. Bray. 1986. Population dynamics of bison in the Henry Mountains, Utah. Journal of Mammalogy 67:503-511.

Yodzis, P. 1989. Introduction to Theoretical Ecology. Harper & Row, New York, New York, USA.