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Relative allocation to horn and body growth in bighorn rams varies with resource availability

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Males may allocate a greater proportion of metabolic resources to maintenance than to the development of secondary sexual characters when food is scarce, to avoid compromising their probability of survival. We assessed the effects of resource availability on body mass and horn growth of bighorn rams (*Ovis canadensis*) at Ram Mountain, Alberta, Canada over 30 years. The number of adult ewes in the population tripled during our study, and the average mass of yearling females decreased by 13%. We used the average mass of yearling females as an index of resource availability. Yearling female mass was negatively correlated with the body mass of rams of all ages, but it affected horn growth only during the first three years of life. Yearly horn growth was affected by a complex interaction of age, body mass, and resource availability. Among rams aged 2–4 years, the heaviest individuals had similar horn growth at high and at low resource availability, but as ram mass decreased, horn growth for a given body mass became progressively smaller with decreasing resource availability. For rams aged 5–9 years, horn growth was weakly but positively correlated with body mass, and rams grew slightly more horn for a given body mass as resource availability decreased. When food is limited, young rams may direct more resources to body growth than to horn growth, possibly trading long-term reproductive success for short-term survival. Although horn growth of older rams appeared to be greater at low than at high resource availability, we found no correlation between early and late growth in horn length for the same ram, suggesting that compensatory horn growth does not occur in our study population. Young rams with longer horns were more likely to be shot by sport hunters than those with shorter horns. Trophy hunting could select against rams with fast-growing horns. *Key words:* bighorn sheep, body mass, horn size, *Ovis canadensis*, population density, reproductive strategy, resource allocation, sexual selection. *[Behav Ecol 15:305–312 (2004)]*

Most large mammals require several years to complete body growth, and when resources are scarce, young and growing individuals face a trade-off between allocation of metabolic resources to growth and to reproduction. Studies of female reproductive strategy in ungulates (Albon et al., 1983; Festa-Bianchet and Jorgenson, 1998) suggest that at high population density, females reduce investment in reproduction in favor of somatic growth and accumulation of fat reserves, presumably increasing survival to the detriment of current reproduction. Young bighorn ewes (*Ovis canadensis*) postpone primiparity when resources are scarce (Jorgenson et al., 1993a), and age of primiparity is often the first vital rate affected by increasing population density in ungulates (Gaillard et al., 2000). Possibly because of a flexible resource-allocation strategy, adult female mass in bighorn sheep varies little with changes in population density (Leblanc et al., 2001). Young males, however, may not have as much flexibility in resources allocation as young females, and consequently their physical development may be more affected by resource availability.

Little is known about how male mammals allocate metabolic resources to growth and to reproduction according to food availability. Because male reproductive success typically depends on male-male combat, males are generally expected to adopt a riskier strategy than females to achieve the greatest possible development of weapons (antlers and horns) used in competition for estrous females, and consequently suffer a survival cost, particularly when resources are scarce (Clutton-Brock, 1988). If males directed more resources to body growth rather than horn or antler growth when food was scarce, they might increase their survival probability, possibly to the detriment of their short-term reproductive success.

In bighorn sheep, male reproductive success increases with horn size for mature males, who father the greatest number of lambs (Coltman et al., 2002; Hogg and Forbes, 1997). Consequently, investment in horn growth can be considered a reproductive investment. It should be noted, however, that while about 75% of asymptotic horn growth takes place by age 4 (Jorgenson et al., 1998), horn length does not play a substantial role in the mating success of rams younger than 6–7 years (Coltman et al., 2002). Young rams fertilize ewes using coursing tactics (Hogg, 1988; Hogg and Forbes, 1997), whose success is independent of their dominance rank. Horn size determines the outcome of male-male combats that establish social rank (Geist, 1971), and social rank determines priority in access to estrous ewes only for the largest males, aged 7 years and older (Hogg, 2000). Consequently, investment in horn growth by young rams will not improve their reproductive success until a few years later. Ram age may therefore affect the relative allocation of resources to body and horn growth. Young rams may devote more resources to body growth when food is scarce because horn size is not as important a determinant of reproductive success as it is for older rams. On the other hand, unless there is much potential for compensatory growth, young rams may be selected to always grow as much horn as possible to maximize lifetime reproductive success.

Leblanc et al. (2001) found that because population density had greater effects on body growth of rams than of ewes,

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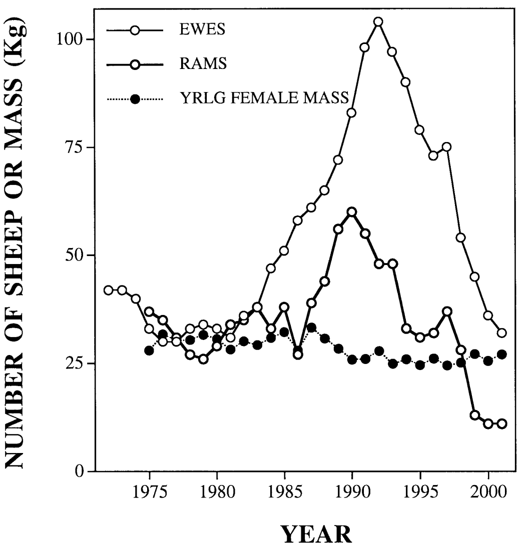

Figure 1
Number of adult bighorn ewes and rams and average mass (kg) of yearling ewes adjusted to 5 June at Ram Mountain, Alberta, 1975–2001. Yearly sample sizes for yearling female mass ranged from 2 to 19 and averaged 7.5.

sexual dimorphism among 4-year-old sheep decreased sharply with increasing density. Jorgenson et al. (1998) reported that density had negative effects on horn growth of young rams. Neither study, however, examined how ram horn growth varied in relation to individual body mass as resource availability changed.

Here we first explored the relationship between body mass and horn growth. We expected that the largest rams would grow the largest horns. Horns are energetically costly because they can make up more than 15% of a ram's body weight (Blood et al., 1970) and are a major source of heat loss during winter (Picard et al., 1996). Because they are costly, horns may be an honest signal of individual quality, as has been suggested for the antlers of some deer (Ditchkoff et al., 2001; Folstad and Karter, 1992). We then examined the effect of resource availability and individual mass on horn growth to test the hypothesis that, as resource availability decreases, rams allocate a greater proportion of resources to mass gain to the detriment of horn growth. Because we previously reported that 4-year-old rams may have higher horn growth at high than at low density (Jorgenson et al., 1998), and because some studies have suggested that male bovids with reduced horn growth early in life show compensatory growth in later years (Côté et al., 1998; Pérez-Barbería et al., 1996), we also looked for evidence of compensatory growth. To do so, we tested whether rams with poor horn growth early in life showed an increase in horn growth during later years compared to rams with greater horn growth early in life. Finally, because harvest of bighorn rams in our study area and in much of their range is determined by regulations based on horn morphology, we looked for evidence that sport hunting may select against young rams with fast-growing horns.

METHODS

Ram Mountain (52°N, 115°W) is a mountainous outcrop in west-central Alberta, Canada, with approximately 38 km^2 of alpine and subalpine habitat used by bighorn sheep. Sheep were captured from late May to early October in a corral trap baited with salt. We individually marked rams with colored Allflex plastic ear tags. Almost all rams were first caught as lambs or yearlings; those caught as adults were aged by counting the horn annuli. We have precise data on population size and individual survival from 1975 because from then on more than 95% of the population was marked in most years. We censused the study area at least once a week during the trapping period, and we noted the identity of all sheep seen. The yearly resighting probability of surviving rams was >95%, and emigration was extremely rare (Jorgenson et al., 1997). We recorded body mass and horn measurements at each capture. Most males aged 1–3 years were captured at least twice each summer, but many older males were only caught once a year, usually in June or July. We adjusted body mass to 5 June each year using individual rates of mass gain for rams caught more than once in the same year and age-specific regressions on date of capture for rams caught only once. More details about capture frequency and mass adjustment procedures are in Festa-Bianchet et al. (1996).

Horn annuli form overwinter when horn growth stops and are obvious in rams up to 10 years of age. We measured the length and base circumference of each annulus, usually in the year after it was formed. We measured some annuli in rams captured 2 or 3 years after the annulus had formed, leading to a larger sample size for annuli measurements than for age-specific body mass. Until 1981, yearly removals of 12–24% of adult ewes kept the population at 95–110 sheep (Jorgenson et al., 1993b). After 1981, the population increased, peaking at 232 in 1991. The number of ewes tripled during the study, while the number of rams doubled (Figure 1). After 1992 the population declined, partly because of density-dependent changes in age of primiparity (Gallant et al., 2001) and in lamb survival (Portier et al., 1998), partly because 11 adult and 3 yearling ewes were removed in 1997, and partly because of an apparent increase in cougar (*Puma concolor*) predation after 1997.

The hunting season for "legal" rams lasted from late August to the end of October. The definition of "legal" ram was based on horn size: until 1995, rams could be shot if their horns described at least 4/5 of a curl. From 1996 onward, only full-curl rams could be harvested. Harvests were limited only by the availability of legal rams. Registration of harvested rams is compulsory. About two or three rams a year were shot by hunters until 1995 (Jorgenson et al., 1993b), but only two were shot over the 5 years from 1996 to 2000.

In previous studies, we used the number of adult ewes as a measure of population density and, consequently, resource availability (Jorgenson et al., 1998). In recent years, however, as density declined (Figure 1), there appeared to be a lag in population response, suggesting that the decrease in density was not accompanied by an increase in resource availability. Consequently, we searched for a better measure of resource availability and selected the average mass of yearling ewes in early June. Yearling ewes are weaned but still growing (Festa-Bianchet et al., 1996), and their mass should reflect how resource availability is affected by both sheep population density and vegetation productivity. Indeed, as population density declined in 1992–2000, mass of yearling ewes did not recover (Figure 1). We did not use the mass of yearling rams because in 2 years there were no yearling rams in the population. An earlier analysis using two phases of population density ("low" up to 1987 and "high" afterward) to estimate resource availability gave similar results to those presented here. The mass of yearling female moose (*Alces alces*) has also been used as an index of resource availability (Adams and Pekins, 1995).

Rams orphaned by ewe removals during the early years of the study had smaller horns than nonorphaned rams at 4–5

Table 1

ANOVA table for linear mixed effects models describing the effects of age and resource availability (RA, measured by the average mass of yearling ewes in early June) on mass, horn annular length, and annular base circumference for bighorn sheep rams at Ram Mountain, Alberta

	Body mass[a]		Annuli length[b]		Annuli base[c]	
Term	Coeff (SE)	*t* (*p*)	Coeff (SE)	*t* (*p*)	Coeff (SE)	*t* (*p*)
Intercept	18.83 (7.19)	2.62 (<.01)	−6.26 (2.86)	−2.19 (<.05)	2.42 (2.38)	1.02 (>.05)
Age	4.77 (1.59)	3.00 (<.005)	2.87 (0.69)	4.18 (<.001)	7.23 (0.51)	14.14 (<.001)
Exp(age)	−0.067 (0.004)	−14.83 (<.001)	−0.0020 (0.0009)	−2.26 (<.05)	−0.040 (0.001)	−26.40 (<.001)
RA	0.32 (0.25)	1.28 (.20)	1.03 (0.10)	10.18 (<.001)	0.16 (0.08)	1.97 (<.05)
Age × RA	0.24 (0.06)	4.30 (<.001)	−0.18 (0.02)	−7.57 (<.001)	−0.032 (0.017)	−1.84 (>.05)
Exp(age) × RA			0.00008 (0.00003)	2.43 (<.05)		
Age × exp(age)	0.0069 (0.0005)	14.2 (<.001)			0.0041 (0.0001)	25.09 (<.001)

[a] 558 observations from 158 individuals, 77.2% of total variance explained.

[b] 694 observations from 182 individuals, 77.7% of variance explained.

[c] 693 observations from 182 individuals, 86.8% of variance explained.

years of age (Festa-Bianchet et al., 1994) and were excluded from our analyses. Our sample included rams aged 2–9 years, monitored between 1975 and 2000.

Because the first horn annulus is often worn off during social interactions, we only included measurements of the second and later annuli in our analyses. In most cases, both horns were measured, and analyses were based on the larger of the two annuli. When only one horn was measured, we used the available measurement. Fluctuating asymmentry was greater than the measurement error, but small. For length, it ranged from 1 to 3% for annuli 2–6 and increased to 5–6% for later years. For circumference, it was less than 2% for all annuli (Demers, 1999).

We first examined how the effects of resource availability on body mass and growth in horn length and circumference varied with age, using linear mixed effects models implemented by SPLUS (Insightful, Seattle, Washington). Year and identity were fitted as random effects, and yearling ewe mass, exponential functions of age, and their second-order interactions were fitted as fixed effects. We assessed model goodness-of-fit using Akaike's information criterion (Pinheiro and Bates, 2000). We then tested how the relationships between horn length increments and either age-specific mass or horn base circumference varied with resource availability. Horn growth has a nonlinear relationship with ram age (Jorgenson et al., 1998), and an exponential function of age fitted our data better than polynomial or logarithmic functions. To test for compensatory horn growth, we used generalized linear models (GLMs) to model late growth (cumulative horn length at ages 4 and 5, or basal circumference at age 5) as a function of earlier growth (cumulative horn length between ages 2 and 3, or basal circumference at age 3) and resource availability at age three as a main effect and as an interaction with early growth.

Hunters could only kill rams with horns describing at least 4/5 of a curl. About 5% of rams reached that minimum horn size at 4 years of age, and 20–60% did so at 5–6 years, but at high population density several rams never became legal (Jorgenson et al., 1998). Therefore, our sample of horn measurements of older males could be biased if young rams with fast-growing horns were more likely to be shot than young rams with slow-growing horns. We tested for a potential selective effect of hunting by comparing rams that were shot at age 5 or younger with those that survived past their 5th year. To do this we modeled the probability of being shot at age 5 or younger as a function of cumulative horn growth from ages 2 to 4, base circumference at age 4, and mass at age 4 using GLMs with binomial error structure (i.e., logistic regressions).

Because we used mixed-effects models, our analyses accounted for repeated measurements of the same individuals in different years. Horn annulus length one year can be independent of the length of the annuli in previous years and could vary with age, resource availability, and other factors. Annulus base circumference, however, cannot be independent of base circumference in previous years because horn annuli are formed around a permanent bony core and cannot shrink from one year to the next.

RESULTS

Resource availability, measured as the average early-June mass of yearling ewes, varied substantially during our study and had a negative effect on body mass of rams of all ages (Table 1; Figure 2). The average mass of yearling ewes adjusted to 5 June decreased from 30.3 kg in 1975–1987 to 26.4 kg in 1988–1997 and ranged yearly from 24.5 to 33.3 kg, a difference of 26% (Figure 1). The negative effects of resource availability on yearly horn growth, however, decreased with age, and after age 5 rams may grow more horn when resources are scarce than when they are abundant (Figure 2). Annulus base circumference was independent of population density after about 5 years of age (Figure 2).

We focused our analyses on the relationship between annulus length, individual mass, and population density. We also compared annulus length with annulus base, taking into account the effects of population density. For rams aged 2–4 years, the relationship between body mass and annulus length was steeper when resource availability was low (Table 2; Figure 3). Relatively light rams grew less horn for a given body mass at low than at high resource availability, but for heavy rams horn growth appeared independent of resource availability. For rams older than 4 years, the relationship between body mass and horn growth had similar slopes at high and at low levels of resource availability. The effect of resource availability was weak, but opposite to that found for younger rams: for a given body mass, rams grew less horn when resources were more abundant (Figure 3). Note, however, that the absolute amount of horn grown at 2–4 years is much greater than that grown at later ages (Figure 2). In this analysis, random effects contributed 7.6% of the total variance, possibly because much of the yearly variation was accounted for by the fixed effects of density and age.

We found little evidence of compensatory horn growth (Figure 4): the length of horn grown during the second and the third year of life was not correlated with horn growth during the fourth and fifth years (Table 3). The positive

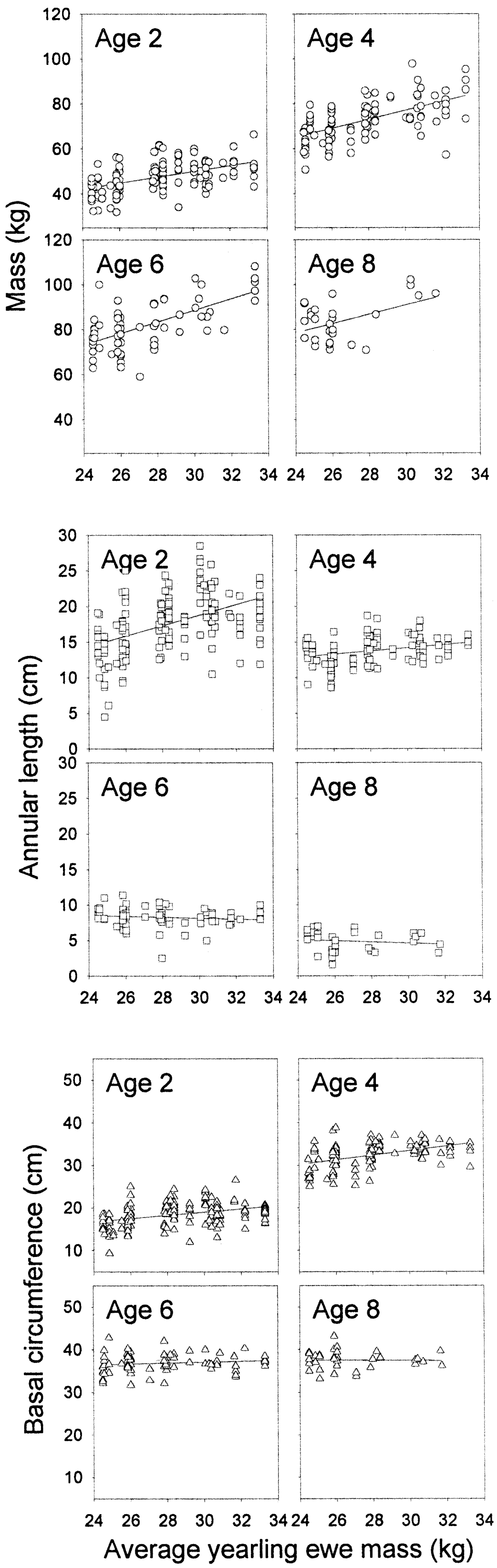

Figure 2
Effects of ram age and average mass of yearling ewes on body mass, mean annular horn length, and basal circumference of bighorn rams at Ram Mountain, Alberta.

Table 2
ANOVA table from mixed effects model describing the relationship between horn annulus length and body mass of bighorn sheep rams in relation to age and resource availability (RA, the average mass of yearling ewes in early June) at Ram Mountain, Alberta

Term	Coefficient (SE)	*t* (*p*)
Intercept	−51.54 (11.05)	−4.66 (<.001)
Age	10.32 (3.46)	2.99 (<.005)
Exp(age)	0.016 (0.003)	6.03 (<.001)
RA	2.28 (0.39)	5.78 (<.001)
Body mass	1.01 (0.18)	5.62 (<.001)
Age × exp(age)	−0.0016 (0.0003)	−5.75 (<.001)
Age × RA	−0.44 (0.13)	−3.51 (<.001)
Age × mass	−0.17 (0.04)	−4.01 (<.001)
RA × mass	−0.027 (0.006)	−4.32 (<.001)
RA × mass × age	0.0050 (0.0015)	3.30 (<.005)

$N = 556$ observations from 156 individuals, 80.0% of variance explained.

correlation between the base circumference of the third and fifth annuli of the same ram (Table 3) was inevitable because of horn geometry. The only evidence of compensatory growth was at the population rather than at the individual level: rams appeared to grow slightly more horn at ages 6–8 years at low than at high resource availability (Figure 2), confirming the results of Jorgenson et al. (1998) that were based on comparing whole-horn (rather than annuli) measurements with population density. That result, however, could have been affected by the selective hunting harvest of rams with fast-growing horns (see below).

The youngest rams legally harvested were 4.5 years of age during the late-summer hunting season. No ram younger than 4 years had legal horns. The probability of being shot before 6 years of age was independent of both body mass in June at age 4 or base circumference of the fourth annulus, but it increased with the cumulative amount of horn grown at 2–4 years of age (Figure 5).

DISCUSSION

Our analyses produced three main results. First, they revealed that as resource availability decreases, young bighorn rams allocate relatively more resources to body than to horn growth, suggesting a conservative strategy that favors body maintenance over investment in secondary sexual characters. Second, contrary to expectations, we found little evidence of compensatory horn growth. Third, hunting mortality of young rams suggests that trophy hunting may select against individuals with fast-growing horns.

We had previously shown that population density had a negative effect on body mass and total horn length of bighorn rams (Jorgenson et al., 1998; Leblanc et al., 2001). The analyses reported here confirm a negative effect of resource availability on horn and body growth of rams. The impact of resource scarcity on annulus length is limited to the first few years of life, but it is lifelong for body mass and annulus base circumference.

Yearling ewe body mass reflects the environmental conditions experienced by bighorn sheep associated with nursery groups. Most rams switch gradually from nursery groups of ewes, lambs, and young males to bachelor groups of adult rams at 2–4 years of age (Festa-Bianchet, 1991). When resource availability was low, young rams in nursery bands experienced high intraspecific competition, with a negative influence on horn growth. High ewe numbers (and low

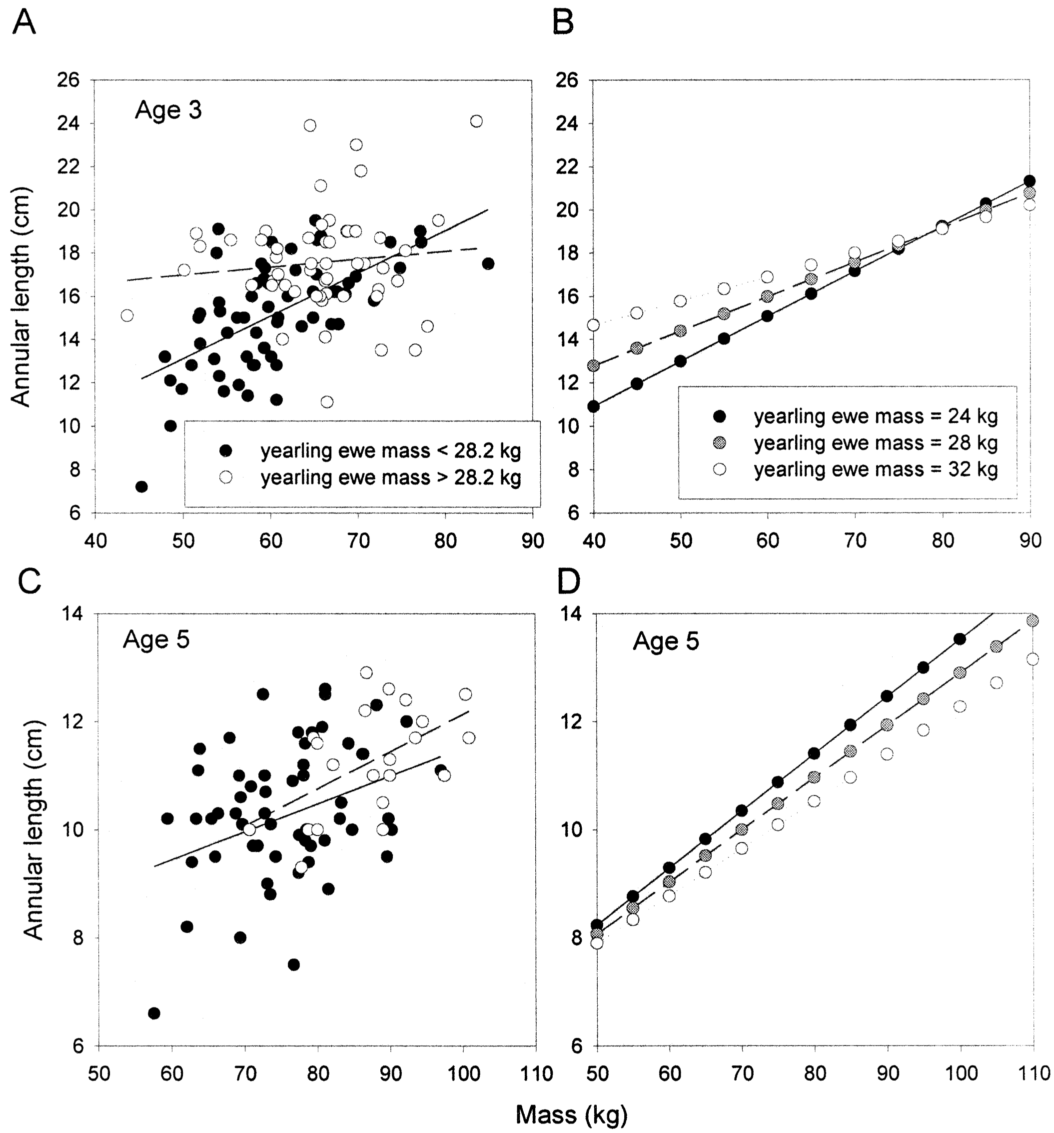

Figure 3
(A, C) The relationship between horn annulus length and body mass for bighorn rams aged 3 and 5 years in years when the average mass of yearling ewes was above and below the long-term average. (B, D) The predicted length of horn annuli grown at 3 and at 5 years of age at low, intermediate, and high levels of resource availability, measured by the average mass of yearling ewes, according to ram body mass.

yearling ewe mass) were also associated with increased lamb mortality, later age of primiparity, lower yearling survival, and lower mass of yearlings of both sexes (Jorgenson et al., 1993a, 1997; Leblanc et al., 2001; Portier et al., 1998). After rams joined bachelor groups at about 3–4 years of age, however, resource availability measured by yearling ewe mass had no effect on the length of new horn annuli. Although the number of ewes tripled during our study, the numbers of males only doubled (Figure 1), partly because ram hunting continued and partly because the natural life expectancy of ewes is longer than that of rams (Jorgenson et al., 1998; Loison et al., 1999). The foraging range of adult rams include areas distant from escape terrain. Those areas are not used by ewes, as they are more sensitive to the risk of predation (Geist, 1971). Jorgenson et al. (1998) reported that age-specific ram horn length was independent of the number of rams in the population. The variability in ram numbers during our study appeared insufficient to produce density-dependent changes in horn or body growth.

As resources become scarce, young rams allocate an increasing proportion of those resources to body growth rather than to horn growth. That allocation strategy may increase the probability of survival, possibly at the cost of decreased lifetime reproductive success. Rams 2 years of age and older can father lambs (Coltman et al., 2002; Hogg and Forbes, 1997), but horn length does not affect reproductive success of rams younger than about 7 years (Coltman et al., 2002). Consequently, by allocating more resources to body growth rather than to horn growth, young rams may not compromise their short-term reproductive success. Heavy young rams appeared to grow as much horn at high as at low density (Figure 3), possibly because increased allocation to body growth may not affect their survival. The relationship between mass and survival of young rams is complex because the heaviest rams may be more active during the rut and possibly suffer higher mortality as a consequence, as reported for feral sheep (Stevenson and Bancroft, 1995). At Ram Mountain, however, the smallest rams aged 3 and 4 years

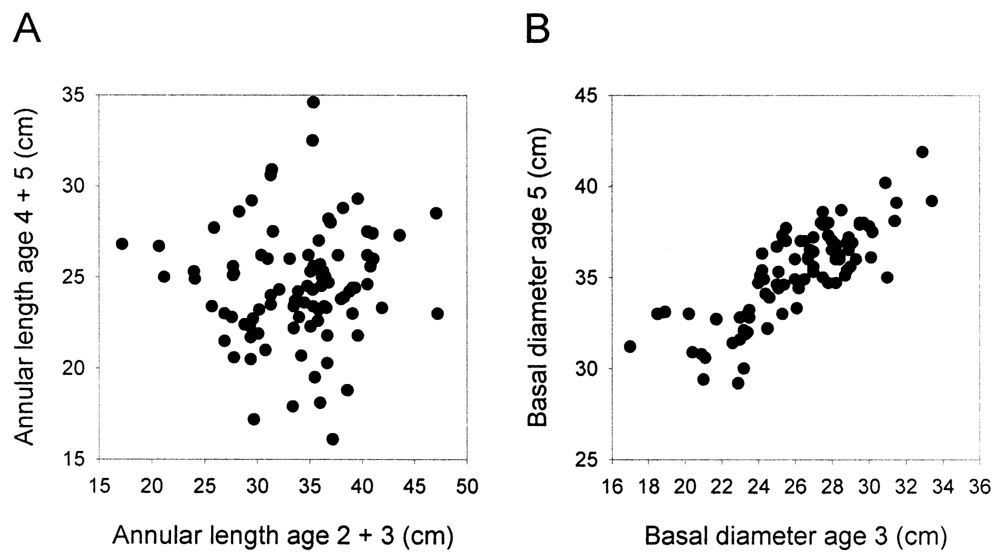

Figure 4
Lack of compensatory horn growth in bighorn rams. Growth in horn length from the ages 4 to 5 (A) and base circumference at age 5 (B) compared with growth in horn length at ages 2 to 3 and base circumference at age 3.

appeared to have lower survival than other rams, although the difference was not significant (Festa-Bianchet et al., 1997). Life expectancy of ewes was correlated with their body mass as young adults (Bérubé et al., 1999), and a similar trend may exist for rams in unhunted populations. By allocating more resources to body growth and less to horn growth, the smaller young rams may trade long-term reproductive success for short-term survival. That allocation pattern was reversed in later years, when rams grew more horn for a given body mass at low than at high resource availability (Figure 3). By age 5, however, absolute horn growth had decreased considerably compared with ages 2–4 (Jorgenson et al., 1998).

The relationship between body mass and horn growth of young rams at low population density was surprisingly weak (Figure 3). That weak phenotypic correlation suggests a potential for hunter selection to act on horn growth directly. Horn size may then evolve independent of body mass if the genetic correlation between these two traits is also weak (Lynch, 1999; Roff, 1996).

We found no evidence of compensatory growth in horn length at the individual level. Compensatory horn growth within the age range that we examined has been reported for mountain goats (*Oreamnos americanus*; Côté et al., 1998) and Cantabrian chamois (*Rupicapra pyrenaica*; Pérez-Barbería et al., 1996), two species in which more than 90% of asymptotic horn growth occurs during the first 3 years of life. In Dall sheep (*Ovis dalli*), which have an age-specific horn growth pattern similar to bighorn sheep, Bunnell (1978) reported compensatory growth at an advanced age (8–9 years), for which we had an inadequate sample. In Alpine ibex (*Capra ibex*), Togo et al. (1999) reported compensatory horn growth for females but not for males. Given that horn length is correlated with reproductive success for males older than about 6 years (Coltman et al., 2002), there may be no advantage for rams that grew large horns early in life to limit horn growth in later years. Consequently, there may be little opportunity for rams with reduced horn growth in early life to ever catch up (Metcalfe and Monaghan, 2001). The apparent population-level trend for greater horn growth at high than at low density for annuli 6–8 (Figure 2) and the greater horn growth for a given body mass of rams older than 5 years (Figure 3) suggest weak compensatory growth, insufficient to make up for the lower growth at 2–4 years (Jorgenson et al., 1998). The lack of compensatory growth at the individual level, however, may indicate that the apparent compensation seen at the population level is due in part to higher hunting mortality of young rams with fast-growing horns at low population density, when the proportion reaching "legal" status at 6–7 years of age was much greater than at high density (Jorgenson et al., 1998).

Finally, our results are consistent with the possibility that trophy hunting may select against large-horned rams (Colt-

Table 3
ANOVA table for general linear models of compensatory horn growth by bighorn sheep rams

Horn length from ages 4–5 ($n = 89$)			Horn base at age 5 ($n = 86$)		
Term	Coefficient (SE)	t (p)	Term	Coefficient (SE)	t (p)
Intercept	24.44 (0.33)	<.001	Intercept	18.73 (1.30)	14.5 (<.001)
			Horn base at age 3	0.63 (0.05)	12.9 (<.001)
Rejected terms					
Horn length from ages 2–3	−0.015 (0.069)	−0.21 (>.05)			
Resource availability	0.18 (0.13)	1.33 (>.05)	Resource availability	0.14 (0.07)	1.94 (>.05)
Horn length × RA	0.018 (0.030)	0.57 (>.05)	Horn base × RA	−0.023 (0.026)	−0.89 (>.05)

Growth at 4 and 5 years of age in annular length and base circumference is modeled as a function of earlier growth (age 2–3) and of resource availability (RA, the average mass of yearling ewes in early June) experienced at age 3. Terms were removed from full models in a reverse stepwise fashion if $p > .05$.

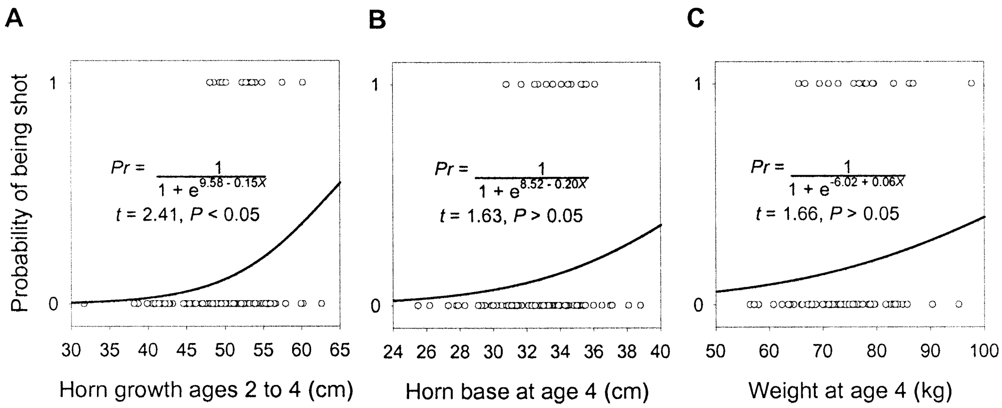

Figure 5
Logistic regression of the probability that a bighorn ram would be shot by a hunter before the age of 6 in relation to cumulative horn growth between ages 2 and 4 (A), horn base circumference at age 4 (B), and body mass at age 4 (C). Observed data and fitted model functions.

man et al., 2003). Rams with fast-growing horns were at greater risk of being shot before 6 years of age than rams with slow-growing horns. Given the lack of compensatory growth in horn length, and because more than 75% of asymptotic horn growth takes place during the first 4 years of life (Jorgenson et al., 1998), rams with short horns by age 4 remain small-horned over their lifetime. Those rams may have a selective advantage under the current hunting regime because many of their competitors with fast-growing horns will be shot. The heritability of horn size is substantial (Coltman et al., 2003). Artificial selection for slow-growing horns would be compounded by the fact that horn size does not affect the reproductive success of young rams (Coltman et al., 2002): hunters remove rams with fast-growing horns before those large horns have a chance to increase the ram's fitness. The weak association between body mass and horn size also allows selection for rams with large bodies and slow-growing horns; that phenotype would be very successful in the clashing combat typical of this species (Geist, 1971), while avoiding the cost of large horns during the hunting season. Given the high demand for trophy rams and the potential to use trophy hunting as part of a conservation strategy (Leader-Williams et al., 2001), further investigation of its potential selective effects is highly desirable.

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