



## Heterogeneity in male horn growth and longevity in a highly sexually dimorphic ungulate

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In sexually dimorphic ungulates, sexual selection favoring rapid horn growth in males may be counterbalanced by a decrease in longevity if horns are costly to produce and maintain. Alternatively, if early horn growth varied with individual quality, it may be positively correlated with longevity. We studied Alpine ibex *Capra ibex* in the Gran Paradiso National Park, Italy, to test these alternatives by comparing early horn growth and longevity of 383 males that died from natural causes. After accounting for age at death, total horn length after age 5 was positively correlated with horn growth from two to four years. Individuals with the fastest horn growth as young adults also had the longest horns later in life. Annual horn growth increments between two and six years of age were independent of longevity for ibex whose age at death ranged from 8 to 16 years. Our results suggest that growing long horns does not constrain longevity. Of the variability in horn length, 22% could be explained by individual heterogeneity, suggesting persistent differences in phenotypic quality among males. Research on un hunted populations of sexually dimorphic ungulates documents how natural mortality varies according to horn or antler size, and can help reduce the impact of sport hunting on natural processes.

Male secondary sexual characters (SSC) may have evolved through sexual selection to increase the attractiveness of males as potential partners, their fighting ability, or both (Darwin 1871, Andersson 1994). Many studies have reported positive correlation between the size, color or complexity of SSC and mating success (mammals: Kruuk et al. 2002; birds: Hill 1991; fishes: Miller and Brooks 2005; arthropods: Mappes et al. 1996). SSCs are thought to be energetically demanding to grow and maintain, and there is often much variability in their expression within a population, because only high-quality individuals can grow large traits (Zahavi 1975). However, little is known about what fitness tradeoffs they may involve (Reznick et al. 2000, Kotiaho 2001).

Life history theory predicts that tradeoffs between reproduction and survival should shape the evolution of SSCs (Stearns 1992, Roff 2002). If SSCs are costly, a positive selection on these characters (via increased fecundity) could be counterbalanced by a negative effect on survival (Møller 1989, Clinton and Le Boeuf 1993, Brooks 2000). According to this theory, males that quickly grow large SSCs may reproduce at a young age, but because of the energetic costs of reproduction (through combats or courtship), they may suffer a decrease in survival. Males with slower SSC growth may survive to reproduce at an older age (Geist 1971). Alternatively, individual hetero-

geneity in the capacity to acquire nutrients and allocate them to SSCs could lead to phenotypic variability in their expression (van Noordwijk and De Jong 1986). High-quality individuals could acquire more resources than their conspecifics, and grow large SSCs without a tradeoff with survival (Reznick et al. 2000, Service 2000). Therefore, size, color or complexity of SSCs could be positively correlated with other fitness-related traits (Kodric-Brown et al. 2006), including survival (Møller and Alatalo 1999, Jennions et al. 2001).

In ungulates, much attention has been paid to the role of horns and antlers as SSCs. In polygynous species, males fight to obtain access to estrous females. In wild and feral sheep, males with large horns usually dominate other males and have a greater chance to reproduce (*Ovis canadensis*: Coltman et al. 2002 ; *O. aries*: Preston et al. 2003, Robinson et al. 2006). The reproductive advantage for large-horned males is substantial. A dominant bighorn ram can sire up to a third of all offspring during one mating season (Coltman et al. 2002). Horns, however, are thought to be costly because they require energy and nutrients to grow, maintain (including heat loss during winter (Picard et al. 1996)), and carry (Geist 1966a). Life history theory would then predict that large horns should have a fitness cost. On the other hand, heterogeneity in individual quality could produce a positive relationship between horn growth

and longevity (Reznick et al. 2000), because weaker individuals may have small horns and die young (Service 2000, Cam et al. 2002).

Although Geist (1966a) suggested four decades ago that horn growth rate and survival may be negatively correlated in bighorn sheep, it is only recently that empirical studies have looked for a survival cost of growing long horns (Robinson et al. 2006, Loehr et al. 2007). In addition to their fundamental value, such studies are important for ungulate management because the selective effects of trophy hunting (which increases the mortality of males with long horns) may be reduced if hunting mimicked natural mortality. In hunted populations, males with rapidly growing horns are at risk of harvest at a young age (Festa-Bianchet et al. 2004). However, the potential selective effect of trophy hunting on early horn growth is controversial (Coltman et al. 2003, Loehr et al. 2007), partly because little is known about the relationship between horn growth and longevity in the absence of hunting mortality. Understanding how natural mortality covaries with horn size is central to test for tradeoffs between sexual and natural selection in the evolution of SSCs, and to assess the potential selective effects of hunting.

Here we explore the relationships between horn growth rate and longevity in an un hunted population of Alpine ibex *Capra ibex*. Ibex are long-lived and strongly sexually dimorphic, with condition-dependent horn growth in males (Giacometti et al. 2002, von Hardenberg et al. 2004). Data on horn growth of Alpine ibex males found dead from winter starvation for a population protected since 1922 were analyzed by von Hardenberg et al. (2004) who found that horn growth decreased in the two years preceding death. Here we examine the same sample to contrast the hypothesis that sexual selection favoring rapid horn growth at young age is counterbalanced by a decrease in longevity (Geist 1966a, Robinson et al. 2006, Loehr et al. 2007), with the alternative that horn growth and longevity are positively correlated because they both depend on individual quality.

## Material and methods

Between 1988 and 1997, park wardens in the Gran Paradiso National Park (GPNP), Italian Alps (45°26'N, 7°08'E), collected all ibex skulls found during regular foot patrols. No hunting is allowed in the Park and there are no large predators. The main causes of death are winter starvation, senescence or accidents such as avalanches. Because park wardens frequently patrol their assigned area, they find ibex carcasses in the year of death. Since horn growth stops during winter forming a distinct growth ring or annulus, it is possible to know age at death of each individual by counting the annuli (Geist 1966b). Ibex skulls were cleaned and annual horn growth increments measured to the nearest 0.5 mm with a caliper along the center of the posterior curvature. The first growth increment is often worn or broken and it was excluded from analyses. Because von Hardenberg et al. (2004) had shown a decline in growth during the final two years of life, independently of the age at death, we excluded from analyses horn increments grown by each ibex in the two years before its death. Similarly to von Hardenberg et al. (2004), we also

excluded individuals with unknown year of death and ibex that had clearly died in avalanches. Less than 5% of ibex appeared to have died in avalanches, and we excluded them because avalanches may kill a random sample of ibex males. von Hardenberg et al. (2004) provide more details on skull collections and horn measurements.

A fundamental assumption of our study is that there are no biases in skulls collection. Such biases are unlikely because wardens systematically search the park to recover all ibex skulls as part of their duties.

## Statistical analyses

We used a linear regression model to test if the length of horn grown between 2–4 years of age was correlated with horn growth after age 5. Because horn length increases with age and is correlated with longevity (Fig. 1a), we also included log-transformed longevity as an explanatory variable in the analysis. Thus, horn length grown after age 5 was a relative measure, controlled for longevity (Fig. 2). A positive correlation of horn length at 2–4 years of age and after age 5 would suggest persistent individual differences in phenotypic quality. A negative correlation would indicate compensatory

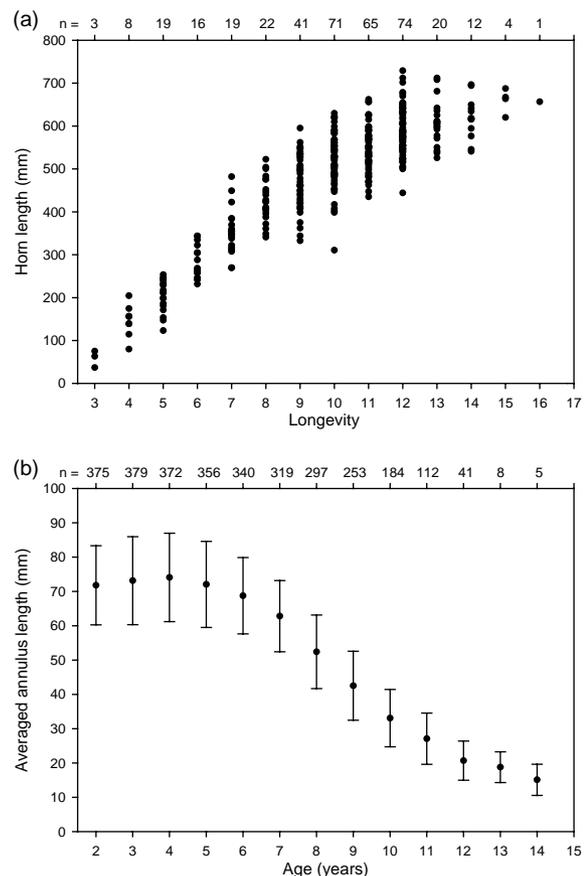


Fig. 1. (a) Positive relationship between horn length (mm) and age at death for 375 male ibex collected by Park Wardens in the Gran Paradiso National Park, Italy, from 1988 to 1997. The first and last annual horn growth increments are not included. (b) Relationship between annual increment horn length and age ( $n = 383$ , mean  $\pm$  SD). Sample sizes differ because eight individuals are not included in (a) as not all of their increments were measured.

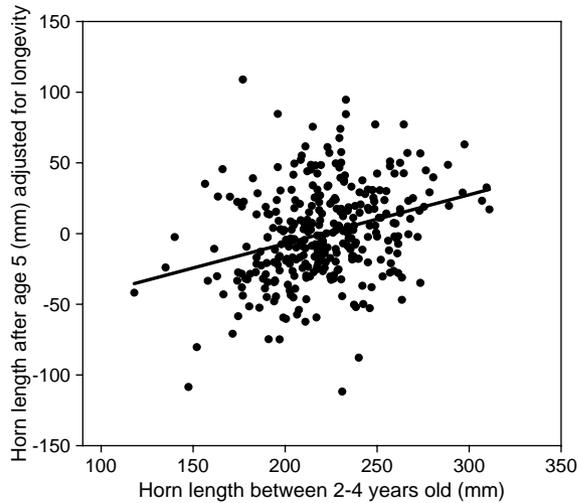


Fig. 2. Relationship between the relative measure of horn length grown after age 5, controlled for longevity, and horn growth between two and four years of age ( $n = 328$ ,  $r^2 = 0.094$ ) for male ibex from the Gran Paradiso National Park, Italy, 1988 to 1997.

growth. We defined as “young age” horn growth between two and four years of age because average increment length increases slightly until age 4 and then decreases (Fig. 1b).

In a second analysis, we used a linear mixed effects model (Pinheiro and Bates 2000) to test if longevity was related to early annual horn growth for males that survived beyond eight years of age. Survival of male ibex between two and 12 years of age is much higher than that of other ungulates, and less than 15% of 2-year-old males die before eight years of age (Toigo et al. 1997, Loison et al. 1999). In this analysis, we used annual horn growth increments between two and six years of age as a measure of “early horn growth” common to our entire sample. We did not use age class 2–4 as in the previous analysis because we wanted to consider all horn increments grown two or more years before death by individuals that survived to at least eight years of age. Of 383 ibex males in our sample, only 17% died before eight years of age. To avoid pseudo-replication due to several annual horn growth increments measured on the same horn at different ages (Machlis et al. 1985), and to calculate the variance in annual horn growth increments attributable to individual “qualities”, we fitted male identity (ID) as a random term. We fitted the year during which each increment was grown as a fixed term (18-level factor) to account for year-specific environmental variability (Postma 2006) that can affect horn growth (Giacometti et al. 2002, von Hardenberg et al. 2004). We also fitted age and longevity as fixed predictor terms of annual horn growth increments between two and six years of age. The significance of the fixed terms was assessed with conditional F-tests. We used this causal statistical approach because we could measure many increments on a given male but had only one measure of longevity per individual. Therefore, we cannot use mixed models to estimate the proportion of variation in longevity attributable to individual quality (Steele and Hogg 2003). We assessed significance of the random term ID using a log-likelihood ratio (LRT) test comparing models with and without the term (Steele and Hogg 2003). We checked for a possible bias for the LRT statistics under a  $\chi^2$  distribution

(Pinheiro and Bates 2000) by comparing this model selection for the random term with a model selection based on the Akaike information criterion (AIC). We checked graphically for normality of residuals and homogeneity of variance. We conducted all analyses using the R 2.1.1 statistical package using the restricted maximum likelihood estimation procedure.

## Results

### Testing individual heterogeneity

Horn length grown after age 5, adjusted for longevity, was weakly positively correlated with horn growth at 2–4 years of age ( $\beta = 0.35$ ,  $SE = 0.059$  mm,  $t = 5.83$ ,  $r^2 = 0.094$ ,  $p < 0.001$ , Fig. 2). A comparison of total horn length grown after age 3, adjusted for age at death, and increment length at age 2 also revealed a positive correlation ( $\beta = 1.50$ ,  $SE = 0.218$  mm,  $t = 6.89$ ,  $r^2 = 0.127$ ,  $p < 0.001$ ), confirming the result obtained with age class 2–4. In the linear mixed model of annual horn growth increments between two and six years for individuals that survived beyond eight years, the random term ID was highly significant ( $\chi^2 = 543.80$ ,  $DF = 1$ ,  $p < 0.001$ ,  $n = 318$ ,  $AIC = 11602.43$  vs  $12261.98$  when removing ID from the model). ID explained 22% of the between-males variance in annual horn growth ( $(\sigma_{ID}^2 / \sigma_{total}^2) \times 100$ ). For a given male, adding a first-order autoregressive process of the within-subject error increased substantially the fit of the model ( $p = 0.525$ ,  $\chi^2 = 137.95$ ,  $DF = 1$ ,  $p < 0.001$ ,  $AIC = 11466.47$  vs  $11602.43$  for the same full model without the correlation structure), suggesting that ibex with good growth one year were likely to have above-average growth in other years.

### Age-specific horn growth and longevity

We tested whether early annual horn growth increments were related to longevity in a linear mixed effect model with ID as a random term. In the final model, variation in increment length between two and six years of age was best explained by a quadratic relationship with age (age:  $\beta = 7.600$ ,  $SE = 1.054$  mm,  $F_{1,1244} = 11.164$ ,  $p < 0.001$ ; age<sup>2</sup>:  $\beta = -1.022$ ,  $SE = 0.128$  mm,  $F_{1,1244} = 73.274$ ,  $p < 0.001$ , Table 1) and yearly differences ( $F_{17,1244} = 5.501$ ,  $p < 0.001$ ). More importantly, after taking into account age and year effects, longevity was independent of annual horn

Table 1. Linear mixed model of the effects of age and longevity on horn growth between two and six years of age from 1581 annual horn growth increments measured on 318 male ibex that survived to at least eight years of age. We fitted ID as random term and year as fixed term in both models. Wardens collected ibex skulls in the Gran Paradiso National Park, Italy, from 1988 to 1997.

Terms	DF	Estimates	SE	F	p
Full model					
Age	1,1244	7.757	1.063	11.148	0.001
Age <sup>2</sup>	1,1244	-1.020	0.128	73.208	<0.001
Longevity	1,316	-0.438	0.387	1.28	0.259
Final model					
Age	1,1244	7.6	1.054	11.146	<0.001
Age <sup>2</sup>	1,1244	-1.023	0.128	73.201	<0.001

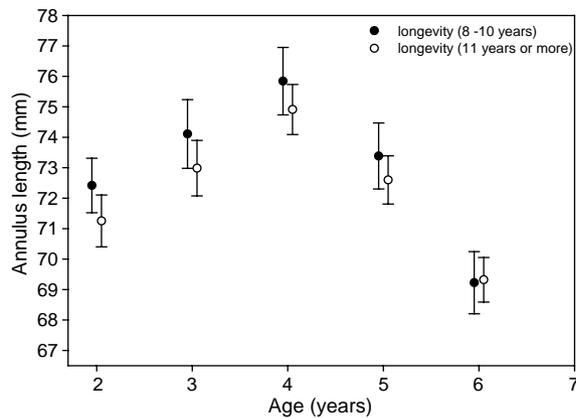


Fig. 3. Length ( $\pm$ SE) of the annual horn growth increments grown between two and six years of age for 134 male ibex that died when aged 8 to 10 years and 176 individuals that survived over 11 years of age in the Gran Paradiso National Park, Italy, 1988 to 1997.

growth increments between two and six years, for individuals whose longevity ranged from eight to 16 years ( $F_{1,316} = 1.279$ ,  $p = 0.259$ , Table 1). Figure 3 illustrates this result by comparing individuals that died between eight and 10 years with individuals that survived beyond that age. Despite the marginal but consistently longer annual horn growth between two and five years old for males that lived between eight and 10 years, logistic regression (family binomial with logit link function) suggested that the probability of surviving past 10 years was not related to the horn growth between two to five years of age ( $\chi^2 = 0.86$ ,  $DF = 1$ ,  $p = 0.36$ ). Over this period, the mean cumulative horn length only differed by 1.4% (4 mm) between the two longevity classes.

## Discussion

Using a large sample of un hunted wild polygynous ungulates that died of natural causes, we tested two opposing hypotheses relating early horn growth and longevity in males. We found persistent individual variation in ability to grow horns. Our results suggest that males with fast-growing horns early in life were able to grow longer horns without any apparent longevity cost. Because male ibex do not compensate for reduced horn growth at young age by increasing growth in later years (Toïgo et al. 1999), persistent individual differences lead to much variability in total horn length among mature males. After controlling for age and the year when a horn increment was grown, about a quarter of this phenotypic variability was explained by individual quality.

It is likely that the length of ibex horns is correlated with reproductive success, as reported for other polygynous ungulates with a similar mating system (Coltman et al. 2002, Preston et al. 2003). Despite their association with reproductive benefits, Pomiankowski and Møller (1995) found that high variability in sexually selected traits is common in nature. We also found much individual heterogeneity in horn size, and some males were unable

to grow long horns independently of their longevity. Hence we suggest that ibex horns could be an honest signal of condition (Preston et al. 2003, von Hardenberg et al. 2004, Malo et al. 2005 von Hardenberg et al. 2007). Assuming that horn growth and maintenance are costly, our results would also be consistent with the Handicap principle (Zahavi 1975), which predicts a positive correlation between the size, color or intensity of costly SSCs and the quality of their bearer. Individuals could advertise their quality if they are able to bear costly displays without compromising their survival (Zahavi 1975). von Hardenberg et al. (2007) found that ibex horn growth was positively correlated with multilocus heterozygosity and suggested that long-horned males were of better genotypic quality. Therefore, horn size could potentially guide mate selection by females, or help establish dominance rank among males while avoiding potentially costly fights between males of different “quality” (Pelletier and Festa-Bianchet 2006). Contrary to our expectation, however, we found no relationship between early horn growth and longevity. Males with slow-growing horns may increase their survival by limiting their reproductive effort. As they age, males with rapidly growing horns probably experience an increase reproductive benefit (Coltman et al. 2002).

Our findings do not exclude the possibility that there may be a survival cost for mature males with the largest horns, after a few years of intense reproductive activity. Geist (1966a, 1971) suggested that rapidly-growing males would participate in rutting activities at a young age and suffer increased mortality through injuries or exhaustion. Recent suggestions that Dall’s sheep, *Ovis dalli*, rams with rapidly-growing horns suffer a survival cost of reproduction as young as 5–6 years (Loehr et al. 2007) ignore data on age-specific reproductive behavior and reproductive success of males of polygynous ungulates. Geist (1966a) suggested a tradeoff between horn growth and longevity by comparing bighorn rams that did and did not survive to 12 years of age. We now know that 12-year-old bighorn rams are well into survival senescence (Loison et al. 1999) and that dominant rams obtain high reproductive success at 7–10 years of age (Coltman et al. 2002). In male ibex, survival senescence becomes evident at about 10–12 years of age and the age-related decrease in survival is very rapid thereafter (Toïgo et al. 2007). We speculate that males with fast-growing horns may make a strong reproductive effort when aged 10–14 years, possibly leading to increased mortality. Such an age-dependent tradeoff may explain the weak trend for males with the longest horns not to survive to the very oldest ages (Fig. 1a). Because of the small sample of males aged 12 years and older, we could not test statistically for this age dependent tradeoff. It remains possible, however, that for mature males with large horns that take an active part in the rut, survival may both increase because of high individual quality and decrease because of high reproductive effort.

Our results underline the importance of studying un hunted populations of ungulates to understand the relationship between horn growth and natural mortality. In feral sheep, Robinson et al. (2006) found that males with larger horns gained in annual breeding success but suffered a decrease in longevity. In that population, the largest male lambs can participate in the rut but experience a survival cost

(Stevenson and Bancroft 1995). Because Robinson et al. (2006) did not look at age-specific costs of long horns, it remains unclear whether this cost also affects adult rams. Clinton and Le Boeuf (1993) reported that some male elephant seals *Mirounga angustirostris* that attempted to breed for the first time suffered a decrease in survival, and found a positive, but not significant, relationship between mating success and survival for 'established' breeding males. Nonetheless, high-quality males enjoy high survival through their prime reproductive years in many other polygynous mammals. For example, Pelletier et al. (2006) found that longevity was correlated with mating effort for bighorn rams aged 2–5 years. Heavier young males participated more in the rut than lighter males of the same age (Pelletier 2005). In fallow deer *Dama dama*, mature males that reproduce are larger (McElligott et al. 2001) and enjoy higher survival than non-reproducers (McElligott et al. 2002).

In conclusion, we found significant individual heterogeneity in the capacity to grow horns but no effect of horn growth on longevity. We suggest that age-specific horn growth during young age is a correlate of individual quality. This suggestion has substantial implications for ungulate management and conservation, because of the potential impact of artificial selection through trophy hunting (Loehr et al. 2007). We suggest that any tradeoff between early horn growth and longevity would only affect individuals that survived past their prime reproductive years. Hunting regulations that allow the harvest of males with large horns when younger than about 10 years would not mimic natural mortality and could select for small horn size (Coltman et al. 2003). Behavioral and paternity data are required to provide a better understanding of the relationships between horn size, reproductive effort and reproductive success, all of which could affect the age-dependent tradeoff between horn size and longevity.

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