




Long-term studies of bighorn sheep and mountain goats reveal fitness costs of reproduction

Marco Festa-Bianchet^{1,2}  | Steeve D. Côté^{2,3}  | Sandra Hamel⁴  | Fanie Pelletier^{1,2}

¹Département de biologie, Université de Sherbrooke, Sherbrooke, Québec, Canada

²Centre d'études nordiques, Québec City, Québec, Canada

³Département de biologie, Université Laval, Sainte-Foy, Québec, Canada

⁴Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries, and Economics, UiT The Arctic University of Norway, Tromsø, Norway

Correspondence

Marco Festa-Bianchet
Email: m.festa@usherbrooke.ca

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Abstract

1. Fitness costs of reproduction are expected when resources are limited. Costs drive the evolution of life-history strategies and can affect population dynamics if females change their allocation of resources to reproduction.
2. We studied fitness costs of reproduction in mountain ungulates in Alberta, Canada. We monitored two populations of bighorn sheep (*Ovis canadensis*) for 44 and 30 years, and one of mountain goats (*Oreamnos americanus*) for 30 years. Both species are highly iteroparous.
3. Heterogeneity in individual reproductive potential makes fitness costs of reproduction difficult to detect and quantify without manipulations. In capital breeders, individual differences can be partly accounted for by considering body mass and other correlates of reproductive potential. Long-term monitoring can reveal costs that only manifest under stressful conditions such as disease or resource scarcity.
4. Despite individual differences in reproductive potential, we detected fitness costs of reproduction in females. Costs, in terms of mass gain and survival, are almost entirely born by subsequent offspring, as mothers prioritize their own maintenance and survival. Costs are greater for primiparous females, decrease with increasing body mass and increase as resource availability declines, and sons are costlier than daughters. Costs may increase for senescent females that appear to reduce allocation to reproduction. In bighorn sheep, costs mostly involve reduced mass gain and lower survival of subsequent offspring. In mountain goats, costs include reductions in mass gain, subsequent fecundity and juvenile survival.
5. In males, fitness costs derive mostly from attempts to reproduce rather than from siring success and likely depend upon individual competitiveness. In the absence of selective harvests, dominant males may enjoy high fitness and possibly lower costs compared to subordinates.
6. The conservative reproductive tactic of mountain ungulate females likely explains why density dependence mostly involves later primiparity and lower recruitment, but rarely affects adult survival. Future research will seek to better account for heterogeneity in reproductive potential, assess cumulative reproductive costs and investigate the potential effects of fathers on maternal allocation tactics.

KEYWORDS

individual differences, long-term monitoring, mountain ungulates, population dynamics, predation, reproductive potential, reproductive strategies, wildlife conservation

1 | INTRODUCTION

When resources are limited, allocation trade-offs among components of reproductive success lead to fitness costs of reproduction (Stearns, 1992). As pointed out by Williams (1966), greater allocation to current reproduction may reduce residual reproductive value. Fitness costs affect the evolution of life-history strategies and can drive changes in population growth. Reproductive allocation decisions may vary with resource availability, potentially leading to density-dependent population growth (Bardsen & Tveraa, 2012). The study of fitness costs in wild populations may allow better assessment of the potential impacts of environmental changes.

In mammals, lactation is the energetically costlier part of female reproduction (Gittleman & Thompson, 1988) and should have a fitness cost if it uses resources that cannot be recovered before the next reproduction. In species where adult females have a high survival rate and multiple reproductive opportunities, the costs of reproduction are expected to be expressed mostly as reduced maternal care. That is because in these “slow” species, the reproductive value of mothers is much greater than that of offspring (Gaillard & Yoccoz, 2003; Hamel et al., 2010). In contrast, when females have high mortality and a limited number of reproductive opportunities, costs often include a reduction in maternal survival, as expected when the reproductive value of offspring is not much lower than that of mothers (Hamel et al., 2010). Costs of reproduction in male mammals are poorly documented, partly because their evaluation requires a molecular assessment of paternity. If costs result from interactions with other males, they may not be closely correlated with siring success (Festa-Bianchet, 2012). The energy and injury costs of male–male interactions may explain why male mortality is typically higher than female mortality in polygynous mammals (Toïgo & Gaillard, 2003).

Quantifying the fitness costs of reproduction in wild mammals is challenging. The strong mother–offspring recognition mechanisms, and often the difficulty of accessing newborns, make experimental manipulations of reproduction difficult. Litter size manipulations have been performed for small mammals (Skibieli, Speakman, & Hood, 2013). To our knowledge, only two studies have examined the costs of reproduction in wild large mammals by manipulating reproductive effort. In feral sheep (*Ovis aries*), contraceptive implants increased female survival, but did not improve subsequent breeding performance (Tavecchia et al., 2005). In Eastern grey kangaroos (*Macropus giganteus*), females prevented from reproducing for one year subsequently gave birth earlier and their offspring had higher survival compared with control females (Gélin, Wilson, Coulson, & Festa-Bianchet, 2015).

If reproductive effort is not manipulated experimentally, to detect costs one must rely on correlations between reproduction and

survival or in reproductive success over subsequent episodes for the same individual. Performance over consecutive reproductive opportunities, however, is affected by individual reproductive potential (Weladji et al., 2008). As pointed out by van Noordwijk and de Jong (1986), if individual variation in resource acquisition is large compared to variation in resource allocation, life-history traits will show positive correlations. That is because individuals that have acquired a large quantity of resources can reproduce without fitness costs, while individuals in poor condition may be unable to reproduce in consecutive breeding seasons or may die even if they do not reproduce. Several environmental and individual variables affect resource acquisition and allocation, and can thereby affect the costs of reproduction. For example, reproductive costs may vary with female age, parity, offspring sex and resource availability (Archie, Altmann, & Alberts, 2014; Descamps, Boutin, McAdam, Berteaux, & Gaillard, 2009). Thus, the costs of reproduction in the wild may not be evident only if monitoring includes a range of individual and environmental characteristics.

Long-term studies of individually marked vertebrates have advanced our knowledge of life histories in the wild (Clutton-Brock & Sheldon, 2010a). Three characteristics of these studies make them particularly valuable for understanding how fitness costs of reproduction affect individual reproductive success, reproductive tactics and population dynamics. First, data collected over many years can account for changes in the environment. Relevant variables include population density, diseases, parasites, forage abundance and predation risk. Long-term studies quantify natural variability in factors that affect the costs of reproduction. Second, the effects of age, cohort and other characteristics such as body mass and mass change can be taken into account, especially when individuals are measured repeatedly. Third, by monitoring individuals from birth to death, these studies can compare how allocation to reproduction at different life stages may affect subsequent survival and reproductive success, elucidating possible long-term effects of allocation tactics. Information on which traits distinguish successful and unsuccessful individuals as ecological conditions change can provide a mechanistic understanding of how reproductive allocation affects subsequent fitness components and therefore influence population dynamics.

Here, we examine how our long-term studies of mountain ungulates advanced understanding of the fitness costs of reproduction in wild large herbivores. We replicated similar monitoring techniques in three populations of two species sharing similar habitats, social organization, antipredator tactic and life-history traits. The presence of effective predators allowed us to quantify reproductive costs within an ecological setting likely similar to that prevalent during the evolution of these species. By monitoring three populations, we

examined how costs of reproduction varied with ecological conditions and among populations.

2 | FITNESS COSTS OF REPRODUCTION IN LARGE MAMMALS

Several long-term studies of marked individuals have addressed the fitness costs of reproduction in large mammals, particularly females. Despite the confounding effects of individual heterogeneity in reproductive potential (Bardsen, Tveraa, Fauchald, & Langeland, 2010; Weladji et al., 2008), some found measurable fitness costs, usually expressed as reduced reproductive performance the year after a juvenile or litter was weaned. Most costs were induced by lactation rather than gestation (Froy, Walling, Pemberton, Clutton-Brock, & Kruuk, 2016). As expected given the much higher reproductive value of mothers compared to juveniles (Gaillard & Yoccoz, 2003), survival costs of reproduction for mothers are rare, but have been reported for both red deer (*Cervus elaphus*) and feral sheep (Clutton-Brock et al., 1996; Froy et al., 2016). Survival costs have also been reported in pinnipeds (Desprez et al., 2014; Hadley, Rotella, & Garrott, 2007).

Fitness costs of reproduction derive from resource limitation. For example, in feral sheep, costs of reproduction are greatest when resources are scarce, both at the individual level and at the population level (Tavecchia et al., 2005). In Alpine ibex (*Capra ibex*), costs of reproduction decrease for females released into unoccupied habitat, where forage is likely more abundant (Rughetti, Dematteis, Meneguz, & Festa-Bianchet, 2015). Kangaroos terminate lactation if they cannot gain sufficient resources to maintain body mass (Gélin, Wilson, Cripps, Coulson, & Festa-Bianchet, 2016). Moreover, primiparous or young mothers are often smaller than multiparous ones (Martin & Festa-Bianchet, 2012). They may suffer greater fitness costs of reproduction than older females because they sustain at the same time the energetic costs of reproduction and of their own growth (Clutton-Brock, Guinness, & Albon, 1983; Green & Rothstein, 1991; Tavecchia et al., 2005).

In male mammals, reproduction has been associated with costs such as reduced feeding time, increased effort in searching for mates or injuries from fighting. For instance, studies of harvested male ungulates reveal substantial mass loss during the rut (Forsyth, Duncan, Tustin, & Gaillard, 2005; Mason et al., 2012; Yoccoz, Mysterud, Langvatn, & Stenseth, 2002). Very few studies, however, have addressed whether these energetic costs lead to fitness costs in terms of survival or future reproduction. Only 3 of 12 studies on this topic detected fitness costs of reproduction in males (Hamel et al., 2010). Experimental evidence from castrated feral sheep suggested a strong survival cost of competing for reproduction (Stevenson & Bancroft, 1995), but this study did not quantify a relationship between siring success and fitness costs. In polygynous mammals, mating success is largely driven by intrasexual competition (Preston, Stevenson, Pemberton, Coltman, & Wilson, 2003). Consequently, males face greater uncertainty over the benefits of a given allocation than over its costs, and the correlation between reproductive effort

and success is likely much weaker in males than that in females. Siring success in moose (*Alces alces*) is related to early development, suggesting that heterogeneity in reproductive potential is also important for males, but it is mostly determined by competitiveness (Markussen et al., 2018). Because very few studies measured both siring success and mating effort, it is difficult to distinguish between a cost of reproduction and a cost of trying to reproduce (Festa-Bianchet, 2012).

3 | THE FIELD STUDIES

Our studies in Alberta, Canada (Figures S1–S5), monitored thousands of marked individuals over decades. All were motivated by conservation concerns, and initiated either by or in collaboration with provincial wildlife biologists. Our basic procedure was to mark all animals and monitor survival, growth and reproduction from birth to death.

The Ram Mountain bighorn sheep program began in 1971 when biologists from Alberta Fish & Wildlife assembled a corral trap (Figure 1) to recapture sheep multiple times between late May and early October. All yearling and adult females, and over 95% of adult males, have been marked since 1975. In the last three decades, over 80% of adult females were recaptured three times or more each year. This study initially simulated a hunting season on females. Annual removal of 14%–32% of females from 1972 to 1980 (Jorgenson, Festa-Bianchet, & Wishart, 1993) provided an experimental manipulation of density, age structure and the duration of maternal care, leading to insights into evolutionary and population ecology (Festa-Bianchet, Jorgenson, & Wishart, 1994; Jorgenson et al., 1993). After 1981, the population increased, peaked in 1992 and then declined (Figure 2). Another 14 ewes were removed in 1997. Numbers declined rapidly in 1997–2001, partly because of cougar (*Puma concolor*) predation (Festa-Bianchet et al., 2006), then stagnated at about 40 for several years. Thirty-two sheep were transplanted to



FIGURE 1 Clockwise from top left: the bighorn sheep trap at Ram Mountain, mountain goats near box traps and a remotely controlled weigh scale at Caw Ridge, a mountain goat female and a kid, and a group of bighorn rams at Sheep River, Alberta, Canada. Photos by M. Festa-Bianchet, F. Dulude-deBroin, E. Bélanger, F. Pelletier

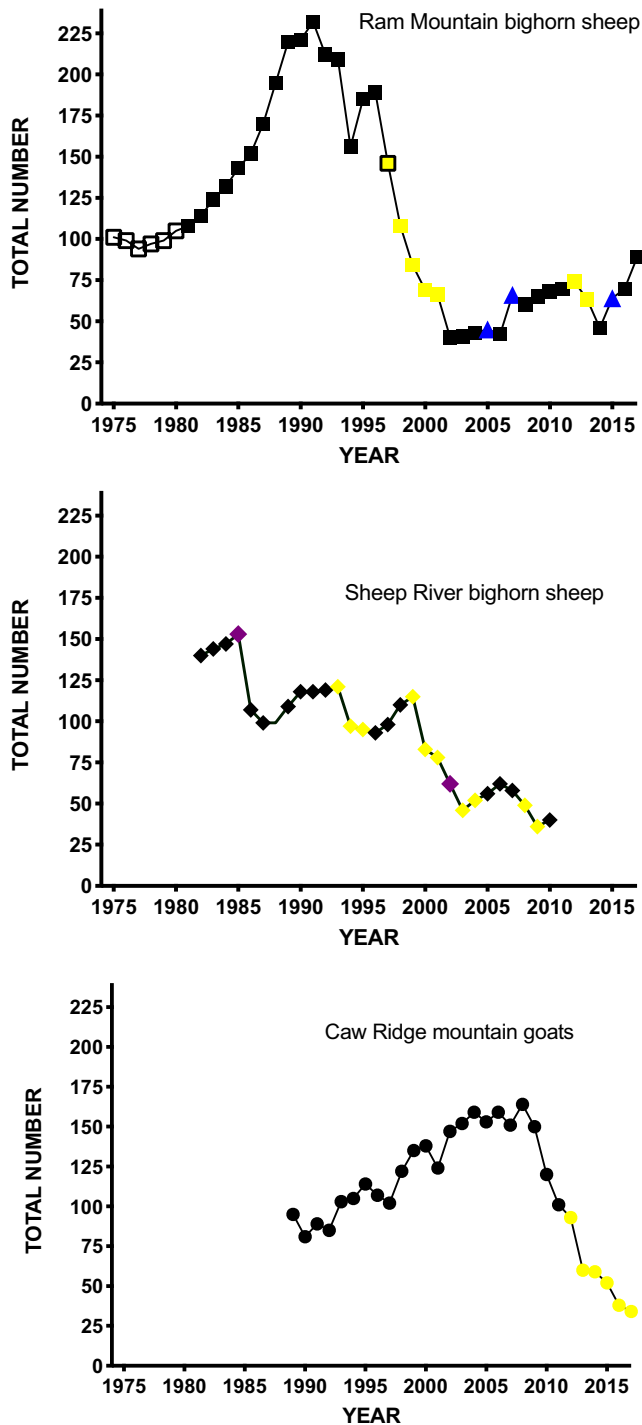


FIGURE 2 Size of three study populations of mountain ungulates in Alberta, Canada, based on total counts in June for Ram Mountain and Caw Ridge, in March for Sheep River. Yellow symbols indicate years of high cougar predation. At Ram Mountain, open symbols indicate experimental female removals (1997 coincided with the start of a predation episode), blue triangles transplants into the population. At Sheep River, purple symbols indicate pneumonia epizootics

Ram Mountain between 2003 and 2015, from a population about 130 km to the north-west (Poirier, Coltman, Pelletier, Jorgenson, & Festa-Bianchet, 2019). Trophy hunting ended in 2010 (Pigeon,

Festa-Bianchet, Coltman, & Pelletier, 2016); 64 males were shot between 1972 and 2007. There was no legal hunting of females, and only one was known to be poached. We attempted an experiment with contraceptive implants in 1996–1997, but soon after the population crashed (Festa-Bianchet et al., 2006). Of 10 contracepted females, six never reproduced again, mostly because of high mortality. The experiment produced no useful data. The Ram Mountain study has monitored 1,175 bighorn sheep. Over 11,000 captures produced data on seasonal and lifetime changes in mass. Ewe captures in late May and early June allow direct inspection of lactation status, providing information on neonatal mortality. The Ram Mountain population is demographically but not genetically isolated. There is a small population on Shunda Mountain, about 4 km away across the North Saskatchewan River. At least nine males born on Ram Mountain were later seen or shot on Shunda.

Other populations in the Rocky Mountains are separated by about 30 km of unsuitable habitat, mostly coniferous forest. Permanent immigration is rare: over 44 years, we documented one female and five male immigrants. In some years, however, many lambs are sired by non-resident rams that arrive for the rut, as typical of bighorn sheep (Hogg, 2000).

The Sheep River bighorn sheep program began because of concerns about pneumonia, an exotic disease transmitted from domestic sheep (Cassirer et al., 2018). Lungworms (*Protostrongylus* spp.) were then thought to be one cause of pneumonia (Samson, Holmes, Jorgenson, & Wishart, 1987). Wildlife managers were concerned that high population density and an early return to the winter range in autumn could increase lungworm infection. A marking program to monitor migratory behaviour and lungworm infection began in 1981. By 1985, all adult ewes were marked. Nearly all sheep were only captured once, with a dart gun (Jorgenson, Samson, & Festa-Bianchet, 1990). In 2000–2010, however, an electronic platform scale baited with salt allowed us to weigh sheep without recapturing them (Bassano, Hardenberg, Pelletier, & Gobbi, 2003). A combination of pneumonia and cougar predation in the late 2000s led to a decrease in population size (Bourbeau-Lemieux, Festa-Bianchet, Gaillard, & Pelletier, 2011), fidelity to the winter range and monitoring effort. Here, we consider data collected between 1981 and 2010, when 787 sheep were marked and monitored. About 70% were captured at 3–6 months of age. Sheep River bighorns are part of a metapopulation, with substantial seasonal range overlap with other female groups and males roving up to 80 km searching for mating opportunities (Festa-Bianchet, 1986a, 1986b). In 1981–2010, the population was mostly demographically isolated. Non-resident rams arrived for the rut, while some resident rams left (Hogg, 2000). Trophy hunting of males with horns describing at least 4/5 of a curl (Festa-Bianchet, 1989b) was allowed outside the winter range, and a few permits were issued for females. In 1981–2010, 35 males and four females were legally harvested. At least 14 males were poached.

Research on mountain goats at Caw Ridge began with the marking of 17 individuals in 1987–1988. The first full field season was in 1989.

Again, the study was motivated by management concerns. Numbers of mountain goats in Alberta had declined, and the hunting season was closed in 1988. Managers were concerned about low juvenile survival; therefore, our initial objective was to measure juvenile mortality and identify its causes. Mountain goat females are more aggressive than females of most other ungulates (Fournier & Festa-Bianchet, 1995), and we investigated how social behaviour affects reproductive success (Côté & Festa-Bianchet, 2001). Mountain goats are more sensitive to human activities, including research, than bighorn sheep (Côté, 1996; Côté, Festa-Bianchet, & Fournier, 1998; Côté, Hamel, St-Louis, & Mainguy, 2013). We captured goats in traps baited with salt (Figure 1), but in 1998 we stopped trapping kids or lactating females (Côté et al., 1998). Since 2001, we weigh goats on platform scales baited with salt (Figure 1). The proportion of marked goats increased from 72% in 1990 to 87% in 1995. Kids were monitored through their association with marked mothers, and 98% of older goats were marked since 1993. As of 2018, 462 mountain goats have been marked. Population size increased from about 80–160 in the first 20 years of monitoring and then declined to about 30 during the last decade (Figure 2). Mountain goats appear more likely to disperse than bighorn sheep. We documented 17 immigrants, all males. At least 33 males emigrated, and possibly three females. Similar to bighorn sheep, some resident males left for the rut and non-residents arrived; therefore, the population was not genetically isolated. There was no sport hunting of mountain goats on Caw Ridge and no known cases of poaching.

In all populations, it was extremely rare for a marked animal to reappear after not having been seen during a field season. Most exceptions were emigrant male sheep that were seen or shot elsewhere (5 at Sheep River and 21 at Ram Mountain). For example, for bighorn sheep at Ram Mountain, the resighting probability was 95% for males and over 99% for females (Jorgenson, Festa-Bianchet, Gaillard, & Wishart, 1997; Loison, Festa-Bianchet, Gaillard, Jorgenson, & Jullien, 1999). Our annual estimates of population size are accurate because animals were seen multiple times each season.

Bighorn sheep and mountain goats share several characteristics (Table 1). Although there was a possible case of twinning at Ram Mountain and a definite one at Caw Ridge, litter size in both species was essentially fixed at 1. Both species require open foraging areas near escape terrain in summer and relatively snow-free areas near escape terrain in winter. Those habitat requirements generate a

patchy distribution and often lead to seasonal migrations (Merkle et al., 2016). Both sexes are philopatric and use rocks and cliffs to avoid courting predators such as wolves (*Canis lupus*), coyotes (*Canis latrans*) and grizzly bears (*Ursus arctos*) (Figures S2–S3). That tactic relies on tradition, with well-marked trails between feeding areas and seasonal ranges. Consequently, the size of a population's range is mostly independent of density (Festa-Bianchet & Côté, 2008) so that population size and density are equivalent. Females rarely venture far from escape terrain. All females in a population use the same home range (Festa-Bianchet & Côté, 2008; Festa-Bianchet, 1986a, 1991), so that differences in survival and reproduction cannot be attributed to forage characteristics within individual home ranges, unlike in species where individuals have distinct home ranges (McLoughlin et al., 2007).

As with any research, our study has limitations. First, field work was year-round at Sheep River, but at Caw Ridge and Ram Mountain it was usually limited to May–September. For three years, however, goats were also observed during the rut, in November and early December. Second, we rarely knew natural causes of death because few carcasses were found, especially of juveniles. Third, as population sizes declined (Figure 2), small sample sizes limited statistical power. Our study populations, however, are representative of most mountain ungulate populations in North America, which typically exist in small patches of suitable habitat and rarely exceed 250 individuals. Finally, our research relies on correlative evidence: we compare reproductive allocation or success in consecutive years by the same individuals, accounting for potential confounding variables such as density, environmental conditions, female mass and mass changes, offspring sex and mass. Although those variables partly reflect individual reproductive potential, ideally the costs of reproduction should be measured by manipulating individual reproductive effort.

4 | DETECTING COSTS OF REPRODUCTION DESPITE INDIVIDUAL HETEROGENEITY

Our research suggests that females modulated allocation to reproduction based on reproductive potential (van Noordwijk & de Jong, 1986). Repeatedly, we found positive correlations among fitness components, rather than the negative correlations predicted by

Traits	Mountain goats	Bighorn sheep (SR)	Bighorn sheep (RM)
Age of primiparity	4.7 (3.7–5.5)	3.2 (2.1–5.6)	3.3 (2.2–5.5)
Survival to 1 year, both sexes	0.56 (0.19–0.92)	0.35 (0.07–0.73)	0.47 (0.09–0.80)
Yearling survival, both sexes	0.83 (0.50–1.00)	0.81 (0.50–1.00)	0.80 (0.20–1.00)
Prime-aged female survival	0.90 (0.65–1.00)	0.91 (0.63–1.00)	0.92 (0.74–1.00)
Max female longevity	18	18	19
Max male longevity	15	13	14
Peak mass, females (kg)	84 (72–87)	77 (75–79)	71 (68–74)
Peak mass, males (kg)	116 (103–134)	134 (124–141)	105 (99–111)

TABLE 1 Life-history characteristics of bighorn sheep and mountain goats. For age of primiparity and survival, the mean and annual range are presented. “Prime age” is 2–9 years for mountain goats and 2–7 years for bighorn sheep. “Peak mass” is the estimated maximum mass in summer, averaged for females aged 4–12 years and for males aged 5–12 years. The range for mass is among annual age classes. Sheep River (SR) and Ram Mountain (RM) are two bighorn sheep study areas

life-history theory (Stearns, 1992). Those correlations were largely explained by individual differences likely associated with reproductive potential, mainly body mass and age. At Ram Mountain, for females that survived to at least 8 years, mass at age 6 explained 24% of variability in longevity (Bérubé, Festa-Bianchet, & Jorgenson, 1999). Females that died before age 11 were 6% lighter than those that survived to 11 years or older. The same study found no negative effect of reproductive success at 2–7 years of age on longevity or on reproductive success later in life. Instead, it found positive relationships, which became not statistically significant when changes in density were accounted for (Bérubé et al., 1999). At Sheep River, ewes primiparous at 2 years were more likely to reproduce again at age 3 than ewes that did not reproduce at age 2 (Festa-Bianchet, 1989a). Effects of reproductive potential were evident also at the individual level: at Ram Mountain, ewes had higher reproductive success in years when they were heavier than their long-term average mass, suggesting that they were in better condition (Festa-Bianchet, 1998). After accounting for female mass, previous reproductive success and population density, female identity as a random variable still explained a significant proportion of variance in reproductive success, suggesting individual heterogeneity in reproductive potential (Festa-Bianchet, Gaillard, & Jorgenson, 1998). At high density, survival was lower for older (8–14 years) ewes that did not reproduce than for those that reproduced, suggesting that some ewes in poor condition died despite allocating all resources to maintenance (Festa-Bianchet et al., 1998). The same study reported that fertility of multiparous ewes increased if they had produced a lamb the previous year. Martin and Festa-Bianchet (2010) found that maternal effort and overwinter survival were correlated at Ram Mountain. At Sheep River, ewe longevity was positively correlated with reproductive success up to age 9, which was in turn correlated with reproductive success after age 9 (Festa-Bianchet & King, 2007). At Ram Mountain, early primiparity did not reduce longevity and was positively associated with lifetime reproductive success (Martin & Festa-Bianchet, 2012). High density at birth reduced both longevity and lifetime reproductive success, particularly when density during adulthood was also high (Pigeon & Pelletier, 2018). In mountain goats (Panagakis, Hamel, & Côté, 2017), heavier and dominant females tended to attain primiparity earlier and had higher reproductive success early in life. Early primiparity and reproductive success were both positively related to late reproductive success. Clearly, females allocated resources to reproduction when they could afford to do so.

Costs of reproduction became more evident when an individual index of reproductive potential, described mostly by mass and longevity, was taken into account. In mountain goats (Figure 3f), heavy and dominant females showed no cost of reproduction, whereas light and subordinate females that gave birth had a lower probability of reproducing the following year compared with non-reproductive females (Hamel, Côté, Gaillard, & Festa-Bianchet, 2009). For the heaviest bighorn ewes, no cost of reproduction was detectable (Festa-Bianchet et al., 1998; Hamel et al., 2009). Our study animals had a fixed litter size of one, and therefore, changes in litter size were not part of their reproductive tactic. It is likely that, for those

in good condition, the energetic costs of lactation were entirely recovered by foraging during summer. Lactating mountain goats spent more time grazing and more time ruminating while lying compared to non-lactating females (Hamel & Côté, 2008). Mass, however, was not the sole determinant of reproductive potential, as cohort effects on reproductive success remained substantial even after differences in mass were accounted for, generating positive correlations between survival and reproduction (Pigeon, Festa-Bianchet, & Pelletier, 2017). Early environmental conditions also affected variation in female reproductive potential of cohorts of both species (Hamel et al. 2009).

5 | THE CONSERVATIVE REPRODUCTIVE TACTIC OF FEMALE CAPITAL BREEDERS: TRANSFER COSTS TO OFFSPRING

Bighorn sheep and mountain goat females show the typical age-specific survival pattern of most ungulates (Gaillard, Viallefont, Loison, & Festa-Bianchet, 2004): those surviving to the age of primiparity experience 5–7 years of annual survival near 90% and then 3–5 years of survival well over 50% (Loison et al., 1999). Adult survival is mostly independent of weather or population density, but can be reduced by predation (Bourbeau-Lemieux et al., 2011; Festa-Bianchet et al. 2006) or disease (Cassirer et al., 2018). Juvenile survival, instead, varies with density, weather and predation (Gaillard, Festa-Bianchet, & Yoccoz, 1998). Consequently, the reproductive value of mothers is much higher than that of juveniles, and females are expected to restrain allocation to reproduction so as not to compromise their own survival, possibly leading to environmental canalization of a conservative reproductive tactic (Gaillard & Yoccoz, 2003). Our research supports that expectation. The only survival cost of reproduction we documented was during a pneumonia epizootic at Sheep River: young ewes that first reproduced as 2-year-olds were more likely to die than ewes that had postponed primiparity (Festa-Bianchet, 1989a) (Figure 3c). Apparently, ewes that allocated resources to reproduction before completing growth had a weaker immune response and were killed by an exotic disease. A similar disease-induced cost of reproduction was reported for female Alpine ibex (Garnier, Gaillard, Gauthier, & Besnard, 2016). Allocation to reproduction appeared to reduce resistance to parasites, as lactating ewes shed more lungworm larvae than non-lactating ones (Festa-Bianchet, 1989a; Pelletier, Page, Ostiguy, & Festa-Bianchet, 2005). We did not detect any other survival costs of reproduction for either bighorn sheep (Festa-Bianchet et al., 1998) or mountain goats (Hamel, Côté, & Festa-Bianchet, 2010). Reproduction reduced mass gain: young and senescent lactating ewes gained less mass during summer than non-lactating ones (Martin & Festa-Bianchet, 2010) and young lactating mountain goats gained less mass than non-lactating ones (Hamel & Côté, 2009). Those somatic costs, however, did not affect survival.

Nearly all maternal fitness costs of reproduction were transferred to the subsequent offspring (Figure 3). Females appeared to allocate resources to reproduction only if that allocation did not compromise their survival or growth, with important consequences for individual

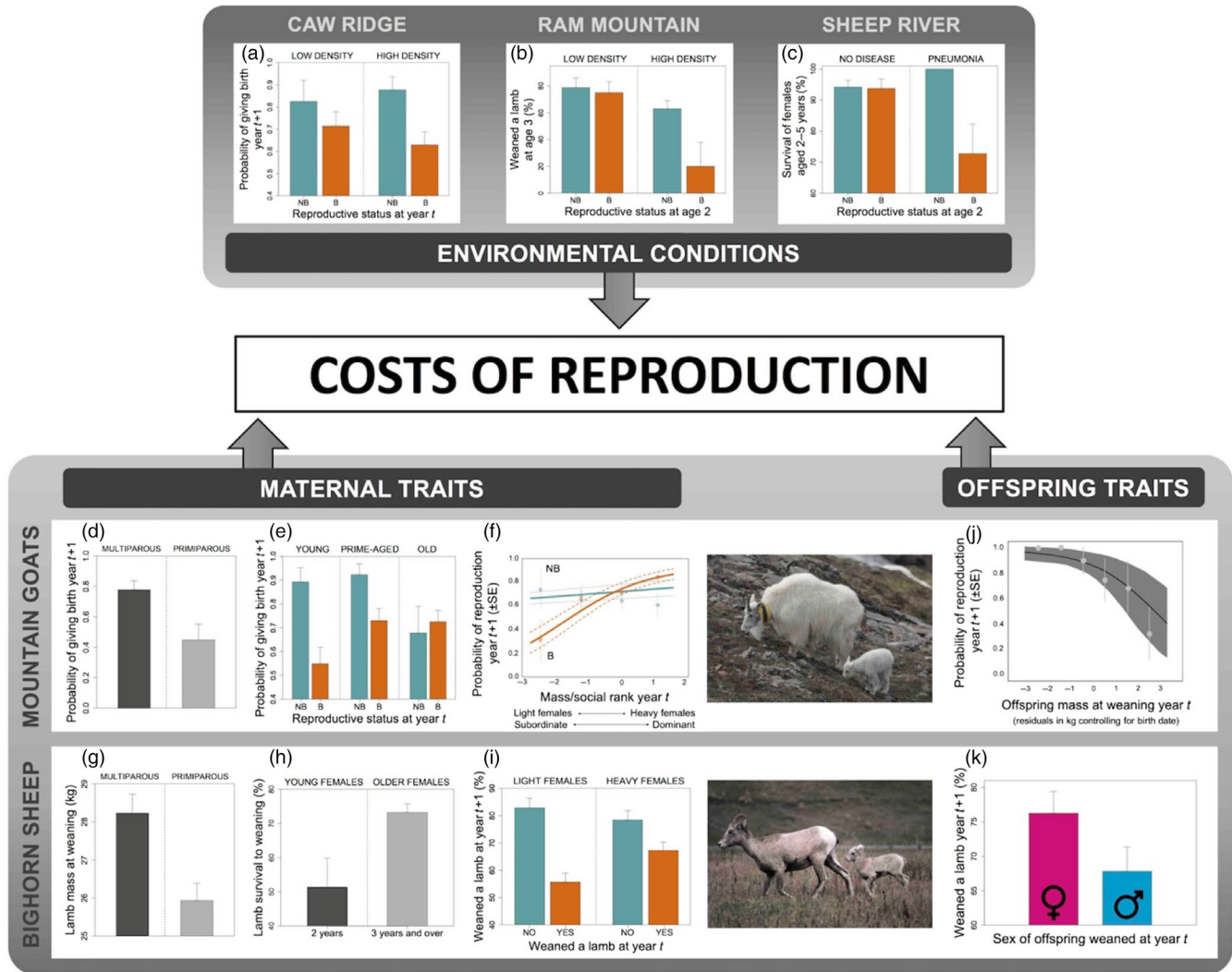


FIGURE 3 Costs of reproduction in three populations of mountain ungulates according to environmental conditions (a, b: population density; c: pneumonia), maternal traits (d, g: primiparity; e, h: age, f, i: mass/social rank) and offspring traits (j: weaning mass; k: sex). Green: non-breeding females (NB); brown: breeding females (B). Panels with percentages report standard errors as $\sqrt{p(1-p)/n}$, where p is the proportion and n the total sample size for each category. Other panels include standard errors from model estimations. In addition, panels f and j show the mean and SE of the raw data in discretized intervals of the covariate. Note that panels are not on the same scale. [a: adapted from Hamel, Côté, & Festa-Bianchet, 2010; b, h: adapted from Festa-Bianchet et al., 1995; c: adapted from Festa-Bianchet, 1989a; d, e: reproduced from Hamel, Côté, & Festa-Bianchet, 2010; f: reproduced from Hamel et al. 2009; g: reproduced from Martin & Festa-Bianchet, 2012; i: adapted from Festa-Bianchet et al., 1998; j: adapted from Hamel et al., 2011; k: adapted from Bérubé et al., 1999.]

fitness and population dynamics. Ewes that were small as yearlings prolonged growth and nearly caught up in mass with larger ewes by the age of 7, by both delaying primiparity and reducing allocation to maternal care, as suggested by the lower survival of their lambs (Marcil-Ferland, Festa-Bianchet, Martin, & Pelletier, 2013). Similarly, female goats that were light as juveniles caught up in mass over a few years by delaying reproduction and lowering reproductive effort compared to heavy juveniles (Hamel, Yoccoz, & Gaillard, 2017). Bighorn ewes decreased reproductive allocation in response to both resource scarcity and previous reproductive effort: they first ensured their own summer mass gain and allocated only surplus energy to their young (Martin & Festa-Bianchet, 2010). Heavier ewes, which have a greater reproductive potential, were less likely to decrease

lamb weaning mass with increasing density (Réale & Festa-Bianchet, 2000). As density increased, ewes allocated fewer resources to reproduction and more to growth or maintenance. Those changes in allocation led to the somewhat paradoxical result of heavier adult mass at high density for ewes born at intermediate or high density (Pigeon & Pelletier, 2018). This conservative reproductive tactic has important consequences for population dynamics, because females delay primiparity and reduce maternal care when resources are scarce, leading to lower recruitment (Festa-Bianchet, Jorgenson, Bérubé, Portier, & Wishart, 1997; Martin & Festa-Bianchet, 2012). Fitness costs in bighorn sheep were mostly expressed through reduced lamb survival, as 92% of ewes aged 3 years and older lactated (Pigeon & Pelletier, 2018). In mountain goats, multiparous females

skipped reproduction in about 22% of years, and fitness costs included reproductive pauses (Hamel, Côté, & Festa-Bianchet, 2010). Reproduction had no effect on summer survival of kids the following year, but kids whose mothers had skipped reproduction the previous year were 2.5 times more likely to survive the winter than kids whose mothers had reproduced (Hamel, Côté, & Festa-Bianchet, 2010).

6 | COSTS ARE CONTEXT-DEPENDENT

The costs of reproduction increase when resources are scarce. For bighorn sheep, the reduction in weaning success the year after weaning a lamb was greater for lighter ewes (Figure 3i), increased with population density (Figure 3b) and peaked for light ewes at high density (Festa-Bianchet et al., 1998). Differences in costs of reproduction among populations also appeared related to body mass, which likely reflects reproductive potential. Ewes at Sheep River are about 10% heavier than at Ram Mountain (Table 1). Reproductive costs were detected at Ram Mountain but were much less evident at Sheep River (Festa-Bianchet, 1989a) that never experienced the high density recorded at Ram Mountain. It seems likely that most ewes at Sheep River had the same high reproductive potential as the largest ewes at Ram Mountain, for which we could not detect any reproductive costs (Hamel et al., 2009). As the Ram Mountain population doubled (Figure 1), summer mass gain by lactating ewes decreased by 9%, but the mass gain of lambs decreased by 22%, likely explaining why lamb mortality was strongly density-dependent while ewe mortality was not (Festa-Bianchet & Jorgenson, 1998). We found similar context-dependent changes for mountain goats, where fitness costs of reproduction could only be detected at high density (Figure 3a). At peak density, weaning a kid reduced reproductive success the following year by 25% (Hamel, Côté, & Festa-Bianchet, 2010).

7 | AGE MODULATES COSTS OF REPRODUCTION: PRIMIPARITY AND SENESCENCE

Young females experienced high reproductive costs, likely because they bore the energetic costs of reproduction while completing body growth (Figure 3h). As mentioned above, young ewes at Sheep River had higher mortality during a pneumonia epizootic if they had been primiparous at age 2 (Festa-Bianchet, 1989a). At Ram Mountain, ewes primiparous at age 2 were lighter at age 4 than ewes that postponed primiparity, but did not show a reduction in subsequent reproductive success. When density increased, 2-year-old ewes stopped reproducing (Festa-Bianchet, Jorgenson, Lucherini, & Wishart, 1995), suggesting strong selection against early primiparity when environmental conditions deteriorate. The effects of density on primiparity were somewhat independent of mass: at low density, most yearling ewes that weighed 50 kg lactated at age two, but yearlings that weighed 50 kg at high density delayed primiparity (Martin & Festa-Bianchet, 2012). Primiparous ewes lost about 15%

more mass overwinter during gestation compared to multiparous females, and gained about 6% less mass than multiparous females over the summer while lactating. By age 6, however, ewe mass was independent of age at primiparity (Martin & Festa-Bianchet, 2012). Primiparous ewes also weaned smaller lambs (Figure 3g; Martin & Festa-Bianchet, 2012). In mountain goats, the probability of parturition was 4.5 times greater for multiparous females than for those that were primiparous the previous year (Figure 3d). Primiparity, however, had no detectable effects on survival of either mothers or offspring (Hamel, Côté, & Festa-Bianchet, 2010). Costs of reproduction were not detected in female goats older than 9 years (Figure 3e).

The onset of reproductive senescence in both species occurs at about 13 years, 4–5 years after the start of actuarial senescence (Festa-Bianchet & Côté, 2008; Festa-Bianchet & King, 2007; Jorgenson et al., 1997). Older females appear to reduce allocation to reproduction and, as reported in chamois (*Rupicapra rupicapra*) (Morin, Rughetti, Rioux-Paquette, & Festa-Bianchet, 2016) and ibex (Rughetti et al., 2015), there may be more variability in reproductive potential among senescent than prime-aged females. Older females appear increasingly conservative in their reproductive allocation, with a greater frequency of reproductive pauses. Bighorn ewes are less likely to reproduce as they approach death, and, independently of age at death, their reproductive effort decreases in the last 2 years of life (Martin & Festa-Bianchet, 2011a). In addition, older females reduce allocation to sons, possibly to avoid survival costs (Martin & Festa-Bianchet, 2011b). In mountain goats, survival of females aged 10 years and older was positively correlated with offspring weaning mass. Apparently, some older females in deteriorating condition were unable to provide much maternal care and then died the following winter (Hamel, Côté, & Festa-Bianchet, 2011).

8 | SONS ARE COSTLIER, BUT ADAPTIVE SEX RATIO MANIPULATION IS RARE

In sexually dimorphic mammals, sons tend to be heavier at birth and at weaning, require more maternal care and often lead to greater reproductive costs than daughters (Froy et al., 2016; Hogg, Hass, & Jenni, 1992). Sexual dimorphism at weaning is 10% in bighorn sheep and 6% in mountain goats (Festa-Bianchet & Côté, 2008). We found more consistent evidence of a greater fitness cost of sons than of daughters in sheep than in goats. At Sheep River, ewes shed more lungworm larvae in faeces after weaning a son than after weaning a daughter (Festa-Bianchet, 1989a). In both sheep populations, survival to weaning was about 10%–12% lower if the mother had weaned a son the previous year than if she had weaned a daughter (Figure 3k). At Ram Mountain, the differential cost of sons increased with density: survival to 1 year of lambs born following a brother compared to survival following a sister was 82% at low density, but only 43% at high density (Bérubé, Festa-Bianchet, & Jorgenson, 1996). Lamb sex had no effects on maternal survival, but lambs born after a brother had lower summer mass gain than lambs born after a sister (Martin &

Festa-Bianchet, 2010). In mountain goats, there was no differential cost of reproduction according to offspring sex at birth (Hamel et al., 2011), but there may be a greater cost of sons that survive the winter, as 35% of mothers of yearling males but only 17% of mothers of yearling females skipped reproduction the following year (Charest-Castro, Leblond, & Côté, 2018). The interspecific difference in the cost of sons may be related to the much greater frequency of prolonged maternal care in mountain goats that frequently nurse yearlings of both sexes, compared to bighorn sheep that usually wean their lambs in late autumn (Figure 4 and Section 9). Offspring sex ratio in early life, however, did not affect longevity in either species (Douhard, Festa-Bianchet, Hamel, et al., 2019).

Bighorn ewes avoid producing sons in consecutive years unless they are in good condition (Douhard, Festa-Bianchet, & Pelletier, 2016). In addition, under favourable environmental conditions, senescent ewes produce more daughters, while when conditions are poor they produce more sons but skip more reproductive opportunities (Martin & Festa-Bianchet, 2011b). Overall, however, despite fitting the assumptions of the Trivers-Willard theory for adaptive offspring sex ratio manipulation (Trivers & Willard, 1973), neither species shows the predicted manipulation of offspring sex ratio (Blanchard, Festa-Bianchet, Gaillard, & Jorgenson, 2004; Hamel, Festa-Bianchet, & Côté, 2016).

9 | COSTS OF PROTRACTED MATERNAL CARE AND LONG-TERM COSTS

The duration of maternal care is an important topic in evolutionary biology because it can affect fitness and may involve a parent-offspring conflict (Trivers, 1974). The strong seasonality of the Canadian Rockies likely truncates maternal care: in autumn, forage quality drops and mothers appear to stop producing milk (Festa-Bianchet, 1988). If the offspring survives the winter, however, its reproductive value increases substantially, as yearling survival is much higher than juvenile survival (Gaillard, Festa-Bianchet, Yoccoz, Loison, & Toïgo, 2000). Therefore, in some circumstances the best maternal tactic may be to continue caring for a yearling rather than produce a new offspring. Our results on prolonged maternal care suggest that it is a form of “making the best of a bad job”.

Bighorn sheep mothers usually do not associate with their yearlings (Festa-Bianchet, 1991). At high population density at Ram Mountain, however, a few ewes continued to care for their yearlings (L'Heureux, Lucherini, Festa-Bianchet, & Jorgenson, 1995). Most of these ewes had not produced a new lamb, and we detected no clear fitness benefits of prolonged association for yearlings. Extended care may have compensated for poor initial condition. In mountain goats, prolonged mother-offspring associations are frequent

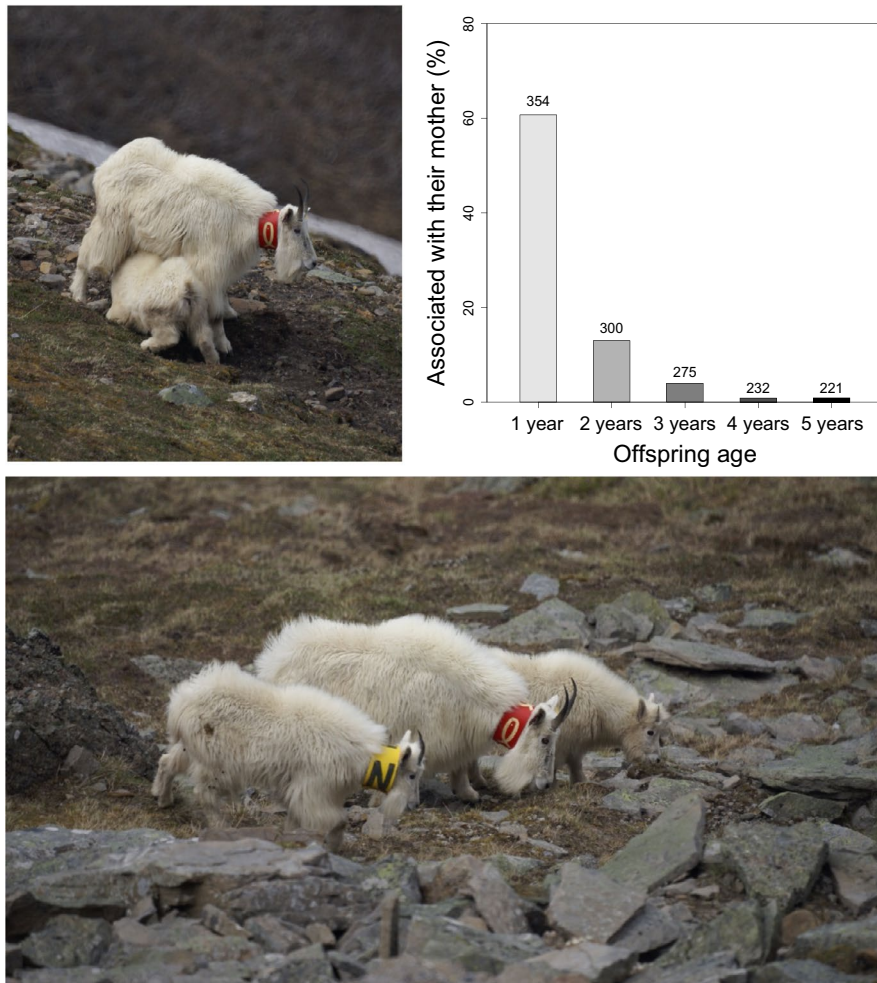


FIGURE 4 Prolonged mother-offspring associations in mountain goats (sample sizes above each bar). Bottom: a 14-year-old female associated with her two-year-old and yearling daughters (2012, Caw Ridge). The yearling daughter is suckling in the top picture. The mother had given birth that year but her kid died. Photos by S. Hamel

(Figure 4). Mothers are more likely to associate with their yearling if they are not nursing a new kid, but association with 2-year-olds is independent of current reproduction. We found no evidence that association with a yearling or a 2-year-old reduced subsequent reproductive success. Prolonged associations did not increase offspring survival or growth, again suggesting that prolonged care may compensate for an initial disadvantage (Charest-Castro et al., 2018). We found no retroactive costs of reproduction: in mountain goats, reproduction did not affect the survival or growth of offspring born the previous year (Gendreau, Côté, & Festa-Bianchet, 2005).

10 | WHAT MECHANISMS LEAD TO COSTS OF REPRODUCTION IN FEMALES AND CAN THEY COMPENSATE?

Some fitness costs in females appeared to derive from somatic costs, as depleted body stores may reduce ability to reproduce in the subsequent year. Considerations of mass changes in relation to reproductive costs, however, must take into account that seasonal mass changes of 20%–30% are a normal part of the biology of bighorn sheep (Douhard, Guillemette, Festa-Bianchet, & Pelletier, 2018; Pelletier, Réale, Garant, Coltman, & Festa-Bianchet, 2007) and mountain goats (Festa-Bianchet & Côté, 2008). Changes in mass are not necessarily beneficial or detrimental. Mass changes are related to initial mass: some individuals show less mass loss because they have little mass to lose (Pelletier et al., 2007). We only measured mass changes in survivors, potentially creating an “invisible fraction” (Hadfield, 2008) if those that lost much mass died. In bighorn sheep, mass loss overwinter, both relative and absolute, is under positive selection, presumably because ewes that gain more resources in summer then use them in winter for both maintenance and reproduction (Pelletier et al., 2007). Nevertheless, we did find evidence that mass loss, presumably reflecting energetic costs, sometimes led to fitness costs. Bighorn ewes lost more mass in winter when their lamb survived to 1 year. That somatic cost of reproduction may have led to their lower subsequent reproductive success (Festa-Bianchet, 1998). Mass gain by lambs was lower if their mother had lost relatively more mass over the previous winter (Douhard et al., 2018). At high density at Ram Mountain, ewes that weaned lambs tended to lose mass, or gain less mass, from one autumn to the next compared to ewes that did not wean lambs (Festa-Bianchet et al., 1998). At low density, mountain goat mothers that weaned heavy kids had a lower probability of parturition the following year than mothers of lighter kids (Figure 3j), suggesting a direct trade-off between allocation to reproduction in subsequent years. At high density, however, that relationship disappeared as the probability of parturition decreased by more than half (Hamel et al., 2011). Bighorn ewes also showed a trade-off between allocation to reproduction in consecutive years, as weaning a lamb one year reduced the weaning mass of the sibling produced the following year by about 10% (Feder, Martin, Festa-Bianchet, Bérubé, & Jorgenson, 2008). Ewes that weaned a lamb

delayed their subsequent parturition by about a week, and late birth decreased lamb survival (Feder et al., 2008).

Although for both species reproduction partly relies upon stored somatic resources, forage intake during spring and summer also sustains lactation. Foraging behaviour was affected by reproductive effort. Lactating goats spent more time foraging and increased bite rate, resulting in a >40% increase in forage intake at the peak of lactation compared with non-lactating females (Hamel & Côté, 2008, 2009). They also increased time spent ruminating while resting and had a faster chewing rate than non-lactating females, likely allowing a faster forage processing rate. Mountain goats nursing sons spent more time foraging than those nursing daughters (Hamel & Côté, 2008), suggesting compensation for the greater energetic costs of sons, as reported in kangaroos (Gélin, Wilson, Coulson, & Festa-Bianchet, 2013). At Sheep River, lactating bighorn ewes spent more time foraging and had faster bite rates than non-lactating ewes, but compensation was only evident in autumn and there was no effect of lamb sex (Ruckstuhl & Festa-Bianchet, 1998). At Ram Mountain, lactating ewes had a faster ruminating rate than non-lactating ewes, suggesting a greater effort in food processing to compensate for the energetic costs of lactation (Blanchard, 2005).

11 | MALES: COST IS IN TRYING, NOT IN SUCCEEDING

Very few studies address the fitness costs of reproduction in male mammals. Several studies used mass loss to examine how male ungulates allocate resources to reproduction (Forsyth et al., 2005; Mason et al., 2012; Mysterud et al., 2008), but winter mass loss by bighorn males at Ram Mountain was independent of siring success (Douhard et al., 2018). At Sheep River, mating effort was unrelated to male overwinter survival, and longevity was positively correlated with mating effort at 2–5 years of age (Pelletier, Hogg, & Festa-Bianchet, 2006). In both species, dominant males adopt the highly successful, and possibly not very costly, tactic of serially defending single oestrous females (Hogg, 1988; Mainguy, Côté, Cardinal, & Houle, 2008). At Sheep River, males that defended oestrous ewes did not spend less time foraging than subordinate males that adopted the alternative and much less successful courting tactic (Pelletier, 2005). Mass loss during the rut was not correlated with rutting effort (Pelletier, 2005). Because large rams can satisfy their food requirements with less foraging time than smaller rams, they can devote more time to rutting activities. The difference in foraging time is substantial: in early autumn, a 60-kg male will forage for about 60% of the time, but a 130-kg male will spend only about 40% of its time foraging. Among rams aged 6 years and older, dominant ones spend less time foraging (31%) than subordinates (45%) (Pelletier & Festa-Bianchet, 2004). The energetic cost of attempting to reproduce appeared to compromise the immune system, as the faecal count of lungworm larvae during the rut was correlated with rutting effort (Pelletier et al., 2005).

Horn growth is associated with high rank and possibly high reproductive success in males (Martin, Festa-Bianchet, Coltman, &

Pelletier, 2016). There is little evidence that rapid horn growth carries a longevity cost. In bighorn sheep, adult male survival is independent of early horn growth, which is positively associated with yearling survival (Bonenfant, Pelletier, Garel, & Bergeron, 2009). The same is true in Alpine ibex, where early and later horn growth is correlated (Bergeron, Festa-Bianchet, Hardenberg, & Bassano, 2008). Horn growth appears associated with lowered survival only for very old ibex males that may be past their reproductive peak (Toigo, Gaillard, & Loison, 2013). When resources are scarce, small males appear to adopt a conservative tactic, by allocating preferentially to mass rather than to horn growth (Festa-Bianchet, Coltman, Turelli, & Jorgenson, 2004), as also reported for red deer (Myrseth, Meisingset, Langvatn, Yoccoz, & Stenseth, 2005). Therefore, our results suggest that successful males enjoy positive correlations among fitness components, as reported for moose (Markussen et al., 2018). That is not surprising because the key to male reproductive success is social dominance, achieved through large mass and horn size in bighorns (Martin et al., 2016; Pelletier & Festa-Bianchet, 2006) and mostly body mass in mountain goats (Mainguy, Côté, Festa-Bianchet, & Coltman, 2009). Fitness costs in males are more likely to derive from attempts to achieve high dominance status than from the reproductive consequences of high rank.

In bighorn sheep, males with rapidly growing horns were at risk of hunting mortality, leading to an evolutionary decrease in horn size over time (Pigeon et al., 2016). Hunting re-distributed siring success among survivors of the hunting season and shortened the life expectancy of males that would likely have been successful breeders in its absence (Festa-Bianchet & Myrseth, 2018), thereby possibly limiting our ability to measure reproductive costs. Trophy hunting also led to a negative correlation between early development and longevity (Douhard, Festa-Bianchet, Landes, & Pelletier, 2019) because males that developed under favourable conditions were shot at a younger age, as reported in other populations of mountain sheep (Douhard, Festa-Bianchet, Pelletier, Gaillard, & Bonenfant, 2016; Hengeveld & Festa-Bianchet, 2011).

12 | CONCLUSIONS

Long-term studies of wild animals have advanced our understanding of ecology, evolution and conservation (Clutton-Brock & Sheldon, 2010b; Festa-Bianchet, Douhard, Gaillard, & Pelletier, 2017). Because few long-term studies are replicated, the potential effects of local differences are unknown. Our studies of mountain ungulates illustrate how costs of reproduction vary among populations. They also reveal some remarkable consistencies, such as the effects of resource availability, age and the transfer of costs to juveniles (Figure 3). Our 104 population-years of monitoring provide five main insights into fitness costs of reproduction in the wild. In females, (a) costs of reproduction are detectable, (b) vary with resource availability and (c) are mostly borne by juveniles. Changes in allocation to reproduction when resources are scarce (d) partly explain density dependence in population growth. In males, (e) costs

of reproduction are mostly driven by reproductive effort, not by siring success.

Individual differences in reproductive potential lead to an underestimate of reproductive costs in correlational studies. Our research, however, shows that by accounting for individual characteristics such as mass, field studies can obtain estimates of fitness costs that provide an understanding of their implications for evolutionary ecology and population dynamics in natural systems. We detected fitness costs of reproduction in the Ram Mountain population of bighorn sheep and in mountain goats. In contrast, most analyses of Sheep River bighorn sheep failed to reveal fitness costs. Two reasons could explain these inter-population differences. First, bighorn sheep at Sheep River never reached the density when reproduction appeared limited by resource availability and were instead limited by predation and disease. Second, we were better able to account for individual heterogeneity in reproductive potential at Ram Mountain and Caw Ridge because we measured mass of both mothers and offspring, and other variables such as social dominance in mountain goats.

The fitness costs of reproduction are shifted almost entirely from mothers to subsequent offspring, partly explaining why studies of ungulate population dynamics generally find that juvenile survival is highly variable from year to year and strongly affected by resource availability (Gaillard et al., 1998; Hamel et al., 2010). These results are as expected given that our study species are at the “slow” end of the life-history continuum (Hamel et al., 2010). Ungulate populations often show density dependence in age of primiparity and juvenile survival, while adult female survival is typically independent of population density (Bonenfant, Gaillard, et al., 2009). We suggest that reduced allocation to reproduction when resources are scarce is the main mechanism explaining differences in density dependence among vital rates (Bardson & Tveraa, 2012). In heavily hunted populations, maternal allocation may change if harvest leads to a very strong truncation of longevity. In brown bears (*Ursus arctos*), protection of family groups from sport hunting appears to favour females that keep their offspring for an extra year (Van de Walle, Pigeon, Zedrosser, Swenson, & Pelletier, 2018). In ungulates, we may expect greater allocation to reproduction if female life expectancy was drastically shortened. That evolutionary response has been frequently reported in fishes, but there is no evidence so far that it has occurred in hunted ungulates (Kuparinen & Festa-Bianchet, 2017). Harvest rates may be insufficient to shift the advantage in reproductive value from mothers to offspring. A key issue worthy of investigation is what proportion of variability in juvenile survival can be explained by maternal care. The higher that proportion, the stronger the selection for increased allocation to reproduction.

13 | NEXT STEPS

Our understanding of fitness costs of reproduction in wild mammals would be improved if heterogeneity in reproductive potential

was better estimated. Mixture models are one promising avenue because they allow considering individual reproductive potential by objectively classifying individuals into categories sharing similar early growth or life-history traits, while controlling for classification uncertainty and covariation among life-history traits (Descamps, Gaillard, Hamel, & Yoccoz, 2016; Hamel et al., 2018, 2017). Furthermore, joint models can also account for covariation among life-history traits (Cam, Link, Cooch, Monnat, & Danchin, 2002; Hamel et al., 2018), increasing our ability to detect reproductive trade-offs (Descamps et al., 2016). Although experimental manipulations, such as contraception, may provide clearer insights, they remain problematic because of the large sample required and the need to account for environmental variation. Our study populations are currently at low density and contraception would be counterproductive for other research goals.

More research is needed on the cumulative costs of reproduction (Kroeger, Blumstein, Armitage, Reid, & Martin, 2018), in combination with better quantification of individual differences in reproductive potential. Cumulative costs may elucidate the mechanisms of reproductive and survival senescence in both sexes (Moyes et al., 2006). In particular, we hope to investigate how females change reproductive allocation over multiple years in response to lactation-induced reductions in summer mass gain, accounting for the effects of offspring sex, maternal initial mass, resource availability and age (Martin & Festa-Bianchet, 2010). Finally, we expect that research on potential conflicts between parents on maternal allocation and offspring sex ratio will provide new insights into maternal allocation strategies and fitness costs of reproduction. The role of fathers in the allocation strategies of mammalian mothers has generally received little attention (Edwards & Cameron, 2014). Yet, our research suggests that paternal traits may affect not only the relative fitness of male and female offspring (Mainguy et al., 2009; Martin, Festa-Bianchet, Coltman, & Pelletier, 2014), but also maternal care according to offspring sex (Douhard, Festa-Bianchet, Coltman, & Pelletier, 2016). These results suggest that the costs of reproduction for females may be affected by characteristics of their mate (Sheldon, 2000), with important implications also for the study of mate choice. In particular, if maternal and paternal interests diverge, there is a potential for intersexual conflict (Douhard, Festa-Bianchet, Coltman, et al., 2016; Douhard, Festa-Bianchet, & Pelletier, 2016) with unknown consequences for the fitness costs of reproduction in females.

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AUTHORS' CONTRIBUTIONS

All authors contributed to the planning and execution of the field studies and to writing the manuscript. All gave final approval for publication.

DATA ACCESSIBILITY

This paper is a synthesis of previous publications and does not use new data.

ORCID

Marco Festa-Bianchet  <https://orcid.org/0000-0002-2352-3379>

Steeve D. Côté  <https://orcid.org/0000-0002-4875-1917>

Sandra Hamel  <https://orcid.org/0000-0003-1126-8814>

REFERENCES

- Archie, E. A., Altmann, J., & Alberts, S. C. (2014). Costs of reproduction in a long-lived female primate: Injury risk and wound healing. *Behavioral Ecology and Sociobiology*, *68*, 1183–1193.
- Bardsen, B. J., & Tveraa, T. (2012). Density-dependence vs. density-independence – linking reproductive allocation to population abundance and vegetation greenness. *Journal of Animal Ecology*, *81*, 364–376. <https://doi.org/10.1111/j.1365-2656.2011.01913.x>
- Bardsen, B. J., Tveraa, T., Fauchald, P., & Langeland, K. (2010). Observational evidence of risk-sensitive reproductive allocation in a long-lived mammal. *Oecologia*, *162*, 627–639. <https://doi.org/10.1007/s00442-009-1537-0>
- Bassano, B., Hardenberg, A. V., Pelletier, F., & Gobbi, G. (2003). A method to weigh free-ranging ungulates without handling. *Wildlife Society Bulletin*, *31*, 1205–1209.
- Bergeron, P., Festa-Bianchet, M., von Hardenberg, A., & Bassano, B. (2008). Heterogeneity in male horn growth and longevity in a highly sexually dimorphic ungulate. *Oikos*, *117*, 77–82. <https://doi.org/10.1111/j.2007.0030-1299.16158.x>
- Bérubé, C. H., Festa-Bianchet, M., & Jorgenson, J. T. (1996). Reproductive costs of sons and daughters in Rocky Mountain bighorn sheep. *Behavioral Ecology*, *7*, 60–68.
- Bérubé, C., Festa-Bianchet, M., & Jorgenson, J. T. (1999). Individual differences, longevity, and reproductive senescence in bighorn ewes. *Ecology*, *80*, 2555–2565. [https://doi.org/10.1890/0012-9658\(1999\)080\[2555:IDLARS\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[2555:IDLARS]2.0.CO;2)
- Blanchard, P. (2005). On lactation and rumination in bighorn ewes (*Ovis canadensis*). *Journal of Zoology*, *265*, 107–112. <https://doi.org/10.1017/S0952836904006077>
- Blanchard, P., Festa-Bianchet, M., Gaillard, J.-M., & Jorgenson, J. T. (2004). Maternal condition and offspring sex ratio in polygynous ungulates: A case study of bighorn sheep. *Behavioral Ecology*, *16*, 274–279. <https://doi.org/10.1093/beheco/arl153>

- Bonenfant, C., Gaillard, J. M., Coulson, T., Festa-Bianchet, M., Loison, A., Garel, M., ... Duncan, P. (2009). Empirical evidence of density-dependence in populations of large herbivores. *Advances in Ecological Research*, 41, 313–357.
- Bonenfant, C., Pelletier, F., Garel, M., & Bergeron, P. (2009). Age-dependent relationship between horn growth and survival in wild sheep. *Journal of Animal Ecology*, 78, 161–171. <https://doi.org/10.1111/j.1365-2656.2008.01477.x>
- Bourbeau-Lemieux, A., Festa-Bianchet, M., Gaillard, J. M., & Pelletier, F. (2011). Predator-driven component Allee effects in a wild ungulate. *Ecology Letters*, 14, 358–363. <https://doi.org/10.1111/j.1461-0248.2011.01595.x>
- Cam, E., Link, W. A., Cooch, E. G., Monnat, J. Y., & Danchin, E. (2002). Individual covariation in life-history traits: Seeing the trees despite the forest. *The American Naturalist*, 159, 96–105.
- Cassirer, E. F., Manlove, K. R., Almberg, E. S., Kamath, P. L., Cox, M., Wolff, P., ... Besser, T. E. (2018). Pneumonia in bighorn sheep: Risks and resilience. *Journal of Wildlife Management*, 82, 32–45.
- Charest-Castro, K., Leblond, M., & Côté, S. D. (2018). Costs and benefits of post-weaning associations in mountain goats. *Behaviour*, 155, 295–326. <https://doi.org/10.1163/1568539X-00003490>
- Clutton-Brock, T. H., Guinness, F. E., & Albon, S. D. (1983). The costs of reproduction to red deer hinds. *Journal of Animal Ecology*, 52, 367–383.
- Clutton-Brock, T. H., & Sheldon, B. C. (2010a). Individuals and populations: The role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology and Evolution*, 25, 562–573. <https://doi.org/10.1016/j.tree.2010.08.002>
- Clutton-Brock, T. H., & Sheldon, B. C. (2010b). The seven ages of *Pan*. *Science*, 327, 1207–1208. <https://doi.org/10.1126/science.1187796>
- Clutton-Brock, T. H., Stevenson, I. R., Marrow, P., MacColl, A. D., Houston, A. I., & McNamara, J. M. (1996). Population fluctuations, reproductive costs and life-history tactics in female Soay sheep. *Journal of Animal Ecology*, 65, 675–689.
- Côté, S. D. (1996). Mountain goat responses to helicopter disturbance. *Wildlife Society Bulletin*, 24, 681–685.
- Côté, S. D., & Festa-Bianchet, M. (2001). Reproductive success in female mountain goats: The influence of maternal age and social rank. *Animal Behavior*, 62, 173–181.
- Côté, S. D., Festa-Bianchet, M., & Fournier, F. (1998). Life-history effects of chemical immobilization and radio collars in mountain goats. *Journal of Wildlife Management*, 62, 745–752.
- Côté, S. D., Hamel, S., St-Louis, A., & Mainguy, J. (2013). Do mountain goats habituate to helicopter disturbance? *Journal of Wildlife Management*, 77, 1244–1248. <https://doi.org/10.1002/jwmg.565>
- Descamps, S., Boutin, S., McAdam, A. G., Berteaux, D., & Gaillard, J. M. (2009). Survival costs of reproduction vary with age in North American red squirrels. *Proceedings of the Royal Society B*, 276, 1129–1135. <https://doi.org/10.1098/rspb.2008.1401>
- Descamps, S., Gaillard, J. M., Hamel, S., & Yoccoz, N. G. (2016). When relative allocation depends on total resource acquisition: Implication for the analysis of trade-offs. *Journal of Evolutionary Biology*, 29, 1860–1866. <https://doi.org/10.1111/jeb.12901>
- Desprez, M., Harcourt, R. G., Hindell, M. A., Cubaynes, S., Gimenez, O., & McMahon, C. R. (2014). Age-specific cost of first reproduction in female southern elephant seals. *Biology Letters*, 10, 20140264. <https://doi.org/10.1098/rsbl.2014.0264>
- Douhard, M., Festa-Bianchet, M., Coltman, D. W., & Pelletier, F. (2016). Paternal reproductive success drives sex allocation in a wild mammal. *Evolution*, 70, 358–368. <https://doi.org/10.1111/evo.12860>
- Douhard, M., Festa-Bianchet, M., Hamel, S., Nussey, D. H., Côté, S. D., Pemberton, J. M., & Pelletier, F. (2019). Maternal longevity and offspring sex in wild ungulates. *Proceedings of the Royal Society B*, 286, 20181968. <https://doi.org/10.1098/rspb.2018.1968>
- Douhard, M., Festa-Bianchet, M., Landes, J., & Pelletier, F. (2019). Trophy hunting mediates sex-specific associations between early-life environmental conditions and adult mortality in bighorn sheep. *Journal of Animal Ecology*, 88(5), 734–745. <https://doi.org/10.1111/1365-2656.12970>
- Douhard, M., Festa-Bianchet, M., & Pelletier, F. (2016). Maternal condition and previous reproduction interact to affect offspring sex in a wild mammal. *Biology Letters*, 12, 20160510. <https://doi.org/10.1098/rsbl.2016.0510>
- Douhard, M., Festa-Bianchet, M., Pelletier, F., Gaillard, J. M., & Bonenfant, C. (2016). Changes in horn size of Stone's sheep over four decades correlate with trophy hunting pressure. *Ecological Applications*, 26, 309–321. <https://doi.org/10.1890/14-1461>
- Douhard, M., Guillemette, S., Festa-Bianchet, M., & Pelletier, F. (2018). Drivers and demographic consequences of seasonal mass changes in an alpine ungulate. *Ecology*, 99, 724–734. <https://doi.org/10.1002/ecy.2141>
- Edwards, A. M., & Cameron, E. Z. (2014). Forgotten fathers: Paternal influences on mammalian sex allocation. *Trends in Ecology and Evolution*, 29, 158–164. <https://doi.org/10.1016/j.tree.2013.12.003>
- Feder, C., Martin, J. G. A., Festa-Bianchet, M., Bérubé, C., & Jorgenson, J. (2008). Never too late? Consequences of late birthdate for mass and survival of bighorn lambs. *Oecologia*, 156, 773–781. <https://doi.org/10.1007/s00442-008-1035-9>
- Festa-Bianchet, M. (1986a). Seasonal dispersion of overlapping mountain sheep ewe groups. *Journal of Wildlife Management*, 50, 325–330. <https://doi.org/10.2307/3801922>
- Festa-Bianchet, M. (1986b). Site fidelity and seasonal range use by bighorn rams. *Canadian Journal of Zoology*, 64, 2126–2132. <https://doi.org/10.1139/z86-326>
- Festa-Bianchet, M. (1988). Nursing behaviour of bighorn sheep: Correlates of ewe age, parasitism, lamb age, birthdate and sex. *Animal Behavior*, 36, 1445–1454. [https://doi.org/10.1016/S0003-3472\(88\)80215-X](https://doi.org/10.1016/S0003-3472(88)80215-X)
- Festa-Bianchet, M. (1989a). Individual differences, parasites, and the costs of reproduction for bighorn ewes (*Ovis canadensis*). *Journal of Animal Ecology*, 58, 785–795. <https://doi.org/10.2307/5124>
- Festa-Bianchet, M. (1989b). Survival of male bighorn sheep in southwestern Alberta. *Journal of Wildlife Management*, 53, 259–263. <https://doi.org/10.2307/3801344>
- Festa-Bianchet, M. (1991). The social system of bighorn sheep: Grouping patterns, kinship and female dominance rank. *Animal Behaviour*, 42, 71–82. [https://doi.org/10.1016/S0003-3472\(05\)80607-4](https://doi.org/10.1016/S0003-3472(05)80607-4)
- Festa-Bianchet, M. (1998). Condition-dependent reproductive success in bighorn ewes. *Ecology Letters*, 1, 91–94. <https://doi.org/10.1046/j.1461-0248.1998.00023.x>
- Festa-Bianchet, M. (2012). The cost of trying: Weak interspecific correlations among life-history components in male ungulates. *Canadian Journal of Zoology*, 90, 1072–1085. <https://doi.org/10.1139/z2012-080>
- Festa-Bianchet, M., Coltman, D. W., Turelli, L., & Jorgenson, J. T. (2004). Relative allocation to horn and body growth in bighorn rams varies with resource availability. *Behavioral Ecology*, 15, 305–312. <https://doi.org/10.1093/beheco/arh014>
- Festa-Bianchet, M., & Côté, S. D. (2008). *Mountain goats: Ecology, behavior and conservation of a mountain ungulate*. Washington, DC: Island Press.
- Festa-Bianchet, M., Coulson, T., Gaillard, J. M., Hogg, J. T., & Pelletier, F. (2006). Stochastic predation and population persistence in bighorn sheep. *Proceedings of the Royal Society B-Biological Sciences*, 273, 1537–1543.
- Festa-Bianchet, M., Douhard, M., Gaillard, J. M., & Pelletier, F. (2017). Successes and challenges of long-term field studies of marked ungulates. *Journal of Mammalogy*, 98, 612–620. <https://doi.org/10.1093/jmammal/gyw227>

- Festa-Bianchet, M., Gaillard, J.-M., & Jorgenson, J. T. (1998). Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. *The American Naturalist*, *152*, 367–379.
- Festa-Bianchet, M., & Jorgenson, J. T. (1998). Selfish mothers: Reproductive expenditure and resource availability in bighorn ewes. *Behavioral Ecology*, *9*, 144–150. <https://doi.org/10.1093/behec/9.2.144>
- Festa-Bianchet, M., Jorgenson, J. T., Bérubé, C. H., Portier, C., & Wishart, W. D. (1997). Body mass and survival of bighorn sheep. *Canadian Journal of Zoology*, *75*, 1372–1379.
- Festa-Bianchet, M., Jorgenson, J. T., Lucherini, M., & Wishart, W. D. (1995). Life-history consequences of variation in age of primiparity in bighorn ewes. *Ecology*, *76*, 871–881. <https://doi.org/10.2307/1939352>
- Festa-Bianchet, M., Jorgenson, J. T., & Wishart, W. D. (1994). Early weaning in bighorn sheep, *Ovis canadensis*, affects growth of males but not of females. *Behavioral Ecology*, *6*, 21–27.
- Festa-Bianchet, M., & King, W. J. (2007). Age-related reproductive effort in bighorn sheep ewes. *Écoscience*, *14*, 318–322. [https://doi.org/10.2980/1195-6860\(2007\)14\[318:AREIBS\]2.0.CO;2](https://doi.org/10.2980/1195-6860(2007)14[318:AREIBS]2.0.CO;2)
- Festa-Bianchet, M., & Mysterud, A. (2018). Hunting and evolution: Theory, evidence, and unknowns. *Journal of Mammalogy*, *99*, 1281–1292. <https://doi.org/10.1093/jmammal/gyy138>
- Forsyth, D. M., Duncan, R. P., Tustin, K. G., & Gaillard, J.-M. (2005). A substantial energetic cost to male reproduction in a sexually dimorphic ungulate. *Ecology*, *86*, 2154–2163. <https://doi.org/10.1890/03-0738>
- Fournier, F., & Festa-Bianchet, M. (1995). Social dominance in adult female mountain goats. *Animal Behavior*, *49*, 1449–1459.
- Froy, H., Walling, C. A., Pemberton, J. M., Clutton-Brock, T. H., & Kruuk, L. E. B. (2016). Relative costs of offspring sex and offspring survival in a polygynous mammal. *Biology Letters*, *12*, 20160417. <https://doi.org/10.1098/rsbl.2016.0417>
- Gaillard, J.-M., Festa-Bianchet, M., & Yoccoz, N. G. (1998). Population dynamics of large herbivores: Variable recruitment with constant adult survival. *Trends in Ecology and Evolution*, *13*, 58–63. [https://doi.org/10.1016/S0169-5347\(97\)01237-8](https://doi.org/10.1016/S0169-5347(97)01237-8)
- Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N. G., Loison, A., & Toïgo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics*, *31*, 367–393. <https://doi.org/10.1146/annurev.ecolsys.31.1.367>
- Gaillard, J. M., Viallefont, A., Loison, A., & Festa-Bianchet, M. (2004). Assessing senescence patterns in populations of large mammals. *Animal Biodiversity and Conservation*, *27*, 47–58.
- Gaillard, J.-M., & Yoccoz, N. G. (2003). Temporal variation in survival of mammals: A case of environmental canalization? *Ecology*, *84*, 3294–3306. <https://doi.org/10.1890/02-0409>
- Garnier, A., Gaillard, J. M., Gauthier, D., & Besnard, A. (2016). What shapes fitness costs of reproduction in long-lived iteroparous species? A case study on the Alpine ibex. *Ecology*, *97*, 205–214. <https://doi.org/10.1890/15-0014.1>
- Gélin, U., Wilson, M. E., Coulson, G., & Festa-Bianchet, M. (2013). Offspring sex, current and previous reproduction affect feeding behaviour in wild eastern grey kangaroos. *Animal Behaviour*, *86*, 885–891. <https://doi.org/10.1016/j.anbehav.2013.08.016>
- Gélin, U., Wilson, M. E., Coulson, G., & Festa-Bianchet, M. (2015). Experimental manipulation of female reproduction demonstrates its fitness costs in kangaroos. *Journal of Animal Ecology*, *84*, 239–248. <https://doi.org/10.1111/1365-2656.12266>
- Gélin, U., Wilson, M., Cripps, J., Coulson, G., & Festa-Bianchet, M. (2016). Individual heterogeneity and offspring sex affect the growth–reproduction trade-off in a mammal with indeterminate growth. *Oecologia*, *180*, 1127–1135. <https://doi.org/10.1007/s00442-015-3531-z>
- Gendreau, Y., Côté, S. D., & Festa-Bianchet, M. (2005). Maternal effects on post-weaning physical and social development in juvenile mountain goats (*Oreamnos americanus*). *Behavioral Ecology and Sociobiology*, *58*, 237–246. <https://doi.org/10.1007/s00265-005-0938-2>
- Gittleman, J. L., & Thompson, S. D. (1988). Energy allocation in mammalian reproduction. *American Zoologist*, *28*, 863–875. <https://doi.org/10.1093/icb/28.3.863>
- Green, W. C. H., & Rothstein, A. (1991). Trade-offs between growth and reproduction in female bison. *Oecologia*, *86*, 521–527. <https://doi.org/10.1007/BF00318318>
- Hadfield, J. D. (2008). Estimating evolutionary parameters when viability selection is operating. *Proceedings of the Royal Society B*, *275*, 723–734.
- Hadley, G. L., Rotella, J. J., & Garrott, R. A. (2007). Evaluation of reproductive costs for Weddell seals in Erebus Bay, Antarctica. *Journal of Animal Ecology*, *76*, 448–458. <https://doi.org/10.1111/j.1365-2656.2007.01219.x>
- Hamel, S., & Côté, S. D. (2008). Trade-offs in activity budget in an alpine ungulate: Contrasting lactating and nonlactating females. *Animal Behaviour*, *75*, 217–227. <https://doi.org/10.1016/j.anbehav.2007.04.028>
- Hamel, S., & Côté, S. D. (2009). Foraging decisions in a capital breeder: Trade-offs between mass gain and lactation. *Oecologia*, *161*, 421–432. <https://doi.org/10.1007/s00442-009-1377-y>
- Hamel, S., Côté, S. D., & Festa-Bianchet, M. (2010). Maternal characteristics and environment affect the costs of reproduction in female mountain goats. *Ecology*, *91*, 2034–2043. <https://doi.org/10.1890/09-1311.1>
- Hamel, S., Côté, S. D., & Festa-Bianchet, M. (2011). Tradeoff between offspring mass and subsequent reproduction in a highly iteroparous mammal. *Oikos*, *120*, 690–695. <https://doi.org/10.1111/j.1600-0706.2011.19382.x>
- Hamel, S., Côté, S. D., Gaillard, J. M., & Festa-Bianchet, M. (2009). Individual variation in reproductive costs of reproduction: High-quality females always do better. *Journal of Animal Ecology*, *78*, 143–151. <https://doi.org/10.1111/j.1365-2656.2008.01459.x>
- Hamel, S., Festa-Bianchet, M., & Côté, S. D. (2016). Offspring sex in mountain goat varies with adult sex ratio but only for mothers in good condition. *Behavioral Ecology and Sociobiology*, *70*, 123–132. <https://doi.org/10.1007/s00265-015-2031-9>
- Hamel, S., Gaillard, J. M., Douhard, M., Festa-Bianchet, M., Pelletier, F., & Yoccoz, N. G. (2018). Quantifying individual heterogeneity and its influence on life-history trajectories: Different methods for different questions and contexts. *Oikos*, *127*, 687–704. <https://doi.org/10.1111/oik.04725>
- Hamel, S., Gaillard, J. M., Yoccoz, N. G., Loison, A., Bonenfant, C., & Descamps, S. (2010). Fitness costs of reproduction depend on life speed: Empirical evidence from mammalian populations. *Ecology Letters*, *13*, 915–935. <https://doi.org/10.1111/j.1461-0248.2010.01478.x>
- Hamel, S., Yoccoz, N. G., & Gaillard, J. M. (2017). Assessing variation in life-history tactics within a population using mixture regression models: A practical guide for evolutionary ecologists. *Biological Reviews*, *92*, 754–775. <https://doi.org/10.1111/brv.12254>
- Hengeveld, P. E., & Festa-Bianchet, M. (2011). Harvest regulations and artificial selection on horn size in male bighorn sheep. *Journal of Wildlife Management*, *75*, 189–197. <https://doi.org/10.1002/jwmg.14>
- Hogg, J. T. (1988). Copulatory tactics in relation to sperm competition in Rocky Mountain bighorn sheep. *Behavioral Ecology and Sociobiology*, *22*, 49–59. <https://doi.org/10.1007/BF00395697>
- Hogg, J. T. (2000). Mating systems and conservation at large spatial scales. In M. Apollonio, M. Festa-Bianchet, & D. Mainardi (Eds.), *Vertebrate mating systems* (pp. 214–252). Singapore: World Scientific.
- Hogg, J. T., Hass, C. C., & Jenni, D. A. (1992). Sex-biased maternal expenditure in Rocky Mountain bighorn sheep. *Behavioral Ecology and Sociobiology*, *31*, 243–251.
- Jorgenson, J. T., Festa-Bianchet, M., Gaillard, J.-M., & Wishart, W. D. (1997). Effects of age, sex, disease, and density on survival of bighorn

- sheep. *Ecology*, 78, 1019–1032. [https://doi.org/10.1890/0012-9658\(1997\)078\[1019:EOASDA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[1019:EOASDA]2.0.CO;2)
- Jorgenson, J. T., Festa-Bianchet, M., & Wishart, W. D. (1993). Harvesting bighorn ewes: Consequences for population size and trophy ram production. *Journal of Wildlife Management*, 57, 429–435. <https://doi.org/10.2307/3809267>
- Jorgenson, J. T., Samson, J., & Festa-Bianchet, M. (1990). Field immobilization of bighorn sheep with xylazine hydrochloride and antagonism with idazoxan. *Journal of Wildlife Diseases*, 26, 522–527.
- Kroeger, S. B., Blumstein, D. T., Armitage, K. B., Reid, J. M., & Martin, J. A. (2018). Cumulative reproductive costs on current reproduction in a wild polytocous mammal. *Ecology and Evolution*, 8, 11543–11553. <https://doi.org/10.1002/ece3.4597>
- Kuparinen, A., & Festa-Bianchet, M. (2017). Harvest-induced evolution: Insights from aquatic and terrestrial systems. *Philosophical Transactions of the Royal Society B*, 372, 20160036. <https://doi.org/10.1098/rstb.2016.0036>
- L'Heureux, N., Lucherini, M., Festa-Bianchet, M., & Jorgenson, J. T. (1995). Density-dependent mother-yearling association in bighorn sheep. *Animal Behavior*, 49, 901–910.
- Loison, A., Festa-Bianchet, M., Gaillard, J.-M., Jorgenson, J. T., & Jullien, J.-M. (1999). Age-specific survival in five populations of ungulates: Evidence of senescence. *Ecology*, 80, 2539–2554. [https://doi.org/10.1890/0012-9658\(1999\)080\[2539:ASSIFP\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[2539:ASSIFP]2.0.CO;2)
- Mainguy, J., Côté, S. D., Cardinal, É., & Houle, M. (2008). Mating tactics and mate choice in relation to age and social rank in male mountain goats. *Journal of Mammalogy*, 89, 626–635. <https://doi.org/10.1644/07-MAMM-A-234R.1>
- Mainguy, J., Côté, S. D., Festa-Bianchet, M., & Coltman, D. W. (2009). Father-offspring phenotypic correlations suggest intralocus sexual conflict for a fitness-linked trait in a wild sexually dimorphic mammal. *Proceedings of the Royal Society of London B*, 276, 4067–4075. <https://doi.org/10.1098/rspb.2009.1231>
- Marcil-Ferland, D., Festa-Bianchet, M., Martin, A. M., & Pelletier, F. (2013). Despite catch-up, prolonged growth has detrimental fitness consequences in a long-lived vertebrate. *The American Naturalist*, 182, 775–785. <https://doi.org/10.1086/673534>
- Markussen, S. S., Herfindal, I., Loison, A., Solberg, E., Haanes, H., Røed, K. H., ... Saether, B.-E. (2018). Determinants of age at first reproduction and lifetime breeding success revealed by full paternity assignment in a male ungulate. *Oikos*, 128(3), 328–337. <https://doi.org/10.1111/oik.05494>
- Martin, A. M., Festa-Bianchet, M., Coltman, D. W., & Pelletier, F. (2014). Sexually antagonistic association between paternal phenotype and offspring viability reinforces total selection on a sexually selected trait. *Biology Letters*, 10, 20140043. <https://doi.org/10.1098/rsbl.2014.0043>
- Martin, A. M., Festa-Bianchet, M., Coltman, D. W., & Pelletier, F. (2016). Demographic drivers of age-dependent sexual selection. *Journal of Evolutionary Biology*, 29, 1437–1446. <https://doi.org/10.1111/jeb.12883>
- Martin, J. G. A., & Festa-Bianchet, M. (2010). Bighorn ewes transfer the costs of reproduction to their lambs. *The American Naturalist*, 176, 414–423. <https://doi.org/10.1086/656267>
- Martin, J. G. A., & Festa-Bianchet, M. (2011a). Age-independent and age-dependent decreases in reproduction of females. *Ecology Letters*, 14, 576–581. <https://doi.org/10.1111/j.1461-0248.2011.01621.x>
- Martin, J. G. A., & Festa-Bianchet, M. (2011b). Sex ratio bias and reproductive strategies: What sex to produce when? *Ecology*, 92, 441–449. <https://doi.org/10.1890/09-2413.1>
- Martin, J. G. A., & Festa-Bianchet, M. (2012). Determinants and consequences of age of primiparity in bighorn ewes. *Oikos*, 121, 752–760. <https://doi.org/10.1111/j.1600-0706.2011.19962.x>
- Mason, T. H. E., Stephens, P. A., Willis, S. G., Chirichella, R., Apollonio, M., & Richards, S. A. (2012). Intra-seasonal variation in reproductive effort: Young males finish last. *The American Naturalist*, 180, 823–830. <https://doi.org/10.1086/668082>
- McLoughlin, P. D., Gaillard, J.-M., Boyce, M. S., Bonenfant, C., Messier, F., Duncan, P., ... Klein, F. (2007). Lifetime reproductive success and composition of the home range in a large herbivore. *Ecology*, 88, 3192–3201. <https://doi.org/10.1890/06-1974.1>
- Merkle, J. A., Monteith, K. B., Aikens, E. O., Hayes, M. M., Hersey, K., Middleton, A. D., ... Kauffman, M. J. (2016). Large herbivores surf waves of green-up during spring. *Proceedings of the Royal Society B*, 283, 20160456. <https://doi.org/10.1098/rspb.2016.0456>
- Morin, A., Rughetti, M., Rioux-Paquette, S., & Festa-Bianchet, M. (2016). Older conservatives: Reproduction in female Alpine chamois (*Rupicapra rupicapra*) is increasingly risk-averse with age. *Canadian Journal of Zoology*, 94, 311–321.
- Moyes, K., Coulson, T., Morgan, B. J. T., Donald, A., Morris, S. J., & Clutton-Brock, T. H. (2006). Cumulative reproduction and survival costs in female red deer. *Oikos*, 115, 241–252. <https://doi.org/10.1111/j.2006.0030-1299.15200.x>
- Mysterud, A., Bonenfant, C., Loe, L. E., Langvatn, R., Yoccoz, N. G., & Stenseth, N. C. (2008). The timing of male reproductive effort relative to female ovulation in a capital breeder. *Journal of Animal Ecology*, 77, 469–477. <https://doi.org/10.1111/j.1365-2656.2008.01365.x>
- Mysterud, A., Meisingset, E., Langvatn, R., Yoccoz, N. G., & Stenseth, N. C. (2005). Climate-dependent allocation of resources to secondary sexual traits in red deer. *Oikos*, 111, 245–252. <https://doi.org/10.1111/j.0030-1299.2005.14197.x>
- Panagakakis, A., Hamel, S., & Côté, S. D. (2017). Influence of early reproductive success on longevity and late reproductive success in an alpine ungulate. *The American Naturalist*, 189(6), 667–683. <https://doi.org/10.1086/691388>
- Pelletier, F. (2005). Foraging time of rutting bighorn rams varies with individual behavior, not mating tactic. *Behavioral Ecology*, 16, 280–285. <https://doi.org/10.1093/beheco/arih162>
- Pelletier, F., & Festa-Bianchet, M. (2004). Effects of body mass, age, dominance and parasite load on foraging time of bighorn rams, *Ovis canadensis*. *Behavioral Ecology and Sociobiology*, 56, 546–551. <https://doi.org/10.1007/s00265-004-0820-7>
- Pelletier, F., & Festa-Bianchet, M. (2006). Sexual selection and social rank in bighorn rams. *Animal Behaviour*, 71, 649–655. <https://doi.org/10.1016/j.anbehav.2005.07.008>
- Pelletier, F., Hogg, J. T., & Festa-Bianchet, M. (2006). Male mating effort in a polygynous ungulate. *Behavioral Ecology and Sociobiology*, 60, 645–654. <https://doi.org/10.1007/s00265-006-0208-y>
- Pelletier, F., Page, K. A., Ostiguy, T., & Festa-Bianchet, M. (2005). Fecal counts of lungworm larvae and reproductive effort in bighorn sheep, *Ovis canadensis*. *Oikos*, 110, 473–480.
- Pelletier, F., Réale, D., Garant, D., Coltman, D. W., & Festa-Bianchet, M. (2007). Selection on heritable seasonal phenotypic plasticity of body mass. *Evolution*, 61, 1969–1979. <https://doi.org/10.1111/j.1558-5646.2007.00160.x>
- Pigeon, G., Festa-Bianchet, M., Coltman, D. W., & Pelletier, F. (2016). Intense selective hunting leads to artificial evolution in horn size. *Evolutionary Applications*, 9, 521–530. <https://doi.org/10.1111/eva.12358>
- Pigeon, G., Festa-Bianchet, M., & Pelletier, F. (2017). Long-term fitness consequences of early environment in a long-lived ungulate. *Proceedings of the Royal Society B*, 284, 20170222. <https://doi.org/10.1098/rspb.2017.0222>
- Pigeon, G., & Pelletier, F. (2018). Direct and indirect effects of early-life environment on lifetime fitness of bighorn ewes. *Proceedings of the Royal Society B*, 285, 20171935. <https://doi.org/10.1098/rspb.2017.1935>
- Poirier, M.-A., Coltman, D. W., Pelletier, F., Jorgenson, J. T., & Festa-Bianchet, M. (2019). Genetic decline, restoration and rescue of an

- isolated ungulate population. *Evolutionary Applications*. <https://doi.org/10.1111/eva.12706>
- Preston, B. T., Stevenson, I. R., Pemberton, J. M., Coltman, D. W., & Wilson, K. (2003). Overt and covert competition in a promiscuous mammal: The importance of weaponry and testes size to male reproductive success. *Proceedings of the Royal Society B*, *270*, 633–640. <https://doi.org/10.1098/rspb.2002.2268>
- Réale, D., & Festa-Bianchet, M. (2000). Mass-dependent reproductive strategies in wild bighorn ewes: A quantitative genetic approach. *Journal of Evolutionary Biology*, *13*, 679–688. <https://doi.org/10.1046/j.1420-9101.2000.00205.x>
- Ruckstuhl, K. E., & Festa-Bianchet, M. (1998). Do reproductive status and lamb gender affect the foraging behavior of bighorn ewes? *Ethology*, *104*, 941–954. <https://doi.org/10.1111/j.1439-0310.1998.tb00043.x>
- Rughetti, M., Dematteis, A., Meneguz, P. G., & Festa-Bianchet, M. (2015). Age-specific reproductive success and cost in female Alpine ibex. *Oecologia*, *178*, 197–205. <https://doi.org/10.1007/s00442-014-3192-3>
- Samson, J., Holmes, J. C., Jorgenson, J. T., & Wishart, W. D. (1987). Experimental infection of free-ranging Rocky Mountain bighorn sheep with lungworms (*Protostrongylus* spp.; Nematoda: Protostrongylidae). *Journal of Wildlife Diseases*, *23*, 396–403.
- Sheldon, B. C. (2000). Differential allocation: Tests, mechanisms and implications. *Trends in Ecology and Evolution*, *15*, 397–402. [https://doi.org/10.1016/S0169-5347\(00\)01953-4](https://doi.org/10.1016/S0169-5347(00)01953-4)
- Skibieli, A. L., Speakman, J. R., & Hood, W. R. (2013). Testing the predictions of energy allocation decisions in the evolution of life-history trade-offs. *Functional Ecology*, *27*, 1382–1391. <https://doi.org/10.1111/1365-2435.12130>
- Stearns, S. C. (1992). *The evolution of life histories*. Oxford, UK: Oxford University Press.
- Stevenson, I. R., & Bancroft, D. R. (1995). Fluctuating trade-offs favour precocial maturity in male Soay sheep. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *262*, 267–275.
- Tavecchia, G., Coulson, T. N., Morgan, B. J. T., Pemberton, J. M., Pilkington, J., Gulland, F. M. D., & Clutton-Brock, T. H. (2005). Predictors of reproductive cost in female Soay sheep. *Journal of Animal Ecology*, *74*, 201–213. <https://doi.org/10.1111/j.1365-2656.2005.00916.x>
- Toigo, C., & Gaillard, J. M. (2003). Causes of sex-biased adult survival in ungulates: Sexual size dimorphism, mating tactic or environment harshness? *Oikos*, *101*, 376–384. <https://doi.org/10.1034/j.1600-0706.2003.12073.x>
- Toigo, C., Gaillard, J. M., & Loison, A. (2013). Alpine ibex males grow large horns at no survival cost for most of their lifetime. *Oecologia*, *173*, 1261–1269. <https://doi.org/10.1007/s00442-013-2700-1>
- Trivers, R. L. (1974). Parent-offspring conflict. *American Zoologist*, *14*, 249–264.
- Trivers, R. L., & Willard, D. E. (1973). Natural selection of parental ability to vary the sex ratio of offspring. *Science*, *179*, 90–92. <https://doi.org/10.1126/science.179.4068.90>
- Van de Walle, J., Pigeon, G., Zedrosser, A., Swenson, J. E., & Pelletier, F. (2018). Hunting regulation favors slow life histories in a large carnivore. *Nature Ecology and Evolution*, *9*, 1100. <https://doi.org/10.1038/s41467-018-03506-3>
- van Noordwijk, A. J., & de Jong, G. (1986). Acquisition and allocation of resources: Their influence on variation in life history tactics. *The American Naturalist*, *128*, 137–142. <https://doi.org/10.1086/284547>
- Weladji, R. B., Loison, A., Gaillard, J. M., Holand, O., Mysterud, A., Yoccoz, N. G., ... Stenseth, N. C. (2008). Heterogeneity in individual quality overrides costs of reproduction in female reindeer. *Oecologia*, *156*, 237–247. <https://doi.org/10.1007/s00442-008-0961-x>
- Williams, G. C. (1966). Natural selection, the cost of reproduction, and a refinement of Lack's principle. *The American Naturalist*, *100*, 687–690.
- Yoccoz, N. G., Mysterud, A., Langvatn, R., & Stenseth, N. C. (2002). Age- and density-dependent reproductive effort in male red deer. *Proceedings of the Royal Society B*, *269*, 1523–1528.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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