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SEX-SPECIFIC GROWTH IN ALPINE CHAMOIS

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Studying between-sex differences in body growth has strong implications for understanding life-history tactics of animals. We used age and carcass mass data from 2,312 female and 2,622 male alpine chamois (*Rupicapra rupicapra*) harvested in the French Alps to model the sex-specific body growth patterns of this species. Males were heavier (asymptotic body mass: 29.6 kg) than females (22.3 kg), with an adult sexual size dimorphism of 32.4%. Sexual size dimorphism originated from both differences in body growth after 1.5 years of age and differences in length of the growth period. Females reached asymptotic body mass almost 3 years earlier (3.5 years) than males (6.2 years). We also found that females 1st reproduced before achieving asymptotic growth, at 78% of their asymptotic body mass. Between-sex differences in growth patterns in this species are most likely due to stronger selection pressure for larger size in males than in females due to intrasexual competition.

Key words: Bauges, carcass mass, French Alps, life-history tactic, monomolecular model, *Rupicapra rupicapra*, sexual size dimorphism

An individual's contribution to future generations is expected to depend on the size and age at which the animal matures (Stearns 1992). In ungulates, fecundity of females is strongly influenced by body mass so that fast-growing females reproduce earlier in life than slow-growing females (Albon et al. 1983; Gaillard et al. 1992; Garel et al. 2005; Reimers 1983; Sæther and Haagenrud 1983; Sadleir 1969). For males of polygynous species, access to females depends on intrasexual competition and body size positively influences male reproductive success (Clutton-Brock et al. 1988; McElligott et al. 2001; Skogland 1989). In both sexes, the duration and the rate of growth are thus closely linked to lifetime reproductive success (Stearns 1992).

Because resources are generally limiting, energy must be allocated to competing functions (Cody 1966; Williams 1966). For instance, growth is often traded for reproduction (Stearns 1992). Several empirical studies have shown that reproducing early has a negative influence on body growth in both males (Garel et al. 2006; Mysterud et al. 2003) and females (Clutton-Brock et al. 1983; Green and Rothstein 1991; Sand 1998). Growth patterns also covary with mortality patterns (Stearns and Koella 1986) independently of body size (Pontier et al. 1993), and are thus expected to reflect the selective pressures acting on animals (Sibly et al. 1985).

In polygynous species, males and females exhibit widely divergent tactics of growth in relation to reproduction, generally leading to marked sexual dimorphism in size (sexual size dimorphism [SSD]—Jarman 1983; Ralls 1977). Such tactics reflect intrasexual selection among males for access to females and competitive selection on females for access to food (Andersson 1994). Consequently, sexual selection often favors larger males through rapid early growth and delayed maturation, whereas females are selected to mature early at the expense of structural size (Andersson 1994; Ralls 1977).

Studies on how growth patterns vary among age and sex classes in dimorphic species (e.g., Festa-Bianchet et al. 1996; Garel et al. 2006; Isaac 2006; Leader-Williams and Ricketts 1982; Leberg and Smith 1993; Sweitzer and Berger 1997) therefore have strong implications for the understanding of life-history evolution (Stearns 1992; Stearns and Koella 1986) and SSD (Stamps 1993). In this study, we used data on body mass of alpine chamois (*Rupicapra rupicapra*) harvested in

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the French Alps to model patterns of sex-specific growth in this polygynous ungulate. Although growth patterns have been previously investigated for this species (Bassano et al. 2003; Schröder 1971), previous studies have used descriptive statistics instead of specific growth modeling and have relied on smaller sample sizes and on a more restricted set of age classes than the present study.

In mammals, growth patterns have often been modeled using a family of growth equations (Gaillard et al. 1997; Zullinger et al. 1984). Because alpine chamois are precocious and juveniles have a much higher mortality than adults (Henderson and Clarke 1986; Loison et al. 1999), leading to the expectation of a high postnatal growth rate (Case 1978), growth should be well fitted by the monomolecular model that includes a decelerating growth rate from birth onward (Gaillard et al. 1997). We expected male chamois to be larger and to have a higher rate of growth than females, as previously suggested for this species (Bassano et al. 2003; Schröder 1971). Moreover, in polygynous ungulates, selective pressures on size and growth rate are expected to be stronger on males than on females (Andersson 1994; Clutton-Brock et al. 1988). We also investigated whether the age at 1st reproduction in females (1.5 years of age in this population—Pioz et al. 2008) corresponded to the age at which females have reached about 80% of their adult body mass, as observed in other large herbivores (Gaillard et al. 2000).

MATERIALS AND METHODS

Study area.—The study was conducted in the eastern part of the Bauges massif (45°40′N, 6°13′E, 350–2,217 m above sea level), in the northern French Alps. The study site encompasses the national game and wildlife reserve of the Bauges (5,205 ha), occupying the highest part of the massif, and adjacent areas (5,800 ha). The Bauges range is a typical subalpine massif of 86,000 ha covered by forests up to about 1,500 m, and by cliffs and open grasslands between 1,700 m and 2,200 m. The chamois population has been monitored by the Office National de la Chasse et de la Faune Sauvage since 1977 in collaboration with local hunting managers. Hunting occurred both within and outside the reserve and was based on quotas. During the study period (1977–2007) the population increased from ≥ 600 chamois (in 1979) to $\geq 1,400$ chamois (in 2004), corresponding to a density range of ≥ 6–15 chamois/km^2.

Data.—We used data from chamois shot both within and outside the wildlife reserve (n = 4,934) during the hunting seasons from early September to late February. Hunters recorded date, age, sex, and carcass mass. Data sampling was in accordance with guidelines approved by the American Society of Mammalogists (Gannon et al. 2007). Age determination was based on counts of horn growth annuli (Schröder and Von Elsner-Schak 1985). Age was measured in years assuming that chamois were born on 1 June (mean birth date in this population [see Loison 1995:99]). Shooting date was transformed to Julian date with day 1 beginning on 1 September except in leap years (years with 366 days) when 1 September was actually day 2 to account for the difference of 1 day regarding the last hunting season. Measurements of carcass mass (± 100–500 g) were made in 3 ways, either as complete carcass mass (n = 301), partially eviscerated carcass mass (minus digestive tract; n = 2,255), or eviscerated carcass mass (minus all internal organs, blood, and digesta; n = 2,657). Using chamois for which at least 2 different measures of mass were taken (± 100 g), we examined the relationships between eviscerated carcass mass (most frequently measured) and the 2 other masses, and transformed all other measures into eviscerated carcass mass (Solberg et al. 2008).

Before estimating body growth, we 1st adjusted for variation in shooting date because body mass of chamois is expected to change during the hunting season (Schröder 1971). We split the data into age and sex classes. We pooled ages for which <40 carcass masses were available (animals older than 9 years in males and animals older than 13 years in females). We used additive models (Wood 2006) to account for potential nonlinear relationships between carcass mass and shooting date, and adjusted the mass to 15 October (4.5 months after 1 June). Fifteen October corresponded to the median shooting date and to the start of the prerut period (Loison 1995) just before adult males begin to loose weight (present study; see also Schröder 1971). Therefore, SSD was expected to peak on 15 October. Animals killed during the hunting season were 0.38, 1.38, … years of age. We used the exact value to model growth and half-age classes (e.g., 0.5, 1.5, … years) in the text.

Statistical analysis.—We adjusted carcass mass data to a monomolecular growth model (France et al. 1996). We measured sex-specific differences using the following equation:

$$W_t = \gamma - (\gamma - W_0)e^{-\beta t}, \qquad (1)$$

where W_t is the carcass mass (kg) at time t (in years), γ is the asymptotic carcass mass, β describes the decay in the growth rate, and W_0 is the carcass mass at t = 0 (i.e., carcass mass at birth), which was set to a fixed value of 1.7 kg, that is, 72% of the live birth mass (~2.4 kg) according to the relationship between eviscerated and complete carcass mass (see ''Results''). We predicted live birth mass from 18 newborns (ages ranging from 1 to 10 days) trapped in the field with aid of a dog and 2 captive animals with repeated measurements. We estimated the parameters of the monomolecular model using nonlinear least-square estimates (Bates and Watts 1988). We used the age when 99% of γ was achieved (age$_{99\%}$) as an estimate of the length of the period of active body growth (Garel et al. 2006; Sand et al. 1995).

We computed confidence intervals (2.5% and 97.5% quantiles) of growth parameters by simulating 1,000 bootstrap replicates from the fitted models. We simulated new data by assuming, for a given sex j and age k, that an observation i is the random realization of a normal distribution of mean μ_{jk} and standard deviation σ_{jk}. We only simulated data for sample size ≥ 15 in a given sex and age class. Mean values of γ and β were computed from these bootstrap replicates to assess to what extent least-square estimates were biased (we assessed

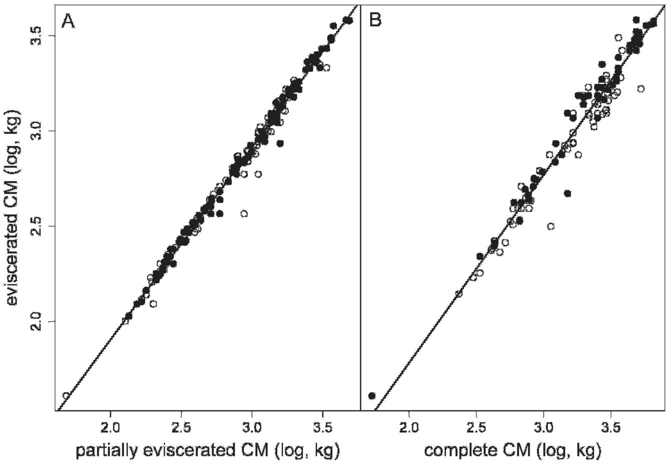

FIG. 1.—Isometric relationships between eviscerated carcass mass (CM, kg, log-transformed) and A) partially eviscerated carcass mass (kg, log-transformed) and B) complete carcass mass (kg, log-transformed) in harvested alpine chamois (*Rupicapra rupicapra*) in the Bauges mountain range, French Alps (filled circles = males; open circles = females). Plain lines were estimated by linear regressions (A: intercept = −0.112 $[-0.154; -0.070]_{95\%}$, slope = 1.008 $[0.994; 1.023]_{95\%}$, $n = 209$, $r = 0.995$; B: intercept = −0.357 $[-0.488; -0.226]_{95\%}$, slope = 1.008 $[0.968; 1.048]_{95\%}$, $n = 121$, $r = 0.977$).

bias from, e.g., $\gamma_{sim} - \gamma$ [Efron and Tibshirani 1993]). We performed all analyses using R 2.6.0 (R Development Core Team 2007).

RESULTS

There were strong positive relationships between eviscerated carcass mass and both partially eviscerated carcass mass (Fig. 1A) and complete carcass mass (Fig. 1B). In autumn, eviscerated carcass mass constituted about 92% of partially eviscerated carcass mass and 72% of complete carcass mass. Given asymptotic body masses estimated from the monomolecular models (Table 1), these results indicated that adult live body mass on 15 October was about 31.0 kg (22.3 kg mean eviscerated carcass mass/0.72 conversion factor for full carcass mass) in females and 41.1 kg (29.6 kg/0.72) in males. Estimations of live body mass for females were in agreement with observations of adult females (>3 years) trapped and weighed in September (30.9 kg, $n = 27$).

When the parameter was not fixed, the carcass mass at birth predicted by the monomolecular model was close to 7.3 kg in both sexes, that is, far from the biological observations (~1.7 kg). This result probably arose due to the lack of data during the early growth period (before 4.5 months) and led us to fix this parameter in the model. Estimates of growth parameters (Table 1) did not vary in both sexes by more than 0.6% and 6.5% for γ and β, respectively, when birth mass varied from 1 kg to 2.4 kg compared to a reference value of 1.7 kg. The model underestimated body mass in 0.5-year-old males (average residual: 3.2 kg). However, the overall fit of the growth curves to the data was satisfactory given the simple form (3 parameters) of the model (Figs. 2A and 2B).

Monomolecular models indicated that males were heavier and experienced active growth in body mass for a longer period than females (Table 1; Figs. 2A and 2B). Parameter estimates did not show any bias (absolute differences between least-square estimates and bootstrap estimates were <0.01 for all parameters). Adult males weighed approximately 32.4% more than adult females and reached 99% of their adult body mass almost 3 years later than females. Old age classes of females were lighter than expected from the monomolecular model (Fig. 2A; females older than 15 years: 8 positive residuals, 20 negative residuals, 1-sided binomial test, $P = 0.02$).

According to the raw data, SSD was marked from 2.5 years of age onward (mean ± *SD*; males = 23.3 ± 3.5 kg; females = 20.9 ± 2.8 kg; $n = 425$, $t = 7.5$, $d.f. = 302.7$, $P < 0.001$, SSD = 11.4%), although between-sex differences in carcass mass were already apparent at 0.5 years of age (males = 11.6 ± 2.0 kg; females = 11.1 ± 2.2 kg; $n = 1{,}096$, $t = 4.3$, $d.f. = 1{,}090.9$, $P < 0.001$, SSD = 4.8%) and 1.5 years (males = 18.5 ± 2.9 kg; females = 17.5 ± 2.6 kg; $n = 1{,}213$, $t = 6.4$, $d.f. = 1{,}157.3$, $P < 0.001$, SSD = 5.9%). At the end of the period of active growth in body mass of females (3.5 years; Table 1), SSD was equal to 21.7% (raw data at 3.5 years: males = 26.7 ± 3.7 kg; females = 21.9 ± 3.0 kg). In females, carcass mass at 1.5 years of age (age at primiparity for this population—Pioz et al. 2008) corresponded to 78% of asymptotic carcass mass estimated from the monomolecular model (Table 1).

DISCUSSION

Results from our study were in accordance with previous research on alpine chamois in that adult males were

TABLE 1.—Sex-specific parameters computed from monomolecular growth curves fitted to carcass mass data of harvested alpine chamois (*Rupicapra rupicapra*) in the Bauges massif, French Alps, period 1977–2007 (see Figs. 2A and 2B and ''Materials and Methods'' for details).

		Sex	
Biological meaning	Parameters	Females	Males
Model characteristics	n	2,312	2,622
	r^2	0.71	0.77
Adult carcass mass	γ	22.3 kg $[22.2; 22.5]_{95\%}$	29.6 kg $[29.3; 29.9]_{95\%}$
Decay rate in carcass growth	β	1.31 $[1.27; 1.37]_{95\%}$	0.73 $[0.71; 0.76]_{95\%}$
Time of active body growth	$Age_{99\%}$	3.5 years $[3.3; 3.6]_{95\%}$	6.2 years $[6.0; 6.4]_{95\%}$

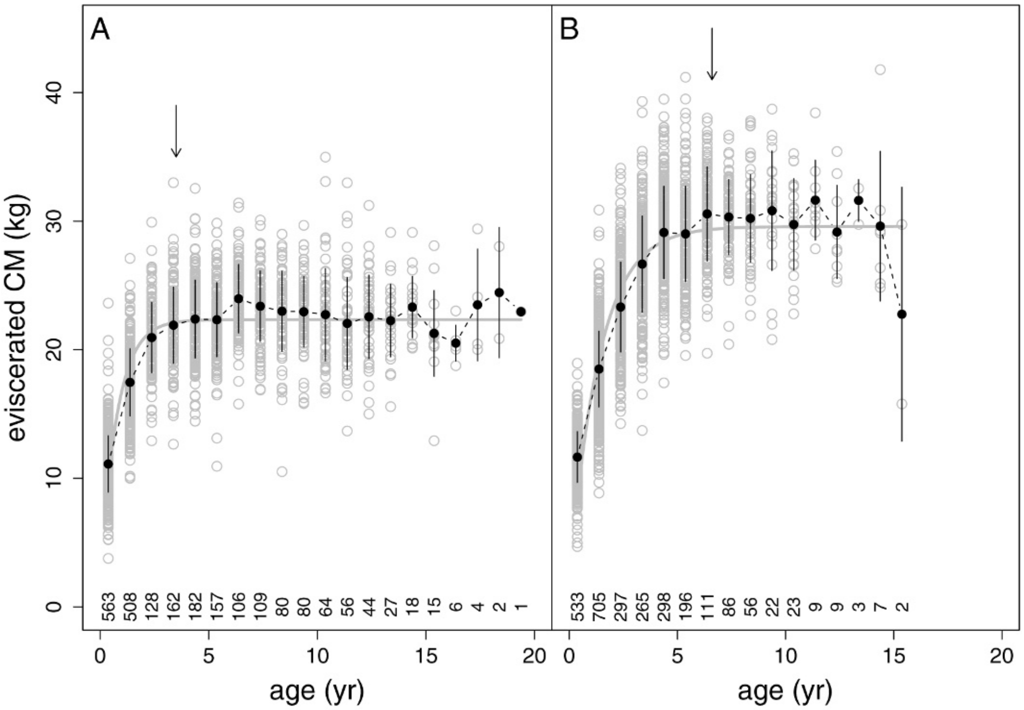

FIG. 2.—Growth pattern of harvested alpine chamois (*Rupicapra rupicapra*; A: females $n = 2{,}312$; B: males $n = 2{,}622$) in the Bauges mountain range, French Alps, period 1977–2007. Plain line corresponds to the monomolecular growth curve fitted to carcass mass data (see Table 1 for parameter estimates). Deleting the very low body mass value of a male of 15.5 years has no effect on the fit of male growth curve. Filled black circles correspond to mean values (± *SD*). Arrows indicated age at which animals reach 99% of the asymptotic body mass estimated from the growth curve (i.e., end of the period of active body growth). Numbers below the curves correspond to the sample size for each age class.

significantly heavier than adult females (SSD of 32.4%—Bassano et al. 2003; Christie 1964; Schröder 1971; Storch 1989). Our analyses further indicated that SSD increased with age up to about 6 years and was due to the combination of a higher rate of growth and a longer period of growth by male chamois (Schröder 1971; see also Garel et al. 2006; Houston et al. 1989; Jarman 1983; Leberg and Smith 1993). As reported in other ungulates with higher levels of SSD (Clutton-Brock et al. 1982; Fandos and Vigal 1988; Leader-Williams and Ricketts 1982), we observed an early development of SSD from the age of 2.5 years onward (Figs. 2A and 2B). Similarly, the duration of active growth in body mass among males was close to that of larger and more sexually dimorphic ungulates (Festa-Bianchet et al. 1996; Garel et al. 2006). Between-sex differences in body growth were only marked in alpine chamois >1.5 years, which corresponded to age at 1st reproduction of females (Pioz et al. 2008). Both sexes thus had relatively similar growth rate during their first 2 years of life, whereas in bighorn sheep (*Oris canadensis*) between-sex differences in growth became marked within several months of birth (Festa-Bianchet et al. 1996). This finding might suggest a relatively more conservative growth tactic among male alpine chamois compared to bighorn sheep (Festa-Bianchet et al. 1996). For male alpine chamois, survival to old age rather than a risky growth tactic would thus be the most important factor affecting reproductive success. Finally, although the most reliable way to study senescence patterns is to achieve longitudinal data (Nussey et al. 2008), our results also provide evidence of declining body mass at old ages in female chamois (see Schröder [1971] for males).

The sex-specific differences in body growth observed in our study may have been due to sex-specific differences in resource allocation for growth and reproduction. In both males and females natural selection and sexual selection are expected to favor rapid development to sexual maturity (Andersson 1994; Fisher 1930). Among female ungulates, sexual maturity depends closely on reaching a threshold body mass (reviewed by Gaillard et al. 2000), after which energy is primarily allocated to reproduction (Clutton-Brock et al. 1982). As reported for other species of large ungulates (Gaillard et al. 2000), this threshold in body mass corresponded to ~80% of asymptotic carcass mass of female alpine chamois, indicating that female chamois begin reproducing before achieving asymptotic growth. In contrast, in social systems that promote intrasexual competition for mates (Weckerly 1998), males tend to delay maturity because early reproduction is likely to have negative effects on body growth (Garel et al. 2006; Mysterud et al. 2003). Males are expected to benefit by growing as fast and as large as possible to ensure early access to estrous females (Andersson 1994), thereby gaining mass and experience before allocating resources to reproduction (Stearns 1992). Accordingly, examination of field data indicates that the majority of male alpine chamois in this population 1st became reproductively active at ~4.5 years of age, when they had achieved 96% of their asymptotic body mass (Table 1).

Differences in growth tactics between sexes also involve differences in how males and females allocate resources between growth and reproduction. Although females can allocate resources to growth or to reproduction by varying their age at primiparity, males are more limited in redirecting resources to growth from reproduction (Festa-Bianchet et al. 2000). In such conditions, SSD is expected to be strongly dependent on growth of males and, thereby, on any factor acting upon it. Several studies have shown that increasing population density negatively affects SSD, likely because of competition for resources (Leberg and Smith 1993; Leblanc et al. 2001; Pépin et al. 1996; Solberg and Sæther 1994), whereas favorable environmental conditions lead to increased SSD (Garel et al. 2006). However, measuring and comparing SSD remains a challenging task for ecologists. Males and females present differences in the timing and magnitude of seasonal variation in body mass related to their reproductive cycle (Festa-Bianchet et al. 1996; Leader-Williams and Ricketts 1982). Most of the reproductive effort of polygynous males occurs during a relatively short rutting season, during which feeding activities are usually sacrificed for mating activities (Bobek et al. 1990; McElligott et al. 2003; Mysterud et al. 2005; Willisch and Ingold 2007). In contrast, reproductive effort among females is spread over several months of gestation and lactation (Sadleir 1969). Females therefore experience less intra-annual variation in body mass than do males (Leader-Williams and Ricketts 1982; Schröder 1971). Hence, adjusting carcass mass after the rutting period (e.g., at 15 January) would have led to a much lower SSD (6.5%) than when carcass mass was adjusted before the onset of decrease in body condition of adult males. Measuring SSD before the mating period could be the best alternative because SSD is at its maximum, providing more power to detect intra- and interspecific variation. To investigate factors affecting SSD, standardization across studies is required. To achieve this goal we encourage ecologists studying growth patterns to use growth models (Zullinger et al. 1984), and to control for any factors that may confound age-dependent changes in body mass. These aspects have not been fully investigated in previous studies on alpine chamois, thereby limiting opportunities for between-study comparisons. These are important issues for studies in evolutionary ecology because growth patterns are crucial components for the evolution of reproductive patterns among organisms (Stearns and Koella 1986).

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