Journal of Wildlife Management 74(5):1024–1029; 2010; DOI: 10.2193/2009-335

Management and Conservation Article

Compensatory Growth Limits Opportunities for Artificial Selection in Alpine Chamois

MARCO RUGHETTI, *Département de biologie and Centre d'études Nordiques, Université de Sherbrooke, Sherbrooke, Québec J1K 2R1, Canada*
MARCO FESTA-BIANCHET,[1] *Département de biologie and Centre d'études Nordiques, Université de Sherbrooke, Sherbrooke, Québec J1K 2R1, Canada*

ABSTRACT In ungulates, big males with large weapons typically outcompete other males over access to estrous females. In many species, rapid early growth leads to large adult mass and weapon size. We compared males in one hunted and one protected population of Alpine chamois (*Rupicapra rupicapra*) to examine the relationship between horn length and body mass. We assessed whether early development and hunter selectivity affected age-specific patterns of body and horn size and whether sport hunting could be an artificial selection pressure favoring smaller horns. Adult horn length was mostly independent of body mass. For adult males, the coefficient of variation of horn length (0.06) was <50% of that for body mass (0.16), suggesting that horn length presents a lower potential for selection and may be less important for male mating success than is body mass. Surprisingly, early development did not affect adult mass because of apparent compensatory growth. We found few differences in body and horn size between hunted and protected populations, suggesting the absence of strong effects of hunting on male phenotype. If horn length has a limited role in male reproductive success, hunter selectivity for males with longer horns is unlikely to lead to an artificial selective pressure on horn size. These results imply that the potential evolutionary effects of selective hunting depend on how the characteristics selected by hunters affect individual reproductive success.

KEY WORDS body mass, chamois, compensatory growth, horn length, *Rupicapra rupicapra*, selective hunting, sexual selection.

In polygynous mammals, body size is often a major determinant of male–male competition and larger adult males have high reproductive success (e.g., elephant seals [*Mirounga angustirostris*], Haley et al. 1994; brown bears [*Ursus arctos*], Zedrosser et al. 2007). In many large herbivores, male mating success also increases with size of horns, antlers, and tusks that evolved as intraspecific weapons (Geist 1966, Andersson 1994). Recent studies found that in ungulates, siring success increases with a male's age, social rank, and body or weapon size (Pemberton et al. 1992, Coltman et al. 2002, Mainguy et al. 2009). These characteristics tend to be correlated; weapon size typically increases with age, and large males are usually dominant and have large horns or antlers (Coltman et al. 2002, Mainguy et al. 2009).

Because of the fitness payoff of high dominance rank, males in sexually dimorphic ungulates favor rapid body and weapon growth over accumulation of fat reserves (Clutton-Brock et al. 1985). Typically, rapid early development is associated with large adult mass and reproductive success (Kruuk et al. 1999, Coltman et al. 2002). Multiyear patterns of horn growth in males may reflect the relative importance of horn size in securing access to females. For example, in bighorn sheep (*Ovis canadensis*) and Alpine ibex (*Capra ibex*), which fight by clashing horns, horn size contributes to a male's fitness. In these species, horn length is correlated with body mass and there is no compensatory growth; males with poor early growth typically remain small through life (Toïgo et al. 1999, Festa-Bianchet et al. 2004). In species that fight by attempting to hook or stab the opponent, such as chamois (*Rupicapra rupicapra*) or mountain goats (*Oreamnos americanus*), horn size may not have a strong effect on male mating success, and individuals with poor horn growth early in life increase growth in later years (Pérez-Barbería et al. 1996, Côté et al. 1998, Mainguy et al. 2009). Compensatory growth can only occur if individuals with rapid early development reduce growth in subsequent years compared to individuals with slow early development. Therefore, one should not expect compensatory horn or body growth without countervailing selection against excessive development of these traits.

Individual horn growth patterns are affected by a complex interaction of age, resource availability, and genotype (Festa-Bianchet et al. 2004, Mysterud et al. 2005). Sport hunting can have both ecological and evolutionary consequences on phenotypic traits (Coltman et al. 2003, Garel et al. 2007, Femberg and Roy 2008). Hunting could increase body mass and horn size by reducing population density (Gordon et al. 2004). If mass and horn size are genetically correlated, trophy hunting can reduce body and horn size by selectively removing males with large horns (Coltman et al. 2003, 2005; Festa-Bianchet 2007). Because empirical data comparing hunted and unhunted populations remain scarce, however, we know little about the effects of hunting on patterns of horn and body growth.

Similar to mountain goats, chamois horns develop quickly early in life, reaching about 95% of asymptotic length by 4 years of age (Bassano et al. 2003). Chamois are less sexually dimorphic than mountain goats; males are 20–30% heavier than females, whereas mountain goat males are about 40% heavier than females (Bassano et al. 2003, Festa-Bianchet and Côté 2008, Garel et al. 2009). Compensatory horn growth in chamois suggests that, as in mountain goats, variability in horn length is not important for male reproductive success (Pérez-Barbería et al. 1996, Mainguy et al. 2009). We compared a hunted and a protected

[1] *E-mail: m.festa@Usherbrooke.ca*

population of chamois to examine the relationship between early horn growth and adult horn and body size in males. We also examined whether sport hunting affected age-specific phenotype of chamois through removal of males with longer horns. Because for male ungulates body mass is typically an important fitness trait, and because individuals with strong early growth typically enjoy high survival and remain large through life, we predicted that large yearlings should develop into large adults (Festa-Bianchet et al. 2000, Malo et al. 2005, Vanpé et al. 2007, Bonenfant et al. 2008). Finally, because hunting has potentially opposite ecological and evolutionary effects on horn growth, we expected that, compared to the protected population, chamois in the hunted population would have longer horns early in life but would show an age-related apparent decline in early growth (Storch 1989, Coltman et al. 2003, Garel et al. 2007). If hunters preferentially harvest males with long horns, those with shorter horns may have longer life expectancy, eventually leading to an artificial selection pressure.

STUDY AREA

We monitored chamois in the Alpi Marittime Natural Park and in the adjacent Comprensorio Alpino Cuneo 4 (CACN4), in the southwestern Alps of Piedmont, Italy, near the border with France (44°12′N, 07°16′E). Narrow valleys and steep mountains dominate the landscape. Forests of beech (*Fagus sylvatica*) are predominant at valley bottom and are replaced by conifers (*Picea abies*, *Abies alba*, and *Larix decidua*) as altitude increases, giving way to alpine pastures at higher elevations. Rocks and moraines cover 47% of the Park and about 29% of CACN4. Ibex is the only other mountain ungulate, abundant in the Park and in small isolated populations in CACN4. Roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*) are present mainly under 1,200-m elevation. Red deer (*Cervus elaphus*) are abundant in CACN4. Wolves (*Canis lupus*) are permanent residents in the Park and in CACN4. Cattle graze all study areas during summer.

METHODS

Populations and Measures of Individual Life-History Traits

We analyzed data from 282 males captured in the Park in April–May 1991–2008 and 770 males shot in October–November in CACN4, 1996–2008. Data included age, body mass (eviscerated mass for harvested animals), total horn length, and foot length. We measured foot length from the tip of the hoof, along the ventral surface to the tip of the calcaneus. We precisely determined age by counting horn annuli (Schroder and Elsner-Schack 1985). We measured horn length from tip to base along the frontal surface. Horn growth stops during winter, forming a distinct growth ring or annulus (Pérez-Barbería et al. 1996). After the second summer, horn increments decrease in length and after the fifth summer they are only about 1 mm each. We knew the length of the first 4 increments for all animals captured in the Park and for 170 males shot in CACN4 from 2006 to 2008. We combined horn increments grown during the first and second summers (L2) for all analyses, because it was not possible to distinguish them (Schroder and Elsner-Schack 1985). We did not collect all measurements for all animals, so sample sizes vary across analyses.

Because we collected data in different seasons, mass and early horn growth in study populations were not directly comparable. Therefore, we limited interpopulation comparisons to season-independent measurements: completed horn increment and foot and horn length of males aged $\geq$5 years, and of yearlings. For males $\geq$5 years, skeletal growth is completed and horns grow $<$1 mm each summer. After establishing that no horn growth occurred between September and May for yearlings, we compared those shot in autumn (aged 16–18 months) with those (aged 22–24 months) captured the following April–May.

Chamois hunting in CACN4 was based on sex- and age-specific quotas. Hunting permits were either specific to an adult male or allowed harvest of an adult female or a yearling of either sex. Harvest plans sought to harvest approximately 10% of chamois that were counted during spring surveys by local game wardens and volunteers. The hunting season was divided into 3 periods, and additional permits were issued near the end of each period if sex–age quotas were not filled. In 2001–2007, the 472 males legally harvested accounted on average for 14% of the number of males counted during spring surveys. Harvest of yearling chamois during 2001–2007 was 22.5% of the number observed during censuses, but because about 60% of harvested yearlings were males, it is likely that hunting pressure was higher on yearlings than on older males.

Statistical Analysis

To assess the correlation between horn length and body mass in chamois we fitted a linear regression for each age class with horn length as the response variable. Asymptotic mass was reached at 4.5 years of age in CACN4 and at 5 years in the Park ($P < 0.05$, Least Significant Difference tests; Sokal and Rohlf 1995); therefore, we considered the following age (yr) classes: 2, 3, 4, and $\geq$5 in the Park and 1.5, 2.5, 3.5, and $\geq$4.5 in CACN4. Most chamois in our study areas are born in May; therefore, they were near their approximate birth dates when captured in the Park in April–May, and about 6 months older during the autumn hunting season.

To compare early development with adult mass, we fitted a linear regression using L2 as an explicative variable and adult mass as the response variable. Because 95% of the asymptotic mass was reached after 4 years in both populations, we used 3 age classes in the Park for which we had an adequate sample (2 yr, 3 yr, and $\geq$4 yr) and only 2 in CACN4 (1.5 yr and $\geq$4.5 yr).

To test for compensatory body growth we analyzed data for the Park population, for which we had the largest sample. From the regression between L2 and mass for 2-year-olds (slope = 0.87, SE = 0.142, $t_{31} = 6.12$, $P < 0.001$, $R^2 = 0.54$) we estimated mass at 2 years from the L2 measurement for 32 4-year-old chamois. By subtracting the estimated mass at 2 years from mass at capture, we obtained

Table 1. Linear regression of total horn length and body mass for 234 male chamois captured from 1991 to 2008 in Parco Naturale Alpi Marittime (Park) and for 749 male chamois shot in Comprensorio Alpino Cuneo 4 (CACN4), Italy, from 1996 to 2008.

Chamois age (yr)	Slope	SE	*t*-value	*P*	R^2	df
Park						
2	0.569	0.078	7.287	≤0.001	0.61	34
3	0.161	0.090	1.785	0.083	0.09	34
4	0.075	0.065	1.151	0.258	0.04	33
≥5	0.056	0.050	1.115	0.267	0.01	125
CACN4						
1.5	0.519	0.036	14.273	≤0.001	0.45	248
2.5	0.306	0.049	6.179	≤0.001	0.37	66
3.5	0.070	0.039	1.808	0.074	0.04	90
≥4.5	0.072	0.023	3.126	0.002	0.03	337

an estimated mass gain from 2 years to 4 years. We then calculated the Pearson correlation coefficient between mass gain from 2 years to 4 years and estimated body mass at 2 years.

We compared horn growth of the hunted and unhunted populations using the mixed model: $L = age \times population$, where L are lengths of the L2, L3, and L4 horn increments and *age* is the corresponding age for that increment (2 yr, 3 yr, 4 yr). This model accounted for individual variability and year of birth as random effects. We confronted models by likelihood ratio tests (LRT; Sokal and Rohlf 1995).

We used linear regression to compare the residual of total horn length on age with foot length (an index of skeletal size) for males >5 years, which had completed skeletal growth.

RESULTS

In the hunted population, date of harvest had no effect on foot length ($t_{92} = 1.309$, $P = 0.19$) or on total horn length ($t_{92} = 1.257$, $P = 0.21$) of chamois aged 1.5 years. Similarly, foot length of 2-year-old males did not increase over April–May in the Park ($t_{30} = -0.340$, $P = 0.73$). Therefore, because yearlings shot in autumn had stopped growing, we could compare their horn and foot measurements with those of 2-year-olds captured the following spring in the Park. Body mass and horn length were correlated for 2-year-old males in the Park and for yearlings in the hunted population (Table 1; Figs. 1, 2). The correlation weakened as chamois aged, so that for males aged ≥5 years, mass and horn length were weakly correlated in the hunted population and not correlated in the Park. For males >5 years, horn length had a weak linear relationship with age (horn length = 22.89 + 0.11 (age), $t_{165} = 2.29$, $R^2 = 0.03$, $P = 0.007$).

Horn growth over the first 2 summers (L2) was not a good predictor of adult mass (Table 2; Fig. 3). In the Park, 2-year-olds in spring showed a correlation between L2 and mass, but for males aged ≥3 years L2 was not correlated with mass. The hunted population revealed a similar pattern in that horn length and body mass were correlated for yearlings but not for adults (Table 2). For the Park

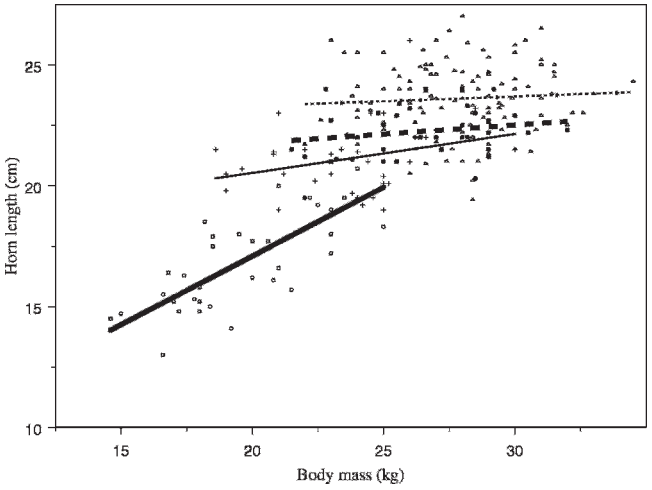

Figure 1. Total horn length and body mass for 234 male chamois captured in April and May 1991–2008 in the Parco Naturale Alpi Marittime, Italy. Lines and symbols correspond to the following age classes: 2 years, bold solid line and empty circles; 3 years, thin solid line and crosses; 4 years, bold dashed line and solid circles; ≥5 years, thin dashed line and triangles.

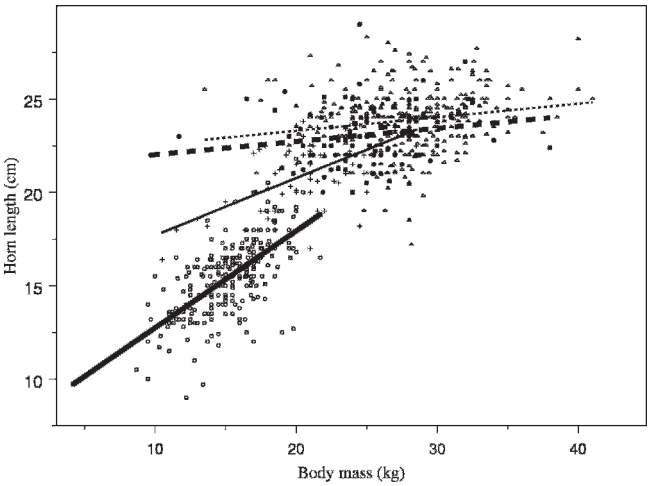

Figure 2. Total horn length in relation to eviscerated body mass for 749 male chamois shot in Comprensorio Alpino Cuneo 4, Italy, 1996 to 2008. Lines and symbols correspond to the following age classes: 1.5 years, bold solid line and empty circles; 2.5 years, thin solid line and crosses; 3.5 years, bold dashed line and solid circles; ≥4.5 years, thin dashed line and triangles.

Table 2. Linear regression of the length of horn grown over the first 2 years of life (L2) and body mass for 239 male chamois captured in Parco Naturale Alpi Marittime (Park) from 1991 to 2008, 245 yearling males shot in Comprensorio Alpino Cuneo 4 (CACN4) from 1996 to 2008, and 61 males aged ≥4.5 years shot from 2006 to 2008, in Italy. For CACN4 age classes 2.5 years and 3.5 years are not reported because sample size was <20. Because chamois were shot in autumn, for yearlings L2 is total length of the horn.

Chamois age (yr)	Slope	SE	*t*-value	*P*	R^2	df
Park						
2	0.870	0.142	6.116	≤0.001	0.55	31
3	0.416	0.349	1.193	0.242	0.04	30
≥4	0.169	0.116	1.452	0.148	0.01	172
CACN4						
1.5	0.775	0.060	12.859	≤0.001	0.40	245
≥4.5	−0.199	0.227	−0.875	0.385	0.01	61

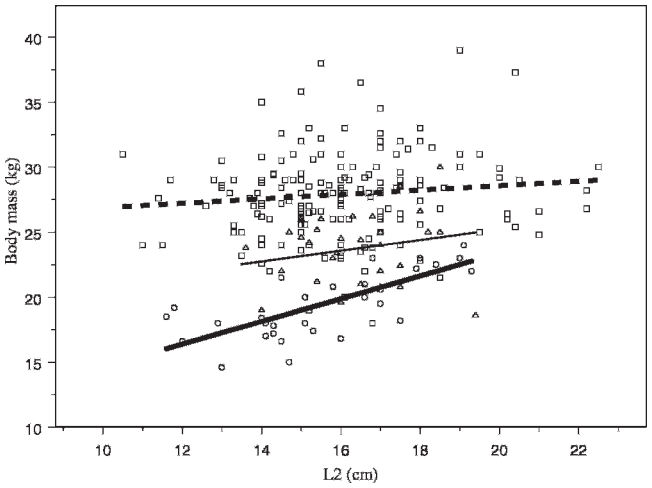

Figure 3. Relationship between body mass and length of the first 2 horn increments (L2) for 239 males chamois captured in April and May in the Parco Naturale Alpi Marittime, Italy, 1991 to 2008. Lines and symbols correspond to the following age classes: 2 years, bold solid line and circles; 3 years, thin solid line and triangles; ≥4 years, bold dashed line and squares.

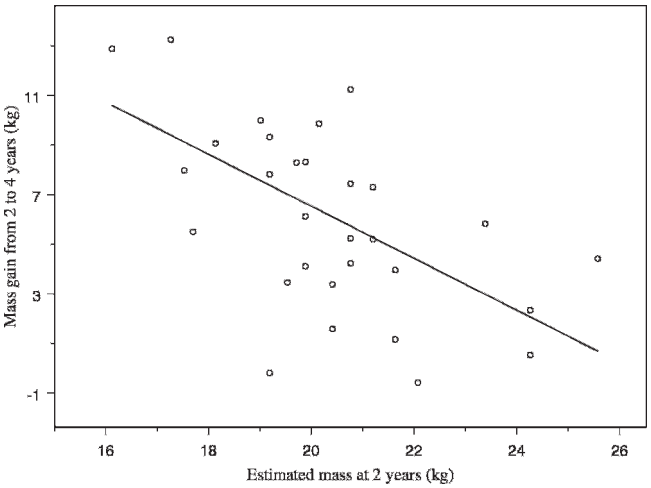

Figure 4. Correlation between estimated body mass at 2 years of age, based on length of horn grown over the first 2 years of life, and gain in mass from 2 years to 4 years of age for 32 4-year-old male chamois captured in April and May in the Parco Naturale Alpi Marittime, Italy, 1991 to 2008 (Pearson correlation coeff. = −0.59, $t_{30} = -3.97$, $P < 0.001$).

population, mass at age 2 years estimated from the L2 annulus was negatively correlated with estimated mass gain over the following 2 years (Fig. 4); heavier 2-year-olds gained less mass than lighter 2-year-olds over the next 2 years.

Over the first 4 summers of life, chamois in the Park grew shorter horn increments than those in the hunted population (Table 3; LRT = 3.899, $P = 0.048$). The effect of population, however, only explained <1% of variance. Year of birth did not explain the difference in horn growth between the Park and CACN4 populations (LRT = 4.782, $P = 0.188$). The relationship between horn and foot length in yearlings did not differ between populations (general model: horn length = foot length × population; foot length and population interaction $t_{160} = 0.556$, $P = 0.579$; population $t_{161} = 1.525$, $P = 0.129$; final model horn length = foot length; slope = 0.68, SE = 0.08, $t_{162} = 9.00$, $P < 0.001$, $R^2 = 0.33$). For adult males, foot length was weakly related to total horn length (slope = 0.17, SE = 0.04, $t_{633} = 4.06$, $P < 0.001$, $R^2 = 0.025$) and there was no difference in slope between populations ($t_{632} = 1.42$, $P = 0.16$). For males >5 years, foot length in the hunted population was 1 cm longer than in the Park (analysis of variance [ANOVA], $F_{1,249} = 41.681$, $P < 0.001$). Based on the relationship between foot length and mass of harvested chamois (mass = −16.85 + 1.25 × foot length, $R^2 = 0.20$, $P < 0.001$), 1 cm difference in foot length corresponded to a difference of about 1 kg or 3% of average mass in autumn. Horn length, however, was the same in both populations (horn length corrected for age, ANOVA, $F_{1,248} = 0.013$, $P = 0.91$; Park: $\bar{x} = 23.6$ cm, SD = 1.51 cm; CACN4: $\bar{x} = 23.9$ cm, SD = 1.53 cm). For males ≥5 years old in the hunted population, the coefficient of variation in body mass (0.16) was more than double the coefficient of variation in horn length (0.06).

DISCUSSION

Our research produced 3 main results. First, horn size did not appear to be an important fitness-related characteristic of male chamois. Second, in addition to confirming strong compensatory horn growth, our data suggest an unexpected compensatory growth in mass. Third, artificial selection on phenotypic traits of hunted chamois appears unlikely because of compensatory growth in both horn size and body mass.

In many polygynous ungulates, such as red deer (Kruuk et al. 2002), fallow deer (*Dama dama*; McElligott et al. 2001), bighorn sheep (Coltman et al. 2002), and ibex (von Hardenberg et al. 2007), horn or antler length and body size are known or strongly suspected to be correlated with male reproductive success. In ibex and bighorn sheep, horn length is correlated with body mass and there is no compensatory growth (Toïgo et al. 1999, Festa-Bianchet et al. 2004). For rupicaprini, however, horn length may play a minor role in determining access to mates. In mountain goats, mass affects male reproductive success but horn length is not important (Mainguy et al. 2009). We found a correlation between horn length and body mass for young males but not for adult males (Figs. 1, 2). That lack of correlation, coupled with compensatory horn growth, suggests that in adult males horn length should be under weak selective pressure, which has important implications for chamois management because it suggests that the target of selective hunting (horn size) may have weak fitness effects.

In wild sheep, horn growth over successive years is positively correlated (Bonenfant et al. 2008) and horn size is a strong determinant of male fitness, genetically correlated with other fitness-related traits (Coltman et al. 2005). By removing males with rapid horn growth before they obtain high mating success, trophy hunters have a strong evolutionary impact (Coltman et al. 2003). In rupicaprini

Table 3. Mixed model comparing horn growth pattern of males in a hunted and an unhunted population of chamois: $L = age \times population$, where L are measurements of horn increments for the first 2, 3, and 4 summers of life and *age* is the age of the animal for that increment (2 yr, 3 yr, 4 yr). We set individual (*id*) and year of birth as random effects.

Effect	Value	SE	df	*t*-value	*P*-value	SD, intercept	SD, slope
Fixed							
Intercept	−0.167	0.385	595	−0.434	0.664		
Age	10.827	0.232	595	46.716	≤0.001		
Age^2	−1.294	0.038	595	−34.168	≤0.001		
Population, unhunted	−0.337	0.171	300	−1.976	0.049		
Random							
Approx. 1 + age | id						3.132	0.705
SD, residual						0.534	

such as mountain goat (Côté et al. 1998), chamois (Pérez-Barbería et al. 1996), and Japanese serow (*Capricornis crispus*; Miura et al. 1987), horns show compensatory growth and no or little dimorphism, suggesting a weak role of horn length in male reproductive success. Combat in these species involves attempts to gore the adversary from an antiparallel position or during high-speed chases (Geist 1978, Lovari and Locati 1991). Thus, once horns reach an optimal size, additional growth may not improve fighting ability and may even compromise it, possibly through increased risk of horn breakage.

Although compensatory horn growth in rupicaprini may have a phylogenetic component, body size dimorphism varies among species (Hernández Fernández and Vrba 2005). Sexual dimorphism is about 40% in mature mountain goats (Festa-Bianchet and Côté 2008), and the Japanese serow is not sexually dimorphic (Miura and Maruyama 1986), whereas chamois sexual dimorphism is 25–32% depending on age, season, and population (Bassano et al. 2003, Garel et al. 2009). In chamois, the much higher coefficient of variation of mass compared to horn length suggests that mass may have greater potential for sexual selection and may better explain individual differences in mating success, as reported for mountain goats (Mainguy et al. 2008). Although little is known about the chamois mating system, available data do not suggest that horn length affects access to mates. Dominant males appear to tend single estrous females and drive away competing males with spectacular chases over hundreds of meters (Lovari and Locati 1991, von Hardenberg et al. 2000). Horn length may not be as important in determining mating success as other characteristics such as agility and strength. Data on individual male reproductive success are required to test our suggestions.

Unexpectedly, we found evidence of compensatory body growth. Horn growth over the first 2 years, which in yearlings was correlated with mass, explained almost no variability in mass among 4-year-olds. Males that had rapid mass gain and horn growth over the first 2 years of life apparently experienced reduced growth over the following 2 years compared to males with slow early development. Consequently, large yearlings did not necessarily develop into the largest adults. Evidence we found of compensatory body growth in chamois has important implications both for sport hunting and for our understanding of ungulate mating tactics. Many management jurisdictions have a specific harvest plan for yearling chamois, but even if they selectively harvested large yearlings, hunters would be unlikely to affect the phenotype of adult males, because yearling mass and horn length were not strongly related to adult characteristics. It is surprising that male chamois that initially grow rapidly later experience reduced growth, losing their early advantage in mass. Perhaps chamois face a trade-off such that males larger than a given threshold are disadvantaged. Observation on Apennine chamois (*Rupicapra pyrenaica*), however, suggest that dominant males had longer horns and were older than their competitors (Lovari and Locati 1991). Natural selection against small individuals does not necessarily imply that selection always favors larger males. Once a threshold size is achieved, further growth may not increase fitness (Pelletier et al. 2007). Repeated measurements of body mass of the same individuals are required to better understand this surprising result.

Without data on male reproductive success, we speculate that agility and speed, rather than body and horn size, may affect male mating success. Females do not form large, defensible groups but tend to be scattered over wide areas of rough terrain. Limited opportunities to monopolize estrous females may weaken the selective pressure for large size. Similar arguments have been proposed for roe deer, a cervid comparable in size and sexual dimorphism to chamois (Vanpé et al. 2008).

MANAGEMENT IMPLICATIONS

Possible evolutionary effects of selective hunting should depend on both the characteristics preferred by hunters and the relevance of those characteristics for reproductive success. For ungulates, it is important to consider age-specific horn and body growth patterns, relationships between horn growth in different years for the same individual, and their effects on mating success. In chamois, horns showed strong compensatory growth, horn length may play a minor role in mating success, males with rapid early growth did not develop into the largest adults, and adult males showed a weak correlation between horn length and body mass. Our results suggest that because of the behavioral ecology of chamois, selective hunting for large-horned males should not lead to a strong artificial evolutionary pressure.

ACKNOWLEDGMENTS

Funding for this project was provided by the Piemonte Region, the Alpi Marittime Natural Park, and the Natural Sciences and Engineering Research Council of Canada. We thank the Park Rangers for logistic support and help with fieldwork. We extend special thanks to managers of the Comprensorio Alpino Cuneo 4 for their collaboration in collecting data. An earlier draft of the manuscript benefited from critical comments by J. Martin.

LITERATURE CITED

Andersson, M. B. 1994. Sexual selection. Princeton University Press, Princeton, New Jersey, USA.

Bassano, B., A. Perrone, and A. von Hardenberg. 2003. Body weight and horn development in Alpine chamois, *Rupicapra rupicapra* (Bovidae, Caprinae). Mammalia 67:65–73.

Bonenfant, C., F. Pelletier, M. Garel, and P. Bergeron. 2008. Age-dependent relationship between horn growth and survival in wild sheep. Journal of Animal Ecology 76:161–171.

Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. Nature 313:131–133.

Coltman, D. W., M. Festa-Bianchet, J. T. Jorgenson, and C. Strobeck. 2002. Age-dependent sexual selection in bighorn rams. Proceedings of the Royal Society B 269:165–172.

Coltman, D. W., P. O'Donoghue, J. T. Jorgenson, J. T. Hogg, and M. Festa-Bianchet. 2005. Selection and genetic (co)variance in bighorn sheep. Evolution 59:1372–1382.

Coltman, D. W., P. O'Donoghue, J. T. Jorgenson, J. T. Hogg, C. Strobeck, and M. Festa-Bianchet. 2003. Undesirable evolutionary consequences of trophy hunting. Nature 426:655–658.

Côté, S. D., M. Festa-Bianchet, and K. G. Smith. 1998. Horn growth in mountain goats (*Oreamnos americanus*). Journal of Mammalogy 79:406–414.

Femberg, P. B., and K. Roy. 2008. Ecological and evolutionary consequences of size-selective harvesting: how much do we know? Molecular Ecology 17:209–220.

Festa-Bianchet, M. 2007. Ecology, evolution, economics, and ungulate management. Pages 183–202 *in* T. E. Fulbright and D. G. Hewitt, editors. Wildlife science: linking ecological theory and management applications. CRC Press, Boca Raton, Florida, USA.

Festa-Bianchet, M., D. W. Coltman, L. Turelli, and J. T. Jorgenson. 2004. Relative allocation to horn and body growth in bighorn rams varies with resource availability. Behavioral Ecology 15:305–312.

Festa-Bianchet, M., and S. D. Côté. 2008. Mountain goats. Island Press, Washington, D.C., USA.

Festa-Bianchet, M., J. T. Jorgenson, and D. Réale. 2000. Early development, adult mass, and reproductive success in bighorn sheep. Behavioral Ecology 11:633–639.

Garel, M., J.-M. Cugnasse, D. Maillard, J.-M. Gaillard, A. J. M. Hewison, and D. Dubray. 2007. Selective harvesting and habitat loss produce long-term life history changes in a mouflon population. Ecological Applications 17:1607–1618.

Garel, M., A. Loison, J.-M. Jullien, D. Dubray, D. Maillard, and J.-M. Gaillard. 2009. Sex-specific growth in alpine chamois. Journal of Mammalogy 90:954–960.

Geist, V. 1966. The evolutionary significance of mountain sheep horns. Evolution 20:558–566.

Geist, V. 1978. On weapons, combat and ecology. Pages 1–54 *in* L. Krames, editor. Aggression, dominance and individual spacing. Volume 4. Plenum Press, New York, New York, USA.

Gordon, I. J., A. J. Hester, and M. Festa-Bianchet. 2004. The management of wild large herbivores to meet economic, conservation and environmental objectives. Journal of Applied Ecology 41:1021–1031.

Haley, M. P., C. J. Deutsch, and B. J. LeBoeuf. 1994. Size, dominance and copulatory success in male northern elephant seals, *Mirounga angustirostris*. Animal Behaviour 48:1249–1260.

Hernández Fernández, M., and E. S. Vrba. 2005. A complete estimate of the phylogenetic relationships in Ruminantia: a dated species-level supertree of the extant ruminants. Biological Reviews 80:269–302.

Kruuk, L. E. B., T. H. Clutton-Brock, K. E. Rose, and F. E. Guinness. 1999. Early determinants of lifetime reproductive success differ between the sexes in red deer. Proceedings of the Royal Society B 266:1655–1661.

Kruuk, L. E. B., J. Slate, J. M. Pemberton, S. Brotherstone, F. Guinness, and T. Clutton-Brock. 2002. Antler size in red deer: heritability and selection but no evolution. Evolution 56:1683–1695.

Lovari, S., and M. Locati. 1991. Temporal relationships, transitions and structure of the behavioural repertoire in male Apennine chamois during the rut. Behaviour 119:77–103.

Mainguy, J., S. Côté, E. Cardinal, and M. Houle. 2008. Mating tactics and mate choice in relation to age and social rank in male mountain goats. Journal of Mammalogy 89:626–635.

Mainguy, J., C. Steeve, M. Festa-Bianchet, and D. Coltman. 2009. Siring success and gender-dependent paternal effects in a sexually dimorphic ungulate, the mountain goat. Proceedings of the Royal Society B 276:4067–4075.

Malo, A. F., E. R. S. Roldan, J. Garde, A. J. Soler, and M. Gomendio. 2005. Antlers honestly advertise sperm production and quality. Proceedings of the Royal Society B 272:149–157.

McElligott, A. G., M. P. Gammell, H. C. Harty, D. R. Paini, D. T. Murphy, J. T. Walsh, and T. J. Hayden. 2001. Sexual size dimorphism in fallow deer (*Dama dama*): do larger, heavier males gain greater mating success? Behavioral Ecology and Sociobiology 49:266–272.

Miura, S., I. Kita, and M. Sugimura. 1987. Horn growth and reproductive history in female Japanese serow. Journal of Mammalogy 68:826–836.

Miura, S., and N. Maruyama. 1986. Winter weight loss in Japanese serow. Journal of Wildlife Management 50:336–338.

Mysterud, A., E. J. Solberg, and N. G. Yoccoz. 2005. Ageing and reproductive effort in male moose under variable levels of intrasexual competition. Journal of Animal Ecology 74:742–754.

Pelletier, F., T. H. Clutton-Brock, J. M. Pemberton, S. Tuljapurkar, and T. Coulson. 2007. The evolutionary demography of ecological change: linking trait variation and population growth. Science 315:1571–1574.

Pemberton, J. M., S. D. Albon, F. E. Guinness, T. H. Clutton-Brock, and G. A. Dover. 1992. Behavioral estimates of male mating success tested by DNA fingerprinting in a polygynous mammal. Behavioral Ecology 3:66–75.

Pérez-Barbería, F. J., L. Robles, and C. Nores. 1996. Horn growth pattern in Cantabrian chamois *Rupicapra pyrenaica parva*: influence of sex, location and phaenology. Acta Theriologica 41:83–92.

Schroder, W., and I. V. Elsner-Schack. 1985. Correct age determination in chamois. Pages 65–70 *in* S. Lovari, editor. The biology and management of mountain ungulates. Croom Helm, London, United Kingdom.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research. W. H. Freeman, London, United Kingdom.

Storch, I. 1989. Condition in chamois populations under different harvest levels in Bavaria. Journal of Wildlife Management 53:925–928.

Toïgo, C., J. M. Gaillard, and J. Michallet. 1999. Cohort affects growth of males but not females in alpine ibex (*Capra ibex ibex*). Journal of Mammalogy 80:1021–1027.

Vanpé, C., J. M. Gaillard, P. Kjellander, A. Mysterud, P. Magnien, D. Delorme, G. V. Laere, F. Klein, O. Liberg, and A. J. M. Hewison. 2007. Antler size provides an honest signal of male phenotypic quality in roe deer. American Naturalist 169:481–493.

Vanpé, C., P. Kjellander, M. Galan, J.-F. Cosson, S. Aulagnier, O. Liberg, and A. J. M. Hewison. 2008. Mating system, sexual dimorphism, and the opportunity for sexual selection in a territorial ungulate. Behavioral Ecology 19:309–316.

von Hardenberg, A., B. Bassano, M. Festa-Bianchet, G. Luikart, P. Lanfranchi, and D. W. Coltman. 2007. Age-dependent genetic effects on a secondary sexual trait in male Alpine ibex, *Capra ibex*. Molecular Ecology 16:1969–1980.

von Hardenberg, A., B. Bassano, A. Peracino, and S. Lovari. 2000. Male alpine chamois occupy territories at hotspots before the mating season. Ethology 106:617–630.

Zedrosser, A., E. Bellemain, P. Taberlet, and J. Swenson. 2007. Genetic estimates of annual reproductive success in male brown bears: the effects of body size, age, internal relatedness and population density. Journal of Animal Ecology 76:368–375.

Associate Editor: Hall.