Age-dependent relationship between horn growth and survival in wild sheep

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Summary

1. Trade-offs in resource allocation underline the evolution of life-history traits but their expression is frequently challenged by empirical findings. In large herbivores, males with large antlers or horns typically have high mating success. The fitness costs of large horns or antlers have rarely been quantified although they are controversial.

2. Here, using detailed longitudinal data on $n = 172$ bighorn (*Ovis canadensis*, Shaw) and the capture–mark–recapture methodology, we tested whether early horn growth leads to a survival cost in rams ('trade-off' hypothesis) or if males that can afford rapid horn growth survive better than males of lower phenotypic quality ('phenotypic quality' hypothesis). We also quantified how hunting increased survival costs of bearing large horns.

3. We found an age-specific relationship between horn growth and survival. In all age classes, natural survival was either weakly related to (lambs, adult rams) or positively associated (yearling rams) with early horn growth. Hunting mortality was markedly different from natural mortality of bighorn rams, leading to an artificial negative association between early horn growth and survival. Beginning at age 4, the yearly harvest rate ranged from 12% for males with the smallest horns up to more than 40% for males with the largest horns.

4. Growing large horns early in life is not related to any consistent survival costs, hence supporting the phenotypic quality hypothesis in males of a dimorphic and polygynous large herbivores. Rapid horn growth early in life is, however, strongly counter selected by trophy hunting. We suggest that horn size is a very poor index of reproductive effort and that males modulate their mating activities and energy allocation to horn growth to limit its impact on survival.

Key-words: bighorn, horn growth, individual heterogeneity, selective harvesting, sexual selection, survival, trade-offs.

Introduction

Trade-off in resource allocation is a keystone concept of the theory of life-history trait (LHT) evolution (Roff 1992; Stearns 1992). Trade-offs may arise when resources or time are limited, so that the energy devoted to one trait cannot be used for another (Cody 1966; Williams 1966; van Noordwijk & de Jong 1986). For instance, increased body growth may lower survival (Metcalfe & Monaghan 2001) or reproduction (Gadgil & Bossert 1970; Stearns 1976). However, the assumption of trade-offs in LHT evolution has been repeatedly questioned (Tuomi, Hakala & Haukioja 1983; Reznick 1985; Bell &

Koufopanou 1986; Arnold 1992). In favourable environments, some individuals may not experience a trade-off (Bérubé, Festa-Bianchet & Jorgenson 1999; Tavecchia *et al.* 2005) suggesting that high-quality individuals have enough resources to allocate much energy to several functions at the same time ('phenotypic quality' hypothesis, Reznick, Nunney & Tessier 2000). Accordingly, recent empirical results suggest that trade-offs are not consistently expressed in individuals of high phenotypic quality (Roff & Fairbairn 2007; Weladji *et al.* 2008).

In dimorphic species, factors determining reproductive success differ between the sexes, potentially leading to different allocation trade-offs between males and females (Clutton-Brock, Guinness & Albon 1982; Clutton-Brock, Albon & Guinness 1985). Sexual selection can favour the development

Table 1. Overview of secondary sexual characteristics and different life-history traits (LHT) in large herbivores (non-exhaustive list). We report whether the relationship between horn or antler characteristics and the measured LHT was positive (+), negative (−) or tested but not significant (0)

Species	Horn measurement	Related with …	Effect	Data	Reference
Alpine ibex *Capra ibex*, L.	Increment length (t and $t + 1$)	Survival between t and $t + 1$	(+)	Skull recovery $n = 6142$	von Hardenberg *et al.* (2004)
Alpine ibex	Early horn growth	Longevity	(0)	Skull recovery, $n = 318$	Bergeron *et al.* (2008)
Bighorn *Ovis canadensis*, Shaw	Horn size classes	Mating success Dominance	(+) (+)	Marked individuals, $n = ?$	Singer & Zeingenfuss (2002)
Bighorn	Horn size	Mating success	(+)	Unknown, $n = ?$	Geist (1966a)
Bighorn	Horn growth	Longevity	(−)	Skull recovery, $n = 38$	
Bighorn	Horn size	Mating success	(+)	CMR‡, $n = 176$	Coltman *et al.* (2002)
Bighorn	Horn size	Longevity	(+)	CMR, $n = ?$	Coltman *et al.* (2005)
	Horn size	Mating success	(0)	CMR, $n = ?$	
	Horn size	Lifetime reproductive success	(0)	CMR, $n = ?$	
Red deer *Cervus elaphus*, L.	Antler asymmetry	Annual and lifetime breeding success	(−)	CMR, $n = ?$	Kruuk *et al.* (2003)
Red deer	Relative antler size	Sperm velocity Test size	(+) (+)	Harvest, $n = 198$	Malo *et al.* (2005)
Red deer	Antler mass at t	Annual and lifetime breeding success	(+)* (+)	CMR, $n = ?$	Kruuk *et al.* (2002)
Soay sheep *Ovis aries*, L.	Horn type (Scurred and unscurred)	Survival between t and $t + 1$	(−)†	CMR, $n = ?$	Moorcroft *et al.* (1996)
Soay sheep	Horn type (scurred and unscurred)	Reproductive performance	(+)§	CMR, $n = ?$	Clutton-Brock *et al.* (1997)
Soay sheep	Horn size	Breeding success	(+)	CMR, $n = ?$	Robinson *et al.* (2006)¶
	Horn size	Longevity	(−)		
Soay sheep	Horn size	Consort success	(+)	CMR, $n = 34$	Preston, Stevenson & Wilson (2003)
	Horn size	Mating success	(−)		
Woodland caribou *Rangifer tarandus*, L.	Relative antler size	Resource acquisition	(+)	$n = 40$	Barrette & Vandal (1986)

*stronger relationship for young deer; †density-dependent relationship; ‡capture–mark–recapture; §age dependent; ¶many other horn-related effects were shown.

of exaggerated secondary sexual characters (SSC; Darwin 1871; Ralls 1977; Andersson 1994). Large secondary sexual characters such as antlers or horns in large herbivores are honest signals of individual quality (*e.g.* Clutton-Brock *et al.* 1979; Solberg & Sæther 1993; Vanpé *et al.* 2007). High-quality males can grow large horns, resist higher parasitic loads, fight for longer times and enjoy higher fitness than low-quality ones (Coltman *et al.* 2002; Pelletier *et al.* 2005; Pelletier, Hogg & Festa-Bianchet 2006). In males, higher fitness may result from better quality sperm, female choice (Byers & Waits 2006), successful defence of mating partners (Clutton-Brock 1988) or a combination of all processes (Table 1). The fitness costs of carrying large sexual characters should, however, limit their evolution (Partridge & Endler 1987; Møller & de Lope 1994; Zuk & Kolluru 1998; Allen & Levinton 2007).

Most large herbivores are polygynous, sexually dimorphic in size with males growing horns or antlers (Short & Balaban 1994). For prime-aged males, the size of secondary sexual characters often correlates positively with reproductive success throughout positive correlations between the size of horns or antlers and dominance rank, access to resources and sperm quality (Table 1). Although it is often suggested that, for a given body size, larger weapons should also carry larger fitness costs (*sensu* Stearns 1976), there is little empirical

evidence of such costs in large herbivores (Table 1). For instance, longevity was unrelated to horn size in bighorn but positively correlated in alpine ibex (Table 1). Reduced longevity of large-horned males has only been reported for lambs of Soay sheep (Robinson *et al.* 2006). The expression of any survival costs of growing large secondary sexual characters may only be evident under unfavourable ecological conditions (Toïgo & Gaillard 2003).

Harvesting by humans becomes a selective pressure (Sutherland 1990; Thelen 1991; Ratner & Lande 2001; Ernande, Dieckmann & Heino 2004) on secondary sexual characters when it affects the fitness costs and benefits of heritable traits. In large mammals, artificial selection is particularly likely for horns or antlers that are targeted by trophy hunters (Ginsberg & Milner-Gulland 1994; Festa-Bianchet 2003; Gordon, Hester & Festa-Bianchet 2004; Milner, Nilsen & Andreassen 2007). Evolutionary consequences of hunting in mammals were strongly suggested in European mouflon *O. aries*, L. (Garel *et al.* 2007) and clearly apparent in bighorn sheep (Coltman *et al.* 2003). Because large-horned males are shot before their peak reproductive age, hunting favours males with slower horn growth (Festa-Bianchet *et al.* 2004). Coltman *et al.* (2003) showed that 30 years of trophy hunting selected for males with smaller body size and shorter horns.

Here we investigate the relationship between horn growth early in life and longevity in the hunted population of bighorn sheep on Ram Mountain, Alberta, Canada. We analyse longevity of bighorn rams and use capture–mark–recapture techniques (CMR, Lebreton *et al.* 1992) to analyse their age-specific annual survival estimated from marked bighorn rams. We test two hypotheses: (i) the 'trade-off' hypothesis that predicts a negative relationship between horn growth and age at death or age-specific annual survival (Geist 1966a), and (ii) the 'phenotypic quality' hypothesis predicting a positive relationship between horn growth and age at death or age-specific annual survival because males that can afford rapid horn growth survive better than males of lower phenotypic quality (Reznick *et al.* 2000). We also investigate to what extent hunting affects the relationship between survival and early horn growth (Coltman *et al.* 2003; Festa-Bianchet *et al.* 2004) to test the hypothesis that trophy hunting is likely to mimic natural mortality (Loehr *et al.* 2006).

Material and Methods

STUDY SITE

Bighorn sheep were monitored on Ram Mountain (52·2°N, 115·5°W), Alberta, from 1975 to 1997. Survival analyses were stopped in 1997 because of cougar (*Puma concolor*, L.) predation that profoundly affected the survival pattern of bighorn in our study population (Festa-Bianchet *et al.* 2006). We examined the survival of 172 individually marked rams for which horn measurements were available. Age of a few individuals was determined by counting horn increments (Geist 1966b) but 93% were caught as lambs so their exact age was known. From 1972 to 1980, yearly removals of 12–24% of adult ewes (Jorgenson *et al.* 1993a) kept the total population at 94–105 sheep. When ewe removals were stopped, the population increased, peaking at 232 sheep in 1992. To account for the potential effects of variation in density and climate on survival, we allowed for time-variation in survival rate before analysing the horn effect.

The definition of a legal male for sport hunting in Alberta is based on horn development and there were no quotas. At Ram Mountain, until 1995, any male with at least one horn that described a minimum of 4/5 curl could be legally harvested. From 1996 onwards, only full-curl rams could be harvested. Although only 0–6 males were harvested each year (average of 2·4 males a year, all aged 4 years and older, Jorgenson, Festa-Bianchet & Wishart 1993b), the hunting pressure was high since rams with 'legal' horns had about a 40% yearly probability of being harvested each year (Coltman *et al.* 2003). Hunting was allowed from late August to the end of October. All hunters that harvested a bighorn ram were required by law to register their kill.

DEFINITION OF MEASUREMENTS USED

For male lambs (between 0 and 1 year of age) and yearling (between 1 and 2 years of age), we used horn length standardized for the julian date of observation as a predictor of survival (later refered to as 'horn length'). For rams 2 years of age and older, we used the horn growth (centimetres) between 1 and 4 years of age (i.e. horn growth as yearlings, 2 and 3 year olds and later referred to as 'horn growth'). This corresponds to increments 2 to 4 and accounts for approximately 75% of the asymptotic horn length (Jorgenson, Festa-Bianchet &
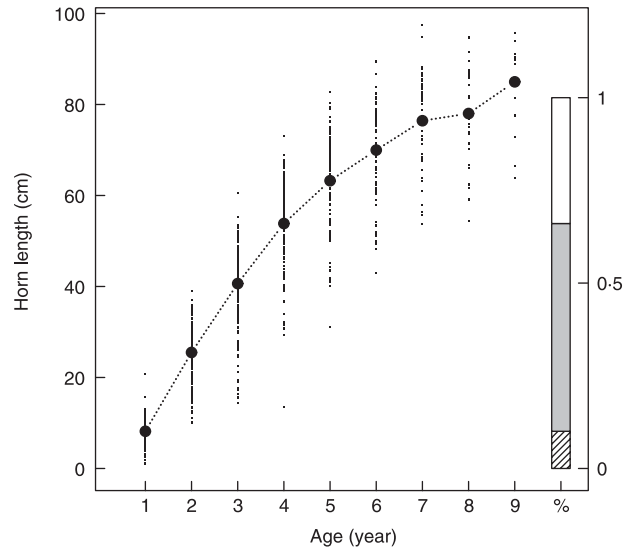
Fig. 1. Age-specific horn length (adjusted for capture date) in bighorn rams from Ram Mountain population of bighorn sheep (Alberta, Canada). Large black dots are the average values of horn length for a given age (*n* = 879 measurements). The right-hand bar (percentage) represents the percentage of asymptotic horn length completed between age 1 and 4 (increments 2 to 4, in gray); growth between 0 and 1 year of age (first increment, dashed) was omitted because of wear.

Wishart 1998, see also Fig. 1). To estimated horn growth, we omitted the first increment because its tip is rapidly worn out (Geist 1966b; Bunnell 1978). For all age classes, we arbitrarily chose to use the left horn measurement (as the absence of directional asymmetry has been shown is several ungulate species e.g., von Hardenberg *et al.* 2004). We thus assimilated horn growth between 1 and 4 years old to a relative measure of energy allocation to the production of secondary sexual characters (Festa-Bianchet *et al.* 2004; Coltman *et al.* 2005). At Ram Mountain, survival was monitored by repeated censuses of marked animals. Annual resighting probability exceeded 95% and emigration was rare (Jorgenson *et al.* 1997). Consequently, males that disappeared were considered dead when missing in two consecutive years (see Loison, Langvatn & Solberg 1999, for a similar approach).

STATISTICAL ANALYSES

We log-transformed annual increment length and modelled its variation with age using linear mixed models (LMM, see Pinheiro & Bates 2000). Increment length was the response variable, age (covariable) and julian date (for lambs and yearlings) were entered as fixed effects (*n* = 879 measurements). Ram identity was fitted as a random effect on both intercept and slope. Some individuals did not survive to age 4, or missed 1 or 2 measurements of horn increment accounting, respectively, for 14·2% and an additional 4·2% point of all rams. LMM were then used to predict missing values allowing us to compare allocation to horn growth by rams dying at any age > 2 years. In a second step, relationships between age at death and horn growth were investigated using linear models (MacCullagh & Nelder 1989). Linear and polynomial (up to third order) terms of horn growth on age at death were tested with standard F-tests. All analyses were run in R 2·6·1 (R Development Core Team 2007).

In large herbivores, survival from birth to weaning (*juvenile summer survival*) may respond differently to climate or density than survival from weaning to 1 year (Gaillard *et al.* 2000). We first assessed the

strength of the relationship between juvenile summer survival probability (noted π) and lamb horn length with a binomial regression (MacCullagh & Nelder 1989), accounting for annual variation in juvenile summer survival (Portier *et al.* 1998).

Before modelling annual survival and harvest rates, we performed a goodness-of-fit (GOF) test (Burnham *et al.* 1987; Pradel, Wintrebert & Gimenez 2003) implemented in U-Care (Choquet *et al.* 2003). We then estimated the *overall survival rate* of bighorn rams (noted φ; $n = 172$) with single state CMR models (Lebreton *et al.* 1992). Overall survival was estimated from all mortality sources including hunting. This analysis provided us with the observed pattern of mortality of rams, testing for the effect of age class (1–2 years, 2–5 years, 5–8 years and older than 8 years of age) and horn length or horn growth. Age classes were derived from Festa-Bianchet, Gaillard & Côté (2003). The prime-age (2–8 years) class was further split into pre- and post-age of peak reproduction to account for potential effect of reproductive effort with age. We tested the effect of horn growth on overall survival by entering horn growth as an individual covariate in the CMR models (Cooch & White 2007) where overall survival (φ) was linearly related to horn growth on the logit scale (β_h). We also compared the overall age-specific survival of rams dying from different 'fate' (natural death vs. harvested).

We then compared overall survival rates with *natural survival rates* (noted φ; $n = 172$) for a given age class. To estimate natural survival rates, we removed hunting mortality by censoring individuals in the year they were shot, so that hunting mortality was excluded (see Jorgenson *et al.* 1997; Langvatn & Loison 1999). We could thus use a multi-state capture–recapture modelling framework (MS-CR, Lebreton & Pradel 2002) to assess the survival cost of growing large horns early in life for bighorn rams, separating natural from hunting mortality to test for a trade-off between horn growth and natural survival. We used two states: live recaptured (*A*) and harvested (*H*). A multi-state model can be expressed as a time-dependent transition matrix (ψ) with its associated vectors of survival (φ) and capture (*p*) probabilities (Nichols *et al.* 1994) as follows:

$$\begin{bmatrix} \phi^A & \phi^H \end{bmatrix}_t \begin{bmatrix} \psi^{A,A} & (1-\psi^{A,A}) \\ \psi^{H,A} & (1-\psi^{H,A}) \end{bmatrix}_t \begin{bmatrix} p^A \\ p^H \end{bmatrix}_t,$$

where, 'harvested' (*H*) is an absorbing state: an individual cannot move from state *H* to state *A* ($\phi^H = 0$ and $\psi^{H,A} = 0$, see Table 2 for a definition of superscripts and subscripts). According to this parameterization, p^H was set to 1. This approach allowed us to estimate annual natural survival (ϕ_t^A, the probability to survive from year *t* to year $t + 1$), resighting (p_t^A, probability to be seen at year *t*) and harvest rates ($1 - \psi_t^{A,A}$, probability to be shot between year *t* and year $t + 1$ conditional on survival) according to year (from 1975 to 1997), age class (1–2 years, 2–5 years, 5–8 years and older than 8 years of age) and horn growth (see above). For lambs and yearlings, which are not subjected to hunting, this parameterization reduces to a single-state model where lamb survival (from birth to one year of age, ϕ_{juv}) and yearling survival (ϕ_{year}) are estimated. Note that for lambs and yearlings, natural survival equals overall survival (ϕ_{juv} and ϕ_{year}). We replicated the same approach as for (φ) to investigate the effect of horn length on ϕ_{juv} and ϕ_{year} and of horn growth on adult natural survival (ϕ^A) and harvest rates ($1 - \psi^{A,A}$).

We used the information theoretic approach with the Akaike information criterion corrected for sample size (AIC_c, Burnham & Anderson 1998) to select a set of best models among the candidate models. AIC_c weights (w_i) were computed to assess the relative likelihood of a given model to be the best among the set of candidate models (Buckland, Burnham & Augustin 1997). Capture–recapture modelling used MARK 5·0 (White & Burnham 1999).

Results

HORN GROWTH

The horn length of lambs and yearlings increased with measurement date ($\beta_{jul} = 0.064 \pm 0.002$, $t = 30.936$, $P < 0.001$). In yearlings, horn growth rate was slightly reduced at the end of the summer as shown by the marginally significant second order coefficient of Julian date ($\beta_{jul} = 0.107 \pm 0.004$, $t = 27.225$, $P < 0.001$; $\beta_{jul}^2 = -6.4 \times 10^{-5} \pm 3.2 \times 10^{-5}$, $t = -1.957$, $P = 0.051$). The LMM predictions at the average Julian date of horn measurement were 3·82 cm for lambs (28 August) and 16·04 cm for yearlings (16 July).

For adult males, the LMM model of horn growth had the following structure:

$$l_{ij} = \mu + \beta_1 \times age + \beta_2 \times age^2 + \beta_3 \times age^3 + \sigma_\mu + \sigma_{age} + \varepsilon_{ij},$$

where l_{ij} is the log-transformed horn growth of individual *j* between age *i* and $i + 1$ ($i > 1$, ignoring the first increment), μ is the average of the log-transformed length of the second increment and β's the coefficient of the polynomial model linking horn growth to age; the random structure included a random effect of individual identity on the intercept (σ_μ) and the slope (σ_{age}); ε_{ij} is the error term.

Estimated coefficients of the third order polynomial model describing ram horn growth were: $\beta_1 = 0.194 \pm 0.059$, $\beta_2 = -0.069 \pm 0.013$ and $\beta_3 = 3.17 \times 10^{-3} \pm 8.55 \times 10^{-4}$. The two random components were highly significant ($\sigma_\mu = 0.300$, $\chi^2 = 31.978$, d.f. = 1, $P < 0.001$; $\sigma_{age} = 0.069$, $\chi^2 = 123.686$, d.f. = 1, $P < 0.001$) and between-individual differences in growth trajectories accounted for 23·2% of variance in horn growth. For a given ram, increment length at age *i* was positively correlated with increment length at age $i + 1$ as revealed by a significant first-order autoregressive coefficient of the within-subject error ($\rho_1 = 0.154$, $\chi^2 = 5.138$, d.f. = 1, $P = 0.023$).

The correlation between observed values and LMM predictions was $r = 0.93$. We are thus confident that missing increment measurements were accurately estimated from LMM and could be entered as horn growth in the CMR analyses. Horn growth of rams aged between 2 and 4 years varied among cohorts (ANOVA: $F_{34,198} = 6.648$, $P < 0.001$). To account for such cohort effects, horn growth between 1 and 4 years was corrected by the year of birth. We made no attempt to model horn growth as a function of covariates such as density or climate and assumed that most variation in horn growth was accounted for by environmental conditions around birth. However, since hunting rules rely on absolute horn length, this correction for cohort variation in horn growth was used to model survival but not hunting rates.

HORN GROWTH VS. AGE AT DEATH

When natural and hunting mortality were pooled, horn growth from 1 to 4 years of age and age at death was negatively and significantly correlated (Fig. 2). When increment lengths estimated by LMM were included, a similar negative relationship
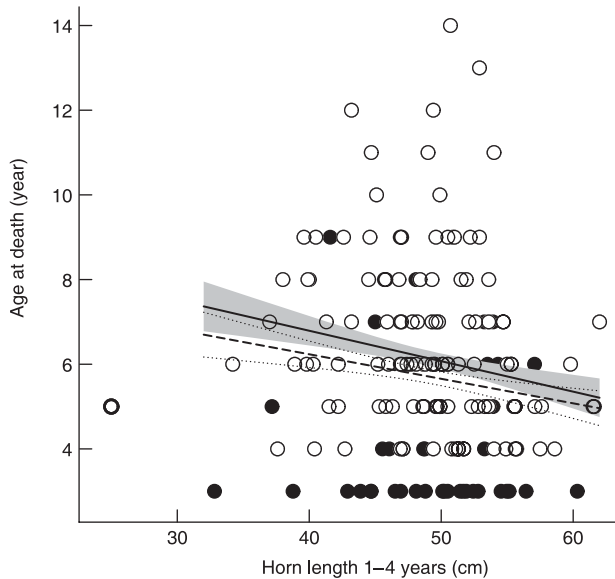
Fig. 2. Relationships between horn growth (in centimetres) from 1 to 4 years of age and age at death in rams from Ram Mountain population of bighorn sheep (Alberta, Canada). Black dots are estimates from the age-specific horn growth with a linear mixed model for rams where one or two of the three horn increments were not measured directly (see text). Only rams that survived to 3 years of age and older are included and one outlier removed (thick open circle). Males on Ram Mountain are hunted for trophy and the figure includes rams dying from natural and artificial causes. The shaded area indicates the 95% confidence limits of the predictions of the best model including only points for which all three horn increments were measured ($\beta = -0.072 \pm 0.032$, $n = 119$, $P = 0.029$, $r^2 = 0.039$). The dashed and dotted lines are the predictions and associated standard deviation of the best model describing the full data set, including the estimated values.

between horn growth and age at death was found (robust estimate: -0.058 ± 0.029, $P = 0.050$, $n = 166$ with one outlier removed; Fig. 2). As expected from the negative relationship between horn growth and age at death, rams with the greatest early horn growth (> 54 cm) died on average 1.08 ± 0.45 years earlier than rams with smaller horns (≤ 54 cm). Density ($\beta = 0.011 \pm 0.010$), cause of death (shot or natural death, $\beta = 0.501 \pm 0.179$) or its interactions with horn growth ($\beta = -0.061 \pm 0.082$) had no effect on longevity (all *P*-values > 0.20).

HORN GROWTH VS. SURVIVAL OF BIGHORN RAMS

Lamb summer survival

At first glance, lamb survival to weaning (juvenile summer survival) appeared strongly and positively related to horn length ($\beta = 0.871 \pm 0.155$, $t = 5.619$, $P < 0.001$). This relationship, however, was no longer significant once the annual variation in lamb summer survival was accounted for ($\beta = 0.290 \pm 0.238$, $t = 1.218$, $P = 0.223$). The final model for lamb summer survival thus only comprised annual-variation (Table 3) and did not show any sign of overdispersion (residual deviance was 262.07 for 335 d.f.).

Overall survival

Our data adequately fit the full time-dependent model (P_t, φ_t, Lebreton *et al.* 1992): $\chi^2 = 15.711$, d.f. = 34, $P = 0.996$. The dispersion parameter was set to $\hat{c} = 1$ (Lebreton *et al.* 1992).

As expected, there was a marked effect of age on overall survival [P(fate), $\varphi(.)$ vs. P(fate), φ(age); $\Delta AIC_c = -102.52$] and harvested rams tended to have a lower overall survival than other rams [Table 4; P(fate), φ(age) vs. P(fate), φ(age × fate); $\Delta AIC_c = 0.80$]. Most of the variation in survival between harvested and nonharvested rams was explained by horn growth between 1 and 4 years (Table 4). Overall survival of large-horned rams was negatively related to horn growth at any age ($\beta_h = -0.050 \pm 0.018$, $t = -2.770$, $P < 0.01$; Fig. 4a), in agreement with the negative relationship between horn growth and longevity when hunting mortality was not accounted for (Fig. 2).

Natural survival

GOF tests suggested that the bighorn data did not deviate from the full time-dependent model ($\psi_t^{S,S}$, ϕ_t^S, p_t^S: $\chi^2 = 12.434$, d.f. = 48, $P = 0.988$; see Table 2 for model specifications) so we set the dispersion parameter to $\hat{c} = 1$.

We could not differentiate between a model with age-dependent resighting [p^A(age), $\phi^A(.)$, $\psi^{A,H}(.)$, $\Delta AIC_c = 0.00$, $w_i = 0.30$] or a model with a constant resighting [$p^A(.)$, $\phi^A(.)$, $\psi^{A,H}(.)$, $\Delta AIC_c = 0.75$, $w_i = 0.29$] so the model with constant resighting was retained as it had the fewest parameters (see also Festa-Bianchet *et al.* 2003). The average resighting rate (p^A) was 0.98 ± 0.005 for all age classes.

Average natural survival of male lambs from year t to $t + 1$ (ϕ_{juv}) was 0.56 ± 0.03 but was highly variable from year to year (Table 4). Lambs are not subjected to hunting, therefore their natural survival equals their overall survival. The model including time-dependent survival had twice as much statistical support as the model including both time-dependent survival and lamb horn length ($\beta_h = 0.117 \pm 0.165$, $t = 0.709$, $P = 0.360$). Natural survival of yearling and adult rams was $\phi_{year} = 0.70 \pm 0.03$ and $\phi^A = 0.82 \pm 0.02$ respectively. We found evidence that survival of yearling (ϕ_{year}) varied positively with horn length (Table 4, Fig. 3), the model including horn length at 1 year of age being 3 times better supported than the model

Table 2. Notations, factors and biological significance of the tested factors in the capture–mark–recapture (CMR) modelling of mountain sheep rams

Notation	Biological meaning
t	Time dependence
.	Constant rate
Age	Age effect considering 3 age classes from 2 to 5, from 5 to 8 and older than 8 years
Horn	Standardized horn length; individual covariate
Fate	Whether the animal was shot or not
×	Interaction term
Exponent	State–S (*A* – live recaptured; *H* – harvested)

Table 3. Modelling summer juvenile survival of male lambs (π) at Ram Mountain, Alberta, Canada ($n = 333$); k is the number of estimated parameters, ΔAIC_c the difference in AIC_c between the *ith* model and the best model (lowest AIC_c) and w_i the AIC_c weight (Burnham & Anderson 1998). 'yr' is the year effect *i.e.* accounts for the annual variation in juvenile summer survival and 'horn' is the standardized horn length as lamb

i	Model description	k	ΔAIC_c	w_i
1	$logit(\pi) = \mu + B_{yr}$	25	0·00	0·75
2	$logit(\pi) = \mu + B_{yr} + \beta_1 \times horn$	26	2·20	0·25
3	$logit(\pi) = \mu + \beta_1 \times horn$	2	14·41	0·00
4	$logit(\pi) = \mu$	1	54·69	0·00
5	$logit(\pi) = \mu + B_{yr} + \beta_1 \times horn + \beta_{yr} \times horn$	50	64·00	0·00

with survival independent of horn length; time-variation in ϕ_{year} had not support (Table 4). The effect of horn length on expected yearling survival was positive ($\beta_h = 0\cdot285 \pm 0\cdot153$, $t = 1\cdot182$, $P = 0\cdot060$). For adult rams, the model with a simple effect of age classes had the best statistical evidence ($w_i = 0\cdot61$), being almost three times more supported than the model with an additive effect of horn growth and age class on survival ($w_i = 0\cdot22$; Table 4). The slopes relating expected survival rate with horn growth on the logit scale were all not significant: $\beta_h = 0\cdot008 \pm 0\cdot038$ ($t = 0\cdot210$, $P = 0\cdot416$) for rams aged 2–5 years, $\beta_h = -0\cdot058 \pm 0\cdot071$ ($t = -0\cdot817$, $P = 0\cdot207$) between 5
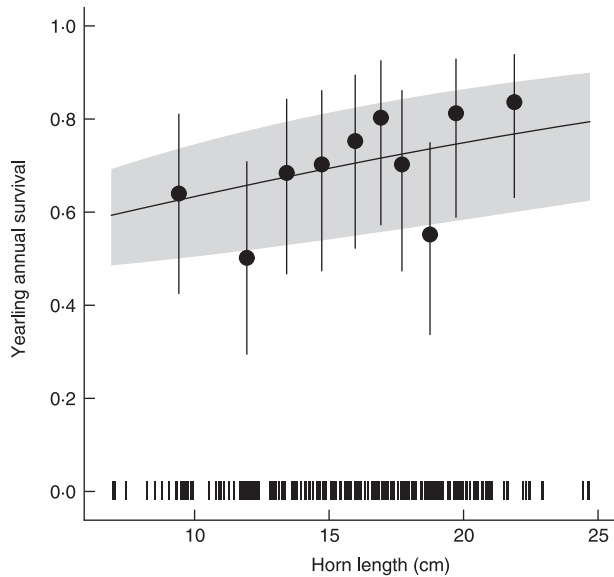
and 8 years and $\beta_h = 0\cdot073 \pm 0\cdot133$ ($t = 0\cdot548$, $P = 0\cdot292$) for rams older than 8 years of age (Fig. 4b). This analysis shows that, at any age class, rams growing large horns early in life had a similar natural survival than rams growing small horns.

Harvest probability

The annual harvest rate of bighorn rams ($\psi^{A,H}$) was in average $0\cdot090 \pm 0\cdot013$ but increased linearly, on the logit scale, with early horn growth (Table 4). For rams between 2 and 5 years, the probability to be shot ($\psi^{A,H}_{2-5} = 0.006 \pm 0.013$) increased from $0\cdot02 \pm 0\cdot01$ for the smallest horn-length class to $0\cdot12 \pm 0\cdot03$ for the largest-horned males (Fig. 4c). No ram younger that 4 years was ever harvested or classified as 'legal' by the field crew. The same increase in harvest probability with horn growth was found for males aged 5 to 8 years ($\psi^{A,H}_{>8} = 0.18 \pm 0.08$) and males older than 8 years ($\psi^{A,H}_{5-8} = 0.17 \pm 0.03$). The common slope relating harvest rate to early horn growth for all age classes was $0\cdot140 \pm 0\cdot035$ ($t = 4\cdot117$, $P < 0\cdot001$). For a given age class, rams with rapid horn growth early in life had up to 2·5 times more risk of being shot than rams with slow horn growth (Fig. 4c).

Discussion

Our analyses suggest that the relationship between natural survival and early horn production of male sheep is age

Table 4. Modelling overall survival (φ), harvest ($\psi^{A,H}$) and natural survival (ϕ) probabilities of bighorn rams at Ram Mountain, Alberta, Canada; k is the number of estimated parameters, ΔAIC_c the difference in AIC_c between the *ith* model and the best model (lowest AIC_c) and w_i the AIC_c weight (Burnham & Anderson 1998). See Table 2 for a biological definition of the terms used in model specification.

Probability	i	Model description	k	ΔAIC_c	w_i
Overall survival	1	$P(fate), \varphi(age + horn)$	8	0·00	0·68
	2	$P(fate), \varphi(age \times horn)$	10	2·01	0·24
	3	$P(fate), \varphi(age)$	7	5·82	0·04
	4	$P(fate), \varphi(age \times fate)$	10	6·62	0·03
	5	$P(fate), \varphi(age + fate)$	8	7·66	0·01
	6	$P(fate), \varphi(horn)$	4	35·27	0·00
	7	$P(fate), \varphi(.)$	3	108·34	0·00
	8	$P(fate), \phi(fate)$	4	110·16	0·00
Lamb survival	1	$p^A(.), \phi_{juv}(t)$	25	0·00	0·57
	2	$p^A(.), \phi_{juv}(t + horn)$	26	1·40	0·29
	3	$p^A(.), \phi_{juv}(horn)$	5	2·71	0·14
	4	$p^A(.), \phi_{juv}(.)$	4	28·17	0·00
	5	$p^A(.), \phi_{juv}(t \times horn)$	54	37·45	0·00
Yearling survival	1	$p^A(.), \phi_{year}(horn)$	7	0·00	0·68
	2	$p^A(.), \phi_{year}(.)$	6	1·51	0·32
	3	$p^A(.), \phi_{year}(t)$	29	15·20	0·00
	4	$p^A(.), \phi_{year}(t + horn)$	30	17·26	0·00
Adult survival and harvest	1	$p^A(.), \phi^A(age), \psi^{A,H}(age + horn)$	10	0·00	0·61
	2	$p^A(.), \phi^A(age + horn), \psi^{A,H}(age + horn)$	11	2·04	0·22
	3	$p^A(.), \phi^A(age), \psi^{A,H}(age \times horn)$	12	3·43	0·11
	4	$p^A(.), \phi^A(age \times horn), \psi^{A,H}(age + horn)$	13	5·01	0·05
	5	$p^A(.), \phi^A(age), \psi^{A,H}(age)$	12	15·85	0·00
	6	$p^A(.), \phi^A(age + horn), \psi^{A,H}(age)$	9	16·61	0·00
	7	$p^A(.), \phi^A(age \times horn), \psi^{A,H}(age)$	10	18·64	0·00
	8	$p^A(.), \phi^A(.), \psi^{A,H}(age + horn)$	6	55·32	0·00
	9	$p^A(.), \phi^A(age), \psi^{A,H}(.)$	7	74·01	0·00
	10	$p^A(.), \phi^A(t), \psi^{A,H}(.)$	25	117·41	0·00
	11	$p^A(.), \phi^A(.), \psi^{A,H}(.)$	3	129·31	0·00

Fig. 3. Relationship between annual survival (between 1 and 2 years of age) and standardized horn length of yearling bighorn sheep from Ram Mountain population (Alberta, Canada). The straight line is the expected survival according to horn length [$\text{logit}(\phi_{year}) = 0.864 + 0.285 \pm 0.153 \times \text{horn}$, $t = 1.182$, $P = 0.060$]. The gray shading is the 95% confidence limits of model predictions. Thick marks are the individual horn length and black dots the average survival of yearlings rams (±95% confidence limits; horn classes were chosen to have all the same number of individuals; $n = 214$).

different from natural mortality. As natural and artificial selection pressures change as rams age, the investigation of age-specific selection patterns is strongly recommended. Our results reinforce the conclusions of previous study on the Ram Mountain population suggesting that trophy hunting can have undesirable evolutionary consequences (Coltman *et al.* 2003).

HORN GROWTH AND SURVIVAL

Males of polygynous and dimorphic ungulates reduce the energy allocation to horn or antler growth when resource availability is low (Toïgo, Gaillard & Michallet 1999; Festa-Bianchet *et al.* 2004; Mysterud *et al.* 2005). If horn growth one year reduces body condition, then one would expect a redirection of energy allocation the following year, at the expense of horn growth. The positive correlation in the length of successive horn increments suggests that growing large horns does not lead to a detectable horn cost production. Early horn growth was either unrelated to or positively associated with natural survival for bighorn rams as lambs, yearlings and adults (Fig. 4b). In this bighorn population, the negative relationship between longevity and early horn growth (Fig. 2) may be caused by preferential hunting on rams aged 5 and older that grew large horns (Fig. 4c). Overall, we found no persuasive evidences of survival costs of growing large horns, as found in other large herbivore species (Table 1).

Our results are more concordant with the predictions of the 'individual quality' than the 'trade-off' hypothesis. Indeed, rams that had grown the largest horns had similar natural survival than rams that had grown smaller horns (Table 4; Fig. 4b). Since large-horned rams are also the heaviest ($r = 0.61$ between horn length and body mass, Coltman *et al.* 2005), they appear to be of high phenotypic quality. The expectation that large horns would be associated with decreased survival is based on the assumption that rams with large horns will make a greater expenditure in reproduction during the rut than small-horned rams (Geist 1966a; Loehr *et al.* 2006;
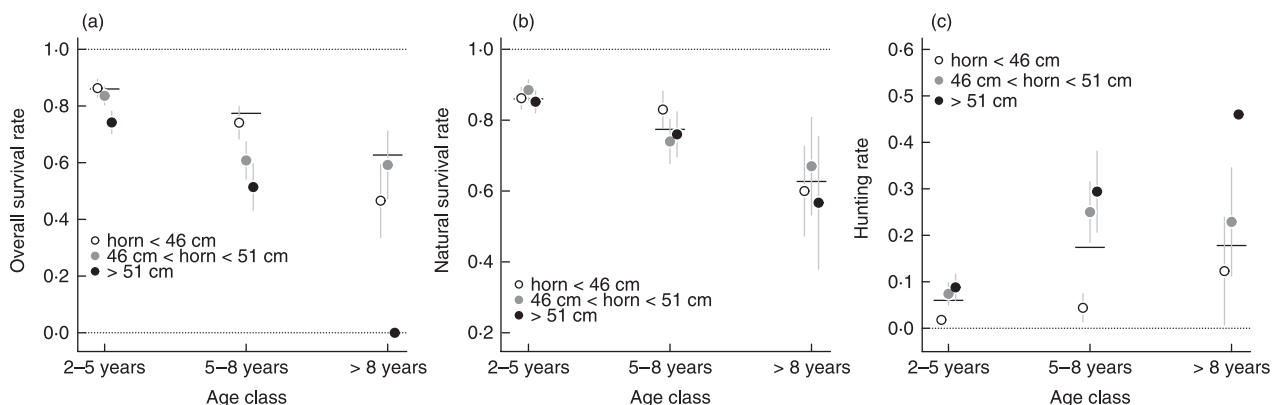
dependent. In all age classes but yearlings was natural survival unrelated to early horn growth. Yearling rams growing large horns better survived than those growing small horns. We provide no support to the contention that rapid horn growth should lower male survival (Geist 1966a; Loehr *et al.* 2006; Robinson *et al.* 2006), as no negative effect of horn growth was detected once hunting mortality was accounted for. On the other hand, hunting profoundly modifies age-specific survival of rams, most critically for large-horned ones, and leads to a pattern of artificial mortality that is sharply

Fig. 4. Age-specific (mean ± sd) overall survival (a), natural survival (b) and harvest (c) of bighorn rams at Ram Mountain (Alberta, Canada) according to early horn-growth (horn growth between 1 and 4 years). In (a), pooling natural and hunting mortality gives the false impression of a survival cost of horns for rams. Natural survival rates (b) show no survival costs of large horn. Harvest rates are highly dependent on age and horn-growth between 1 and 4 years. No harvest occurred before 4 years of age. In panels (a) and (b), horizontal lines indicate the average age-specific natural survival rates. In panel (c), horizontal lines are the averages of the age-specific hunting rates.

Robinson *et al*. 2006). As males modulate their mating activities according to their social rank, age (Pelletier *et al*. 2006) or body size (McElligott *et al*. 2003), males with very different mating tactics can have similar natural survival rates as adults while having different individual characteristics. If rams of low quality limit their reproductive effort and allocate more resources to maintenance than to horn growth (Festa-Bianchet *et al*. 2004), they may achieve natural survival rates similar to those of large-horned rams. We therefore suggest that horn size is a very poor index of reproductive effort. On the other hand, individuals having large horns are more likely to be dominants (Geist 1971; Hogg 1987). Dominant could have preferential access to food resources than subordinates (Table 1, see also Tomback *et al*. 1989) and so, may be able to cope with possible higher energy demand of growing large horns. In bighorn, however, rams of all social status seem to have equal access to food resource (Fanie Pelletier, personal observation).

Young adults may have different tactics of energy allocation than prime-age males. Contrary to our results, a study of Soay sheep reported a survival cost of growing large horns in lambs (Robinson *et al*. 2006). In ungulates, the degree of participation of young males into reproduction is linked to the relative proportion of young and prime-age males in the population (Komers, Messier & Gates 1994) and lead to lower early body growth (reindeer, Mysterud *et al*. 2003; moose, *Alces alces*, L. Garel *et al*. 2006). In the Soay population, male lambs (that represent up to 50% of the males, Clutton-Brock & Coulson 2002) heavier than the average participate actively in rutting and suffer increased mortality (Stevenson & Bancroft 1995). Rutting by male lambs is a highly unusual situation for wild large herbivores (Clutton-Brock *et al*. 1982) and is likely to be related to past domestication of this species. The negative relationship between early horn-growth and longevity in Soay rams may be due mainly to the mating costs incurred by large male lambs. A study on mating behaviour of bighorn rams reported that large young adults (yearlings and 2 years old rams) are more active during the rut than smaller ones (Pelletier *et al*. 2006). Although an altered age-structure by hunting of adult rams may favour a substantial energy allocation to reproduction while still growing in body size (asymptotic body mass is reached at 5 years of age), the most active young males during rut also enjoyed longer longevity (Pelletier *et al*. 2006) which is consistent with our analysis of survival.

Taken as a whole, the positive or weak relationship between horn growth and survival observed at most ages suggests that conservative tactics of energy allocation, typical of adult females of large herbivores (Festa-Bianchet & Jorgenson 1998; Gaillard & Yoccoz 2003), may also apply to males (Yoccoz *et al*. 2002; Festa-Bianchet & Côté 2008). In alpine ibex, pro-longed body mass gain likely reduces the survival costs of sexual dimorphism (Toïgo *et al*. 2007) but the same may apply to bighorn. Indeed, the two species of large herbivores in which the production of secondary sexual characters was negatively correlated with longevity (Table 1) showed rapid body growth (percentage of adult body mass completed as a yearling in females: 80% in Soay sheep, 81% in red deer) compared to

bighorn (59%, Festa-Bianchet & Côté 2008, p. 107). Consequently, the smallest amount of energy allocated to body growth in bighorn may be diverted to maintenance, reducing the expression of trade-offs between survival and horn production.

HUMAN INDUCED TRADE-OFFS

In mature bighorn rams (> 7 years), large size (Pelletier & Festa-Bianchet 2006) and large horns (Hogg & Forbes 1997; Coltman *et al*. 2002) determine the outcome of male–male interactions. Horn size is also a major determinant of male social status (Geist 1971; Hogg 1987). Dominant rams defend oestrous ewes and achieve high reproductive success (Hogg & Forbes 1997). By selectively removing individuals with large horns beginning at 4 years of age, hunting may advantage rams with slower horn growth (Coltman *et al*. 2003; Festa-Bianchet *et al*. 2004). The harvest rates at Ram Mountain (Fig. 4c) implies a strong potential for artificial directional selection in favour of slow horn growth. Large-horned rams were almost four times as likely to be shot as small-horned rams. Comparing male age-structures in hunted and non-hunted populations of bighorn and thinhorn sheep, Singer & Zeingenfuss (2002) indirectly supported our findings by showing the greater hunting pressure imposed on large-horned rams relatively to small-horned ones. Biased harvest of males with large horns or antlers is likely to occur in most sport-hunted populations of large herbivores (Murphy, Singer & Nichols 1990; Solberg *et al*. 2000).

Hunting impacts populations of large herbivores by affecting social structure, sex ratio, population stability and population growth rate (Milner *et al*. 2007). Because hunting mortality patterns are different from the natural mortality (compare Fig. 4a and 4b), harvest affects the relationships between age, phenotype and reproductive success (Festa-Bianchet 2003). There is now overwhelming evidence, from different taxonomic groups (including plants, fishes and mammals), that harvesting by humans can be a strong selective pressure (Fenberg & Roy 2008). For instance, the intense size-selective fishing mortality of cod *Gadus morhua*, L. selects for an earlier age at maturation (Olsen *et al*. 2004). In many harvested populations, most natural selection pressures on males are likely weak compared to hunting, so that human harvest is one of the major current evolutionary force (Palumbi 2001). Several models suggest that selective harvesting based on phenotype can lead to rapid evolutionary changes (Sutherland 1990; Thelen 1991; Ratner & Lande 2001; Ernande *et al*. 2004). However, we still have very limited empirical studies documenting evolutionary response in the wild. This is because most studies exploring the consequences of human-driven changes on natural population only collect phenotypic information (Gienapp *et al*. 2008). Studies comparing male survival for several populations with variable level of hunting would be very beneficial to understand both the direct and indirect effects of hunting on the evolution of male life history. At Ram Mountain, however, artificial selection for smaller horn size appears to have resulted, at least partly, in genetic changes (Coltman *et al*. 2003).

Conclusion

In large herbivores, the length of secondary sexual characters is generally positively correlated with mating success and survival or longevity (Table 1, this study) but for young adults. Working on observational data, where replicated experimental manipulations cannot be carried out, we can hardly account for changes in the male age structure that may have indirect effects on young male survival. Our results nevertheless highlight the importance of exploring the age-dependent patterns of selection to understand the impact of harvesting in wild species, using an appropriate methodology. The different selective forces (natural and artificial) acting on male sheep survival are clearly antagonistic: while natural selection favour large-horned males, artificial selection select for smaller horned one. This supports the contention that hunting-induced mortality is sharply different from natural mortality. Several wild species have now been exploited by human for many decades or even centuries. A major challenge for both evolutionary and population biologists will be to evaluate the relative importance of natural and artificial selection in shaping the evolution of life history of harvested wild species.

Acknowledgements

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