Seasonal changes in sexual size dimorphism in northern chamois

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Abstract

In many polygynous mammals, sexual size dimorphism (SSD) is thought to have evolved through sexual selection, because larger males prevail in male–male combat and secure access to estrous females. SSD is often correlated with higher age-specific mortality of males than of females, possibly because males have higher nutritional requirements and riskier growth and reproductive tactics. In adult chamois *Rupicapra rupicapra*, sexual dimorphism in skeletal size was about 5%, but dimorphism in body mass was highly seasonal. Males were about 40% heavier than females in autumn but only 4% heavier in spring. For a given skeletal size, males were heavier than females only in autumn. Chamois sexual dimorphism appears mainly due to greater summer accumulation of fat and muscle mass by males than by females. Male mass declines rapidly during the rut. Limited dimorphism in skeletal size combined with substantial but seasonal dimorphism in mass has not been reported in other sexually dimorphic ungulates. Seasonal changes in mass allow males to achieve large size for the rut by accumulating body resources during summer. The use of these resources over the rut may reduce mortality associated with sustaining a large size over the winter.

Introduction

Sexual size dimorphism (SSD) is common in mammals (Andersson, 1994), where males are often larger than females. The most dimorphic groups are the Macropodidae, Primates, Mustelidae, Pinnipedia and Artiodactyla (Weckerly, 1998). Typically, SSD in mammals is thought to arise through sexual selection (Darwin, 1871). In polygynous systems, males should be under stronger selection than females for large body and weapon size, because defeating other males leads to very high fitness returns (Coltman *et al.*, 2002; Kruuk *et al.*, 2002; Mainguy *et al.*, 2009). As a consequence, young males often have higher growth rates than young females, tend to accumulate fewer fat reserves and suffer higher age-specific mortality, especially during periods of resource scarcity (Clutton-Brock, Albon & Guinness, 1985; Toïgo & Gaillard, 2003). The interspecific relationship between sexual dimorphism and the level of polygyny, however, has been questioned (Isaac, 2005). Several other factors are correlated with dimorphism, such as, body size (Loison *et al.*, 1999*b*), habitat type (Jarman, 1974; Pérez-Barberia, Gordon & Pagel, 2002), latitude (Quin, Smith & Norton, 1996; Storz *et al.*, 2001) and the distribution and abundance of resources (Weckerly, 1998; Isaac & Johnson, 2003). An understanding of the factors affecting the relationship among SSD, sexual differences in survival and polygyny could shed light on the evolution of male reproductive strategies.

In large herbivores, SSD also appears to be affected by mating tactics (Clutton-Brock, 1989). In many bovids and cervids, where access to females depends mainly on male–male combat (Andersson, 1994), sexual dimorphism is very evident (Loison *et al.*, 1999*b*); but in some polygynous groups such as equids or camelids, dimorphism is weak, possibly because male–male competition depends on speed, agility and aggressiveness, which may not be dependent on body size (Linklater, 2000).

Sexual dimorphism in size is often assumed to correlate with sexual differences in survival. Male survival is thought to be reduced by two main causes (Toïgo & Gaillard, 2003). First, polygyny may directly decrease male survival, if males adopt a riskier growth strategy than females to gain and maintain large body and weapon size (Kruuk *et al.*, 2002). Second, because males are larger than females, they have greater nutritional requirements (Clutton-Brock *et al.*, 1985). For temperate ungulates, a decrease in body condition after the rut and at the beginning of winter may reduce male survival (Festa-Bianchet, Gaillard & Côté, 2003; Forsyth *et al.*, 2005). However, in some species with limited polygyny and SSD, such as roe deer *Capreolus capreolus* (Gaillard, Delorme & Jullien, 1993; Vanpé *et al.*, 2008), males show substantially lower survival than females, similar to ungulates with much greater sexual dimorphism (Loison *et al.*, 1999*a*).

SSD is correlated with sex-specific body growth patterns (Festa-Bianchet *et al.*, 1996), energy allocation trade-offs

(Clutton-Brock, Guinness & Albon, 1982; Festa-Bianchet, Gaillard & Jorgenson, 1998) and mating tactics (Clutton-Brock, 1989). It may also lead to age-specific sexual differences in survival (Clutton-Brock *et al.*, 1985; Promislow, 1992) and in the variance of reproductive success among individuals (Vanpé *et al.*, 2008), although environmental conditions and mating system may be the ultimate causes of these correlations (Loison *et al.*, 1999a; Toïgo & Gaillard, 2003). Previous studies, however, have generally assumed that sexual differences in mass are associated with differences in structural size, and little attention has been paid to the possibility that dimorphism may partly originate from size-independent differences in mass, through sex-specific seasonal or permanent accumulation of muscle mass or fat deposits (Soderquist, 1995). These differences are important because they may affect both male reproductive tactics and the potential costs of sexual dimorphism.

We studied two populations of northern chamois *Rupicapra rupicapra* to examine how age-specific SSD in body mass and skeletal size varied according to season. Previous reports (Loison *et al.*, 1999a; Bassano, Perrone & von Hardenberg, 2003; Garel *et al.*, 2009) suggest that males are 20–30% heavier than females, but most data were collected in summer–autumn. In the closely related Pyrenean chamois *Rupicapra pyrenaica*, no mass dimorphism was evident during winter (Crampe *et al.*, 1997). Garel *et al.* (2009) reported that SSD in their study population of northern chamois dropped from 32 to 6% from September to January. We expected to find weaker mass dimorphism in spring than in autumn, because studies of other ungulates report that larger individuals lose more mass over winter (Pelletier *et al.*, 2007). In addition, we sought to examine whether SSD in chamois reflected seasonal changes in resource accumulation rather than differences in skeletal size.

Materials and methods

Study area

We studied two chamois populations: Alpi Marittime Natural Park and the neighboring Comprensorio Alpino Cuneo 4 (CN4), in the south-western Alps of Piedmont, Italy, near the border with France ($44°12'$N, $7°16'$E). In the Park, chamois were captured in April–May and released elsewhere in the Alps for reintroduction programs. In CN4, chamois were hunted from mid-September to late December with a pause between November 20 and December 4.

Both study areas have typical alpine habitat and rugged topography, with rocks and moraines covering 47% of the Park and 29% of CN4. Forests dominated by beech *Fagus sylvatica* at low elevation are replaced by mixed forest of conifers *Larix decidua* and *Picea abies* at higher elevations. Vegetation above tree line includes shrubs and alpine pastures.

Chamois data

For both, captured (323 females and 278 males) and harvested (677 females and 758 males) chamois, we noted sex, age, foot length, body mass (live for the Park and eviscerated or partially eviscerated in CN4) and date of capture or death. Age can be determined with precision by the number of horn annuli (Schroder & Elsner-Schack, 1985). Most chamois in this area are born in May, therefore they were close to their approximate birth dates when captured in the Park in April–May, and about 6 months older during the fall hunting season. Because some harvested chamois were eviscerated and others partially eviscerated (with heart, liver and lungs), we first estimated the age-specific difference in mass in the two groups, then subtracted this difference from partially eviscerated mass to estimate eviscerated mass (Garel *et al.*, 2009). Management plans in CN4 aim to harvest about 10% of chamois counted during ground surveys each spring. Because ground surveys inevitably underestimate population size, the actual harvest rate is probably lower; therefore, it is unlikely that changes in body mass over the hunting season could be due to selective harvest.

Statistical analysis

We used a multiple regression analysis to compare hind foot length, as an index of skeletal size (Rughetti & Festa-Bianchet, 2010), according to age, sex and population. After accounting for age, we compared body mass of males and females in both populations using ANOVA. We used an ANCOVA to describe mass as a function of hind foot length with age and sex as covariates. We log-transformed hind foot length and body mass because of their allometric relationship and removed three outliers (0.8% of the dataset). For this analysis, we fitted a model for each population and for CN4 we only considered chamois harvested during the first 50 hunting days after the season opened on September 15, before males started to rapidly lose mass (see "Results"). We quantified sexual dimorphism as the ratio of average male over female mass. We used regression to model variation in mass separately for males and females according to harvest date, because changes in mass over time differed according to sex (see "Results"). A Shapiro–Wilk test confirmed that after accounting for sex and age, body mass of Park chamois was normally distributed ($W = 0.999$, $P = 0.98$). In CN4 females, body mass was normally distributed after accounting for age ($W = 0.997$, $P = 0.34$); and the same was true for males after accounting for age and harvest date ($W = 0.996$, $P = 0.21$). To select final models, we started with a full model including all variables of interest and their interactions and simplified it using a stepwise procedure based on the Akaike Information Criterion with second-order adjustment (AIC_c) to correct for small-sample bias (Burnham & Anderson, 2002). When the difference between two models was <2 AIC_c units, we selected the most parsimonious model (Burnham & Anderson, 2002). All analyses were conducted in R (http://www.r-project.org). All *P*-values were considered significant at a level of 0.05. All means are presented as ± 1 SD, except regression coefficients for which SE are used.

Results

In early autumn, male chamois were about 40% heavier than females (Figs 1 and 2). After the rut, male body mass decreased, whereas female mass did not change (Fig. 2). By early winter, males and females had similar body mass (Fig. 2).

Sex and population accounted respectively for 25 and 7% of the variance in hind foot length in adult chamois (4 years and older) (Table 1). In CN4, foot length was longer than in the Park but the difference was only 3.3% in males and 2.6% in females. Sexual dimorphism in hind foot length was 1.05 in CN4 (male = 35.8 ± 1.3, female = 34.1 ± 1.3) and 1.04 in the Park (male = 34.6 ± 1.6, female = 33.1 ± 1.4). Within each population, males were larger than females but the difference in hind foot length was $<5\%$. No sexual dimorphism in mass was evident in the Park in spring (Fig. 1) after accounting for age (ANOVA, $P = 0.44$). Mass dimorphism for chamois aged 4–10 years, however, was evident in CN4 in autumn (Fig. 1; average dimorphism over all ages: 1.41 ± 0.04). After accounting for age, chamois aged 4 years and older captured in spring in the Park, exhibited no sex difference in the regression of mass on hind foot length (Table 2, Fig. 3). For the same hind foot length, however, males harvested in autumn in CN4 were about 1.4 times heavier than females (Table 2, Fig. 4).

Mass of adult males increased from September 15 to October 15, when 70% of males were harvested (mass = age + date; age: slope = -0.192 ± 0.066, $P = 0.004$; date: slope = 0.052 ± 0.026, $P = 0.046$) and was not affected by the interaction between age and harvest date (mass = age + date vs. mass = age $\times$ date, $\Delta AIC_c = 1.566$). Male mass peaked around October 12 (Fig. 2), then decreased (Table 3). In the last 2 weeks of December, males were about 35% lighter than those harvested between October 9 and 15 and their mass did not differ from that of

females harvested at the same time (ANOVA, $P = 0.12$, 14 males, 40 females). Seasonal changes in adult male mass were independent of age (Table 4). The age of adult males was independent of harvest date (regression of age on date: slope = 0.009 ± 0.006, $P = 0.16$).

Females showed no change in mass over the hunting season (Table 3). About 70% of females were harvested during the first month of hunting. After accounting for age, horn length did not vary over the hunting season for either males aged 4 years and older (horn length = age + date; age: slope = 0.055 ± 0.026, $P = 0.03$; date: slope = -0.007 ± 0.005, $P = 0.18$) or females aged 3 years and older (age: slope = 0.262 ± 0.021, $P < 0.0001$; date: slope = -0.004 ± 0.006, $P = 0.47$).

Discussion

As suggested by Garel *et al.* (2009), SSD in adult Alpine chamois is almost entirely seasonal; males gain much more mass than females from late spring to early autumn, then lose it during autumn. Differences in skeletal size and in horn or body growth patterns between our two study populations were minor (Rughetti & Festa-Bianchet, 2010). Therefore, our results were not affected by the comparison of different populations. In CN4 by late December, males weighed the same as females, suggesting that by the following spring the near absence of mass dimorphism that we found in the Park population would also exist within the adjacent CN4 population.

Temporal changes in mass in CN4 population were not due to hunter selectivity. Neither age nor horn length of harvested males was related to harvest date, suggesting that the decrease in male mass in November–December was not due to selective removal of large males early in the season. In addition, the average mass of harvested males increased
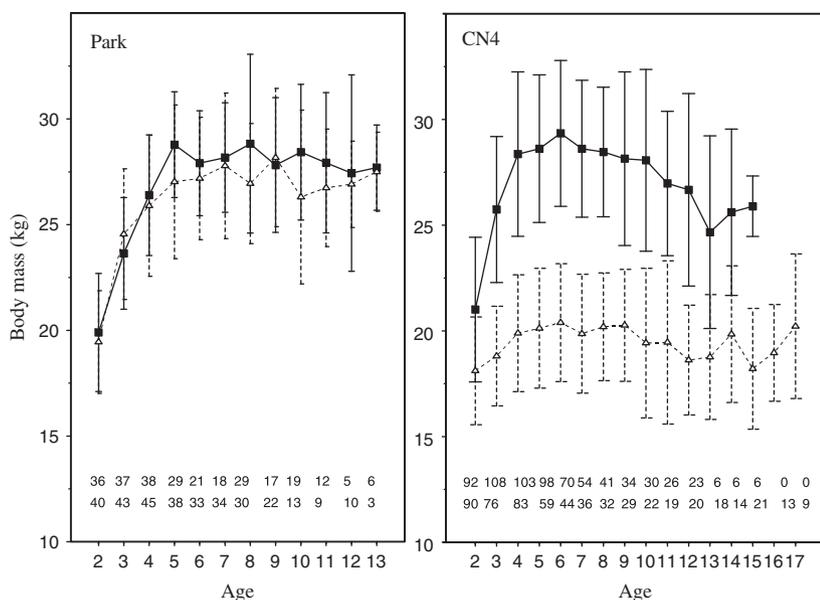

Figure 1 Park: age-specific mean live body mass ($\pm$ SD) for 323 females (dashed line and triangles) and 278 male chamois *Rupicapra rupicapra* (solid line and squares) captured in April–May 1992–2008 in the Alpi Marittime Natural Park, Italy. CN4: age-specific mean eviscerated body mass ($\pm$ SD) for 585 females (dashed line and triangles) and 697 male chamois (solid line and squares) harvested in Comprensorio Alpino Cuneo 4 during the first 50 hunting days (September 15 to November 4), Italy, 1996–2008. Numbers indicate sample sizes, with males over females.
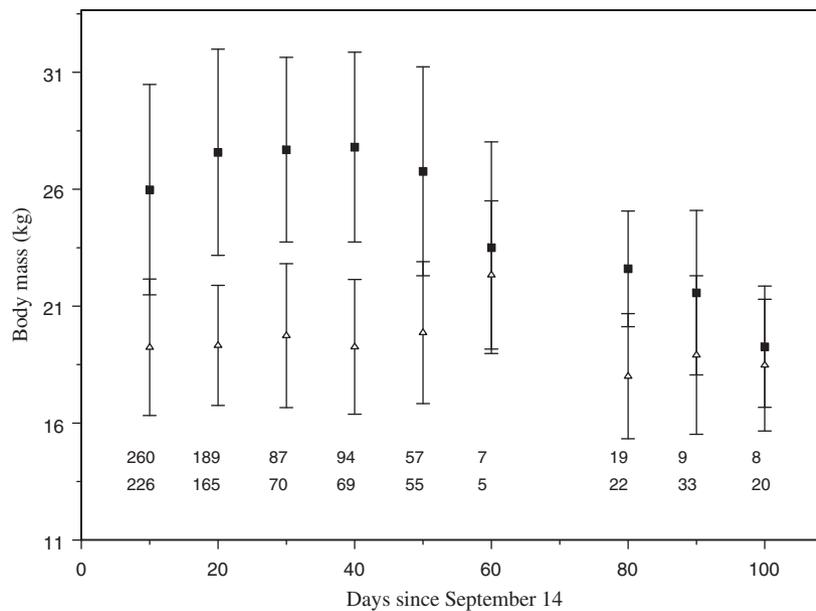
Figure 2 Eviscerated body mass averaged ($\pm$ SD) every 10 days over the hunting season for males (4 years and older, squares) and females (3 years and older, triangles) chamois *Rupicapra rupicapra* harvested in Comprensorio Alpino Cuneo 4, Italy, in September–December, 1996–2008. Numbers indicate sample sizes, with males over females.

Table 1 ANOVA table for hind foot length (cm) as a function of age (years), sex and population, for chamois aged 4 years and older harvested in the Comprensorio Alpino Cuneo 4 (CN4) from 1996 to 2008, or captured in the Alpi Marittime Natural Park from 1992 to 2008

	d.f.	Sum of squares	Pr(*F*)
Age	1	3.098	–
Sex (male)	1	992.526	–
Population	1	278.128	–
Age:sex (male)	1	19.514	0.0011
Age:population (CN4)	1	15.435	0.0037
Sex (male):population (CN4)	1	5.499	0.0827
Residuals	1458	2658.560	

Terms were added sequentially.

Table 2 ANCOVA of body mass (log transformed, kg) as a function of hind foot length (hfl; log transformed, cm), age (years), and sex for chamois *Rupicapra rupicapra* aged 4 years and older harvested in the Comprensorio Alpino Cuneo 4 from 1996 to 2008 (September 15 to November 4) or captured in the Alpi Marittime Natural Park in April–May from 1992 to 2008

Population	Coefficient	SE	Pr ($>|t|$)
Park			
hfl	1.560	0.182	–
Sex (male)	1.598	0.939	–
hfl:sex (male)	−0.460	0.266	0.08
CN4			
hfl	1.632	0.118	<0.000
Sex (male)	0.283	0.010	<0.000
Age	−0.006	0.001	<0.000

Model R^2: Park = 0.23, d.f. = 389; CN4 = 0.70, d.f. = 901.

over the first month of hunting (Table 3 and Fig. 2). Therefore, although harvested animals cannot be considered a random sample of the population, the changes in mass reflect actual seasonal variations.

We suspect that hunters seek chamois with longer horns, but our analysis suggests that they are unable to selectively remove most long-horned individuals of either sex in CN4, because horn length was independent of harvest date. In CN4 male, age-specific survival is independent of horn length (Rughetti & Festa-Bianchet, 2010), possibly because of the relatively light harvest rate.

Adult male chamois were 1.4 times heavier than females in autumn, but sexual mass dimorphism was only 1.04 and not significant in spring. Skeletal size dimorphism, measured by hind foot length, was <1.05 and was independent of population or season. The limited dimorphism in skeletal size and the absence of dimorphism in mass in spring suggest that the substantial dimorphism during the rut is due to sexual differences in seasonal mass gain, which may involve

the accumulation of both body fat and muscle tissue. Other species of ungulates may have similar sexual differences in patterns of seasonal changes in mass and condition. In Cantabrian chamois *Rupicapra pyrenaica parva*, males began the rutting season with kidney fat three times higher than that of females, but by early spring kidney fat of males was half that of female (Pérez-Barbería, Mutuberria & Nores, 1998). In Himalayan tahr *Hemitragus jemlahicus* in New Zealand, kidney fat of males was 25% greater than that of females before the rut, and 25% lower after the rut (Forsyth *et al*., 2005).

In other sexually dimorphic ungulates, dimorphism in hind foot length ranges from 1.07 to 1.09 against 1.45–1.60 in body mass [reindeer *Rangifer tarandus* (Leader-Williams & Ricketts, 1982), bighorn sheep *Ovis canadensis* (Blood, Flook & Wishart, 1970), mountain goats *Oreamnos americanus* (Festa-Bianchet & Côté, 2008) and mule deer
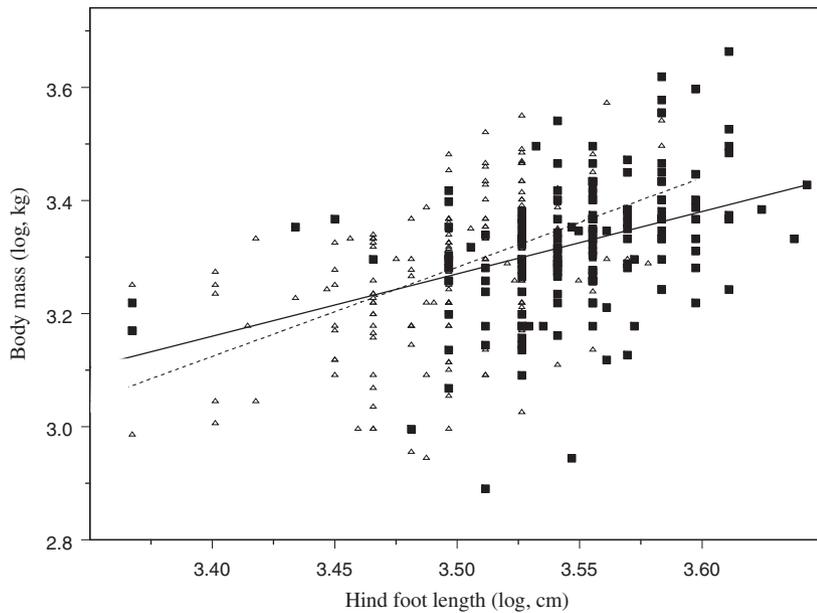
Figure 3 Log-transformed live body mass in relation to log-transformed foot length for 393 chamois *Rupicapra rupicapra* aged 4 years and older captured in the Alpi Marittime Natural Park, Italy, from 1992 to 2008. Females, dashed line and triangles; males, solid line and squares.
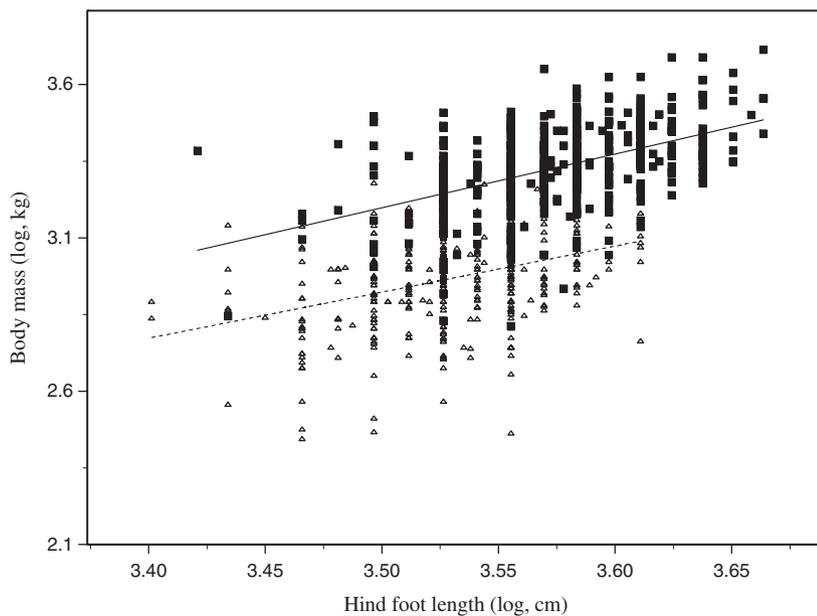

Figure 4 Log-transformed eviscerated body mass in relation to log-transformed foot length for 997 chamois *Rupicapra rupicapra* aged 4 years and older harvested in the Comprensorio Alpino Cuneo 4, Italy, from 1996 to 2008. Females, dashed line and triangles; males, solid line and squares.

Odocoileus hemionus (Anderson, Medin & Bowden, 1974)]. In roe deer, sexual dimorphism is slight in both body mass and skeletal size, with minor seasonal changes (Hewison *et al.*, 1996; Andersen, Duncan & Linnell, 1998); a dimorphism in hind foot length of 1.04–1.05 corresponds to a mass dimorphism of 1.06–1.07 (Pettorelli *et al.*, 2002; Hewison *et al.*, 2009). Therefore, chamois have limited skeletal dimorphism, and are more similar to roe deer than other species with larger sex difference in mass. In other sexually dimorphic ungulates, mass dimorphism is evident also in spring, for example, in bighorn sheep (Festa-Bianchet *et al.*, 1996) and mountain goats (Festa-Bianchet & Côté, 2008), with seasonal changes of 20–30% of body mass for both

sexes (Leader-Williams & Ricketts, 1982; Berger & Peacock, 1988; Festa-Bianchet *et al.*, 1996). So far, chamois is the only ungulate for which sexual dimorphism during the rut appears mostly due to seasonal changes in mass.

In several sexually dimorphic ungulates [red deer *Cervus elaphus* (Catchpole *et al.*, 2004), mountain goat and bighorn (Loison *et al.*, 1999*a*; Festa-Bianchet *et al.*, 2003)], the lower survival of males compared with females may derive partly from the riskier growth strategy adopted by males to gain and maintain large body and weapon size (Clutton-Brock *et al.*, 1985) and to the higher absolute energetic requirements of males (Demment & Van Soest, 1985). Male ibex *Capra ibex* deviate from the general pattern, because

Table 3 Effects of age (years) and date of harvest on body mass (kg) of male (4 years and older) and female (3 years and older) chamois *Rupicapra rupicapra* harvested in Comprensorio Alpino Cuneo 4 from 1996 to 2008 from mid-September to late December

Sex	Coefficient	SE	Pr($>|t|$)
Males			
Age	−0.242	0.056	<0.0001
Date	0.124	0.023	<0.0001
Date^2	−0.002	0.0002	<0.0001
Females			
Age	−0.066	0.029	0.02
Date	−0.007	0.005	0.15

Model R^2: males = 0.186, d.f. = 523; females = 0.01, d.f. = 566.

Table 4 Selection procedure for model of male chamois *Rupicapra rupicapra* in Table 3 based on the Akaike Information Criterion with second order adjustment (AIC$_c$; Burnham & Anderson, 2002)

Model	d.f.	AIC$_c$
Mass = age + date + date^2 + age:date + age:date^2	7	2848.210
Mass = age + date + date^2 + age:date	6	2846.209
Mass = age + date + date^2	**5**	**2844.628**
Mass = age + date	4	2901.54

Selected model is in bold.

they have high survival until about 10 years of age, despite being more sexually dimorphic than most ungulates (Toïgo *et al.*, 2007). Male ibex may favor survival at the expense of rapid growth and reproductive effort, reaching a very large size after 11–12 years of growth (Toïgo *et al.*, 2007; Willisch & Neuhaus, 2009). After this age, they suffer very high mortality, presumably related to rutting activities (Toïgo *et al.*, 2007; Willisch & Neuhaus, 2009). Although no published data exist on long-term monitoring of marked, known-age adults of both sexes, available evidence suggests that sexual dimorphism in the survival of prime-aged (about 3–9 years) chamois may be less than in most other ungulates (Bocci, Canavese & Lovari, 2010), a result confirmed for the closely related Pyrenean chamois (Loison *et al.*, 1999*a*).

Male chamois may have evolved a unique strategy to achieve high body mass for the rut while avoiding the high maintenance costs associated with large body size when resources are scarce. In winter and spring, the energetic requirement for maintenance should be similar for males and females, because size dimorphism is small (Hayssen & Lacy, 1985) (Fig. 1). Male energetic expenditure during the rut could mainly rely on fat and muscle tissue accumulated over the summer, as suggested for reindeer (Leader-Williams & Ricketts, 1982). Male chamois deplete their accumulated fat reserve over the rut, and by the end of the breeding season they have similar mass (and presumably body condition) as females. Although data comparing survival of individuals with known mass changes are necessary to test our hypothesis, evidence from bighorn sheep suggests that individuals with greater seasonal mass changes had greater fitness (Pelletier *et al.*, 2007).

In bighorn sheep (Coltman *et al.*, 2002), mountain goat (Mainguy *et al.*, 2009) and ibex (Willisch, 2009), a few dominant males sire the majority of offspring in each rut, although subordinate males obtain matings using alternative tactics (Hogg & Forbes, 1997). In mountain goats and bighorn sheep, males appear to be under strong selective pressure for rapid growth in skeletal size and body mass. The seasonality of SSD in chamois may suggest selection for a less risky male reproductive tactics, possibly associated with a low level of polygyny, similar to roe deer (Vanpé *et al.*, 2008).

Acknowledgments

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