

The cost of trying: weak interspecific correlations among life-history components in male ungulates

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Abstract: Life-history trade-offs are well known in female mammals, but have seldom been quantified for males in polygynous species. I compared age-specific mass, weapon size, survival, and reproductive success of males in eight species of ungulates, and found weak interspecific correlations among life-history traits. Young males tended to have higher reproductive success in rapidly-growing than in slow-growing species, and in species where horns or antlers reached near-asymptotic size over the first few years of life. There was no clear interspecific trade-off between early reproduction and early survival. Reproductive senescence was evident in most species. Generation length, calculated as the mean age of fathers, was negatively correlated with the reproductive success of young males and positively with life expectancy of 3-year-olds, but not with early mortality. The main determinant of male reproductive success in polygynous ungulates is the ability to prevail against competing males. Consequently, the number and age structure of competitors should strongly affect an individual's ability to reproduce, making classic trade-offs among life-history traits very context-dependent. Most fitness costs of reproduction in male ungulates likely arise from energy expenditure and injuries sustained while attempting to mate. Individual costs may be weakly correlated with fitness returns.

Key words: life history, reproductive effort, age-specific, sexual dimorphism, reproductive strategies, ungulates.

Résumé : Les compromis entre les traits d'histoire de vie sont bien documentés chez les femelles des mammifères. Par contre, ils ont été peu étudiés pour les mâles chez des espèces polygynes. Dans cette étude, j'ai comparé les changements en masse, taille des armements, survie et succès reproducteur des mâles en fonction de leur âge, et ce, chez huit espèces d'ongulés. Mes analyses interspécifiques suggèrent des faibles corrélations entre traits d'histoire de vie. Le succès reproducteur des jeunes mâles tendait à être plus important pour les espèces avec une croissance rapide et pour les espèces dont les cornes ou bois atteignent des dimensions quasi-asymptotiques durant les premières années de vie. Aucun compromis évident n'a été détecté entre reproduction et survie en bas âge. Une sénescence reproductive était évidente pour la majorité des espèces. La durée de génération, estimée par l'âge moyen des pères, avait une corrélation négative avec le succès reproducteur des jeunes mâles et une corrélation positive avec l'espérance de vie des mâles âgés de 3 ans, mais n'avait aucune corrélation avec le taux de mortalité des jeunes mâles. Chez les ongulés polygynes, la variable la plus importante pour le succès reproducteur des mâles est la capacité à combattre les compétiteurs. Par conséquent, le nombre et la structure d'âge des compétiteurs devraient affecter la capacité d'un individu à se reproduire. Les compromis entre traits d'histoire de vie devraient varier selon le contexte. La plupart des coûts en aptitude phénotypique de la reproduction pour les ongulés mâles sont probablement dus aux coûts énergétiques et au risque de blessures lors des tentatives d'accouplement. Les coûts individuels pourraient avoir une faible corrélation avec le succès reproducteur.

Mots-clés : histoire de vie, effort reproducteur, âge-spécifique, dimorphisme sexuel, stratégies de reproductive strategies, ongulés.

Introduction

Based on the assumption of limited resources, life-history theory predicts trade-offs between fitness components (Stearns 1992). That prediction has been confirmed by many studies of females, especially when individual heterogeneity in reproductive potential was accounted for (Therrien et al. 2007; Bårdsen et al. 2008; Wilson et al. 2009; Bouwhuis et al. 2010; Hamel et al. 2010). Similarly, interspecific comparisons often reveal predictable patterns of covariation among life-history traits (Shine and Schwarzkopf 1992; Gilbert and Manica 2010). There have been fewer attempts to explore fitness trade-offs among males in wild populations, possibly because paternity is more difficult to measure than maternity.

Although most studies of male reproduction have considered energetic costs (Lane et al. 2010), some have also found fitness consequences, such as negative impacts of mating on subsequent mating success or on survival (Stevenson and Bancroft 1995; Janowitz and Fischer 2010; Jordan and Brooks 2010).

In polygynous species, the factors limiting reproductive success of males and females are fundamentally different. Although a female's reproduction is mostly limited by her ability to obtain resources, a male's reproduction mostly depends on his ability to outcompete rival males and on the number of females he can fertilize (Clutton-Brock 1988). Differences in limiting factors generate important differences in

Received 25 April 2012. Accepted 10 July 2012. Published at www.nrcresearchpress.com/cjz on 14 August 2012.

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expected trade-offs among fitness components. For example, a female that invests heavily in reproduction may improve her current reproductive success at the cost of a decrease in subsequent reproduction (Clutton-Brock 1991). Natural selection may then favor different allocation to current and future reproduction according to a host of ecological, genetic, and environmental variables (Roff and Fairbairn 2007). A male, however, could suffer substantial fitness costs while attempting to mate but obtain no reproductive success if other males monopolize access to females. Conversely, some dominant males may secure matings by simply threatening opponents. Thus, correlations between effort and success that do not account for age structure or dominance rank of potential competitors should be weaker in males than in females. If access to mates is mostly determined by differences in resource acquisition (Houle 1991), trade-offs in allocation may have little influence in siring success. Here, I compare data on male age-specific survival, growth, and reproduction in ungulates to quantify trade-offs between these life-history components.

The fitness costs of reproduction in males may vary with age. For example, in northern elephant seals (*Mirounga angustirostris* (Gill, 1866)), where males attain high mating success at 9–13 years of age, mating behavior increased mortality in males aged 7–8 years, but not in older males (Clinton and LeBoeuf 1993). In females, age differences in reproductive costs are usually ascribed to an allocation trade-off between reproduction and maintenance: females that reproduce before completing body growth typically suffer high fitness costs of reproduction (Descamps et al. 2006; Martin and Festa-Bianchet 2011). In males, a similar trade-off may involve risk of injury, especially in species where mature males are larger and stronger than younger ones (Festa-Bianchet and Côté 2008; Bergeron et al. 2010). In females, many life-history trade-offs are correlated with the “speed of life”, measured as the generation time, or the mean age of mothers, which typically increases with body mass (Gaillard et al. 2005). For iteroparous species such as ungulates, which only produce one or a few juveniles per parturition, the range of combinations of female life-history traits is constrained by demography. Some combinations of life-history trait are unlikely, as they may lead to population extinction. For example, a species where females are limited to one offspring per breeding opportunity and most females die before reproducing is unlikely to persist (Kraus et al. 2005). In polygynous species, however, one or a few males could fertilize all females in the population so that covariations in male life-history traits may be less constrained by demography compared with female traits. For example, high mortality of young males would not necessarily be correlated with high reproductive success at a young age. There have been no attempts to compare male life-history traits to male generation length.

Most ungulates are sexually dimorphic, polygynous, or promiscuous, and only females provide parental care. Females rarely wean more than two offspring a year and many species are monotocous (Gaillard et al. 2000). Consequently, lifespan is the main determinant of variability in female fitness (Clutton-Brock 1988). In females, rapid early growth usually correlates with earlier primiparity, and large adult size with greater reproductive success, often through lowered costs of reproduction (Festa-Bianchet et al. 1998; Hamel et al. 2009) and greater longevity (Bérubé et al. 1999; Nussey

et al. 2011). The reproductive success of males, on the other hand, is primarily dependent upon the number of potential mates and the competitive ability of other males (Myysterud et al. 2003; Preston et al. 2003). Because male mating success is mostly determined through contest competition, large males with big antlers or horns (“weapons”) usually achieve high mating success (McElligott et al. 2001; Coltman et al. 2002; Kruuk et al. 2002; Mainguy et al. 2009). These trends, however, are not universal; for example, in pronghorn (*Antilocapra americana* (Ord, 1815)), male mating success is unrelated to either body size or horn length (Byers et al. 1994), and in American bison (*Bison bison* (L., 1758)), body mass is unrelated to the number of copulations observed (Wolff 1998). Varying effectiveness of mate choice by females may explain these differences (Clutton-Brock and McAuliffe 2009), but the key sexual difference in most species is that female reproduction is limited by absolute body size or condition, while male reproduction is limited by relative size. Large weapons provide high reproductive success only if competitors do not have even larger weapons.

Ungulates are long-lived, grow for many years after weaning, and their survival and reproduction are strongly age-dependent (Gaillard et al. 1998). In most species, age-specific survival of males is lower than that of females, particularly when resources are limited (Clutton-Brock et al. 1985; Toïgo and Gaillard 2003). Sexual differences in survival are often attributed to differences in reproductive strategies (Toïgo and Gaillard 2003; Kraus et al. 2008). Because males can potentially father many offspring in a single breeding season, they may adopt a risky strategy as the pay-offs of achieving high dominance status are potentially very high. There are, however, some notable exceptions to the pattern of sexual dimorphism in survival. Alpine ibex (*Capra ibex* L., 1758) are among the most dimorphic ungulates known, yet survival of males and females aged 1–9 years is nearly identical (Toïgo et al. 2007). In red deer (*Cervus elaphus* L., 1758) aged 4–9 years, survival of males and females is very similar (Catchpole et al. 2004), and survival of pre-senescent adult chamois (genus *Rupicapra* Blainville, 1816) may not differ by sex (Gonzalez and Crampe 2001; Bocci et al. 2010). Survival of young adult males may be related to the opportunity to mate at different ages. In species where alternative mating tactics lead to some paternities, such as bighorn sheep (*Ovis canadensis* Shaw, 1804) (Hogg and Forbes 1997), young males may take more risks than in species where reaching a large size at an advanced age appears essential to obtain access to estrous females (Pemberton et al. 1992; Willis and Neuhaus 2009).

Males prevented from reproducing may have high survival, as demonstrated by castrated feral Soay rams (*Ovis aries* L., 1758) (Stevenson and Bancroft 1995), but no study of mammals has shown that individual male reproductive success and reproductive costs are correlated. On the contrary, there is evidence that highly successful males do not suffer a survival cost of reproduction (McElligott et al. 2002; Pelletier et al. 2006; Bergeron et al. 2008; Bonenfant et al. 2009). Given that mating success is mostly determined through male–male contests, one may expect selection for rapid growth in body and weapon size (Kruuk et al. 2002), but it is unknown whether there are any interspecific patterns of covariation between early growth in body and weapon size,

age-specific survival, and age-specific reproductive success. Survival and growth rate of young males may be negatively correlated for two reasons. First, rapid growth could carry a survival cost (Stamps et al. 1998), as could early participation in reproduction (Stevenson and Bancroft 1995). Second, if male size and competitive ability increase over many years, selection may favor survival of young males until they are large enough to achieve high reproductive success (Willisch and Neuhaus 2009), similarly to the apparent selection for high survival in ungulate females (Gaillard and Yoccoz 2003).

Several studies examined the possible costs of reproduction in male ungulates by quantifying mass loss over the rut. Typically, prime-aged adults lose more mass than young or senescent males. These patterns of mass loss have been attributed to differences in age-specific reproductive effort (Yoccoz et al. 2002; Forsyth et al. 2005; Mysterud et al. 2005). At the individual level, however, there is little indication that mass loss during the rut is related to reproductive success or that it affects survival. For example, in male fallow deer (*Dama dama* (L., 1758)), mass loss during the rut was related to neither mating success nor to behaviors associated with mating success (McElligott et al. 2003). In bighorn sheep, young males that were most active during the rut had longer life expectancy than less active males (Pelletier et al. 2006). Mass loss during the rut does not necessarily imply a fitness cost, because some males may have greater energy stores to devote to mating activities (Lidgard et al. 2004; Rughetti and Festa-Bianchet 2011). Overwinter mass loss in female bighorn sheep is positively related to fitness traits (Pelletier et al. 2007).

An interspecific analysis of life-history trade-offs in male ungulates could explain why age-specific survival of males tends to be lower and more variable than that of females (Gaillard et al. 2000), and shed light on interspecific variability in age-specific body and weapon size. It would also be useful for the management of ungulates, where sport hunting often leads to selective mortality of larger males (Coltman et al. 2003; Garel et al. 2007; Hengeveld and Festa-Bianchet 2011). Given its implication for the evolutionary consequences of selective hunting, the relationship between early growth and survival is the subject of debate. Studies based on individual monitoring suggest that rapid early growth is not correlated with life expectancy (Bergeron et al. 2008; Bonenfant et al. 2009). If males that quickly reach large body or weapon size made a strong reproductive effort, however, they may suffer high mortality (Loehr et al. 2006), as shown for male lambs in feral sheep (Stevenson and Bancroft 1995). It is unknown whether early growth and survival of young adult males are correlated across species. This paper has three objectives: (1) compare age-specific reproductive success for eight species of ungulates; (2) test the hypothesis that siring success and mortality of young males are correlated; (3) examine whether relative growth of young males is correlated with their reproductive success and mortality.

Materials and methods

I included all species with available age-specific data on mass, weapon size, survival, and reproductive success of males (Table 1). All survival estimates used capture–mark–recapture

(CMR) models based on monitoring known-age marked individuals (Lebreton et al. 1992). Most reproductive success estimates were based on paternity assignments using CER-VUS (Kalinowski et al. 2007) with 95% statistical confidence, although the study of roe deer (*Capreolus capreolus* (L., 1758)) used 80% (Vanpé et al. 2009a). Paternity assignments for ibex used MasterBayes (Hadfield et al. 2006). In fallow deer, reproductive success was estimated from observed copulations, which in the study population accurately measure paternity (Say et al. 2003). Mating systems varied among species. Tending, where a dominant male defends a single estrous female, was the main tactic for bighorn sheep, mountain goats (*Oreamnos americanus* (de Blainville, 1816)), feral sheep, and ibex. Fallow deer in Phoenix Park use a variety of territorial and nonterritorial strategies, but most matings are outside territories (Moore et al. 1995). Red deer on Rum defend harems, while roe deer defend territories. Male pronghorns can defend territories, harems, or individual females (Byers 1997). Data used here are from years when males did not defend territories (J.A. Byers, personal communication).

When available, I used data on survival, mass, and weapon size from the populations that provided data on reproductive success (Table 1). There are no data on reproductive success of male chamois (*Rupicapra rupicapra* (L., 1758)), and estimates of survival for males aged 1 and 2 years are biased because many male chamois of this age disperse (Loison et al. 1999, 2008). A. Loison provided age-specific CMR estimates for male chamois at Les Bauges, France, and I used these data to estimate life expectancy of 3-year-old males. P. Kjellander provided data on antler length and eviscerated mass of fallow deer in Sweden. There were no age-specific data on horn length available for pronghorn for the National Bison Range. Instead, I used data from the Nebraska sample in Mitchell and Maher (2006). All regional samples suggested an asymptote by 2 or 3 years of age (Mitchell and Maher 2006). For red deer, I used pre-rut mass of eviscerated deer in Norway (Yoccoz et al. 2002). Deer in Norway are likely heavier than on Rum, but age-specific relative mass should be similar. For ibex, data on age-specific survival are from Toïgo et al. (2007) for a reintroduced population in France, while data on mass and horn length (excluding the first annulus that is subject to age-specific wear) are from the Gran Paradiso National Park in Italy (Bergeron et al. 2008).

Mass was measured live for bighorn sheep, mountain goats, pronghorn, Soay sheep, and roe deer, but as eviscerated mass for red deer, fallow deer, and chamois. For comparisons across species, the mass of the latter three species was increased by 30% to account for removed viscera (Garel et al. 2009).

Data on age-specific male reproductive success are available for only one population of each species, with the exception of bighorn sheep where three populations have been monitored (Hogg and Forbes 1997; Coltman et al. 2002; Hogg et al. 2006). To illustrate possible intraspecific variability, I included a comparison of those three populations. For the interspecific analysis, I used data from Ram Mountain, which has the most data on body mass and horn size, the longest time series, and the largest number of assigned paternities. Age-specific siring success of bighorn rams at Sheep

Table 1. Sources of information on age-specific size, survival, and reproductive success of ungulate males.

Species	Mass	Weapon size	Survival	Reproductive success (<i>N</i>)	Sites
Bighorn sheep (<i>Ovis canadensis</i>)	Own data	Own data	Own data	Own data (289)	Ram Mountain, Alberta
Mountain goat (<i>Oreamnos americanus</i>)	Mainguy et al. 2008	Own data	Own data	Mainguy et al. 2009 (96)	Caw Ridge, Alberta
Red deer (<i>Cervus elaphus</i>)	Yoccoz et al. 2002	Nussey et al. 2009	Catchpole et al. 2004	Nussey et al. 2009 (1510)	Mass: Norway. Other data: Rum, Scotland
Pronghorn (<i>Antilocapra americana</i>)	J. Byers	Mitchell and Maher 2006	Byers 1997	J. Byers (212)	Horn size: Nebraska. Other data: National Bison Range, Montana
Soay sheep (<i>Ovis aries</i>)	Robinson et al. 2006	Robinson et al. 2006	Clutton-Brock and Pemberton 2004	Robinson et al. 2006 (1668)	St. Kilda, Scotland
Alpine ibex (<i>Capra ibex</i>)	Bergeron et al. 2010	Bergeron et al. 2008	Toigo et al. 2007	Willisch et al. 2012 (50)	Size: Gran Paradiso, Italy. Survival: Belledonne, France. Reproduction: Les Diablerets, Switzerland
Roe deer (<i>Capreolus capreolus</i>)	J.-M. Gaillard	Vanpé et al. 2007	Loison et al. 1999	Vanpé et al. 2009a, 2009b (90)	Reproduction: Bogesund, Sweden. Other data: Trois-Fontaines, France
Fallow deer (<i>Dama dama</i>)	P. Kjellander	P. Kjellander	McElligott et al. 2002	McElligott and Hayden 2000; A. McElligott (2016)	Reproduction and survival: Phoenix Park, Ireland. Size: Koberg, Sweden
Chamois (<i>Rupicapra rupicapra</i>)	Rughetti and Festa-Bianchet 2010	Rughetti and Festa-Bianchet 2010	A. Loison	na	Size: Piedmont, Italy. Survival from age 3: Les Bauges, France

Note: Names of individuals indicate personal communications. For reproductive success, numbers in parentheses indicate copulations seen for fallow deer, paternity assignments for all other species. Sport hunting of males in populations with data on paternity occurred at Ram Mountain (bighorn sheep), Les Diablerets (ibex), and Bogesund (roe deer). na, not available.

River, Alberta (246 paternities), and the National Bison Range, Montana (240 paternities), was provided by J.T. Hogg.

To compare early development with survival and reproductive success among species, I used data for 3-year-olds, the minimum age at which males bred in all species. I calculated the following:

- *Maximum mass/maximum weapon size*: mean mass of the heaviest age class and mean weapon length for the age class with the longest horns or antlers (Fig. 1).
- *Relative mass*: age-specific mass as a percentage of maximum mass.
- *Relative weapon size*: age-specific length of horns or antlers compared with maximum length. Roe deer show senescence in antler size (Vanpé et al. 2007; Nussey et al. 2009), while red deer do not (Nussey et al. 2009). Horn length cannot decrease with age other than through breakage, wear, or selective survival (Figs. 1, 2).
- *Early adult survival*: the proportion of yearling males that survived to 4 years. With rare exceptions, yearling males do not receive maternal care. I chose survival to age 4 to compare it with relative size and reproductive success at age 3, as survival to age 4 indicates the proportion of yearlings that survive through age 3. All estimates of survival exclude hunter kills. Sport hunting occurred for bighorn sheep, ibex, and roe deer.
- *Relative reproductive success*: the reproductive success at each age relative to the success of the age with most pater-

nities per male (Fig. 3). Assessment of male reproductive success in ungulates is fraught with difficulties. It is affected by adult sex ratio: the more female-biased the sex ratio, the greater the mean male reproductive success (Clutton-Brock et al. 1997). In open populations, unsampled nonresident males may immigrate during the rut, siring an unknown number of offspring, and resident males may sire offspring outside the study population (Hogg 2000). The proportion of juveniles sampled for molecular analyses will also affect the estimate of male reproductive success: one can determine the reproductive success of each female by simply noting the presence of an offspring, but to accurately estimate reproductive success of any male, all juveniles must be sampled. Consequently, comparisons of male reproductive success among studies cannot use absolute values but must rely on relative measures.

To account for possible nonindependence among species-specific trait values generated by phylogenetic inertia (Felsenstein 1985), statistical analyses were adjusted for phylogeny (Appendix Fig. A1) based on a taxonomy-based phylogeny of Artiodactyla (Wilson and Reeder 1993). The analysis used phylogenetic generalized least squares (PGLS) models (Freckleton et al. 2002), which quantify the phylogenetic signal (called λ). The λ value was consistently not different from 0 and was at times different from 1 (see Appendix Table A1) and parameter estimates remained unchanged when

Fig. 1. Age-specific relative mass for males of nine species of ungulates. Mass is reported for each age as a percentage of the heaviest age class.

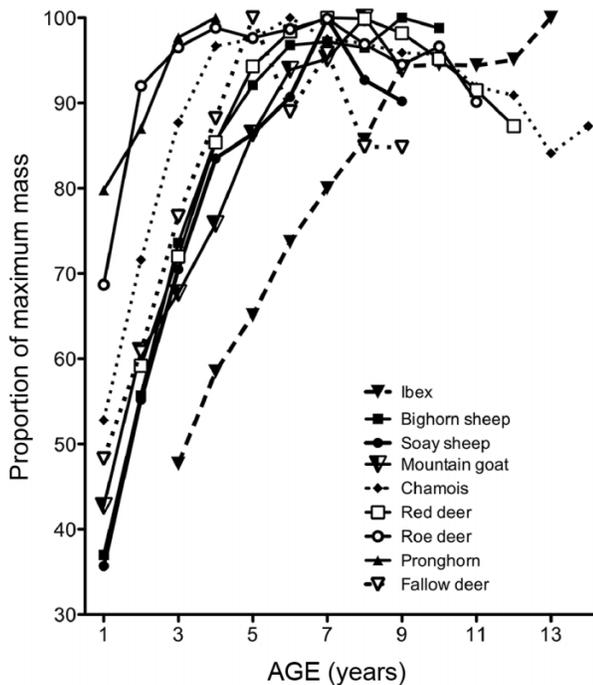
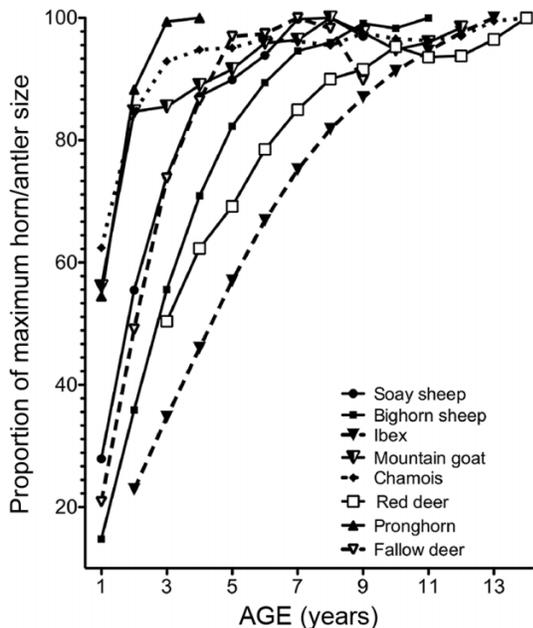
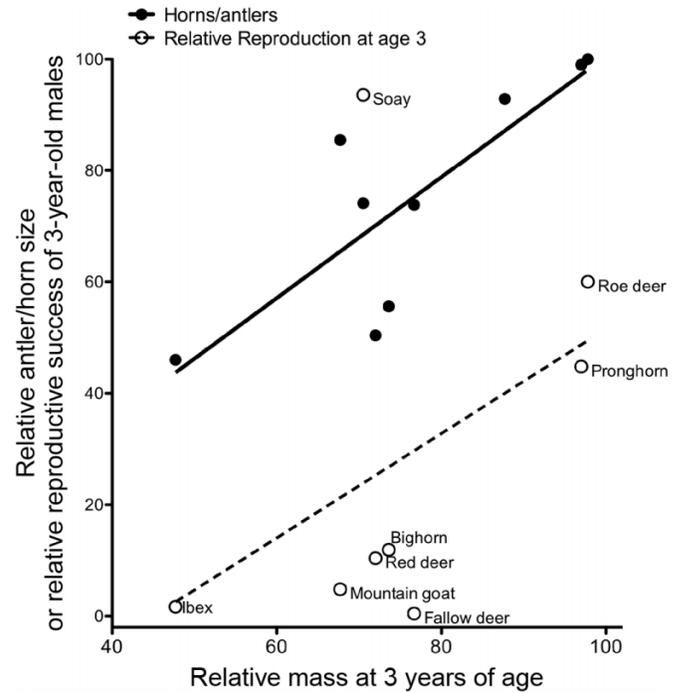


Fig. 2. Age-specific relative horn or antler size for males of eight species of ungulates. Size is reported for each age as a percentage of the size for the largest age class.



using PGLS or general linear models (GLM). I therefore only report standard GLM analyses with the exception of the comparison of mass at age 3 and maximum mass. Measurements of mass and horn size were log-transformed before analyses. For variables reported as proportions (relative mating success, relative early mass, early mortality), a logit transformation was applied.

Fig. 3. Mass of 3-year-old males as a proportion of maximum adult mass compared with relative weapon size and relative reproductive success of 3-year-old males. Data are shown for eight species of ungulates, listed near their relative reproductive success. The relationship of relative mass at age 3 and relative reproduction is significant if Soay sheep are excluded.



Soay sheep are feral animals that were introduced to the St. Kilda archipelago by people (Clutton-Brock and Pemberton 2004) and have many characteristics, such as breeding by male lambs and frequent episodes of mass starvation, that are not shared by wild ungulates. Therefore, some analyses were repeated excluding this species.

Results

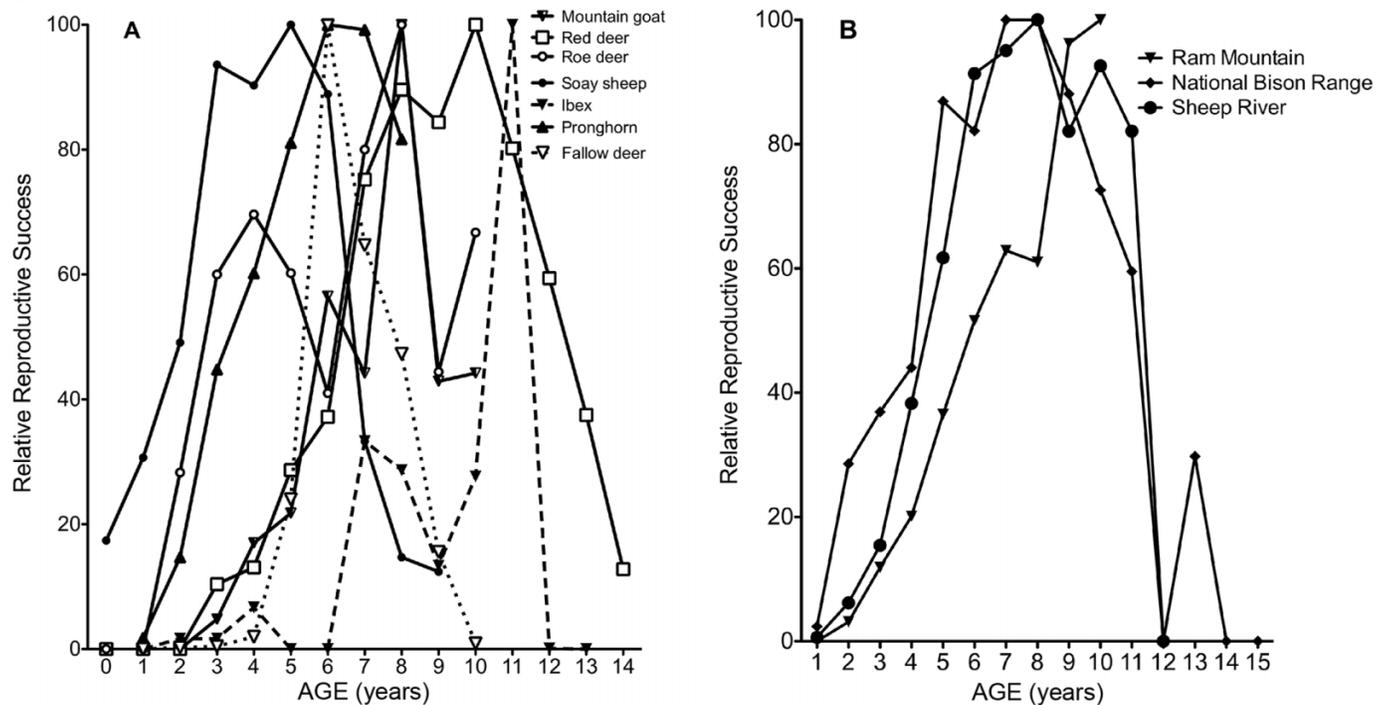
Growth in mass and weapon size

There were substantial interspecific differences in growth patterns in both mass (Fig. 1) and weapon size (Fig. 2). The proportion of maximum mass achieved by age 3 ranged from 48% for ibex to 98% for roe deer. Regression of the natural logs of mass at age 3 and maximum mass adjusted for phylogeny suggested isometry (slope 0.81 (CI: 0.60 to 1.02), $r^2 = 0.89$, $N = 9$, $P = 0.0002$) between early growth and maximum mass. Weapon size at age 3 was over 92% of its maximum for roe deer, chamois, and pronghorn, but it was only about 50% of maximum for red deer and ibex. Weapon size by age 3 increased with maximum weapon size (slope = 0.56 (CI: 0.33 to 0.80), $r^2 = 0.77$, $N = 9$, $P = 0.002$): species with small horns or antlers showed faster early growth than species with large weapons. Relative weapon size and mass at age 3 were correlated (slope = 1.09 (CI: 0.41 to 1.76), $r^2 = 0.67$, $N = 9$, $P = 0.007$) (Fig. 3).

Early growth and reproductive success

The proportion of mass achieved by age 3 was not related to the relative mating success of 3-year-olds (slope on a logit scale 0.78 (CI: -0.31 to +1.88), $r^2 = 0.25$, $N = 8$, $P = 0.21$).

Fig. 4. Age-specific reproductive success of males in (A) seven ungulate species and (B) three populations of bighorn sheep, relative to the age class with maximum success.



That analysis was strongly affected by feral sheep, where 3-year-olds weigh 30% less than 6-year-olds but their reproductive success is over 93% of maximum (Fig. 4A). In wild species with rapid early growth, such as pronghorn and roe deer, 3-year-olds weigh over 90% of maximum mass but only enjoy reproductive rates of about 45% and 60% of maximum, respectively (Fig. 3). The regression of early growth and early reproduction excluding feral sheep is significant ($r^2 = 0.95$, $P = 0.0002$) despite the small sample size. There was a positive relationship between relative weapon length and relative reproductive success of 3-year-olds on the logit scale (slope 0.57 (CI: 0.21 to 0.93), $r^2 = 0.65$, $N = 8$, $P = 0.027$).

Early growth and survival

The speed of early growth and survival of young males were not correlated. There was no detectable relationship between relative mass at 3 years and mortality between 1 and 4 years (slope 0.51 (CI: -0.66 to 1.68), $r^2 = 0.13$, $N = 8$, $P = 0.44$) (Fig. 5A). Log-transformed maximum mass was not correlated with log life expectancy of 3-year-olds (slope 0.46 (CI: -0.18 to 1.10), $r^2 = 0.22$, $N = 9$, $P = 0.20$). Life expectancy of 3-year-olds was just 1.1 years for Soay sheep. For wild species, it averaged 5.2 years, ranging from 3.3 years for fallow deer to 8.5 years for ibex. I examined this relationship for individual bighorn sheep and mountain goats, two species where mass correlates with male reproductive success (Coltman et al. 2002; Mainguy et al. 2009). Male longevity was independent of mass as a 3-year-old in both species (bighorn sheep: slope -0.02 (CI: -0.09 to 0.04), $r^2 = 0.007$, $N = 102$, $P = 0.41$ (males shot by hunters were excluded); mountain goats: slope -0.04 (CI: -0.22 to 0.14), $r^2 = 0.009$, $N = 30$, $P = 0.61$).

Age-specific survival and reproductive success

Adult male survival differed among species (Fig. 6). Less than 10% of yearling Soay rams survived to age 6 (Clutton-Brock and Pemberton 2004). Age-specific natural survival of bighorn sheep, mountain goats, roe deer, and fallow deer was broadly similar: 19%–36% of yearlings survived to 8 years of age. Pronghorn had higher survival than most other species until about 7 years of age, then suffered rapid senescence (Byers 1997). Ibex had high survival up to 10 years of age, then showed rapid senescence (Toïgo et al. 2007). The survival pattern of red deer on Rum was unique: many disappeared at ages 1 and 2, but from ages 3 to 9 their survival was as high as that of ibex, and nearly identical to that of female red deer of the same age (Catchpole et al. 2004). More red deer and ibex survived to old age than in other species: their life expectancy at 3 years was 7.7 and 8.5 years, while it averaged 3.8 years for the other species. Earlier analyses revealed survival senescence for most species (Loison et al. 1999; Catchpole et al. 2004; Toïgo et al. 2007).

There were substantial differences in age-specific relative reproductive success (Figs. 4A, 4B). The age at which males first attained a reproductive success of at least 10% of that of the most successful age class was 0 in feral sheep, which can breed as lambs. It was 2 years in pronghorn and roe deer, 3 years in red deer and bighorn sheep, 4 years in mountain goats, 5 years in fallow deer, and 7 years in ibex. The oldest males had lower reproductive success than prime-aged males in all species except bighorns at Ram Mountain. Bighorn rams in two other populations, however, showed reproductive senescence after about 8 years of age (Fig. 4B). Reproductive senescence (Vanpé et al. 2009a) and a decrease in antler size (Vanpé et al. 2007) have been reported in old male roe deer.

Fig. 5. For males of eight species of ungulates: (A) mortality from 1 to 4 years of age compared with the mass of 3-year-olds relative to the mass of the largest age class; (B) relative reproductive success of 3-year-olds, measured as a percentage of the age class with the highest reproductive success, compared with mortality from 1 to 4 years of age.

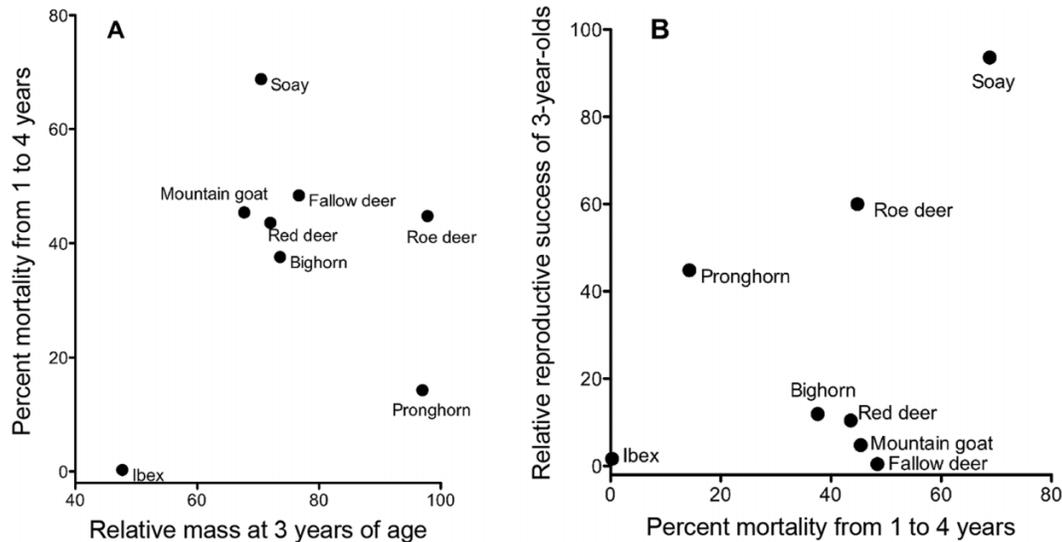
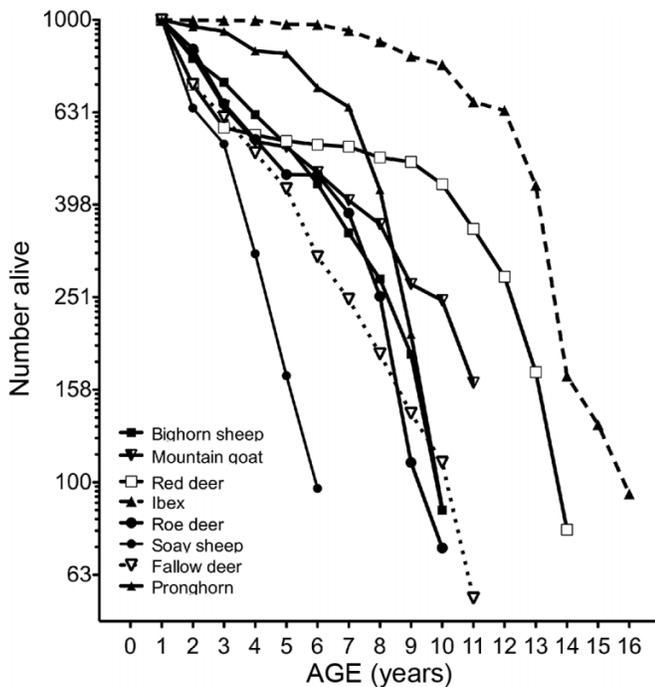


Fig. 6. Survival of a cohort of 1000 yearling males for eight species of ungulates, based on age-specific survival rates calculated from capture-mark-recapture models.



In red deer, however, male reproductive senescence is not accompanied by senescence in antler size (Nussey et al. 2009). Reproductive senescence has also been reported for male bison (Wolff 1998).

Reproductive senescence may be due to weakening of selective pressures with age, as few individuals survive to old age (Hamilton 1966). It is therefore important to quantify survival to an age when senescence in reproduction becomes obvious. I calculated the proportion of yearlings surviving to the age when relative reproductive success declines by at least 50% from its peak (Figs. 4A, 4B, 6). Bighorn sheep at

Ram Mountain did not show reproductive senescence and the reproductive success of the oldest male pronghorns declined only slightly after a peak at 6–7 years of age. For the other six species, on average, 23% of yearling males survived into reproductive senescence, varying from 0.8% in Soay rams to 64% in ibex.

Early reproduction and survival

The relative reproductive success of 3-year-olds was not correlated with mortality between 1 and 4 years of age (Fig. 5B) (slope 0.59 (CI: -0.11 to 1.29), $r^2 = 0.31$, $P = 0.15$). Almost all yearling male ibex survived to 4 years of age, and in this species few males reproduce before age 7 (Willisch et al. 2012). At the other extreme, about 69% of yearling Soay rams, which can sire offspring as lambs (Robinson et al. 2006), died before age 4. On the other hand, 3-year-old male pronghorns approach 50% of peak reproduction (Figs. 4A, 4B), yet over 85% of yearlings survived to age 4 (Fig. 6). Among these, 3-year-olds rarely reproduce in bighorn sheep, red deer, fallow deer, and mountain goat, but have high reproductive success in roe deer. Almost half (48%) of yearling fallow deer die before 4 years of age, yet mating success of 3-year-olds is less than 0.5% of that of males aged 6 (Figs. 4A).

Interspecific differences in longevity

Some of the interspecific differences presented above could be explained by differences in life expectancy. Not surprisingly, the log-transformed age at which males, on average, achieved 50% of peak reproductive success increased with the log-transformed median life expectancy of yearlings (slope 0.29 (CI: 0.16 to 0.42), $r^2 = 0.84$, $N = 6$, $P = 0.011$). The age by which 50% of yearlings died ranged from 4 years in Soay sheep to 13 years in ibex (Fig. 6), and was 6 years in the two species (bighorn sheep and mountain goats) coexisting with large predators (Festa-Bianchet et al. 2006; Festa-Bianchet and Côté 2008). In the nine species considered

here, the log-transformed median life expectancy of yearlings was unrelated to relative mass by age 3 ($P = 0.73$; $P = 0.18$ excluding Soay sheep, with a negative trend) and was independent of log maximum mass ($P = 0.20$).

A slow-fast continuum?

Calculated as the mean age of fathers, generation time averaged 6.3 years (SD = 2.2 years) and ranged from 2 years in Soay sheep to 9.1 years in ibex. It had a nearly significant correlation with maximum mass (log-log scale, slope 0.51 (CI: 0.06 to 0.96), $r^2 = 0.45$, $N = 8$, $P = 0.07$) but not with relative mass at 3 years (slope -0.06 , $r^2 = 0.04$, $N = 8$, $P = 0.64$). As expected, the life expectancy of 3-year-olds increased and their reproductive success decreased with longer generation time (using log-transformed values, life expectancy: slope 1.27 (CI: 0.95 to 1.59), $r^2 = 0.91$, $N = 8$, $P = 0.0002$; logit of relative reproductive success: slope -0.24 (CI: -0.37 to -0.11), $r^2 = 0.70$, $N = 8$, $P = 0.009$) (Fig. 7). Mortality between 1 and 4 years was not correlated with generation time (logit of mortality and log of generation time: slope -2.29 (CI: -5.27 to 0.69), $r^2 = 0.27$, $N = 8$, $P = 0.18$) (Fig. 7). Pronghorns have a short generation time despite high survival of young males, and survival from yearling to 4 years of age is about 50%–60% in five species (fallow deer, mountain goat, bighorn sheep, roe deer, red deer) whose generation times range from 5 to 8.5 years (Fig. 7).

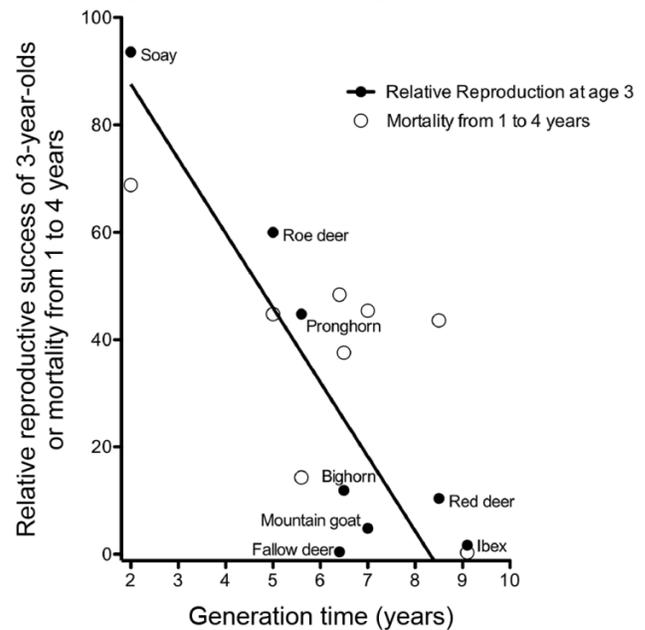
Discussion

Age-specific survival and growth in male ungulates vary widely among species but are not consistently correlated with differences in age-specific reproductive success. These results are not simply a function of interspecific differences in life expectancy, because there appears to be no correlation between early growth and early mortality, or between early mortality and generation time. The fast-slow continuum often identified in life-history traits of females (Fisher et al. 2002; Gaillard and Yoccoz 2003) was only partly confirmed for males, because mortality and reproductive success of young males were not correlated across species.

Not surprisingly, if Soay sheep were excluded, rapid early growth was correlated with early reproduction: when young males are small, they are easily outcompeted by older males. The apparent inconsistency of Soay sheep underlines the importance of relative size of competing males. The study population of feral sheep undergoes drastic changes in male age structure as most adult males die during crashes (Coulson et al. 2001). Although 3-year-olds are 20%–30% lighter than rams aged 5–6 years, few rams survive to age 5 (Fig. 6). Males born in a postcrash year find themselves aged 3 years in a population with many females and few if any older competitors. These 3-year-old males have high reproductive success. Changes in age structure inevitably affect the relative reproductive success of males of different ages. In bison, if older males are removed, young males have high reproductive success (Komers et al. 1994). Because mating success requires competition with other males, it is somewhat independent of absolute trait values and instead depends on the distribution of traits in competitors.

Neither rapid growth nor early reproductive success appeared to be correlated with mortality of young adults. In

Fig. 7. Relative reproductive success of 3-year-old males (●, solid line) and mortality from 1 to 4 years of age (○) compared with male generation length of eight species of ungulates.



both fallow deer and ibex, survival to a threshold age (6 and 11 years, respectively) is key to male reproductive success (Fig. 4A). Yet, although 66% of yearling ibex survive to 11 years, only 31% of yearling fallow deer live to 6 years. Roe deer and pronghorn grow very rapidly in both mass and weapon size, both species can defend territories, and both were studied in populations with no predation on adults. Yet, mortality of roe deer from 1 to 4 years was more than three times that of pronghorn (Figs. 5A, 5B).

Selection may favor riskier behavior in species where alternative mating tactics allow young males to obtain some paternities, leading to higher mortality among young males. My analysis, however, provides limited support for that hypothesis. In ibex, there are few mating opportunities for males younger than 7 years, and that species shows slow growth and high survival of males aged 1–9 years (Figs. 1, 2, 6) (Toigo et al. 2007). At the other extreme, in feral sheep, male lambs can sire offspring, mortality of young males is very high, and there is a survival cost of reproduction for male lambs (Stevenson and Bancroft 1995). Roe deer may also fit this pattern, with high mating success and substantial mortality of young males (Figs. 5A, 5B). High mortality of young roe deer may arise from interactions among males setting up territories (Wahlström 1994; Vanpé et al. 2008, 2009b). Young male pronghorn, however, combine faster growth, substantially greater survival, and much higher reproductive success than young males in most other species. Young fallow deer and mountain goats suffer high mortality, yet obtain very little reproductive success (Fig. 5B). In mountain goats, very rapid horn development among young males (Fig. 2) does not lead to siring success (Fig. 3). In this species, body mass, not horn size, determines access to estrous females (Mainguy et al. 2009).

Male chamois show a different growth-survival pattern than any other species, but their age-specific reproductive success is unknown. They achieve over 90% of asymptotic

size by age 3, yet survival of adult males is very high (Loison et al. 1994; Gonzalez and Crampe 2001; Bocci et al. 2010) and young adults cannot defend territories (von Hardenberg et al. 2000). The mating success of territorial and nonterritorial males, however, is unknown.

My analysis was limited by low statistical power and by the unavailability of all types of data for the same population. Because of the difficulties inherent in monitoring wild known-age male ungulates and in sampling enough offspring to estimate age-specific paternity, data are only available for eight species. Sample sizes or proportion of total offspring sampled are limited for ibex (Willisch et al. 2012) and roe deer (Vanpé et al. 2009a), possibly explaining the sudden drop in reproductive success of ibex between 11 and 12 years of age, and the apparent decrease in reproductive success of male roe deer between 4 and 6 years (Fig. 4A). Sport hunting of the ibex population truncated its age structure: only three animals older than 11 years were present (Willisch et al. 2012), whereas in unhunted populations, many males survive beyond 12 years (Toigo et al. 2007). In an unhunted ibex population, males aged 10–13 years have high dominance rank (Bergeron et al. 2010), and either maintain their mass or continue to gain mass (Fig. 1). Therefore, it is likely that the peak reproductive success of ibex extends over that range of ages, rather than being limited to 11-year-olds. In roe deer, a high proportion of fawns were not sampled, so the drop in reproductive success of males aged 5–6 years (Fig. 4A) may be due to sampling error. Low statistical power dictates a cautious approach to the interpretation of results. Some of the nonsignificant relationships that I report here have high determination coefficients and appear biologically plausible (Yoccoz 1991). Available data, however, reject the hypothesis of a positive interspecific relationship between early growth and mortality of young adults. That contention is supported by intraspecific analyses showing that rapidly-growing young males do not suffer greater mortality than slow-growing ones (Bergeron et al. 2008; Bonenfant et al. 2009), a pattern reversed by trophy hunting (Coltman et al. 2003; Garel et al. 2007; Bonenfant et al. 2009). In fallow deer, successful breeders enjoy higher survival than unsuccessful ones, and reproduce over several years (McElligott et al. 2002). Costs of reproduction in male ungulates could arise mostly from failed attempts at reproduction by subordinates, while dominants may enjoy high fitness with little cost (Pelletier 2005; Pelletier et al. 2006), because male reproductive success is mostly limited by the presence of superior competitors. When there are no clear dominance relationships, the mating system may shift (Byers and Kitchen 1988) and possibly change the distribution of reproductive costs according to male phenotype.

With the exception of bighorn sheep and mountain goats, all studies included in this analysis involved populations where large predators had been extirpated. Although the survival of adult males was not particularly lower in bighorns and mountain goats than in other species, predation can substantially reduce the survival of adult ungulates (Sinclair et al. 2003; Festa-Bianchet et al. 2006; Owen-Smith and Mills 2008; Bourbeau-Lemieux et al. 2011). There is some evidence that male ungulates are particularly vulnerable to predation during and soon after the rut (Knopff et al. 2010). Predation could affect male reproductive success by changing

both the adult sex ratio and the age structure of competing males. In species where reproductively successful males are highly visible or spatially predictable, they may suffer high predation (Fitzgibbon 1990). I found that for most species over a third of yearling males lived to reproductive senescence. This proportion may be lower in populations exposed to natural predation regimes. On the other hand, trophy hunting, by selectively removing the largest males, can strongly affect the distribution of male reproductive success (Coltman et al. 2003; Festa-Bianchet 2007). In many populations, the success of many males may depend upon the survival or death of just one competitor. Consequently, selective pressures on size and growth may be inconsistent from year to year (Coltman et al. 1999) and relationships between mass, weapons size, and reproductive success are unlikely to be linear (Coltman et al. 2002).

The high mortality of young males documented in sexually dimorphic mammals is often attributed to a risky strategy to maximize growth (Clutton-Brock et al. 1985). My analysis and research on intraspecific variability in male reproductive success (Clinton and LeBoeuf 1993; McElligott et al. 2002) suggest that for males, fitness risks, and rewards are not necessarily correlated. Most trade-offs likely occur at the level of resource acquisition rather than allocation (Houle 1991), and successful males may not suffer reproductive costs because they have acquired large amounts of resources to allocate to reproduction. Costs of reproduction in polygynous males may best be studied by examining the consequences of individual behavior on energetic expenditure, parasite infection, and survival (Pelletier 2005; Pelletier et al. 2005) rather than by looking for correlates of individual reproductive success. It is likely that those costs will vary across species, populations, and years in accordance with mating system, resource availability, and age structure. For example, young roe deer may suffer high mortality while fighting for territory acquisition, and young bighorn sheep and mountain goats may suffer high mortality because of the energy expended in attempting to mate through alternative tactics. Adult red deer may have high survival and high mating success because high mortality of young deer means that in most years there are few males aged 8–11 years. Young red deer are competitively inferior (Pemberton et al. 1992) and old ones are senescent (Nussey et al. 2009). In ibex, many males survive to 10–13 years, and strong competition within these age classes may lead to high mortality (Toigo et al. 1997). An interesting contrast with ibex is provided by northern elephant seals, where peak mating success is also at 11–13 years, but only 2.8% of yearling males survive to 11 years, when they enjoy high mating success without a strong increase in mortality (Clinton and LeBoeuf 1993). For males in many polygynous mammals, the fitness cost of trying to reproduce are likely much higher than the costs of actually reproducing.

Acknowledgements

I am very grateful to the Natural Sciences and Engineering Research Council of Canada (NSERC) for financial support for my long-term research on evolutionary ecology and conservation of large mammals. Many people assisted me by providing unpublished data, discussion, or comments on earlier drafts of the manuscript: J. Byers, S.D. Côté, J.-M. Gaillard, P. Kjellander, A. Loison, A. McElligott, P. Neuhaus,

F. Pelletier, D. Nussey, J.-M. Gaillard also provided substantial help with statistical analyses. The Department of Zoology of the University of Melbourne was a gracious host during the writing of the manuscript.

References

- Bårdsen, B.-J., Fauchald, P., Tveraa, T., Langeland, K., Yoccoz, N.G., and Ims, R.A. 2008. Experimental evidence of a risk-sensitive reproductive allocation in a long-lived mammal. *Ecology*, **89**(3): 829–837. doi:10.1890/07-0414.1. PMID:18459345.
- Bergeron, P., Festa-Bianchet, M., von Hardenberg, A., and Bassano, B. 2008. Heterogeneity in male horn growth and longevity in a highly sexually dimorphic ungulate. *Oikos*, **117**(1): 77–82. doi:10.1111/j.2007.0030-1299.16158.x.
- Bergeron, P., Grignolio, S., Apollonio, M., Shipley, B., and Festa-Bianchet, M. 2010. Secondary sexual characters signal fighting ability and determine social rank in Alpine ibex (*Capra ibex*). *Behav. Ecol. Sociobiol.* **64**(8): 1299–1307. doi:10.1007/s00265-010-0944-x.
- Bérubé, C., Festa-Bianchet, M., and Jorgenson, J.T. 1999. Individual differences, longevity, and reproductive senescence in bighorn ewes. *Ecology*, **80**(8): 2555–2565. doi:10.1890/0012-9658(1999)080[2555:IDLARS]2.0.CO;2.
- Bocci, A., Canavese, G., and Lovari, S. 2010. Even mortality patterns of the two sexes in a polygynous, near-monomorphic species: is there a flaw? *J. Zool. (Lond.)*, **280**(4): 379–386. doi:10.1111/j.1469-7998.2009.00672.x.
- Bonenfant, C., Pelletier, F., Garel, M., and Bergeron, P. 2009. Age-dependent relationship between horn growth and survival in wild sheep. *J. Anim. Ecol.* **78**(1): 161–171. doi:10.1111/j.1365-2656.2008.01477.x. PMID:19120602.
- Bourbeau-Lemieux, A., Festa-Bianchet, M., Gaillard, J.-M., and Pelletier, F. 2011. Predator-driven component Allee effects in a wild ungulate. *Ecol. Lett.* **14**(4): 358–363. doi:10.1111/j.1461-0248.2011.01595.x. PMID:21320261.
- Bouwhuis, S., Charmantier, A., Verhulst, S., and Sheldon, B.C. 2010. Individual variation in rates of senescence: natal origin effects and disposable soma in a wild bird population. *J. Anim. Ecol.* **79**(6): 1251–1261. doi:10.1111/j.1365-2656.2010.01730.x. PMID:20646122.
- Byers, J.A. 1997. American pronghorn. University of Chicago Press, Chicago.
- Byers, J.A., and Kitchen, D.W. 1988. Mating system shift in a pronghorn population. *Behav. Ecol. Sociobiol.* **22**: 355–360.
- Byers, J.A., Moodie, J.D., and Hall, N. 1994. Pronghorn females choose vigorous mates. *Anim. Behav.* **47**(1): 33–43. doi:10.1006/anbe.1994.1005.
- Catchpole, E.A., Fan, Y., Morgan, B.J.T., Clutton-Brock, T.H., and Coulson, T. 2004. Sexual dimorphism, survival and dispersal in red deer. *J. Agric. Biol. Environ. Stat.* **9**(1): 1–26. doi:10.1198/1085711043172.
- Clinton, W.L., and LeBoeuf, B.J. 1993. Sexual selection's effects on male life history and the pattern of male mortality. *Ecology*, **74**(6): 1884–1892. doi:10.2307/1939945.
- Clutton-Brock, T.H. (Editor). 1988. Reproductive success. University of Chicago Press, Chicago.
- Clutton-Brock, T.H. 1991. The evolution of parental care. Princeton University Press, Princeton, N.J.
- Clutton-Brock, T.H., and McAuliffe, K. 2009. Female mate choice in mammals. *Q. Rev. Biol.* **84**(1): 3–27. doi:10.1086/596461. PMID:19326786.
- Clutton-Brock, T.H., and Pemberton, J.M. (Editors). 2004. Soay sheep: dynamics and selection in an island population. Cambridge University Press, Cambridge.
- Clutton-Brock, T.H., Albon, S.D., and Guinness, F.E. 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature*, **313**(5998): 131–133. doi:10.1038/313131a0.
- Clutton-Brock, T.H., Rose, K.E., and Guinness, F.E. 1997. Density-related changes in sexual selection in red deer. *Proc. R. Soc. Lond. B Biol. Sci.* **264**(1387): 1509–1516. doi:10.1098/rspb.1997.0209. PMID:9364790.
- Coltman, D.W., Smith, J.A., Bancroft, D.R., Pilkington, J., MacColl, A.D.C., Clutton-Brock, T.H., and Pemberton, J.M. 1999. Density-dependent variation in lifetime breeding success and natural and sexual selection in Soay rams. *Am. Nat.* **154**(6): 730–746. doi:10.1086/303274. PMID:10600616.
- Coltman, D.W., Festa-Bianchet, M., Jorgenson, J.T., and Strobeck, C. 2002. Age-dependent sexual selection in bighorn rams. *Proc. R. Soc. Lond. B Biol. Sci.* **269**(1487): 165–172. doi:10.1098/rspb.2001.1851. PMID:11798432.
- Coltman, D.W., O'Donoghue, P., Jorgenson, J.T., Hogg, J.T., Strobeck, C., and Festa-Bianchet, M. 2003. Undesirable evolutionary consequences of trophy hunting. *Nature*, **426**(6967): 655–658. doi:10.1038/nature02177. PMID:14668862.
- Coulson, T., Catchpole, E.A., Albon, S.D., Morgan, B.J.T., Pemberton, J.M., Clutton-Brock, T.H., Crawley, M.J., and Grenfell, B.T. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. *Science*, **292**(5521): 1528–1531. doi:10.1126/science.292.5521.1528. PMID:11375487.
- Descamps, S., Boutin, S., Berteaux, D., and Gaillard, J.-M. 2006. Best squirrels trade a long life for an early reproduction. *Proc. R. Soc. Lond. B Biol. Sci.* **273**(1599): 2369–2374. doi:10.1098/rspb.2006.3588. PMID:16928640.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *Am. Nat.* **125**(1): 1–15. doi:10.1086/284325.
- Festa-Bianchet, M. 2007. Ecology, evolution, economics, and ungulate management. *In* *Wildlife science: linking ecological theory and management applications*. Edited by T.E. Fulbright and D.G. Hewitt. CRC Press, Boca Raton, Fla. pp. 183–202.
- Festa-Bianchet, M., and Côté, S.D. 2008. Mountain goats: ecology, behavior and conservation of a mountain ungulate. Island Press, Washington, D.C.
- Festa-Bianchet, M., Gaillard, J.-M., and Jorgenson, J.T. 1998. Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. *Am. Nat.* **152**(3): 367–379. doi:10.1086/286175. PMID:18811445.
- Festa-Bianchet, M., Coulson, T., Gaillard, J.-M., Hogg, J.T., and Pelletier, F. 2006. Stochastic predation events and population persistence in bighorn sheep. *Proc. R. Soc. Lond. B Biol. Sci.* **273**(1593): 1537–1543. doi:10.1098/rspb.2006.3467. PMID:16777749.
- Fisher, D.O., Blomberg, S.P., and Owens, I.P.F. 2002. Convergent maternal care strategy in ungulates and macropods. *Evolution*, **56**(1): 167–176. PMID:11915851.
- Fitzgibbon, C.D. 1990. Why do hunting cheetahs prefer male gazelles? *Anim. Behav.* **40**(5): 837–845. doi:10.1016/S0003-3472(05)80984-4.
- Forsyth, D.M., Duncan, R.P., Tustin, K.G., and Gaillard, J.-M. 2005. A substantial energetic cost to male reproduction in a sexually dimorphic ungulate. *Ecology*, **86**(8): 2154–2163. doi:10.1890/03-0738.
- Freckleton, R.P., Harvey, P.H., and Pagel, M. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. *Am. Nat.* **160**(6): 712–726. doi:10.1086/343873. PMID:18707460.
- Gaillard, J.-M., and Yoccoz, N.G. 2003. Temporal variation in survival of mammals: a case of environmental canalization? *Ecology*, **84**(12): 3294–3306. doi:10.1890/02-0409.
- Gaillard, J.-M., Festa-Bianchet, M., and Yoccoz, N.G. 1998.

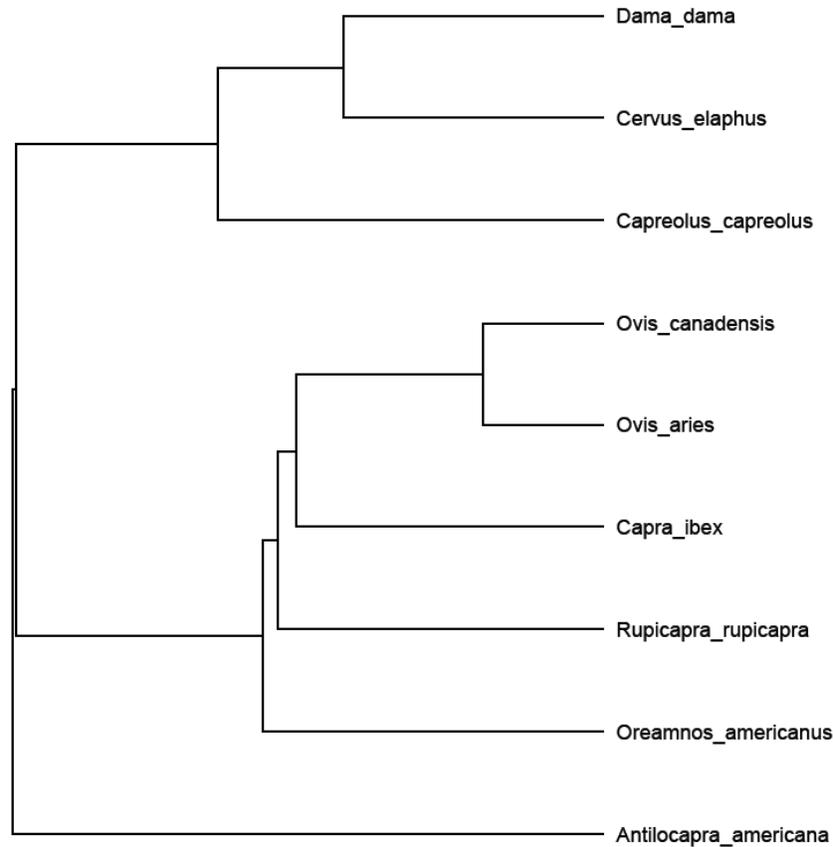
- Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends Ecol. Evol.* **13**(2): 58–63. doi:10.1016/S0169-5347(97)01237-8. PMID:21238201.
- Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A., and Toigo, C. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annu. Rev. Ecol. Syst.* **31**(1): 367–393. doi:10.1146/annurev.ecolsys.31.1.367.
- Gaillard, J.-M., Yoccoz, N.G., Lebreton, J.-D., Bonenfant, C., Devillard, S., Loison, A., Pontier, D., and Allainé, D. 2005. Generation time: a reliable metric to measure life-history variation among mammalian populations. *Am. Nat.* **166**(1): 119–123, discussion 124–128. doi:10.1086/430330. PMID:15937795.
- Garel, M., Cugnasse, J.-M., Maillard, D., Gaillard, J.-M., Hewison, A.J.M., and Dubray, D. 2007. Selective harvesting and habitat loss produce long-term life history changes in a mouflon population. *Ecol. Appl.* **17**(6): 1607–1618. doi:10.1890/06-0898.1. PMID:17913127.
- Garel, M., Loison, A., Jullien, J.-M., Dubray, D., Maillard, D., and Gaillard, J.-M. 2009. Sex-specific growth in Alpine chamois. *J. Mammal.* **90**(4): 954–960. doi:10.1644/08-MAMM-A-287.1.
- Gilbert, J.D.J., and Manica, A. 2010. Parental care trade-offs and life-history relationships in insects. *Am. Nat.* **176**(2): 212–226. doi:10.1086/653661. PMID:20528469.
- Gonzalez, G., and Crampe, J.P. 2001. Mortality patterns in a protected population of isards (*Rupicapra pyrenaica*). *Can. J. Zool.* **79**(11): 2072–2079. doi:10.1139/z01-173.
- Hadfield, J.D., Richardson, D.S., and Burke, T. 2006. Towards unbiased parentage assignment: combining genetic, behavioural and spatial data in a Bayesian framework. *Mol. Ecol.* **15**(12): 3715–3730. doi:10.1111/j.1365-294X.2006.03050.x. PMID:17032269.
- Hamel, S., Côté, S.D., Gaillard, J.-M., and Festa-Bianchet, M. 2009. Individual variation in reproductive costs of reproduction: high-quality females always do better. *J. Anim. Ecol.* **78**(1): 143–151. doi:10.1111/j.1365-2656.2008.01459.x. PMID:18700872.
- Hamel, S., Gaillard, J.-M., Yoccoz, N.G., Loison, A., Bonenfant, C., and Descamps, S. 2010. Fitness costs of reproduction depend on life speed: empirical evidence from mammalian populations. *Ecol. Lett.* **13**(7): 915–935. doi:10.1111/j.1461-0248.2010.01478.x. PMID:20482573.
- Hamilton, W.D. 1966. The moulding of senescence by natural selection. *J. Theor. Biol.* **12**(1): 12–45. doi:10.1016/0022-5193(66)90184-6. PMID:6015424.
- Hengeveld, P.E., and Festa-Bianchet, M. 2011. Harvest regulations and artificial selection on horn size in male bighorn sheep. *J. Wildl. Manage.* **75**(1): 189–197. doi:10.1002/jwmg.14.
- Hogg, J.T. 2000. Mating systems and conservation at large spatial scales. In *Vertebrate mating systems*. Edited by M. Apollonio, M. Festa-Bianchet, and D. Mainardi. World Scientific, Singapore. pp. 214–252.
- Hogg, J.T., and Forbes, S.H. 1997. Mating in bighorn sheep: frequent male reproduction via a high-risk “unconventional” tactic. *Behav. Ecol. Sociobiol.* **41**(1): 33–48. doi:10.1007/s002650050361.
- Hogg, J.T., Forbes, S.H., Steele, B.M., and Luikart, G. 2006. Genetic rescue of an insular population of large mammals. *Proc. R. Soc. Lond. B Biol. Sci.* **273**(1593): 1491–1499. doi:10.1098/rspb.2006.3477. PMID:16777743.
- Houle, D. 1991. Genetic covariance of fitness correlates: what genetic correlations are made of and why it matters. *Evolution*, **45**(3): 630–648. doi:10.2307/2409916.
- Janowitz, S., and Fischer, K. 2010. Costing reproduction: effects of mating opportunity on mating success in male *Bicyclus anynana* butterflies. *Behav. Ecol. Sociobiol.* **64**(12): 1999–2006. doi:10.1007/s00265-010-1011-3.
- Jordan, L.A., and Brooks, R.C. 2010. The lifetime costs of increased male reproductive effort: courtship, copulation and the Coolidge effect. *J. Evol. Biol.* **23**(11): 2403–2409. doi:10.1111/j.1420-9101.2010.02104.x. PMID:20825547.
- Kalinowski, S.T., Taper, M.L., and Marshall, T.C. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Mol. Ecol.* **16**(5): 1099–1106. doi:10.1111/j.1365-294X.2007.03089.x. PMID:17305863.
- Knopff, K.H., Adams Knopff, A., Kortello, A., and Boyce, M.S. 2010. Cougar kill rate and prey composition in a multiprey system. *J. Wildl. Manage.* **74**: 1435–1447.
- Komers, P.E., Messier, F., and Gates, C.C. 1994. Plasticity of reproductive behaviour in wood bison bulls: when subadults are given a chance. *Ethol. Ecol. Evol.* **6**(3): 313–330. doi:10.1080/08927014.1994.9522984.
- Kraus, C., Thomson, D.L., Künkele, J., and Trillmich, F. 2005. Living slow and dying young? Life-history strategy and age-specific survival rates in a precocial small mammal. *J. Anim. Ecol.* **74**(1): 171–180. doi:10.1111/j.1365-2656.2004.00910.x.
- Kraus, C., Eberle, M., and Kappeler, P.M. 2008. The costs of risky male behaviour: sex differences in seasonal survival in a small sexually monomorphic primate. *Proc. R. Soc. Lond. B Biol. Sci.* **275**(1643): 1635–1644. doi:10.1098/rspb.2008.0200. PMID:18426751.
- Kruuk, L.E.B., Slate, J., Pemberton, J.M., Brotherstone, S., Guinness, F., and Clutton-Brock, T. 2002. Antler size in red deer: heritability and selection but no evolution. *Evolution*, **56**(8): 1683–1695. PMID:12353761.
- Lane, J.E., Boutin, S., Speakman, J.R., and Humphries, M.M. 2010. Energetic costs of male reproduction in a scramble competition mating system. *J. Anim. Ecol.* **79**(1): 27–34. doi:10.1111/j.1365-2656.2009.01592.x. PMID:19674182.
- Lebreton, J.-D., Burnham, K.P., Clobert, J., and Anderson, D.R. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* **62**(1): 67–118. doi:10.2307/2937171.
- Lidgard, D.C., Boness, D.J., Bowen, D.W., and McMillan, J.I. 2004. State-dependent male mating tactics in the grey seal: the importance of body size. *Behav. Ecol.* **16**(3): 541–549. doi:10.1093/beheco/ari023.
- Loehr, J., Carey, J., Hoefs, M., Suhonen, J., and Ylönen, H. 2006. Horn growth rate and longevity: implications for natural and artificial selection in thinhorn sheep (*Ovis dalli*). *J. Evol. Biol.* **20**(2): 818–828. doi:10.1111/j.1420-9101.2006.01272.x. PMID:17305848.
- Loison, A., Gaillard, J.-M., and Houssin, H. 1994. New insight on survivorship of female chamois (*Rupicapra rupicapra*) from observation of marked animals. *Can. J. Zool.* **72**(4): 591–597. doi:10.1139/z94-081.
- Loison, A., Festa-Bianchet, M., Gaillard, J.-M., Jorgenson, J.T., and Jullien, J.-M. 1999. Age-specific survival in five populations of ungulates: evidence of senescence. *Ecology*, **80**(8): 2539–2554. doi:10.1890/0012-9658(1999)080[2539:ASSIFP]2.0.CO;2.
- Loison, A., Darmon, G., Cassar, S., Jullien, J.-M., and Maillard, D. 2008. Age- and sex-specific settlement patterns of chamois (*Rupicapra rupicapra*) offspring. *Can. J. Zool.* **86**(6): 588–593. doi:10.1139/Z08-031.
- Mainguy, J., Côté, S.D., Cardinal, É., and Houle, M. 2008. Mating tactics and mate choice in relation to age and social rank in male mountain goats. *J. Mammal.* **89**(3): 626–635. doi:10.1644/07-MAMM-A-234R.1.
- Mainguy, J., Côté, S.D., Festa-Bianchet, M., and Coltman, D.W. 2009. Father-offspring phenotypic correlations suggest intralocus

- sexual conflict for a fitness-linked trait in a wild sexually dimorphic mammal. *Proc. R. Soc. Lond. B Biol. Sci.* **276**(1675): 4067–4075. doi:10.1098/rspb.2009.1231. PMID:19740880.
- Martin, J.G.A., and Festa-Bianchet, M. 2011. Determinants and consequences of age of primiparity in bighorn ewes. *Oikos*, **121**(5): 752–760. doi:10.1111/j.1600-0706.2011.19962.x.
- McElligott, A.G., and Hayden, T.J. 2000. Lifetime mating success, sexual selection and life history of fallow bucks (*Dama dama*). *Behav. Ecol. Sociobiol.* **48**(3): 203–210. doi:10.1007/s002650000234.
- McElligott, A.G., Gammell, M.P., Harty, H.C., Paini, D.R., Murphy, D.T., Walsh, J.T., and Hayden, T.J. 2001. Sexual size dimorphism in fallow deer (*Dama dama*): do larger, heavier males gain greater mating success? *Behav. Ecol. Sociobiol.* **49**(4): 266–272. doi:10.1007/s002650000293.
- McElligott, A.G., Altwegg, R., and Hayden, T.J. 2002. Age-specific survival and reproductive probabilities: evidence for senescence in male fallow deer (*Dama dama*). *Proc. R. Soc. Lond. B Biol. Sci.* **269**(1496): 1129–1137. doi:10.1098/rspb.2002.1993. PMID:12061956.
- McElligott, A.G., Naulty, F., Clarke, W.V., and Hayden, T.J. 2003. The somatic cost of reproduction: what determines reproductive effort in prime-aged fallow bucks? *Evol. Ecol. Res.* **5**: 1239–1250.
- Mitchell, C.D., and Maher, C.R. 2006. Horn growth in male pronghorns *Antilocapra americana*: selection for precocial maturation in stochastic environments. *Acta Theriol.* **51**(4): 405–409. doi:10.1007/BF03195187.
- Moore, N.P., Kelly, P.F., Cahill, J.P., and Hayden, T.J. 1995. Mating strategies and mating success of fallow (*Dama dama*) bucks in a non-lekking population. *Behav. Ecol. Sociobiol.* **36**(2): 91–100. doi:10.1007/BF00170713.
- Mysterud, A., Holand, Ø., Røed, K.H., Gjøstein, H., Kumpula, J., and Nieminen, M. 2003. Effects of age, density and sex ratio on reproductive effort in male reindeer (*Rangifer tarandus*). *J. Zool. (Lond.)*, **261**(4): 341–344. doi:10.1017/S0952836903004114.
- Mysterud, A., Solberg, E.J., and Yoccoz, N.G. 2005. Ageing and reproductive effort in male moose under variable levels of intrasexual competition. *J. Anim. Ecol.* **74**(4): 742–754. doi:10.1111/j.1365-2656.2005.00965.x.
- Nussey, D.H., Kruuk, L.E.B., Morris, A., Clements, M.N., Pemberton, J., and Clutton-Brock, T.H. 2009. Inter- and intrasexual variation in aging patterns across reproductive traits in a wild red deer population. *Am. Nat.* **174**(3): 342–357. doi:10.1086/603615. PMID:19653847.
- Nussey, D.H., Coulson, T., Delorme, D., Clutton-Brock, T.H., Pemberton, J.M., Festa-Bianchet, M., and Gaillard, J.-M. 2011. Patterns of body mass senescence and selective disappearance differ across three species of free-living ungulates. *Ecology*, **92**(10): 1936–1947. doi:10.1890/11-0308.1. PMID:22073785.
- Owen-Smith, N., and Mills, M.G.L. 2008. Shifting prey selection generates contrasting herbivore dynamics within a large-mammal predator–prey web. *Ecology*, **89**(4): 1120–1133. doi:10.1890/07-0970.1. PMID:18481536.
- Pelletier, F. 2005. Foraging time of rutting bighorn rams varies with individual behavior, not mating tactic. *Behav. Ecol.* **16**(1): 280–285. doi:10.1093/beheco/arl162.
- Pelletier, F., Page, K.A., Ostiguy, T., and Festa-Bianchet, M. 2005. Fecal counts of lungworm larvae and reproductive effort in bighorn sheep, *Ovis canadensis*. *Oikos*, **110**(3): 473–480. doi:10.1111/j.0030-1299.2005.14120.x.
- Pelletier, F., Hogg, J.T., and Festa-Bianchet, M. 2006. Male mating effort in a polygynous ungulate. *Behav. Ecol. Sociobiol.* **60**(5): 645–654. doi:10.1007/s00265-006-0208-y.
- Pelletier, F., Réale, D., Garant, D., Coltman, D.W., and Festa-Bianchet, M. 2007. Selection on heritable seasonal phenotypic plasticity of body mass. *Evolution*, **61**(8): 1969–1979. doi:10.1111/j.1558-5646.2007.00160.x. PMID:17683438.
- Pemberton, J.M., Albon, S.D., Guinness, F.E., Clutton-Brock, T.H., and Dover, G.A. 1992. Behavioral estimates of male mating success tested by DNA fingerprinting in a polygynous mammal. *Behav. Ecol.* **3**(1): 66–75. doi:10.1093/beheco/3.1.66.
- Preston, B.T., Stevenson, I.R., Pemberton, J.M., Coltman, D.W., and Wilson, K. 2003. Overt and covert competition in a promiscuous mammal: the importance of weaponry and testes size to male reproductive success. *Proc. R. Soc. Lond. B Biol. Sci.* **270**(1515): 633–640. doi:10.1098/rspb.2002.2268. PMID:12769464.
- Robinson, M.R., Pilkington, J.G., Clutton-Brock, T.H., Pemberton, J.M., and Kruuk, L.E.B. 2006. Live fast, die young: trade-offs between fitness components and sexually antagonistic selection on weaponry in Soay sheep. *Evolution*, **60**(10): 2168–2181. PMID:17133873.
- Roff, D.A., and Fairbairn, D.J. 2007. The evolution of trade-offs: where are we? *J. Evol. Biol.* **20**(2): 433–447. doi:10.1111/j.1420-9101.2006.01255.x. PMID:17305809.
- Rughetti, M., and Festa-Bianchet, M. 2010. Compensatory growth limits opportunities for artificial selection in Alpine chamois. *J. Wildl. Manage.* **74**(5): 1024–1029. doi:10.2193/2009-335.
- Rughetti, M., and Festa-Bianchet, M. 2011. Seasonal changes in sexual size dimorphism in northern chamois. *J. Zool. (Lond.)*, **284**(4): 257–264. doi:10.1111/j.1469-7998.2011.00800.x.
- Say, L., Naulty, F., and Hayden, T.J. 2003. Genetic and behavioural estimates of reproductive skew in male fallow deer. *Mol. Ecol.* **12**(10): 2793–2800. doi:10.1046/j.1365-294X.2003.01945.x. PMID:12969481.
- Shine, R., and Schwarzkopf, L. 1992. The evolution of reproductive effort in lizards and snakes. *Evolution*, **46**(1): 62–75. doi:10.2307/2409805.
- Sinclair, A.R.E., Mduma, S., and Brashares, J.S. 2003. Patterns of predation in a diverse predator–prey system. *Nature*, **425**(6955): 288–290. doi:10.1038/nature01934. PMID:13679915.
- Stamps, J.A., Mangel, M., and Phillips, J.A. 1998. A new look at relationships between size at maturity and asymptotic size. *Am. Nat.* **152**(3): 470–479. doi:10.1086/286183. PMID:18811453.
- Stearns, S.C. 1992. *The Evolution of life histories*. Oxford University Press, Oxford.
- Stevenson, I.R., and Bancroft, D.R. 1995. Fluctuating trade-offs favour precocial maturity in male Soay sheep. *Proc. R. Soc. Lond. B Biol. Sci.* **262**(1365): 267–275. doi:10.1098/rspb.1995.0205. PMID:8587885.
- Therrien, J.-F., Côté, S.D., Festa-Bianchet, M., and Ouellet, J.-P. 2007. Conservative maternal care in an iteroparous mammal: a resource allocation experiment. *Behav. Ecol. Sociobiol.* **62**(2): 193–199. doi:10.1007/s00265-007-0453-8.
- Toïgo, C., and Gaillard, J.-M. 2003. Causes of sex-biased adult survival in ungulates: sexual size dimorphism, mating tactic or environment harshness? *Oikos*, **101**(2): 376–384. doi:10.1034/j.1600-0706.2003.12073.x.
- Toïgo, C., Gaillard, J.-M., and Michallet, J. 1997. Adult survival pattern of the sexually dimorphic Alpine ibex (*Capra ibex ibex*). *Can. J. Zool.* **75**(1): 75–79. doi:10.1139/z97-009.
- Toïgo, C., Gaillard, J.-M., Festa-Bianchet, M., Largo, É., Michallet, J., and Maillard, D. 2007. Sex- and age-specific survival of the highly dimorphic Alpine ibex: evidence for a conservative life-history tactic. *J. Anim. Ecol.* **76**(4): 679–686. doi:10.1111/j.1365-2656.2007.01254.x. PMID:17584373.
- Vanpé, C., Gaillard, J.-M., Kjellander, P., Mysterud, A., Magnien, P., Delorme, D., Laere, G.V., Klein, F., Liberg, O., and Hewison, A.J.M.

2007. Antler size provides an honest signal of male phenotypic quality in roe deer. *Am. Nat.* **169**(4): 481–493. doi:10.1086/512046. PMID:17273980.
- Vanpé, C., Kjellander, P., Galan, M., Cosson, J.-F., Aulagnier, S., Liberg, O., and Hewison, A.J.M. 2008. Mating system, sexual dimorphism, and the opportunity for sexual selection in a territorial ungulate. *Behav. Ecol.* **19**(2): 309–316. doi:10.1093/beheco/arm132.
- Vanpé, C., Gaillard, J.-M., Morellet, N., Kjellander, P., Liberg, O., Delorme, D., and Hewison, A.J.M. 2009a. Age-specific variation in male breeding success of a territorial ungulate species, the European roe deer. *J. Mammal.* **90**(3): 661–665. doi:10.1644/08-MAMM-A-137R.1.
- Vanpé, C., Morellet, N., Kjellander, P., Goulard, M., Liberg, O., and Hewison, A.J.M. 2009b. Access to mates in a territorial ungulate is determined by the size of a male's territory, but not by its habitat quality. *J. Anim. Ecol.* **78**(1): 42–51. doi:10.1111/j.1365-2656.2008.01467.x. PMID:18752539.
- von Hardenberg, A., Bassano, B., Peracino, A., and Lovari, S. 2000. Male alpine chamois occupy territories at hotspots before the mating season. *Ethology*, **106**(7): 617–630. doi:10.1046/j.1439-0310.2000.00579.x.
- Wahlström, L.K. 1994. The significance of male–male aggression for yearling dispersal in roe deer (*Capreolus capreolus*). *Behav. Ecol. Sociobiol.* **35**: 409–412. doi:10.1007/BF00165843.
- Willisch, C.S., and Neuhaus, P. 2009. Alternative mating tactics and their impact on survival in adult male Alpine ibex (*Capra ibex ibex*). *J. Mammal.* **90**(6): 1421–1430. doi:10.1644/08-MAMM-A-316R1.1.
- Willisch, C.S., Biebach, I., Koller, U., Bucher, T., Marreros, N., Ryser-Degiorgis, M.-P., Keller, L.F., and Neuhaus, P. 2012. Male reproductive pattern in a polygynous ungulate with a slow life-history: the role of age, social status and alternative mating tactics. *Evol. Ecol.* **26**(1): 187–206. doi:10.1007/s10682-011-9486-6.
- Wilson, D.E., and Reeder, D.A.M. 1993. *Mammal species of the world. A taxonomic and geographic reference.* 2nd ed. Smithsonian Institution Press, Washington, D.C., and London, U.K.
- Wilson, A.J., Pemberton, J., Pilkington, J.G., Clutton-Brock, T.H., and Kruuk, L.E.B. 2009. Trading offspring size for number in a variable environment: selection on reproductive investment in female Soay sheep. *J. Anim. Ecol.* **78**(2): 354–364. doi:10.1111/j.1365-2656.2008.01489.x. PMID:19302125.
- Wolff, J.O. 1998. Breeding strategies, mate choice, and reproductive success in American bison. *Oikos*, **83**(3): 529–544. doi:10.2307/3546680.
- Yoccoz, N.G. 1991. Use, overuse, and misuse of significance tests in evolutionary biology and ecology. *Bull. Ecol. Soc. Am.* **72**: 106–111.
- Yoccoz, N.G., Mysterud, A., Langvatn, R., and Stenseth, N.C. 2002. Age- and density-dependent reproductive effort in male red deer. *Proc. R. Soc. Lond. B Biol. Sci.* **269**(1500): 1523–1528. doi:10.1098/rspb.2002.2047. PMID:12184820.

Appendix A

Figure A1 and Table A1 appear on the following page.

Fig. A1. The phylogeny of ungulates used to test for phylogenetic inertia. Data from Wilson and Reeder (1993).**Table A1.** Values of λ , the phylogenetic signal estimated with phylogenetic generalized least squares (PGSL) models (Freckleton et al. 2002) for the relationships tested in the paper.

Relationship	λ	$P = 0$	$P = 1$
Mass at age 3 and maximum mass	0.47	0.49	0.40
Weapon size by age 3 and maximum weapon size	0.00007	1.00	0.29
Early growth and early reproduction for seven wild species	0.00007	1.00	0.08
Relative weapon length and reproduction of 3-year-olds	0.00007	1.00	0.03
Relative mass at 3 years and mortality from 1 to 4 years	0.00007	1.00	0.16
Maximum mass and life expectancy of 3-year-old males	0.00007	1.00	0.08
Relative reproduction at 3 years and mortality from 1 to 4 years	0.00007	1.00	0.03
Age of 50% of peak reproduction and yearling life expectancy	0.00007	1.00	0.08
Median life expectancy of yearlings and relative mass by age 3	0.00007	1.00	0.02
Median life expectancy of yearlings and maximum mass	0.00007	1.00	0.06
Generation time and maximum mass	0.00007	1.00	0.15
Generation time and relative mass at 3 years	0.00007	1.00	0.19
Life expectancy of 3-year-olds and generation time	0.00007	1.00	0.03
Relative reproductive success of 3-year-olds and generation time	0.00007	1.00	0.18
Mortality between 1 and 4 years and generation time	0.00007	1.00	0.24

Note: None of the estimated λ values were significantly different from 0, and some were significantly different from 1.