

Ecological and evolutionary effects of selective harvest of non-lactating female ungulates

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Summary

1. Female ungulates are often selectively harvested according to their reproductive status. Because ungulate population growth depends heavily on adult female survival, it is crucial to understand the effects of this selective harvest. Recent studies revealed persistent individual differences in female reproductive potential, with a positive correlation of reproductive success over consecutive years. If current reproduction is correlated with lifetime reproductive success, then selective harvest of non-lactating females should remove individuals of low reproductive potential, with lower impact on population growth than random harvest. If lifetime reproductive success has a genetic basis, selective harvest may also increase the proportion of successful females.

2. We used an individual-based model to understand the short-term effects of harvest intensity and hunter selectivity on population dynamics, accounting for both heterogeneity in reproductive potential and orphan survival. We also explored the long-term effect of harvest as a selective pressure on female heterogeneity.

3. Selective harvest of non-lactating females reduced survival to primiparity compared to random harvest, because of high harvest rates of pre-reproductive females. After primiparity, however, females of higher reproductive potential had higher survival under selective than random harvest. Therefore, the overall effect on population dynamics depends on a trade-off between a high harvest of pre-reproductive females and a reduced harvest of reproductive females with high reproductive potential.

4. Female heterogeneity and the length of the pre-reproductive period affected this trade-off. Over the short term, high heterogeneity in reproductive potential of pre-reproductive females made selective harvest the most effective strategy to maintain a high population growth rate. With low heterogeneity and little effects of orphaning on juvenile mortality, however, random harvest had a lower impact on population growth than selective harvest. Over the long term, selective female harvest may increase the proportion of successful reproducers in the population.

5. *Synthesis and applications.* Selective harvests of non-lactating females appear justified only if female heterogeneity in reproductive potential and/or orphan mortality are very high. Because pre-reproductive females will be subject to intense harvest, selective harvest may reduce population growth rate compared to random harvest in species with late primiparity, especially if most pre-reproductive female normally survive to primiparity. When heterogeneity in reproductive potential and orphan mortality are low, random female harvest appears preferable to selective harvest.

Key-words: female harvest, individual heterogeneity, lactating females, lifetime reproductive success, orphaning, population dynamics, selective hunting

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Introduction

In several ungulate populations in Europe and North America, sport hunting is the main cause of adult mortality (Langvatn & Loison 1999; McCorquodale 1999; Ballard *et al.* 2000; Festa-Bianchet 2003; Mysterud, Solberg & Yoccoz 2005; Milner *et al.* 2006). Harvest may have strong effects on population dynamics (Milner, Nilsen & Andreassen 2007; Femberg & Roy 2008), and potential evolutionary effects on phenotype and life-history traits [(Proaktor, Coulson & Milner-Gulland 2007; Pigeon *et al.* 2016), but see (Mysterud 2011; Rivrud *et al.* 2013)]. In ungulates, survival of adult females has higher elasticity for population growth compared to reproductive parameters or to survival of other age-sex classes (Gaillard, Festa-Bianchet & Yoccoz 1998; Gaillard *et al.* 2000). In hunted populations, reproductive females often experience lower harvest mortality than non-reproductive ones, either because regulations discourage harvest of females with offspring at heel, or because hunters are reluctant to shoot these females (Solberg *et al.* 2000; Ericsson *et al.* 2001; Nilsen & Solberg 2006; Mysterud, Yoccoz & Langvatn 2009; Rughetti & Festa-Bianchet 2011). Therefore, information on how the magnitude and selectivity of female harvest may affect population dynamics is essential to understand the effects of harvest on large herbivores. This issue, however, has received little attention (Rughetti & Festa-Bianchet 2014), and hence the consequences of selective harvest of non-lactating females remain mostly unknown.

Hunting regulations favour the harvest of non-lactating females because removing a lactating female may decrease her offspring's growth [*Oreamnos americanus* (Gendreau, Côté & Festa-Bianchet 2005); *Rangifer tarandus* (Weladji *et al.* 2003); *Capreolus capreolus* (Andersen *et al.* 2000)] and survival [*Alces alces* (Testa 2004); *Cervus elaphus* (Andres *et al.* 2013), but see *Ovis canadensis* (Festa-Bianchet, Jorgenson & Wishart 1994)]. Little is known, however, about the consequences of orphaning near the time of weaning, when hunting usually takes place (Holand *et al.* 2012; Rughetti & Festa-Bianchet 2014).

Rughetti & Festa-Bianchet (2014) using empirical data on chamois (*Rupicapra rupicapra*) showed that selective harvest of non-lactating females leads to increased mortality of pre-reproductive females aged 2–3 years, with strong negative impacts upon population growth. Pre-reproductive females are considered 'adults' by hunting regulations, and have a very high reproductive value. That study, however, did not consider the possible consequences of heterogeneity in reproductive potential. Recent studies (Weladji *et al.* 2008; Hamel *et al.* 2009a,b) reveal that some females reproduce every year while others fail repeatedly, leading to a positive correlation between current and lifetime reproductive success. Harvesting a lactating female could then potentially remove an individual with high reproductive potential, with greater impacts on population dynamics compared to a random harvest with

respect to reproductive status. Furthermore, reproductive success in large herbivores typically peaks in prime-aged females and then decreases with age (Gaillard *et al.* 2000). At high density or under harsh environmental conditions, females may delay primiparity (Festa-Bianchet *et al.* 1995) or skip reproduction (Hamel *et al.* 2009a). Therefore, the potential consequences of selective harvest of non-lactating females on population dynamics should also vary according to female lifetime reproductive schedule.

Intense harvest of pre-reproductive females and selective harvest of non-lactating adult females may also have long-term evolutionary consequences on reproductive strategies (Proaktor, Coulson & Milner-Gulland 2007). Lifetime reproductive success should have low heritability because genes that increase fitness should be rapidly fixed (Fisher 1958; Mousseau & Roff 1987). Empirical studies, however, have documented some heritability of lifetime reproductive success (see McFarlane *et al.* 2014 for a review). If female reproductive potential has some additive genetic variance, selective harvest of non-lactating females may remove individuals with low reproductive potential, ultimately increasing population growth despite the removal of pre-reproductive adults. Surprisingly, no attempt has been made to assess whether and how selective harvest may have potential evolutionary consequences on female heterogeneity.

We used long-term data of individually marked mountain goats (*Oreamnos americanus*) to construct an individual-based model (IBM) to evaluate the short-term ecological effects and long-term evolutionary consequences of selective harvest of non-lactating females in wild ungulate populations. We did not seek to evaluate management practices for mountain goats, whose harvest is typically male-biased (Festa-Bianchet & Côté 2008). We used mountain goats as a model because females show high heterogeneity in reproductive potential (Hamel, Côté & Festa-Bianchet 2010) and because data on individual lifetime performance are available. Females reach asymptotic mass at about 7 years (Festa-Bianchet & Côté 2008). Reproductive success increases from 3 to 6 years of age, peaks at 7–12 years, and declines slightly at older ages (Festa-Bianchet & Côté 2008). Primiparity is usually at 4 or 5 years, but ranges from 3 to 8 years (Festa-Bianchet & Côté 2008). Survival of females >2 years old is high until about age 10, then declines (Hamel, Côté & Festa-Bianchet 2010).

Using an IBM to simulate different scenarios, we first evaluated how harvest intensity and selectivity may affect population dynamics when accounting for heterogeneity in reproductive potential. We tested whether selective harvest of non-lactating females improved population growth. If current reproduction is correlated with lifetime reproductive success, selective harvest should favour survival of females with high reproductive potential compared to random harvest. High harvest mortality of pre-reproductive females (Rughetti & Festa-Bianchet 2014), however, may eliminate the demographic

advantage of selective harvest. Second, we evaluated the role of harvest as a potential selective pressure on reproductive strategies. If lifetime reproductive success has additive genetic variance, selective harvest could reinforce natural selection by removing females with low reproductive potential. Harvest independent of female reproductive status should not have any selective effects on reproductive potential.

Materials and methods

POPULATION DATA

We used data from mountain goats at Caw Ridge (54 N, 119 W), Alberta, Canada, from 1993 to 2012, when 99% of females 1 year and older were individually marked. For each year, survival to 1 June, parturition rate and reproductive success, defined as production of a kid that survived to 15 September, were available for all marked females. We also recorded kid summer and winter survival defined, respectively, as survival from birth to weaning (15 September) and from weaning to the following 1 June. We used the number of females aged 1 year and older to measure population density. More information on the mountain goat study is provided elsewhere (Festa-Bianchet & Côté 2008; Hamel, Côté & Festa-Bianchet 2010).

OVERVIEW

Purpose

We modelled two main scenarios. Over the short term, the model sought to understand how harvest intensity and hunter selectivity affected population dynamics, accounting for heterogeneity in reproductive potential and orphan survival. In the long-term scenario, the model explored the role of harvest as a selective pressure on heterogeneity in reproductive potential and its consequences for population dynamics. For both analyses, we used an IBM considering only females and followed the protocol for IBMs in Grimm *et al.* (2006). All analyses were conducted in R (R Development Core Team 2014).

State variables and scales

The model accounted for three hierarchical scales: individual, population and environmental conditions including management. Individuals were characterized by three state variables: age, potential lifetime reproductive success (pLRS), and reproductive status. The pLRS was the number of offspring that a female could wean during her lifetime if not harvested. Young of the year and 1-year-old females were referred to as kids and yearlings. Females 2 years and older were referred to as adults. After the hunting season, kids were classified as orphan or not.

Process overview and scheduling

The model has a 1-year time step. Adult females give birth in summer, summer mortality affects kid survival to weaning, then harvest and winter mortality affects survival of kids, yearling and adult females. Harvest was considered random when independent of female reproductive status and selective when only

non-lactating females were harvested. Harvest rate was the ratio of the annual harvest over population size. Ungulate hunting regulations are often distinct for adults and yearlings (Rughetti & Festa-Bianchet 2011). Harvest rate was therefore estimated separately for adult and yearling females. Harvest of yearling females was random and there was no kid harvest. Sex ratio at birth was assumed to be one (Côté & Festa-Bianchet 2001).

DESIGN CONCEPTS

Management was characterized by harvest rate and hunter avoidance of lactating females. The model accounted for density dependence in kid summer survival, and for environmental stochasticity in summer survival of kids and in winter survival and reproduction of all animals.

DETAILS

Initialization and input

Each simulation began with the age structure obtained from empirical data, with frequencies from yearling to age 16: 0.098, 0.098, 0.091, 0.082, 0.080, 0.080, 0.075, 0.067, 0.063, 0.061, 0.054, 0.046, 0.041, 0.027, 0.019, 0.018 animals, for a total of 250 females. We ran 500 simulations over 80 and 250 years for the short- and long-term scenarios. In both scenarios, the population was not harvested for the first 50 years to reach a stable age distribution and equilibrium size. For the short-term scenario, we first assumed equal survival of orphans and non-orphans. We modelled female harvest rates of 0.03 and 0.09 based on knowledge of goat harvest rate (Hamel *et al.* 2006) and on initial inspection of simulations to avoid unsustainable harvest in the short term. For each rate, we simulated random and selective harvest. Finally, we repeated the analysis assuming that orphaned kids were half as likely as non-orphans to survive the winter. Because there are no data on orphan mountain goat survival, we decreased survival by 0% and 50% based on results from other ungulates (Rughetti & Festa-Bianchet 2014). For the long-term analysis, we simulated non-harvest, random harvest and non-lactating female harvest, assuming equal survival of orphans and non-orphans.

Submodels

Female reproduction and natural survival. Parameter estimates were derived from empirical data (Appendix S1, Supporting Information). We then used estimates from these models as parameters in the equations of the IBM to simulate individual survival and reproduction. Survival of females aged 2 years and older (S), survival of yearlings (S_y), and parturition rate for females aged 5 years and older (R_5), 4 (R_4) and 3 (R_3) years were modelled following equations in Table 1.

For each equation (Table 1), parameters inside the squared brackets were estimated from models fitted with empirical data. We simulated environmental stochasticity with $U \times SD$. U was selected at random for each new simulated year from a normal distribution with a mean of zero and a standard deviation of one. SD was the standard deviation of year set as a random intercept in the selected model (Appendix S1). The IBM model accounted for stochasticity in overwinter survival (U_s), reproduction (U_r)

Table 1. Equations used to simulate survival and reproduction. Parameters were estimated from 112 female mountain goats monitored at Caw Ridge, Canada, from 1993 to 2012 for which lifetime data were available. See Supporting Information for model selection. S and S_y are survival of females aged 2 years and older and survival of yearlings respectively. SK_s and SK_w are respectively summer and winter survival of kids. R_5 , R_4 and R_3 are the probability to give birth for females aged 5 years and older (R_5), 4 years (R_4) and 3 years respectively. pR is reproductive success the previous year and $pLRS$ the individual potential lifetime reproductive success. In each equation, $U \times SD$ simulates environmental stochasticity. See main text for details

Main equations	SD
(1) $\text{Logit}(S) = [1.23 - 0.24 \times \text{Age} + 2.12 \times pLRS - 0.14 \times \text{Age} \times pLRS] + U_s \times SD_s$	$SD_s = 0.76$
(2) $\text{Logit}(S_y) = [2.15] + U_{s_y} \times SD_{S_y}$	$SD_{S_y} = 0.85$
(3) $\text{Logit}(R_5) = [-4.22 + 0.98 \times \text{Age} - 0.07 \times \text{Age}^2 - 3.56 \times pR + 0.67 \times pLRS + 0.21 \times \text{Age} \times pLRS] + U_r \times SD_{R_5}$	$SD_{R_5} = 0.96$
(4) $\text{Logit}(R_4) = [-1.82 + 0.39 \times pLRS] + U_r \times SD_{R_4}$	$SD_{R_4} = 0.74$
(5) $\text{Logit}(R_3) = [-2.93] + U_r \times SD_{R_3}$	$SD_{R_3} = 0$
(6) $\text{Logit}(SK_s) = [1.09 - 0.53 \times \text{Density}] + U_{k_s} \times SD_{SK_s}$	$SD_{SK_s} = 0.68$
(7) $\text{Logit}(SK_w) = [1.66] + U_{k_w} \times SD_{SK_w}$	$SD_{SK_w} = 0.76$

and kid survival over summer (U_{k_s}). In equation 3 (Table 1), pR was reproductive status at weaning the previous year to account for potential reproductive costs. Once the probability of reproduction or survival was obtained from the main equations, demographic stochasticity was modelled independently for each female by binomial sampling of that probability.

Kid survival, density dependence and orphan mortality. At Caw Ridge population size increased from 63 to 128 goats 1 year and older over 20 years, then decreased abruptly. We recently found evidence of a small effect of high density on kid survival (Théoret-Gosselin, Hamel & Côté 2015). To avoid unrealistic population growth over long-term simulations, we modelled the effect of density on kid survival using only years of high density. We used a threshold population size of 120 animals (S. Hamel, unpublished data), including about 60 females, when the effect of density appeared important. We used equations 6 and 7 in Table 1 to model kid summer (SK_s) and winter (SK_w) survival (see Appendix S1 for model selection).

Density refers to the number of yearling and adult females. Density dependence only affected kid summer survival (Supporting Information). SD_{SK_s} and SD_{SK_w} were estimated using the null model fitted with the complete data set to estimate an annual variability in kid survival over all years. In the simulations, the negative effect of density began at 200 females instead of about

60 in the real population, to allow a higher carrying capacity while keeping the same shape of the density response. A higher carrying capacity avoided population sizes prone to extinction under simulated harvests.

In the short-term analysis, we compared different effects of female hunting mortality on the survival of orphans. The probability of an orphaned kid to survive (Sk_{orph}) was $Sk_{orph} = SK_w \times (1 - K_{hm})$, where K_{hm} is the lower survival of an orphan compared to a non-orphan, either 0 or 0.5. In the long-term scenario, we set $K_{hm} = 0$, to focus the attention on the evolutionary effect of harvest on female heterogeneity, without the confounding effects of orphaning on population dynamics.

Heritability of lifetime reproductive success. Females with greater $pLRS$ are potentially better reproducers. We used $pLRS$ to simulate heterogeneity and to test which harvest regime increased survival of females with high reproductive potential. In the short-term analysis, we assumed no heritability of $pLRS$ and assigned to kids a $pLRS$ selected at random from the empirical distribution obtained from cohorts with complete lifetime data (Fig. 1). Only few individuals survived and reproduced until older ages (Fig. 1). Of 78 females from cohorts monitored until death and used as input for $pLRS$ in the model, 24 never reproduced; all these females except one died before age 5. Female reproductive value peaks at 4 years (Fig. 1).

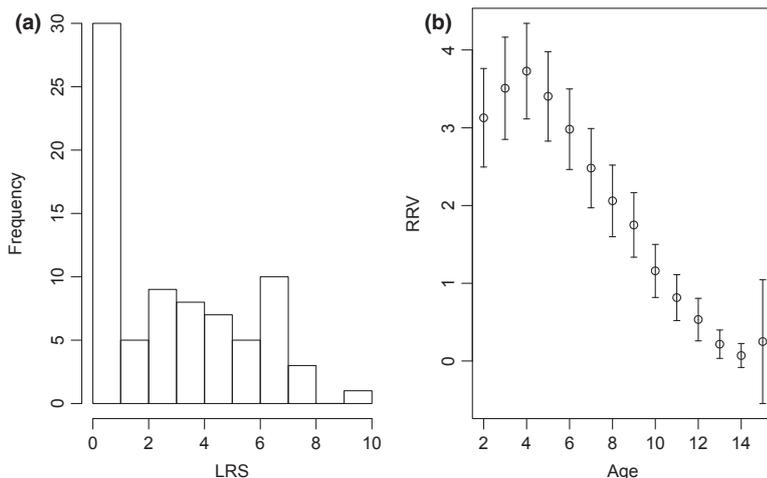


Fig. 1. Lifetime reproductive success (LRS) and age-specific residual reproductive value ($RRV \pm SE$) of female mountain goats monitored at Caw Ridge (Canada, 1993–2012). The figure reports only 78 individuals of cohorts with complete lifetime data.

In the long-term analysis, we assumed that a kid recruited in the population had a 0.9 probability to receive a pLRS assigned at random from the parental generation before selection acted on, and a 0.1 probability of receiving the pLRS of her mother. This procedure simulated a moderate heritability of 0.1 in lifetime reproductive success, while constraining variability in pLRS between 0 and 10 (Fig. 1). There are very few empirical data to select a heritability value for lifetime reproductive success, and 0.1 appears reasonable (McFarlane *et al.* 2014).

Results

SHORT-TERM SCENARIO

Given the distribution of pLRS used as input in the model, the simulated population decreased over time under both harvest rates (Fig. 2). Most of this decrease was due to harvest, while orphan mortality had a smaller effect (Fig. 3). Compared to random harvest, selective harvest had a positive effect on population size only when orphan mortality was increased by 50% (Fig. 3b and d), especially under 9% harvest (Fig. 3d). Assuming no effect of orphaning on kid survival, and 3% harvest, no difference in population size was detected between random and selective harvest (Fig. 3a). With 9% harvest, the randomly harvested population was 4% larger than the selectively harvested one (SE = 0.02, Fig. 3c).

The probability to survive to a given age was modelled as a function of pLRS and harvest regime (Fig. 4). With 9% harvest, females aged 2 and 3 years suffered greater mortality under selective than random harvest (Figs 4 and 5). From age four on, the probability to survive until a

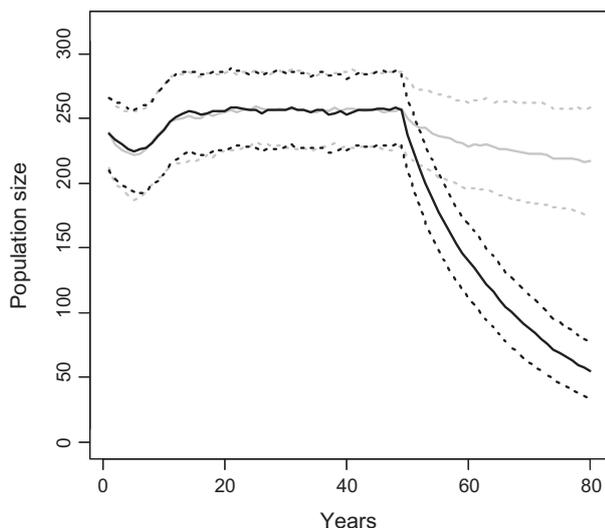


Fig. 2. Variation in population size over time under 0.09 (black) and 0.03 (grey) harvest rates, with harvest beginning at year 50. Results were averaged over 500 simulations (averages presented by solid lines and SD by dashed lines), based on empirical data from mountain goats at Caw Ridge (Canada, 1993–2012). Simulations assumed random harvest and no difference in mortality between orphan and non-orphan kids.

given age for females with above-average pLRS decreased more rapidly under random than under selective harvest (Fig. 4). At older ages, females with high pLRS were more likely to survive under selective than random harvest (Fig. 4). On the contrary, age-specific survival of females with low pLRS tended to be lower under selective than random harvest, with little differences at older ages. The difference in age-specific survival according to pLRS between random and selective harvest increased with harvest rate (Fig. 4).

LONG-TERM SCENARIO

Under both harvest scenarios, population size first decreased then recovered (Fig. 6). Random harvest, however, had a smaller impact than selective harvest, and average population size was as much as 15% higher for the former than the latter, although this difference decreased over time.

Average pLRS in new cohorts increased over time under both harvest regimes and in the non-harvested population (Fig. 7), but did so more rapidly under selective harvest. Therefore, selective harvest led to a faster increase in the frequency of good reproducers compared to random harvest.

Discussion

Our results revealed complex relationships between harvest intensity, orphan mortality, heritability and heterogeneity in female reproductive potential. Selective harvest increased survival of females with high reproductive potential, leading to a positive effect on population size only when survival of pre-reproductive females had limited consequences on population growth and assuming high orphan mortality. The main driver of population dynamics was harvest rate (Myrsetrud 2011). Over the long term, selective harvest may promote an increased frequency of good reproducers if enough additive genetic variance in reproductive potential allows an evolutionary response.

SHORT-TERM SCENARIO

Over the short term and assuming no heritability in reproductive success, much of the decrease in population size over time was due to harvest intensity and to a much lesser extent orphan mortality. Compared to random harvest, selective harvest had a strong positive effect on population size only when harvest intensity and orphan mortality were high (Fig. 3d), in contrast with predictions for Alpine chamois, where selective harvest reduced population size because of intense removals of pre-reproductive females (Rughetti & Festa-Bianchet 2014). Therefore, heterogeneity in reproductive potential can have a strong effect on population dynamics of ungulates under selective female harvest.

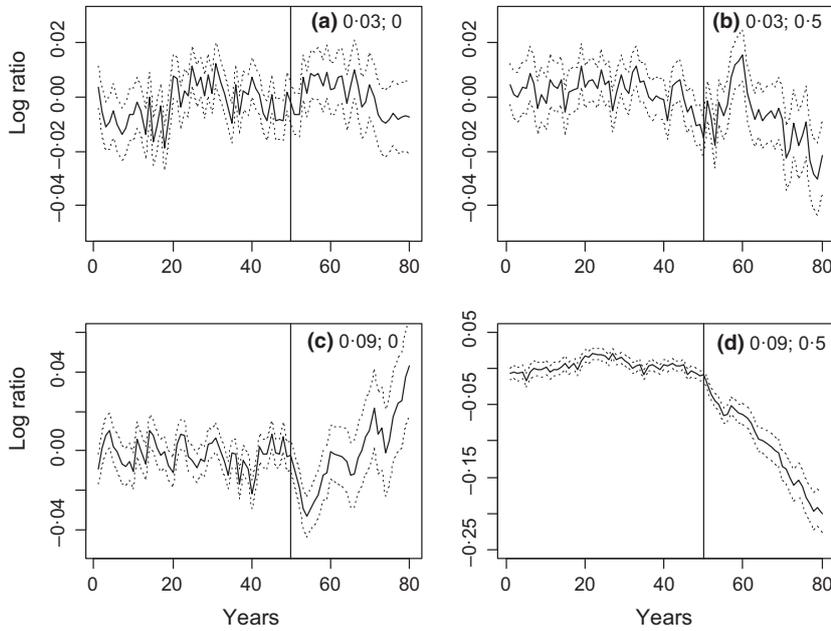


Fig. 3. Variation in the log ratio (solid line) of average female population size under random vs. selective harvest. Values greater than zero indicate that population size was larger under random than selective harvest of females with respect to reproductive status. SD (dotted lines) were estimated by 1000 bootstrapped samples each year. Numbers in panels refer to harvest rate (0.09; 0.03) and to the decrease in winter survival of orphans compared to non-orphans (0; 0.5). Results were averaged over 500 simulations based on empirical data from mountain goats at Caw Ridge (Canada, 1993–2012). Harvest started in year 50: vertical line. Note the different scale of the y axes among panels.

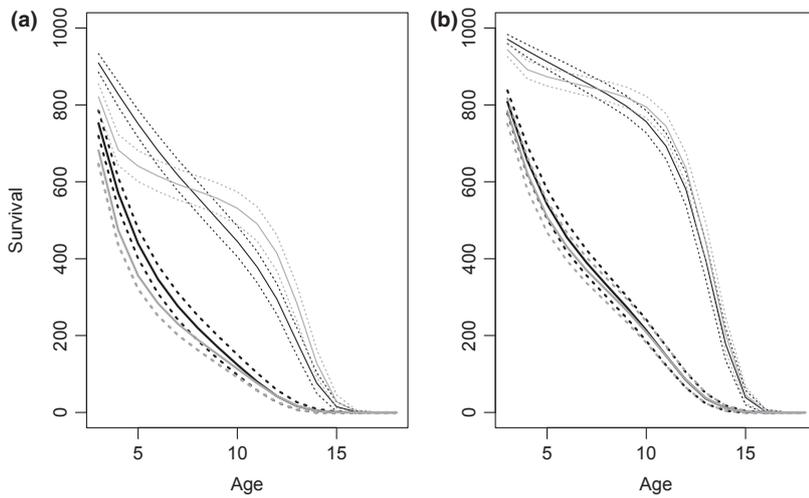


Fig. 4. Simulated survivorship of mountain goats under random (black) and selective harvest (grey), for females with a potential lifetime reproductive success higher (thin line) and lower (bold line) than the population average. Survival is the number of individuals from a cohort of one thousand 2-year-old females surviving to a given age. Harvest rate is 0.09 (a) and 0.03 (b). Results were averaged over 500 simulations (averages presented by solid lines and SD by dashed lines), based on empirical data from mountain goats at Caw Ridge (Canada, 1993–2012).

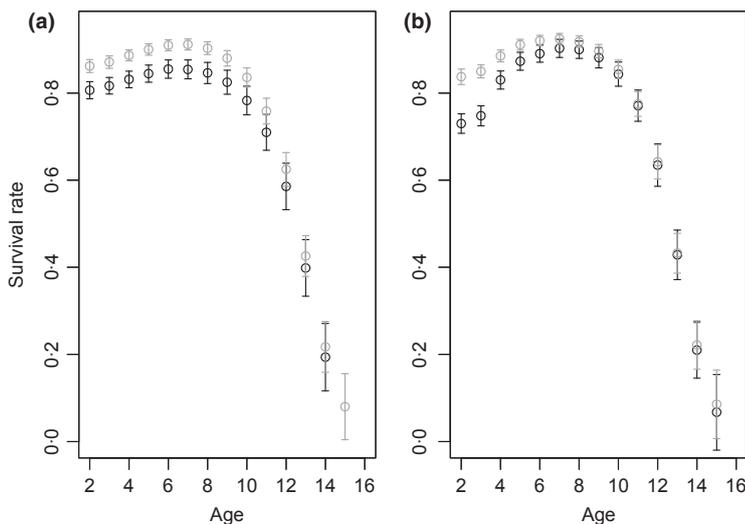


Fig. 5. Age-specific probability that a female mountain goat would survive the hunting season under random (a) and selective harvest with respect to reproductive status (b). Harvest rates are 0.09 (black) and 0.03 (grey). Data were simulated over 30 years for 500 simulations (averages presented by circles and SD by bars), based on empirical data from mountain goats at Caw Ridge (Canada, 1993–2012). See text for details about the simulations.

Fig. 6. Variation in population size over 250 years under random (grey zone and bold line in a), selective harvest (oblique lines and thin line in a) and in the non-harvested scenario (b). Harvest rate was 0.09. Results were averaged over 500 simulations (averages presented by solid lines and SD by zones), based on empirical data from mountain goats at Caw Ridge (Canada, 1993–2012).

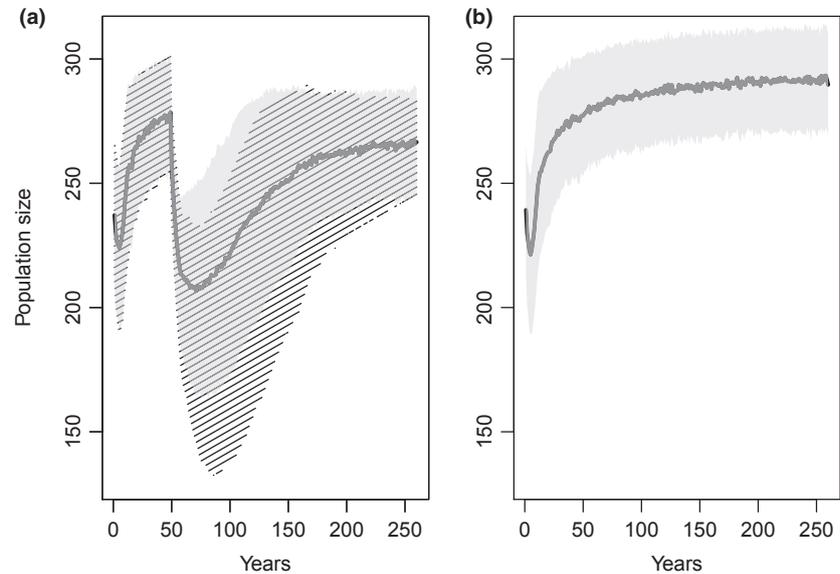
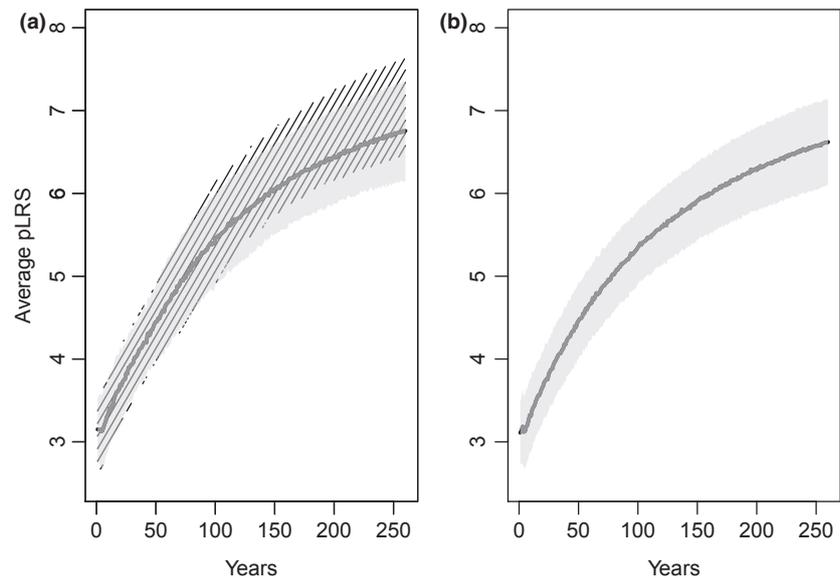


Fig. 7. Variation in average potential lifetime reproductive success (pLRS) in new cohorts over 250 years under random (grey zone and bold line in a), selective harvest (oblique lines and thin line in a) and in the non-harvested scenario (b). Harvest rate was 0.09. Results were averaged over 500 simulations (averages presented by solid lines and SD by zones), based on empirical data from mountain goats at Caw Ridge (Canada, 1993–2012).



Under random harvest, female survival was independent of reproductive status or reproductive potential. Compared to random harvest, selective harvest of non-lactating females increased the mortality of pre-reproductive females and decreased that of mature females of high reproductive potential (Fig. 4). Under selective harvest the higher mortality of pre-reproductive females was independent of pLRS. For females that survived to primiparity, selective harvest increased survival of those with high pLRS, which were more likely to have a kid at heel every hunting season (Hamel *et al.* 2009b). Therefore, the overall impact of selective hunting upon population dynamics depends on a trade-off between increased harvest of pre-reproductive females and reduced harvest of reproductive females with high pLRS (Fig. 4). A simulation of chamois harvest (Rughetti & Festa-Bianchet 2014) showed that heavy harvest of pre-reproductive females negated the potential benefits on population dynamics of sparing

lactating females, by removing young females with high reproductive value (Rughetti & Festa-Bianchet 2014). In the absence of hunting, young female ungulates generally experience high survival and have high reproductive potential (Gaillard *et al.* 2000). In mountain goats, however, reproductive value peaked at age 4 and then decreased (Fig. 1). Reproductive value increased with age among pre-reproductive females because of the selective disappearance of poor reproducers (van de Pol & Verhulst 2006): 31% of females died before 5 years without weaning a kid. For mountain goats, we simulated substantial individual heterogeneity based on empirical data, with about a third of females entering the simulated population but disappearing before 5 years of age, so that reproductive potential peaked at age 4. Therefore, the effects of hunter selectivity for reproductive status on population dynamics appear to depend strongly upon the level of female heterogeneity in reproductive potential and the age

when reproductive value peaks. The empirical distribution of female goats entering the population as 2-year-olds was skewed towards poor reproducers (Fig. 1), and this skew reduced the negative effect of high pre-reproductive harvest mortality. In mountain goats, survival of pre-reproductive females has little influence on population growth (Hamel *et al.* 2006). Therefore, despite reducing harvest mortality of young females, random harvest was less effective in increasing growth rate in mountain goats than in chamois (Rughetti & Festa-Bianchet 2014). This result highlights the importance of female heterogeneity on population dynamics, and cautions against generalizations from single-species or single-population studies.

In most ungulates, primiparity varies from 2 to 4 years (Gaillard *et al.* 2000) and in poor habitats females may delay primiparity independently of weather or density (Gaillard *et al.* 2000). By increasing mortality of pre-reproductive females, selective harvest may reduce population growth in species with late primiparity, but its overall effects depend on the level of heterogeneity in female reproductive potential. Large variance in lifetime reproductive success and a distribution skewed toward poor reproducers at young ages decrease the negative effect of pre-reproductive mortality on population dynamics.

We used lifetime weaning success as a proxy of fitness. However, fitness depends also on offspring survival (Hunt *et al.* 2004). A strong reproductive cost in term of decreased postweaning survival of subsequent offspring may substantially decrease the positive effects of selective compared to random harvest on population growth rate.

LONG-TERM SCENARIO

The results of the long-term simulation were strongly dependent on our assumptions for distribution and heritability of pLRS. These data are lacking for most hunted species. Therefore, rather than using these results as a prescription for wildlife management, we underline what our analyses revealed about mechanisms that can drive the population dynamics of ungulates.

In the short-term analysis, the variance and the distribution of heterogeneity in reproductive potential of new female cohorts remained constant over time (Fig. S1). In the long-term scenario we explored the potential evolutionary effect of harvest on heterogeneity in reproductive potential, by considering a moderate heritability of pLRS. In all scenarios (harvested and non-harvested) natural and artificial selection favoured the survival of females of greater reproductive potential (Fig. 7). Random harvest had no selective effects because it reduced life expectancy equally for all females. On the contrary, selective harvest imposed strong directional selection, increasing the frequency of individuals with higher pLRS faster than natural selection in non-hunted populations. The strength of this effect will depend on the heritability of LRS. In most empirical studies, additive genetic variance of LRS is near

zero, leading to the expectation of no evolutionary response (Coltman *et al.* 2005; McFarlane *et al.* 2014), but in some cases there may be enough additive genetic variance to respond to selection (Kruuk *et al.* 2000; Wilson *et al.* 2005). Assuming moderate heritability of LRS, our long-term simulated scenario suggested a strong evolutionary effect on female heterogeneity due to the additive effects of natural and artificial selection.

Our results indicate that female heterogeneity affected population dynamics. After 50 years, the effect of harvest on population dynamics in the evolutionary scenario was no longer comparable to that observed in the short-term scenario because the average female heterogeneity in reproductive potential (Fig. 7) and its variance (Fig. S2) had changed. The frequency of long-lived and reproductively successful females increased with selection (Fig. 7), so that the population sustained a higher level of harvest over time, allowing recovery after the initial decrease (Fig. 6a). At $t = 50$, a 2-year-old female recruited in the population was more likely to have high potential fitness than at $t = 0$. Consequently, by removing young non-reproductive females, selective harvest had a negative effect on population size (Fig. 6a).

In ungulates, longevity is the main determinant of lifetime reproductive success (Clutton-Brock 1988), and females adopt a conservative reproductive strategy. The harvest-induced decrease in life expectancy should select for high reproductive investment in early life. Although simulations support this hypothesis (Proaktor, Coulson & Milner-Gulland 2007), there is no empirical evidence for it (Mysterud, Yoccoz & Langvatn 2009). Early primiparity may reduce future reproduction and possibly survival (Hamel *et al.* 2010). If early primiparity had a strong fitness cost, strong selective harvest of non-lactating females that increases pre-reproductive mortality may select for a reproductive strategy opposite to that shaped by natural selection.

MANAGEMENT IMPLICATIONS

When the primary aim of female harvest is to maximize hunting opportunities rather than control population growth, management should favour the survival of females with high reproductive potential. Our results suggest that selective harvest of non-lactating females increased survival of females with high reproductive potential after they had reached reproductive age, but the positive effect on population dynamics was sharply reduced by pre-reproductive adult female mortality. In species with delayed primiparity, strong heterogeneity may reduce the negative impact of pre-reproductive adult female mortality under selective compared to random harvest, in particular if females of low reproductive potential normally suffer high natural mortality before primiparity. This is inevitable as hunters would be unable to distinguish pre-reproductive from older females. A strong positive effect on population growth rate of selective

compared to random harvest should be expected only if both orphan mortality and harvest rate are high. Otherwise, a policy that simply sets a female quota with no prescriptions about selective harvest would be just as effective but easier to implement.

Our long-term scenario shows that harvest could affect the distribution of female heterogeneity in reproductive success, potentially even leading to an evolutionary response that may allow a greater level of harvest. Further investigation of the genetic basis of lifetime reproductive success in hunted ungulates is required before the results of this modelling exercise can be included in management decisions.

Authors' contributions

M.R. and M.F.-B. conceived the ideas; M.F.-B., S.C. and S.H. collected the data; M.R. analysed the data; M.R., M.F.-B., S.C. and S.H. led the writing of the manuscript. All authors wrote and revised drafts of the manuscript and gave final approval for publication.

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Data accessibility

Data used in this article are provided as part of the main text and supporting information.

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Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. Model selection (Table S1–S5).

Appendix S2. Variability in potential lifetime reproductive success (Figs S1 and S2).