

THE LENGTH OF GROWING SEASON AND ADULT SEX RATIO AFFECT SEXUAL SIZE DIMORPHISM IN MOOSE

MATHIEU GAREL,^{1,2,5} ERLING JOHAN SOLBERG,³ BERNT-ERIK SÆTHER,² IVAR HERFINDAL,²
AND KJELL-ARILD HØGDA⁴

¹Laboratoire de Biométrie et Biologie Évolutive (UMR 5558), Centre National de la Recherche Scientifique (CNRS),
Université Lyon 1, 43 boulevard du 11 novembre, 69622, Villeurbanne Cedex, France

²Department of Biology, Norwegian University of Science and Technology, NO-7491 Trondheim, Norway

³Norwegian Institute for Nature Research, Tungasletta 2, NO-7485 Trondheim, Norway

⁴Norut Information Technology AS, NO-9291, Tromsø, Norway

Abstract. While factors affecting body growth have been extensively studied, very little is known about the factors likely to affect the sexual size dimorphism (SSD) in polygynous mammals. Based on the carcass mass of 24 420 male and female moose recorded in 14 Norwegian populations, we examine three hypotheses to explain geographical variation in SSD. First, SSD is expected to decrease when the relative density of animals (for a given habitat quality) increases, because resource limitation at high population densities is assumed to affect body growth of males more than females. Second, because males are selected to invest in growth more than females, environmental seasonality and related improvement of the forage quality during the short and intense growing season are expected to increase SSD. Third, by decreasing the proportion of adult males in the population, resulting in start of rutting earlier in life, hunting may decrease the SSD by increasing the reproductive cost of young males. We found that males grew faster and for a longer time of their life than did females and thus were heavier (~24%) when they reached adulthood. Sexual size dimorphism was independent of density but was higher in areas with short growing seasons. The low SSD in populations with largely adult female-biased sex ratios (males per female) shows that male body growth decreases with a decreasing proportion of adult males in the population. Our results indicate that geographical variation in moose SSD is influenced by divergent responses in the sexes to ecological factors affecting body growth.

Key words: *biased sex ratio; carcass mass; density; hunting; monomolecular model; moose; normalized difference vegetation index (NDVI); Norway; plant phenology; sexual size dimorphism.*

INTRODUCTION

In sexually dimorphic species adult males and females differ consistently in size, coloring, shape, or adornment, and dimorphism can also imply differences in smell, calls, and aspects of behavior (Darwin 1871, Ralls 1977, Jarman 1983, Shine 1989). However, in most vertebrate species, sexual size dimorphism (SSD) is the most common form (Ralls 1977, Fairbairn 1997, Loison et al. 1999a, Perez-Barberia et al. 2002). In birds (Wiley 1974) and mammals (Ralls 1976, Jarman 1983, Loison et al. 1999a), male-biased SSD predominates, reaching its greatest extreme in larger species of the mammalian orders Primates, Pinnipedia, Proboscidea, and Artiodactyla (Ralls 1977, Alexander et al. 1979, Weckerly 1998), in which males may weigh 2–8 times as much as females (Ralls 1977, Fairbairn 1997, Weckerly 1998). Several hypotheses have been proposed to account for the SSD (Darwin 1871, Trivers 1972, Ralls 1977, Hedrick and Temeles 1989, Shine 1989, Fairbairn 1997, Weckerly 1998, Loison et al.

1999a, Perez-Barberia et al. 2002), most suggesting the extensive role of sexual selection for the evolution of SSD.

The strength of selection for SSD would depend on the intensity of competition among males and, accordingly, studies have shown that SSD among vertebrates is closely associated with the level of polygyny (Wiley 1974, Ralls 1977, Jarman 1983, Loison et al. 1999a, Perez-Barberia et al. 2002). In polygynous mammals, SSD results from different selection pressure on male and female growth tactics in relation to reproduction (Trivers 1972, Ralls 1977, Clutton-Brock et al. 1988, Andersson 1994, Post et al. 1999). Such tactics reflect sexual selection on males for access to females and competitive selection on females for access to food. Consequently, sexual selection favors large male size through rapid early growth to large adult body size and delayed maturation, whereas females are selected to invest in improved body condition and early sexual maturity at the expense of structural size (Trivers 1972, Ralls 1977, Clutton-Brock et al. 1988, Andersson 1994). Under such a trade-off between growth and reproduction, factors affecting animal growth are expected to elicit divergent responses in the sexes that

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⁵ E-mail: mgarel@biomserv.univ-lyon1.fr

exacerbate or constrain SSD (Trivers 1972, Clutton-Brock et al. 1982, Sæther and Haagenrud 1985, Leberg and Smith 1993, Stamps 1993, Post et al. 1999, Leblanc et al. 2001).

Despite the importance of sex-specific body growth for variation in different life history characters (Stamps 1993, Gaillard et al. 2000), very little is known about the factors likely to affect SSD (Leblanc et al. 2001). However, long-term individual-based population studies have increased our understanding of factors affecting body mass in ungulates (Sæther 1997, Gaillard et al. 2000), thereby providing a suitable framework for an understanding of the mechanisms that influence SSD. Body masses of large ungulates are known to vary according to density-dependent food limitation and stochastic environmental variation (Sæther 1997) and indirectly to hunting as a response to changes in density or structural composition of the population (Clutton-Brock and Lonergan 1994, Ginsberg and Milner-Gulland 1994, Solberg and Sæther 1994, Langvatn and Loison 1999, Solberg et al. 1999, 2000, Laurian et al. 2000, Coltman et al. 2003, Sæther et al. 2003). Based on sex-specific effects of such factors on body growth, and by mainly focusing on ungulates living in seasonal environments that breed seasonally, we propose three hypotheses to explain variation in SSD.

First, density dependence in growth and body mass has long been recognized in several ungulate species (for a review see Fowler [1987]). For a given habitat quality (Van Horne 1983), a high population density affects body mass by increasing intraspecific competition for food and by decreasing resource quality and availability (e.g., Skogland 1985). In highly dimorphic ungulates (SSD > 20%; Ruckstuhl and Neuhaus 2000), males have greater absolute energy requirements than females due to allometric constraints (Fairbairn 1997), higher basic metabolic rates (Demment and Van Soest 1985), and higher energy expenditure during the rut (Clutton-Brock et al. 1982). Accordingly, males have been found to be more sensitive to food limitation than females (Clutton-Brock et al. 1982, Clutton-Brock and Albon 1985, Owen-Smith 1993, Rose et al. 1998, Loison et al. 1999b, Réale and Boussès 1999). We thus expect that SSD decreases when relative (to the habitat quality) density (Van Horne 1983) increases.

Second, geographical patterns of variation in body mass of many species have been reported to be closely related to temperature (e.g., in ungulates [Langvatn and Albon 1986, Sand et al. 1995]). To explain such a pattern, Bergmann (1847) proposed that larger phenotypes should be favored as the ambient temperature decreases due to their superior ability to store heat and/or fat reserves. However, this hypothesis has been widely debated (for a review see Ashton et al. [2000] and Meiri and Dayan [2003]) leading to other ecological and evolutionary hypotheses to supplement or replace Bergmann's original explanation (McNab 1971, Boyce 1979, Lindstedt and Boyce 1985, Geist 1987). One al-

ternative explanation (Langvatn and Albon 1986) is that body mass increases with increasing latitude or altitude because forage quality improves along these gradients (Klein 1964, Albon and Langvatn 1992, Van Soest 1994). Indeed, short growing seasons in higher latitudes and altitudes are related to fast-growing plants with higher nutritional quality and digestibility (Bliss 1962, 1971, Klein 1965, 1970, Van Soest 1994). Increasing the seasonality of the environment may thus either constrain the SSD by increasing the environmental harshness (Clutton-Brock et al. 1982, Clutton-Brock and Albon 1985, Réale and Boussès 1999) or, due to the improvement of the forage quality, have the opposite effect since males are selected to invest more in growth than females (Trivers 1972, Ralls 1977, Clutton-Brock et al. 1988, Andersson 1994).

Third, several ungulate populations are subject to intense harvesting, predominantly on juveniles and adult males (Sutherland 2001), to maximize the annual harvesting yield (Caughley 1977, Sæther et al. 2001). An indirect effect of such a strategy is that the proportion of adult males in the populations decreases, with several potential life history consequences (Ginsberg and Milner-Gulland 1994, Solberg and Sæther 1994, Noyes et al. 1996, Mysterud et al. 2002, 2003, Solberg et al. 2002, Festa-Bianchet 2003, Holand et al. 2003, Milner-Gulland et al. 2003, Sæther et al. 2003, 2004, Bonenfant et al. 2004). One suggested effect is that young males increase their reproductive investment during the rut due to reduced competition from older males (Solberg and Sæther 1994, Mysterud et al. 2002, 2003, Sæther et al. 2003, Bonenfant et al. 2004). Because rutting is energetically expensive due to higher activity and reduced feeding (Clutton-Brock et al. 1982, Miquelle 1990), early breeding may decrease further body growth (Stevenson and Bancroft 1995). Thus, we predict that the SSD should be lower in populations with low adult male:adult female ratios.

In this study, we analyzed geographical variations in sexual size dimorphism of 14 Norwegian moose (*Alces alces*) populations experiencing varying degrees of male-biased harvesting and density. We examined the effect of environmental seasonality by relating the variation in SSD with the variation in climatic harshness and plant phenology. We used the normalized difference vegetation index (NDVI) derived from satellite data (Reed et al. 1994, Kerr and Ostrovsky 2003, Turner et al. 2003) to assess geographical variation in plant phenology, and we used winter temperature and snow depth as measures of winter harshness. In addition, we compared the variation in SSD with the variation in latitude and altitude, two other proxies of environmental conditions commonly used in such studies (Langvatn and Albon 1986, Hjeljord and Histøl 1999, Ericsson et al. 2002). Because birth mass is approximately the same among sexes (Andersen and Sæther 1996, Schwartz 1998), SSD can arise when males grow faster, for a longer time, or both, than females (Jarman



FIG. 1. Location of the six Norwegian regions from which moose data were collected in 14 municipalities.

1983, Southwood 1988). Therefore, within each population we fitted a sex-specific growth curve to estimate the adult body size, the decay rate, and the time of active body growth for each sex. Such an approach was made possible by taking the advantage of a large number of carcass mass measurements ($n = 24\,420$) collected from harvested moose ranging from calves to 21 yr of age.

METHODS

Study areas

Moose data were collected from 14 municipalities along a north–south gradient covering the most important regions with moose harvest in Norway (Fig. 1; Appendix A). These moose populations have been monitored annually since 1991 as part of the National Monitoring of Cervids in Norway. All study areas are situated within the boreal vegetation zones. The study areas in Nordland ($n = 3$ municipalities), Nord-Trøndelag ($n = 1$), and Hedmark ($n = 2$) regions are located mainly in coniferous forests of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), whereas in Troms ($n = 1$) and Oppland ($n = 4$), a large

part of the study area is covered by birch (*Betula pubescens*) in addition to Scots pine. Forests in Vestfold ($n = 3$) consist mainly of Scots pine, Norway spruce, and birch in the interior and coniferous trees mixed with birch, oak (*Qercus robur*), and to some extent beech (*Fagus sylvatica*) along the coast. For further information on the study areas, see Sæther and Heim (1993), Solberg and Sæther (1994), Sæther et al. (1996), and Hjeljord and Histøl (1999).

Population data

Environmental characteristics.—We used eight phenology variables (Appendix A and Table 1; Fig. 2a) computed from the normalized difference vegetation index (NDVI) to assess variation in vegetation phenology among populations (Reed et al. 1994). The NDVI is derived from the ratio of red to near-infrared reflectance ($NDVI = [NIR - RED]/[NIR + RED]$, where NIR and RED are the amounts of near infrared and red light reflected by the vegetation). Data were generated from the Global Inventory Modelling and Mapping Studies (GIMMS) data set. This data set includes the maximum value NDVI composite for 15-d

TABLE 1. Description of phenology variables used in the analyses (see Fig. 2a).

Phenology variable	Abbreviation	Description
Onset of spring	os	week number of spring during which NDVI value represent birch leaf burst
Onset of autumn	oa	week number in autumn during which NDVI values fall below the same value used to calculate onset of spring
Length of growing season	lgs	no. weeks between onset of spring and onset of autumn
Peak time	pt	week number in summer during which NDVI values reach their highest value
Peak value	pv	NDVI value at peak time
Length of spring	ls	no. weeks between onset of spring and peak time
Derived spring NDVI	ds	NDVI value at onset of spring minus NDVI value at previous orbit of NOAA (15 d earlier); used as measure of spring flush of vegetation
Integrated NDVI	int	sum of all NDVI values for one growing season; used as measure of habitat productivity
Seasonality index	si	first axis of PCA based on os, oa, pt, pv, ds, and int (see above)

periods covering July 1981 through 2002, computed from the advanced very high resolution radiometer (AVHRR) onboard the afternoon-viewing NOAA satellite series (Turner et al. 2003). Spatial resolution was approximately 8×8 km.

Variation in the NDVI is known to be strongly correlated with aboveground net primary productivity, leaf area in canopy, and absorbed photosynthetic active radiation (e.g., Kerr and Ostrovsky 2003). Therefore NDVI is assumed to reflect variation in plant phenology. For instance, in the Northern Hemisphere, NDVI values will be low during winter, rise rapidly during spring to a high summer level, and then fall during autumn (Fig. 2b). We described the shape of the NDVI curve by using the eight following variables (see also Reed et al. 1994): onset of spring (os), onset of autumn (oa), length of growing season (lgs), peak time (pt), peak value (pv), length of spring (ls), derived spring NDVI (ds) and integrated NDVI (Table 1 and Fig. 2a). In the following, we used integrated NDVI (int) as a measure of habitat productivity (see *Sex ratio and density*). All parameters were calculated annually for each pixel in the GIMMS data set, and mean values were calculated for municipalities, using pixels with the center inside the municipality and below the tree limit. For further details on the GIMMS data set and processing, especially concerning treatment of noise caused by cloud cover and other atmospheric conditions, see, e.g., Tucker et al. (2001).

We used both the means of the monthly mean temperature and mean snow depth from December to February as a measure of winter severity (Appendix A). For municipalities with no weather station, we used values from the closest weather station that was located in a similar climate type (e.g., coastal, continental).

In each municipality, we computed mean altitude for areas below the tree limit only (Appendix A). However, because the tree limit varies extensively between study areas due to large variation in climate, we adjusted the altitude (from Moen 1999) by dividing the tree line with mean altitude for the municipality. The estimated altitude then refers to altitude relative to the climatic

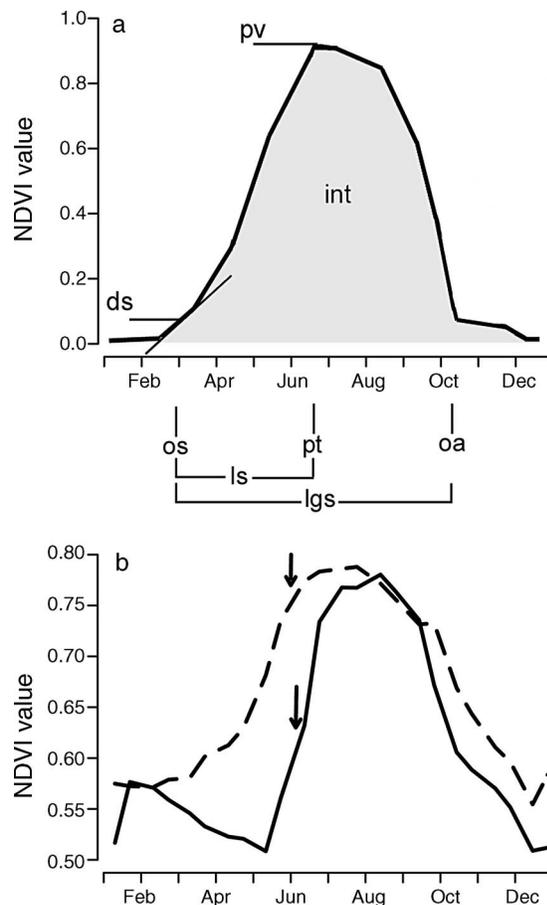


FIG. 2. (a) Schematic presentation of phenology variables derived from annual normalized difference vegetation index (NDVI) curves. Abbreviations are: os, onset of spring; oa, onset of autumn; lgs, length of growing season; pt, peak time; pv, peak value; ls, length of spring; ds, derived spring NDVI; int, integrated NDVI (see Table 1 for descriptions). (b) Changes in NDVI values through the year for a northern (solid line, Troms) and southern (dashed line, Vestfold) area of Norway (see Fig. 1). Arrows indicate mean date of birth for moose in corresponding areas (Sæther et al. 1996).

tree line and not the absolute altitude in each municipality.

Sex ratio and density.—The adult sex ratio was estimated based on hunters' observations of moose recorded during the hunting season (Solberg and Sæther 1999; Appendix A) that usually reflect the variation in population sex ratio quite well (Solberg et al. 2002). In accordance with Solberg et al. (2002, 2005), we assumed that males and females were equally observable. We estimated the yearly population sex ratio as the observed number of adult (≥ 1 -yr-old) males divided by the observed number of adult females. Variation in population absolute density was estimated by the number of moose harvested per square kilometer of moose inhabitable habitat (i.e., below tree limit, but see Solberg et al. [2004]; Appendix A). During the study period, the harvest per square kilometer has been quite stable, indicating that the harvest approximately equals the annual production of moose. Under such conditions, annual harvest is assumed to constitute between 33% and 44% of the absolute moose winter density, depending on the local age and sex structure (Solberg et al. 2005). Accordingly, absolute winter moose density was assumed to vary between 2.3 and 3.0 times the annual harvest per square kilometer.

Theoretical analyses based on the ideal free distribution have suggested that density should increase with habitat productivity (Fretwell and Lucas 1970). To assess the density effects on SSD, we adjusted the population density estimates (the annual harvest per square kilometer) for the interpopulation variations in habitat quality (Van Horne 1983). We estimated the relative density in each population as the residuals from the regression of population density against integrated NDVI (Appendix A). We used in the regression all populations in Norway for which we had density and integrated NDVI estimates. In the following, density thus refers to the density relative to habitat productivity.

Moose data

We used data from 12 421 males and 11 999 females killed during the hunting seasons for the period 1991–2003. Hunters recorded date, locality, sex, and carcass mass and collected the lower jawbone for age determination. Carcass mass was equal to body mass minus head, skin, metapodials, bleedable blood, and viscera and was weighted to the nearest kilogram. Carcass mass constitutes on average 50% of total body mass (Wallin et al. 1996). For calves and yearlings, the ontogenic development and the pattern of tooth replacement in the lower jawbone determined age, whereas for older animals (from 2.5 to 21.5 yr old in our study), age was estimated in the laboratory by counting the number of layers in the secondary dentine of the incisor (Haagenrud 1978, Hamlin et al. 2000).

Statistical analysis

Growth pattern.—To model body growth, we used a monomolecular curve (i.e., a monotonic concave increase [see, e.g., France et al. 1996: Fig. 2]), that accounts for a rapid initial growth followed by a levelling off without inflection point. This growth pattern is typical of precocious mammals such as moose (Gaillard et al. 1997). We characterized sex-specific differences in each municipality by the following equation (France et al. 1996):

$$M_t = \gamma - (\gamma - M_0)e^{-\beta t} \quad (1)$$

where M_t is the carcass mass (in kilograms) at time t (in years), γ is the asymptotic value equal to adult carcass mass, M_0 is the carcass mass at $t = 0$ (carcass mass at birth), which was set to a fixed value of 6.5 kg (50% of the live birth mass; Andersen and Sæther 1996, Wallin et al. 1996), and β describes the decay in the growth rate. The parameters of the curves were estimated by using nonlinear least-squares estimates (Bates and Watts 1988). We used the age when 99% of γ was achieved ($\text{age}_{99\%}$) as an estimate of the length of the period of active body growth (for a similar approach, see Sand et al. [1995]).

Before estimating body growth, we first adjusted for variation in killing date because body mass of moose changed during the hunting season (from 25 September to 31 October). The decrease was stronger in males than in females (Solberg et al. 2004), probably because of higher activity and feeding suppression in males during the rut (Schwartz et al. 1987, Miquelle 1990). Similarly, adults (≥ 2.5 yr old) tend to lose more mass than yearlings. Calves are mainly found to increase in body mass during the hunting season. We calculated relative body mass from the regression of carcass mass on killing date after splitting the data on municipality, age, and sex, and adjusted the mass to 1 October (4 mo after mean birth date; Sæther et al. 1996).

Analysis procedure.—First, we used the residuals from the regression of male estimates on female estimates as a measure of SSD (Ranta et al. 1994). We thus obtained for each parameter (γ and β) two indices of relative SSD (SSD γ and SSD β). Positive values of SSD γ and negative values of SSD β indicated males with relatively higher carcass mass and lower decay rate. We did not compute such an index for $\text{age}_{99\%}$, as this parameter was highly correlated with β (for males, $r = 0.99$, $df = 12$, $P < 0.001$; for females, $r = 1$, $df = 12$, $P < 0.001$) and would not supply additional biological information to our study.

Second, we analyzed the variation in SSD indices in relation to interpopulation variation in density, sex ratio, and environmental variables (Appendix A). Because the environmental variables were highly correlated (I. Herfindal, *unpublished data*), we first introduced the effects of sex ratio and density in the models (see the first and third hypotheses in *Introduction*) and

then either the effects of latitude and altitude, the effects of temperature and snow depth (environmental harshness), or the effects of plant phenology (the second hypothesis). We introduced one phenology variable at a time because these variables were also highly intercorrelated. We did not use integrated NDVI because we included this variable into our estimate of density (see *Population data: Sex ratio and density* above). We accounted for the interaction between density and sex ratio and for the first-order interactions between these two variables and the environmental variables. Higher order interactions were excluded due to the small number of study sites ($n = 14$).

We also performed a principal component analysis (PCA) based on os, oa, pt, pv, ds, and int (Table 1). We did not use lgs and ls that were completely included, respectively, in os and oa and in os and pt (see Fig. 2a). In addition to the phenology variables, we also used the coordinates of each population along the first axis of the PCA as a measure of seasonality (seasonality index; Table 1 and Appendix A). The first axis explained 74.2% of the variability among populations in plant phenology. Positive coordinates indicated a highly seasonal environment with short growing season and low productivity (correlation coefficients with os = 0.98, $df = 12$, $P < 0.001$; oa = -0.88, $P < 0.001$; pt = 0.89, $P < 0.001$; pv = -0.93, $P < 0.001$; ds = 0.27, $P = 0.35$; int = -1, $P < 0.001$). The second axis referred only to the spring flush of vegetation (correlation coefficient with ds = -0.96, $df = 12$, $P < 0.001$) and was therefore not included in the analysis.

Finally, environmental factors influencing SSD γ and SSD β are expected to elicit divergent growth response in the sexes. We accounted for this hypothesis by regressing γ and β against the best explanatory variables selected in the SSD analysis. We included sex as a fixed factor in the regressions and used an ANCOVA to test for the interaction between males and females.

Model selection.—Model selection was based on Akaike Information Criterion (AIC) with second-order adjustment of the AIC (AIC_c) to correct for small-sample bias (Burnham and Anderson 1998). This criterion is based on the principle of parsimony and is well-adapted when performing multiple comparisons between non-nested models. The most parsimonious model (i.e., lowest AIC_c) was selected as the best model. We computed Akaike weights (AIC_c weights) to compare the relative performance of models rather than only their absolute AIC_c value (Burnham and Anderson 2001). Weights can be interpreted as the probability that a model is the best model given the data and the set of candidate models. Thus, the strength of evidence in favor of one model (M1) over another (M2) is simply the ratio of their Akaike weights ($AIC_c^{w_{ratio}} = AIC_c^{w_{M1}} / AIC_c^{w_{M2}}$). When the difference in AIC_c (ΔAIC_c) is greater than 2, there is considerable support for a real difference between models (Burnham and Anderson 1998). We thus reported only models that differed in

AIC_c from the best model by ≤ 2 , which can be considered as the set of the most likely models (models with $\Delta AIC_c > 2$ are at least more than three times less supported by the data than the best model).

Parameters were weighted by the sample size within municipality at each step of the analysis (SSD estimation, SSD analysis, and parameter-specific regressions). All analyses were performed using R version 1.9.1 (R Development Core Team 2004).

RESULTS

Growth pattern

Variation in γ and β among populations was 23.9% (range 204.6–268.9 kg) and 40.4% (0.56–0.94), respectively, for males and 18.9% (172.7–212.9 kg) and 23.3% (0.92–1.20) for females (Appendix B). Males were heavier ($F = 88.1$, $df = 1, 26$, $P < 0.001$), grew faster ($F = 73.8$, $df = 1, 26$, $P < 0.001$), and had active body growth for longer time ($F = 95.4$, $df = 1, 26$, $P < 0.001$) than females. On average, adult males weighed approximately 24% more than adult females and reached 99% of their adult body mass ~ 2 yr later than females (Appendix B).

Sexual size dimorphism

Sexual size dimorphism analysis.—Among the set of most likely models (i.e., $\Delta AIC_c \leq 2$ with the best model), all models included the effect of sex ratio (Table 2). Similarly, all models accounted independently either for an effect of three phenology variables (the length of growing season, the onset of autumn, and the onset of spring) or for an effect of the seasonality index. These four environmental variables were highly correlated (correlation coefficients ranged from 0.84 to 0.99), which is why they were both included in the selected models. Our results suggested, however, that the length of the growing season was probably the best explanatory variable. Indeed, models with an effect of the length of growing season were ≥ 1.7 times (e.g., SSD β $AIC_c^{w_{ratio}} = 0.17/0.10$) more supported by the data than models including onset of spring or onset of autumn (Table 2). A model including the seasonality index as a replacement for the length of growing season had the same weight in the data only for SSD β . Environmental seasonality seems thus better accounted for by the length of the growing season than by any other measure of the phenology pattern. For SSD β , the two best models accounted for additive effects of sex ratio and the seasonality index or for additive effects of sex ratio and the length of growing season, whereas for SSD γ data supported both a model with an additive effect and a model with an interaction between sex ratio and the length of growing season.

Models that considered only sex ratio or a phenology variable, such as length of growing season, had no support in the data compared to the best models (e.g., sex ratio + lgs), emphasizing that both sex ratio and

environmental seasonality strongly affected SSD (models with only sex ratio or with only lgs compared to a model with sex ratio + lgs: $AIC_c w_{\text{ratio}} < 0.005$ both for SSD γ and SSD β). Altitude, latitude, temperature, and snow depth were never selected as the best explanatory variables (Table 2). Models that included one of these variables as a replacement for the length of the growing season obtained little support (e.g., model with sex ratio + altitude compared to a model with sex ratio + lgs, for SSD γ : $AIC_c w_{\text{ratio}} = 0.07$, for SSD β : $AIC_c w_{\text{ratio}} = 0.10$; $AIC_c w_{\text{ratio}}$ were lower with the three other variables both for SSD γ and SSD β). Similarly, models including derived spring values were not supported compared to a model that included the length of the growing season (for SSD γ and SSD β $AIC_c w_{\text{ratio}} < 0.005$). This indicates that spring flush of vegetation also explained poorly the variation in SSD.

The models predicted that SSD γ decreases and SSD β increases in municipalities with low proportions of males (Table 2). Under such conditions, males relative to females were smaller and had higher decay rates. Similarly, the relative male body size and decay rate were higher and lower, respectively, in areas with short growing seasons, late onset of spring, and early onset of autumn. The interaction between sex ratio and the length of the growing season indicated that SSD γ was more affected by the sex ratio in areas with a short growing season (Fig. 3).

Among models selected, no density effect was recorded on SSD γ and only one model supported such an effect on SSD β (Table 2). Coefficients indicated that males relative to females had higher decay rate in municipalities with high density. Such a model, however, was more than two times less supported than the best model ($AIC_c w_{\text{ratio}} = 2.3$; Table 2). Moreover, including a density effect in the best models (e.g., model with sex ratio + lgs) resulted in a decrease of AIC_c of 5.1 for SSD γ and of 2.6 for SSD β .

Regression analysis.—Sex ratio affected the growth parameters of males, whereas no such effect was recorded on female parameter estimates (Fig. 4a, b; interaction between sex ratio and sex for β : $F = 5.3$, $df = 1, 24$, $P = 0.03$). Although not significant ($F = 3.5$, $df = 1, 24$, $P = 0.08$), possibly due to the low sample size ($n = 14$), the same pattern was recorded for γ .

For the analyses regarding the effect of plant phenology, γ tended to decrease more for males than for females when the length of the growing season increased (Fig. 4c; interaction term for γ : $F = 3.05$, $df = 1, 24$, $P = 0.09$). The decay rate increased with the length of growing season ($F = 13.00$, $df = 1, 25$, $P = 0.001$) in a similar way for both sexes (interaction term for β : $F = 1.38$, $df = 1, 24$, $P = 0.25$; Fig. 4d). Corresponding patterns were observed in analyses including the onset of spring, the onset of autumn, and the seasonality index, but these results are not presented.

DISCUSSION

Sexual size dimorphism in Norwegian moose

Most studies recognize the extensive evidence of the importance of sexual selection in explaining the evolution of SSD (Darwin 1871, Trivers 1972, Ralls 1977, Hedrick and Temeles 1989, Shine 1989, Fairbairn 1997), whereas the relative contribution of ecological factors to variation in SSD is still unclear (e.g., Shine 1989). In our study, adult males were heavier ($\sim 24\%$) and grew faster and for a longer time than did adult females. This growth pattern is consistent with earlier findings in this species (Sæther and Haagenrud 1985, Schwartz et al. 1987, Sand et al. 1995) and confirms that SSD results from sex-specific differences in body growth (Trivers 1972, Ralls 1977, Clutton-Brock et al. 1982, Andersson 1994). However, we also found (Table 2 and Fig. 4) that variations in sex ratio and plant phenology were able to elicit divergent growth responses of males and females. Accordingly, our results support that SSD results from a combination of sexual selection and sex-specific responses to variation in environmental conditions. Thus, sex differences in strategies of body growth due to sexual selection promote divergent responses to ecological factors that ultimately affect SSD (Sæther and Haagenrud 1985, Stamps 1993, Sand et al. 1995, Loison et al. 1999a, Post et al. 1999, Leblanc et al. 2001).

Density effects

Our results suggested that population density explained only a small proportion of the variance in the data (Table 2). Except for the three municipalities in Vestfold (Fig. 1), the data set used in the present analysis are from areas north of the “high density” municipalities and could therefore be less affected by density dependence. Based on the harvest statistics (Appendix A) and the proportion of calves in the populations (see *Methods: Population data: Sex ratio and density*), the absolute winter density of moose was less than 1.62 moose/km² (median = 0.72 moose/km²) in study areas north of Vestfold (in Vestfold, range 1.42–3.33 moose/km²; median with all municipalities = 0.87 moose/km²); that is probably, regardless of the habitat productivity, well below the ecological carrying capacity (Messier 1994, Sæther et al. 1996). Accordingly, Sand et al. (1995) reported no density-dependent effects on the geographical variation in moose body mass in 14 Swedish populations experiencing quite similar environmental conditions as in our study and varying in absolute density from 0.31 to 1.32 moose/km² (median = 0.92 moose/km²). More generally, several studies have suggested that density dependence in moose body mass is likely to occur only at high population densities (Messier and Crête 1984, Sæther et al. 1996, Hjeljord and Histøl 1999, Ferguson et al. 2000).

Part of the reason for the lack of any strong effect of density may also be that relative density estimates

TABLE 2. Modeling the variation in two indices of sexual size dimorphism (SSD) in 14 Norwegian moose populations in relation to sex ratio, relative density, adjusted altitude, latitude, snow depth, winter temperature, and phenology variables (Table 1, Appendix A).

Model	ΔAIC_c	AIC_c weights	Intercept
SSD γ			
Sex ratio + lgs	0.00	0.22	15.42 \pm 18.97
Sex ratio + lgs + sex ratio \times lgs	0.05	0.22	-143.79 \pm 78.55
Sex ratio + os	1.28	0.12	-179.82 \pm 30.46
Sex ratio + os + sex ratio \times os	1.79	0.09	56.52 \pm 123.60
SSD β			
Sex ratio + si	0.00	0.20	0.42 \pm 0.06
Sex ratio + lgs	0.35	0.17	0.03 \pm 0.10
Sex ratio + os	1.33	0.10	1.01 \pm 0.16
Density + sex ratio + oa	1.72	0.09	-2.45 \pm 0.90

Notes: A "plus" (+) sign corresponds to additive effects, and a "times" (\times) sign corresponds to interactions between factors. Only models with $\Delta AIC_c \leq 2$ compared to the best model are reported, together with their parameter estimates (\pm SE). Null models had a ΔAIC_c of 16.69 and 19.53 for SSD γ and SSD β , respectively. See Table 1 for abbreviations of model variables.

remain rough measures of density. By scaling density (harvest per kilometer) with primary production (Appendix A), we tried to account for spatial variation in resource availability. However, this supposes that primary production correlates with availability of moose forage. Moose is a selective browser, and therefore not all trees and bushes are as attractive as forage (Andersen and Sæther 1996, Renecker and Schwartz 1998). For instance, some trees are almost never eaten (e.g., Norway spruce), but may still constitute the most common tree species in many areas. This problem with confounding variables is present in all comparative studies of interpopulation variation in life history characteristics and population dynamics. We still conclude that density did not seem to explain a large proportion of the geographical variation in SSD, at least at the range of density that we observed. However, more information is needed on factors limiting the density of Norwegian moose populations.

Environmental seasonality

Environmental seasonality appears to be more important than density-dependent food limitation in explaining geographical variation in SSD (Table 2). Despite the environmental harshness, seasonality exacerbates the SSD probably due to the improvement of the forage quality related to short growing seasons (Langvatn and Albon 1986, Albon and Langvatn 1992, Van Soest 1994). Such results may be sought in the sex-specific differences in resource allocation to growth and reproduction. In both sexes, natural and sexual selection are expected to favor rapid development to sexual maturity (Fisher 1930, Andersson 1994), and males and females should therefore grow faster in populations living under favorable conditions. However, because maturity in ungulate females depends closely on a mass threshold (Sadleir 1969, Sæther and Heim 1993, Hewison 1996, Sand 1996, Gaillard et al. 2000), females may invest in their lifetime reproductive success rather than body growth once

this threshold is achieved (Trivers 1972, Clutton-Brock et al. 1982, Albon et al. 1987). In contrast, males will, under good environmental condition, benefit by growing as large as possible to ensure access to females (Trivers 1972) and to increase their survival probability (e.g., Festa-Bianchet et al. 1997, Coté and Festa-Bianchet 2001), both of which are important components of the reproductive success in male ungulates (Owen-Smith 1993, McElligott et al. 2001). Accordingly, moose living in areas with short and intense summers grew faster, for a longer time, and to a larger body mass than moose living in areas with long growing seasons, and these differences in forage quality affected the growth of males more than the growth of females (Table 2).

Such differences of growth among sexes did not appear in the same clear way when we considered the growth parameters of each sex independently (see Fig. 4c, d). This is probably because high environmental seasonality not only involves better forage quality, but also a longer period of food shortage during winter. Therefore, the two sexes may also be selected to invest in growth in order to increase their fasting endurance (Boyce 1978, 1979, Lindstedt and Boyce 1985). By considering growth parameters independently of the population (Fig. 4), such a selection may react simultaneously to the divergent effects between sexes of forage quality, which in turn may explain why the sex difference in growth pattern supported by SSD analysis (Table 2) did not appear more clearly in the regression analysis (Fig. 4c, d).

Several mechanisms have been invoked to explain how altitudinal or latitudinal gradients in environmental seasonality affect the quality of vegetation during the growing season (Klein 1965, 1970, Langvatn and Albon 1986, Albon and Langvatn 1992, Sæther and Heim 1993, Van Soest 1994). First, cooler weather and long daylight enhance diet quality by reducing the catabolic night time metabolism. Under such conditions

TABLE 2. Extended.

First term	Second term	Third term	Interaction
136.99 ± 22.73	-4.39 ± 0.94
478.02 ± 165.63	4.00 ± 4.13	...	-17.92 ± 8.64
137.13 ± 23.82	5.33 ± 1.23
-369.63 ± 259.40	-5.84 ± 5.80	...	24.01 ± 12.25
-0.89 ± 0.12	-0.03 ± 0.006
-0.91 ± 0.12	0.02 ± 0.005
-0.91 ± 0.13	-0.03 ± 0.007
0.17 ± 0.07	-0.78 ± 0.12	0.07 ± 0.02	...

the stem:leaf ratios and the proportion of fibrous tissue of low digestibility increase more slowly (Bliss 1962, 1971, Klein 1970, Van Soest 1994, Langvatn et al. 1996). Second, areas with a short growing season are often associated with more snow-rich winters. This leads to extended periods of snowmelt in the spring, which in turn extend the period with available food plants at an early phenological stage. At such a stage, plants are rich in nitrogen and digestible energy and often low in structural and defense compounds (Klein 1970, Albon and Langvatn 1992). Third, long daylight hours allow for higher photosynthetic activity and, thus, rapid growth rates that improve the quality of vegetation (Bliss 1962, 1971, Klein 1970). Finally, it is suggested that even small differences in digestibility and quality of forage plants have large effects on body mass gain due to a “multiplier” effect (White 1983, Sæther et al. 1996, Mysterud et al. 2001). Indeed, high forage digestibility increases both the relative metabolic energy intake and the absolute herbage intake (Van Soest 1994, Langvatn et al. 1996), probably because animals use less time for rumination when eating high-quality/digestible forage (Sæther and Andersen 1990, Van Soest 1994, Mysterud et al. 2001).

The timing of birth in relation to the vegetation phenology may also contribute to the explanation of the difference in SSD among populations. The nutritional and digestible qualities of plants are usually higher at an early stage of the growing season (Bliss 1962, 1971, Klein 1965, 1970, Sæther and Andersen 1990, Albon and Langvatn 1992). Because the difference in birth date between areas with short and long growing seasons is quite small while the variation in advancement of spring is large (Fig. 2b), calves born in localities with a short growing season therefore may take more advantage of the good feeding conditions during their first summer. This might also explain why a skewed sex ratio, which may lead to delayed calving date (see *Sex ratio effects* below), may have more profound effects in SSD γ when the growing season is short (Fig. 3). Calves born under such conditions will have less time to compensate for a poor fit between the birth date and the good feeding conditions.

Sex ratio effects

Several studies have suggested that a female-biased sex ratio could affect male growth (Solberg and Sæther 1994, Singer and Zeigenfuss 2002, Festa-Bianchet 2003, Mysterud et al. 2003, 2005, Sæther et al. 2003), but so far few studies have successfully investigated this hypothesis. For instance, Solberg and Sæther (1994) showed that adult males were smaller when population density was high and sex ratio low, but were unable to separate the effect of density and sex ratio on body mass variation. Indeed, a covariation between sex ratio and density is commonly encountered in ungulate populations (Clutton-Brock and Lonergan 1994, Clutton-Brock et al. 2002), limiting the possibility of disentangling the effect of each factor on the variation of young body mass. In the present study, however, no

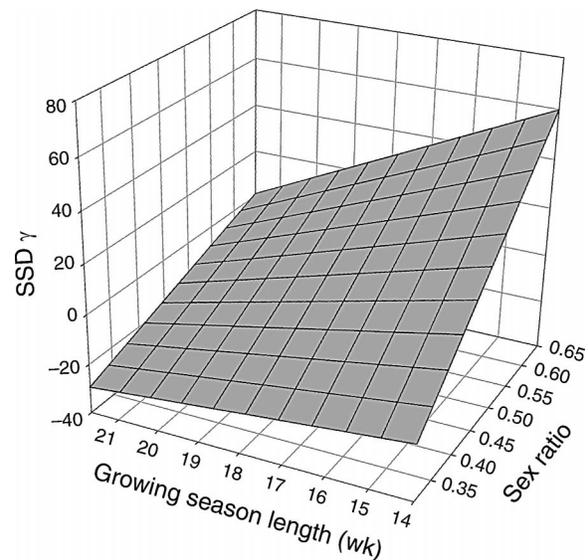


FIG. 3. Predicted values of sexual size dimorphism of adult carcass mass (SSD γ) from a model including an interaction between sex ratio (adult male : adult female) and the length of growing season (see Table 2). Predictions were made from the range of observed values for each variable (Appendix A).

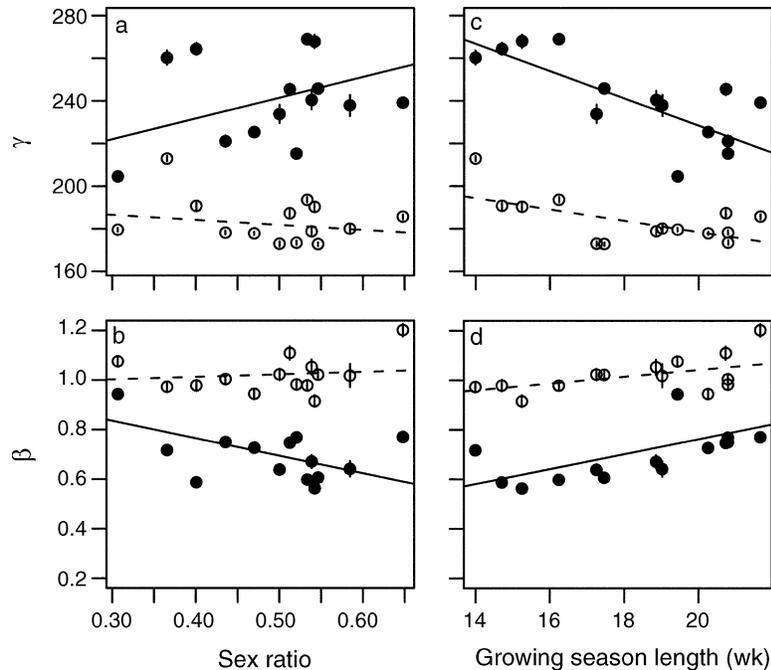


FIG. 4. Regression between the best explanatory variables (sex ratio, panels a and b; growing season, panels c and d) selected in the sexual size dimorphism analysis (see Table 2) and the growth parameters (γ , the adult [asymptotic] carcass mass, and β , the decay in growth rate) for males (solid circles, solid line) and females (open circles, dashed line) (means \pm SE). The regression analyses were weighted by sample size.

such strong correlation existed between density and sex ratio ($r = -0.31$, $n = 14$, $P = 0.28$).

In addition to the increasing rutting cost of young males when the proportion of males decreases, variation in sex ratio may also have other biological consequences that can explain variation in SSD. In a number of studies, breeding and/or calving have been found to be delayed and less synchronous in populations with female-biased sex ratio and a young male age structure (Noyes et al. 1996, Holand et al. 2003, Sæther et al. 2003), possibly due to a lack of acceptable males during the rut (Ballard et al. 1991, Komers et al. 1999). In turn, delayed birth is known to affect offspring body size in ungulates (Albon et al. 1987, Sæther et al. 2003), which is closely related to the subsequent body growth (Albon et al. 1987, Clutton-Brock et al. 1992, Lindström 1999). As males are often found to be less able to compensate for a bad start in life than females (Toigo et al. 1999, Festa-Bianchet et al. 2000, Leblanc et al. 2001, Solberg et al. 2004), a female-biased sex ratio may thus affect SSD not only through male reproductive investments, but more generally by affecting the behavioral ecology of rutting (Noyes et al. 1996, Myrsterud et al. 2002, Holand et al. 2003, Sæther et al. 2003).

By affecting the growth pattern and body mass, female-biased sex ratio could have both short- and long-term demographic effects on the population dynamics. Indeed many life history traits of ungulates, such as survival (Guinness et al. 1978, Clutton-Brock et al.

1992, Gaillard et al. 1998, Rose et al. 1998, Lindström 1999) and reproduction (Albon et al. 1987, Sæther and Heim 1993, Lindström 1999, Festa-Bianchet et al. 2000), are closely related to body growth (see Gaillard et al. [2000] for a review). So far, effects of sex ratio variation on body growth have received little attention (but see Myrsterud et al. 2003). Our results suggest that such studies should strongly be encouraged.

CONCLUSION

Our results support the hypotheses (1) that SSD is influenced by sexual differences in the response to variation in factors affecting body growth (Sæther and Haagenrud 1985, Sand et al. 1995, Loison et al. 1999a, Post et al. 1999, Leblanc et al. 2001) and (2) that sexual dimorphism in polygynous ungulates varies according to the environmental quality (Clutton-Brock et al. 1982, Leberg and Smith 1993, Réale and Boussès 1999). Moreover, absence of strong density effects is in line with the expectation that density dependence in large mammals mainly occurs at high density (Fowler 1987, Sæther et al. 1996).

We also call attention to the use of satellite-derived environmental data in studies of large-scale variations in body mass of ungulates. Such studies have usually focused on latitude (Geist 1987, Sand et al. 1995), climate (Sæther 1985, Langvatn and Albon 1986, Sand et al. 1995, Langvatn et al. 1996), and/or altitude effects (Hjeljord and Histøl 1999, Ericsson et al. 2002) as proxies of environmental conditions. In the present

study, however, the phenology variables derived from annual NDVI curves gave by far a better fit to the data, indicating that such variables are more able to assess large-scale variation in forage quality. Few ecological studies have yet taken advantage of such data to examine the manner in which population processes are affected by vegetation patterns (but see Pettorelli et al. 2005). This is unfortunate as they are easy and freely available and cover all terrestrial areas of the world with a relatively high temporal resolution (Reed et al. 1994, Kerr and Ostrovsky 2003, Turner et al. 2003). We argue that researchers should consider carefully large-scale variables that seem able to partly reflect some ecological processes that local variables fail to capture (Hallett et al. 2004).

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APPENDIX A

Environmental and population characteristics recorded during the study period, 1991–2003, for 14 Norwegian moose populations (*Ecological Archives* E087-044-A1).

APPENDIX B

Sex-specific adult body mass (γ) and decay rate (β) estimated from monomolecular growth curves fitted to carcass mass data from 14 Norwegian moose populations (1991–2003 period) (*Ecological Archives* E087-044-A2).