RESEARCH ARTICLE

Horn Growth and Reproduction in a Long-Lived Male Mammal: No Compensation for Poor Early-Life Horn Growth

C. S. Willisch · I. Biebach · N. Marreros · M.-P. Ryser-Degiorgis · P. Neuhaus

Abstract Secondary sexual traits in males of polygynous species are important determinants of reproductive success. It is, however, unknown if and how the development of continuously growing traits at different life-stages is related to reproduction in long-lived male mammals. In this study, we evaluated the relationship of early and late horn growth on social status and reproduction in long-lived male Alpine ibex (*Capra ibex*). For this, we analysed individual horn growth and assessed its effect on dominance and reproduction. No evidence was detected for compensatory horn growth, as late-life horn growth positively depended on early-life horn growth in males. Still, individuals with longer horn segments grown during early adulthood experienced a stronger age-dependent length decline in annual horn growth during the late development. Accordingly, a divergence between individual growth potential and realized horn growth late in life has to be assumed. Residual age-specific horn length and length of early grown horn segments both positively affected dominance and reproductive success, whereas, contrary to our expectation, no significant effect of the length of horn segments grown

during the late development was detected. Suspected higher somatic costs incurred by high-quality males during their late development might at least partly be responsible for this finding. Overall, our study suggests that the total length of horns and their early development in long-lived male Alpine ibex is a reliable indicator of reproductive success and that individuals may be unable to compensate for poor early-life growth performance at a later point in life.

Keywords Compensatory growth · Life-history · Longevity · Male fitness · Ungulate

Introduction

In polygynous species sexual selection is expected to be stronger in males than in females. As a consequence, phenotypic variation in secondary sexual characters as determinants of individual reproductive success is thought to be particularly pronounced in males (Andersson 1994; Shuster and Wade 2003). Accordingly, many studies have shown that male reproductive success increases with the expression of these traits (e.g., Møller 1989; Kruuk et al. 2002). However, the production of secondary sexual characters is energetically costly. At any point in their life organisms must therefore carefully trade their investments into these traits against investments into other competing functions, such as reproductive behaviour, growth or survival (Stearns 1992).

Besides ornaments male weapons are probably the most elaborate secondary sexual structures in animals (Andersson 1994). Irrespective of the taxa they play a major role in establishing dominance relationships through combat and assessment contests in the direct competition between males for access to female mating partners (Emlen 2008).

C. S. Willisch (✉) · I. Biebach
Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland
e-mail: willichristian@yahoo.com

N. Marreros · M.-P. Ryser-Degiorgis
Centre for Fish and Wildlife Health, Vetsuisse Faculty, University of Bern, Länggass-Strasse 122, 3001 Bern, Switzerland

P. Neuhaus
Department of Biological Sciences, University of Calgary, 2500 University Dr. NW, Calgary, AB T2N 1N4, Canada

Furthermore, they appear to provide an honest signal of male quality (Zahavi 1975; Vanpé et al. 2007; von Hardenberg et al. 2007) and they can be important for female mate choice (Emlen 2008).

In ungulates, well-known forms of weapons are the horns of bovids and the antlers of cervids (Caro et al. 2003). Horns and antlers have been shown to be important determinants or indicators of reproductive success in different species (red deer, *Cervus elaphus*: Kruuk et al. 2002; roe deer, *Capreolus capreolus*: Vanpé et al. 2010; Soay sheep, *Ovis aries*: Preston et al. 2001; bighorn sheep, *Ovis canadensis*: Coltman et al. 2002). Thus, individual reproductive success in male ungulates typically increases with the size or mass of horns and antlers.

In contrast to antlers that are casted and rebuilt every year, horns are permanent structures that remain throughout an animal's entire life. Their overall length is the outcome of continuing growth over multiple years. A steady annual development is consequently very important. Horn growth is strongly condition-dependent (Festa-Bianchet et al. 2004; Bergeron et al. 2010). Because of that only high-quality individuals are capable of building big-sized horns (von Hardenberg et al. 2007; Bergeron et al. 2008). Morphological studies suggest that annual growth rates of horns and the corresponding variation are typically decreasing as animals become older (Côté et al. 1998; Bassano et al. 2003; Festa-Bianchet et al. 2004).

According to life history theory, all organisms have to find strategies how to invest their limited energy into current and future reproduction (Stearns 1992). Because horns are the result of an energetically costly and continuing growth processes (Toïgo et al. 2013), the following questions arise: Do males exhibit differences in their individual, age-dependent horn growth strategies? And if yes, how do these strategies relate to their reproductive behaviour and success? It has several times been shown that the overall size of weapons is related to the reproductive behaviour of individual male ungulates (Clutton-Brock et al. 1988a; Stevenson et al. 2004), and that early development of horns positively affects male reproductive success (Robinson et al. 2008). However, up to now it is unknown if the relationship between reproduction and the age-specific growth of secondary sexual traits varies among individuals, and if males may compensate for poor early growth later on.

In this study we used male Alpine ibex (*Capra ibex*) as model organism to investigate the relationship between age-specific horn growth and individual reproductive behaviour and success, respectively. Alpine ibex are sexually dimorphic animals (Loison et al. 1999). Males are long-lived and enjoy very high annual survival until the age of 12–13 years (Toïgo et al. 2007). They do not reach asymptotic body size until the age of 8 years and they grow impressively large horns that can exceed 1 m in length (Lüps et al. 2007). The production as well as the carrying of horns are likely to impose significant costs to males (Toïgo et al. 2013). Not surprisingly annual horn growth varies positively with body mass (Bergeron et al. 2010) suggesting that horn growth is condition-dependent. Further, environmental factors are known to affect horn growth through the nutritional status of the animal (Giacometti et al. 2002; Buentgen et al. 2014). In male Alpine ibex horn size is an important determinant of dominance (Bergeron et al. 2010) and dominance itself is an important factor determining access to receptive females during the rut (see below). Accordingly, reproductive success has recently been shown to depend to a major extent on the dominance of males (Willisch et al. 2012).

In order to get an idea of the prevailing horn growth strategies in the study population we first evaluated individual horn growth of male Alpine ibex. For this we checked if horn development early in life was related to horn development later in life. Based on previous findings on horn growth in male Alpine ibex (Bergeron et al. 2010; Toïgo et al. 2013) we expected a positive relationship. A negative relationship, on the other hand, is an indication for compensatory growth (see e.g., Toïgo et al. 1999; Festa-Bianchet et al. 2004) or an indication for somatic costs of early horn growth or activities closely linked with early horn growth (McElligott et al. 2003). We then examined the role of horn length as an indicator for social rank (since access to oestrus females in male Alpine ibex is largely depending on social rank; Willisch and Neuhaus 2009, 2010) and for reproductive success of individual males. Because of the expectedly positive relationship mentioned above, we predicted total horn length, and horn growth during early and late stages of their physical development to be positively related to social rank and reproduction.

Materials and Methods

Study Area and Animals

The study was carried out between November 2005 and January 2010 in the Alpine ibex population 'Cape au Moine' north of Les Diablerets, Switzerland (46°22′N, 07°09′E; 1,700–2,550 m elevation). The study area measured approximately 13.2 km² and consisted of a steep mountain ridge that was characterized by extensive alpine pastures interspersed with rocky cliffs. In winter Alpine ibex inhabited the south-facing slopes of the ridge that were often free of snow due to solar radiation and avalanches.

Population size ranged between 220 and 270 animals containing approximately 100–120 females, 80–100 males

and 40–65 juveniles. The juvenile/female ratio varied between 0.40 and 0.55, and the male/female ratio between 0.75 and 0.90. Female Alpine ibex with their offspring built groups of up to 50 animals and were permanently resident in the study area. Males lived year-round in fission–fusion societies where individuals were free to join or to leave groups. Part of the males roamed between this population and two adjacent ones. Composition of males during the rut varied, as a consequence, markedly from year to year. At the time of the study, a total of 170 different males (>2 years of age) that were at least once present in the study area could be individually identified due to ear tags or morphological traits (Willisch and Neuhaus 2009).

Mating System

The rut of Alpine ibex takes place in winter. In our study area the rut started with the first females coming into oestrus in early December lasting about 4–6 weeks until about mid-January. Receptive females were only moderately synchronized in time showing a patchy distribution leading to a high level of intra-male competition (Willisch and Neuhaus 2009). Males tried to get mating access to receptive females by making use of two dominance-based alternative mating tactics (Willisch and Neuhaus 2010). The primary tactic 'tending' was adopted only by dominant males. They monopolized access to single receptive females by following, courting and defending them persistently against competitors with the aim of finally getting to copulate with them. Subordinate males, on the other hand, adopted a sneaking tactic termed 'coursing'. Normally, they would wait in the vicinity of a receptive female and the tending male in order to get temporary mating access. Situations favouring coursing male copulations typically arose suddenly when tended females started to run or when they moved or stood too far away from the tending male (Willisch and Neuhaus 2009). Recent paternity analyses showed that reproductive success in male Alpine ibex in the study population was heavily skewed towards old, dominant males often making use of the tending tactic during the rut, while subordinate, young males using mostly the coursing tactic had much lower chances siring offspring (Willisch et al. 2012). Up to now, the role of females in the mating system of Alpine ibex remains largely unknown. In comparison to other ungulate species with less male-imposed (e.g., fallow deer, *Dama dama*: Clutton-Brock et al. 1988b; African topi, *Damaliscus lunatus*: Bro-Jørgensen 2002, 2007, red deer: Clutton-Brock et al. 1982, roe deer: Vanpé et al. 2009) or more promiscuous (e.g., bighorn sheep: Hogg and Forbes 1997; Soay sheep: Preston et al. 2001) mating systems in Alpine ibex possibilities for female mate choice appear to be limited (Willisch 2009).

Behavioural Observations

Each year between 2005 and 2010 from November to January (i.e., during the pre-rut and the rut) behavioural observations on individually identifiable male Alpine ibex were carried out in order to establish yearly dominance hierarchies. The dominance relationships were determined based on records of (1) male–male dyads (individuals were considered winners of agonistic encounters when they displaced or mounted their opponents, or when they were seen following their opponents after a fight), and (2) situations in which males were trying to get access to receptive females by the use of the two alternative mating tactics (Willisch and Neuhaus 2010). Data were collected using different sampling techniques (Willisch and Neuhaus 2009, 2010; Willisch et al. 2012) including continuous focal animal sampling of individual males (applied in winters 2005–2006, 2006–2007, 2007–2008), scan sampling of all receptive females visible in the area and their associated males (applied in all winters), as well as ad libitum sampling of all observed male–male interactions (applied in all winters). Sampling methods aimed in the collection of dominance data for all males. In case of the continuous focal animal sampling effort was distributed as equally as possible among identifiable males present in the study area (Willisch and Neuhaus 2010). In order to rank individual males within yearly dominance hierarchies, we decided to include for each observation period only the data of males that were observed to interact with at least 3 other individuals (i.e., 2005–2006: 25 males, 2006–2007: 47 males, 2007–2008: 56 males, 2008–2009: 26 males, 2009–2010: 17 males). In total, dominance data of 99 different individuals were used. There was no significant difference in age-specific horn length between males with dominance data available and those without (C.S. Willisch, unpublished data). Standardized dominance indices (the so-called dominance abilities) were inferred within a Bayesian framework for all individuals and years as described below.

Horn Measurements

Annual horn increments (i.e., the horn annuli) of captured individuals and animals shot or found dead were determined using measuring tape and photographs. In addition, horn increments of free-ranging males were multiply estimated (≤8 times) by the photogrammetric approach described by Willisch et al. (2013). In total horn measurements of 106 different males were available. For the analyses we calculated different measures of horn length (Fig. 1):

Total horn length (TH): Summed up length of all horn annuli except the one produced as kid (i.e., increment '0';
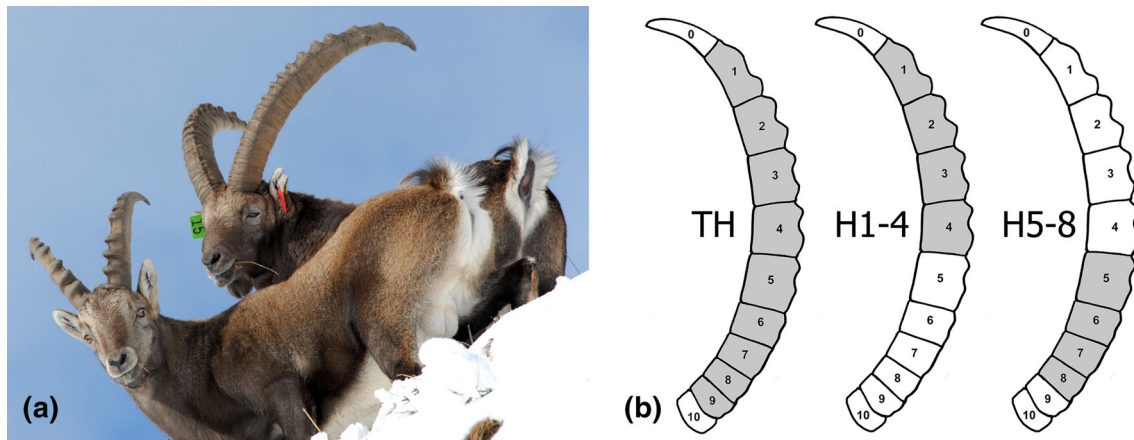
Fig. 1 Photograph illustrating the size of male Alpine ibex (*Capra ibex*) horns depending on the age of males **a**. The animals are 4½ (*left*) and 10½ years old (*right*). In **b** the 3 line-drawings show a horn of a 10½ years old male and the corresponding annuli (in *grey*) that were used to calculate TH, H1-4 and H5-8 (for details see text). The *numbers inside the annuli* correspond with the ages when the annuli were grown (0: annulus grown as kid, 1: annulus grown as yearling, and so on)

this annulus becomes worn out as males are aging) and the one produced in the year of observation (Fig. 1).

Length of horn segment 1–4 (H1-4): Summed up length of the horn annuli produced at the ages of 1–4 years (Fig. 1). Because male Alpine ibex become full-grown at an age of about 8 years (Lüps et al. 2007), we defined the period of 1–4 years of age to be the stage of early development in the life of male Alpine ibex. Similar to TH, the first horn increment produced as kid (i.e., increment '0') is not included in this measure because it can be worn or broken, especially in older males.

Length of horn segment 5–8 (H5-8): Summed up length of the horn annuli produced at the ages of 5–8 years (Fig. 1). This period can be viewed as stage of late development in the life of male Alpine ibex.

Genetic Data

DNA samples of kids born in years 2006 and 2007, and samples of their mothers and potential fathers were collected. The aim was to sample all kids born in the study area in those years together with the samples of their mothers. Furthermore, we also tried to obtain DNA samples of all males that were present during the two corresponding rutting periods in the winters 2005–2006 and 2006–2007 respectively. The DNA samples were genotyped at up to 32 microsatellite loci. Details on genetic data including information on sample storage, DNA extraction, locus-specific genotyping success and error rates, expected heterozygosity and identity analyses can be found in Willisch et al. (2012).

In total, DNA samples of 70 kids (2 of them were twins, i.e., from the same mother), 67 mothers and 100 potential fathers entered the paternity analyses. Of the 68 identifiable

males which had been observed during the two corresponding rutting seasons 85.0 % had been successfully sampled and genotyped. Remaining DNA samples of males in the data set originated from unidentifiable animals (aged 1–5 years) which had been sampled in the study area (Willisch et al. 2012). Data on horn measurements were available for 72 of the males that entered the paternity analyses.

Statistical Analyses

The analyses of the dominance data were performed in WinBugs (Spiegelhalter et al. 2003). Individual dominance abilities, which reflect their relative social status among each other, were inferred in a Bayesian framework based on the method of paired comparisons under the Bradley-Terry model (Adams 2005). The model assumes that the probability that an individual A defeats an individual B is a function of the difference in dominance between the two individuals (Romero and Castellanos 2010). The covariates age and the various measures of horn length were centred and fitted in different models. Their effects were inferred simultaneously with the dominance abilities using Bayesian regression analyses. For the analyses we run simultaneously two Markov chains of 150,000 iterations. Burn-in was 50,000 resulting in a sample size of 200,000 per model. Priors were set to constrain the range of possible dominance abilities between −15 and 15. Standard vague priors were set for regression coefficients (mean of zero, variance of 1,000), the standard deviation of variation around the regression line was assigned a prior distribution with a uniform density between 0 and 1,000 (for details see Adams 2005). Because the dominance data consisted of multiple subsets gathered during five consecutive years we

Table 1 Parameter estimates based on linear mixed-effects models: a) influence of age on total horn length (TH), b) influence of segment length 1–4 (H1-4) on segment length 5–8 (H5-8)

Model	N	Factor	Effect size	SE	D.f.	T-value	p value
a) TH $\sim$ Age + Age^2	106	Age	100.4	7.82	89	14.72	<0.0001
		Age^2	−3.2	0.48	89	−6.76	<0.0001
b) H5-8 $\sim$ H1-4	42	H1-4	0.29	0.08	31	3.66	0.0009

In all analyses animal ID and birth year of animals were included as random factors. For details see text

included animal identity as random factor in the analyses. According to Adams (2005) the Bayesian inference of dominance abilities under the Bradley-Terry model outperforms other methods often used in behavioural studies.

Willisch et al. (2012) recently inferred paternity in Alpine ibex using the same genetic data as in this study. In accordance with them, we reanalysed the pedigree data in a Bayesian framework using the R package MasterBayes (Version 2.42; Hadfield et al. 2006). Similar to the analyses of the dominance data, also the pedigree reconstruction and the estimation of the different parameters of interest occurred simultaneously in a so-called full-probability model. We fitted models with various measures of horn length and age as covariates. Missing horn length data were accounted for by replacing them with 0 (zero) and fitting a secondary binary variable (missing vs. not missing) as interactions with the variable age (J.D. Hadfield, pers. comm.). Markov chains were run for 1.1 million iterations, with a burn-in of 100,000 iterations and a thinning interval of 1,000. Priors were set for the number of unknown sires, as well as for the different parameter estimates. The unknown sires priors were lognormal distributed and weakly informative with a mean of log(15) and a sigma of 0.75. For the other parameter estimates priors with means of zero (i.e. no effect) and variances of pi (which is the closest normal-inverse-logit transformation to a uniform prior on the probability scale) for categorical variables and of 0.02 and 1,000 for continuous or mixed variables were used (J.D. Hadfield, pers. comm.).

The results for the different parameters estimates derived from the Bayesian analyses of the dominance and the pedigree data were all summarized by the medians and the corresponding 95 % credible intervals.

Linear mixed-effects models (Pinheiro and Bates 2000) were used to investigate horn growth patterns in male Alpine ibex. To account for cohort effects we included animal ID and the birth year of animals as random factors in the models.

Results

Horn Growth Patterns

Total horn length of male Alpine ibex is strongly age-dependent (Table 1) and there is a steady increase in the length of horns with increasing age (Fig. 2). The average length of annually grown horn increments is steadily decreasing with increasing age of males (Table 2). Variation coefficients further reveal that relative differences in annuli growth are initially (i.e., up to an age of 5–7 years) becoming smaller with increasing age of males, but then tend to increase again.

The linear mixed-effects model shows that the length of horn segment H1-4 has a positive impact on the length of the segment H5-8 (Table 1; Fig. 2). Comparison of the horn growth trajectories of males with short- (H1-4 $\leq$299.9 mm), medium- (300.0 mm $\leq$ H1-4 $\leq$ 349.9 mm) and long-sized H1-4 segments (H1-4 $\geq$350.0 mm) indicates, however, that the age-dependent decline in annuli length between the ages of 5–8 years is negatively related to the length of H1-4 for these three groups (Fig. 3; group: $F_{2;60} = 5.6$, $p = 0.006$; age: $F_{1;161} = 179.4$, $p < 0.0001$; group * age: $F_{2;161} = 24.5$, $p < 0.0001$). Thus, the yearly decline in annuli length grown between 5 and 8 years of age is strongest in the group of males with long H1-4 segments, whereas there is a less marked decline for the group with medium-sized H1-4 segments. Only a slight age-dependent decline is evident for the group of males with short H1-4 segments (Fig. 3). No significant variation between groups differing in H1-4 segment length can be found in lengths of horn annuli produced at ages $\geq$9 years (Fig. 3; group: $F_{2;21} = 0.2$, $p > 0.05$; age: $F_{1;42} = 196.4$, $p < 0.0001$; group * age: $F_{2;42} = 2.6$, $p > 0.05$). Hence, the length of annuli grown at ages $\geq$9 years do not differ according to the segment length grown during early development; only do they negatively decrease with increasing age of males.

Dominance

Bayesian regression models show that age of male Alpine ibex has a strong positive impact on dominance (Table 3). Individual dominance abilities increase steadily until the age of 10–12 years but slightly decline thereafter (Fig. 4). The analyses further demonstrate that the residual age-specific horn length also has a strong positive effect on dominance (Table 3, Fig. 5). Considering the impact of the horn lengths produced at different stages it turns out that dominance increases with the segment length of horns produced during their early development, i.e. H1-4 (Fig. 5), but not during their late development, i.e. H5-8 (Table 3).

Fig. 2 Growth patterns of male Alpine ibex (*Capra ibex*) horns. The total horn length (TH) in relation to the age of 106 males is displayed in figure (**a**). Figure **b** shows the intra-individual relationship between the horn segment length 1–4 (H1-4) and the horn segment length 5–8 (H5-8) of 42 males
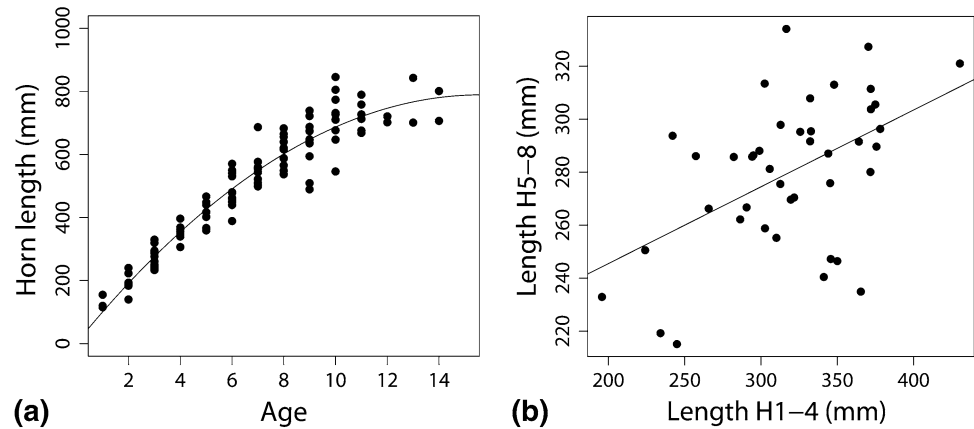

(a)

(b)

Table 2 Average annual horn growth in male Alpine ibex (*Capra ibex*) depending on their age

Horn annulus	n	Mean	SD	CV
0[a]	106	69.3	22.0	0.32
1	106	92.1	20.7	0.22
2	103	81.8	14.5	0.18
3	97	81.7	12.7	0.16
4	86	79.4	11.0	0.14
5	76	75.7	10.1	0.13
6	68	71.9	9.1	0.13
7	55	68.3	9.1	0.13
8	44	60.1	8.8	0.15
9	33	51.9	7.6	0.15
10	22	43.1	7.1	0.16
11	13	33.3	6.9	0.21
12	6	29.0	3.5	0.12
13	4	22.5	7.2	0.32
14	2	22.4	1.3	0.06

Displayed are the sample sizes (n), the mean annuli lengths (in mm), standard deviations (SD) and coefficients of variation (CV)

[a] The first horn increment 0 may be worn or broken, especially in older males

Paternity

Despite differing parameterisation the four models used to infer paternity result in similar pedigrees. Overall the number of unknown sires varies between 8.8 and 10.5 depending on the model. Paternity has been determined for 60–64 kids, which represents 85–88 % of all sampled kids. Considering the commonly used confidence levels of 80 and 95 % for the paternity assignments the four models report likely fathers for 71–73 and 59–62 % of the sampled kids, respectively (Table 4). The two twin kids in the sample were assigned two different fathers at the 80 % confidence level, one of them being 10 years old during the rut and the other being 4 years old.
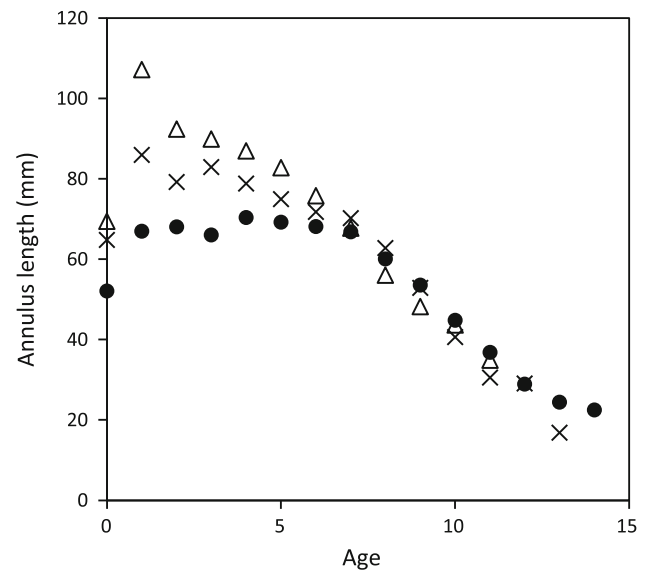

Fig. 3 Horn growth trajectories of male Alpine ibex (*Capra ibex*) depending on their early life horn growth. Displayed are the mean annuli lengths (y axis) produced at certain ages of three Alpine ibex male groups based on their horn segment lengths 1–4 (H1-4). Symbols: *filled circles*: males with H1-4 ≤299.9 mm (n = 20); *x signs*: males with H1-4 between 300.0 and 349.9 mm, (n = 36); *open triangles*: males with H1-4 ≥350.0 mm (n = 29)

Models show that reproductive success is positively depending on the age of males and as well on the size of their horns. The age-specific residual horn length has a positive effect on the likelihood of paternity (Table 4, Fig. 6). The number of offspring is, furthermore, also increasing with the segment length H1-4 (Fig. 6), whereas the length of horn segment H5-8 does apparently not contribute significantly to it (Table 4).

Discussion

The present study demonstrates that social status and reproductive success in male Alpine ibex are both related

Table 3 Results of the Bayesian regression analyses of individual dominance abilities in male Alpine ibex (*Capra ibex*) for the differently parameterised models using WinBugs (for details see text)

Model	Factor	Effect size
Model 1		
A + A^2	A	1.52 (1.27 to 1.79)*
	A^2	−0.18 (−0.24 to −0.13)*
Model 2		
A + A^2 + RTH	A	1.52 (1.29 to 1.79)*
	A^2	−0.17 (−0.23 to −0.12)*
	RTH	0.016 (0.005 to 0.027)*
Model 3		
A + A^2 + H1-4 + H5-8	A	1.43 (1.16 to 1.72)*
	A^2	−0.15 (−0.21 to −0.09)*
	H1-4	0.0051 (0.0013 to 0.0090)*
	H5-8	0.0006 (−0.0033 to 0.0046)
Model 4		
A + A^2 + H1-4	A	1.45 (1.21 to 1.71)*
	A^2	−0.15 (−0.21 to −0.09)*
	H1-4	0.0055 (0.0018 to 0.0093)*
Model 5		
A + A^2 + H5-8	A	1.46 (1.17 to 1.76)*
	A^2	−0.17 (−0.24 to −0.11)*
	H5-8	0.0018 (−0.0021 to 0.0057)

Presented values are medians followed by the 95 % credible intervals in brackets. Explanatory variables are age (A), age-specific residuals of total horn length (RTH), horn segments length 1–4 (H1-4) and horn segments length 5–8 (H5-8). All horn measures are in mm

Significant effects are indicated by an '*'
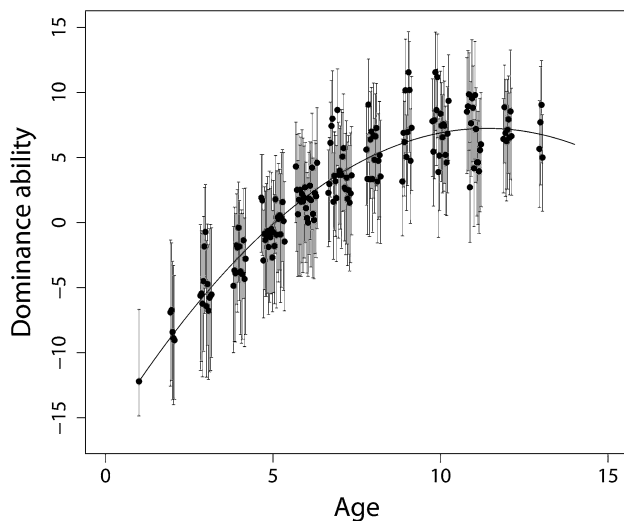
Fig. 4 Individual dominance abilities of 99 individual male Alpine ibex (*Capra ibex*) depending on their age between 2005 and 2006 and 2009–2010 (n$_{total}$ = 171). Displayed values are the medians and the corresponding 95 % credible intervals based on the Bayesian dominance analysis

to horn size. Hence, the longer the horns of males are the better they perform in intra-sexual conflicts and the more successful they are in terms of reproduction. Although it is reasonable to assume that other physical parameters, such as body size or weight (Bergeron et al. 2010), are also playing an important role in intra-male competition, horn size is likely to influence directly the fighting ability of individual males. Thus, in escalated agonistic interactions male Alpine ibex are known to fight fiercely with their horns. Besides from pushing they frequently clash with their horns. For the most vigorous clashes male Alpine ibex go upright on their hind legs and then strike their opponent by descending fast onto their front legs delivering an extremely forceful blow in a bent downward movement (Alvarez 1990). Because the momentum of such clashes increases with the size and the weight of horns, males with bigger horns can deliver stronger strikes to their opponents than short-horned males. Having long horns is therefore decisive in escalated fights in male Alpine ibex and mediates significant advantages to their bearers. Furthermore, it is very likely that the length of horns can also be used by competitors to visually assess the fighting ability of a male. However, since fighting strength is besides from horn size and skeletal size to a large extent also condition-dependent (see above), the utility of an irreversible trait, such as horn size, to assess the actual competitiveness of an opponent is limited (Jennings et al. 2006). Still, since the rutting season of Alpine ibex takes place in winter, under harsh environmental conditions in steep and dangerous terrain, males are well-advised to evaluate the strength of their opponents before engaging in risky fights. To do so, visual assessments might involve multiple physical traits being indicative for an individual's actual state, such as body size and conditioning (Jennings et al. 2006). Additionally, also behavioural aspects might enter the assessments of opponents. Especially useful might be information on male performance during previous contests with other males. The fact that fighting males are often observed by bystanders may be an indication for this (C.S. Willisch, unpublished data).

Because dominance in male Alpine ibex varies with the size of horns and because the adoption of the alternative mating tactics and thus also mating access in Alpine ibex is strongly dominance-dependent (Willisch and Neuhaus 2010; Willisch et al. 2012) it is not surprising that the reproductive success itself is as well positively related with the horn size of individual males. Hence, in Alpine ibex the high reproductive success of males with long horns is likely to result from their advantages in intra-male competition. The extent to which the relationship between male horn size and reproductive success is further enhanced by the process of female mate choice remains unclear. It seems reasonable to assume that female Alpine ibex are

Fig. 5 Relationship of individual horn growth patterns and the age-specific dominance abilities of male Alpine ibex (*Capra ibex*). Age-specific residual dominance abilities are plotted against **a** the age-specific residual horn length ($n_{total} = 171$; $n_{males} = 99$) and **b** the horn segment length 1–4 (H1-4) ($n_{total} = 128$; $n_{males} = 69$)
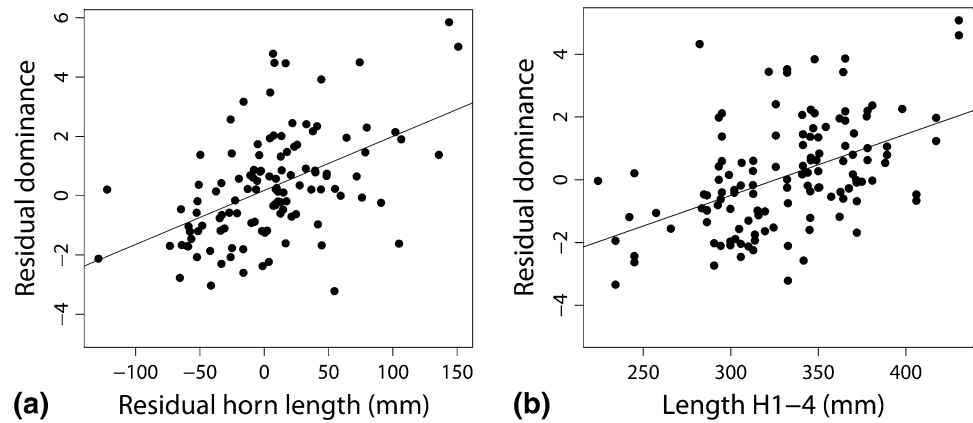
able to assess the quality of individual males by evaluating them visually (see above). Since horn size in male Alpine ibex is a sign of genetic quality (von Hardenberg et al. 2007) this trait might serve females to choose among potential mating partners. However, as the mating system of Alpine ibex is male-imposed, the contribution of female choice to the evolution of long horns in male Alpine ibex appears to be limited—at least compared to other ungulate species with less male-imposed or more promiscuous mating systems (e.g., Clutton-Brock et al. 1982; Preston et al. 2001; Vanpé et al. 2010).

Considering the high selective pressure to which secondary sexual traits in polygynously breeding males, such as Alpine ibex are exposed, our result that horn size in male Alpine ibex is related to their dominance and reproductive success is fitting well into the general theory (Andersson 1994). Previous studies provided evidence for the size and/or expression of such traits being positively related to male dominance (Alpine ibex: Bergeron et al. 2010; red deer: Appleby 1982) and reproduction (red deer: Kruuk et al. 2002; bighorn sheep: Coltman et al. 2002; Soay sheep: Preston et al. 2001). However, to our knowledge this study is the first to show under natural conditions that not all developmental stages of a long-lived animal's ontogeny are contributing equally to these relationships.

Although the early development of horns has recently been identified to be indicative for the reproductive success in male ungulates (Robinson et al. 2008), it was up to now not clear if long-lived organisms attaining high reproductive rewards very late in life (such as male Alpine ibex; Willisch et al. 2012) can compensate for poor early-life growth performance. In this respect the results of our study provide new insights into how individuals may govern investments into secondary sexual traits during different developmental stages of their life in order to maximize rewards later on. The results suggest that in male Alpine ibex the early development of horns is a suitable predictor of individual reproductive success, whereas the late

development of horns does not seem to relate significantly to it. Consequently, it seems rather unlikely that individuals showing poor growth early in life are able to compensate for that later on.

Given the finding that the length of the horn segment H1-4 is positively correlated with the length of H5-8 (see also, Toïgo et al. 2013) the lack of any positive effect of the late-grown horn segment H5-8 on social status and reproductive success is yet not trivial to understand. The fact that males with long H1-4 segments experience a stronger age-dependent decline in annuli length between the ages of 5–8 years than males with shorter H1-4 segments may, however, at least partly contribute to the explanation of this phenomenon. Thus, the age-dependent decline in horn growth during the late development is more pronounced in males growing long horn segments early in life. As a consequence, the relative differences in the horn segment lengths among males diminish as they get older. The smaller the inter-individual variation in the length of the H5-8 segments is, the harder it finally becomes to infer statistically significant relationships between H5-8 and other variables, such as dominance and reproductive success.

The finding that the length of the horn segment H1-4 is positively related to the length of the segment H5-8 suggests that individual differences in the growth rate of horns in principal persist throughout the entire development of male Alpine ibex. Accordingly animals growing long horn annuli early in life are likely to grow also long annuli late in life. The lack of any negative relationship indicates that male Alpine ibex—in contrast to females (Toïgo et al. 1999)—are apparently not able to compensate for poor early-life growth performance at a later point in life. Although environmental factors are known to affect annual horn growth (Giacometti et al. 2002; Buentgen et al. 2014) consistent horn length differences over multiple years are therefore a likely sign of individual heterogeneity in male Alpine ibex (Bergeron et al. 2008; Toïgo et al. 2013).

Table 4 Results of the Bayesian paternity analyses in male Alpine ibex (*Capra ibex*) for the differently parameterised models using Master-Bayes (for details see text)

Model	Factor	Effect size	Paternities assigned at the 80 and 95 % confidence level	Number of unknown sires
Model 1				
A + RTH	A	0.26 (0.16 to 0.36)*	51 and 44	9.45 (3.64 to 19.87)
	RTH	0.0089 (0.0032 to 0.0146)*		
Model 2				
A + H1-4 + H5-8	A	0.12 (−0.06 to 0.32)	51 and 43	10.40 (3.98 to 21.65)
	H1-4	0.011 (0.004 to 0.019)*		
	H5-8	−0.002 (−0.012 to 0.007)		
Model 3				
A + H1-4	A	0.24 (0.13 to 0.36)*	51 and 43	10.45 (4.23 to 22.75)
	H1-4	0.012 (0.005 to 0.018)*		
Model 4				
A + H5-8	A	0.08 (−0.09 to 0.30)	50 and 41	8.76 (3.20 to 19.36)
	H5-8	−0.0008 (−0.01 to 0.09)		

Presented values are medians followed by the 95 % credible intervals in brackets. Explanatory variables are age (A), age-specific residuals of total horn length (RTH), horn segments length 1–4 (H1-4) and horn segments length 5–8 (H5-8). All horn measures are in mm

Note: Secondary binary variables that were fitted to account for missing data are not reported

Significant effects are indicated by an '*'

Yet, the stronger age-dependent decline in annuli growth at the ages of 5–8 years in males with long H1-4 segments denotes that there seems to be a certain discrepancy in the individual growth potential (based on the early life annuli length) and the realized growth during the late development. Although it is very difficult to reveal the ultimate causes for this pattern, it is (based on the positive relationship between the absolute horn lengths during early and late development discussed above) unlikely that it is due to compensatory growth (Toïgo et al. 2013). If compensatory effects cannot be responsible for the observed negative relationship in male Alpine ibex it might be possible that the discrepancy in realized growth and growth potential is a result of somatic costs. Comparable to our data, in adult male fallow deer body mass loss during the rut was positively related with initial body mass suggesting that heavier males lost more weight than lighter ones (McElligott et al. 2003). Not surprisingly fighting behaviour of male fallow deer contributed to the mass loss as well indicating that investments into costly behaviours can markedly impair the physical development of males. Since fighting in male Alpine ibex is considered to be a very costly activity (Willisch and Neuhaus 2010) one can imagine that also in this species well-developed and more dominant males may suffer from a more pronounced annual horn growth depression than poorly-developed, subordinate males.

The idea that the age-dependent decline in annuli length until the age of about 8 years is representing a sort of somatic costs is particularly interesting with respect to a recent study evaluating the survival costs of horn growth in Alpine ibex (Toïgo et al. 2013). Thus, in the mentioned study early horn growth was not found to impair future survival of males until a very high age of about 12 years. Accordingly, it seems that early horn growth has no immediate survival consequences for male Alpine ibex whereas it conveys high reproductive success later in life. On the other hand, horn growth may be depressed to a certain point by reproduction related activities until an age of about 8 years (see also, McElligott et al. 2003). Taken together, our results and the findings of Toïgo et al. (2013) therefore indicate that investments into reproduction related behaviours might not be traded against survival but to a limited degree against future annual horn growth in male Alpine ibex. Considering that dominance at an advanced age of ≥9 years (Willisch and Neuhaus 2010; Willisch et al. 2012) is the crucial factor determining whether a male gets unrestricted mating access to receptive females or not it may be beneficial, particularly for well-developed individuals, to slow down annual horn growth during the late development while maintaining a high yearly survival. From this point of view, the observed patterns with respect to growth, survival and reproduction exhibited by male Alpine ibex are fitting well with the supposedly slow life

Fig. 6 Effect of **a** the age-specific residual horn length ($n_{total} = 106$; $n_{males} = 72$) and **b** the horn segment length 1–4 (H1-4) ($n_{total} = 69$; $n_{males} = 46$) on the mean age-specific residual offspring number of male Alpine ibex (*Capra ibex*)
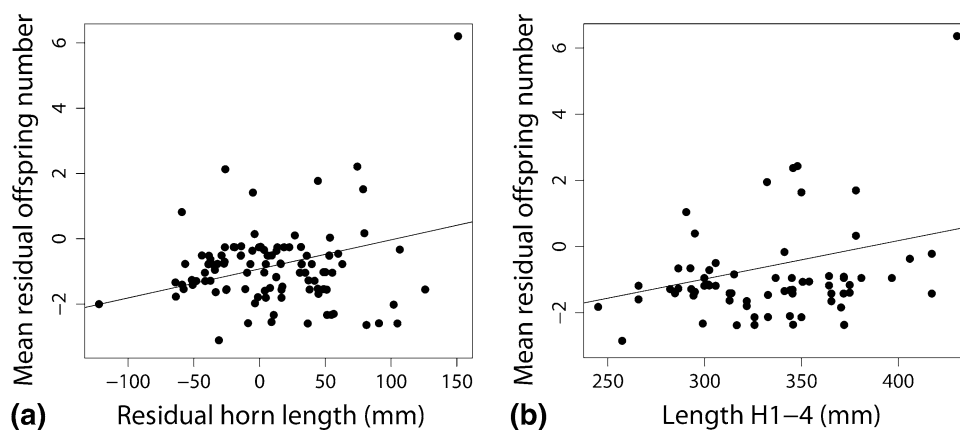
history strategy of these animals (Willisch et al. 2012; Toïgo et al. 2013).

Conclusion

Overall, our study provides support for the idea that early development of secondary sexual traits in long-lived polygynous male mammals is a reliable indicator of dominance and reproductive success later in life. In this regard, it is in line with studies evaluating the effect of early development of morphological traits in general on reproduction in males (e.g., for horns: Robinson et al. 2008; for antlers: Clutton-Brock et al. 1982; for body weight: Kruuk et al. 1999) and also in females (body size/weight: Beauplet and Guinet 2007; but see Kruuk et al. 1999). The fact that the late development of horns does not significantly affect reproduction of individual male Alpine ibex further denotes that not all developmental stages of an animal's life are contributing equally to its reproductive success and that it may be impossible for individuals with reduced early growth to compensate for these effects later in life. The extent of somatic costs incurred in the growth of secondary sexual traits may, furthermore, also vary with the specific life-history strategies of the species under consideration. Consequently, the supposed trade-offs in energy investments into growth, survival and reproduction (Stearns 1992) can considerably differ among species.

References

Adams, E. S. (2005). Bayesian analysis of linear dominance hierarchies. *Animal Behaviour, 69*, 1191–1201.

Alvarez, F. (1990). Horns and fighting in male Spanish ibex, *Capra pyrenaica*. *Journal of Mammalogy, 71*(4), 608–616.

Andersson, M. (Ed.). (1994). *Sexual selection* (pp. 1–599). Princeton: Princeton University Press.

Appleby, M. C. (1982). The consequences and causes of high social rank in red deer stags. *Behaviour, 80*, 259–273.

Bassano, B., Perrone, A., & Von Hardenberg, A. (2003). Body weight and horn development in Alpine chamois, *Rupicapra rupicapra* (Bovidae, Caprinae). *Mammalia, 67*(1), 65–73.

Beauplet, G., & Guinet, C. (2007). Phenotypic determinants of individual fitness in female fur seals: Larger is better. *Proceedings of the Royal Society B-Biological Sciences, 274*(1620), 1877–1883.

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*(1), 77–82.

Bergeron, P., Grignolio, S., Apollonio, M., Shipley, B., & Festa-Bianchet, M. (2010). Secondary sexual characters signal fighting ability and determine social rank in Alpine ibex (*Capra ibex*). *Behavioral Ecology and Sociobiology, 64*, 1299–1307.

Bro-Jørgensen, J. (2002). Overt female mate competition and preference for central males in a lekking antelope. *Proceedings of the National Academy of Sciences of the United States of America, 99*(14), 9290–9293.

Bro-Jørgensen, J. (2007). Reversed sexual conflict in a promiscuous antelope. *Current Biology, 17*(24), 2157–2161.

Buentgen, U., Liebhold, A., Jenny, H., Mysterud, A., Egli, S., Nievergelt, D., et al. (2014). European springtime temperature synchronises ibex horn growth across the eastern Swiss Alps. *Ecology Letters, 17*(3), 303–313.

Caro, T. M., Graham, C. M., Stoner, C. J., & Flores, M. M. (2003). Correlates of horn and antler shape in bovids and cervids. *Behavioral Ecology and Sociobiology, 55*(1), 32–41.

Clutton-Brock, T. H., Albon, S. D., & Guinness, F. E. (1988a). Reproductive success in male and female red deer. In T. H. Clutton-Brock (Ed.), *Reproductive success* (pp. 325–343). Studies of individual variation in contrasting breeding systems. Chicago: The University of Chicago Press.

Clutton-Brock, T. H., Green, D., Hiraiwa-Hasegawa, M., & Albon, S. D. (1988b). Passing the buck: Resource defence, lek breeding and mate choice in fallow deer. *Behavioral Ecology and Sociobiology, 23*, 281–296.

Clutton-Brock, T. H., Guinness, F. E., & Albon, S. D. (1982). *Red deer*. Behavior and ecology of two sexes. Chicago: The University of Chicago Press.

Coltman, D. W., Festa-Bianchet, M., Jorgenson, J. T., & Strobeck, C. (2002). Age-dependent sexual selection in bighorn rams. *Proceedings of the Royal Society of London Series B-Biological Sciences, 269*(1487), 165–172.

Côté, S. D., Festa-Bianchet, M., & Smith, K. G. (1998). Horn growth in mountain goats (*Oreamnos americanus*). *Journal of Mammalogy, 79*(2), 406–414.

Emlen, D. J. (2008). *The evolution of animal weapons* (pp. 387–413). Annual Reviews: Annual Review Of Ecology Evolution And Systematics. Palo Alto.

Festa-Bianchet, M., Coltman, D. W., Turelli, L., & Jorgenson, J. T. (2004). Relative allocation to horn and body growth in bighorn rams varies with resource availability. *Behavioral Ecology, 15*(2), 305–312.

Giacometti, M., Willing, R., & Defila, C. (2002). Ambient temperature in spring affects horn growth in male alpine ibexes. *Journal of Mammalogy, 83*(1), 245–251.

Hadfield, J. D., Richardson, D. S., & Burke, T. (2006). Towards unbiased parentage assignment: Combining genetic, behavioural and spatial data in a Bayesian framework. *Molecular Ecology, 15*(12), 3715–3730.

Hogg, J. T., & Forbes, S. H. (1997). Mating in bighorn sheep: Frequent male reproduction via a high-risk "unconventional" tactic. *Behavioral Ecology and Sociobiology, 41*(1), 33–48.

Jennings, D. J., Gammell, M. P., Carlin, C. M., & Hayden, T. J. (2006). Is difference in body weight, antler length, age or dominance rank related to the number of fights between fallow deer (*Dama dama*)? *Ethology, 112*(3), 258–269.

Kruuk, L. E. B., Clutton-Brock, T. H., Rose, K. E., & Guinness, F. E. (1999). Early determinants of lifetime reproductive success differ between the sexes in red deer. *Proceedings of the Royal Society of London Series B-Biological Sciences, 266*(1429), 1655–1661.

Kruuk, L. E. B., Slate, J., Pemberton, J. M., Brotherstone, S., Guinness, F., & Clutton-Brock, T. (2002). Antler size in red deer: Heritability and selection but no evolution. *Evolution, 56*(8), 1683–1695.

Loison, A., Gaillard, J. M., Pelabon, C., & Yoccoz, N. G. (1999). What factors shape sexual size dimorphism in ungulates? *Evolutionary Ecology Research, 1*(5), 611–633.

Lüps, P., Blöchlinger, B., Schmid, P., & Zuber, M. (2007). Ontogenese und Variabilität verschiedener Körpermerkmale des Steinwildes *Capra i. ibex* im Berner Oberland (Schweizer Alpen). *Beiträge zur Jagd- und Wildforschung, 32*, 495–510.

McElligott, A. G., Naulty, F., Clarke, W. V., & Hayden, T. J. (2003). The somatic cost of reproduction: What determines reproductive effort in prime-aged fallow bucks? *Evolutionary Ecology Research, 5*(8), 1239–1250.

Møller, A. P. (1989). Viability costs of male tail ornaments in a swallow. *Nature, 339*(6220), 132–135.

Pinheiro, J. C., & Bates, D. M. (2000). *Mixed-effects models in S-Plus*. New York: Springer Verlag.

Preston, B. T., Stevenson, I. R., Pemberton, J. M., & Wilson, K. (2001). Dominant rams lose out by sperm depletion: A waning success in siring counters a ram's high score in competition for ewes. *Nature, 409*(6821), 681–682.

Robinson, M. R., Pilkington, J. G., Clutton-Brock, T. H., Pemberton, J. M., & Kruuk, L. E. B. (2008). Environmental heterogeneity generates fluctuating selection on a secondary sexual trait. *Current Biology, 18*(10), 751–757.

Romero, T., & Castellanos, M. A. (2010). Dominance relationships among male hamadryas baboons (*Papio hamadryas*). *Journal of Ethology, 28*(1), 113–121.

Shuster, S. M., & Wade, M. J. (2003). *Mating systems and strategies*. Princeton: Princeton University Press.

Spiegelhalter, D., Thomas, A., Best, N., & Lunn, D. (2003). *WinBUGS. User manual, version 1.4*. Cambridge: MRC Biostatistics Unit.

Stearns, S. C. (1992). *The evolution of life histories*. New York: Oxford University Press.

Stevenson, I. R., Marrow, P., Preston, B. T., Pemberton, J. M., & Wilson, K. (2004). Adaptive reproductive strategies. In J. Pemberton & T. H. Clutton-Brock (Eds.), *Soay sheep. Dynamics and selection in a island population*. Cambridge: Cambrigde University Press.

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. *Journal of Animal Ecology, 76*(4), 679–686.

Toïgo, C., Gaillard, J.-M., & Loison, A. (2013). Alpine ibex males grow large horns at no survival cost for most of their lifetime. *Oecologia, 173*(4), 1261–1269.

Toïgo, C., Gaillard, J. M., & Michallet, J. (1999). Cohort affects growth of males but not females in alpine ibex (*Capra ibex ibex*). *Journal of Mammalogy, 80*(3), 1021–1027.

Vanpé, C., Gaillard, J.-M., Kjellander, P., Liberg, O., Delorme, D., & Hewison, A. J. M. (2010). Assessing the intensity of sexual selection on male body mass and antler length in roe deer *Capreolus capreolus*: Is bigger better in a weakly dimorphic species? *Oikos, 119*(9), 1484–1492.

Vanpé, C., Gaillard, J.-M., Kjellander, P., Mysterud, A., Magnien, P., Delorme, D., et al. (2007). Antler size provides an honest signal of male phenotypic quality in roe deer. *American Naturalist, 169*(4), 481–493.

Vanpé, C., Morellet, N., Kjellander, P., Goulard, M., Liberg, O., & Hewison, A. J. M. (2009). Access to mates in a territorial ungulate is determined by the size of a male's territory, but not by its habitat quality. *Journal of Animal Ecology, 78*(1), 42–51.

von Hardenberg, A., Bassano, B., Festa-Bianchet, M., Luikart, G., Lanfranchi, P., & Coltman, D. (2007). Age-dependent genetic effects on a secondary sexual trait in male Alpine ibex, *Capra ibex*. *Molecular Ecology, 16*(9), 1969–1980.

Willisch CS. 2009. The ecology of reproduction in long-lived male Alpine ibex (*Capra ibex*): The role of age, dominance and alternative mating tactics. [PhD thesis]. Neuchâtel: Université de Neuchâtel. 1-106 p.

Willisch, C. S., Biebach, I., Koller, U., Bucher, T., Marreros, N., Ryser-Degiorgis, M.-P., et al. (2012). Male reproductive pattern in a polygynous ungulate with a slow life-history: The role of age, social status and alternative mating tactics. *Evolutionary Ecology, 26*(1), 187–206.

Willisch, C. S., Marreros, N., & Neuhaus, P. (2013). Long-distance photogrammetric trait estimation in free-ranging animals: A new approach. *Mammalian Biology, 78*, 351–355.

Willisch, C. S., & Neuhaus, P. (2009). Alternative mating tactics and their impact on survival in adult male Alpine ibex (*Capra ibex ibex*). *Journal of Mammalogy, 90*(6), 1421–1430.

Willisch, C. S., & Neuhaus, P. (2010). Social dominance and conflict reduction in rutting male Alpine ibex *Capra ibex*. *Behavioral Ecology, 21*(321), 380.

Zahavi, A. (1975). Mate selection: A selection for a handicap. *Journal of Theoretical Biology, 53*(1), 205–214.