

Effects of selective harvest of non-lactating females on chamois population dynamics

Marco Rughetti^{1*} and Marco Festa-Bianchet²

¹Département de biologie, Université de Sherbrooke, Sherbrooke, QC J1K 2R1, Canada; and ²Département de biologie, Centre d'études nordiques, Université de Sherbrooke, Sherbrooke, QC J1K 2R1, Canada

Summary

1. In large mammals, regulations or hunter preference often lead to selective harvest of non-lactating females, with unknown impacts upon population growth. Because female survival has very high elasticity effects on population growth, an assessment of the magnitude and selectivity of female harvest is crucial to understand population dynamics of sport-hunted ungulates. Hunting accounts for most mortality of adult chamois *Rupicapra rupicapra* and regulations typically discourage the harvest of lactating females as orphaned kids have reduced survival rates.

2. We used an individual-based model, produced from empirical data, to explore the effects of selective removal of non-lactating females on chamois population dynamics.

3. Harvest intensity had much stronger effects on female population dynamics than selectivity for reproductive status. Selective harvest of non-lactating females had very weak effects on population size and then only at a high harvest rate and under strong selectivity. Assuming no difference in winter survival between orphaned and non-orphaned kids, harvest of non-lactating females decreased population size at equilibrium compared to a random female harvest, whereas the opposite was true when assuming 50% lower survival of orphaned kids.

4. Selective harvest of non-lactating females may avoid the negative effects of orphaning on juvenile survival, but increases mortality of pre-reproductive females that normally enjoy high survival and have high reproductive value.

5. *Synthesis and applications.* The impact of selective harvest of non-lactating females upon population dynamics is likely to be more affected by the age structure of lactating and non-lactating females rather than by the survival of orphan and non-orphan juveniles. High harvest of pre-reproductive females has undesirable effects on population dynamics, which must be considered alongside any cultural preferences of hunters when developing hunting regulations or policies.

Key-words: age structure, female harvest, orphaning, population dynamics, selective hunting

Introduction

Sport harvest of large mammals is typically male-biased, to satisfy hunter preferences (Ginsberg & Milner-Gulland 1994; Nilsen & Solberg 2006) and to maintain population size and hence hunting opportunities (Langvatn & Loison 1999; Solberg *et al.* 1999). Often, however, females are harvested to maintain populations within certain density objectives (Festa-Bianchet 2007). Hunters may avoid harvesting lactating females (Mysterud 2011). Hunter preference for non-reproducing females was reported in brown

bears *Ursus arctos* (Bischof *et al.* 2009), moose *Alces alces* (Solberg *et al.* 2000; Ericsson 2001; Nilsen & Solberg 2006), chamois (Rughetti & Festa-Bianchet 2011) and red deer *Cervus elaphus* (Mysterud, Yoccoz & Langvatn 2009). Even when hunting regulations do not directly discourage the harvest of lactating females, hunters are often reluctant to harvest females with offspring at heel because of cultural reasons (Nilsen & Solberg 2006; Mysterud 2011; Rughetti & Festa-Bianchet 2011). Harvest of reproductive females may increase mortality of orphaned offspring. For example, in Sweden, hunting regulations prohibit the harvest of brown bears in family groups, as females have an important effect on survival of dependent offspring (Bischof *et al.* 2009). In ungulates, the effect of

*Correspondence author. Corso Dante Livio Bianco 12010 Valdieri (CN), Italy. E-mail: marco_rughetti@libero.it

orphaning near the end of lactation on juvenile survival has only been measured in a handful of species. In big-horn sheep *Ovis canadensis*, experimental removal of mothers in September did not affect lamb survival (Festa-Bianchet, Jorgenson & Wishart 1994), whereas in red deer, orphaning before 1 year of age increased mortality for both male and female orphans compared to non-orphans (Andres *et al.* 2013).

Harvesting of females according to reproductive status may also become a selective pressure. Although theory suggests that high female harvest rate may select for greater reproductive effort early in life (Proaktor, Coulson & Milner-Gulland 2007), empirical evidence does not support that hypothesis for ungulates (Mysterud, Yoccoz & Langvatn 2009). Reproductive status is the main factor affecting hunter selectivity in the harvest of large mammal females (Mysterud 2011), and adult female survival has very high elasticity effects on population growth rate (Gaillard, Festa-Bianchet & Yoccoz 1998; Gaillard *et al.* 2000). Therefore, assessment of the magnitude and the selectivity of female harvest is crucial to understanding the population dynamics of sport-hunted ungulates.

Alpine chamois are hunted in most of their distribution, where hunting probably accounts for most mortality of adults. Males are mostly hunted for their horns, although hunter selectivity for chamois horn size is unlikely to have ecological or evolutionary consequences (Rughetti & Festa-Bianchet 2010). On the contrary, females are selectively harvested according to their reproductive status (Rughetti & Festa-Bianchet 2011). Females produce one offspring usually in early May (Rughetti & Festa-Bianchet 2010), and primiparity is between two and 4 years (Houssin, Loison & Gaillard 1993; Rughetti & Festa-Bianchet 2011). Harvest of non-lactating females may prevent orphaning, which may reduce survival (Andres *et al.* 2013) and body growth of juveniles, particularly males (Festa-Bianchet, Jorgenson & Wishart 1994; Andres *et al.* 2013). There are, however, no published data on the effects of orphaning on chamois kid survival. Rughetti and Festa-Bianchet (2011) pointed out a potential perverse consequence of harvesting non-lactating females: many hunters took 2-year-old females, which are pre-reproductive and therefore non-lactating in most populations (Bauer 1985; Crampe *et al.* 2004; Rughetti & Festa-Bianchet 2011), but enjoy very high natural survival (Loison, Gaillard & Houssin 1994; Loison *et al.* 1999) and have very high reproductive potential.

Little is known about how selective removal of non-lactating females may affect ungulate population dynamics. Here we use empirical data on chamois to construct an individual-based model to quantify the likely consequences of hunter selectivity for non-lactating females. We evaluated how varying levels of harvest and selectivity for non-lactating females could affect (i) population size at equilibrium, (ii) age structure, (iii) hunting mortality of different age classes and (iv) recruitment. By comparing

the likely ecological consequences of random and selective harvest of females with respect to their reproductive status, we sought to identify which management practice would have the least impact on population dynamics.

Materials and methods

We used an individual-based model of a population of female chamois. Only the female portion of the population was modelled. Population dynamics emerged from empirical data extracted from the literature on survival and reproduction of long term studied chamois populations in the European Alps and Pyrenees (Tables 1 and 2, and online Supporting information). We follow Grimm *et al.* (2006) in describing our model. All analyses were conducted in R (R Development Core Team 2012).

OVERVIEW

State variables and scales

The model accounted for four hierarchical scales: individual, age class, population and environment. We assumed that any changes in male population size would not affect female fecundity or offspring survival, because the proportion of males in hunted chamois populations does not approach the very low levels that affect fecundity in ungulates (Milner-Gulland *et al.* 2003; Rughetti & Festa-Bianchet 2010). Individuals were characterized by two state variables: age and reproductive status. Young of the year and 1-year-old females were referred to as kids and yearlings. Adult females (2 years and older) were grouped into four age classes: 2 years, 3 years, adults (4–8 years) and senescent (9 years and older), based on differences in natural survival and reproductive rates (Loison, Jullien & Menaut 1999). After the

Table 1. Input parameters and assumptions of the individual-based model of female chamois population dynamics

Parameters	Description	Values used
Demography		
S_a	Density-dependent winter survival	Nonlinear function of n^*
R_a	Density-dependent reproductive success	Nonlinear function of n^*
n	Female population size	500 (at time step $t = 0$)
K	Female carrying capacity	500
Sex ratio at birth		1
Abiotic environment		Constant
K_{hm}	Additional mortality of orphan kids	0; 0.5
Hunting management		
HP_y	Yearling harvest rate	5%, 10% and 15%
HP_r	Adult female harvest rate	5%, 10% and 15%
CF	Parameter simulating hunter avoidance of lactating females. $0 < CF < 1$	1–0 (step 0.1)

*See eqns 1 and 5 in the main text.

Table 2. Age-class-specific survival and reproduction used to simulate density dependence in female chamois. *K*, carrying capacity; *n*, population size

	Increasing population; low density $n \rightarrow 0$	Stable population; high density $n = K$
Reproduction R_a		
2 years old	0.70 (e, i)	0.05 (a, c, j, k)
3 years old	0.80 (i)	0.30 (c, j, k)
Adults (4–8 years)	0.95 (i)	0.70 (c, j, k)
Senescent (9 years and older)	0.90 (d, i)	0.60 (c, j, k)
Survival S_a		
Kids	0.90 (b, g, i)	0.47 (b, g, i)
Yearlings	0.95 (g, f)	0.90 (g, f)
2 years old	0.97 (f, g, h, i)	0.95 (f, g, h, i)
3 years old	0.97 (f, g, h, i)	0.95 (f, g, h, i)
Adults (4–8 years)	0.97 (f, g, h, i)	0.95 (f, g, h, i)
Senescent (9 years and older)	0.90 (g, i)	0.70 (g, i)

a) Bauer (1985); b) Bonenfant *et al.* (2009); c) Crampe *et al.* (2004); d) Gaillard *et al.* (2000); e) Houssin, Loison & Gaillard (1993); f) Loison *et al.* (1999); g) Loison, Gaillard & Houssin (1994); h) Loison, Jullien & Menaut (1999); i) Loison *et al.* (2002); j) Morin (2013); k) Rughetti & Festa-Bianchet (2011). See supporting information for further details.

hunting season, kids were classified as orphan or not. Environment was characterized by female population size, harvest rate and hunter avoidance of lactating females. ‘Population size’ refers to the number of females. The abiotic environment was assumed to be constant.

Process overview and scheduling

The model had a 1-year time step (Fig. 1). Population size reduced overwinter survival and reproduction. Harvest rate affected female survival, and for a given level of harvest, mortality of non-lactating females increased with hunter avoidance of lactating females. Yearling harvest was random and there was no kid harvest, as is typical of most hunted populations of chamois. Hunting of lactating females affected indirectly overwinter survival of orphaned kids.

DESIGN CONCEPTS

We compared simulations with survival of orphaned kids either equal to or half that of non-orphans. We assumed that environmental stochasticity was constant because we sought to compare population dynamics under random removal of females and with selective removal of non-lactating females.

DETAILS

Initialization

Simulations began with the stationary age structure obtained from age-specific survival rates (Table 2) and included 59 yearlings, 53 2-year-olds, 50 3-year-olds, 216 adult and 123 senescent females, for a total of 500. Other input parameters are summarized in Table 1.

Input

For each harvest scenario, we ran 1000 simulations over 100 years. We first assumed equal survival of orphans and non-orphans. We modelled female harvest rates of 5%, 10% and 15% based on available information on chamois harvest in the Western Alps, and used these rates in all analyses. For each rate, we simulated several harvest scenarios increasing the proportion of non-lactating females harvested, to simulate hunter avoidance of lactating females. Finally, we repeated the analysis assuming that orphaned kids were half as likely as non-orphaned kids to survive the winter. Because there are no published data on survival of orphaned chamois kids, we chose our categories of 0% and 50% decrease in survival from available knowledge on the effects of orphaning in other ungulates (Table 3).

Submodels

Female reproduction. To simulate density-dependent reproduction, we used a logistic function:

$$R_a = \frac{1}{1 + \exp(+b(\frac{n}{K} - q))} \quad \text{eqn 1}$$

(Collier & Kremetz 2007; Myserud & Bischof 2010) where R_a is the probability of a female of age class *a* to have a kid in

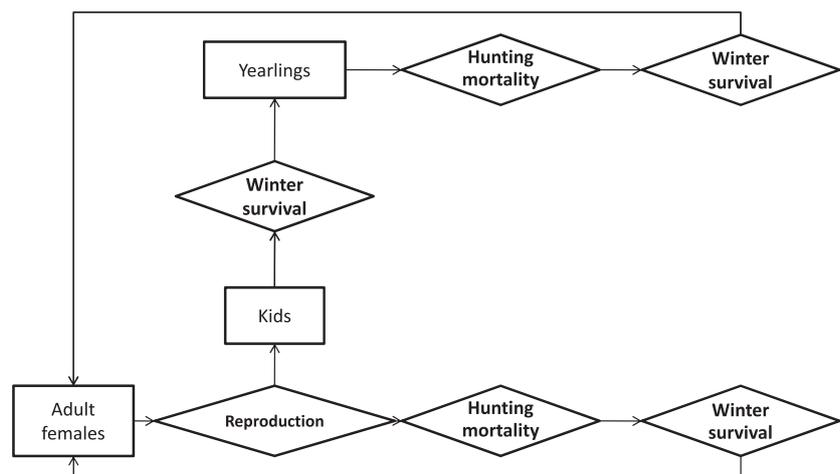


Fig. 1. Chamois population dynamics model showing transitions between age classes, processes and causes of these transitions.

Table 3. Survival of orphan and non-orphan juveniles in north-temperate ungulates, listed in order of orphan sample size

Species	Sex	Sample size (orphans; non-orphans)	Survival rate as % (orphans; non-orphans)	Weaning status at orphaning	Reduced survival of orphans?	Cause of adult female mortality	References
<i>Cervus elaphus</i>	M	74; 912	*	Near weaning	Yes	Natural and culls	a
<i>Cervus elaphus</i>	F	55; 893	*	Near weaning	Yes	Natural and culls	a
<i>Ovis canadensis</i>	M	33; 63	76; 84	2–4 weeks before weaning	No (1 year) [†]	Manipulation experiment	b
<i>Ovis canadensis</i>	F	24; 75	83; 85	2–4 weeks before weaning	No (1 year) [†]	Manipulation experiment	b
<i>Odocoileus virginianus</i>	Both	21; 31	One non-orphan died	Weaned	No (Overwinter)	Manipulation experiment	c
<i>Alces alces</i>	Both	17; 13	88; 100	Weaned	No (to April)	Manipulation experiment	d
<i>Odocoileus virginianus</i>	M	15; 19	87; 53	Weaned	No [‡]	Hunting, poaching, vehicles	e
<i>Odocoileus virginianus</i>	Both	14; 10	79; 100	Weaned	Yes (to October 9)	Manipulation experiment	f
<i>Odocoileus virginianus</i>	F	13; 94	/	Weaned	No (annual survival)	Vehicles or capture mortality	g
<i>Rangifer tarandus</i>	Both	12; 24	/	Weaned	No (to March 16)	Manipulation experiment	h
<i>Rangifer tarandus</i>	Both	8; 120	62; 78	Mostly already weaned	Unclear	Hunting	i

a) Andres *et al.* (2013); b) Jorgenson, Festa-Bianchet & Wishart (1993); Festa-Bianchet, Jorgenson & Wishart (1994); c) Woodson *et al.* (1980); d) Jolicoeur & Crête (1988); e) Hölzenbein & Marchinton (1992a,b); f) Giuliano *et al.* (1999); g) Etter *et al.* (1995); h) Holand *et al.* (2012); i) Joly (2000).

*Andres *et al.* (2013) estimated the effect of orphaning on the risk of death as 3.41 and 1.67 times higher for males and females orphans, respectively, compared to non-orphans. They did not provide survival rates.

[†]No difference in survival at 2 years too.

[‡]Authors suggested that non-orphans suffered higher predation rate than orphans because of their higher emigration rate.

September (Morin 2013), n is the number of females in the population and K is the carrying capacity. q and b are the parameters to be estimated and can be calculated as:

$$q = \log(R_0/(1 - (R_0)))$$

$$b = q - \log(R_k/(1 - (R_k)))$$

where q is the intercept of the model in eqn 1 for $n = 0$ and R_0 is the probability to reproduce for $n = 0$. b is the slope of the model in eqn 1 and R_k is the probability to reproduce for $n = K$. When $n \gg K$ (n tends towards infinity), R_a tends to zero. Using data from Table 2, we estimated a and b for each age class. Demographic stochasticity of reproduction acted independently on all females and was modelled by binomial sampling with probability R_a (Sæther, Engen & Solberg 2001; Akçakaya 2002).

Hunting mortality. Harvest rate was the ratio of the annual harvest over the current population size. As is typical of hunting regulations (Rughetti & Festa-Bianchet 2010), harvest rate was estimated separately for adult (HP_f) and yearling females (HP_y ; Table 1) as the probability of an individual being harvested if hunters took females randomly within an age class. Harvest rate of adult females, however, could vary as a function of reproductive status. For each year time step of the simulation, the number of yearlings ($n_{\text{yearlings}}$), lactating ($n_{\text{lact.F}}$) and non-lactating ($n_{\text{non-lact.F}}$) adult females in the harvest were obtained from the following equations:

$$n_{\text{yearlings in the harvest quota}} = n_{\text{yearlings in the population}} * HP_y \quad \text{eqn 2}$$

$$n_{\text{lact.F in the harvest quota}} = n_{\text{lact.F in the population}} * HP_f * CF \quad \text{eqn 3}$$

$$n_{\text{non-lact.F in the harvest quota}} = n_{\text{non-lact.F in the population}} * HP_f * (1 - (CF * P_p)) / (1 - P_p) \quad \text{eqn 4}$$

To simulate hunter avoidance of lactating females, we introduced a correction factor CF which was the ratio of the proportion of lactating females in the harvest (P_h) over the proportion of lactating females in the overall population of adult females (P_p): $CF = P_h/P_p$. We varied CF from 0 to 1 with a step of 0.1; CF = 1 indicated that harvest was independent of reproductive status. A decreasing CF indicated increasing avoidance of lactating females. For example, given $P_p = 0.8$ and imposing CF = 0.9, the frequency of lactating adult females in the harvest was $0.8 * 0.9 = 0.72$. With CF = 0, only non-lactating females were harvested. When $CF \neq 1$, adult female hunting mortality depends on HP_f , P_p and CF. Therefore, harvest rate of non-lactating females increased with both the proportion of lactating females in the population and hunter avoidance of lactating females. Once age classes (yearling and adults) and harvest rates specific to each reproductive status were determined, the simulation removed individuals randomly from the population. Given $CF = P_h/P_p$, we can obtain eqn 4 from $n_{\text{non-lact.F in the harvest quota}} = n_{\text{non-lact.F in the population}} * HP_f * (1 - P_h) / (1 - P_p)$ through elementary algebra.

Winter survival. To simulate density dependence in survival, we used the same logistic function as for reproduction:

$$S_a = \frac{1}{1 + \exp(+b(\frac{n}{k}) - q)} \quad \text{eqn 5}$$

where S_a is the probability of a female of age class a to survive. Similar to reproduction, q and b can be calculated as:

$$q = \log(S_0 / (1 - (S_0)))$$

$$b = q - \log(S_k / (1 - (S_k)))$$

where S_0 is the probability of a female to survive the winter when $n = 0$ and S_k is the probability to survive when $n = K$. Using data from Table 2, we estimated a and b for each age class. Because natural survival of prime-aged female chamois is very high and appears independent of most changes in weather or density (Loison, Jullien & Menaut 1999; Loison *et al.* 1999, 2002; Gaillard *et al.* 2000), for survival of females aged 2–8 years, we rearranged eqn 5 so that when $n \gg K$, S_a only decreased to 0.9. Therefore, prime-age survival varied between 0.97 and 0.90. Demographic stochasticity of survival acted independently on all females and was modelled by binomial sampling with probability S_a (Akçakaya 2002).

Recruitment and population growth. Assuming an even birth sex ratio, the numbers of female kids (n_K) in autumn was given by:

$$n_K = \left(\sum_{i=1}^n \text{binom}(R_a, i) \right) * 1/2 \quad \text{eqn 6}$$

Density dependence in winter survival of kids was modelled by eqn 5 using data from Table 2. We compared scenarios with different effects of female hunting mortality on the survival of orphaned kids. Given S_{kid} as the overwinter survival of non-orphaned, the probability of an orphaned kid to survive (S_{orph}) was:

$$S_{\text{orph}} = S_{\text{kid}} * (1 - K_{\text{hm}}) \quad \text{eqn 7}$$

where K_{hm} is the difference in survival of an orphaned compared to a non-orphaned kid, either 0 or 0.5. Demographic stochasticity of survival acted independently on all kids and was modelled by binomial sampling (Akçakaya 2002).

Results

For harvest rates of 5%, 10% and 15%, the population reached a stable age distribution and equilibrium size after about 15, 20 and 40 years, respectively, under both random and selective harvest. For harvest rates of 5%, 10% and 15%, and random harvest of females, population size at equilibrium averaged, respectively, 1.6%, 4.9% and 14.3% greater when orphaning had no effects on survival compared to when it halved kid survival.

Hunter preference for non-lactating females led to an increased proportion of 2-year-olds in the harvest and a decrease in the proportion of adult females harvested (Fig. 2). Assuming no effect of orphaning on kid survival ($K_{\text{hm}} = 0$), increased harvest of non-lactating females lowered female population size at equilibrium compared to a random harvest (Fig. 3). With $K_{\text{hm}} = 0.5$, we obtained the opposite result. For a harvest rate of 5%, there was no effect of selective harvesting on population size at equilibrium, whereas for rates of 10% and 15%, population size increased, respectively, by 0.6% and 4.8% when hunters removed only non-lactating females compared to a random harvest (Fig. 3).

An increase in harvest rate skewed the age structure towards younger females (Fig. 4). When hunters removed only non-lactating females ($CF = 0$, Fig. 4), however, the proportion of adult and senescent females were, respectively, lower (by 1.4%, 3.0% and 4.4% for harvest rates

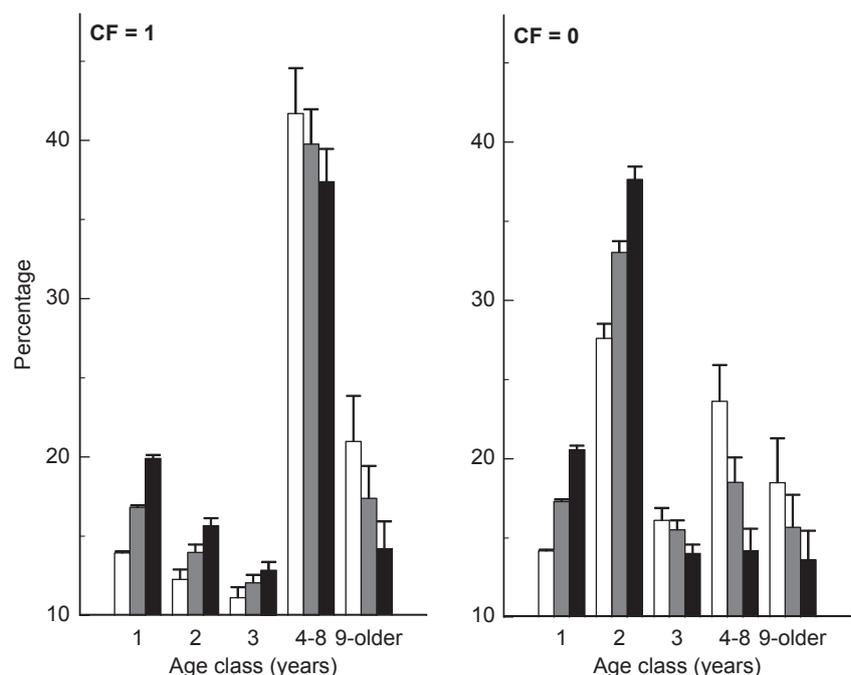


Fig. 2. Age distribution of harvested female chamois (+SD) under varying harvest rates (5% white, 10% grey and 15% black bars) and hunter preference for non-lactating females (CF = 1: harvest independent of reproductive status; CF = 0: only non-lactating females harvested). Data are averages of 1000 simulations over 100 years.

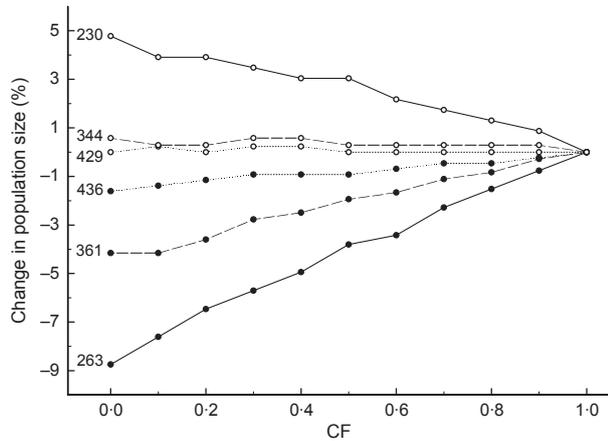


Fig. 3. Relative change in female population size under increasing hunter selectivity for non-lactating chamois (CF = 1: female harvest independent of reproductive status; CF = 0: only non-lactating females harvested). Results are based on 1000 simulations over 100 years. Harvest rates were set at 5%, 10% and 15% (dotted, dashed and solid lines), and survival of orphaned kids was either equal (solid circles) or half as much (empty circles) as that of non-orphaned kids. Numbers on the left side of the figures indicate population size at equilibrium under random harvest of adult females (CF = 1). Carrying capacity was 500 females. Populations reached equilibrium after 15, 20 and 40 years, respectively, for harvest rates of 5%, 10% and 15%.

of 5%, 10% and 15%) and higher (by 1.4%, 3.4% and 11.4% for corresponding harvest rates; Fig. 4) compared to random harvest (CF = 1, Fig. 4).

Compared to random harvest, selective harvesting of non-lactating females increased hunting mortality of 2- and 3-year-olds and lowered that of adult and senescent females. When only non-lactating females were harvested, at harvest rates of 5%, 10% and 15%, hunting mortality of 2-year-old females more than doubled, increasing by 2.22, 2.31 and 2.34 times compared to ran-

dom female harvest. For 3-year-olds, the corresponding increases were 1.52, 1.45 and 1.36 times. On the contrary, hunting mortality of adult and senescent females was reduced, respectively, to 0.58, 0.49, 0.40 and 0.82, 0.74, 0.67 times compared to random harvests at female harvest set at 5%, 10% and 15%.

Assuming no effect of orphaning on kid survival, and given a population size of 263 females and harvest rate of 15%, the age structure obtained from random harvest (dark bars and CF = 1 in Fig. 4) remained stationary from year t to $t + 1$, whereas with selective harvest of non-lactating females (dark bars and CF = 0 in Fig. 4), the number of animals removed by hunting and natural mortality was higher than the number of yearlings recruited (Fig. 5), leading to a decline in population size. When the survival of orphaned kids was reduced by 50%, given the same population of 230 females and a harvest rate of 15%, the age structure obtained from random harvest (dark bars and CF = 1 in Fig. 4) remained stationary from year t to $t + 1$, but with selective harvest of non-lactating females (dark bars and CF = 0 in Fig. 4), the number of yearlings recruited was higher than the number of animals that died (Fig. 5), allowing an increase in population size.

Discussion

Our simulations showed how harvest selectivity for reproductive status in female chamois may affect age-specific mortality, age structure and population dynamics (Fig. 3). Harvest intensity is typically the main factor driving dynamics of hunted populations of ungulates (Myrsetrud 2011). Our simulations suggest that the effect of selective harvest of non-lactating female chamois on population size was much weaker than that attributable to changes in harvest rate, and was evident only at high harvest rate and with strong selectivity (Fig. 3). Crucially, however,

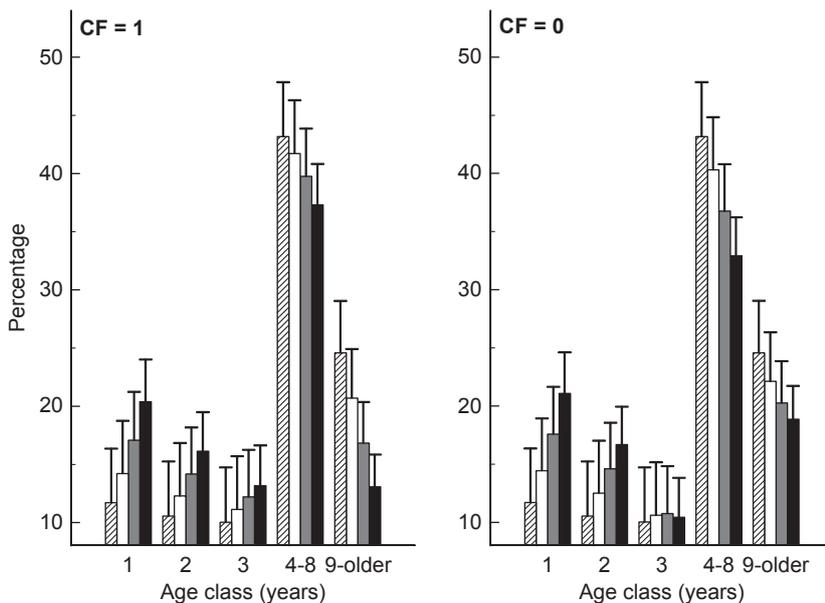
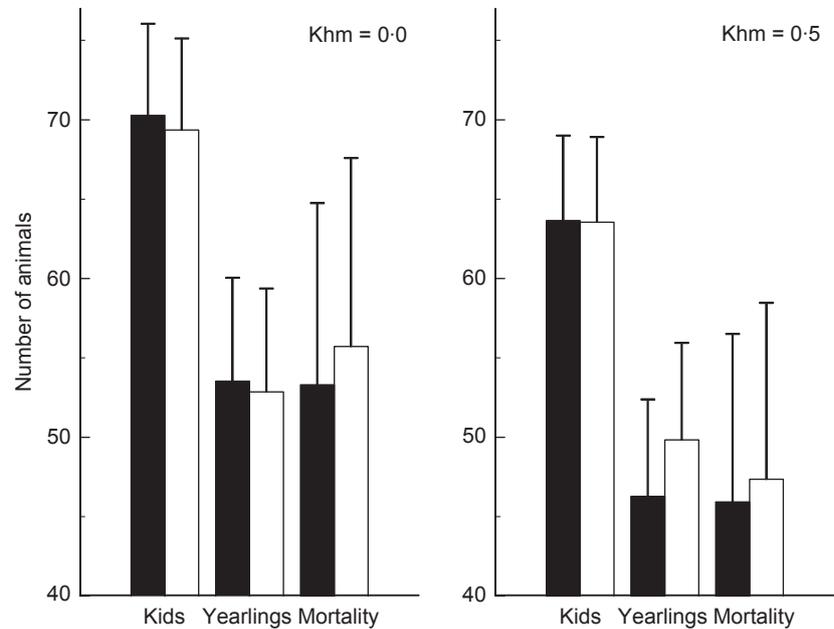


Fig. 4. Population age class structure at equilibrium with SD under varying harvest rate (5% white, 10% grey and 15% black bars), and hunter preference for non-lactating female chamois (CF = 1: harvest independent of reproductive status; CF = 0: only non-lactating females harvested). Data are from 1000 simulations over 100 years. Hatched columns indicate the age class structure of a non-hunted population.

Fig. 5. Simulated chamois population recruitment and mortality with 15% harvest rate, when orphaning does not affect kid survival ($K_{hm} = 0$) or assuming 50% lower survival of orphaned kids ($K_{hm} = 0.5$). Black bars indicate the yearly numbers of kids and yearlings recruited in the population and the number of females that die from natural and hunting mortality, with SD ($n = 1000$ simulations), given the age structure produced from random harvest (black bars and $CF = 1$ in Fig. 4). White bars report estimates given the age structure produced when only non-lactating females are harvested (black bars and $CF = 0$ in Fig. 4). The two panels show estimates.



the impact of selectivity for non-lactating females on population dynamics depends on the survival of orphaned kids. When orphaning in our model population had no effect on kid survival, removing non-lactating females reduced population growth, leading to a lower population size at equilibrium compared to a random harvest of adult females. On the contrary, when assuming a decrease in survival of 50% for orphaned kids, our simulation suggested a slight increase in population size at equilibrium, but only under strong harvest rate and selectivity (Fig. 3). With light harvest rates, the effects of hunters' preference for non-lactating females are negligible, and with high harvest rate, selectivity for non-lactating females must be very strong to cause an appreciable change in population size. Given that regulations or hunter preferences against harvest of lactating females are common for large herbivores, our research suggests that it is crucial to document the impact of orphaning on juvenile growth and survival. That information, however, requires data on individually marked animals in hunted populations. In the literature, there are very few data on orphan ungulate survival and none for chamois (Table 3). Only two studies monitored a large sample size of orphans. In bighorns, there was no difference in survival between lambs orphaned at 3–5–4 months and non-orphans (Festa-Bianchet, Jorgenson & Wishart 1994), whereas in red deer, calves orphaned before 12 months suffered natural mortality higher by about 1.67 times for females and 3.41 times for males compared to non-orphans (Andres *et al.* 2013), although the actual mortality rates were not reported. For bighorns, orphaning had no effects on mass at 1 year, age at primiparity, lifetime reproductive success and longevity for females, whereas orphaned males had smaller horns and were lighter than non-orphans as adults (Festa-Bianchet, Jorgenson & Wishart 1994). Similar to bighorn, in red deer, orphaning had no effect in the likelihood of

reproduction for females, but reduced antler growth (Andres *et al.* 2013). Andres *et al.* (2013) monitored the offspring of adult females that died of natural mortality, which in large herbivores is typically very low (Gaillard *et al.* 2000). Therefore, female red deer may not have been very good mothers in their last reproduction, leading to an overestimate of orphan mortality. Maternal care is particularly important in spring and summer when lactation plays a crucial role for offspring growth (Gerard & Hansen 1992). In temperate herbivores, harvest is typically in early autumn, after juveniles have completed much of their pre-winter body growth (Festa-Bianchet, Jorgenson & Wishart 1994) and are either weaned or near weaning, therefore orphaning may have a weak impact on offspring survival. Although empirical data are necessary to test whether orphaning affects survival of chamois kids, our review of available knowledge in ungulates (Table 3) suggests that a reduction in survival of 50% for orphans is a very conservative choice.

Our models accounted for potential effects of orphaning on offspring survival, but other effects should also be considered, such as a decrease in male body mass or weapon growth (Festa-Bianchet, Jorgenson & Wishart 1994; Andres *et al.* 2013) that may negatively affect future reproduction. Orphaned females may be more likely to emigrate if they have a lower social rank (Etter *et al.* 1995) and their future reproduction may be compromised. Otherwise, as suggested by empirical data (Rughetti & Festa-Bianchet 2011), our results confirm that increasing harvest selectivity for non-lactating females mostly increases the mortality of 2- and, to a lesser extent, 3-year-olds. Those age classes enjoy high natural survival and have high reproductive potential (Loison, Gaillard & Houssin 1994; Gaillard *et al.* 2000).

High mortality of pre-reproductive females may select for a reproductive strategy of high investment in early life,

possibly reducing natural survival and longevity (Proaktor, Coulson & Milner-Gulland 2007). Longevity is the main determinant of female reproductive success (Clutton-Brock 1988), but heavy harvest of non-lactating female may artificially select for a reproductive strategy opposite to natural selection. High mortality of pre-reproductive females occurs in chamois populations with strong selectivity for non-lactating females, where Rughetti and Festa-Bianchet (2011) reported that 43% of female harvested were 2–3 years old, compared to 28% in populations with light selectivity.

Harvest mortality of 2- and 3-year-old female chamois increased with increasing hunter selectivity because most of these young females do not reproduce in stable populations. In large herbivores, primiparity is mostly at 2 or 3 years (Gaillard *et al.* 2000). Some species delay primiparity to 4–5 years (mountain goat *Oreamnos americanus*; Festa-Bianchet, Urquhart & Smith 1994), or mostly reproduce at 3 years in established populations such as chamois (Rughetti & Festa-Bianchet 2011) and ibex *Capra ibex* (Michallet *et al.* 1994). High population density may delay primiparity, but if harvested populations are kept below carrying capacity, density dependence should not play a major role in the relationship between selective harvest and age-specific mortality. Populations on poor habitat may delay primiparity independently of weather or density (Gaillard *et al.* 2000). In such cases, selective harvest may further increase mortality of pre-reproductive females, as documented in chamois. Selective harvest of non-lactating females is more likely to occur for ungulates living in open habitats, where observation of offspring at heel is easier than in forest-dwelling species such as many deer.

Our analysis is relevant for management practices that seek to minimize the impact of harvest on population growth. Hunters and managers of large mammals often assume that harvest of non-lactating females has a lower impact on population growth than a random harvest of adult females, because orphans are expected to suffer high mortality. When most non-lactating females are pre-reproductive, however, our work suggests that female harvest irrespective of reproductive status has an impact on population dynamics either equivalent to or in some cases lower than selective harvest of non-lactating females. There is little evidence that orphaning near the time of weaning strongly reduces the survival of juvenile ungulates (Table 3). One may speculate that mortality of orphans may increase in harsh winters, because of lower body weight compared to non-orphans, in particular for males (Festa-Bianchet, Jorgenson & Wishart 1994). In large herbivores, however, juvenile survival is naturally low and variable (Gaillard *et al.* 2000); therefore, high mortality of offspring is not exceptional. Our results suggest that a slight decrease in female harvest rate would be much more effective in allowing population growth than an increase in selective harvest of non-lactating females. On the contrary, intense removal of non-lactating females

would focus hunting mortality on pre-reproductive females that in natural population enjoy high survival and have the highest reproductive value. The ecological and potential evolutionary effects of non-lactating female harvest merit attention in management of large herbivores.

Although it is possible that lactating females have on average higher reproductive potential than non-lactating ones (Hamel *et al.* 2009), that argument is unlikely to be of concern when regulations or hunter preferences concentrate the harvest on pre-reproductive females. In many populations of chamois, almost all 2-year-olds are non-lactating, regardless of individual differences in reproductive potential. Another important issue is that of cultural preferences, as some hunters are unwilling to harvest females with kids at heel. Our previous work, however, shows that regulations have a much stronger role than cultural preferences in harvest selectivity: where penalties for harvesting lactating females are low, many fewer 2-year-olds are shot (Rughetti & Festa-Bianchet 2011). Currently, in many parts of the Alps, hunters are penalized if they harvest a lactating female. We suggest that removing that penalty would have no effect on chamois population dynamics, while leaving hunters with the opportunity to select a non-lactating female if they wish.

In ungulates, the survival of pre-reproductive females is a more important determinant of population growth than juvenile survival (Gaillard, Festa-Bianchet & Yoccoz 1998). Our results suggest that when harvest rate is light, the level of selectivity for non-reproductive females has negligible effects on population dynamics. When harvest rate is high, however, harvest selectivity becomes an important issue because of its potential ecological and evolutionary consequences. Depending on the effects of orphaning on juvenile survival, selective harvest may either increase or decrease population growth rate compared to random harvest. To further illuminate the best harvest strategy, it is essential to obtain more information on the effects of orphaning on juvenile ungulates.

Acknowledgements

We thank the Parco Naturale Alpi Marittime, Comprensorio Alpino Cuneo 4 and Verbano Cusio-Ossola 2 for allowing access to the data. Funding was provided by the Natural Sciences and Engineering Research Council of Canada. We also thank Simona Imperio and an anonymous reviewer for insightful comments on previous draft of this paper.

Data accessibility

All data used in this manuscript have already been published in scientific literature. Descriptions of all data sources and references can be found in Supporting information.

References

- Akçakaya, H.R. (2002) Estimating the variance of survival rates and fecundities. *Animal Conservation*, **5**, 333–336.
- Andres, D., Clutton-Brock, T.H., Kruuk, L.E.B., Pemberton, J.M., Støppler, K.V. & Ruckstuhl, K.E. (2013) Sex differences in the conse-

- quences of maternal loss in a long-lived mammal, the red deer (*Cervus elaphus*). *Behavioral Ecology and Sociobiology*, **67**, 1249–1258.
- Bauer, J.J. (1985) Fecundity patterns of stable and colonising chamois population of New Zealand and Europe. *The Biology and Management of Mountain Ungulates* (ed. S. Lovari), pp. 154–165. Croom Helm, London, UK.
- Bischof, R., Swenson, J.E., Yoccoz, N.G., Mysterud, A. & Gimenez, O. (2009) The magnitude and selectivity of natural and multiple anthropogenic mortality causes in hunted brown bears. *Journal of Animal Ecology*, **78**, 656–665.
- Bonenfant, C., Gaillard, J.M., Coulson, T., Festa-Bianchet, M., Loison, A., Garel, M. *et al.* (2009) Empirical evidence of density dependence in populations of large herbivores. *Advances in Ecological Research*, **41**, 313–357.
- Clutton-Brock, T.H. (1988) Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems, *Reproductive success* p. 538. University of Chicago Press, Chicago, Illinois, USA.
- Collier, B.A. & Kremenetz, D.G. (2007) Uncertainty in age-specific harvest estimates and consequences for white-tailed deer management. *Ecological Modelling*, **201**, 194–204.
- Crampe, J.-P., Caens, P., Florence, E., Gaillard, J.-M. & Loison, A. (2004) Variations de la reproduction en fonction de l'âge chez les femelles dans une population d'Isard (*Rupicapra pyrenaica pyrenaica*) protégée du Parc National des Pyrénées. *El sarrío pirenaico Rupicapra p. pyrenaica: Biología, Patología y Gestión*. (eds J. Herrero, E. Escudero, D. Fernández de Luco & R. García-González), pp. 207–214. Publicaciones del Consejo de Protección de la Naturaleza de Aragón, Zaragoza, Spain.
- Ericsson, G. (2001) Reduced cost of reproduction in moose *Alces alces* through human harvest. *Alces*, **37**, 61–69.
- Etter, D.R., Nixon, C.M., Sullivan, J.B. & Thomas, J.A. (1995) Emigration and survival of orphaned female deer in Illinois. *Canadian Journal of Zoology*, **73**, 440–445.
- Festa-Bianchet, M. (2007) Ecology, evolution, economics, and ungulate management. *Wildlife Science: Linking Ecological Theory and Management Applications* (eds T.E. Fulbright & D.G. Hewitt), pp. 183–202. CRC Press, Boca Raton, Florida, USA.
- 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., Urquhart, M. & Smith, K.G. (1994) Mountain goat recruitment: kid production and survival to breeding age. *Canadian Journal of Zoology*, **72**, 22–27.
- 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.
- Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. & Toigo, C. (2000) Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics*, **31**, 367–393.
- Gerard, J.-F. & Hansen, C.R. (1992) Social affinities and the basis of the social organization of a Pyrenean chamois (*Rupicapra pyrenaica*) population on open mountain range. *Behavioural Processes*, **28**, 111–122.
- Ginsberg, J.R. & Milner-Gulland, E.J. (1994) Sex-biased harvesting and population dynamics in ungulates: implications for conservation and sustainable use. *Conservation Biology*, **8**, 157–166.
- Giuliano, W.M., Demarais, S., Zaiglin, R.E. & Sumner, M.L. (1999) Survival and movements of orphaned white-tailed deer fawns in Texas. *The Journal of Wildlife Management*, **63**, 570–574.
- Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J. *et al.* (2006) A standard protocol for describing individual-based and agent-based models. *Ecological Modelling*, **198**, 115–126.
- 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.
- Holand, Ø., Weladji, R.B., Mysterud, A., Roed, K., Reimers, E. & Nieminen, M. (2012) Induced orphaning reveals post-weaning maternal care in reindeer. *European Journal of Wildlife Research*, **58**, 589–596.
- Hölzenbein, S. & Marchinton, R.L. (1992a) Emigration and mortality in orphaned male white-tailed deer. *The Journal of Wildlife Management*, **56**, 147–153.
- Hölzenbein, S. & Marchinton, R.L. (1992b) Spatial integration of maturing-male white-tailed deer into the adult population. *Journal of mammalogy*, **73**, 326–334.
- Houssin, H., Loison, A. & Gaillard, J.-M. (1993) Participation à la reproduction des femelles de chamois (*Rupicapra rupicapra*) en fonction de leur âge dans une population alpine chassée. *Gibier, Faune Sauvage*, **10**, 39–45.
- Jolicoeur, H. & Crête, M. (1988) Winter survival and habitat use of orphaned and non-orphaned moose calves in southern Quebec. *Canadian Journal of Zoology*, **66**, 919–924.
- Joly, K. (2000) Orphan caribou, *Rangifer tarandus*, calves: are-evaluation of overwinter survival data. *Canadian Field-Naturalist*, **114**, 322–323.
- Jorgenson, J.T., Festa-Bianchet, M. & Wishart, W.D. (1993) Harvesting bighorn ewes: consequences for population size and trophy ram production. *The Journal of Wildlife Management*, **57**, 429–435.
- Langvatn, R. & Loison, A. (1999) Consequences of harvesting on age structure, sex ratio and population dynamics of red deer *Cervus elaphus* in central Norway. *Wildlife Biology*, **5**, 213–223.
- Loison, A., Gaillard, J.-M. & Houssin, H. (1994) New insight on survivorship of female chamois (*Rupicapra rupicapra*) from marked animals. *Canadian Journal of Zoology*, **72**, 591–597.
- Loison, A., Jullien, J.M. & Menaut, P. (1999) Relationship between chamois and isard survival and variation in global and local climate regimes: contrasting examples from the Alps and Pyrenees. *Ecological Bulletins*, **47**, 126–136.
- 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.
- Loison, A., Toigo, C., Appolinaire, J. & Michallet, J. (2002) Demographic processes in colonizing populations of isard (*Rupicapra pyrenaica*) and ibex (*Capra ibex*). *Journal of Zoology*, **256**, 199–205.
- Michallet, J., Loison, A., Gaillard, J.-M. & Gauthier, D. (1994) Valeur de critères biométriques externes pour la détermination de l'âge du bouquetin des Alpes (*Capra ibex ibex*): rôle du sexe et de l'habitat. *Gibier, Faune Sauvage*, **11**, 99–118.
- Milner-Gulland, E.J., Bukreeva, O.M., Coulson, T., Lushchekina, A.A., Kholodova, M.V., Bekenov, A.B. & Grachev, I.A. (2003) Reproductive collapse in saiga antelope harems. *Nature*, **422**, 135.
- Morin, A. (2013) *Age-dependent costs of reproduction in female Alpine chamois (Rupicapra rupicapra)*. Master thesis, pp. 22–66. Université de Sherbrooke, QC J1K 2R1, Canada.
- Mysterud, A. (2011) Selective harvesting of large mammals: how often does it result in directional selection? *Journal of Applied Ecology*, **48**, 827–834.
- Mysterud, A. & Bischof, R. (2010) Can compensatory culling offset undesirable evolutionary consequences of trophy hunting? *Journal of Animal Ecology*, **79**, 148–160.
- Mysterud, A., Yoccoz, N.G. & Langvatn, R. (2009) Maturation trends in red deer females over 39 years in heavily harvested populations. *Journal of Animal Ecology*, **78**, 595–599.
- Nilsen, E.B. & Solberg, E.J. (2006) Patterns of hunting mortality in Norwegian moose (*Alces alces*) populations. *European Journal of Wildlife Research*, **52**, 153–163.
- Proaktor, G., Coulson, T. & Milner-Gulland, E.J. (2007) Evolutionary responses to harvesting in ungulates. *Journal of Animal Ecology*, **76**, 669–678.
- R Development Core Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rughetti, M. & Festa-Bianchet, M. (2010) Compensatory growth limits opportunities for artificial selection in Alpine chamois. *The Journal of Wildlife Management*, **74**, 1024–1029.
- Rughetti, M. & Festa-Bianchet, M. (2011) Effects of early horn growth on reproduction and hunting mortality in female chamois. *Journal of Animal Ecology*, **80**, 438–447.
- Sæther, B.-E., Engen, S. & Solberg, E.J. (2001) Optimal harvest of age-structured populations of moose *Alces alces* in a fluctuating environment. *Wildlife Biology*, **7**, 171–190.
- Solberg, E.J., Sæther, B.E., Strand, O. & Loison, A. (1999) Dynamics of a harvested moose population in a variable environment. *Journal of Animal Ecology*, **68**, 186–204.
- Solberg, E.J., Loison, A., Sæther, B.E. & Strand, O. (2000) Age-specific harvest mortality in a Norwegian moose *Alces alces* population. *Wildlife Biology*, **6**, 41–52.
- Woodson, D.L., Reed, E.T., Downing, R.L. & McGinnes, B.S. (1980) Effect of fall orphaning on white-tailed deer fawns and yearlings. *The Journal of Wildlife Management*, **44**, 249–252.

Received 16 January 2014; accepted 7 April 2014
Handling Editor: J. du Toit

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Data S1. Details on data on female survival and reproduction.

Fig. S1. Changes in reproductive rate of 2 (red)-, 3 (black)-year-old, adult (green) and senescent (yellow) females according to the number of chamois in the population.

Fig. S2. Changes in survival rate for kids (red), yearlings (orange), prime-aged (2–8 years old; black) and senescent (yellow) females according to the number of chamois in the population.