

Older conservatives: reproduction in female Alpine chamois (*Rupicapra rupicapra*) is increasingly risk-averse with age

A. Morin, M. Rughetti, S. Rioux-Paquette, and M. Festa-Bianchet

Abstract: In long-lived mammals, costs of reproduction may vary with age. The terminal investment hypothesis predicts greater reproductive effort as females approach the end of their life expectancy. We monitored 97 individually marked female Alpine chamois (*Rupicapra rupicapra* (L., 1758)) between 2007 and 2013 to determine how age-specific reproduction affected body mass and subsequent reproductive success. We captured and weighed females between April and August and monitored reproductive success from April to October through mother–kid associations. Reproductive success was strongly age-dependent and peaked at 70% for prime-aged females (4–7 years). Reproductive senescence began at 8 years, earlier than reported by other studies of ungulates. There was no clear evidence of reproductive costs in any age class. Reproductive success was very heterogeneous for old females, suggesting variability in the onset of senescence. Old females were less likely to reproduce in poor years despite being heavier than prime-aged females, suggesting reproductive restraint in late life rather than terminal investment. Female mass remained stable from May to August with no effect of lactation. Our results suggest that chamois reproductive strategy becomes increasingly conservative with age, resulting in no detectable costs of reproduction.

Key words: *Rupicapra rupicapra*, Alpine chamois, individual heterogeneity, age, reproductive costs, conservative strategy, terminal investment.

Résumé : Chez les mammifères longévives, les coûts de la reproduction peuvent varier selon l'âge. L'hypothèse de l'investissement terminal prédit que l'effort reproducteur devrait augmenter chez les femelles approchant la fin de leur espérance de vie. Nous avons suivi 97 femelles chamois des Alpes (*Rupicapra rupicapra* (L., 1758)) marquées individuellement dans le Parco Naturale Alpi Marittime (Italie) entre 2007 et 2013 afin d'étudier l'effet de la reproduction sur la masse corporelle et le succès reproducteur suivant des femelles, en relation avec l'âge. Nous avons capturé et pesé les femelles entre avril et août et suivi le succès reproducteur d'avril à octobre. Les femelles entre 4 et 7 ans avaient une fécondité élevée (70 %), mais la sénescence commençait à 8 ans, plus tôt que l'indiquent les études sur d'autres ongulés. Aucune classe d'âge ne montrait un coût évident de la reproduction. Pour les vieilles femelles, le succès reproducteur était très hétérogène, suggérant de la variabilité dans l'âge de début de la sénescence. Leur probabilité de reproduction diminuait lors des mauvaises années et elles étaient plus lourdes que les femelles adultes, suggérant de la restreinte reproductrice plutôt qu'un investissement terminal. Le statut reproducteur n'affectait pas la masse, qui demeurait stable de mai à août. Nos résultats suggèrent une stratégie de reproduction très conservatrice, surtout pour les vieilles femelles, qui ne cause aucun coût détectable de la reproduction.

Mots-clés : *Rupicapra rupicapra*, chamois des Alpes, hétérogénéité individuelle, âge, coûts de la reproduction, stratégie conservatrice, investissement terminal.

Introduction

Life-history theory predicts that because individuals have access to a limited amount of resources, they should allocate those resources optimally among growth, survival, and reproduction to maximize fitness (Williams 1966; Stearns 1992). Because reproduction is energetically costly (Gittleman and Thompson 1988; Robbins 1993), investment in current reproduction should result in trade-offs with survival or future reproduction (Stearns 1992; Roff 2002; but for a review of other mechanisms explaining trade-offs see Harshman and Zera 2007).

Different species use different strategies to optimize resource allocation between current reproduction, growth, survival, and future reproduction. Many large mammals are capital breeders that rely partly on accumulated resources to satisfy the energy requirements of gestation and especially lactation (Gittleman and Thompson

1988; Robbins 1993). Seasonally breeding temperate ungulates rely on energy stores mostly for gestation because of the scarcity of resources during winter (Albon and Langvatn 1992; Gonzalez and Crampe 2001). Because of the short vegetation growing season, the accumulation of fat reserves for subsequent winter survival and reproduction conflicts with the high energetic needs of lactation (Clutton-Brock et al. 1982; Therrien et al. 2007; Bårdsen et al. 2008). Lactating females often fail to accumulate as much fat as nonreproductive ones during summer, resulting in lower autumn body condition (Green and Rothstein 1991; Festa-Bianchet et al. 1998; Testa and Adams 1998), indicating an energetic cost of reproduction. As body condition of females generally influences reproductive success (Cameron et al. 1993; Testa and Adams 1998; Stewart et al. 2005), those energetic costs may result in fitness costs (Jönsson 1997). Long-lived large-mammal females have evolved a conservative reproductive strategy, favoring their own survival by restraining allocation

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to reproduction (Gaillard et al. 2000b), especially when resources are scarce (Festa-Bianchet and Jorgenson 1998; Therrien et al. 2007; Hamel et al. 2010b). As a result, the annual reproductive success of female ungulates is much more variable than their survival (Gaillard and Yoccoz 2003), and its fitness costs are mostly expressed as reduced future reproductive success rather than lowered maternal survival (Hamel et al. 2010b).

Females in poor body condition may reduce reproductive allocation either by lowering fecundity (moose, *Alces alces* (L., 1758): Testa 2004; elk, *Cervus elaphus* L., 1758: Stewart et al. 2005), or by reducing pre- or post-birth maternal care. For large ungulates, reduced maternal care could involve reduced frequency or duration of nursing, lower volume of milk, milk containing less fat, or lower protection against predators. These changes could in turn decrease offspring birth mass, growth (bison, *Bison bison* (L., 1758): Green and Rothstein 1991; bighorn sheep, *Ovis canadensis* Shaw, 1804: Martin and Festa-Bianchet 2010; reindeer, *Rangifer tarandus* (L., 1758): Bårdsen et al. 2010), survival (moose: Testa 2004), or reproductive success (bison: Green and Rothstein 1991). Reductions in fecundity, offspring survival, or performance are nonexclusive costs of reproduction, therefore more than one component of reproductive success can be affected by previous reproduction.

Although trade-offs between fitness components are a central assumption of life-history theory (Clutton-Brock 1991; Stearns 1992; McNamara and Houston 1996) and the conservative strategy of ungulates makes them sensitive to reproductive costs, only half the studies of ungulates report such costs (Hamel et al. 2010b). Many studies even report positive correlations (Sand 1998; Loison et al. 2002; Weladji et al. 2008), thus the prevalence of reproductive costs of reproduction in ungulates remains ambiguous. This ambiguity partly arises from the difficulty of measuring the costs of reproduction accurately. Of the four approaches listed by Reznick (1985, 1992), the method most used for ungulates is phenotypic correlations because manipulations of reproductive allocation, genetic correlations, and selection experiments are difficult to apply to large wild mammals (Moyes et al. 2006; Gélín et al. 2015). Phenotypic correlations face confounding variables, as individuals generally differ in resource acquisition (van Noordwijk and de Jong 1986) and therefore in reproductive potential (Clutton-Brock et al. 1983; Reznick 1985; Jorgenson et al. 1998; Hamel et al. 2010b). If individuals with high reproductive potential consistently reproduce successfully, then current and subsequent reproductive success will be correlated positively at the population scale, obscuring the expected intraindividual negative relationship (van Noordwijk and de Jong 1986). The strength of reproductive costs and the amount of individual heterogeneity could vary independently. If the amount of individual heterogeneity is unknown, then there is no clear a priori expectation of the direction of the correlation between current and subsequent reproductive success (Wilson and Nussey 2010).

A way to control for individual heterogeneity is to treat individual as a random factor in a mixed model in addition to considering covariates of reproductive success, such as body mass, age, or yearly environmental conditions (Lunn et al. 1994; Festa-Bianchet et al. 1998; Hamel et al. 2010b). As early development can affect reproductive success at all ages (Green and Rothstein 1991; Hamel et al. 2009b; Marcil-Ferland et al. 2013), it must be controlled for by including, for example, early growth rate or age at weaning in the model. Also, when yearly variation in resource availability introduces systematic variation in reproductive allocation, environmental heterogeneity must be controlled for (Hamel et al. 2010b). Studies that control for individual and environmental heterogeneity tend to find costs of reproduction more often than those that do not, but only if they control for variables that are correlated to resource acquisition or reproductive potential, and if their direction and form are correctly modelled (Hamel et al. 2010b).

Age is an important confounding variable in the study of costs of reproduction. In ungulates, reproductive success is generally

higher for prime-aged than for primiparous and senescent females (Gaillard et al. 2000b). As it influences both current and future reproductive success, age must be controlled for. Age can also influence reproductive costs. For some species (Festa-Bianchet et al. 1998; Tavecchia et al. 2005; Descamps et al. 2009), old females may face higher costs than prime-aged ones because of physiological senescence (Jones et al. 2008; Descamps et al. 2009). In other species, however, costs are lower for old females (Green 1990; Beauplet et al. 2006; Hamel et al. 2010a), possibly because of greater experience, larger body mass, or because longevity is positively correlated with reproductive potential. Reproductive tactics could also change when individuals reach old age. The terminal investment hypothesis (Pianka and Parker 1975; Clutton-Brock 1984) predicts that older animals will have a less conservative reproductive tactic compared with younger ones because the residual reproductive potential decreases with age. The evidence for terminal investment in long-lived females, however, is inconsistent, as several studies support the alternative senescence hypothesis, which predicts that reproductive performance will decline with age (Ericsson et al. 2001; Martin and Festa-Bianchet 2011).

We studied the costs of reproduction in female Alpine chamois (*Rupicapra rupicapra* (L., 1758)), a species for which little is known about reproductive costs (Tettamanti et al. 2015). Female chamois are monogamous, with high prime-age survival (97% in an expanding population; Loison et al. 1994) and can live past 19 years of age (Rughetti and Festa-Bianchet 2011). In summer, 82%–100% of prime-aged females are accompanied by a kid (Houssin et al. 1993; Pérez-Barberia et al. 1998; Loison et al. 2002), but it is usually unknown if reproductive failure represents variability in female fecundity or in early juvenile survival. For the Pyrenean chamois (*Rupicapra pyrenaica* Bonaparte, 1845), a closely related species (Masini and Lovari 1988), female survival is very high and stable, whereas juvenile survival is density-dependent (Crampe et al. 2006), suggesting a conservative reproductive strategy. Female chamois should be capital breeders, as they live in a very seasonal environment where they subsist on low-quality forage during winter, the time of gestation, and then gain about 3 kg (12% of the mean mass) in late summer (Pioz et al. 2008a). Rughetti and Festa-Bianchet (2011) found that lactating females were lighter than nonlactating ones in autumn, but it is unknown if this energetic cost of reproduction originates from gestation or lactation and, more importantly, if it leads to fitness costs.

Our 7-year longitudinal study of marked female chamois aims to assess the energetic and fitness costs of reproduction and test the terminal investment hypothesis and the senescence hypothesis. We tested whether resource allocation to gestation during winter reduced spring mass. We expected that spring and summer mass should be lower for lactating females than nonlactating ones. We also sought to determine if the fitness costs of reproduction reduced subsequent reproductive success and how this relationship may vary with age. We expected chamois to show a conservative reproductive strategy, so fitness costs should affect future reproduction rather than survival (Martin and Festa-Bianchet 2010). We expected that females should experience a reduction in reproductive success on years following successful reproduction, and that this reduction should be greater for older females because body condition deteriorates with age. Finally, the terminal investment hypothesis predicts that older females have greater allocation in reproduction; they should therefore have higher reproductive success and (or) lower body mass than prime-aged females. We expected the opposite pattern under the senescence hypothesis.

Materials and methods

Study area and animal population

Alpine chamois were studied from 2007 to 2013 in the Parco Naturale Alpi Marittime (44°12'N, 07°16'E), southwestern Italian Alps. The study area (23 km², elevation 1700–3000 m above sea level) is the Valasco valley. The forest is dominated by European

larch (*Larix decidua* Mill.), Norway spruce (*Picea abies* (L.) Karst.), and Swiss pine (*Pinus cembra* L.), but most of the study area is above treeline, with alpine pastures and shrublands. Rock and scree cover 47% of the park (Bocci et al. 2010). The climate is alpine-suboceanic, with a mean rainfall of 71 mm/month in summer and snowfall of 60 cm/month in winter (Bocci et al. 2010). Alpine ibex (*Capra ibex* L., 1758) are common; roe deer (*Capreolus capreolus* (L., 1758)) are present at the lowest elevations. Cattle graze the valley floor during summer. Golden Eagles (*Aquila chrysaetos* (L., 1758)) and red foxes (*Vulpes vulpes* (L., 1758)) are commonly seen and they could prey on young kids (Bertolino 2003). Wolves (*Canis lupus* L., 1758), a predator of all sex-age classes, are occasional visitors.

There has been no hunting in the Park since 1980. In 2011, a mark-resight estimate (Lincoln-Peterson estimator) applied to block counts conducted by park wardens (Bocci et al. 2010) suggested about 400 chamois in the study area, for a density of 18 individuals/km², which is medium-high for *Rupicapra* (Storch 1989: 6–7 individuals/km²; Allainé et al. 1990: 31 individuals/km²; Pérez-Barbería et al. 1997: 2–22 individuals/km²; Loison et al. 1999: 24–34 individuals/km²). The earliest age of primiparity is 3 years, which is typical of stable populations (Loison 1995; Pérez-Barbería et al. 1998; Crampe et al. 2006). Therefore, we considered all females ≥ 3 years as adults.

In summer 2008, the population suffered an epizootic of keratoconjunctivitis, a disease known to substantially lower female reproductive success, mostly by reducing foraging efficiency and neonatal survival (Loison et al. 1996). That summer was followed by a winter of very deep snow that led to 40% adult female mortality (Rughetti et al. 2011), whereas between 2007 and 2013, mean annual adult female mortality was 24%.

We captured 97 adult females between April and August, 2007–2013, using three techniques: darting with xylazine (Dematteis et al. 2009), a 625 m² rising net (Dematteis et al. 2010), and clover traps baited with salt. We weighed captured chamois with spring scales to the nearest 500 g. We measured hind-foot length and the length of each annual growth increment of the left horn, along the outside curvature. We determined age by the annual horn growth rings (Schröder and Von Elsner-Shack 1985). Kids were considered age 0. We assessed reproductive status by milking for lactation and by abdominal palpation for gestation, an accurate diagnostic for small ruminants after 4 months of pregnancy (Richter and Gotze 1986). We placed VHF radio collars on 67 females and marked all individuals with colored plastic ear tags and collars that allowed identification during observations. All animal-handling methods were approved by the Animal Care Committee of the Université de Sherbrooke, affiliated with the Canadian Council on Animal Care (protocol MFB2012-1).

Measures of reproductive success

Reproductive status was monitored each year from May to October, for 243 female-years, with a mean of 9 sightings/female per year (range 1–30). Chamois form nurseries and kids are not always closely associated with their mother. Therefore, we proceeded in two steps to assign females to reproductive categories. First, for each sighting, we confirmed a mother–kid association only if (i) the female suckled the kid (allo-suckling has not been reported in this species) or (ii) a kid was always next to a marked female, especially when travelling (Ruckstuhl and Ingold 1999). Second, we classified females ≥ 3 years as “barren” if they were seen at least three times and never with a kid, “kid lost during summer” if they were seen at least three times without kid after being seen with a kid, or “weaning” if their kid was seen at least once in September, the monitoring period closest to true weaning in November (Ruckstuhl and Ingold 1994). In 2011–2013, only 3% of females seen three times without a kid were classed as lactating in a later

sighting, against 8% after two sightings and 26% after only one sighting. Reproductive success was only assigned from 30 May because most kids were born in the last week of May.

Since previous reproduction can affect different aspects of current reproduction (Hamel et al. 2010b), we calculated three binary components of individual reproductive success — “fecundity”: whether an adult female produced a kid or not; “offspring survival to weaning”: whether a kid produced survived to September or not; “weaning success”: whether an adult female was accompanied by a kid in September or not. Since 33% of known summer kid mortality occurred in June ($n = 5$), 47% in July ($n = 7$), and 20% in August ($n = 3$), if a female without kid was not seen before July, then it was unknown if she was barren or had lost her kid. Therefore, we only considered females seen before July to calculate fecundity and offspring survival to weaning.

Reproductive status determined at capture was not used to assign a female to a category of reproductive success. Instead, we used it to assess the probability to detect a kid knowing that a female was lactating. Of 35 lactating females captured in June and July, only 4 were classified as barren based on sightings and 2 of these were seen fewer than three times. Kid detection probability for females known to be lactating and seen at least three times was therefore 94%.

Statistical analyses

Defining the age covariate

Before modelling factors affecting reproductive success and mass, we used lowest second-order Akaike’s information criterion (AIC_c) (Burnham and Anderson 2002) to determine what age structure provided the best fit to the data, including only females aged ≥ 3 years. For the effect of age on reproductive success, we tested eight age structures: a linear effect, a linear effect with all females ≥ 10 years pooled, a quadratic effect, a quadratic effect with females ≥ 10 years pooled, age as a categorical variable where each year is one modality, two sets of age classes (3 years = young; 4–7 (or 8) years = prime-aged adults; ≥ 8 (or 9) years = senescent), and a broken-stick model with the break at age 4. We chose the age structure with three classes (3, 4–7, and ≥ 8 years), as it had a weight of 0.63. The second best model had a ΔAIC_c of 2.47 and a weight of 0.18 (Supplementary Table S1 and Supplementary Fig. S1).¹

For the effect of age on mass, we tested a linear effect, a quadratic effect, two broken-stick regressions with breaks at age 4 or 5, a model with one class per age, and a model with three age classes (3, 4–7, and ≥ 8 years). There were five equivalent models with $\Delta\text{AIC}_c < 2$, including the same set of age classes used for reproductive success, which we selected for consistency and because it fitted better with the graphical raw data (Supplementary Table S2 and Supplementary Fig. S2).¹

Components of reproductive success

To understand the relation between the three components of reproductive success (fecundity, offspring survival to weaning, and weaning success), we compared graphically how they covaried according to year and female age.

Effects of age, early growth, and environment on reproductive success

To identify what factors affected the three components of reproductive success, we fitted a generalized linear mixed model (GLMM) of reproductive success with horn growth to age 2 (L2), type of year (good or poor), and age as fixed effects. In female chamois, L2 is an index of early development (Rughetti and Festa-Bianchet 2011) and should partly control for individual heterogeneity. The interaction between age and L2 was also included

¹Supplementary materials are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2015-0153>.

because Rughetti and Festa-Bianchet (2011) reported that early development had a stronger positive effect on young and old females than on prime-aged adults. Years 2007, 2010, 2011, and 2012 were considered “good” because winter mortality of adult females was <19%, 2008 was considered “poor” because of keratoconjunctivitis, and 2009 and 2013 were considered “poor” because winter mortality was 40% and 30%, respectively. We also included the interaction between type of year and age to test if older and younger females were more affected than prime-aged ones during poor years, as well as year and female identity (ID) as random variables to account for repeated measurements. Therefore, our complete model was the following: component of reproductive success = age + L2 + type + age : L2 + age : type + (1 | ID) + (1 | year).

This logistic (logit-link function) model was based on a binomial error structure and fitted with the glmer function of package lme4 (Bates et al. 2014) in R version 3.0.2 (R Foundation for Statistical Computing, Vienna, Austria; available from <https://www.r-project.org/>).

Fitness costs of reproduction

We built a second logistic GLMM to assess the influence of previous reproductive success (weaning_(t-1)) on current reproductive success. We did not include previous reproductive success in the earlier model because the sample size for this variable was much smaller (without weaning_(t-1): *n* = 97 females, 243 observations; with weaning_(t-1): *n* = 68 females, 149 observations). We expected no or weak interactions or correlations between previous reproductive success and other variables except age, which we always kept in the second model.

Although current reproductive success may be affected differently by previous fecundity and previous offspring survival, we only tested the influence of previous weaning success because offspring survival to weaning was very high and we had no data on postweaning survival. We controlled for the variables retained in the previous model: age, type of year, and their interaction. No 2-year-old reproduced, so there was no variability in previous weaning success for 3-year-olds, which were removed from the analysis. The interaction between age and previous weaning success was included in the model to test if costs were stronger for senescent females. We also included the interaction between type of year and previous weaning success to test if the costs of reproduction were stronger after a poor year, and included the interaction between the three variables to test if costs were stronger for senescent females only in poor years. Therefore, the complete model was the following: component of reproductive success = age + type + weaning_(t-1) + age : type + age : weaning_(t-1) + type : weaning_(t-1) + age : type : weaning_(t-1) + (1 | ID) + (1 | year).

To better understand the correlation between previous and current reproductive success for prime-aged and old females, we calculated the number of events where a female had (i) two consecutive successes (high reproductive success), (ii) two consecutive failures (low reproductive success), or (iii) a success followed by a failure or vice versa, the pattern expected under costs of reproduction. With a χ^2 test, we tested if the distribution of 2-year combinations was different between prime-aged and old females.

Somatic costs of reproduction

We obtained mass measurements from April to August. Autumn mass has a strong effect on ungulate reproductive success (Cameron et al. 1993; Festa-Bianchet 1998; Stewart et al. 2005), whereas spring mass is likely affected by winter conditions and reproductive effort (Festa-Bianchet et al. 1996; Festa-Bianchet and Jorgenson 1998) and can be independent of autumn mass (Bårdsen and Tveraa 2012) because heavier females tend to lose more mass during winter (Pelletier et al. 2007). Therefore, we did not consider spring and summer masses as a predictor of reproductive success. Rather, we tested the effect of reproductive status on spring and summer body condition. To do so, we fitted a general linear model

(LM) of mass according to reproductive status at capture (lactating or not), controlling for hind-foot length (foot) and age with the lm function in R. We controlled for possible summer mass gain and for winter severity and keratoconjunctivitis by including Julian date (date) and type of year (type), as well as the interaction between them, to account for possible differences in mass gain between good and poor years. For this analysis, 2008 was considered a good year, as the keratoconjunctivitis peaked in summer and 79% of mass data were collected in May, before the infection. We also included the interaction between hind-foot length and reproductive status to test if bigger females lost more mass than smaller ones when lactating; the interaction between age and reproductive success to test if younger and older females lost more mass than prime-aged ones when lactating; and the interaction between reproductive status and Julian date to control for a potential difference in mass gain during summer between lactating and nonlactating females. Therefore, our complete model was the following: mass ~ foot + age + repro + type + date + foot : repro + age : repro + repro : date + type : date.

Analyses were restricted to adult (≥ 3 years) nongestating females (barren or lactating). From 1 April to 15 June, mass was only available for barren females because all reproductive females that were captured were gestating. A preliminary analysis indicated that the mass of barren females did not vary during this period, so we included these females in the analysis. Values are presented as mean \pm SE.

Model selection

Before the selection of fixed effects, we tested the significance of individual years and female ID as random effects using a likelihood ratio test, comparing the complete models with and without the effects in the ANOVA function in R (Pinheiro and Bates 2000).

For fixed effects, model selection was based on the lowest AIC_c (Burnham and Anderson 2002). We defined a set of candidate models containing the same random-effects structure but different fixed-effects combinations, chosen based on biological hypotheses, and computed the AIC_c of each model. We computed the weight of evidence of each model (w_i), which is the likelihood that a model, given the data, is the best one within the set of competing models. If none of the candidate models had a weight >0.95, we evaluated regression coefficients, their unconditional standard errors, and their 95% confidence intervals by multimodel inference. Model selection and multimodel inference were done with the package AICcmodavg (Mazerolle 2012) in R.

Results

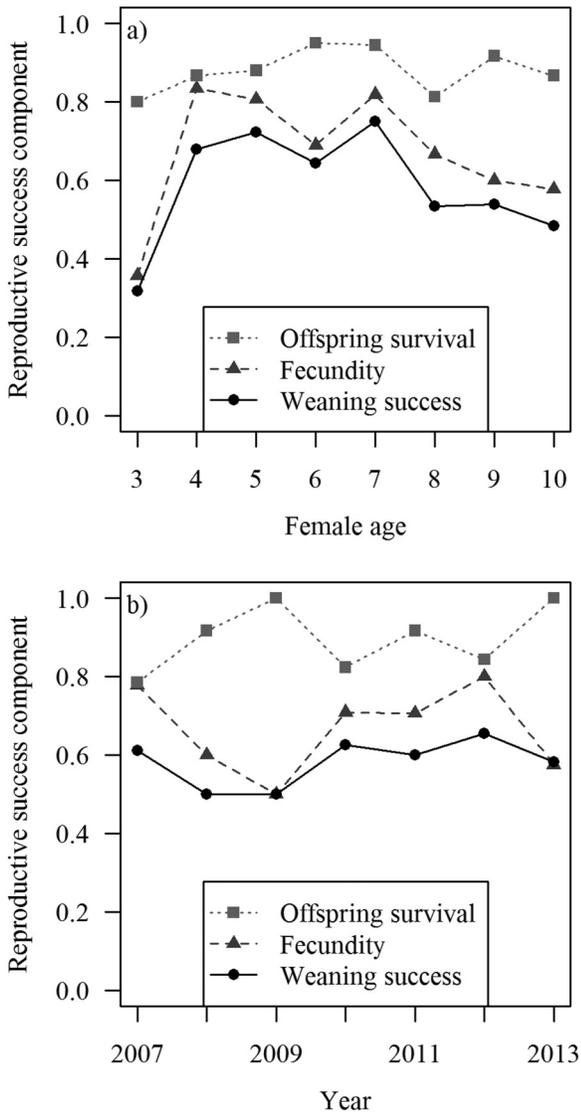
Components of reproductive success

For all adult females, mean (\pm SE) yearly fecundity was 0.69 \pm 0.03 and mean (\pm SE) offspring survival to weaning was 0.89 \pm 0.03, leading to a mean (\pm SE) weaning success of 0.63 \pm 0.03. Fecundity and weaning success varied strongly with female age and year (Figs. 1a, 1b). Offspring survival to weaning varied little with maternal age (Fig. 1a), but varied with year, in a pattern opposite to fecundity (Fig. 1b).

Influence of age, early growth, and winter mortality on weaning success

We fitted both models of factors affecting reproductive success for each of the three response variables (fecundity, offspring survival to weaning, and weaning success). We report only detailed results for weaning success because the results for fecundity were very similar and weaning success is a better proxy for fitness than fecundity. Also, offspring survival to weaning was high and varied little. Detailed results on fecundity and survival to weaning are presented in Supplementary Tables S6–S13¹ and Supplementary Figs. S4 and S5.¹

Fig. 1. Unadjusted (a) age-specific and (b) year-specific fecundity, offspring survival to weaning, and weaning success (presence of an offspring in September) for female Alpine chamois (*Rupicapra rupicapra*) in the Parco Naturale Alpi Marittime, Piedmont, Italy, 2007–2013. Sample size are as follows — fecundity: $n = 86$ females, 184 female-years; offspring survival to weaning: $n = 68$ females, 127 female-years; weaning success: $n = 94$ females, 224 female-years. Values at age 10 are means for all females aged 10–13 years, pooled because of the small sample size (for fecundity: 15 female-years aged 11–13 years).



Model selection of factors affecting weaning success produced three models with $\Delta AIC_c < 2$, whose combined weight of evidence was 0.72 (Supplementary Table S3).¹ All three included age, two included type of year, and one included its interaction with age.

The averaged coefficient estimates (Table 1) showed that age had a strong influence on weaning success, which was lowest for 3-year-olds (0.32 ± 0.11), peaked at ages 4–7 (0.70 ± 0.04), and decreased for older females (0.56 ± 0.08 ; Fig. 2). The effect of poor years was strongly dependent on age class. Poor years had no effect on females aged 4–7 years, but reduced the weaning success of younger and older females. The effect size was strong for both, but the confidence interval included 0 for 3-year-olds, which were only 22 in this sample. The difference between prime-aged and senescent females was stronger in poor years (0.22 ± 0.11) than in

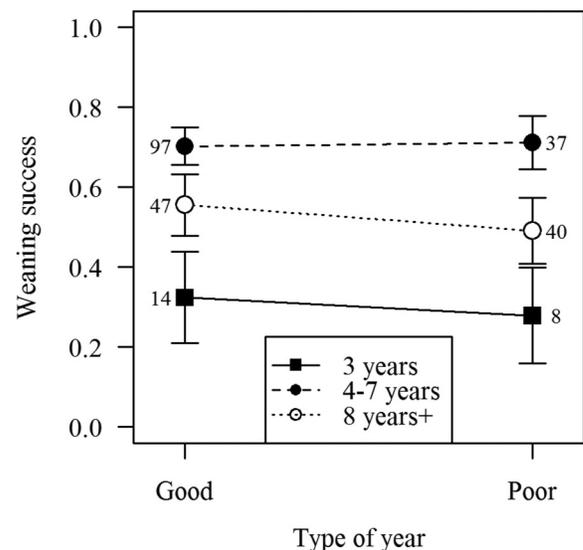
Table 1. Effects of age, horn growth to age 2, and type of year on the weaning success of female Alpine chamois (*Rupicapra rupicapra*) in the Parco Naturale Alpi Marittime, Piedmont, Italy, 2007–2013 ($n = 97$ females, 243 female-years).

Fixed effect	β	SE	95% CI
Intercept	0.98	0.96	-0.89, 0.85
Age ^a			
3 years	-1.69	0.51	-2.69, -0.69
≥ 8 years	-0.76	0.30	-1.35, -0.16
Type ^a			
Poor	-0.23	0.29	-0.81, 0.34
L2	0.02	0.10	-0.17, 0.22
L2 : age			
L2 : 3 years	0.53	0.39	-0.23, 1.30
L2 : ≥ 8 years	0.28	0.20	-0.11, 0.67
Age : type			
3 years : poor	-1.22	1.14	-3.45, 1.01
≥ 8 years : poor	-1.41	0.65	-2.67, -0.14
Random effect	Variance	χ^2 (df)	P
Female identity	0.30	1.47 (1)	0.23

Note: Estimated coefficients (β), standard errors (SE), and 95% confidence intervals (CI) of fixed effects were calculated following a multimodel inference approach and are given in the logit scale. Age is a categorical variable: 3, 4–7, and ≥ 8 years; type: type of year is a categorical variable (“poor year”: 2008, 2009, and 2013; “good year”: 2007 and 2010–2012); L2: horn growth to age 2.

^aPrime-aged females (4–7 years) and good years were considered to be references in the analysis.

Fig. 2. Age-specific weaning success of female Alpine chamois (*Rupicapra rupicapra*) and its interaction with type of year in the Parco Naturale Alpi Marittime, Piedmont, Italy, 2007–2013. Means were predicted by multimodel inference based on models in Supplementary Table S3,¹ with horn growth to age 2 held constant at its mean (12.3 cm). Bars represent one standard error. Numbers refer to female-years.



good years (0.14 ± 0.09). Early horn growth (L2) had no effect for females aged 4–7 years and the effect was slightly positive for younger and older females, but the confidence interval of the interaction between L2 and age class included 0. The effect of year as a random variable was not significant and thus was removed. Female ID as a random variable was not significant, revealing weak individual differences, but was retained to account for re-

peated measurements of the same female in different years (range = 1–6 years/female; mean = 2.5).

Fitness costs of reproduction

Model selection by AIC_c of factors affecting weaning success when considering weaning success the previous year produced two equivalent best models whose combined weight of evidence was 0.63 (Supplementary Table S4).¹ Both models included age, type of year, and their interaction. The second model also included previous weaning success and its interaction with age.

The averaged estimates (Table 2) suggested that the decrease in weaning success with ageing remained similar to the model that did not account for previous reproductive success for previously barren females in good years (4- to 7-year-olds: 0.72 ± 0.08 ; ≥ 8 -year-olds: 0.60 ± 0.15 ; Fig. 3a), but depended on the type of year and on previous weaning success (Figs. 3a, 3b). Poor years decreased weaning success when both age classes were pooled, but the confidence interval just included 0. The interaction between type of year and age was stronger than in the previous model because senescent females suffered a strong decrease in weaning success in poor years (0.25 ± 0.12), whereas prime-aged females did not (0.76 ± 0.10 ; Figs. 3a, 3b). Pooling both age classes, previous reproduction had no effect on weaning success. There was a positive interaction between age and previous weaning success whose confidence interval did not include 0, revealing that previous weaning success affected current weaning success of older females positively but had no effect on weaning success of prime-aged females (Figs. 3a, 3b). In good years, old females that had reproduced successfully the previous year had weaning success similar to that of prime-aged females (0.73 ± 0.12 ; Fig. 3a). The effect of previous reproduction did not interact with type of year, and the lower weaning success for previously barren old females was similar in good and poor years, as those interactions were weak and their confidence intervals included 0. Neither year nor female ID were significant as random factors, but we kept female ID to account for repeated measurements.

Senescent females had more years of weaning failures than prime-aged females and tended to fail more in consecutive years: consecutive failures only occurred on 10% of occasions for prime-aged females, but on 37% of occasions for older females (Table 3). On the contrary, weaning successes in consecutive years occurred in nearly the same proportion for both age classes. Old females changed reproductive status in consecutive years in 29% of occasions, whereas prime-aged females changed status in 49% of occasions ($\chi^2 = 16.13$, $df = 2$, $p < 0.001$).

Somatic costs of reproduction

Adult females weighed, on average, 24.8 kg. Two models of factors affecting female mass had a $\Delta AIC_c < 2$. Both included age and hind-foot length and one included reproductive status at capture (Supplementary Table S5).¹ Their combined weight of evidence was 0.65.

Hind-foot length was positively correlated with mass (Table 4), with a difference of 3 kg or 12% between the smallest (22.9 ± 0.74 kg) and the largest (25.9 ± 0.61 kg) prime-aged female predicted by multimodel averaging. Accounting for hind-foot length, age had a strong effect on mass: females aged 3 years weighed 22.7 ± 0.75 kg or 8% less than prime-aged females (24.7 ± 0.33 kg), whereas senescent females weighed 26.1 ± 0.57 kg or 6% more than prime-aged females (Fig. 4). Mass was not affected by reproductive success at capture, year type, or capture date between April and August. All interactions were weak and their confidence intervals included 0.

Discussion

Five main results emerge from our analysis: (1) fecundity contributes more to variation in reproductive success than offspring summer survival; (2) reproductive senescence begins earlier than

Table 2. Effects of age, previous weaning success, and type of year on the weaning success of female Alpine chamois (*Rupicapra rupicapra*) in the Parco Naturale Alpi Marittime, Piedmont, Italy, 2007–2013 ($n = 68$ females, 149 female-years).

Fixed effect	β	SE	95% CI
Intercept	1.17	0.55	0.10, 2.24
Age ^a			
≥ 8 years	-0.98	0.39	-1.75, -0.22
Weaning _(t-1) ^a			
Success	0.07	0.39	-0.69, 0.84
Type ^a			
Poor	-0.71	0.38	-1.44, 0.03
Age : weaning _(t-1)			
≥ 8 years : success	1.57	0.80	0.01, 3.14
Age : type			
≥ 8 years : poor	-2.01	0.81	-3.60, -0.43
Weaning _(t-1) : type			
Success : poor	-0.42	0.82	-2.04, 1.19
Age : weaning _(t-1) : type			
≥ 8 years : success : poor	-1.28	1.64	-4.49, 1.94
Random effect	Variance	χ^2 (df)	p
Female identity	0.58	0.93 (1)	0.33

Note: Estimated coefficients (β), standard errors (SE), and 95% confidence intervals (CI) of fixed effects were calculated following a multimodel inference approach and are given in the logit scale. Age is a categorical variable: 3, 4–7, and ≥ 8 years; type: type of year is a categorical variable (“poor year”: 2008, 2009, and 2013; “good year”: 2007 and 2010–2012); weaning_(t-1) is weaning success the previous year.

^aPrime-aged females (4–7 years), failure to previous reproductive attempt, and good years were considered to be references in the analysis.

reported for other ungulates, despite an increase in mass for senescent females; (3) individual variation in reproductive success is strong, especially for old females; (4) the effect of previous weaning success and poor years on current reproductive success are age-dependent, but show no evidence for terminal investment; (5) spring–summer mass is age-dependent and is not influenced by reproduction.

Influence of age on reproductive success

Age-specific reproduction of female chamois was broadly similar to that reported for other ungulates, with reproductive success low for younger females, highest for prime-aged females, and declining for old females (Gaillard et al. 2000b). Only 31% of 3-year-olds reproduced, all other surviving females were primiparous at age 4. Primiparity at age 3 is typical for stable *Rupicapra* populations (Loison 1995; Pérez-Barbería et al. 1998; Crampe et al. 2006) and can be delayed to age 4 (Crampe et al. 2004) with low food availability. Because females reach asymptotic size at age 3 (Supplementary Fig. S3),¹ females may have delayed primiparity to avoid a trade-off between reproduction and growth (Bonenfant et al. 2003; Descamps et al. 2009).

Reproductive success started decreasing at age 8, suggesting reproductive senescence. Senescence is a within-individual process and is best analyzed with longitudinal data (van de Pol and Verhulst 2006; Nussey et al. 2008). Because our data span 1–6 years per individual (mean = 2.26), we cannot quantify within-individual changes; therefore, we used a transversal analysis. Reproductive success is often positively correlated to survival so that females surviving to old age are those with above-average reproductive success (Bérubé et al. 1999; Gaillard et al. 2000a; Cam et al. 2002). Such selective disappearance would hide reproductive senescence (Cam et al. 2002), making our estimate of senescence-induced decline in reproductive success conservative. Alternatively, a cohort effect may explain the lower reproductive rate of older females if they were born in years of unfavourable environmental conditions. Also, there could be selective disappearance if females with better reproductive success had survival costs of reproduc-

Fig. 3. Effects of age, type of year (i.e., (a) good year; (b) poor year), and weaning success the previous year on weaning success of female Alpine chamois (*Rupicapra rupicapra*) in the Parco Naturale Alpi Marittime, Piedmont, Italy, 2007–2013. Means were predicted by multimodel inference based on models in Supplementary Table S4.¹ Bars represent one standard error. Numbers refer to female-years.

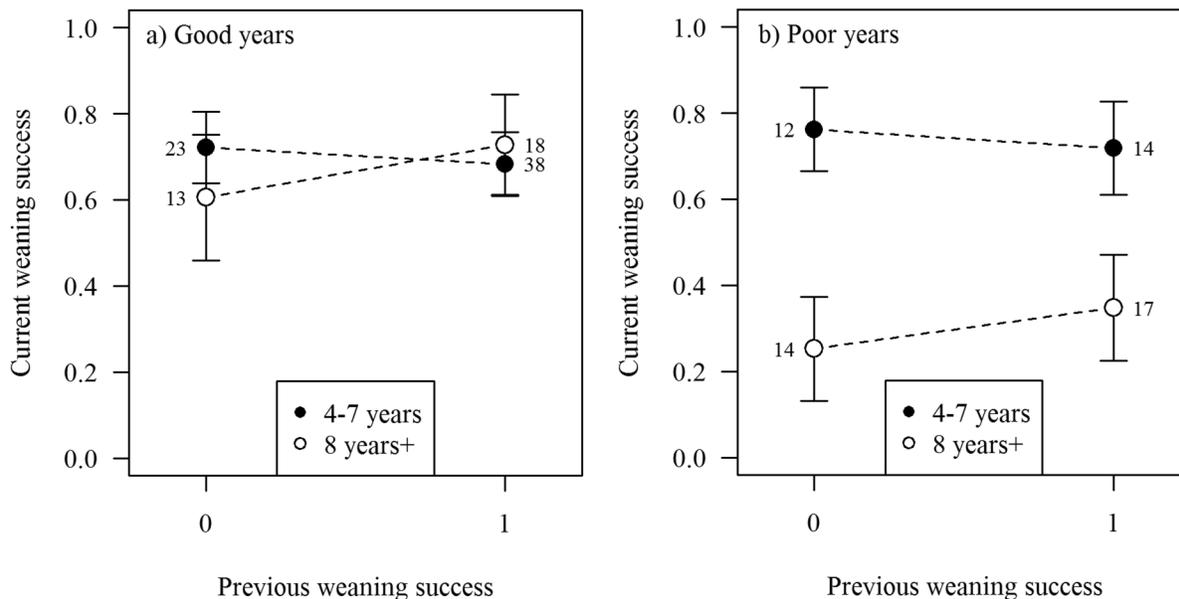


Table 3. Number and proportion of occasions when a female Alpine chamois (*Rupicapra rupicapra*) had consecutive weaning successes, consecutive failures, or a change in weaning success over 2 years in the Parco Naturale Alpi Marittime, Piedmont, Italy, 2007–2013 (n = 68 females, 149 female-years).

	4–7 years		≥8 years	
	Number	Proportion	Number	Proportion
Two successes	35	0.40	21	0.34
Two failures	9	0.10	23	0.37
Change	43	0.49	18	0.29

Table 4. Effects of reproductive status, age, type of year, Julian date, and hind-foot length on spring–summer mass of female Alpine chamois (*Rupicapra rupicapra*) in the Parco Naturale Alpi Marittime, Italy, 2007–2013 (n = 65 females, 81 female-years).

Fixed effect	β	SE	95% CI
Intercept	0.60	10.12	–19.23, 20.43
Age ^a			
3 years	–2.02	0.74	–3.47, –0.57
≥8 years	1.43	0.62	0.21, 2.65
Foot	0.71	0.26	0.19, 1.22
Repro	–0.45	0.55	–1.53, 0.62
Type ^a			
Poor	0.22	0.62	–0.99, 1.44
Date	–0.01	0.01	–0.03, 0.01
Age : repro			
3 years	1.22	1.53	–1.77, 4.21
≥8 years	–0.88	1.42	–3.66, 1.90
Foot : repro	–0.49	0.56	–1.59, 0.61
Repro : date	–0.01	0.03	–0.06, 0.04
Type : date			
Poor	0.06	0.03	0.00, 0.12

Note: Estimated coefficients (β), standard errors (SE) and 95% confidence intervals (CI) were calculated following a multimodel inference approach. Age is a categorical variable: 3, 4–7, and ≥8 years; foot: hind-foot length; repro: reproductive status at capture; type: type of year is a categorical variable (“poor year”: 2008, 2009, and 2013; “good year”: 2007 and 2010–2012); date: day of the year (day 1 is 1 January).

^aPrime-aged females (4–7 years) and good years were considered to be references in the analysis.

tion. Based on results from other ungulates (Jones et al. 2008; Nussey et al. 2008), however, the senescence hypothesis is the most parsimonious to explain the decrease in reproduction with age.

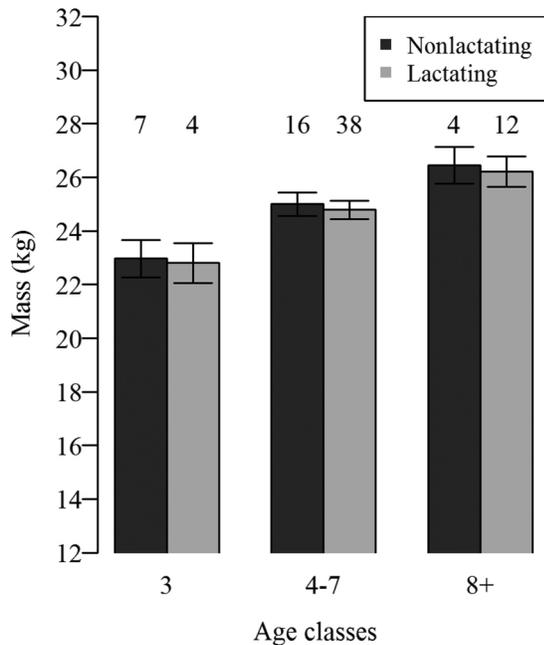
Reproductive senescence began 1–4 years earlier than reported for other ungulates (Gaillard et al. 2000b). Fecundity begins to decline at about 9 years of age in fallow deer (*Dama dama* L., 1758; San José et al. 1999), 12 years in mountain goats (Festa-Bianchet and Côté 2008), and 13 years in bighorn sheep (Bérubé et al. 1999; Festa-Bianchet and King 2007) and red deer (*Cervus elaphus* L., 1758; Clutton-Brock et al. 1982). In other chamois populations, reproductive success is stable until at least 10–14 years (Houssin et al. 1993; Pioz et al. 2008b; Tettamanti et al. 2015), and for *R. pyrenaica*, senescence begins at 12–17 years (Pérez-Barbería et al. 1998; Loison et al. 2002; Crampe et al. 2006), suggesting that early senescence is not simply a characteristic of this genus. Instead, it is likely a consequence of limited resource availability, similarly to red deer, where females born at high density experience earlier senescence (Nussey et al. 2007). The age-specific reproductive pattern of female chamois appears to vary among populations, likely because of differences in resource availability.

Early horn growth did not have a significant influence on reproductive success, even though the tendency confirmed the findings of Rughetti and Festa-Bianchet (2011). Therefore, we did not control for this individual variable in our analysis of reproductive costs.

Components of reproductive success

Weaning success depends on fecundity and offspring survival. It is surprising that 89% of kids survived to weaning. The mean for other ungulates is 64% and only 3 of the 46 populations reviewed by Gaillard et al. (2000b) had survival to weaning higher than what we found. Observational studies commonly underestimate the number of births and overestimate juvenile summer survival

Fig. 4. Effect of age class and reproductive status on spring–summer body mass of adult female Alpine chamois (*Rupicapra rupicapra*) in the Parco Naturale Alpi Marittime, Piedmont, Italy, 2007–2013. Bars show one standard error.



(Sand 1998; Hamel et al. 2010b) because neonatal mortality can be high (Gaillard et al. 2000b) and is rarely detected. Of 28 females captured when gestating, however, only 1 female was classified as barren when resighted, suggesting that neonatal mortality was low and unlikely to strongly bias our estimates of parturition rate and juvenile survival. Many ungulates have high fecundity and variable survival to weaning (Gaillard et al. 2000b), such as roe deer that almost always produce twins (Gaillard et al. 1998) and semidomestic reindeer with 84% fecundity and 75% survival to weaning (Weladji et al. 2008). With low fecundity (69%) and high juvenile survival, chamois in our study area seem to have the opposite strategy. Rughetti et al. (2015) recently found a similar pattern for Alpine ibex, with low fecundity (36% for prime-aged and 21% for senescent females) and 100% juvenile survival to weaning. These two alpine species seem to have a very conservative strategy, reproducing only if weaning probability is high. Alternatively, the scarcity of predators in the Alps could explain this very high juvenile summer survival.

Because survival to weaning was very high, variation in weaning success depended mostly on fecundity. Therefore, the lower reproductive success of young and old females appeared to be due to low fecundity rather than offspring survival. In most vertebrates, juvenile survival is generally more variable than fecundity (Clutton-Brock 1988), but in many studies, juvenile survival includes postweaning survival, which we were unable to assess. In temperate environments, juvenile survival of large mammals is often low during winter, especially at high density (Gaillard et al. 2000b). Of eight marked kids resighted after capture, only three were seen the following summer, suggesting that postweaning juvenile mortality was high and could have a strong influence on reproductive success.

Fitness costs of reproduction

Detectable costs of reproduction were generally weak, but previous reproduction had complex interactions with age and type of year (Table 2). For prime-aged females, reproductive success was independent of previous weaning success: many were able to reproduce 2 or 3 years in a row, indicating that they gained enough

resources to compensate the costs of gestation and lactation. However, some females alternated between success and failure. Our data did not allow us to measure some reproductive costs such as reduced offspring mass, growth, winter survival, or reproductive performance. In reindeer, fecundity is higher for previously lactating females, but those females produce smaller offspring (Bårdsen et al. 2010).

For old females, the positive relationship between previous and current reproductive success (Figs. 3a, 3b) indicated strong individual heterogeneity. Similar to recent results for both chamois (Tettamanti et al. 2015) and ibex (Rughetti et al. 2015), we found a strong tendency for some senescent females to be reproductively successful in consecutive years. Therefore, although female chamois show reproductive senescence, some maintain high reproductive success even at old age, as reported for other ungulates (Côté and Festa-Bianchet 2001; Weladji et al. 2006; Hamel et al. 2009a). This highly heterogeneous decrease in reproductive success suggests that only those females with high reproductive potential reproduce in most years, whereas most old females skip some reproductive opportunities, probably to avoid survival costs (Gaillard and Yoccoz 2003). This pattern suggests reproductive restraint by older females, given that most of the variability in weaning success was caused by fecundity and not by juvenile survival. We also found much greater negative effects of poor years on the reproductive performance of senescent than prime-aged females, suggesting greater reproductive restraint by older females. This supports the suggestion by Rughetti and Festa-Bianchet (2011) that old females adopt a more conservative reproductive strategy than prime-aged females, especially when resources are scarce, as reported for bighorn sheep ewes by Martin and Festa-Bianchet (2011). The relationship between age and mass further supports this hypothesis. Generally, mass decreases at the same time as reproductive success for old ungulate females (Bérubé et al. 1999; Côté and Festa-Bianchet 2001). Old female chamois, however, were heavier than prime-aged ones. Consequently, the decrease in reproductive success with age was not explained by a loss of body condition. Instead, for a given mass, old females had lower reproductive success than prime-aged females. It is unknown if mass influences reproductive success for female chamois, but since it does for most ungulates (Gaillard et al. 2000b), we interpret the mass-specific decrease in reproductive success as a more conservative strategy for old females.

Reproductive restraint at old age, coupled with an increase in mass (Fig. 4), could explain the reduced energetic costs of reproduction of old females observed by Rughetti and Festa-Bianchet (2011) and the absence of costs on future fecundity reported here. Reproductive restraint removes breeding opportunities, lowering fitness (Weladji et al. 2006). However, this strategy may allow the surprisingly high longevity (McNamara et al. 2009) observed in chamois (Rughetti and Festa-Bianchet 2011) and may limit reproductive effort to the most favourable years (Gaillard and Yoccoz 2003) when the costs of reproduction are lower (Festa-Bianchet et al. 1998). This strategy supports the senescence hypothesis rather than the terminal investment hypothesis.

Reproduction and spring–summer body mass

There were no differences in mass between nonreproducing and lactating females between May and August. As in other temperate ungulates, late gestation and early lactation occur during late winter and early spring, when resources are often insufficient to maintain body mass (Albon and Langvatn 1992). Reproductive females should therefore partly rely on endogenous energy reserves for reproduction (Jönsson 1997; Festa-Bianchet et al. 1998). Therefore, the similar mass of females could indicate either that females can compensate for the energetic costs of gestation and early lactation by diverting energy from activity or maintenance (Gittleman and Thompson 1988) or that reproductive females were heavier the previous autumn and used up the extra mass.

Our data cannot distinguish between these two hypotheses, but show no detectable somatic cost of gestation. Rughetti and Festa-Bianchet (2011) found that harvested lactating females were lighter than nonlactating ones in September and October, suggesting a somatic cost of lactation.

Another indication that reproduction reduced mass is that old females were heavier than prime-aged females. By skipping some reproductive opportunities, old females may gain more mass than prime-aged females that reproduce in most years. Similar long-term costs of reproduction on body mass also exist in bison, where older females gain mass and are more often barren than younger females, but produce heavier offspring (Green and Rothstein 1991). Alternatively, if lighter females die at a younger age, selective disappearance may give the impression of an age-related increase in mass where none exists (Nussey et al. 2011).

We found that reproductive success was strongly age-dependent, with old females showing a very conservative strategy including reproductive restraint, limiting reproductive effort to most favorable years. Therefore, our results do not support the terminal investment hypothesis. For prime-aged females, reproductive success was independent of previous weaning success and spring-summer mass was independent of reproductive status, with no detectable costs of reproduction. However, reproductive success was very heterogeneous, reinforcing the need to identify covariates to control for individual heterogeneity to study the costs of reproduction. Here, early growth did not affect reproductive success and could not be used as an individual covariate. The influence of individual variables such as autumn mass, dominance status, birth date, birth mass, mass at primiparity, longevity, and maternal effects on reproductive success need to be further explored in female chamois. Future research should also focus on other fitness components such as offspring mass, growth, reproductive performance, and especially winter survival, as reproduction could affect those variables instead of maternal fecundity or offspring survival to weaning.

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