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Secondary sexual characters signal fighting ability and determine social rank in Alpine ibex (*Capra ibex*)

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Abstract Social dominance is a fundamental aspect of male evolutionary ecology in polygynous mammals because it determines access to estrous females. As it is rarely possible to monitor marked individuals of known morphology, little is known about the determinants of male dominance. We studied the social structure of Alpine ibex males in Gran Paradiso National Park, Italy in 2003, 2006, and 2007. Dominance interactions produced a linear social hierarchy. In ibex males, body mass and horn length are key traits in male-male combat, and both increase with age. We explored the links between age, body mass, horn length, and social rank. Ibex males showed much age-independent phenotypic heterogeneity and rapidly growing males reached high rank at a younger age than slow-growing males. Because there is no trade-off between horn growth and longevity, fast-growing males may face weak potential costs of rapid growth and high fitness benefit of achieving high rank. Violent interactions were more likely to occur between males similar in both mass and horn length, independently of age. We suggest that only high-quality individuals can afford a strategy of rapid growth for both secondary sexual characters, and likely reap substantial fitness benefits.

Keywords Alpine ibex · *Capra ibex* · Dominance · Hierarchy · Horn · Body mass · Sexual selection

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Introduction

In seasonally breeding polygynous mammals, a few dominant males can father a large share of each cohort (Kodric-Brown and Brown 1984; Clutton-Brock 1989), partly because their high social rank allows them to exclude other males from mating. A dominance relationship exists if the outcome of repeated aggressive interactions between two individuals (a dyad) is consistently in favor of one dyad member (Drews 1993). Studies of polygynous ungulates typically report strong positive correlations between male social rank and breeding success (Hogg and Forbes 1997; McElligott et al. 2001; Preston et al. 2003). When fitness depends on being dominant to other males, selection for rapid growth in body or weapon size could lead to sexual dimorphism in morphology, survival, and age-specific reproductive success (Clutton-Brock 1989; Andersson 1994).

Most polygynous ungulates are sexually dimorphic in body mass and weapon size (Short and Balaban 1994). These traits should be under strong sexual selection (Andersson 1994) because they affect male dominance (Geist 1966a; Clutton-Brock 1982; Loison et al. 1999b). Few studies, however, have assessed the role of mass or weapon size in determining male rank (Barrette and Vandal 1986; Alvarez 1990; McElligott et al. 2001; Pelletier and Festa-Bianchet 2006) and very few simultaneously examined how variation in these traits and age may affect male rank or reproductive success (Coltman et al. 2002; Preston

et al. 2003). Because of the difficulty of measuring mass and horn size in free-ranging adult ungulates, little is known about the relative roles and potential interactions between these variables in determining male social rank.

By providing earlier access to high dominance status, rapid growth could allow earlier reproduction, possibly at the expense of survival and future reproductive success (Geist 1971; Stearns 1992; Robinson et al. 2006). Secondary sexual characteristics in ungulates, however, appear to be an honest signal of condition (Malo et al. 2005; Weladji et al. 2005; Vanpé et al. 2007), likely because dominance is frequently challenged by rival males. Because large-horned males in poor condition may face a high risk of injury from fighting, males should be under strong selection to allocate much energy to both maintenance and growth of sexually selected characters (Reznick et al. 2000; Kodric-Brown et al. 2006). Individual heterogeneity could be a major determinant of trait variability (van Noordwijk and De Jong 1986; Vanpé et al. 2007). For example, Coltman et al. (2005) reported positive genetic and phenotypic correlations between horn length and body mass in bighorn sheep (*Ovis canadensis*), two heritable traits correlated with male reproductive success (Coltman et al. 2002; Coltman et al. 2005). Yet, there is little information on the proximal mechanisms involved in the evolution of correlated sexual characters, especially in long-lived species with multiannual growth.

Agonistic interactions between males can escalate to very violent fights and males have evolved various mechanisms to assess opponents and avoid contests when their chances to win cannot overcome potential costs. For instance, ritualized behavior such as parallel walks can prevent escalated fights (Clutton-Brock et al. 1979). As male ungulates age, they become larger and more experienced, therefore rank generally increases with age (Hass and Jenni 1991; Pelletier et al. 2003). Horns and large mass may also be a signal of fighting ability (Geist 1966b; Clutton-Brock 1982), and small males or males in poor condition should avoid escalated fights with superior opponents to prevent injuries (Parker 1974; Clutton-Brock et al. 1979; McElligott et al. 1998). For example, up to 6% of rutting red deer stags (*Cervus elaphus*) are permanently injured each year (Clutton-Brock et al. 1979).

Here, we use 3 years of data on marked Alpine ibex (*Capra ibex*) males to compare the relative roles of horn length, body mass, and age in determining social rank and on behavior during intrasexual aggressive encounters. Ibex are one of the most sexually dimorphic ungulates: fully grown males weigh more than twice as much as females, and male horns are three times as long as female horns (Toïgo et al. 1999). Unlike other dimorphic ungulates (Gaillard et al. 2000), however, ibex show almost no sexual differences in survival from 1 to 11 years of age, when both sexes enjoy very high survival, followed by high mortality of

males aged 12-14 years (Toïgo et al. 2007). Therefore, male reproductive effort may have little effect on survival until an advanced age, unlike other ungulates (Loison et al. 1999a).

Based on research on other ungulates (Barrette and Vandal 1986; Côté 2000a; Pelletier and Festa-Bianchet 2006), we hypothesized that males would form a linear dominance hierarchy during summer. In other species, stable dyadic relationships established in summer hold until the rut (McElligott et al. 2001). We also hypothesized that there would be a positive relationship between horn length and body mass (Coltman et al. 2002), and predicted that it weaken with age because older senescent males may lose body mass. Horns continue to grow after asymptotic body mass is reached and until senescence (Bergeron et al. 2008). We also predicted that the interaction between mass and horn length would be the most important determinant of rank because the effects of a given horn length could be stronger for large males in good condition than for small, possibly senescent, males. Finally, because compared to other ungulates ibex males are surprisingly long-lived and appear to adopt a conservative growth strategy (Toïgo et al. 2007), we predicted that small males will avoid escalated interactions with larger competitors.

Methods

Study area and population

We studied ibex in the Levionaz basin (1,700 ha, 1,700-3,300 m above sea level (a.s.l.)) in the Gran Paradiso National Park (45°26′ N, 7°08′ E), Western Italian Alps, where hunting is prohibited. Large predators such as lynx (*Lynx lynx*) and wolf (*Canis lupus*) have been extirpated for about a century, whereas livestock has been absent for about 15 years. From late May to December, there is a strong sexual segregation and ibex males mostly use high altitude (2,300-3,300 m a.s.l.) cliffs, steep slopes, and alpine meadows where *Carex curvula* and *Festuca* spp. are the dominant graminoids. Males spend the winter at lower altitudes (1,700–2,300 m a.s.l) with conifers (*Picea abies*, *Larix decidua*, and *Pinus cembra*), bushes (*Rhododendron ferrugineum*, *Vaccinium myrtillus*, and *Juniperus communis*) and pastures near villages (Grignolio et al. 2003). Both sexes can reach sexual maturity at age 1.5 and adult males and females only aggregate during the rut (December-January). Kids are born in June. There are suggestions that male social system is based on absolute rank, with a linear hierarchy based on memory of past encounters in small populations and on horn size when assessing strangers (Nievergelt 1966; Schaller 1977; review in Parrini et al. 2009). During the rut, a few high-ranking males defend oestrus females and low-ranking males form coursing groups and mate opportunisti-

cally (reviewed in Parrini et al. 2009). The number of ibex counted in the study area decreased from 108 males, 119 females, and 30 kids and yearlings in 2003 to 77 males, 60 females, and 24 kids and yearlings in 2007. Since 1992, Park wardens have captured males with tranquilizing darts for marking and to evaluate health status (von Hardenberg 2005). We observed 52 males in 2003, 53 in 2006, and 55 in 2007 marked with unique combinations of colored plastic ear tags or radio collars. At capture, we aged males by counting the horn annuli (von Hardenberg et al. 2004).

Dominance data

Ibex males form large bachelor groups in late spring and throughout summer. We observed agonistic interactions ad libitum during 2 weeks per month from March to October 2003, and most days from late April to mid-August 2006 and 2007. We used binoculars (10×42) to record inter-actions during daylight hours, for >650 h of observation each year. We used the following four behaviors as a sign of dominance of male A over male B: (1) mounting: A mounted B; (2) displacement: A walked towards B while threatening it with its horns, and B ran or walked away. Male A would usually forage or rest at the exact site from where B was displaced. In 2006 and 2007, we classified displacements as "escalated" if they involved direct aggressive interactions and as "non-contact" if they did not. (3) Horn fight: after a fight involving frontal horn clashes, sideways slashes and pushing, B avoided A while A attempted to interact with B. (4) Procession: after a horn fight, B walked away and A followed it closely and persistently. All behavior were considered as equal signs of dominance. Interactions with no clear winner were not recorded during observations and were therefore not used to assess rank.

We included interactions at salt licks (24% of all interactions). Côté (2000a) reported differences in the hierarchy of mountain goat (*Oreamnos americanus*) near traps baited with salt and elsewhere. Ibex salt licks, however, were in very open areas where males could easily see each other and, presumably, decide whether or not to interact. Including or excluding interactions recorded at licks did not affect the structure of dominance matrices (see "Results" section).

Only displacements from the salt were recorded in 2003. We recorded three other behaviors in 2006 and 2007: monopolize salt: male A licks the salt and prevents other nearby males from accessing it. We recorded A as dominant only to males that waited to approach the salt after he left. Resist displacement: B tries unsuccessfully to displace A from the salt. Salt scooping: A and B move toward the salt and A prevents B from approaching the salt and B licks the salt after A leaves.

Body measurements

From 2000 to 2007, we repeatedly weighed males every summer with two platform scales located at salt licks (Bassano et al. 2003). Mass gain was linear from May to August (von Hardenberg 2005); therefore, we adjusted the mass of each male to August 1, using a linear mixed effect model (LME, Pinheiro and Bates 2000) with male identity as a random term. This approach controlled for daily fluctuation in mass that may affect the estimation of mass with simple linear models (Pelletier et al. 2007). We adjusted body mass of males weighed at least twice in a summer (Fig. 1a).

Annual horn increments were measured with a caliper along the frontal curvature on males captured or recovered dead. In addition, we measured annual horn increments of free-ranging males on the external side of the horns using parallel laser pointers and a digital camera (Bergeron 2007).
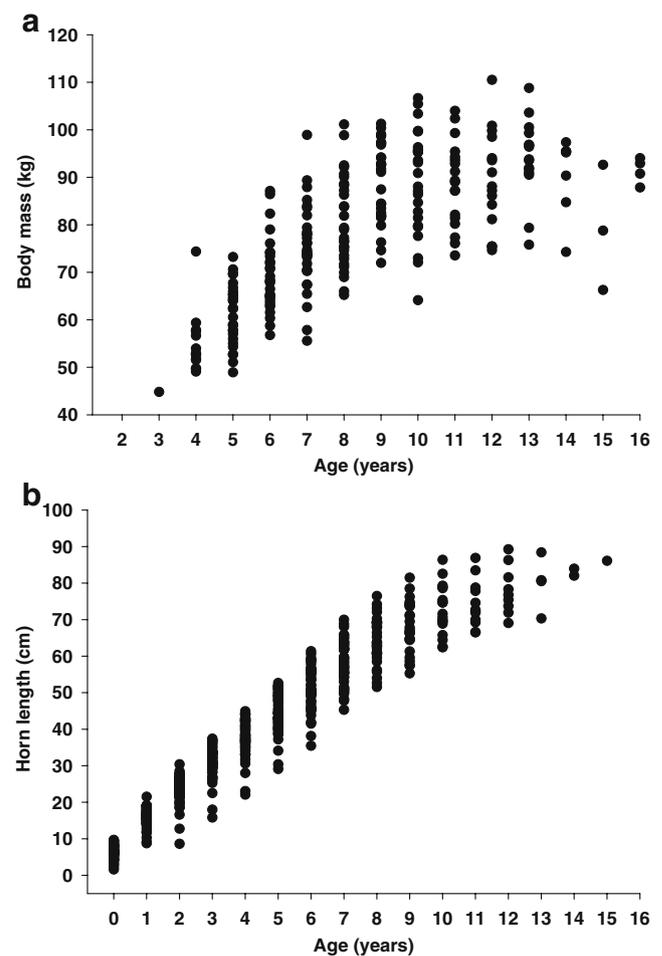
Fig. 1 a Body mass adjusted to August 1 compared to age for Alpine ibex males at Levionaz, Gran Paradiso National Park, Italy, 2000 to 2007 (244 adjusted yearly masses from 83 individuals). b Relationship between age and total horn length (523 yearly measurements from 56 males)

It is easier to measure on photographs the distance between annuli on the external than on the frontal side of the horn. Because most males were first captured when aged 4 years or older, total horn length was the sum of annual horn increments measured along the frontal curvature for the first 4 years of age and of lateral measurements for later ones (Fig. 1b). We considered all annuli because in this population, it was very rare to see substantial breaking or wearing out of the tip of the horns. We used the laser system to measure six frontal horn increments from five males captured when younger than 4 years. We did not include the horn increment grown during the year when rank was determined because most interactions were observed during late spring and summer, before annual horn growth was completed.

Statistical analyses

We calculated social rank separately for 2003, 2006, and 2007 for marked ibex that interacted with at least five other males (Pelletier et al. 2003). We organized all dyads in a dominance matrix using Matman 1.1 for Windows (Noldus Information Technology 2003) and calculated the linearity index h' (de Vries 1995), which is based on the Landau index (Landau 1951), but corrects for unknown relationships (de Vries 1995, 1998). In a linear hierarchy, if A dominates B and B dominates C, then A also dominates C. The value of h' ranges from 0 (no linearity) to 1 (perfect linearity, with all possible dyads observed to interact) and we assessed its significance based on 10,000 randomizations. When linearity is significant but <1, Matman calculates the optimal near-linear order of individuals with a two-steps iterative procedure (1,000 sequential trials, Côté 2000b) that minimizes first the number and then the strength of inconsistencies. An inconsistency occurs when an individual dominates another that has a higher position in the hierarchy. The strength of the inconsistency is the number of rank positions between the two individuals (de Vries 1995, 1998). Each year, we ranked males in a linear hierarchy and calculated the directional consistency (DC) index, the probability that the outcome of an interaction is consistent with earlier encounters of the same dyad. A DC

value of 1 indicates perfect predictability based on previous encounters, and 0 means no predictability (van Hooff and Wensing 1987). The number of males in yearly social hierarchies differed (Table 1). Therefore, to combine data from the 3 years, we calculated the relative rank of each male each year as $1-(\text{rank}/N_i)$ where N_i is the number of males in the hierarchy during year I (Côté 2000b). Males with rank near 1 are dominant; those with rank near 0 are subordinates.

We used LME to investigate the relationship between log-transformed horn length and log-transformed body mass for two age classes (4-7 years old: $n=63$ measures from 30 males; 8–14 years old: $n=55$ measures from 27 males), using all data from 2000 to 2007. At 8–9 years of age, mass gain decelerates (Fig. 1a), and survival decreases (Toïgo et al. 2007). We had no males with measurements of both mass and horn length before 4 years of age. We fitted a two-age-class model with the log of horn length as the response variable and the log of mass, age class, and their interaction as fixed terms. Ibex identity and cohort were fitted as random terms to avoid pseudo-replication (Machlis et al. 1985) and to account for year effects, as mass and horn length were measured on some males during more than 1 year.

We combined social rank of males for all 3 years and explored determinants of rank using 62 observations from 36 males of known rank, mass, horn length, and age. We used a LME with rank as the response variable and mass, horn length, age, and all possible interactions as fixed effects. We centered and reduced the data to allow direct comparison of their effects. We fitted male identity as a random term and year (factor) as a fixed term in all models. Because of strong correlations of age with mass and horn length (Fig. 1, Table 2), we also tested causal hypotheses explaining the patterns of correlation with social rank using path analysis (Shipley 2009). Both analyses led to the same biological conclusions (see electronic supplementary material S1 Appendix for details on the path analysis) and here, we only present the linear mixed model. We also modeled the probability to observe an escalated interaction for all dyads in 2006 and 2007, given the absolute difference in age, mass, and horn length between the members of each dyad, with a logistic LME with interaction type as binary response variable. The full model included the differences in mass,

Table 1 Dominance matrices of Alpine ibex males in Levionaz, Gran Paradiso National Park, Italy

Year	No. of males	Interactions observed	Percent of dyads observed	h'[a]	P value[b]	DC[c]
2003	36	318	30.7	0.15	0.023	0.87
2006	39	491	38.1	0.26	<0.001	0.95
2007	35	514	44.5	0.27	<0.001	0.92

[a] Linearity index

[b] P value associated with the linearity test of the h' index

[c] Directional consistency index in encounter outcome

Table 2 Correlation matrix of age, mass, horn length, and rank of Alpine ibex males in Levionaz, Gran Paradiso National Park, Italy

	Mass	Horn length	Rank
Age	0.63	0.90	0.72
Mass		0.77	0.84
Horn length			0.84

horn length, age, and their interactions. Because dominance is an attribute of two individuals (Barrette and Vandal 1986), we fitted dyad identity as a random term in all models. Model selections were performed using backward procedures, sequentially removing the least significant term ($P>0.05$) from the model based on its P value. All mixed model analyses used R 2.7.1 (www.r-project.org). All estimates are presented±SE.

Results

Social rank

Each year, ibex males established a significantly linear hierarchy (Table 1). The high directional consistency index (Table 1) indicates that for a given dyad, the outcome of an interaction was highly consistent with the result of previous interactions. Interactions at the salt lick did not affect the results. For example, in 2006, h' and DC index were respectively 0.26 and 0.95 (Table 1); removing interactions at the lick increased marginally the linearity index (h'=0.28, $p<0.001$) and the DC index (0.96), but reduced the sample from 39 to 31 individuals and from 491 to 321 interactions. We found significant individual effects (variance component of individual random effect: 95% C.I.=0.026-0.174) in a mixed model with rank as the dependent variable and age and size as independent variables. ID accounted for 26.5% (($\sigma_{ID}^2/\sigma_{total}^2$)×100) of the variance in rank.

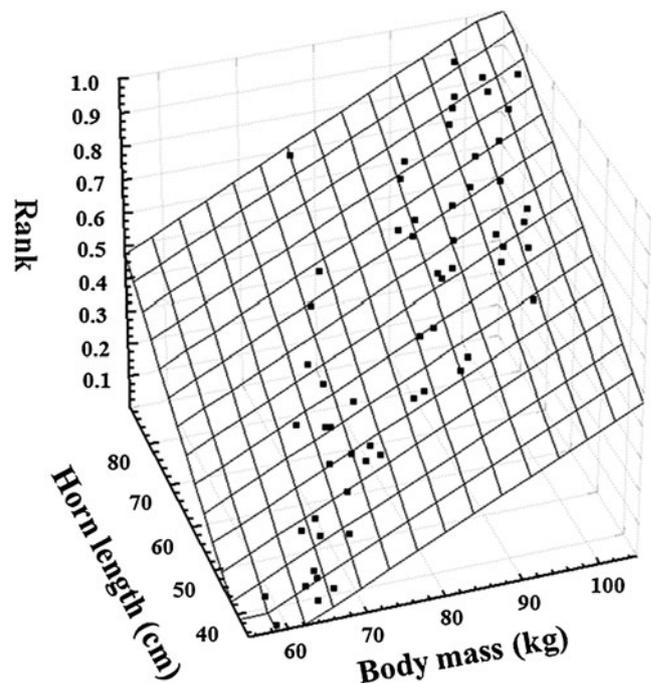### Relationship between body mass and horn length

Although ibex males reached asymptotic mass at 9-10 years (Fig. 1a), the slope of horn length on body mass did not differ between males aged 4-7 and 8-14 years (interaction of mass × age class: 0.017±0.077, $F_{1,114}=0.046$, $P=0.831$, Fig. 2). Heavy males had long horns, independently of age class (body mass: 0.900±0.039, $F_{1,115}=1370.619$, $P<0.001$). For a given mass, males older than 8 years had longer horns than younger males (age class: 0.074±0.014, $F_{1,115}=29.546$, $P<0.001$), as expected given that horns grow through life. The relationship between mass and horn length appeared weaker for older males (age class 4-7: $\sigma^2=0.0051$, age class 8–12: $\sigma^2=0.0079$, Fig. 2).
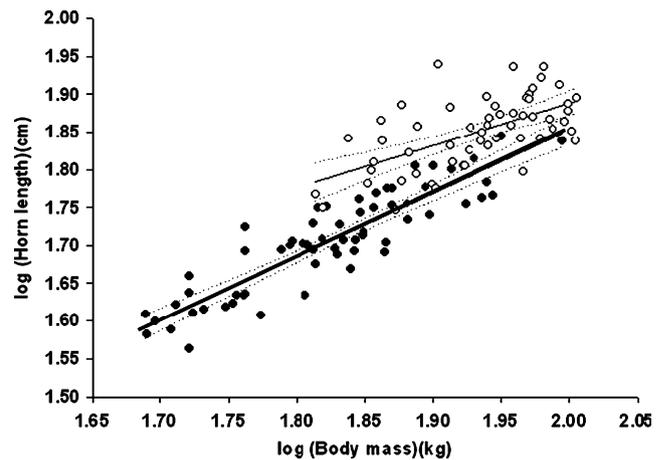
Fig. 2 Relationship between log-transformed horn length and log-transformed mass for ibex males aged 4–7 years (*filled circles*, *thick line*, 63 observations from 30 individuals) and 8–12 years (*open circles*, *thin line*, 55 observations from 27 individuals) in Levionaz, Italy. The slopes are not significantly different (95% confidence intervals represented by *gray dotted lines*)

Dominance

The final mixed effects model suggests that a male's rank is only determined by its secondary sexual characters (mass: 0.14±0.03, t=5.16, $p<0.001$, horn length: 0.14±0.03, t=5.12, $p<0.001$, Fig. 3). Age, interactions, and year effects

Fig. 3 Relationship between body mass, horn length, and social rank for Alpine ibex males aged 5-13 years (62 observations from 36 individuals) in 2003, 2006, and 2007 in Levionaz, Italy. The surface was interpolated from the observed data using a linear smooth function

were not significant. Mass and horn length remained significant even when accounting for a potential effect of age on rank (Table 3). The effect of age on rank decreases with age (Fig. 4), probably because some old large-horned males lose mass (Figs. 1a, 2).

We used a logistic mixed effects model to calculate the probability of an escalated interaction between members of a dyad depending on the difference in mass, horn length, age, and their interactions. We observed 157 non-contact and 95 escalated interactions involving 111 dyads. Consistently with the positive relationship between mass and horn length, both traits affected the probability of escalation (final model: Δ mass: -0.064 ± 0.026, $z=-2.497$, $p=0.012$, Δ horn length: -0.132 ± 0.031, $z=-4.334$, $p<0.001$) even when accounting for a potential effect of age (Table 4). The interactions effects were nonsignificant.

Fig. 4 Age and social rank for Alpine ibex males aged 5-13 years (100 observations from 58 individuals) in 2003, 2006, and 2007 in Levionaz, Italy
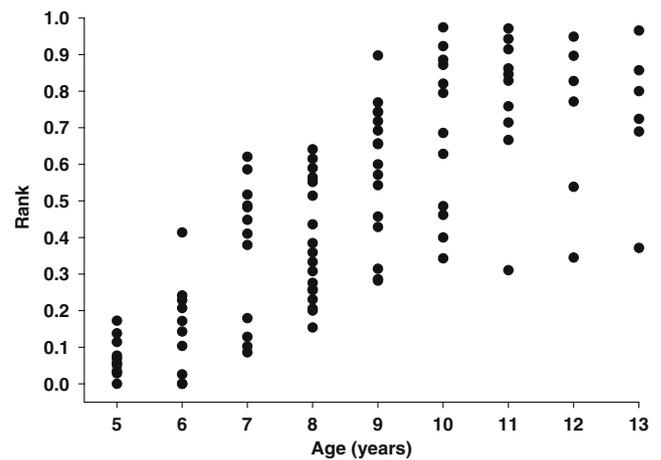
Discussion

In sexually dimorphic polygynous mammals such as ibex, dominance is the key determinant of male reproductive success (Clutton-Brock et al. 1982; Apollonio et al. 1989; Berger and Cunningham 1991; Haley et al. 1994; Hogg and Forbes 1997). As reported for many other polygynous ungulates (Clutton-Brock et al. 1979; Barrette and Vandal 1986; Pelletier and Festa-Bianchet 2006), ibex males formed a linear social hierarchy. However, the linearity index h' was lower in ibex than in bighorn rams, where Pelletier and Festa-Bianchet (2006) found values ranging from 0.33 to 0.57 over 5 years of observations when they saw interactions among 49–71% of possible dyads. The interspecific difference could potentially be due to the large range in age for ibex. At the extreme ages, linearity might be weaker due to the relatively lower competitiveness of young males and old senescent males. In bighorn rams, directional consistency ranged from 0.93 to 0.96, similar to what we found in ibex (0.89-0.95). The highly consistent outcome of interactions within a dyad suggests that individual ranks remained stable over the summer. Rank was strongly affected by mass and horn length, for which the mid-summer measurements used in our analyses are

representative of the early winter rut, as reported for bighorn sheep in a similar habitat (Festa-Bianchet et al. 1996; Pelletier and Festa-Bianchet 2006).

To our knowledge, this is the first analysis of the combined effects of individual mass, age and horn size on male social rank of any wild ungulate. The heaviest males with long horns are at the top of the hierarchy, with age having no direct effect (see also S1 Appendix). Earlier studies of male social rank in ungulates could not distinguish the effects of age from those of mass and other secondary sexual characters correlated with age. For example, Coltman et al. (2002) were unable to tease apart the relative importance of horn length and body mass on reproductive success of bighorn rams. Our results suggest that both variables are important. Pelletier and Festa-Bianchet (2006) found that mass was a strong correlate of rank in bighorn rams, but did not measure horn length. Preston et al. (2003) found that feral rams with long horns had high reproductive success, independently of mass or age. In long-lived, slow-growing species such as Alpine ibex, the effect of age on mass and horn size could be partly buffered by inter-individual heterogeneity. Males seem to be set in a growth strategy from a young age with no

Table 3 Linear mixed model of the effects of body mass, horn length, and age on social rank of male Alpine ibex

Terms	Estimates	SE	t value	p value
Body mass	0.14	0.03	4.970	0.001
Horn length	0.14	0.05	2.685	0.014
Age	0.002	0.04	0.037	0.971

Year was fitted as a fixed term (factor) and ID as a random term

Table 4 Logistic mixed model of the probability to observe an escalated interaction (coded 1) vs. a non-contact interaction (code 0) among marked adult male Alpine ibex, as a function of difference in mass, horn length, and age

Terms	Estimates	SE	t value	p value
Δ Body mass	-0.069	0.026	-2.659	0.008
Δ Horn length	-0.105	0.034	-3.039	0.002
Δ Age	-0.263	0.193	-1.365	0.172

evidence of compensatory growth at old age (Bergeron et al. 2008). Hence, our results do not exclude the possibility that age could affect social rank before 5 years of age. Early growth rate could have lasting effects on social rank later in life. However, during the 3 years of this study, we saw no males younger than 5 years involved in agonistic interactions with males from the main bachelor group.

We found a strong age-independent relationship between body mass and horn length. Fast-growing males reach high rank at a younger age than slow-growing males and may remain dominant for several years. Theories of life-history trade-offs predict a negative relationship between traits that allow early reproduction and survival because of the greater energy expenditure during the rut (Geist 1966b; Robinson et al. 2006). However, despite environmental cohort effects on horn growth (Toïgo et al. 1999), male ibex longevity is independent of growth rate (Bergeron et al. 2008) similar to bighorn rams (Bonenfant et al. 2009). Male ungulates appear to be able to allocate resources to horn growth without affecting survival (Bonenfant et al. 2009). For example, in bighorn sheep and red deer, allocation of resources to horns or antlers relative to body mass increases when condition are favorable (Festa-Bianchet et al. 2004; Mysterud et al. 2005). In soay sheep (*Ovis aries*), however, Robinson et al. (2006) found a negative relationship between horn size and longevity. The life history of soay sheep is very different from that of ibex and bighorn since males can breed as lambs (Robinson et al. 2006). The strength of sexual selection for rapid growth may vary across species and correlate with other aspects of their ecology. Soay sheep rams reach asymptotic horn length and body mass at 4-5 years and few survive beyond 6 years (Stevenson and Bancroft 1995; Robinson et al. 2006). Life expectancy for both bighorn rams and ibex males is greater than for soay sheep rams, but bighorn rams reach asymptotic mass and horn length at a younger age than ibex (Pelletier and Festa-Bianchet 2006; Bonenfant et al. 2009). About half of yearling males will survive to age 6 in bighorn and age 12 in ibex (Festa-Bianchet 2007). Ibex males are especially long-lived and the fitness benefit of surviving many years to achieve high dominance through a conservative growth strategy, including late asymptotic body growth and almost linear horn growth (Fig. 1), may prevail over the benefits of rapid early growth.

Our interpretation of the combined effect of horn length and body mass on dominance implies that young subordinate males may have few opportunities to mate. By avoiding escalated interactions with large males that they are unlikely to beat, small males may reduce the risk of injuries (Geist 1971; Clutton-Brock et al. 1979) and increase their survival. Males benefit from surviving because of the direct positive effect of age on size. A male that survived to 12-13 years of age should reach high rank simply because most males in the population will be younger and therefore smaller. Data on the reproductive success of individuals over their lifetime are required to determine the relative roles of social rank and age-specific size on male fitness.

After accounting for body mass within a dyad, the probability of escalation decreased with increasing difference in horn length. It is likely that interacting males assess the strength of their opponents (Pelletier and Festa-Bianchet 2004) and use that information to determine whether the probability of winning justifies an escalated fight (Hoem et al. 2007). Horn length could be a clue in that assessment, provided it is correlated with body mass and condition as revealed by a male's fighting ability when challenged. Senescent bighorn rams tend to avoid bachelor groups (Hass and Jenni 1991), possibly because their large horns are no longer an honest signal of their condition. Very old male ibex may lose mass (Fig. 1a), and some appeared to avoid other males. Because very old (14+years) males seldom interacted with other males, we could not include them in the hierarchy. Pelletier and Festa-Bianchet (2006) found that bighorn rams older than 7 years were more likely to lose rank as they aged.

In conclusion, male ibex form a linear hierarchy and social rank is likely a strong determinant of reproductive success. Body mass and horn length directly determined social status, while age had no direct effect on rank. Therefore, sexual selection should favor individuals able to obtain sufficient resources for rapid growth. The combined role of horn length and body mass in determining dominance among males could explain the high sexual dimorphism of this species. Currently, however, we do not know if selection acts on both traits simultaneously or on one trait that is genetically correlated with the other. Horn length and body mass co-vary phenotypically in male ibex and their genetic relationship is likely positive, as reported for bighorn rams (Coltman et al. 2005). Observations during the rut could explore changes in the importance of body mass and horn length when animals are exhausted and their secondary sexual characters do not match their condition.

References

Alvarez F (1990) Horns and fighting in male Spanish ibex, *Capra pyrenaica*. J Mammal 71:608–616

Andersson M (1994) Sexual selection. Princeton University Press, Princeton

Apollonio M, Festa-Bianchet M, Mari F (1989) Correlates of copulatory success in a fallow deer lek. Behav Ecol Sociobiol 25:89–97

Barrette C, Vandal D (1986) Social rank, dominance, antler size, and access to food in snow-bound wild woodland caribou. Behaviour 97:118–145

Bassano B, von Hardenberg A, Pelletier F, Gobbi G (2003) A method to weigh free-ranging ungulates without handling. Wildlife Soc B 31:1205–1209

Berger J, Cunningham C (1991) Bellows copulations and sexual selection in bison (*Bison bison*). Behav Ecol 2:1–6

Bergeron P (2007) Parallel lasers for remote measurements of morphological traits. J Wildl Manage 71:289–292

Bergeron P, Festa-Bianchet M, Von Hardenberg A, Bassano B (2008) Heterogeneity in male horn growth and longevity in a highly sexually dimorphic ungulate. Oikos 117:77–82

Bonenfant C, Pelletier F, Garel M, Bergeron P (2009) Age-dependent relationship between horn growth and survival in wild sheep. J Anim Ecol 78:161–171

Clutton-Brock TH (1982) The functions of antlers. Behaviour 79:109–125

Clutton-Brock TH (1989) Mammalian mating systems. Proc R Soc Lond B 236:339–372

Clutton-Brock T, Gibson RM, Guinness FE (1979) The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). Anim Behav 27:211–225

Clutton-Brock TH, Guinness FE, Albon SD (1982) Red deer: behavior and ecology of two sexes. University of Chicago, Chicago

Coltman DW, Festa-Bianchet M, Jorgenson JT, Strobeck C (2002) Age-dependent sexual selection in bighorn rams. Proc R Soc Lond B 269:165–172

Coltman DW, O'Donoghue P, Hogg JT, Festa-Bianchet M (2005) Selection and genetic (co)variance in bighorn sheep. Evolution 59:1372–1382

Côté SD (2000a) Determining social rank in ungulates: a comparison of aggressive interactions recorded at a bait site and under natural conditions. Ethology 106:945–955

Côté SD (2000b) Dominance hierarchies in female mountain goats: stability, aggressiveness and determinations of rank. Behaviour 137:1541–1566

de Vries H (1995) An improved test of linearity in dominance hierarchies containing unknown or tied relationships. Anim Behav 50:1375–1389

de Vries H (1998) Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. Anim Behav 55:827–843

Drews C (1993) The concept and definition of dominance in animal behaviour. Behaviour 125:283–313

Festa-Bianchet M (2007) Ecology, evolution, economics, and ungulate management. CRC Press, Boca Raton

Festa-Bianchet M, Jorgenson JT, King WJ, Smith KG, Wishart WD (1996) The development of sexual dimorphism: seasonal and lifetime mass changes in bighorn sheep. Can J Zool 74:330–342

Festa-Bianchet M, Coltman DW, Turelli L, Jorgenson JT (2004) Relative allocation to horn and body growth in bighorn rams varies with resource availability. Behav Ecol 15:305–312

Gaillard JM, Festa-Bianchet M, Yoccoz NG, Loison A, Toigo C (2000) Temporal variation in fitness components and population dynamics of large herbivores. Annu Rev Ecol Syst 31:367–393

Geist V (1966a) The evolution of horn-like organs. Behaviour 27:175–213

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

Geist V (1971) Mountain sheep, a study in behaviour and evolution. The university of Chicago press, Chicago

Grignolio S, Parrini F, Bassano B, Luccarini S, Apollonio M (2003) Habitat selection in adult males of Alpine ibex, *Capra ibex ibex*. Folia Zool 27:175–213

Haley MP, Deutsch CJ, Leboeuf BJ (1994) Size dominance and copulatory success in male northern elephant seals *Mirounga angustirostris*. Anim Behav 48:1249–1260

Hass CC, Jenni DA (1991) Structure and ontogeny of dominance relationships among bighorn rams. Can J Zool 69:471–476

Hoem SA, Melis C, Linnell JDC, Andersen R (2007) Fighting behaviour in territorial male roe deer *Capreolus capreolus*: the effects of antler size and residence. Eur J Wildl Res 53:1–8

Hogg JT, Forbes SH (1997) Mating in bighorn sheep: frequent male reproduction via a high-risk "unconventional" tactic. Behav Ecol Sociobiol 41:33–48

Kodric-Brown A, Brown JH (1984) Truth in advertising: the kinds of traits favored by sexual selection. Am Nat 124:309–323

Kodric-Brown A, Sibly RM, Brown JH (2006) The allometry of ornaments and weapons. Proc Natl Acad Sci 103:8733–8738

Landau HG (1951) On dominance relations and the structure of animal societies: I. Effect of inherent characteristics. B Math Bioph 13:1–19

Loison A, Festa-Bianchet M, Gaillard J-M, Jorgenson JT, Jullien J-M (1999a) Age-specific survival in five populations of ungulates: evidence of senescence. Ecology 80:2539–2554

Loison A, Gaillard J-M, Pélabon C, Yoccoz NG (1999b) What factors shape sexual size dimorphism in ungulates? Evol Ecol Res 1:611–633

Machlis L, Dodd PWD, Fentress JC (1985) The pooling fallacy: problems arising when individuals contribute more than one observation to the data set. Z Tierpsychol 68:201–214

Malo AF, Roldan ERS, Garde J, Soler AJ, Gomendio M (2005) Antlers honestly advertise sperm production and quality. Proc R Soc Lond B 272:149–157

McElligott AG, Mattiangeli V, Mattiello S, Verga M, Reynolds CA, Hayden TJ (1998) Fighting tactics of fallow bucks (*Dama dama*, Cervidae): reducing the risks of serious conflict. Ethology 104:789–803

McElligott AG, Gammel MP, Harty HC, Paini DR, Murphy DT, Walsh JT, Hayden TJ (2001) Sexual size dimorphism in fallow deer (*Dama dama*): do larger, heavier males gain greater reproductive success? Behav Ecol Sociobiol 49:266–272

Mysterud A, Meisingset E, Langvatn R, Yoccoz NG, Stenseth NC (2005) Climate-dependent allocation of resources to secondary sexual traits in red deer. Oikos 111:245–252

Nievergelt B (1966) Der Alpensteinbock (*Capra ibex*) in seinem Lebensraum. Verlag Paul Parey. Hamburg, Germany

Noldus Information Technology (2003) Matman: Reference Manual 1.1. Wageningen, The Netherlands

Parker GA (1974) Assessment strategy and the evolution of fighting behaviour. J Theor Biol 47:223–243

Parrini F, Cain JW, Krausman PR (2009) *Capra ibex* (Artiodactyla: Bovidae). Mamm sp 830:1–12

Pelletier F, Festa-Bianchet M (2004) Effects of body mass, age, dominance and parasite load on foraging time of bighorn rams, *Ovis canadensis*. Behav Ecol Sociobiol 56:546–551

Pelletier F, Festa-Bianchet M (2006) Sexual selection and social rank in bighorn rams. Anim Behav 71:649–655

Pelletier F, Bauman J, Festa-Bianchet M (2003) Fecal testosterone in bighorn sheep (*Ovis canadensis*): behavioural and endocrine correlates. Can J Zool 81:1678–1684

Pelletier F, Réale D, Garant D, Coltman DW, Festa-Bianchet M (2007) Selection on heritable seasonal phenotypic plasticity of body mass. Evolution 61:1969–1979

Pinheiro JC, Bates DM (2000) Mixed effects models in S and S-Plus. Springer Verlag, New York

Preston BT, Stevenson IR, Pemberton JM, Coltman DW, Wilson K (2003) Overt and covert competition in a promiscuous mammal: the importance of weaponry and testes size to male reproductive success. Proc R Soc Lond B 270:633–640

Reznick D, Nunney L, Tessier A (2000) Big houses, big cars, superfleas and the cost of reproduction. Trends Ecol Evol 15:421–425

Robinson MR, Pilkington JG, Clutton-Brock TH, Pemberton JM, Kruuk LEB (2006) Live fast, die young: trade-offs between fitness components and sexually antagonistic selection on weaponry in soay sheep. Evolution 60:2168–2181

Schaller GB (1977) Mountain monarchs: wild sheep and goats of the Himalaya. University of Chicaco Press, Chicago

Shipley B (2009) Confirmatory path analysis in a generalized multilevel context. Ecology 90:363–368

Short R, Balaban E (1994) The differences between the sexes. Cambridge University Press, Cambridge

Stearns SC (1992) The evolution of life histories. Oxford University Press

Stevenson IR, Bancroft DR (1995) Fluctuating trade-offs favour precocial maturity in male soay sheep. Proc R Soc Lond B 262:267–275

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

Toïgo C, Gaillard J-M, Festa-Bianchet M, Largo E, Michallet J, Maillard D (2007) Sex- and age-specific survival of the highly dimorphic Alpine ibex: evidence for a conservative life history tactic. J Anim Ecol 76:679–686

van Hooff JARAM, Wensing JAB (1987) Dominance and its behavioral measures in a captive wolf pack. In: Frank H (ed) Man and wolf. Junk Publishers, Dordrecht, pp 219–252

van Noordwijk AJ, De Jong G (1986) Acquisition and allocation of resources: their influence on variation in life history tactics. Am Nat 128:137–142

Vanpé C, Gaillard J-M, Kjellander P, Mysterud A, Magnien P, Delorme D, van Laere G, Klein F, Liberg O, Hewison AJM (2007) Antler size provides an honest signal of male phenotypic quality in roe deer. Am Nat 169:481–493

von Hardenberg A (2005) Sénescence, sélection sexuelle et dynamique de population du bouquetin des Alpes (*Capra ibex*). PhD Thesis. Université de Sherbrooke, Sherbrooke, pp 206

von Hardenberg A, Bassano B, del Pilar Zumel Arranz M, Bogliani G (2004) Horn growth but not asymmetry heralds the onset of senescence in male Alpine ibex (*Capra ibex*). J Zool Lond 263:425–432

Weladji RB, Holand Ø, Steinheim G, Colman JE, Gjøstein H, Kosmo A (2005) Sexual dimorphism and intercohort variation in reindeer calf antler length is associated with density and weather. Oecologia 145:549–555