Effects of early horn growth on reproduction and hunting mortality in female chamois

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Summary

1. Environmental conditions during early development can affect the growth patterns of vertebrates, influencing future survival and reproduction. In long-lived mammals, females that experience poor environmental conditions early in life may delay primiparity. In female bovids, annual horn growth increments may provide a record of age-specific reproduction and body growth. Horn length, however, may also be a criterion used by hunters in selecting animals to harvest, possibly leading to artificial selection.

2. We studied three populations of chamois (*Rupicapra rupicapra*) in the western Alps to explore the relationships between female horn length and early growth, age of primiparity and age-specific reproduction. We also compared the risk of harvest to reproductive status and horn length.

3. Early horn growth was positively correlated with body mass in pre-reproductive females and with reproduction in very young and senescent adults. Females with strong early horn growth attained primiparity at an earlier age than those with weak early growth. Horn length did not affect hunter selection, but we found a strong hunter preference for nonlactating females.

4. Our research highlights the persistent effects of early development on reproductive performance in mammals. Moderate sport harvests are unlikely to affect the evolution of phenotypic traits and reproductive strategies in female chamois. A policy of penalizing hunters that harvest lactating females, however, may increase the harvest of 2-year-old females, which have high reproductive potential.

Key-words: horn growth, hunting, primiparity, *Rupicapra rupicapra*, senescence

Introduction

The evolution of reproductive strategies is of central interest in ecology. Because many populations are exploited or otherwise affected by human activities, a simultaneous consideration of natural and artificial selective pressures should provide novel insights and may be required for most large mammals (Festa-Bianchet 2003; Proaktor, Coulson & Milner-Gulland 2007). That approach would be particularly appropriate in cases where natural and artificial selective pressures are thought to be opposite, as in the case of trophy hunting (Coltman *et al*. 2003). Here, we examine how differences in morphology and early development may influence the reproductive success of female chamois (*Rupicapra rupicapra* Linnaeus) exposed to natural and artificial selective pressures.

Environmental conditions during early development can affect the growth patterns of vertebrates (Lindström 1999). Harsh weather, high density or scarce resources decrease juvenile growth rate, reducing body development and eventually future reproductive performance (Madsen & Shine 2000; Gaillard *et al*. 2003; Beauplet *et al*. 2005). Rapid early development is typically associated with large mass and high reproductive success in adults (Lummaa & Clutton-Brock 2002; Beauplet & Guinet 2007; Solberg *et al*. 2008). In polygynous and sexually dimorphic ungulates, males with rapid early growth are typically larger as adults and have higher reproductive success than males with poor early growth (Kruuk *et al*. 1999; Solberg *et al*. 2008). Rapid growth, however, is associated with greater mortality of juvenile males during periods of resource scarcity (Clutton-Brock, Major & Guinness 1985). On the contrary, when resources are scarce, females allocate energy to growth and maintenance rather than to reproduction (Gaillard *et al*. 2000a; Festa-Bianchet, Gaillard & Côté 2003). Females that experience poor environmental conditions early in life can delay primiparity (Festa-Bianchet & Jorgenson 1998; Gaillard *et al*. 2003) and may show compensatory growth later in life. Ungulate females that attain primiparity at an early age are typically heavier than nonreproducing females of the same age

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(Jorgenson *et al.* 1993; Garel *et al.* 2009; Hamel *et al.* 2009a). In bighorn sheep (*Ovis canadensis* Shaw), heavy adult females live longer than light ones (Gaillard *et al.* 1998) and have higher reproductive success at all ages (Bérubé, Festa-Bianchet & Jorgenson 1999). In red deer (*Cervus elaphus* Linnaeus), Nussey *et al.* (2007) found that poor environmental condition early in life decrease the fecundity of senescent females, while females that enjoy favourable environmental conditions during early development have high fecundity at all ages. Good environmental conditions during ontogeny may lower the costs of early primiparity (McElligott, Altwegg & Hayden 2002; Moyes *et al.* 2006) and allow a strong reproductive performance during senescence.

In temperate climates, the horns of bovids stop growing in winter, usually forming a distinct annulus (Bubenik & Bubenik 1990). The growth of each annual horn increment can be affected by environmental conditions (Festa-Bianchet *et al.* 2004), reproduction (Miura, Kita & Sugimura 1987) and early development, as some species show compensatory growth (Pérez-Barbería, Robles & Nores 1996; Festa-Bianchet & Côté 2008). Consequently, horn increments may provide a permanent indication of age-specific body growth. In some species, primiparity is associated with reduced horn growth (Miura, Kita & Sugimura 1987), but we know little about the relationship between early horn development and age-specific female reproductive success.

Because most mountain ungulate populations are subject to sport hunting, it is important to consider the potential eco-logical impacts and artificial selective pressures from human harvest (Festa-Bianchet 2003). Horn length may be a crite-rion used by hunters in deciding which animals to harvest, possibly leading to artificial selection (Festa-Bianchet 2003). Hunters usually seek specific age or sex classes (Milner, Nilsen & Andreassen 2007), decreasing their survival (Bonenfant *et al.* 2008). If hunters preferentially remove individuals with long horns, they may also select against correlated traits, such as large mass (Coltman *et al.* 2003) or possibly early repro-duction. If hunters prefer to harvest females without depen-dent offspring (Festa-Bianchet 2007), however, hunting may increase the mortality of nonlactating females, possibly affecting the evolution of female reproductive strategies (Proaktor, Coulson & Milner-Gulland 2007). Several studies have examined the ecological and evolutionary effects of hunting on males (Femberg & Roy 2008), and simulations suggest that high harvest rates may favour females that make a greater reproductive effort early in life (Proaktor, Coulson & Milner-Gulland 2007). Few studies, however, have empiri-cally evaluated the potential effects of hunting on female reproductive strategy (Mysterud, Yoccoz & Langvatn 2009).

We studied three populations of chamois in the western Alps to explore the relationships between horn increment length in females and early growth, age of primiparity, age-specific reproduction and the risk of sport harvest. We tested six hypotheses (Table 1). We expected that early horn growth would reflect early body growth and predict adult horn length but not adult mass, similarly to what we found for

Table 1. Summary of hypotheses, predictions and populations involved, for a study of reproductive success in female chamois in the western Italian Alps. 'Park' refers to a protected population, while VCO2 and CN4 are hunted populations. Regulations imposed a heavy penalty for harvesting lactating females in VCO2

Hypothesis	Predictions	Populations	Supported (yes, no)
(A) Early horn growth is an index of early rapid development but not of adult mass.	Early horn growth is positively correlated with yearling mass but not with adult mass.	CN4, VCO2, Park	Yes
(B) Early horn growth predicts adult horn length.	Early horn growth is positively correlated with adult horn length.	CN4, VCO2, Park	Yes
(C) Females with rapid early growth reproduce early.	Horn increments grown over the first 2 years of life are correlated with age of primiparity.	CN4, Park[a]	Yes
(D) Females with rapid early growth have greater probability to reproduce when aged 4 years and older.	Horn increments grown over the first 2 years of life are correlated with probability of reproduction.	CN4, Park[a]	No[b]
(E) Hunter prefers to harvest nonlactating females, particularly when heavy penalties apply to the harvest of lactating ones.	Lower frequency of lactating females harvested in VCO2 than in CN4. In VCO2 but not in CN4, as the hunting season progresses, the availability of nonlactating females should decrease and more lactating females will be harvested. In VCO2, the harvest will include more 2-year-old females compared to CN4, because 2-year-old females are unlikely to lactate.	CN4, VCO2, Park[c]	Yes
(F) Hunters prefer to harvest long-horned females where penalties for harvesting lactating females are light.	Length of horn increments grown over the first few years of life will decrease with age at harvest in CN4 but not in VCO2.	CN4, VCO2	No

[a]Not tested in VCO2 because of small sample size.
[b]Yes for senescent females.
[c]Gestation rate in the Park was used as an age-specific control unbiased by hunter selectivity.

males (Rughetti & Festa-Bianchet 2010). We then tested whether horn length as a yearling was positively correlated with the probability to reproduce at all ages. In female chamois, horn growth during the first two summers of life accounts for about 73% of horn length at 5 years (Bassano, Perrone & von Hardenberg 2003; Fig. 1). We expected that horn growth over the first 2 years of life would be correlated with age of primiparity. On the other hand, horn growth in the year of first reproduction can be reduced by the energy cost of lactation (Miura, Kita & Sugimura 1987). For females aged 4 years and older, we expected that rapid early horn growth would be correlated with fecundity.

Finally, we assessed whether horn length and reproductive status affected hunter selection and consequently female survival. We monitored two areas with differing hunting regulations and expected that heavier penalties for the harvest of lactating females would lead to an increase in the proportion of nonlactating females in the harvest. Harvest should then be concentrated on very young and old females that are less likely to lactate than prime-aged females (Crampe *et al.* 2006). If reproductive status did not strongly affect hunter choice, hunter selectivity could be mostly based on horn length, and females with rapid early horn growth could be harvested at a younger age than those with slow growth.

Materials and methods

STUDY AREA

Our study populations included the Alpi Marittime Natural Park (280 km^2), where no hunting is allowed, and the adjacent hunting area CN4 (595 km^2), in south-western Piedmont, Italy, near the border with France (44°12′N, 7°16′E). The second hunted area (VCO2, 727 km^2) is in northern Piedmont near the border with Switzerland (46°12′N, 8°29′E). All study areas have narrow valley and steep mountains. Chamois use areas mostly between 1000 and 3000 m

a.s.l. As altitude increases, forests of beech (*Fagus sylvatica*) are replaced by conifers (*Picea abies, Abies alba* and *Larix decidua*), then alpine pastures at higher elevations. Rocks and moraines cover 47% of the Park and about 25% of VCO2 and CN4. Ibex (*Capra ibex* Linnaeus) is the only other mountain ungulate, abundant in the Park and small isolated populations in CN4. Roe deer (*Capreolus capreolus* Linnaeus) and wild boar (*Sus* scrofa Linnaeus) are present mainly under 1200 m elevation. Red deer are abundant in CN4 and VCO2. Wolves (*Canis lupus* Linnaeus) are permanent residents in the Park and in CN4. Cattle graze all study areas during summer.

POPULATION DATA

In the Park, 374 females aged 2 years and older were captured by dart gun in April–May, mostly 2–6 weeks before parturition, from 1991 to 2008 and released elsewhere for reintroduction programmes. Gestation status was recorded for 319 of these by abdominal palpation. In CN4 and VCO2 respectively, 552 and 495 females aged 2 years and older were harvested from 2000 to 2008. In CN4, the hunting season starts in mid-September and normally ends in mid-December, but 89% of females were harvested in September and October. In VCO2, hunting starts in early September and normally ends in early October. Lactation status was noted for 445 females in CN4 and 380 in VCO2. We included in the analyses data from 11 3-year-old females harvested in CN4 in 2009. Age and body mass (kg) (eviscerated mass for harvested animals) were recorded for all females. Age can be determined precisely by counting the horn annuli (Schroder & Elsner-Schack 1985). Horn length (cm) was measured from tip to base along the frontal surface. Because it is not possible to distinguish the horn increments grown during the first and second summers, we combined growth over the first 2 summers (L2) for all analyses (see (Côté, Festa-Bianchet & Smith 1998), for a similar approach in mountain goats *Oreamnos americanus De Blainiville*). We measured horn increments for all females captured in the Park, 175 shot in CN4 from 2006 to 2009 and 99 shot in VCO2 in 2007 and 2008. Because horn increments grown after the fourth summer of life are generally 2 mm or less, we restricted our analyses to either total horn length or the first four increments.
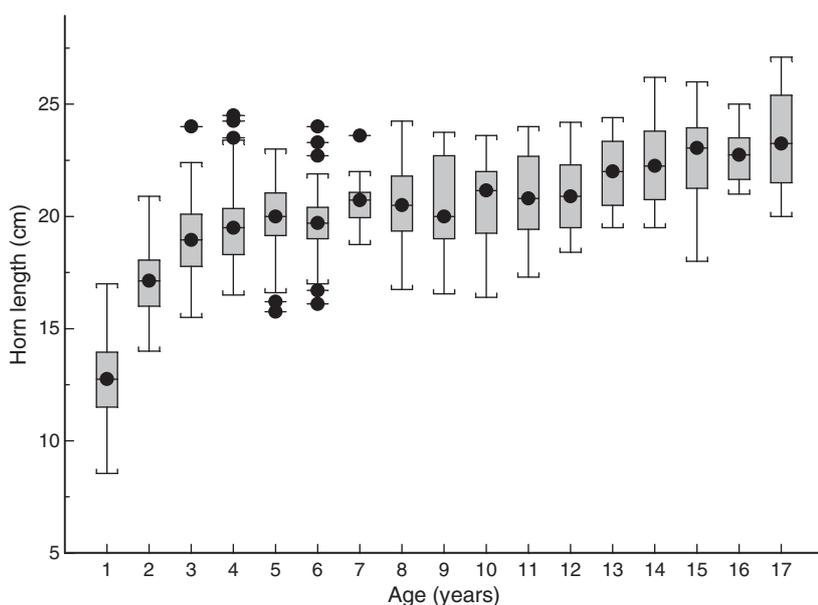
Fig. 1. Box plot of horn length of 717 female chamois aged 2 years and older harvested in autumn in the CN4 hunting area in southern Piedmont, Italy, 2000–2009.

Hunting regulations in Piedmont encourage the harvest of nonlactating females. In both hunting areas, hunters that harvest a nonlactating female increase their position on a merit scale that gives access to permit for adult males, while hunters that harvest a lactating female cannot harvest an adult male in either the current or the successive hunting season. In VCO2, however, regulations provide stronger incentives against shooting lactating females: hunters can have up to four chamois tags during a season but killing a lactating female limits them to two and leads to a fine that increases if the hunter harvests a second lactating female. Consequently, we expected stronger hunter selection for nonlactating females in VCO2 than in CN4. Harvest rate in 2002–2007 varied from 0·09 to 0·13 in CN4 and from 0·11 to 0·15 in VCO2 with an average, respectively, of 10% and 13% of the number of chamois seen during annual censuses. The actual harvest rate, however, was lower, as census counts underestimate population size (Loison *et al.* 2006).

STATISTICAL ANALYSIS

We present statistical methods according to the hypotheses listed in Table 1.

Hypothesis A: To test for a correlation between early horn growth and adult mass, we fitted a linear regression for each age class using horn length (cm) as a yearling as the predictor variable. We considered the following age classes: 2, 3 and 4 years and older in the Park and 1·5, 2·5, 3·5 and 4·5 years and older in CN4 and VCO2. Most chamois in Piedmont are born in late May; therefore, they were near their approximate birth dates when captured in the Park and about 6 months older during the hunting season.

Hypothesis B: To test whether total horn length was a function of horn length as a yearling, we used a multiple linear regression including population as a covariate. We expected a positive effect of early horn growth on adult horn length despite compensatory growth.

Hypothesis C: Because primiparity was mainly at three and 4 years, we used a general linear model with a binomial distribution to estimate the probability that a 3-year-old female would be lactating in autumn in CN4 or pregnant in spring in the Park as a function of early horn growth. Horn increments grown during the third (L3) and fourth (L4) summers of life (when chamois are aged 2 and 3 years) were negatively correlated with L2 (CN4, $r = -0.53$ for L3, $n = 131$ and -0.43 for L4, $n = 99$. Park, $r = -0.57$ for L3, $n = 299$ and -0.37 for L4, $n = 256$). Therefore, we considered the residuals of the regressions of L3 and L4 on L2 (RL3 and RL4), which reflect variation in horn growth in years 3 and 4 that is not explained by L2. We tested the following models: CN4, Logit (P-lactating) = L2 × RL3 × RL4; Park, Logit (P-pregnancy) = L2 × RL3. We expected higher values for RL3 (last increment grown before reproduction) and lower values for RL4 (increment grown while lactating) for females primiparous as 3-year-olds compared to nulliparous 3-year-olds. For the Park, we could not compare RL4 with reproductive status at age 3, because animals were captured in spring, before L4 had finished growing. We did not estimate the probability of early reproduction as a function of L2 in VCO2 because of the small sample of females aged 3 years ($n = 19$, 2 lactating).

Hypothesis D: To assess the effect of early horn growth on reproduction of females aged 4 years and older in CN4 and in the Park, we modelled the probability of reproduction as a function of age, body mass and length of horn grown as a yearling, using general linear models with a binomial distribution: CN4, Logit (P-lactating) = age × age² × mass × L2; Park, Logit (P-pregnant) = age × age² × L2. We included a quadratic effect of age to account for potential senescence. In CN4, harvest date was not included because it did not affect female mass (Rughetti & Festa-Bianchet unpublished data). In the Park, we did not consider the effect of mass because we could not account for foetal mass for pregnant females. We did not analyse data for VCO2 because we measured only 20 lactating females. Because some females in CN4 were eviscerated and others partially eviscerated (with heart, liver and lungs), we first estimated the age-specific difference in mass in the two groups, then subtracted it from partially eviscerated mass to estimate eviscerated mass.

Hypothesis E: We examined whether hunter preference for nonlactating females was stronger in VCO2 than in CN4. We used the frequency of pregnant females in the Park as a control unbiased by hunter selectivity. Because of juvenile mortality, lactation rates should generally be lower than gestation rates, but we assumed that this decrease would not be affected by female age. To compare age effects on reproduction, we fitted a general linear model with a binomial distribution and a cubic smoothing spline procedure (Bartels, Beatty & Barsky 1995). We expected a lower frequency of lactating females in VCO2 than lactating in CN4 or gestating in the Park. We then used a general linear model with a binomial distribution to examine whether the proportion of lactating females in the harvest increased during the hunting season. If hunters prefer to harvest nonlactating females, with the advance of the season the availability of nonlactating females should decrease and more lactating females should be shot. Finally, we compared the age structure of females captured in the Park and harvested in CN4 and VCO2 with a Pearson's chi-squared statistic (Snedecor & Cochran 1980). In VCO2, we expected a greater proportion of young females compared to the Park and CN4 populations, because young females were unlikely to lactate.

Hypothesis F: If hunters prefer to harvest long-horned females, short-horned females should live longer. We fitted a multiple linear regression model to test for a decrease in length of the yearling horn increment with increasing age at harvest (Hengeveld & Festa-Bianchet in press). Because an apparent decrease of L2 may be due to horn tip wear, we repeated the same analysis for horn increments grown during the third and fourth summers of life.

All analyses were conducted in R (R Development Core Team 2009). To select final models, we began with a full model including all variables of interest and their interactions, then simplified it using a stepwise procedure based on *P*-values. To test the fit of logistic regression models, we performed a goodness of fit test from the Design packages (Harrell 2009). Large *P*-values indicate an acceptable fit.

Results

In the Park, horn growth during the first two summers of life was correlated with mass for 2-year-old females captured in April–May; at 3 years the correlation was weak, and for adults it disappeared (Table 2). We found similar patterns in CN4 and VCO2: horn length of yearlings in autumn was correlated with mass, but for older females, horn growth during the first two summers of life explained almost no variability in mass (Table 2).

Total horn length increased rapidly from 2 to 4 years, then changed little with age (Fig. 1). For females aged 4–10 years,

Table 2. Linear regression of body mass as a function of the length of horn grown during the first 2 years of life (L2) for 294 female chamois aged 2, 3, and 4 years and older captured in the Alpi Marittime Natural Park, Italy, from 1991 to 2008, and for 635 females aged 1·5, 3·5, and 4·5 years and older harvested in the hunting areas of CN4 and VCO2 from 2000 to 2009. Age classes with sample size less than 20 are not reported. For harvested yearlings, L2 is the total length of the horn

Age	Slope	SE	t-value	$Pr(> |t|)$	R^2	d.f.
PARK						
2	0·788	0·269	2·933	0·006	0·212	32
3	0·615	0·296	2·081	0·045	0·110	35
4 +	0·050	0·116	0·434	0·664	0·001	221
CN4						
1·5	1·015	0·094	10·837	0·000	0·395	180
3·5	0·140	0·208	0·673	0·505	0·012	38
4·5 +	0·212	0·157	1·354	0·179	0·019	94
VCO2						
1·5	0·906	0·082	11·077	0·000	0·330	249
4·5 +	0·258	0·225	1·145	0·256	0·021	64

horn growth as a yearling explained 26% of the variability in total horn length (horn length = L2 + population; L2, slope = 0·459, SE = 0·043, t_{348} = 10·62, $P < 0·001$; population (Park), intercept = −0·390, SE = 0·191, t_{348} = −2·05, $P = 0·04$; population (VCO2), intercept = −0·934, SE = 0·276, t_{348} = −3·38, $P < 0·001$). Population affected the intercept of the regression of horn growth as a yearling on total horn length but the slopes were similar (length = L2 + population vs. length = L2 × population, $F = 2·51$, $P = 0·5$). Total horn length averaged 20·0 cm (±1·7 SD) in CN4, 19·6 cm (±1·7 SD) in the Park and 19·3 cm (±1·3 SD) in VCO2.

From 2000 to 2008, 4 of 74 (5%) and 12 of 105 (11%) 2-year-old females harvested, respectively, in CN4 and VCO2 were lactating. Of 43 2-year-olds captured in the Park from 1992 to 2008, none was pregnant; therefore, primiparity was mainly at three and 4 years. Horn length at age 2 was positively associated with reproductive status at 3 years, explaining, respectively, 17% and 20% of the probability of being pregnant in the Park or lactating in CN4 (Fig. 2, Table 3). The residuals of the third and fourth horn increments on L2 did not improve the model in either CN4 (RL3: slope = −0·256, SE = 0·371, t_{31} = −0·69, $P = 0·49$; RL4: slope = 0·184, SE = 0·536, t_{30} = 0·34, $P = 0·73$) or the Park (RL3: slope = 0·159, SE = 0·493, t_{32} = 0·32, $P = 0·75$).

In both the Park and CN4, the probability of reproduction declined after about 9–11 years of age (Fig. 3, Tables 4 and 5). After accounting for age, horn growth as a yearling did not affect the probability of gestation for females aged 4 years and older in the Park (slope = 0·078, SE = 0·080, t_{249} = 0·97, $P = 0·33$). In CN4, horn growth as a yearling affected lactation in interaction with age; after accounting for mass, senescent females were more likely to reproduce if they had grown longer horns as yearlings (Table 4, Fig. 2). For females aged 11 years and older in CN4, horn growth as a yearling was 12% longer in 14 lactating than in 13 nonlac-
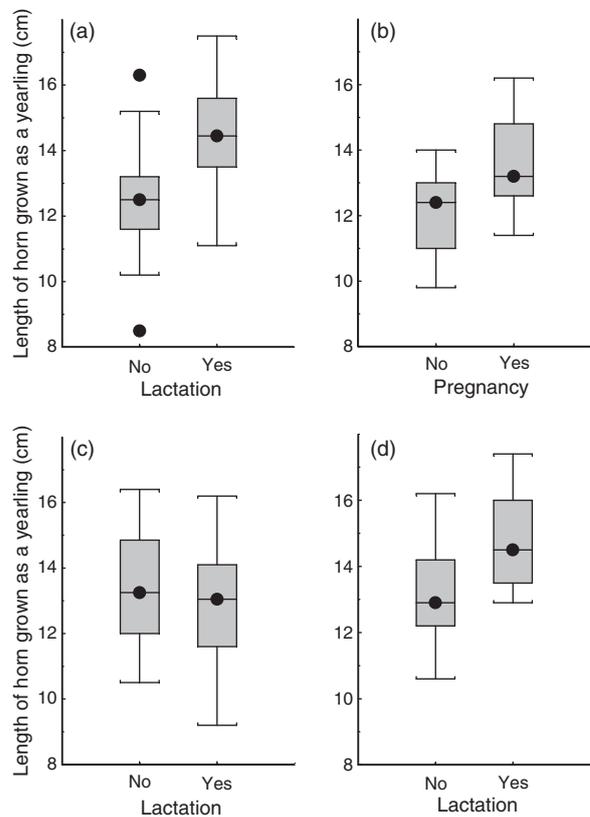

Fig. 2. Box plot of horn length as a yearling (L2) with respect to reproductive status for (a) 39 3·5-year-old female chamois harvested in autumn in the CN4 hunting area, 2006–2009 (b) 39 3-year-old females captured in April–May in the nearby Alpi Marittime Natural Park, 1991–2008 (c) 77 female chamois aged 4–10 years (d) and 27 female chamois aged 11 years and older harvested in autumn in CN4, 2006–2008.

Table 3. Logistic regression of the probability of gestation as function of horn growth during the first two summers of life (L2) for 39 3-year-old females chamois captured in April–May in the Alpi Marittime Natural Park, 1991–2008, and of lactation for 39 3·5-year-old females harvested in autumn in the nearby CN4 hunting area, 2006–2009

	Estimate	Std. error	d.f.	Wald $\chi2$	P-value
PARK					
Intercept	−10·387	4·231	1	6·027	0·0141
L2	0·822	0·330	1	6·225	0·0126
CN4					
Intercept	−9·301	3·320	1	7·862	0·005
L2	0·666	0·244	1	7·436	0·006

Goodness of fit test: Park, $Z = 1·61$, $P = 0·11$; CN4, $Z = −0·49$, $P = 0·62$.

tating ones (ANOVA $F_{1,26}$ = 8·62, $P = 0·007$; lactating mean = 14·8 cm ± 1·4 SD; nonlactating mean = 13·2 ± 1·6 cm) and was correlated with body mass (slope = 0·72, SE = 0·284, t_{26} = 2·52, $P = 0·018$, R^2 = 0·20). Lactating females were lighter than nonlactating ones, and this differ-
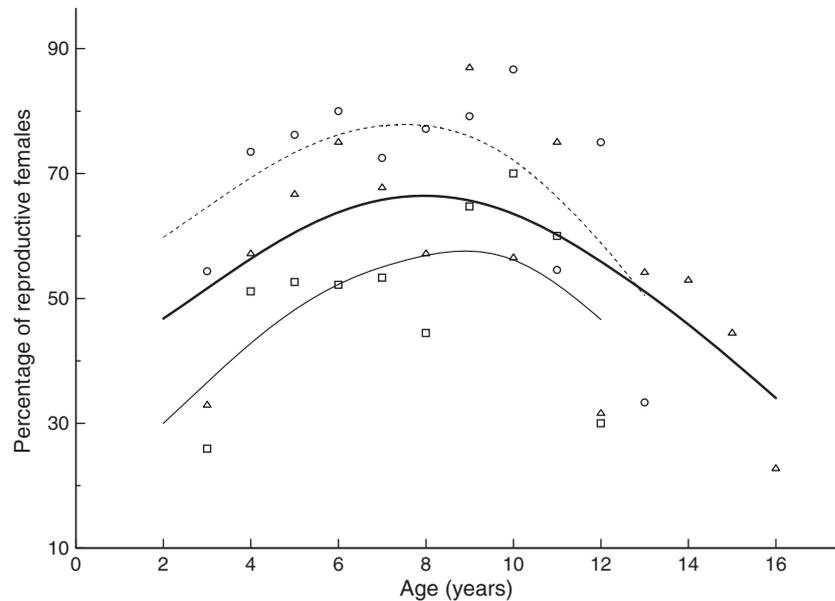
Fig. 3. Percentage of pregnant females among chamois aged 3 years and older captured in April–May in the Alpi Marittime Park (plain dashed line and circles, 319 chamois, 1991–2008,) and of lactating females among those aged 3 years and older harvested in two hunting areas, CN4 (bold solid line and triangles, 455 chamois, 2000–2008,) and VCO2 (plain solid line and squares, 380 chamois, 2000–2008). Lines are cubic smoothed splines.

Table 4. Logistic regression of the probability of lactation for female chamois aged 4 years and older harvested in CN4 from 2006 to 2008 in relation to age, age^2, eviscerated mass and the length of horn grown during the first two summers of life (L2)

	Estimate	Std. error	d.f.	Wald χ^2	P-value
Intercept	49·142	18·388	1	7·140	0·007
Age	−10·236	4·390	1	5·438	0·020
Age^2	0·490	0·240	1	4·170	0·041
L2	−0·275	0·250	1	1·201	0·273
Mass	−2·485	0·947	1	6·875	0·009
Age^2 : L2	0·006	0·003	1	4·477	0·034
Age : mass	0·579	0·234	1	6·126	0·013
Age^2 : mass	−0·033	0·013	1	6·007	0·014

Goodness of fit test: $Z = -0·11, P = 0·91$.

Table 5. Logistic regression of the probability of gestation (Park, 1991–2008) and lactation (hunted populations, 2000–2008) of female chamois aged 4 years and older as a function of age and populations

	Estimate	Std. error	d.f.	Wald χ^2	P-value
Intercept	1·655	0·204	1	65·448	< 0·0001
Age	−0·079	0·020	1	15·109	0·0001
Population (CN4)	−0·588	0·178	1	10·956	0·0009
Population (VCO)	−1·036	0·195	1	28·260	< 0·0001

Goodness of fit test: $Z = -1·15, P = 0·25$.

ence was greater for prime-aged than for senescent females (11 years and older, Table 4). Mean eviscerated mass for lactating females aged 4–10 years was 18·8 kg ($\pm 2·9$ SD) or 10% less than the average of 20·8 kg ($\pm 2·7$ SD) for nonlactating ones. Mean eviscerated mass for lactating senescent

females was 18·2 kg ($\pm 2·6$ SD), only 4% less than the average of 18·9 kg ($\pm 2·2$ SD) for nonlactating ones. For nonlactating females, mass decreased with age (slope = −0·24, SE = 0·10, $t_{37} = -2·29, P = 0·028$), whereas for lactating ones, it was independent of age ($t_{60} = 0·11, P = 0·9$).

For each age class, pregnancy rates in the Park were higher than lactation rates in hunted populations (Fig. 3, Table 5). Among those aged 4–11 years, there were more lactating females harvested in CN4 (66%) than in VCO2 (54%) ($\chi^2 = 6·39$, d.f. = 1, $P = 0·011$). The proportion of lactating females in the harvest increased during the hunting season in VCO2 but not in CN4 (Table 6). The proportion of females aged 2 years harvested in VCO2 was much greater (29%) than for Park captures (11%) or in the CN4 harvest (14%) ($\chi^2 = 55·74$, d.f. = 2, $P < 0·001$; Fig. 4). The proportion of females aged 3–11 years was greater in Park captures (83%) than in CN4 (68%) or VCO2 (63%) harvests ($\chi^2 = 41·68$, d.f. = 2, $P < 0·001$). Correspondingly, the proportion of females aged 12 years and older also differed among populations (Park = 6%, VCO2 = 8%, CN4 = 19%).

For both hunted populations, age of harvested females was independent of either horn growth as a yearling or the length of horn grown from 2 to 4 years of age (Table 7). There was no difference between populations in horn growth as a yearling (Table 7), but for the same growth as yearlings, females in VCO2 grew shorter increments in the following 2 years than in CN4 [regression model: L2–4 = L2 + population; L2, slope = −0·488, SE = 0·064, $t_{143} = -7·63$, $P < 0·001$; population (VCO2), intercept = −1·031, SE = 0·221, $t_{143} = -4·67, P < 0·001$]. The difference in horn growth existed despite yearling females in VCO2 being 7% heavier (15·5 Kg $\pm 2·6$ SD, $n = 340$) than in CN4 (14·5 kg $\pm 3·0$ SD, $n = 237$), a difference that persisted among females 4 years and older [20·6 kg $\pm 2·8$ SD in VCO2 ($n = 340$) and 19·6 kg ± 3 SD in CN4 ($n = 237$)].

Table 6. Logistic regression of the probability of lactation as a function of date of harvest (days since the start of the hunting season) for female chamois aged 2 years and older in the VCO2 and CN4 hunting areas from 2000 to 2008

	Estimate	Std. error	d.f.	Wald χ2	*P*-values
VCO2					
Intercept	−3·460	0·725	1	22·753	< 0·0001
Date	0·300	0·079	1	14·288	0·0002
Date^2	−0·009	0·003	1	10·693	0·001
Date^3	0·00007	0·00003	1	8·410	0·004
CN4					
Intercept	0·037	0·181	1	0·042	0·84
Date	−0·003	0·005	1	0·452	0·50

Goodness of fit test: VCO2, $Z = 0.012$, $P = 0.99$; CN4, $Z = 1.5$, $P = 0.13$.

For females aged 4–10 years, the coefficient of variation in body mass (VCO2 = 0·16, CN4 = 0·15) was greater than that for horn length (VCO2 = 0·09, CN4 = 0·08).

Discussion

Our research produced two key results. First, early development affected the reproductive performance of very young and senescent females, but not of prime-aged adults. Second, sport harvest did not appear to have strong selective effects but it did increase the mortality of nonlactating females.

EARLY DEVELOPMENT AND REPRODUCTIVE POTENTIAL

Horn length as a yearling reflected early development because it was correlated with early body mass. Consequently, horn growth as a yearling provides a permanent record of early development of female chamois. After 9–11 years of age, the probability of reproduction decreased

Table 7. Multiple linear regression of horn length as yearling (L2; d.f. = 244) and horn increment from yearling to 4 years old (L2–4; d.f. = 145) as a function of age of harvest and population (VCO2 and CN4) for females chamois

	Value	Std. error	*t*-value	*P*-value
L2				
Intercept	13·306	0·202	65·925	0·0000
Age	0·010	0·025	0·418	0·68
Population (VCO2)	0·236	0·210	1·123	0·26
L2–4				
Intercept	5·569	0·305	18·255	0·0000
Age	−0·043	0·032	−1·342	0·18
Population (VCO2)	−0·983	0·257	−3·825	0·0002

with age but a strong early development led to higher probabilities of reproduction in very young and senescent females. Female chamois with strong early horn growth attained primiparity at an earlier age than females with lower early growth and had longer horns as adults, despite compensatory horn growth. Because of compensatory horn growth, the length of the third and fourth increments was negatively correlated with horn length as a yearling and appeared independent of age of primiparity. In the Park, early horn growth did not affect reproduction during senescence, possibly because of the limited sample of older females (15, including 12 12-year-olds).

The age of first reproduction is an important trait in the reproductive strategy of female mammals (Clutton-Brock *et al.* 1987; Lindström 1999; Festa-Bianchet, Jorgenson & Réale 2000). Typically, early primiparity is associated with large mass, rapid early development, longer life expectancy and greater fitness (Beauplet & Guinet 2007; Descamps *et al.* 2008; Hamel *et al.* 2009b; Pistorius *et al.* 2008). Good environmental condition in early life and large mass positively affected reproduction at all ages (Bérubé, Festa-Bianchet &
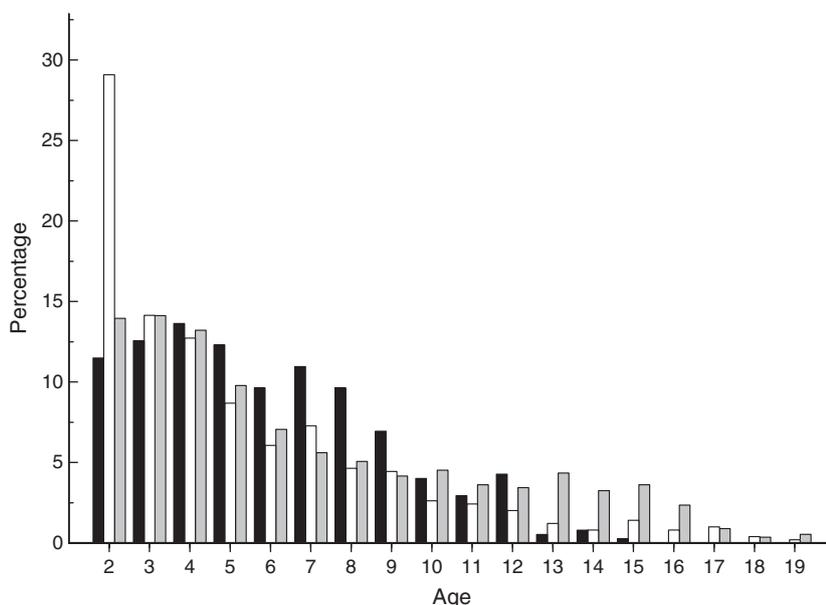
Fig. 4. Age distribution of female chamois captured in the Alpi Marittime Park (dark bars, 374 chamois, 1991–2008) or harvested in CN4 (grey bars, 552 chamois, 2000–2008) and in VCO2 (white bars, 495 chamois, 2000–2008).

Jorgenson 1999; Nussey *et al*. 2007). Adult female chamois with strong early horn growth were apparently able to acquire substantial amounts of resources to allocate to both body growth and reproduction. Strong early horn growth was correlated with a delayed positive fitness consequence by increasing reproduction during senescence, probably because early growth in horn and mass were correlated. Therefore, our data suggest that horn length as a yearling is a reliable index of reproductive potential in young and senescent female chamois. Although early horn growth was not correlated with mass of prime-aged adults, it was associated with the mass of senescent females.

In CN4, female body mass during the hunting season revealed an energetic cost of lactation. Lactating females were lighter than nonlactating ones, as reported for other ungulates (Sæther & Haagenrud 1985; Clutton-Brock *et al*. 1996; Reimers, Holmengen & Mysterud 2005). Prime-aged females therefore faced a trade-off between summer mass gain and lactation. Autumn mass of senescent females, however, appeared independent of lactation status. We suggest that the apparent lower cost of reproduction among older female chamois arises through two mechanisms: first, females that survive to the senescent phase are likely those with a greater reproductive potential as prime-aged adults, as previously reported for bighorn sheep (Bérubé, Festa-Bianchet & Jorgenson 1999) and for roe deer (Gaillard *et al*. 2000b). Second, older females may adopt a conservative reproductive strategy, so that only those in good condition reproduce. Lactating senescent and prime-aged females had similar mass, but nonlactating senescent females were about 10% lighter than nonlactating prime-aged females. Our contention is supported by the positive effect of early horn growth on reproduction among senescent females. Females with rapid horn growth early in life did not reproduce at a greater rate than other females through the prime-aged years, but maintained a high reproductive rate into their later years (Fig. 2).

HUNTER SELECTION

Our results confirmed a strong hunter preference to harvest nonlactating females where harvest of lactating females carries strong penalties. In contrast to our expectations, however, horn length did not appear to affect harvest probability in either hunting area, because the length of horn grown as a yearling did not decline with harvest age, in contrast with recent results for bighorn sheep males (Hengeveld & Festa-Bianchet in press). Therefore, we found no evidence that either hunting regulations or hunter selection favour the survival of females with short horns. We suggest that the relatively low hunting pressure, strong compensatory horn growth and limited variability in horn length among adult females weaken the effects of any hunter selection for long horns, as we reported for males of the same species (Rughetti & Festa-Bianchet 2010). Despite the limited evidence for hunter selection for horn length, however, horn growth trajectories differed between the two hunted populations. In VCO2,

horn increments in the third and fourth summer of life were shorter than in CN4 for the same length of horn grown as yearling. That difference occurred despite heavier mass in VCO2 than in CN4 and may suggest a selective pressure for shorter horns in VCO2. It is unclear whether that pressure is caused by hunting or is due to differences in environmental conditions, but it is in the direction predicted by the apparently stronger hunting pressure in VCO2 than in CN4.

Nonlactating females had a higher probability of being harvested than lactating females. The low age-specific percentage of lactating females in VCO2 (Fig. 3) was likely due to strong hunter preference for nonlactating females rather than to a lower frequency of lactation than in the other two populations. Harvest of lactating females increased with the advance of the hunting season in VCO2 but not in CN4, presumably because as many nonlactating females were harvested early in the season, later on it became difficult for hunters to find females without kids. Hunting culture in Piedmont and generally in Europe tends to frown upon shooting lactating females (Festa-Bianchet 2007). Therefore, in hunted populations, nonlactating females likely suffer greater mortality than lactating females. If this trend was strong, it could select for a strategy of early primiparity and high maternal investment each year, even at a cost of reduced longevity, opposite to the conservative strategy normally favoured by natural selection in long-lived species (Solberg *et al*. 2000; Festa-Bianchet 2003; Proaktor, Coulson & Milner-Gulland 2007). Recent research on Norwegian red deer, however, found no evidence that sport harvests led to earlier primiparity, possibly because much of the harvest focussed on pre-reproductive females and on males (Mysterud, Yoccoz & Langvatn 2009).

The harvest (Fig. 4) of many old animals in both CN4 and VCO2, compared to heavily harvested populations of other species such as Norwegian moose (*Alces alces* Linnaeus) (Mysterud, Solberg & Yoccoz 2005), suggests a relatively weak hunting pressure, as older females are rare in heavily hunted populations (Langvatn & Loison 1999; Solberg *et al*. 2000; Festa-Bianchet 2003). It may also indicate hunter selectivity for old females that have long horns and are unlikely to be lactating (Figs 1 and 3). The scarcity of senescent females captured in the Park could be partly because of a tendency to avoid females that appear very old, as younger females are more useful for reintroduction. We suggest, however, that wardens capturing live females in the Park were more likely to obtain a random sample of the population than hunters in autumn. Although wardens may have avoided females that appeared frail or very small, they were not influenced by lactation status because captures were done before females gave birth.

Because of their low reproductive value, high harvest mortality of old nonlactating females is unlikely to have strong ecological or evolutionary consequences (Festa-Bianchet 2003). Strong hunter selection for nonlactating females in VCO2, however, increased the mortality of 2-year-old females (Fig. 4), an age class with a very high residual reproductive value (Gaillard *et al*. 2000a). Hunting regulations

discouraging the harvest of lactating females seek to reduce the impact of female harvests on population growth, partly based on the assumption that if a lactating female is harvested her kid would likely die. Our results suggest instead that this regulation may increase the impact of female harvests in comparison with a random harvest of lactating and nonlactating females. Because most 2-year-old females are nonlactating, they suffer a disproportionately heavy harvest pressure. Hunters harvest young females with a very high probability to survive to the following year, when they will begin their productive lifespan.

Conclusion

Our research highlights the fundamental importance of early development on reproductive performance in mammals, not only for young adults (Descamps *et al.* 2008; Pistorius *et al.* 2008; Hamel *et al.* 2009b) but also during senescence (Bérubé, Festa-Bianchet & Jorgenson 1999; Nussey *et al.* 2007). We found no evidence that early development affected hunter selectivity. Although some types of selective hunting can lead to evolutionary pressures on morphological traits (Coltman *et al.* 2003; Garel *et al.* 2007), not all forms of sport hunting should be expected to have evolutionary impacts. Hunter selectivity can vary according to many factors (Martinez *et al.* 2005; Mysterud, Trjanowski & Panek 2006), and some sport harvests may not be selective (Bischof *et al.* 2009). Sport harvest did not appear to have strong impacts on the evolution of phenotypic traits and reproductive strategies of female chamois, likely because of a low harvest rate and weak selection for long-horned females. Our research points to two avenues for further investigation on the effects of regulations that protect lactating females. First, the high hunting mortality of nonlactating females creates a fitness cost of nonreproduction and may favour a higher lactation rate (Proaktor, Coulson & Milner-Gulland 2007). Second, the high mortality of pre-reproductive females may decrease population growth more than alternative strategies of female harvest.

Acknowledgements

References

Bartels, R., Beatty, J. & Barsky, B. (1995) *An Introduction to Splines for Use in Computer Graphics and Geometric Modeling.* Morgan Kaufmann, Palo Alto, CA.

Bassano, B., Perrone, A. & von Hardenberg, A. (2003) Body weight and horn development in Alpine chamois, *Rupicapra rupicapra* (Bovidae, Caprine). *Mammalia*, **67**, 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**, 1877–1883.

Beauplet, G., Barbraud, C., Chambellant, M. & Guinet, C. (2005) Interannual variation in the post-weaning and juvenile survival of subantarctic fur seals: influence of pup sex, growth rate and oceanographic conditions. *Journal of Animal Ecology*, **74**, 1160–1172.

Bérubé, C., Festa-Bianchet, M. & Jorgenson, J.T. (1999) Individual differences, longevity, and reproductive senescence in bighorn ewes. *Ecology*, **80**, 2555–2565.

Bischof, R., Swenson, J.E., Yoccoz, N.G., Mysterud, A. & Gimenez, O. (2009) The magnitude and selectivity of natural and multiple anthropogenic mortality causes in hunted brown bears. *Journal of Animal Ecology*, **78**, 656–665.

Bonenfant, C., Pelletier, F., Garel, M. & Bergeron, P. (2008) Age-dependent relationship between horn growth and survival in wild sheep. *Journal of Animal Ecology*, **78**, 161–171.

Bubenik, G.A. & Bubenik, A.B. (eds) (1990) *Horns, Pronghorns, and Antlers: Evolution, Morphology, Physiology, and Social Significance.* Springer-Verlag, New York.

Clutton-Brock, T.H., Major, M. & Guinness, F.E. (1985) Population regulation in male and female red deer. *Journal of Animal Ecology*, **54**, 831–846.

Clutton-Brock, T.H., Major, M., Albon, S.D. & Guinness, F.E. (1987) Early development and population dynamics in red deer. I. Density-dependent effects on juvenile survival. *Journal of Animal Ecology*, **56**, 53–64.

Clutton-Brock, T.H., Stevenson, I.R., Marrow, P., MacColl, A.D., Houston, A.I. & McNamara, J.M. (1996) Population fluctuations, reproductive costs and life-history tactics in female Soay sheep. *Journal of Animal Ecology*, **65**, 675–689.

Coltman, D.W., O'Donoghue, P., Jorgenson, J.T., Hogg, J.T., Strobeck, C. & Festa-Bianchet, M. (2003) Undesirable evolutionary consequences of trophy hunting. *Nature*, **426**, 655–658.

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

Crampe, J.-P., A. Loison, A., Gaillard, J.M., Florence, E., Caens, P. & Appolinaire, J. (2006) Patterns of reproduction of female isard (*Rupicapra pyrenaica pyrenaica*) in a non-hunted population and demographic consequences. *Canadian Journal of Zoology*, **84**, 1263–1268.

Descamps, S., Boutin, S., Berteaux, D. & Gaillard, J.M. (2008) Age-specific variation in survival, reproductive success and offspring quality in red squirrels: evidence of senescence. *Oikos*, **117**, 1406–1416.

Femberg, P.B. & Roy, K. (2008) Ecological and evolutionary consequences of size-selective harvesting: how much do we know? *Molecular Ecology*, **17** 209–220.

Festa-Bianchet, M. (2003) Exploitative wildlife management as a selective pressure for the life-history evolution of large mammals. *Animal Behavior and Wildlife Conservation* (eds M. Festa-Bianchet & M. Apollonio), pp. 191–207. Island Press, Washington, DC.

Festa-Bianchet, M. (2007) Ecology, Evolution, Economics, and Ungulate management. *Wildlife Science: Linking Ecological Theory and Management Applications* (eds T.E. Fulbright & D.G. Hewitt), pp. 183–202. CRC Press, Boca Raton, FL.

Festa-Bianchet, M. & Côté, S.D. (2008) *Mountain goats: ecology, behaviour and conservation of an alpine ungulate*, pp. 265. Island Press, Washington, USA.

Festa-Bianchet, M., Gaillard, J.-M. & Côté, S.D. (2003) Variable age structure and apparent density-dependence in survival of adult ungulates. *Journal of Animal Ecology*, **72**, 640–649.

Festa-Bianchet, M. & Jorgenson, J.T. (1998) Selfish mothers: reproductive expenditure and resource availability in bighorn ewes. *Behavioral Ecology*, **9**, 144–150.

Festa-Bianchet, M., Jorgenson, J.T. & Réale, D. (2000) Early development, adult mass, and reproductive success in bighorn sheep. *Behavioral Ecology*, **11**, 633–639.

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**, 305–312.

Gaillard, J.-M., Andersen, R., Delorme, D. & Linnell, J.D.C. (1998) Family effects on growth and survival of juvenile roe deer. *Ecology*, **79**, 2878–2889.

Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. & Toïgo, C. (2000a) Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics*, **31**, 367–393.

Gaillard, J.M., Festa-Bianchet, M., Delorme, D. & Jorgenson, J. (2000b) Body mass and individual fitness in female ungulates: bigger is not always better. *Proceedings of the Royal Society B-Biological Sciences*, **267**, 471–477.

Gaillard, J.M., Loison, A., Toïgo, C., Delorme, D. & Laere, G.v. (2003) Cohort effects and deer population dynamics. *Écoscience*, **10**, 412–420.

Garel, M., Cugnasse, J.-M., Maillard, D., Gaillard, J.-M., Hewison, A.J.M. & Dubray, D. (2007) Selective harvesting and habitat loss produce long-term

life history changes in a mouflon population. *Ecological Applications*, **17**, 1607–1618.

Garel, M., Solberg, E.J., Sæther, B.-E., Grøtan, V., Tufto, J. & Heim, M. (2009) Age, Size, and Spatiotemporal Variation in Ovulation Patterns of a Seasonal Breeder, the Norwegian Moose (*Alces alces*). *American Naturalist*, **173**, 89–104.

Hamel, S., Côté, S.D., Gaillard, J.-M. & Festa-Bianchet, M. (2009a) Individual variation in reproductive costs of reproduction: high-quality females always do better. *Journal of Animal Ecology*, **78**, 143–151.

Hamel, S., Gaillard, J.-M., Festa-Bianchet, M. & Côté, S.D. (2009b) Individual quality, early life conditions and reproductive success in contrasted populations of large herbivores. *Ecology*, **90**, 1981–1995.

Harrell Jr, F.E. (2009). Design: design package. R package version 2.3-0. Available at: http://CRAN.R-project.org/package=Design.

Hengeveld, P. & Festa-Bianchet, M. (in press) Harvest regulations and artificial selection on horn size in male bighorn sheep. *Journal of Wildlife Management*.

Jorgenson, J.T., Festa-Bianchet, M., Lucherini, M. & Wishart, W.D. (1993) Effects of body size, population density and maternal characteristics on age of first reproduction in bighorn ewes. *Canadian Journal of Zoology*, **71**, 2509–2517.

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 B-Biological Sciences*, **266**, 1655–1661.

Langvatn, R. & Loison, A. (1999) Consequences of harvesting on age structure, sex ratio and population dynamics of red deer *Cervus elaphus* in central Norway. *Wildlife Biology*, **5**, 213–223.

Lindström, J. (1999) Early development and fitness in birds and mammals. *Trends in Ecology and Evolution*, **14**, 343–348.

Loison, A., Appolinaire, J., Jullien, J.M. & Dubray, D. (2006) How reliable are total counts to detect trends in population size of chamois *Rupicapra rupicapra* and *R. pyrenaica*? *Wildlife Biology*, **12**, 77–88.

Lummaa, V. & Clutton-Brock, T. (2002) Early development, survival and reproduction in humans. *Trends in Ecology and Evolution*, **17**, 141–147.

Madsen, T. & Shine, R. (2000) Silver spoons and snake body sizes: prey availability early in life influences long-term growth rates of free-ranging pythons. *Journal of Animal Ecology*, **69**, 952–958.

Martinez, M., Rodrıguez-Vigal, C., Jones, O.R., Coulson, T. & Miguel, A.S. (2005) Different hunting strategies select for different weights in red deer. *Biology Letters*, **1**, 353–356.

McElligott, A.G., Altwegg, R. & Hayden, T.J. (2002) Age-specific survival and reproductive probabilities: evidence for senescence in male fallow deer (*Dama dama*). *Proceedings of the Royal Society B-Biological Sciences*, **269**, 1129–1137.

Milner, J.M., Nilsen, E.B. & Andreassen, H.P. (2007) Demographic side effects of selective hunting in ungulates and carnivores. *Conservation Biology*, **21**, 36–47.

Miura, S., Kita, I. & Sugimura, M. (1987) Horn growth and reproductive history in female Japanese serow. *Journal of Mammalogy*, **68**, 826–836.

Moyes, K., Coulson, T., Morgan, B.J.T., Donald, A., Morris, S.J. & Clutton-Brock, T.H. (2006) Cumulative reproduction and survival costs in female red deer. *Oikos*, **115**, 241–252.

Mysterud, A., Solberg, E.J. & Yoccoz, N.G. (2005) Ageing and reproductive effort in male moose under variable levels of intrasexual competition. *Journal of Animal Ecology*, **74**, 742–754.

Mysterud, A., Trjanowski, P. & Panek, M. (2006) Selectivity of harvesting differs between local and foreign roe deer hunters: trophy stalkers have the first shot at the right time. *Biology Letters*, **2**, 632–635.

Mysterud, A., Yoccoz, N.G. & Langvatn, R. (2009) Maturation trends in red deer females over 39 years in heavily harvested populations. *Journal of Animal Ecology*, **78**, 595–599.

Nussey, D.H., Kruuk, L.E.B., Morris, A. & Clutton-Brock, T.H. (2007) Environmental conditions in early life influence ageing rates in a wild population of red deer. *Current Biology*, **17**, 1000–1001.

Pérez-Barbería, F.J., Robles, L. & Nores, C. (1996) Horn growth pattern in Cantabrian chamois *Rupicapra pyrenaica parva*: influence of sex, location and phenology. *Acta Therioogica*, **41**, 83–92.

Pistorius, P.A., Bester, M.N., Hofmeyr, G.J.G., Kirkman, S.P. & Taylor, F.E. (2008) Seasonal survival and the relative cost of first reproduction in adult female southern elephant seals. *Journal of Mammalogy*, **89**, 567–574.

Proaktor, G., Coulson, T. & Milner-Gulland, E.J. (2007) Evolutionary responses to harvesting in ungulates. *Journal of Animal Ecology*, **76**, 669–678.

R Development Core Team (2009) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, Available at: http://www.R-project.org.

Reimers, E., Holmengen, N. & Mysterud, A. (2005) Life-history variation of wild reindeer (*Rangifer tarandus*) in the highly productive North Ottadalen region, Norway. *Journal of Zoology*, **265**, 53–62.

Rughetti, M. & Festa-Bianchet, M. (2010) Compensatory growth limits opportunities for artificial selection in Alpine chamois. *Journal of Wildlife Management*, **74**, 1024–1029.

Sæther, B.-E. & Haagenrud, H. (1985) Life history of the moose *Alces alces*: relationship between growth and reproduction. *Ecography*, **8**, 100–106.

Schroder, W. & Elsner-Schack, I.V. (1985). Correct age determination in chamois. *The Biology and Management of Mountain Ungulates* (ed S. Lovari), pp. 65–70. Croom-Helm, London, UK.

Snedecor, G.W. & Cochran, W.G. (1980) *Statistical Methods*. Iowa State University Press, Ames, IA.

Solberg, E.J., Loison, A., Saether, B.E. & Strand, O. (2000) Age-specific harvest mortality in a Norwegian moose *Alces alces* population. *Wildlife Biology*, **6**, 41–52.

Solberg, E.J., M, M.G., Heim, M., Grotan, V. & Saether, B.E. (2008) Lack of compensatory body growth in a high performance moose Alces alces population. *Oecologia*, **58**, 485–498.