

Sexual size dimorphism in bighorn sheep (*Ovis canadensis*): effects of population density

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Abstract: Sexual dimorphism is an important characteristic of many mammals, but little is known about how environmental variables may affect its phenotypic expression. The relationships between population size, body mass, seasonal mass changes, and sexual mass dimorphism were investigated using 22 years of data on individually marked bighorn sheep (*Ovis canadensis*) on Ram Mountain, Alberta. The number of adult ewes was artificially maintained low from 1972 to 1981 and then allowed to increase. The body mass of males from 0 to 7 years of age was negatively affected by population density. Female body mass was negatively affected by population density up to 2 years of age. As the number of ewes increased, sexual mass dimorphism of sheep aged 2–7 years declined. Population density had a negative effect on seasonal mass changes of young males and females. Density also had a weak but significant positive effect on yearly mass gain of 2-year-old females, suggesting compensatory growth. Females appear to compensate for resource shortages early in life, while males show a lifelong negative effect. We suggest that these sexual differences are due to the greater flexibility of resource allocation to growth or reproduction by females than by males.

Résumé : Le dimorphisme sexuel est une caractéristique importante chez plusieurs espèces de mammifères, mais peu est connu sur les facteurs qui peuvent influencer son expression phénotypique. La relation entre la taille de la population et le dimorphisme sexuel de masse a été étudiée grâce à une série de 22 années de données sur la masse corporelle individuelle des mouflons d'Amérique (*Ovis canadensis*) de la population de Ram Mountain, Alberta. Le nombre de femelles adultes dans cette population a varié passablement entre 1972 et 1996. La masse des mâles âgés entre 0 et 7 ans a été négativement affectée par l'augmentation de la taille de la population. La masse des femelles a été affectée seulement jusqu'à l'âge de 2 ans. Le dimorphisme sexuel de masse des mouflons âgés entre 2 et 7 ans a diminué avec l'augmentation du nombre de femelles adultes. La densité a eu un effet négatif sur les changements saisonniers de masse des jeunes mâles et femelles. La densité a également eu un léger effet positif sur le gain de masse annuel des femelles de 2 ans. Les jeunes femelles sembleraient être capables de compenser pour une faible croissance survenue tôt dans la vie tandis que l'effet sur les mâles persisterait jusqu'à l'âge adulte. Nous suggérons que ces différences sexuelles sont attribuables à la plus grande flexibilité d'allocation des ressources de la reproduction vers la croissance de la part des femelles.

Introduction

Sexual size dimorphism, a difference in body size between sexually mature males and females, is a fundamental morphological characteristic of many animals, including most ungulates (for a review see Andersson 1994). Sexual size dimorphism has important consequences for ecology, behaviour, population dynamics, and evolution. Body-mass differences between males and females have been associated with differences in diet selection and intake rates (Houston and Shine 1993; Pérez-Barberia and Gordon 1998), habitat use (Clutton-Brock et al. 1987; Ruckstuhl 1998; Kie and Bowyer 1999), growth rates and growth strategies (Georgiadis 1985; Festa-Bianchet et al. 1996), survival rates (Trivers 1972; Clutton-Brock et al. 1982; Jorgenson et al. 1997), metabolic

rates (Hudson and White 1985), and reproductive strategies (Trivers 1972).

Of several evolutionary hypotheses proposed to explain the origin and maintenance of sexual size dimorphism (Ralls 1977; Slatkin 1984), the most widely accepted one is based upon the theory of sexual selection (Darwin 1871). In many species, sexual differences in the factors limiting reproductive success usually favour large size and a rapid growth rate in males, whose reproductive success is usually correlated with strength and weapon size (Ralls 1976; Clutton-Brock et al. 1980). The reproductive success of females, on the other hand, is generally not as dependent on body size as that of males. Consequently, females may adopt a more conservative growth strategy than males, and after achieving a certain amount of body growth, they should invest available resources in reproduction (Trivers 1972; Clutton-Brock et al. 1982).

Despite the ecological and evolutionary importance of sexual dimorphism in animals, very little is known about the environmental factors that may affect the degree of sexual size dimorphism over the short term within a population. A comprehensive assessment of these factors is necessary to understand how dimorphism patterns may have evolved, for two reasons. First, short-term changes in variables such as population density or food availability may hide the long-term evolutionary significance of sexual size dimorphism. If

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the growth of males and females is constrained in different ways by scarcity of resources, short-term changes in dimorphism may be unrelated to selective pressures. Second, temporal changes in environmental factors may lead to adaptive plasticity in the expression of sexual dimorphism. Here we use long-term data on marked bighorn sheep (*Ovis canadensis*) to explore how changes in population density may lead to changes in the degree of sexual size dimorphism.

Density dependence in growth and body mass have long been recognised in populations of large mammals (for a review see Fowler 1987). Population density can influence body size through a decrease in quantity or quality of forage and a resulting increase in intraspecific competition (Klein 1981; Clutton-Brock et al. 1982). In many studies, negative effects of high population density on growth have been reported (Skogland 1983; Skogland 1990; Choquenot 1991; Crête and Huot 1993; Hewison et al. 1996; Sams et al. 1998). Because the sexes are subject to different selective pressures regarding the trade-off between growth and reproduction, the consequences of changes in resource abundance associated with changes in population density should be different for males and females, leading to sex-specific strategies for coping with a decrease in resource availability (Trivers 1972; Iverson 1985; Halliday 1987). The results of studies of bird and mammal species where males are larger than females suggest that males are generally more sensitive than females to environmental stress such as food scarcity or disease (Clutton-Brock et al. 1985; Teather and Weatherhead 1989). The susceptibility of males to food shortage has been attributed to their high energetic needs resulting from large size and a high growth rate (Clutton-Brock et al. 1982). Leberg and Smith (1993) reported a decrease in asymptotic mass for males but not females in white-tailed deer (*Odocoileus virginianus*). A greater effect of density on size and mass of males than of females has also been reported in Alpine ibex (*Capra ibex*) (Toïgo et al. 1999), moose (*Alces alces*) (Solberg and Sæther 1994; Ferguson et al. 2000), and roe deer (*Capreolus capreolus*) (Vincent et al. 1995), and in another study of white-tailed deer (Ashley et al. 1998). We therefore expected that sexual size dimorphism would be negatively correlated with density (Leberg and Smith 1993; Stamps et al. 1997). The relation between population density and sexual size dimorphism could be either an inevitable consequence of limited food availability or the expression of an evolved adaptive strategy by which males restrain growth when resources are scarce (Clutton-Brock et al. 1982).

Our understanding of the population dynamics of ungulates is limited not by the existence of models and theories but by the availability of data on natural populations (Eberhardt 1985; Gaillard et al. 2000). Long-term studies of wild populations where density has been manipulated are essential to assess density-dependent effects on population dynamics (Caughley 1981; Sinclair 1989). The 28-year study of bighorn sheep at Ram Mountain, Alberta, is unique because of the availability of repeated measurements of body mass of marked animals. Population density was manipulated by yearly removals of ewes between 1972 and 1981 and was subsequently allowed to increase (Jorgenson et al. 1993b). With the subsequent threefold increase in the number of ewes, lamb survival rates (Portier et al. 1998) and male horn growth (Jorgenson et al. 1998) declined and the age at primiparity

increased (Gallant 1999), suggesting a decrease in food availability.

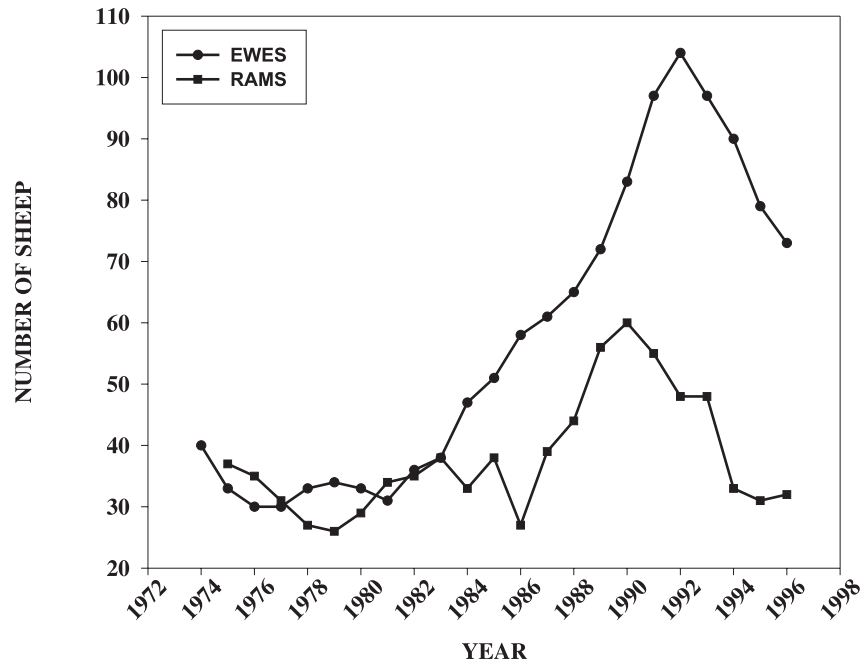
To investigate the effects of changes in population density on body growth and sexual dimorphism, we focused on three questions: (1) Do the effects of population density on growth and body mass vary with age? Because growth patterns change with age (Festa-Bianchet et al. 1996), we expected the effects of population density to be age-specific, with a strong negative effect of increasing population density on body mass of lambs and yearlings of both sexes. Bighorn sheep of both sexes show an increase in mass with age until they are at least 7 years old (Festa-Bianchet et al. 1996). Because of the potential for compensatory growth, we expected the older age-classes to be less affected by population density at birth. (2) Does compensatory growth occur? Compensatory growth is a period of accelerated growth that follows a period of decreased growth due to food restriction or environmental perturbations, but it requires relaxation of the food restriction (Verme 1963; Hudson and White 1985). It has been reported for various species (McAdam and Millar 1999; Badyaev and Martin 2000), including domestic sheep (Oldham et al. 1999) and wild ungulates (Toïgo et al. 1999). Females may direct more resources to growth and fewer to reproduction when food is scarce. The density-dependent increase in age at primiparity and decrease in maternal effort (Festa-Bianchet and Jorgenson 1998; Gallant 1999) reported in our study population suggest that females favoured growth and maintenance over reproduction at high population density. In males, however, the maximum growth rate is expressed when resources are abundant and it is not clear how males could divert resources from reproduction to body growth. We therefore expected the potential for compensatory growth to be greater for females than for males. (3) Do the effects of population density on growth and body mass vary with sex? Because males are usually more affected than females by resource shortages, we expected a stronger effect of population density on body mass and growth of males than of females and a decrease in sexual size dimorphism with increasing population density.

Material and methods

Ram Mountain (52°N, 115°W) is an isolated mountainous outcrop separated from the main Rocky Mountain chain by about 30 km of foothills covered by coniferous forest. Bighorn sheep use about 38 km² of alpine and subalpine habitat at elevations from 1082 to 2173 m. Since 1971, sheep were captured in a corral trap baited with salt, weighed, and marked. Females were marked with individually identifiable canvas or plastic collars and males with numbered and coloured Allflex plastic ear tags. Lambs were marked with Ketchum metal ear tags with attached strips of coloured Safeflag plastic. Multiple captures of almost all ewes were made each year from late May to early October, and over 95% of the population was individually marked in most years. Captured sheep were weighed to the nearest 250 g with a Detecto spring scale whose accuracy was checked monthly with known weights.

Data used in these analyses were collected from 1974 to 1996. Population density was kept low from 1972 to 1981 by annual removals of adult ewes (Jorgenson et al. 1993b). The mean number of ewes 2 years of age and older during this period was 35 and ranged from 30 to 42. After 1981, the number of adult ewes (2 years of age and older) more than tripled, reached 104 in 1992, and then decreased to 73 by 1996 (Fig. 1).

Fig. 1. Numbers of bighorn sheep (*Ovis canadensis*) ewes 2 years of age and older and rams 3 years of age and older on Ram Mountain, Alberta, in 1974–1996.



Sheep were censused by identifying those caught or seen at the trap and observed during ground searches of the study area. Females have very traditional area-use patterns, so changes in population density do not affect the size of their geographic range (Geist 1971; Festa-Bianchet 1986). Population size and population density are therefore approximately equivalent. For consistency with previous studies (Festa-Bianchet et al. 1997; Festa-Bianchet and Jorgenson 1998; Portier et al. 1998), we used the number of adult females (2 years of age and older) in June as the measure of population size. The probability of not seeing a marked sheep in a given year was very low, 0.5% for ewes and 5% for rams (Jorgenson et al. 1997), and almost all sheep that were missed had emigrated to a neighbouring mountain. Bighorn sheep are sexually segregated for most of the year (Geist 1971) and the number of adult rams should have a limited effect on the availability of resources for ewes and lambs. Jorgenson et al. (1998) found that horn growth of rams before they left the nursery groups at 3 years of age was affected by the number of ewes but not by the number of rams in the population. We expected that density in the year of birth may have a long-term effect on individual development (cohort effect), but also that density in a given year could affect mass gain of sheep of all ages in that year. Therefore, we used two measures of density: the number of adult females in the population in the year of birth, and “current” population size, i.e., the number of adult females in the year when age-specific mass or mass change was estimated. Population size at birth and current population size were highly correlated for all age-classes because the population mostly increased over time (Fig. 1). Direct effects of density were assessed by analysing the effect of current population size on seasonal and yearly mass changes, while the effects of conditions during early development were measured by examining the relationship between population size at birth and body mass of different age-classes. For males 3 years of age and older, current population size was the number of adult males (3 years of age and older) in the population. Three-year-old males move from nursery herds to bachelor groups of adult males (Geist 1971; Festa-Bianchet 1991). The number of females is therefore unlikely to affect body growth of adult males (Festa-Bianchet 1991), and horn growth of adult males was independent of the number of ewes (Jorgenson et al. 1998).

Captured sheep were weighed if they had not been processed for at least 3 weeks. We knew the exact age and year of birth of each individual because over 95% of sheep were first captured as lambs or yearlings. Ewes were caught 2–5 times each summer but many rams were only caught once each summer. Over 80% of lambs in the population were caught and tagged each year. Mothers were identified from suckles and associations with marked ewes for over 90% of lambs (Jorgenson et al. 1993a). We adjusted the mass of each sheep with multiple captures to June 5 and September 15 using individual growth rates. Mass of lambs was adjusted to June 15 because for some lambs, mass adjusted to June 5 was much lower than the average birth mass (Hogg et al. 1992). Bighorn sheep experience pronounced seasonal variation in body mass and the mass-adjustment dates were chosen to approximate mass at the beginning and end of the growing season. Because males older than 3 years were rarely caught after July, their mass at the end of the summer was usually not available. More details on capture frequencies and mass adjustments are provided in Festa-Bianchet et al. (1996).

Data analysis

We used parametric statistics to analyse mass at the beginning and end of the summer for sheep aged 0–7 years. We tested for sexual dimorphism in mass and its relationship with population size using analysis of covariance (ANCOVA) (Sokal and Rohlf 1997) in the GLM procedure in SPSS for PC (SPSS Inc. 1997).

We also quantified sexual dimorphism as the percentage of mass by which males were larger than females ((mean male mass – mean female mass / mean male mass) × 100). This index was calculated for each cohort with data for 2 or more individuals of each sex. We regressed this index of dimorphism on population size at birth.

We examined the correlation between the number of adult ewes and three measures of variation in mass: summer gain (mass in September minus mass in June of the same year), yearly gain (mass in June of one year minus mass in June of the previous year), and winter loss (mass in June of one year minus mass in September of the previous year). Within a sex–age class, mass

Table 1. Linear relationship between the number of adult ewes (2 years of age and older) in the year of birth and body mass of male and female bighorn sheep (*Ovis canadensis*) on Ram Mountain, Alberta, in 1974–1996.

	Males				Females			
	<i>n</i>	Slope	<i>r</i> ²	<i>p</i>	<i>n</i>	Slope	<i>r</i> ²	<i>p</i>
Lambs								
Mass on 15 June	124	−0.02	0.03	0.041	126	−0.02	0.05	0.014
Mass on 15 Sept.	145	−0.09	0.16	0.000	134	−0.09	0.20	0.000
Yearlings								
Mass on 5 June	154	−0.09	0.12	0.000	168	−0.07	0.16	0.000
Mass on 15 Sept.	133	−0.16	0.21	0.000	152	−0.13	0.24	0.000
2-year-olds								
Mass on 5 June	110	−0.17	0.29	0.000	154	−0.16	0.30	0.000
Mass on 15 Sept.	94	−0.29	0.42	0.000	131	−0.14	0.19	0.000
3-year-olds								
Mass on 5 June	107	−0.24	0.39	0.000	138	−0.05	0.04	0.022
Mass on 15 Sept.	40	−0.29	0.32	0.000	132	−0.01	0.003	0.561
4-year-olds								
Mass on 5 June	81	−0.29	0.40	0.000	115	−0.02	0.006	0.414
Mass on 15 Sept.	18	−0.38	0.37	0.007	111	−0.03	0.01	0.278
5-year-olds								
Mass on 5 June	61	−0.27	0.39	0.000	105	−0.03	0.02	0.196
Mass on 15 Sept.*	—	—	—	—	95	0.008	0.001	0.795
6-year-olds								
Mass on 5 June	53	−0.33	0.47	0.000	91	−0.09	0.08	0.006
Mass on 15 Sept.*	—	—	—	—	88	−0.05	0.04	0.057
7-year-olds								
Mass on 5 June	26	−0.22	0.31	0.003	87	−0.07	0.07	0.011
Mass on 15 Sept.*	—	—	—	—	82	−0.02	0.006	0.486

Note: Regressions were performed for age-classes between 0 and 7 years and for mass adjusted to the beginning (June 15 for lambs, June 5 for older sheep) and end (September 15) of the summer.

*Insufficient males.

changes were often correlated with individual mass at the beginning (summer gain and yearly gain) or end (winter loss) of the summer: large sheep tend to gain relatively less mass than small sheep (Festa-Bianchet et al. 1996). When testing for density effects on mass changes, therefore, we removed the effect of absolute mass on mass changes by using partial correlation controlling for initial mass. The results of our analyses of mass change are therefore not biased by the possible negative effects of population size on absolute mass.

The September mass of ewes that reproduced as 2-year-olds was negatively affected by their reproductive status, and their lambs were lighter than the lambs of older ewes (Festa-Bianchet et al. 1995). These ewes and their lambs were therefore excluded from the analyses. Males orphaned during the removal experiment in 1972–1981 were also excluded from all analyses because they were lighter than non-orphans (Festa-Bianchet et al. 1994). Statistical analyses were performed with SPSS for PC (SPSS 1997). All probability values are two-tailed unless otherwise specified, with $\alpha = 0.05$.

Results

Population size and body mass

Population size had divergent effects on age-specific mass of males and females. Density in the year of birth negatively affected body mass for males of all age-classes. This effect was weak for male lambs on 15 June but increased by the end of the first growing season and remained highly significant for rams up to 7 years old (Table 1). Population size in the year of birth, on the other hand, had a negative effect

only for young females. From the end of their fourth summer (3 years old on September 15) until they were 7 years old, the mass of ewes was either not affected, or only very weakly affected, by population size (Table 1).

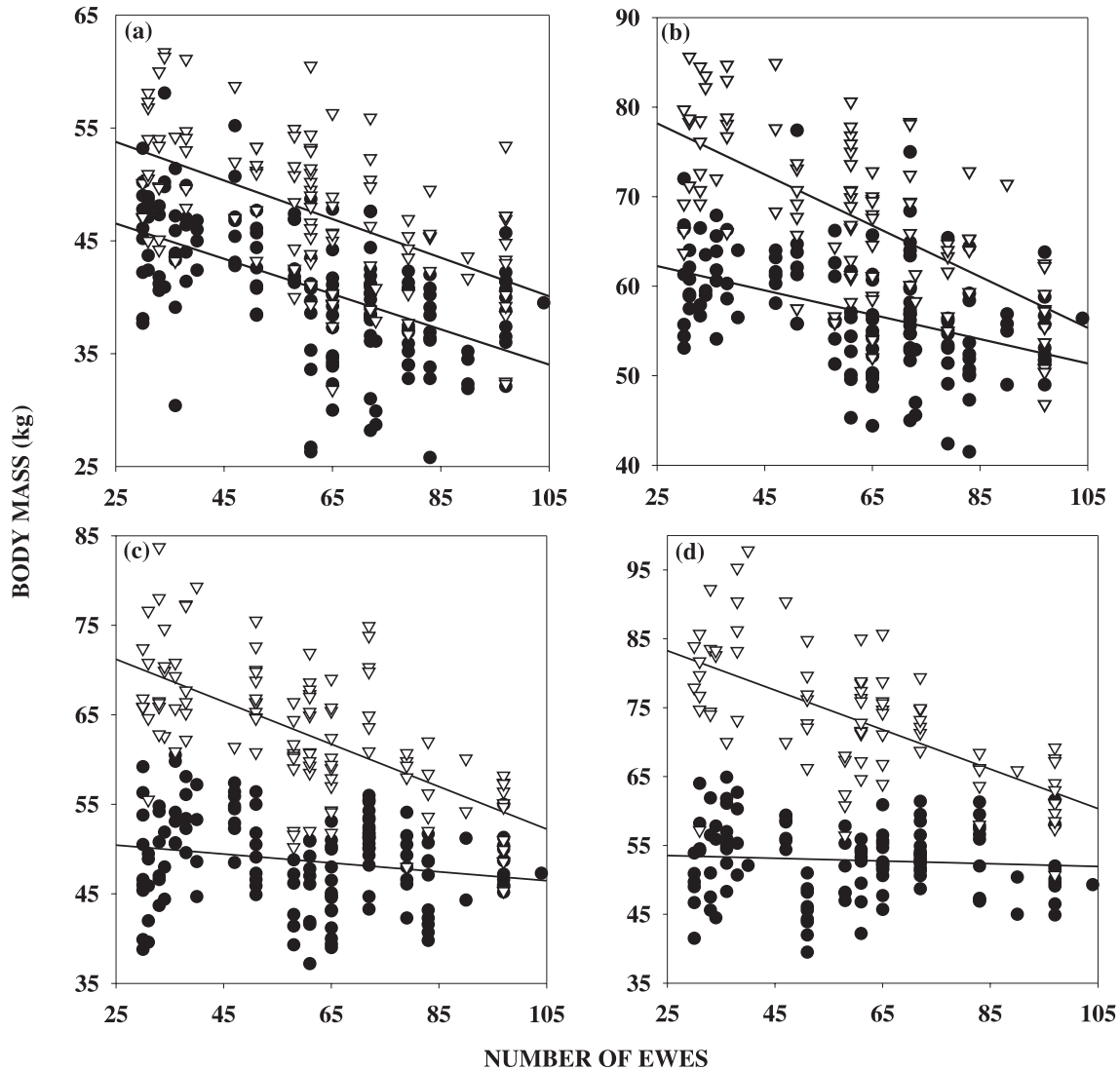
Number of ewes and sexual mass dimorphism

Sexual mass dimorphism of adult bighorn sheep decreased with increasing population size at birth (Fig. 2). ANCOVA (Table 2) revealed that the sex \times number of ewes interaction became significant for mid-September mass at age 2 and remained significant up to 7 years of age for mass in June and September. Sexual mass dimorphism was significant from 1 to 7 years of age. Contrary to our expectations, we found a similar effect of population size on growth of males and of females from 0 to 2 years (Table 2). After age 2, however, population size had a negative effect only for males. Consequently, cohort-specific sexual dimorphism decreased with increasing population density (Fig. 3).

Current population size and seasonal mass changes

Seasonal mass changes were not independent of initial mass (Festa-Bianchet et al. 1996). When individual mass was taken into account through partial correlation, current population size had a negative effect on yearly and seasonal mass changes in most sex–age classes. For males, yearly gain and summer mass gain were negatively affected from 0 to 2 years of age. Lambs and yearlings, but not adults, lost more mass during winter at high than at low population size

Fig. 2. Relationship between the number of adult bighorn ewes in the year of birth and body mass of males (∇) and females (\bullet) at Ram Mountain, Alberta, in 1974–1996. (a) Two-year-olds, mass adjusted to June 5 (females: $y = -0.16x + 50.44$; males: $y = -0.17x + 58.12$). (b) Two-year-olds, mass adjusted to September 15 (females: $y = -0.14x + 65.65$; males: $y = -0.29x + 85.31$). (c) Three-year-olds, mass adjusted to June 5 (females: $y = -0.05x + 51.68$; males: $y = -0.24x + 77.13$). (d) Four-year-olds, mass adjusted to June 5 (females: $y = -0.02 + 54.01$; males: $y = -0.29x + 90.42$).



(Table 3). Population size negatively affected seasonal mass changes of female lambs and yearlings, but was positively correlated with yearly mass gain of 2-year-old ewes (Table 3). Comparisons of correlation coefficients revealed that mass changes were not more affected by population size in males than in females, with the exception of mass gain from 2 to 3 years of age, which decreased with increasing population size for males but increased for females. Seasonal mass changes in adult ewes were not affected by the current number of ewes, and seasonal mass changes in males older than 3 years were not affected by the number of rams (Table 3).

Discussion

Our study provides evidence that changes in population density lead to changes in the degree of sexual size dimorphism. As the number of ewes at birth increased, the degree

of sexual size dimorphism of bighorn sheep aged 2–7 years declined. Contrary to our prediction, however, instead of a greater effect of population size on growth of young males than of young females, we found a persistent effect on males in older age-classes. High population density in the year of birth led to a lifelong negative effect for males, but young adult females appeared to compensate for slow early growth. We suggest that the sexual differences in the effects of population density were due to differences in the reproductive strategies of males and females. Our results underline the importance of distinguishing both sex and age classes when assessing the effect of population density on body growth.

Confirming the results of earlier studies of ungulates (Clutton-Brock et al. 1982; Fowler 1987; Leberg and Smith 1993), high density in the year of birth led to depressed body mass of young bighorn sheep of both sexes. Previous studies have shown that maternal body condition affects

Table 2. ANCOVA comparing the number of ewes in the year of birth and body mass adjusted to June 5 and September 15 for bighorn sheep aged between 0 and 7 years on Ram Mountain, Alberta, in 1974–1996.

Age-class and term	Mass on 5 June			Mass on 15 September		
	<i>n</i>	<i>r</i> ²	<i>p</i>	<i>n</i>	<i>r</i> ²	<i>p</i>
Lambs						
Model	250	0.05	0.009	279	0.23	0.000
No. of ewes			0.002			0.000
Rejected terms						
Sex			0.747			0.190
Sex × no. of ewes			0.987			0.918
Yearlings						
Model	322	0.27	0.000	285	0.40	0.000
No. of ewes			0.000			0.000
Sex			0.002			0.000
Rejected terms						
Sex × no. of ewes			0.512			0.256
2-year-olds						
Model	264	0.45	0.000	225	0.55	0.000
No. of ewes			0.000			0.000
Sex			0.000			0.000
Sex × no. of ewes ^a			—			0.000
Rejected terms						
Sex × no. of ewes ^b			0.588			
3-year-olds						
Model	245	0.66	0.000	172	0.67	0.000
No. of ewes			0.000			0.000
Sex			0.000			0.000
Sex × no. of ewes			0.000			0.000
4-year-olds						
Model	196	0.75	0.000	129	0.65	0.000
No. of ewes			0.000			0.000
Sex			0.000			0.000
Sex × no. of ewes			0.000			0.001
5- to 7-year-olds						
Model	— ^c	— ^c	0.000	— ^d	— ^d	— ^d
No. of ewes			0.000			
Sex			0.000			
Sex × no. of ewes			0.000 ^c			

Note: Body mass is the dependent variable, sex is a factor, and number of ewes is a covariate; *n* is the total number of individuals, males and females, included in the analysis.

^aMass on September 15 only.

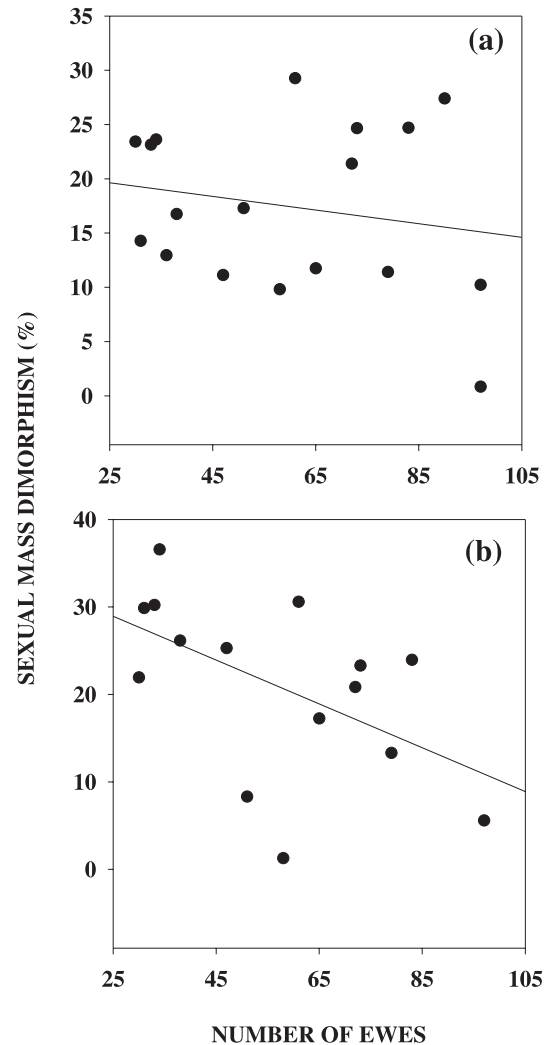
^bMass on June 5 only.

^cResults for 5- (*n* = 166, *r*² = 0.77), 6- (*n* = 145, *r*² = 0.81) and 7-year-old ewes (*n* = 113, *r*² = 0.81) are the same except that *p* = 0.022 for sex × number of ewes at 7 years old.

^dInsufficient males.

foetal growth, birth mass, neonatal growth rate, and milk production (Verme 1963; Festa-Bianchet 1988; Gaillard et al. 1993b). Surprisingly, however, the effect of population size on mid-June mass of lambs was weak. Lambs are about 3 weeks old in mid-June, and this result suggests that birth mass was not strongly affected by changes in population size. As density increased, some lambs were born late (Bérubé 1997) and were therefore younger in mid-June than lambs born at low density. It is therefore all the more surprising

Fig. 3. Relationship between sexual mass dimorphism (percentage of mass by which males are larger than females) and number of adult bighorn ewes at Ram Mountain, Alberta, in 1974–1996. (a) Two-year-olds, mass adjusted to June 5 (*n* = 18 cohorts). (b) Four-year-olds, mass adjusted to September 15 (*n* = 15 cohorts).



that density had no significant negative effect on mass of lambs in mid-June. Alternatively, if small newborns died before we could catch them, our sample may be biased towards heavier lambs and may not provide a reliable assessment of density-dependent changes in birth mass. Other studies have found higher mortality rates in light than in heavy newborn ungulates (Clutton-Brock et al. 1982; Fairbanks 1993). If birth mass decreased with increasing population size, however, neonatal mortality should also increase, but there is very little evidence of density dependence of neonatal mortality in sheep at Ram Mountain (Portier et al. 1998).

The negative effects of population size on body mass increased during the first summer. Carlisle (1982) predicted that parental expenditure will decrease when resource availability is low and population density is high. Réale and Boussès (1995) and Réale et al. (1999) reported that as resource availability decreased, maternal care and maternal

Table 3. Partial correlation between seasonal and yearly mass changes of bighorn sheep and number of ewes in the current year, controlling for individual body mass in June for yearly and summer gain and for body mass in September for winter loss.

Mass change	Age (years)	Males			Females			<i>t</i> test
		<i>n</i>	<i>r</i>	<i>p</i>	<i>n</i>	<i>r</i>	<i>p</i>	<i>p_c</i>
Yearly gain	0	47	-0.38	0.008	50	-0.45	0.001	0.681
	1	98	-0.44	0.000	126	-0.50	0.000	0.610
	2	86	-0.25	0.021	127	0.21	0.017	0.001
	3	57	-0.08	0.562	101	0.16	0.113	—
	4	49	0.18	0.205	93	-0.01	0.918	—
Winter loss	0	50	-0.39	0.005	57	-0.28	0.031	0.541
	1	90	-0.31	0.003	117	-0.26	0.004	0.681
	2	73	-0.16	0.177	108	0.15	0.125	—
	3	24	0.29	0.145	98	0.11	0.279	—
	4*	—	—	—	89	0.05	0.665	—
Summer gain	0	81	-0.31	0.004	76	-0.41	0.000	0.477
	1	129	-0.37	0.000	140	-0.38	0.000	0.912
	2	88	-0.23	0.027	125	-0.08	0.389	—
	3	37	0.05	0.745	126	0.01	0.921	—
	4*	—	—	—	106	-0.15	0.126	—

Note: For males older than 3 years, the number of males in the population was used as a measure of population size. The results of tests comparing correlation coefficients are represented by the probability, *p_c*, for cases in which at least one correlation coefficient was significant. The negative relationship between winter loss and current population size represents increasing mass loss during high-density years.

*Insufficient males.

investment also decreased in mouflon (*Ovis gmelini*). Because the energetic demands of lactation are much greater than those of gestation (Hudson and White 1985), the negative effect of population size on mass at weaning may reflect a decrease in maternal expenditure. Indeed, summer mass gain of adult ewes was independent of density, and ewes reduced their maternal expenditure as the population increased (Festa-Bianchet and Jorgenson 1998).

The effects of population size on mass of males and females diverged at 2 years of age, leading to a decrease in sexual mass dimorphism with increasing population size. Clutton-Brock et al. (1982) also noted that in red deer (*Cervus elaphus*), as density increased, sexual dimorphism declined. While population size in the year of birth had little or no effect for females beyond 2 years of age, it had a permanent negative effect on males. Sexual differences in the plasticity of resource allocation between growth and reproduction may account for the absence of compensatory growth in rams compared with ewes. In polygynous mammals, when females attain adequate body mass for reproduction, growth is usually greatly reduced or stops and most metabolic resources not needed for maintenance and activity are directed to reproduction (Clutton-Brock et al. 1982), presumably because the fitness gain from additional body growth is less than that obtained by reproducing. The reproductive success of males, on the other hand, depends upon competing with other males for oestrous females. The outcome of male-male competition is strongly affected by body mass and body condition (Le Boeuf 1974; Clutton-Brock et al. 1982). Males of most polygynous mammal species are therefore selected to grow as large and as fast as possible. Because the post-weaning body growth of bighorn males is much greater than

that of females (Festa-Bianchet et al. 1996), and horn growth after 3 years of age is independent of population size (Jorgenson et al. 1998), one may assume that males have a high potential for compensatory growth and that mass at weaning would not be strongly correlated with adult mass. Festa-Bianchet et al. (2000), however, reported that weaning mass is more closely correlated with adult mass for males than for females. The more rigid growth strategy of males relative to reproduction may explain this apparent inconsistency. If the age-specific growth rate of bighorn rams is always expressed as the maximum allowed by the available resources, then males that suffer a growth handicap early in life will be unable to compensate for it later in life. Rams that are small as lambs or yearlings therefore become small adults (Festa-Bianchet et al. 2000). Unlike females, young males do not appear to divert resources from reproduction to growth at high population density. The rut occurs in autumn, after seasonal growth has ended. Even if it did not take part in the rut, a young ram would not increase its body growth, although it may increase its probability of survival (Stevenson and Bancroft 1995) or possibly improve its growth the following year if body condition at the end of winter had an effect on subsequent growth. The positive relationship between population size and yearly mass gain of 2-year-old ewes suggests that, unlike young males, females were able to compensate for poor early development. Consequently, the mass of adult females was little affected by population density. We suggest that adult females were able to compensate for negative density effects on early development by postponing primiparity (Jorgenson et al. 1993a; Gallant 1999) and decreasing maternal energy expenditure (Festa-Bianchet and Jorgenson 1998). Compensatory growth has also been found

in female ibex (Toïgo et al. 1999) and in young domestic ewes that were underfed during early development (Oldham et al. 1999).

We expected that the effects of population density on growth would be stronger for males than for females. In many species of polygynous mammals, the large mass and rapid growth of males have been associated with greater susceptibility to diseases and parasites, starvation and predation, higher rates of heat loss, and a shorter life expectancy compared with females (Clutton-Brock et al. 1985). However, we did not find a stronger effect of population size at birth on the mass of male than on female lambs, yearlings, and 2-year-olds. This contradicts the findings of other studies of wild ungulates which showed that young males were more strongly affected by population density than young females (Ashley et al. 1998; Ferguson et al. 2000). Possibly, the sexual differences in mass up to 2 years of age were not sufficient to cause great differences in metabolic requirements. Sexual size dimorphism in bighorn sheep between 0 and 2 years of age only ranges from about 10 to 15%, independently of population size. Ruckstuhl (1998) found that ewes and males up to 2 years of age had similar foraging behaviour, while 3-year-old males behaved more like adult rams; her results suggest that the energetic needs of males and females up to 2 years of age may not be very different.

Previous studies of ungulates have underlined the importance of birth mass and early mass gain on adult mass and lifetime reproductive success (Clutton-Brock et al. 1992; Gaillard et al. 1998; Lindström 1999). In most ungulates, however, body growth continues for many years after weaning, often also after sexual maturity (Blaxter et al. 1982; Georgiadi 1985; Festa-Bianchet et al. 1996). Events occurring after early development can therefore influence adult mass and postweaning growth (Sæther and Heim 1993; Gaillard et al. 1993a; Festa-Bianchet et al. 1996; Festa-Bianchet et al. 2000). Our results suggest a direct effect of population size on growth of yearlings of both sexes and of 2-year-old males. By switching from nursery to bachelor groups at 2 or 3 years of age (Festa-Bianchet 1991), males experienced lower population density and presumably greater forage availability, because the number of males only doubled while the number of ewes more than tripled during our study. Although we could not detect any negative effects of high density on mass gain for either sex beyond 2 years of age, rams were unable to compensate for the conditions experienced during early development, and the negative effect of population size at birth persisted into adulthood.

Clutton-Brock et al. (1982) suggested that the negative relationship between sexual size dimorphism and population density in red deer could be either an unavoidable consequence of higher sensitivity of males to food availability or an adaptive strategy by which males restrain body growth when resources are scarce. Food availability at Ram Mountain was probably reduced because of the increase in the number of ewes; lamb survival and male horn growth decreased (Jorgenson et al. 1998; Portier et al. 1998) and age of primiparity increased (Gallant 1999). High population density also reduced body growth of lambs, yearlings, and 2-year-old females. Our study therefore supports the physiological-constraint hypothesis: rams were small at high density because their growth was limited by resource availability. The

variability seen in horn and body size between populations, which has great importance for trophy ram production, probably originates more from environmental variations than from genetic factors (Geist 1971), and suggestions of adaptive, density-dependent control of growth by males remain untested.

Mass-biased mortality could have potentially affected our results in two ways. First, as pointed out by Jorgenson et al. (1998), mortality of bighorn sheep rams is affected by hunting regulations: harvest of small-horned rams (which are presumably also small-bodied) is prohibited. Therefore, our sample of adult males may have been increasingly biased towards small ones from 4 to 6 years of age, because the largest horned and presumably biggest rams were at greater risk of being shot than the smallest ones. This bias was probably stronger at low population density because at high density many rams never reached the minimum horn size required by hunting regulations (Jorgenson et al. 1998). It is therefore possible that our results concerning the effects of population size on mass of males aged 5 and 6 years slightly underestimate the effects of population density. Secondly, Festa-Bianchet et al. (1997) reported that survival of male and female lambs and of yearling females increased with body mass at high population density. If the survival rate of small sheep is lower at high than at low population density, our data may underestimate the negative effects of population size on mass of adult sheep.

Neither of these two potential biases, however, is likely to affect our suggested explanation for a density-dependent reduction in sexual mass dimorphism. Furthermore, our results suggest that sex differences in growth strategies can promote divergent responses of males and females to environmental perturbations and therefore lead to phenotypic plasticity in the expression of sexual mass dimorphism. Long-term studies of the effects of population density or other environmental factors are important for understanding population fluctuations and reproductive strategies of long-lived species. Future research should therefore consider the effects of winter and summer weather, and their interaction with population density, on the growth of the different sex-age classes. Our results also provide clues to the ecological circumstances required for the evolution of sexual size dimorphism. We suggest that sexually dimorphic growth strategies would be more likely to evolve under conditions of resource abundance than of food scarcity.

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References

- Andersson, M. 1994. Sexual selection. Princeton University Press, Princeton, N.J.
- Ashley, E.P., McCullough, G.B., and Robinson, J.T. 1998. Morphological responses of white-tailed deer to a severe population reduction. *Can. J. Zool.* **76**: 1–5.
- Badyaev, A.V., and Martin, T.E. 2000. Individual variation in growth trajectories: phenotypic and genetic correlations in ontogeny of the house finch (*Carpodacus mexicanus*). *J. Evol. Biol.* **13**: 290–301.
- Bérubé, C. 1997. Les stratégies d'adaptation vitale chez les brebis du mouflon d'Amérique (*Ovis canadensis*) : la reproduction en fonction de l'âge. Ph.D. thesis, Université de Sherbrooke, Sherbrooke, Que.
- Blaxter, K.L., Fowler, V.R., and Gill, J.C. 1982. A study of the growth of sheep to maturity. *J. Agric. Sci.* **98**: 405–420.
- Carlisle, T.R. 1982. Brood success in variable environment: implication for parental care allocation. *Anim. Behav.* **30**: 824–836.
- Caughley, G. 1981. Comments on natural regulation of ungulates (What constitutes a real wilderness?). *Wildl. Soc. Bull.* **9**: 232–284.
- Choquenot, D. 1991. Density-dependent growth, body condition, and demography in feral donkeys: testing the food hypothesis. *Ecology*, **72**: 805–813.
- Clutton-Brock, T.H., Albon, S.D., and Harvey, P.H. 1980. Antlers, body size, and breeding group size in the Cervidae. *Nature (Lond.)*, **285**: 565–567.
- Clutton-Brock, T.H., Guinness, F.E., and Albon, S.D. 1982. Red deer: behavior and ecology of two sexes. University of Chicago, Chicago.
- Clutton-Brock, T.H., Albon, S.D., and Guinness, F.E. 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature (Lond.)*, **313**: 131–133.
- Clutton-Brock, T.H., Major, Albon, S.D., and Guinness, F.E. 1987. Early development and population dynamics in red deer. I. Density-dependent effects on juvenile survival. *J. Anim. Ecol.* **56**: 53–67.
- Clutton-Brock, T.H., Price, O.F., Albon, S.D., and Jewell, P.A. 1992. Early development and population fluctuations in Soay sheep. *J. Anim. Ecol.* **61**: 381–396.
- Crête, M., and Huot, J. 1993. Regulation of a large herd of migratory caribou: summer nutrition affects calf growth and body reserves of dams. *Can. J. Zool.* **71**: 2291–2296.
- Darwin, C. 1871. The descent of man, and selection in relation to sex. D. Appleton, New York.
- Eberhardt, L.L. 1985. Assessing the dynamics of wild populations. *J. Wildl. Manag.* **49**: 997–1012.
- Fairbanks, W.S. 1993. Birthdate, birthweight, and survival in pronghorn fawns. *J. Mammal.* **74**: 129–135.
- Ferguson, S.H., Bisset, A.R., and Messier, F. 2000. The influences of density on growth and reproduction in moose *Alces alces*. *Wildl. Biol.* **6**: 31–39.
- Festa-Bianchet, M. 1986. Site fidelity and seasonal range use by bighorn rams. *Can. J. Zool.* **64**: 2126–2132.
- Festa-Bianchet, M. 1988. Nursing behaviour of bighorn sheep: correlates of ewe age, parasitism, lamb age, birthdate and sex. *Anim. Behav.* **36**: 1445–1454.
- Festa-Bianchet, M. 1991. The social system of bighorn sheep: grouping patterns, kinship and female dominance rank. *Anim. Behav.* **42**: 71–82.
- Festa-Bianchet, M., and Jorgenson, J.T. 1998. Selfish mothers: reproductive expenditure and resource availability in bighorn ewes. *Behav. Ecol.* **9**: 144–150.
- Festa-Bianchet, M., Jorgenson, J.T., and Wishart, W.D. 1994. Early weaning in bighorn sheep, *Ovis canadensis*, affects growth of males but not females. *Behav. Ecol.* **5**: 21–27.
- Festa-Bianchet, M., Jorgenson, J.T., Lucherini, M., and Wishart, W.D. 1995. Life history consequences of variation in age of primiparity in bighorn ewes. *Ecology*, **76**: 871–881.
- Festa-Bianchet, M., Jorgenson, J.T., King, W.J., Smith, K.G., and Wishart, W.D. 1996. The development of sexual dimorphism: seasonal and lifetime mass changes in bighorn sheep. *Can. J. Zool.* **74**: 330–342.
- Festa-Bianchet, M., Jorgenson, J.T., Bérubé, C.H., Portier, C., and Wishart, W.D. 1997. Body mass and survival of bighorn sheep. *Can. J. Zool.* **75**: 1372–1379.
- Festa-Bianchet, M., Jorgenson, J.T., and Réale, D. 2000. Early development, adult mass and reproductive success in bighorn sheep. *Behav. Ecol.* **11**: 633–639.
- Fowler, C.W. 1987. A review of density dependence in populations of large mammals. In *Current mammalogy*. Edited by H.H. Genoways. Plenum Press, New York. pp. 401–441.
- Gaillard, J.M., Delorme, D., and Jullien, J.M. 1993a. Croissance précoce et poids à l'entrée de l'hiver chez le faon de chevreuil (*Capreolus capreolus*). *Mammalia*, **57**: 359–366.
- Gaillard, J.M., Delorme, D., and Jullien, J.M. 1993b. Effects of cohort, sex, and birth date on body development of roe deer (*Capreolus capreolus*) fawns. *Oecologia*, **94**: 57–61.
- Gaillard, J.-M., Andersen, R., Delorme, D., and Linnell, J.D.C. 1998. Family effects on growth and survival of juvenile roe deer. *Ecology*, **79**: 2878–2889.
- Gaillard, J.-M., Festa-Bianchet, M., Delorme, D., and Jorgenson, J. T. 2000. Body mass and individual fitness in female ungulates: bigger is not always better. *Proc. R. Soc. Lond. B Biol. Sci.* **267**: 471–477.
- Gallant, B.Y. 1999. Retardement dans l'âge à la primiparité chez le mouflon d'Amérique : corrélats et conséquences. M.Sc. thesis, Université de Sherbrooke, Sherbrooke, Que.
- Geist, V. 1971. Mountain sheep. University of Chicago Press, Chicago.
- Georgiadis, N. 1985. Growth patterns, sexual dimorphism and reproduction in African ruminants. *Afr. J. Ecol.* **23**: 75–87.
- Halliday, T.R. 1987. Physiological constraints on sexual selection. In *Sexual selection: testing the alternatives*. Edited by J.W.B. and M.B. Andersson. M.B. Interscience, Chichester, England. pp. 247–264.
- Hewison, A.J.M., Vincent, J.P., Bideau, E., Angibault, J.M., and Putman, R.J. 1996. Variation in cohort mandible size as an index of roe deer (*Capreolus capreolus*) densities and population trends. *J. Zool. (Lond.)*, **239**: 573–581.
- Hogg, J.T., Hass, C.C., and Jenni, D.A. 1992. Sex-biased maternal expenditure in Rocky Mountain bighorn sheep. *Behav. Ecol. Soc.* **31**: 243–251.
- Houston, D., and Shine, R. 1993. Sexual dimorphism and niche divergence: feeding habits of the Arafura filesnake. *J. Anim. Ecol.* **62**: 737–748.
- Hudson, J., and White, R.G. 1985. Bioenergetics of wild herbivores. CRC Press Inc., Boca Raton, Fla.
- Iverson, J.B. 1985. Geographic variation in sexual dimorphism in the mud turtle *Kinosteron hirtipes*. *Copeia*, 1985: 388–393.
- Jorgenson, J.T., Festa-Bianchet, M., Lucherini, M., and Wishart, W.D. 1993a. Effects of body size, population density, and maternal characteristics on age at first reproduction in bighorn ewes. *Can. J. Zool.* **71**: 2509–2517.

- Jorgenson, J.T., Festa-Bianchet, M., and Wishart, W.D. 1993b. Harvesting bighorn ewes: consequences for population size and trophy ram production. *J. Wildl. Manag.* **57**: 429–435.
- Jorgenson, J.T., Festa-Bianchet, M., Gaillard, J.-M., and Wishart, W.D. 1997. Effects of age, sex, disease, and density on survival of bighorn sheep. *Ecology*, **78**: 1019–1032.
- Jorgenson, J.T., Festa-Bianchet, M., and Wishart, W.D. 1998. Effects of population density on horn development in bighorn rams. *J. Wildl. Manag.* **62**: 1011–1020.
- Kie, J.G., and Bowyer, R.T. 1999. Sexual segregation in white-tailed deer: density-dependent changes in use of space, habitat selection, and dietary niche. *J. Mammal.* **80**: 1004–1020.
- Klein, D.R. 1981. The problems of overpopulation of deer in North America. *In* Problems in management of locally abundant wild mammals. *Edited by* P.A. Jewell and S. Holt. Academic Press, New York. pp. 119–127.
- Leberg, P.L., and Smith, M.H. 1993. Influence of density on growth of white-tailed deer. *J. Mammal.* **74**: 723–731.
- Le Boeuf, B.J. 1974. Male–male competition and reproductive success in elephant seals. *Am. Zool.* **14**: 167–195.
- Lindström, J. 1999. Early development and fitness in birds and mammals. *Trends Ecol. Evol.* **14**: 343–348.
- McAdam, A., and Millar, J.S. 1999. The effects of dietary protein content on growth and maturation in deer mice. *Can. J. Zool.* **77**: 1822–1828.
- Oldham, J.M., Kirton, A.H., and Bass, J.J. 1999. Compensatory growth in lambs undernourished from birth. *Proc. N.Z. Soc. Anim. Prod.* **59**: 111–113.
- Pérez-Barberia, F.J., and Gordon, I.J. 1998. The influence of sexual dimorphism in body and mouth morphology on diet selection and sexual segregation in cervids. *Acta Vet. Hung.* **46**: 357–367.
- Portier, C., Festa-Bianchet, M., Gaillard, J.-M., Jorgenson, J.T., and Yoccoz, N.G. 1998. Effects of density and weather on survival of bighorn sheep lambs (*Ovis canadensis*). *J. Zool. (Lond.)*, **245**: 271–278.
- Ralls, K. 1976. Mammals in which females are larger than males. *Q. Rev. Biol.* **51**: 245–276.
- Ralls, K. 1977. Sexual dimorphism in mammals: avian models and unanswered questions. *Am. Nat.* **111**: 917–938.
- Réale, D., and Boussès, P. 1995. Effects of ewe age and high population density on the early nursing behaviour of mouflon. *Ethol. Ecol. Evol.* **7**: 323–334.
- Réale, D., Boussès, P., and Chapuis, J.-L. 1999. Nursing behaviour and mother–lamb relationships in mouflon under fluctuating population densities. *Behav. Processes*, **47**: 81–94.
- Ruckstuhl, K.E. 1998. Foraging behaviour and sexual segregation in bighorn sheep. *Anim. Behav.* **56**: 99–106.
- Sæther, B.-E., and Heim, M. 1993. Ecological correlates of individual variation in age at maturity in female moose (*Alces alces*): the effects of environmental variability. *J. Anim. Ecol.* **62**: 482–489.
- Sams, M.G., Lochmiller, R.L., Qualls, C.W.J., and Leslie, D.M.J. 1998. Sensitivity of condition indices to changing density in a white-tailed deer population. *J. Wildl. Dis.* **34**: 110–125.
- Sinclair, A.R.E. 1989. Population regulation in animals. *In* Ecological concepts. *Edited by* J.M. Cherrett. Blackwell Scientific Publications, Oxford. pp. 197–241.
- Skogland, T. 1983. The effects of density dependent resource limitation on size of wild reindeer. *Oecologia*, **60**: 156–168.
- Skogland, T. 1990. Density dependence in a fluctuating wild reindeer herd; maternal vs. offspring effects. *Oecologia*, **84**: 442–450.
- Slatkin, M. 1984. Ecological causes of sexual dimorphism. *Evolution*, **38**: 622–630.
- Sokal, R.R., and Rohlf, F.J. 1997. Biometry: the principles and practice of statistics in biological research. W.H. Freeman and Co., New York.
- Solberg, E.J., and Sæther, B.-E. 1994. Male traits as life-history variables: annual variation in body mass and antler size in moose (*Alces alces*). *J. Mammal.* **75**: 1069–1079.
- SPSS Inc. 1997. SPSS 8.0, version for PC. SPSS Inc., Chicago.
- Stamps, J.A., Losos, J.B., and Andrews, R.M. 1997. A comparative study of population density and sexual size dimorphism in lizards. *Am. Nat.* **149**: 64–90.
- Stevenson, I.R., and Bancroft, D.R. 1995. Fluctuating trade-offs favour precocial maturity in male Soay sheep. *Proc. R. Soc. Lond. B Biol. Sci.* **262**: 267–275.
- Teather, K.L., and Weatherhead, P.J. 1989. Sex-specific mortality in nestling great-tailed grackles. *Ecology*, **70**: 1485–1493.
- Toïgo, C., Gaillard, J.-M., and Michallet, J. 1999. Cohort affects growth of males but not females on alpine ibex (*Capra ibex ibex*). *J. Mammal.* **80**: 1021–1027.
- Trivers, R.L. 1972. Parental investment and sexual selection. *In* Sexual selection and the descent of man. *Edited by* B. Campbell. Aldine Press, Chicago. pp. 136–179.
- Verme, L.J. 1963. Effects of nutrition on growth of white-tailed deer fawns. *Trans. N. Am. Wildl. Nat. Res. Conf.* **24**: 431–443.
- Vincent, J.P., Bideau, E., Hewison, A.J.M., and Angibault, J.M. 1995. The influence of increasing density on body weight, kid production, home range and winter grouping in roe deer (*Capreolus capreolus*). *J. Zool. (Lond.)*, **236**: 371–382.