

Review

Demographic Side Effects of Selective Hunting in Ungulates and Carnivores

JOS M. MILNER,^{*,†‡} ERLEND B. NILSEN,^{*,†} AND HARRY P. ANDREASSEN^{*}

^{*}Hedmark University College, Department of Forestry and Wildlife Management, N-2480 Koppang, Norway

[†]Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, P.O. Box 1066, Blindern,

N-0316 Oslo, Norway.

Abstract: *Selective harvesting regimes are often implemented because age and sex classes contribute differently to population dynamics and hunters show preferences associated with body size and trophy value. We reviewed the literature on how such cropping regimes affect the demography of the remaining population (here termed demographic side effects). First, we examined the implications of removing a large proportion of a specific age or sex class. Such harvesting strategies often bias the population sex ratio toward females and reduce the mean age of males, which may consequently delay birth dates, reduce birth synchrony, delay body mass development, and alter offspring sex ratios. Second, we reviewed the side effects associated with the selective removal of relatively few specific individuals, often large trophy males. Such selective harvesting can destabilize social structures and the dominance hierarchy and may cause loss of social knowledge, sexually selected infanticide, habitat changes among reproductive females, and changes in offspring sex ratio. A common feature of many of the reported mechanisms is that they ultimately depress recruitment and in some extreme cases even cause total reproductive collapse. These effects could act additively and destabilize the dynamics of populations, thus having a stronger effect on population growth rate than first anticipated. Although more experimental than observational studies reported demographic side effects, we argue that this may reflect the quite subtle mechanisms involved, which are unlikely to be detected in observational studies without rigorous monitoring regimes. We call for more detailed studies of hunted populations with marked individuals that address how the expression of these effects varies across mating systems, habitats, and with population density. Theoretical models investigating how strongly these effects influence population growth rates are also required.*

Keywords: big game, population dynamics, selective harvesting, trophy hunting, wildlife exploitation, wildlife management

Efectos Demográficos Secundarios de la Cacería Selectiva en Ungulados y Carnívoros

Resumen: *Los regímenes de cosecha selectiva a menudo son implementados porque las clases de edad y sexo contribuyen distintamente a la dinámica de la población y los cazadores muestran preferencias asociadas con el tamaño corporal y el valor como trofeo. Revisamos la literatura sobre los efectos de esos regímenes de cosecha sobre la demografía del resto de la población (denominados aquí efectos demográficos secundarios). Primero, examinamos las implicaciones de la remoción de la mayor parte de una clase específica de edad o sexo. Tales estrategias de cosecha a menudo sesgan la proporción de sexos de la población hacia hembras y reducen la edad promedio de los machos, lo que consecuentemente puede retardar fechas de nacimiento, reducir la sincronía de nacimientos, retardar el desarrollo de la masa corporal y alterar la proporción de sexos de las crías. Segundo, revisamos los efectos secundarios asociados con la remoción selectiva de relativamente pocos individuos específicos, a menudo machos grandes. Tal cosecha selectiva puede desestabilizar las estructuras sociales y la jerarquía de dominancia y puede provocar la pérdida de conocimiento social, infanticidio seleccionado sexualmente, cambios de hábitat entre hembras reproductivas y cambios en la proporción de sexos de las crías. Una característica común de muchos de los mecanismos reportados es que, a fin de cuentas, deprimen el reclutamiento y en algunos casos extremos causan un colapso reproductivo total. Estos efectos pueden actuar aditivamente y desestabilizar la dinámica de las poblaciones, por lo que tienen un mayor efecto que el esperado sobre la tasa de crecimiento poblacional. Aunque estudios más experimentales que de observación reportaron efectos demográficos secundarios, argumentamos que esto puede reflejar los sutiles mecanismos implicados, que pueden no ser detectados en estudios de observación sin regímenes de monitoreo rigurosos. Hacemos un llamado para la realización de estudios más detallados de poblaciones cazadas utilizando individuos marcados para abordar la variación de esos efectos en sistemas de apareamiento, hábitats y densidades poblacionales diferentes. También se requieren modelos teóricos que investiguen el impacto de estos efectos sobre las tasas de crecimiento poblacional.*

Palabras Clave: caza deportiva, caza mayor, cosecha selectiva, dinámica poblacional, explotación de vida silvestre, gestión de vida silvestre

Introduction

One of the central aspects of conservation biology is the relationship between human exploitation and the conservation of exploited resources. Throughout the world terrestrial mammals are hunted for sport, subsistence, and to control population size (Festa-Bianchet 2003). Hunting thus provides a significant source of meat and income in rural communities and beyond. Nevertheless, there are numerous examples of populations being overharvested, and subsistence hunting may be one of the most urgent current threats to the persistence of species in tropical ecosystems (Robinson & Bennett 2000; Milner-Gulland & Bennett 2003). Over 30% (250 species) of mammals currently listed as endangered on the World Conservation Union (IUCN) Red List are threatened by overexploitation (Baillie et al. 2004). Of these, larger mammal species, especially ungulates and carnivores, are particularly targeted (Baillie et al. 2004; Fig. 1).

Although subsistence hunting may take a random sample of a population, in many other instances—particularly associated with sport hunting of ungulates and carnivores—economic demands, ecological knowledge, and hunter preferences have led to the implementation of selective harvesting regimes (e.g., Ginsberg & Milner-Gulland 1994; Solberg et al. 1999). Here the offtake is focused around predetermined sex and/or age classes or specific individuals. Such selective hunting will, in addition to the obvious direct effects of reducing the population size, also affect the demography of populations by altering age and sex structures (Ginsberg & Milner-Gulland 1994) and potentially disrupting social systems (Swenson et al. 1997). Although such effects have received far less attention than direct overharvesting, they are potentially equally undesirable (Festa-Bianchet 2003) and occur even when the overall offtake is not regarded as excessively high. We sought to synthesize the current knowledge on how selective harvesting regimes affect the performance of populations. We considered the effects of hunting a large proportion of a selected sex and/or age class of the population, so affecting the age and sex structure of the remaining population and hunting specific individuals for trophies, so disturbing social structures and dominance hierarchies. We included recreational or sport hunting for meat and trophies, and poaching and population control where specific individuals or sex/age classes are targeted. We focused on ungulates and carnivores because, with the exception of a vast literature on size-selective exploitation of fish stocks and its consequences (see e.g., Law 2001), these are the groups for which most information regarding selective harvesting is available.

Consequences of Perturbing the Population Age and Sex Structure

Many mammalian populations are strongly structured by age and sex. Because survival rates typically differ among age and sex classes (Gaillard et al. 1998), populations of equal size but differing structures will have different temporal dynamics (Coulson et al. 2001) and will respond differently to stochastic environmental variation (Cameron & Benton 2004). Consequently, by perturbing population sex and age structure, selective harvesting affects population dynamics (Festa-Bianchet 2003).

Theoretically, the most productive populations are those with a female-biased sex ratio (Caughley 1977). Male-biased harvesting regimes have therefore been widely applied to ungulates in North America (McCullough 2001; Stalling et al. 2002), Scandinavia (Langvatn & Loison 1999; Sæther et al. 2004b), and in wildlife cropping schemes in Africa (Ginsberg & Milner-Gulland 1994). Even though a more balanced or slightly female-biased harvest is taken in many European countries (Milner et al. 2006), harvested ungulate populations invariably have mortality patterns that deviate significantly from those in unharvested populations (Ginsberg & Milner-Gulland 1994; Langvatn & Loison 1999). In particular, mortality rates of prime-aged adults, especially males, are considerably higher than in unharvested populations.

Male-biased harvesting regimes have led to severely biased sex ratios; for example, there are 0.05 adult males per female in populations of both North American elk (if not provided, scientific names are in Table 1 or 2) (Noyes et al. 1996) and the central Asian saiga antelope (Milner-Gulland et al. 2003). In addition, the often high harvesting pressure on mature males for trophies results in harvested populations with lower average ages of males and fewer old males than unharvested populations (Langvatn & Loison 1999; Laurian et al. 2000; Apollonio et al. 2003). For example, 70% of all males in a Norwegian moose population are harvested by 3 years of age (Solberg et al. 1999).

In the following we discuss how sex- and age-specific hunting affects various demographic processes. We do not discuss genetic and evolutionary effects in detail because they have been reviewed recently (Harris et al. 2002; Festa-Bianchet 2003).

Proportion of ungulate and carnivore species threatened by harvesting

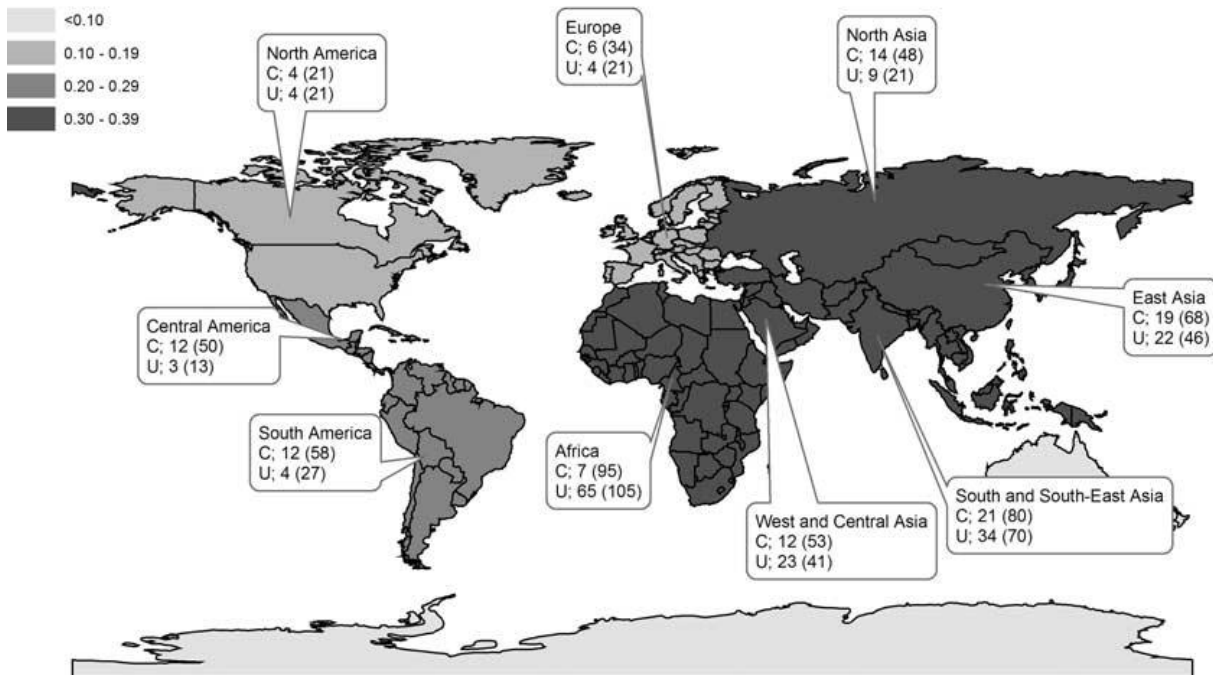


Figure 1. The number of ungulate (U) and carnivore (C) species registered as threatened (all threat categories) at least partly due to harvesting (IUCN 2004) relative to the total number (in parentheses) of ungulate and carnivore species evaluated in each region. Shading represents the approximate proportion of ungulate and carnivore species threatened. There are substantial differences among the regions with the highest proportion of threatened species (0.37) occurring in south and southeast Asia and west and central Asia.

Effects on Reproduction

Although selective harvesting of males leads to female-biased adult sex ratios, this does not necessarily lead to a reduction in fecundity rate because most harvested game species have polygynous mating systems in which a single mature male is capable of inseminating many females (Ginsberg & Milner-Gulland 1994; Mysterud et al. 2002; but see Greene et al. 1998 for monogamous species). Consequently in many cases, recruitment rates are resilient to skewed sex ratios (Table 1) and may even increase because of higher proportion of females in the adult population (Solberg et al. 2000). But there may nonetheless be a sex-ratio threshold below which fecundity collapses. Indeed, if the offtake is strongly male-biased, population crashes due to reduced fecundity can occur at lower overall offtake rates than if a random harvest is taken (Ginsberg & Milner-Gulland 1994). This has been observed in saiga antelope at a ratio of between 0.025 and 0.009 males per female (Milner-Gulland et al. 2003), caribou (*Rangifer tarandus*) at a sex ratio of 0.08 (Bergerud 1974), elk populations with a sex ratio of 0.04 (Freddy 1987), and elephants with a sex ratio of 0.013 (Dobson & Poole 1998). In moose, even moderately, female-biased sex ratios (0.25–0.70) can affect the fecundity of primiparous females, although the fecundity of older females seems to be unaffected (Solberg et al. 2002).

Many populations with low male-to-female ratios also tend to have a low mean male age, which may be a contributing factor to lower fecundity (Solberg et al. 2002). Nevertheless, even though it has been suggested that subadults show immature courtship behavior, are socially disruptive, and prolong the mating season (Squibb 1985; Shackleton 1991; Singer & Zeigenfuss 2002; Stalling et al. 2002), young males are nonetheless capable of achieving paternities successfully (Stevenson & Bancroft 1995; Hogg & Forbes 1997). It is less clear whether they are able to inseminate as many females as old males (Ginsberg & Milner-Gulland 1994). Overall, there is little clear evidence that a reduction in male age affects fecundity rate per se (Table 1). Rather, the literature points toward changes in parturition dates, birth synchrony, and offspring sex ratio with a reduction in male age.

Selective harvesting may also have indirect effects on recruitment through its influence on the mean age of adult females. For example, in an Norwegian moose population in which selective harvesting protects adult females, the resulting increase in average female age led to an increase in both calving rate and twinning rate (Solberg et al. 1999). In other situations, such as game ranching, cropping results in a general reduction in average female age and thus in an increased reproductive rate due to the absence of senescent individuals (Ginsberg & Milner-Gulland 1994).

Table 1. Demographic consequences of a selective-harvesting regime that creates a female-biased adult sex ratio and/or a young average age of males.

Species	Effect of harvesting			Demographic consequence ^a					Reference	
	Q-biased sex ratio	reduced ♂ age	fecundity rate	breeding/ birth date	birth synchrony	offspring sex ratio	offspring survival 1) weight	offspring survival 2) weight		adult ♂ condition
Moose (<i>Alces alces</i>)	X		+							Solberg et al. 1999
	X		- ^b							Solberg et al. 2002
		X				<0 ^c		2) 0		Sæther et al. 2004
	X		0	- ^c	-			2) 0		Sæther et al. 2003
	X		0	-	0			2) 0		Sæther et al. 2003
	X		0	0	0			2) -		Garel et al. 2006
Elk (<i>Cervus elaphus</i>)	X		0	0	0		2) - ^d			Laurian et al. 2000
	X		0							Taquet et al. 1999
	X		0							Courtois & Lamontagne 1999
	X		-							Freddy 1987
	X		- ^e		-				0	Noyes et al. 1996
	X		-							Squibb 1985
Red deer (<i>Cervus elaphus</i>)	X		-							White et al. 2001
	X		0							Bender & Miller 1999
	X		0							Langvaath & Loison 1999
	X		0		+					Koimers et al. 1999
Fallow deer (<i>Dama dama</i>)	X		-							White et al. 2001
	X		0							Ozoga & Verme 1985
Mule deer (<i>Odocoileus hemionus</i>)	X		-							
	X		0							
White-tailed deer (<i>Odocoileus virginianus</i>)	X		0							
	X		0							
Bighorn sheep (<i>Ovis canadensis</i>)	X		0							
	X		0							
Dall sheep (<i>Ovis dalli</i>)	X		0							
	X		0							
Caribou (<i>Rangifer tarandus</i>)	X		0							
	X		0							
Reindeer (<i>Rangifer tarandus</i>)	X		0							
	(X) f		0							
Saiga antelope (<i>Saiga tatarica</i>)	X		0							
	X		0							

^a Key: 0, no effect; +, positive effect; -, negative effect.
^b Primiparous females only, no effect in adult females.
^c Slightly adult sex ratio had significantly stronger effect on calving date than young-male age structure.
^d Offspring size measured by length of hind foot not body weight.
^e Nonsignificant trend.
^f A group of the females were inhibited from mating during their first cycle, thus conceiving in the second cycle. Simulate s skewed sex ratio and/or male age structure.
^g Sex ratio of calves conceived in second estrus.
^h Increased weight loss during the rut.

Effects on Timing and Synchrony of Birth

Timing and synchrony of birth have important implications for demography because of their effects on offspring body weights and survival. Greater birth synchrony leads to higher survival in species with heavy predation of neonates (Sinclair et al. 2000), whereas late-born individuals often have lower survival (Clutton-Brock et al. 1987; Festa-Bianchet 1988) or delayed body mass development (Sæther et al. 2003; Nilsen et al. 2004; Holand et al. 2006). In female ungulates this may lead to a delay in onset of reproduction (Langvatn et al. 1996).

In both reindeer and moose calving is earlier when the adult sex ratio is even rather than female-biased (Holand et al. 2003, Sæther et al. 2003). In addition, timing of calving in moose can be delayed when the male population is restricted to yearlings (Sæther et al. 2003). Similarly, birth dates in fallow deer (Komers et al. 1999), timing of the rut in elk (Noyes et al. 1996), and median date of accepted mounts in Dall sheep (Singer & Zeigenfuss 2002) are all significantly earlier in groups or populations with mature males than when only young males are present, although other studies have shown no such effects (Table 1). Birth synchrony was greater in a moose population with an even sex ratio compared with a population in which the sex ratio was experimentally manipulated toward females (Sæther et al. 2003), whereas birth dates are more synchronous with increasing male age in elk (Noyes et al. 1996) but less synchronous in fallow deer (Komers et al. 1999). By contrast, no effects of male age on rutting behavior or the timing of the birth season were found in bighorn sheep (Shackleton 1991) or in a hunted moose population (Laurian et al. 2000).

Effects on Offspring Sex Ratio

In dimorphic and polygynous species birth size is more strongly correlated with fitness in males than in females (Kruuk et al. 1999). The Trivers-Willard model (Trivers & Willard 1973) predicts that mothers in good condition should therefore produce male offspring because this yields the highest fitness return (Sheldon & West 2004). Nevertheless, other factors such as male quality and timing of breeding may also influence natal sex ratio. For example, if females hesitate to mate with young males and thus conceive late, the model predicts that fitness would be maximized by producing females because late-born offspring generally have lower birth and autumn weights (Holand et al. 2006).

In an experimental study of a Norwegian moose population, a change in male age structure toward younger males led to a reduction in the proportion of male calves born (Sæther et al. 2004b), whereas manipulation of the adult sex ratio had no effect. Similarly, Holand et al. (2006) showed that reindeer conceived in the first estrus are more likely to be male, whereas second-estrus offspring are more likely to be female. They argue that a skewed sex ratio and young male age structure could result in fewer adult females conceiving during the first cycle due to their hesitation to mate with young males. A trend toward more male offspring being sired by older males than by yearling males has also been observed in white-tailed deer (Ozoga & Verme 1985).

Effects on Survival

Participation in rutting activities is energetically costly, and, consequently, winter survival rates of participating males are typically lower than for other individuals (Geist 1971; Stevenson & Bancroft 1995; Jorgenson et al. 1997). Subordinate males may engage in high-risk alternative mating tactics (Hogg & Forbes 1997) and may invest more heavily in reproductive activities when there is either an abundance of females relative to males or a paucity of prime-age males (Squibb 1985; Singer & Zeigenfuss 2002; Mysterud et al. 2003). One might therefore predict that young males will be more involved in the rut and suffer higher winter mortality rates in areas where heavy hunting of mature males occurs (Geist 1971; Murphy et al. 1990). Evidence for the so-called depressed survival hypothesis, however, is equivocal (Singer & Zeigenfuss 2002; Table 1). No effect is seen in Dall sheep populations in which young rams show adult mating behavior in the absence of mature males (Murphy et al. 1990) or in lightly hunted populations of desert bighorn sheep and bighorn sheep (Singer & Zeigenfuss 2002). Higher mortality rates have been detected only among young rams in a heavily hunted Dall sheep population (Singer & Zeigenfuss 2002).

Where selective hunting leads to high adult mortality, populations tend to have a high proportion of juveniles and yearlings. Because overwinter survival of these classes is variable from year to year (Gaillard et al. 1998), such populations are more sensitive to winter mortality in harsh years than unhunted populations, leading to greater population variability (Cameron & Benton 2004; Gordon et al. 2004).

Effects on Body Weights

Another cost to young males participating in the rut is reduced body growth as resources are diverted to reproduction (Stearns 1992). In populations with few mature males, one might expect increased energy expenditure of young males participating in mating behavior to lead to greater weight loss during the rut. This is observed in male reindeer (Mysterud et al. 2003) and moose (Solberg & Sæther 1994; Garel et al. 2006). However, Sæther et al. (2003) found no such effect when mature male moose were removed from a population, although they found an indirect negative effect on calf body weight the following winter due to delayed

parturition dates. Similarly, lower birth and autumn body weights occur in second-estrus offspring in moose (Schwartz & Becker 1994) and reindeer (Holand et al. 2003, 2006). Low mass at birth has implications for other life-history traits such as survival, age and body size at maturity, and lifetime reproductive success (Kruuk et al. 1999).

As a result of expending more energy in avoidance behavior, female fallow deer in an enclosure with only young males lost significantly more body weight than females enclosed with only mature males (Komers et al. 1999). Female white-tailed deer in a low-density hunted population significantly increased their daily movement and home range size in peak and late rut, apparently in response to low availability of adult males (Labisky & Fritzen 1998). By contrast, Singer and Zeigenfuss (2002) found no compelling evidence for any negative effects on ewe energetic of increased harassment of ewes by young rams in hunted mountain sheep populations.

Consequences of Removing a Few Targeted Individuals

Trophy hunting typically targets the largest males or those with impressive ornaments but is generally restricted to relatively few individuals. Nonetheless, a high proportion of individuals that qualify as trophy individuals may be removed each year (Coltman et al. 2003). Species subject to trophy hunting include large carnivores and large horn-, tusk-, or antler-bearing herbivores. Trophy hunting is usually associated with a considerable fee, making it an important tool for wildlife management and conservation programs, particularly in developing countries, where it offers potential benefits for rural economies (Festa-Bianchet 2003). Within Europe and North America, there is also considerable interest in the trophy hunting of some relatively common ungulate species that, are also hunted for meat or population control (Festa-Bianchet 2003; Milner et al. 2006).

In many mammals the largest individuals are also the oldest and, as such, play an important role in leading social groups that benefit from their greater experience. Nevertheless, these are often the same individuals that are typically targeted by trophy hunters because of their size. For example, in elephants, tusk size is related to age, and hunters or poachers focus their efforts on individuals with the largest tusks, including matriarchs (Dobson & Poole 1998). Older matriarchs have social discrimination abilities that are superior to those of young matriarchs, so enabling them to make more appropriate responses during encounters with other elephant groups (McComb et al. 2001). These factors and a greater knowledge of the distribution of resources may result in higher per capita reproductive success for female groups led by older individuals. Consequently, if groups rely on older members for their store of social knowledge, then whole populations may be affected by the removal of a few key individuals (McComb et al. 2001).

Among lions, the absence of males within a pride enables hyenas to drive females and subadults off their kills under certain circumstances, constituting a constant energy drain by forcing them to hunt more frequently (Cooper 1991). In populations where adult males are scarce, due, for example, to trophy hunting, cleptoparasitism by hyenas is likely to increase.

In most species managers assume that sport hunting for trophy males only reduces the overall population size when the rate of male removal is so high that not all females are impregnated. In many cases it is thought that sport hunting of males may even have a positive effect on population growth through compensatory density dependence (McLellan 2005; but see also Miller 1990). In monogamous species and species in which males provide parental care, however selective removal of even a modest number of adult males is predicted to have a stronger impact on population growth than random removals (Greene et al. 1998).

Table 2. Demographic consequences of selective removal of a few specific individuals from a population.

Species	Effect of harvesting		Demographic consequence ^a				Reference
	removal dominant ♂	removal dominant ♀	fecundity rate	offspring sex ratio	offspring survival	adult ♀ condition	
Plains zebra (<i>Equus burchelli</i>)	X		–			–	Hack et al. 2002
Feral horses (<i>Equus caballus</i>)	X		–				Berger 1983
Shackleford Banks horses (<i>Equus caballus</i>)	X		–			–	Rubenstein 1986
Elephants (<i>Loxodonta africana</i>)	X		–				Dobson & Poole 1998
Lion (<i>Panthera leo</i>)	X	X	–		–		McComb et al. 2001
	X			>♂			Pusey & Packer 1994
	X			>♂			Smuts 1978
Brown bear (<i>Ursus arctos</i>)	X				–		Creel & Creel 1997
	X				0		Swenson et al. 1997
	X						Miller et al. 2003
	X		–				Wielgus & Bunnell 2000
	X		– ^b		(–) ^b		Stringham 1983
	X		– ^b		(–) ^b		McCullough 1981
	X				0		McLellan 2005

^a Key: 0, no effect; +, positive effect; –, negative effect.

^b Reduced cub recruitment when adult males were removed, but effects on fecundity rate and offspring survival not distinguished.

Effects on Juvenile Survival

Removal of trophy individuals, especially dominant males, can have far-reaching effects where male replacement is associated with infanticide. Sexually selected infanticide (SSI) can occur when a male gains increased mating success by killing dependent young he has not sired himself (Swenson 2003). By killing unrelated offspring a mature male can reduce the interbirth period and sire the next litter. Furthermore, because males tend to roam over larger areas than females (Nilsen et al. 2005), the turnover of one male can affect several females. For example, in root voles (*Microtus oeconomus*), high male turnover rates severely hamper population growth (Andreassen & Gundersen 2006). Male infanticide occurs primarily in primates, terrestrial carnivores, and some rodents.

Among bears, older males may limit the immigration of younger males (Rogers 1987). Therefore, increasing the mortality rate of old males can result in a higher immigration rate of younger, potentially infanticidal, males (Table 2). In Scandinavian brown bears survival rates of cubs are depressed in areas with high adult-male hunting offtake (juvenile survival 0.98 vs. 0.72 in unhunted and hunted populations, respectively; Swenson et al. 1997). A considerable body of evidence points toward infanticide as the cause of this (Swenson et al. 1997; Swenson 2003). In North American brown bear populations the evidence for SSI due to male turnover is still controversial (McCullough 1981; Stringham 1983; Wielgus & Bunnell 2000; Miller et al. 2003; McLellan 2005). Nevertheless, cases of SSI are extremely difficult to document in the field, and recent studies strongly support the SSI model and the adaptive value of SSI for male brown bears (Bellemain et al. 2006). In hunted black bear (*Ursus americanus*) populations with high male turnover rates, SSI is thought to cause high intraspecific juvenile mortality (LeCount 1987).

Sexually selected infanticide is also well documented in lions (Pusey & Packer 1994), and because trophy hunting is expected to increase the rate of male takeovers, excessive trophy hunting could limit recruitment through the negative effects of infanticide on cub survival (Whitman et al. 2004). Although trophy hunting increases the risk of population extinction, quite extensive trophy hunting could be sustained as long as only old males are targeted (Whitman et al. 2004).

Rare cases of SSI have been documented in some herbivore species (captive red deer: Bartos & Madlafousek 1994; hippopotamus [*Hippopotamus amphibious*]: Lewison 1998; captive plains zebra [*Equus burchelli*]: Pluhacek & Bartos 2005). Although the evidence is somewhat circumstantial, this suggests that similar effects could arise in ungulates under some conditions where trophy hunting for adult males takes place.

Effects on Reproduction

In situations where SSI is not documented the removal of a few adult males may nonetheless have an impact on demography through other mechanisms. For example, when comparing two North American grizzly bear populations, Wielgus and Bunnell (2000) found that reproductive rates were suppressed in the hunted compared with the unhunted population (Table 2). These differences were caused by mature females avoiding food-rich areas inhabited by potentially infanticidal immigrant males (sexual segregation), forcing them to use suboptimal habitats (Wielgus & Bunnell 2000). Subsequent modeling exercises show that this has a strong negative effect on the population growth rate and thus increases the risk of population extinction (Wielgus et al. 2001).

Equids often show highly developed multilevel social organization. Harem-forming feral horses and plains zebras are vulnerable to social instability and a high turnover of harem males (Hack et al. 2002). The selective removal of harem stallions can lead to increased stress levels, reduced grazing time, and loss of body

condition in females subject to harassment from intruding males, resulting in induced abortion (Berger 1983) and lower female reproductive success (Rubenstein 1986). Male takeovers in feral horses led to abortion due to forced copulation in 80% of females <6 months pregnant and due to other stress factors in a further 10% (Berger 1983). Females were subsequently reseeded by new males resulting in a reduced interbirth interval and genetic investment of rival males.

As with the selective hunting of specific age and sex classes, the selective removal of individuals could also affect other birth characteristics. For example, lion populations in which males are hunted, rear a higher proportion of male than female cubs (Smuts 1978; Creel & Creel 1997). According to the sex-allocation theory (Charnov 1982), this could compensate for a high turnover of adult males (Packer & Pusey 1987) but reduces the number of lions that can be sustainably harvested before the availability of females becomes limiting (Greene et al. 1998).

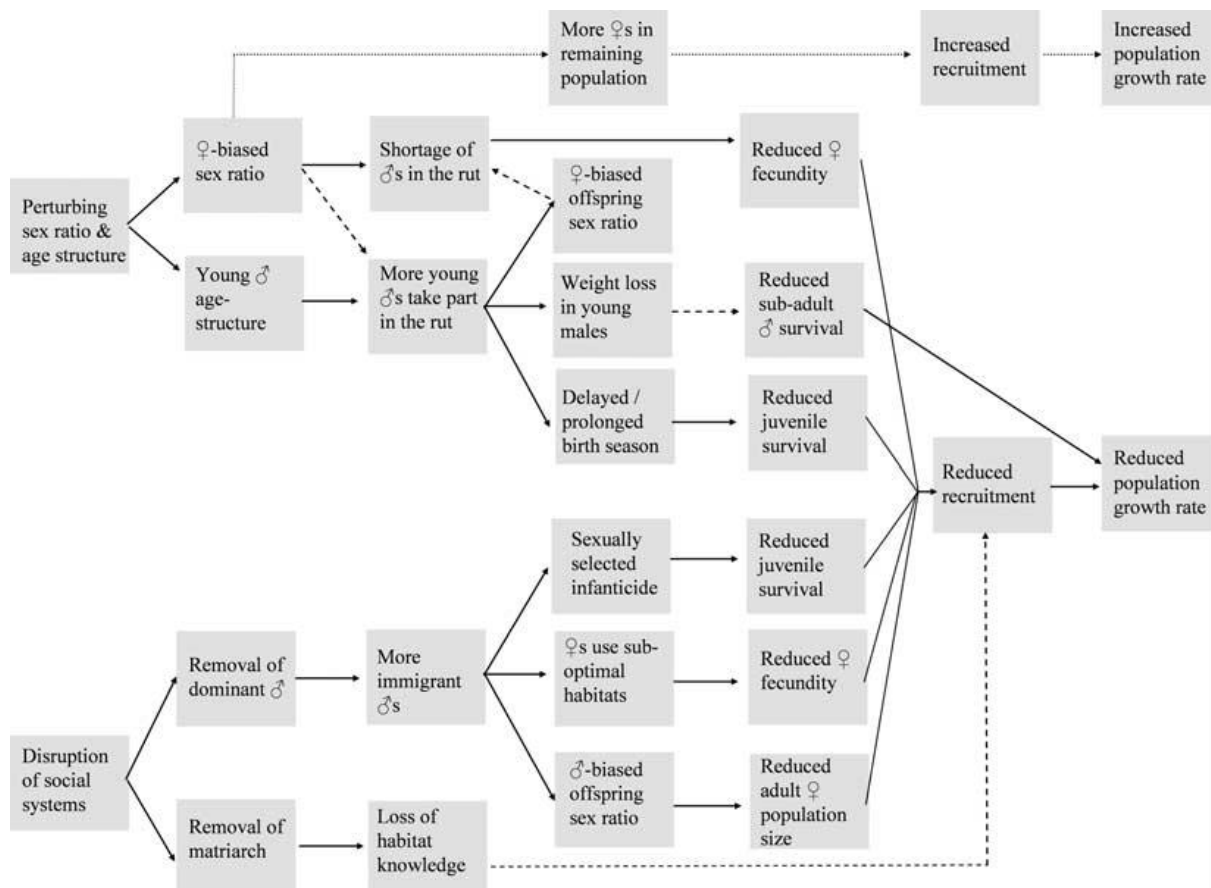


Figure 2. Schematic model of some of the processes and indirect pathways by which selective harvesting may affect population growth rate. Solid lines are mechanisms and effects that are well documented, and dashed lines indicate effects that are less well documented. The dotted lines indicate the path by which selective harvesting can increase population growth rate.

Synthesis and Conclusions

Our review shows that when selective harvesting perturbs the sex or age structure in such a way that the mating system is disrupted, the fecundity and survival of certain sectors of the population and the offspring sex ratio may all be affected. The removal of even a few targeted individuals could have similar consequences. Nevertheless, the evidence for the occurrence of such unintended demographic side effects is somewhat equivocal (Tables 1 & 2), being more common in experimental than observational studies. We believe this arises because such effects are often subtle, indirect, and sometimes involve time lags (Fig. 2). Changes such as shifts in calving date or offspring sex ratio are difficult to detect without detailed monitoring programs, and there is currently a lack of long-term studies of marked individuals in hunted populations (Festa-Bianchet 2003). This limits our understanding of how and when these demographic effects are expressed across different mating systems, habitat types, and population densities.

Many of the processes triggered by selective harvesting indirectly reduce the recruitment of new individuals, thereby potentially reducing the population growth rate (Fig. 2). Recruitment is depressed because females hesitate to mate with young males (e.g., Holand et al. 2006), ovulation is delayed in the absence of

stimulation from mature males (e.g., McComb 1987; Komers et al. 1999), or, more rarely, there are insufficient males for all females to be mated (e.g., Milner-Gulland et al. 2003). Conception rates can be limited by spatial (Myserud et al. 2002) and social (Greene et al. 1998) factors influencing access to mates and by a physical limit to the number of females each male can inseminate (Ginsberg & Milner-Gulland 1994). Although there are clearly differences between monogamous and polygynous mating systems in the ratio of adult males to females necessary for all females to be mated, within polygynous species differences in female group size (solitary individuals, small social groups, or large harems) and male mating behavior (e.g., tending, lekking, or harem holding) also influence access to mates. In addition, mate access may vary within species because group size differs with habitat type (Hewison et al. 1998). Extrapolation of adult sex ratios from domestic populations is not advisable. Generally, daily sperm production, sperm density, and absolute sperm numbers are directly related to testes size (Møller 1989), and most domestic animals have large testes for their body weight (Ginsberg & Milner-Gulland 1994). Under intense competition between males, sperm depletion can occur before the end of the rut, even in species with relatively large testes (Preston et al. 2001).

Although the mechanisms by which selective harvesting could affect population demography are relatively well documented (Fig. 2), the extent to which they affect population growth is still poorly understood (e.g., Wielgus et al. 2001; Whitman et al. 2004). Because the sensitivity of population growth rate to recruitment is generally lower than its sensitivity to adult female survival (Gaillard et al. 2000), demographic side effects that depress recruitment may not have as strong an effect on population growth rate as the direct harvesting of adult females. Nevertheless, because many of these effects are likely to act additively (Fig. 2), they may nonetheless reduce the population growth rate more than first anticipated. Although good estimates are lacking for many parameters, conceptual models would be helpful in suggesting when demographic side effects might start to limit population growth and in guiding empirical data collection.

The occurrence of demographic side effects of selective harvesting has implications for the performance of population viability analyses (PVA). In many of the most commonly used PVA software programs there is an implicit assumption that sex does not matter as long as the number of adult males is ≥ 1 (Brook et al. 2000). Nevertheless, estimated extinction probabilities are affected by both population sex ratio and mating system (Ginsberg & Milner-Gulland 1994; Sæther et al. 2004a). In addition, for small populations, demographic stochasticity in the sex ratio could have a direct negative effect on mean population growth rate (Sæther et al. 2004a). If the abundance of one sex is particularly low, chance events could result in that sex being limiting in certain years. This would be especially important in small, harvested populations and in more abundant populations when the sex ratio is close to the threshold where these effects become important.

Selective harvesting regimes can have destabilizing effects on populations. The young age structure of harvested populations results in less-stable dynamics due to high stochasticity in juvenile survival (e.g., Gordon et al. 2004). Furthermore, if late-born offspring enter the winter with lower body weights (e.g., Holand et al. 2006), they are more likely to be affected by random climatic variation (Festa-Bianchet 1988), which, together with reduced birth synchrony, could result in large interannual fluctuations in juvenile survival. In addition, in species with SSI, the effect of male removal on population growth rate is hard to predict because it depends on the number of offspring killed by immigrant males. In a Scandinavian bear population Swenson et al. (1997) estimated that the removal of one male was equivalent to the removal of 0.5–1.0 females, depending on the extent to which the immigrant male killed the cubs in the area. In such situations harvesting juveniles and females will have more predictable effects.

In response to the demographic side effects discussed here and the evolutionary consequences of selective harvesting (Harris et al. 2002; Festa-Bianchet 2003), wildlife managers are advised to implement harvesting regimes that mimic natural mortality patterns more closely. Because natural mortality is typically higher among juveniles and old individuals (Gaillard et al. 1998), these groups should be targeted (Ginsberg & Milner-Gulland 1994), although this may conflict with economic considerations in some areas (Festa-Bianchet 2003; Milner et al. 2006). Applying a minimum age threshold is a possibility for trophy males if a reliable assessment of age can be made independently from trophy phenotype, which may be well developed at a young age in high-quality males (Whitman et al. 2004). An additional approach would be to consider the timing of the harvest. Currently many temperate ungulates are hunted during the breeding season. If the harvest is delayed until after the rut, older males have the opportunity to breed and could be harvested at the time of year when their reproductive value is lowest (Kokko et al. 2001). In lions the optimal time for hunting a pride male would be as his cubs become independent (Whitman et al. 2004). In this way, and by following natural pride take over intervals, infanticide can be minimized.

We are now starting to understand the mechanisms by which undesirable side effects of selective hunting occur, but much less is known about when they occur and the extent to which they affect population growth. To be able to make firmer predictions about the effects on population growth and viability, both large-scale empirical manipulations of harvesting regimes and theoretical studies, including simulation modeling, are urgently needed. Because most of the effects discussed here operate through recruitment, monitoring recruitment and juvenile sex ratios should be standard routines for managers, in addition to assessment of total population

size. In addition, stronger emphasis should be put on the timing of the harvest. Until the importance of the mechanisms triggered by selective harvesting discussed here are more clearly understood, we urge managers to be cautious in their use of nonrandom harvesting strategies.

Acknowledgments

We thank the Norwegian Research Council for funding J.M.M. and E.B.N. (project 156367/530). Furthermore, we thank colleagues at Hedmark University College for valuable discussions and A.J. Loveridge, M. Festa-Bianchet, and an anonymous referee for helpful comments.

Literature Cited

- Andreassen, H. P., and G. Gundersen. 2006. Male turnover reduces population growth: an enclosure experiment on voles. *Ecology* **87**:88–94.
- Apollonio, M., B. Bassano, and A. Mustoni. 2003. Behavioral aspects of conservation and management in European mammals. Pages 157–170 in M. Festa-Bianchet and M. Apollonio, editors. *Animal behavior and wildlife conservation*. Island Press, Washington, D.C.
- Baillie, J. E. M., C. Hilton-Taylor, and S.N. Stuart. 2004. 2004 IUCN red list of threatened species. A global species assessment. World Conservation Union, Gland, Switzerland, and Cambridge, United Kingdom.
- Bartos, L., and J. Madlafousek. 1994. Infanticide in a seasonal breeder—the case of red deer. *Animal Behaviour* **47**:217–219.
- Bellemain, E., J. E. Swenson, and P. Taberlet. 2006. Mating strategy in relation to sexually selected infanticide in a nonsocial carnivore: the brown bear. *Ethology* **112**:238–246.
- Bender, L., and P. J. Miller. 1999. Effects of elk harvest strategy on bull demographics and herd composition. *Wildlife Society Bulletin* **27**:1032–1037.
- Berger, J. 1983. Induced abortion and social factors in wild horses. *Nature* **303**:59–61.
- Bergerud, A. T. 1974. Rutting behaviour of the Newfoundland caribou. Pages 395–435 in V. Geist and F. Walther, editors. *The behaviour of ungulates and its relation to management*. World Conservation Union, Morges, Switzerland.
- Brook, B. W., M. A. Burgman, and R. Frankham. 2000. Differences and congruencies between PVA packages: the importance of sex ratio for predictions of extinction risk. *Conservation Ecology* **4**: <http://www.ecologyandsociety.org/vol4/iss1/art6/>.
- Cameron, T. C., and T. G. Benton. 2004. Stage-structured harvesting and its effects: an empirical investigation using soil mites. *Journal of Animal Ecology* **73**:996–1006.
- Caughley, G. 1977. *Analysis of vertebrate populations*. John Wiley & Sons, Chichester, United Kingdom.
- Charnov, E. 1982. *The theory of sex allocation*. Princeton University Press, Princeton, New Jersey.
- Clutton-Brock, T. H., M. Major, S. D. Albon, and F. E. Guinness. 1987. Early development and population dynamics in red deer. I. Density-dependent effects on juvenile survival. *Journal of Animal Ecology* **56**:53–67.
- Coltman, D. W., P. O'Donoghue, J. T. Jorgenson, J. T. Hogg, C. Strobeck, and M. Festa-Bianchet. 2003. Undesirable evolutionary consequences of trophy hunting. *Nature* **426**:655–658.
- Cooper, S. M. 1991. Optimal hunting group-size—the need for lions to defend their kills against loss to spotted hyaenas. *African Journal of Ecology* **29**:130–136.
- Coulson, T., E. A. Catchpole, S.D. Albon, B. J. T. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley, and B. T. Grenfell. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. *Science* **292**:1528–1531.
- Courtois, R., and G. Lamontagne. 1999. The protection of cows: its impacts on moose hunting and moose populations. *Alces* **35**:11–29.
- Creel, S., and N. M. Creel. 1997. Lion density and population structure in the Selous Game Reserve: evaluation of hunting quotas and offtake. *African Journal of Ecology* **35**:83–93.
- Dobson, A., and J. Poole. 1998. Conspecific aggregation and conservation biology. Pages 193–208 in T. Caro, editor. *Behavioural ecology and conservation biology*. Oxford University Press, Oxford, United Kingdom.
- Festa-Bianchet, M. 1988. Birthdate and survival in bighorn lambs (*Ovis canadensis*). *Journal of Zoology* **214**:653–661.
- Festa-Bianchet, M. 2003. Exploitative wildlife management as a selective pressure for life-history evolution of large mammals. Pages 191–210 in M. Festa-Bianchet and M. Apollonio, editors. *Animal behavior and wildlife conservation*. Island Press, Washington, D.C.
- Freddy, D. J. 1987. *The White River elk herd: a perspective 1960–85*. Wildlife technical publication. Colorado Division of Wildlife, Fort Collins.
- Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology & Evolution* **13**:58–63.

- Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toïgo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* **31**:367–93.
- Garel, M., E. J. Solberg, B. E. Sæther, I. Herfindal, and K. A. Hogda. 2006. The length of growing season and adult sex ratio affect sexual size dimorphism in moose. *Ecology* **87**:745–758.
- Geist, V. 1971. *Mountain Sheep, a study in behavior and evolution*. University of Chicago Press, Chicago.
- Ginsberg, J. R., and E. J. Milner-Gulland. 1994. Sex-biased harvesting and population-dynamics in ungulates—implications for conservation and sustainable use. *Conservation Biology* **8**:157–166.
- Gordon, I. J., A. J. Hester, and M. Festa-Bianchet. 2004. The management of wild large herbivores to meet economic, conservation and environmental objectives. *Journal of Applied Ecology* **41**:1021–1031.
- Greene, C., J. Ubanhowar, M. Mangel, and T. Caro. 1998. Animal breeding systems, hunter selectivity and consumptive use in wildlife conservation. Pages 271–305 in T. Caro, editor. *Behavioural ecology and conservation biology*. Oxford University Press, Oxford, United Kingdom.
- Hack, M. A., R. East, and D. I. Rubenstein. 2002. Status and Action Plan for the Plains Zebra (*Equus burchellii*). Pages 43–60 in P. D. Moehlman, editor. *Equids: zebras, asses and horses*. World Conservation Union (IUCN) Species Survival Commission Equid Specialist Group, IUCN, Gland, Switzerland.
- Harris, R. B., W. A. Wall, and F. W. Allendorf. 2002. Genetic consequences of hunting: what do we know and what should we do? *Wildlife Society Bulletin* **30**:634–643.
- Heimer, W. E., S. M. Watson and T. C. Smith. 1984. Excess ram mortality in a heavily hunted Dall sheep population. *Symposium Northern Wild Sheep & Goat Council* **4**:425–432.
- Hewison, A. J. M., J.-P. Vincent, and D. Reby. 1998. Social organization of European roe deer. Pages 189–219 in R. Andersen, P. Duncan, and J. D. C. Linnell, editors. *The European roe deer: the biology of success*. Scandinavian University Press, Oslo.
- Hogg, J. T., and S. H. Forbes. 1997. Mating in bighorn sheep: frequent male reproduction via a high-risk “unconventional” tactic. *Behavioral Ecology and Sociobiology* **41**:33–48.
- Holand, Ø., K. H. Roed, A. Mysterud, J. Kumpula, M. Nieminen, and M. E. Smith. 2003. The effect of sex ratio and male age structure on reindeer calving. *Journal of Wildlife Management* **67**:25–33.
- Holand, Ø., A. Mysterud, K. H. Røed, T. Coulson, H. Gjøstein, R. B. Weladji, and M. Nieminen. 2006. Adaptive adjustment of offspring sex ratio and maternal reproductive effort in an iteroparous mammal. *Proceedings of the Royal Society B* **273**:293–299. IUCN (World Conservation Union). 2004. 2004 IUCN Red List of threatened species. IUCN, Gland, Switzerland. Available from <http://www.iucnredlist.org> (accessed February 2006).
- Jorgenson, J. T., M. Festa-Bianchet, J.-M. Gaillard, and W. D. Wishart. 1997. Effects of age, sex, disease, and density on survival of Bighorn sheep. *Ecology* **78**:1019–1032.
- Komers, P., B. Birgesson, and K. Ekvall. 1999. Timing of estrus in fallow deer is adjusted to the age of available mates. *The American Naturalist* **153**:431–436.
- Kokko, H., J. Lindström, and E. Ranta. 2001. Life histories and sustainable harvesting. Pages 301–322 in J. D. Reynolds, G. M. Mace, K. H. Redford, and J. G. Robinson, editors. *Conservation of exploited species*. Cambridge University Press, Cambridge, United Kingdom.
- Kruuk, L. E. B., T. H. Clutton-Brock, K. E. Rose, and F. E. Guinness. 1999. Early determinants of lifetime reproductive success differ between the sexes in red deer. *Proceedings of the Royal Society B* **266**:1655–1661.
- Labisky, R. F., and D. E. Fritzen. 1998. Spatial mobility of breeding female white-tailed deer in a low-density population. *Journal of Wildlife Management* **62**:1329–1334.
- Langvatn, R., S. D. Albon, T. Burkey, and T. H. Clutton-Brock. 1996. Climate, plant phenology, and variation in age at first reproduction in a temperate herbivore. *Journal of Animal Ecology* **65**:653–670.
- Langvatn, R., and A. Loison. 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.
- Laurian, C., J. P. Ouellet, R. Courtois, L. Breton, and S. St-Onge. 2000. Effects of intensive harvesting on moose reproduction. *Journal of Applied Ecology* **37**:515–531.
- Law, R. 2001. Phenotypic and genetic changes due to selective exploitation. Pages 323–342 in J. D. Reynolds, G. M. Mace, K. H. Redford, and J. G. Robinson, editors. *Conservation of exploited species*. Cambridge University Press, Cambridge, United Kingdom.
- LeCount, A. L. 1987. Causes of black bear cub mortality. *International Conference on Bear Research and Management* **7**:75–82.
- Lewison, R. 1998. Infanticide in the hippopotamus: evidence for polygynous ungulates. *Ethology, Ecology & Evolution* **10**:277–286.
- McComb, K. 1987. Roaring by red deer stags advances the date of oestrus in hinds. *Nature* **330**:648–649.
- McComb, K., C. Moss, S. M. Durant, L. Baker, and S. Sayialel. 2001. Matriarchs as repositories of social knowledge in African elephants.

Science **292**:491–494.

McCullough, D. R. 1981. Population dynamics of the Yellowstone grizzly bear. Pages 173–196 in C. W. Fowler and T. D. Smith, editors. Dynamics of large mammal populations. John Wiley & Sons, New York.

McCullough, D. R. 2001. Male harvest in relation to female removals in a black-tailed deer population. *Journal of Wildlife Management* **65**:46–58.

McLellan, B. N. 2005. Sexually selected infanticide in grizzly bears: the effects of hunting on cub survival. *Ursus* **16**:141–156.

Miller, S. D. 1990. Impact of increased bear hunting on survivorship of young bears. *Wildlife Society Bulletin* **18**:462–467.

Miller, S. D., R. A. Sellers, and J. A. Keay. 2003. Effects of hunting on brown bear cub survival and litter size in Alaska. *Ursus* **14**:130–152.

Milner, J. M., C. Bonenfant, A. Mysterud, J.-M. Gaillard, S. Csányi, and N. C. Stenseth 2006. Temporal and spatial development of red deer harvesting in Europe—biological and cultural factors. *Journal of Applied Ecology* **43**:721–734.

Milner-Gulland, E. J., and E. L. Bennett. 2003. Wild meat: the bigger picture. *Trends in Ecology & Evolution* **18**:351–357.

Milner-Gulland, E. J., O.M. Bukreeva, T. Coulson, A. A. Lushchekina, M. V. Kholodova, A. B. Bekenov, and I. A. Grachev. 2003. Reproductive collapse in saiga antelope harems. *Nature* **422**:135.

Møller, A. P. 1989. Ejaculate quality, testes size and sperm competition in primates. *Journal of Human Evolution* **17**:479–488.

Murphy, E. C., F. J. Singer, and L. Nichols. 1990. Effects of hunting on survival and productivity of Dall sheep. *Journal of Wildlife Management* **54**:284–290.

Mysterud, A., T. Coulson, and N. C. Stenseth. 2002. The role of males in the dynamics of ungulate populations. *Journal of Animal Ecology* **71**:907–915.

Mysterud, A., O. Holand, K. H. Roed, H. Gjostein, J. Kumpula, and M. Nieminen. 2003. Effects of age, density and sex ratio on reproductive effort in male reindeer (*Rangifer tarandus*). *Journal of Zoology* **261**:341–344.

Nilsen, E. B., J. D. C. Linnell, and R. Andersen. 2004. Individual access to preferred habitat affects fitness components in female roe deer *Capreolus capreolus*. *Journal of Animal Ecology* **73**:44–50.

Nilsen, E. B., I. Herfindal, and J. D. C. Linnell. 2005. Can intra-specific variation in carnivore home-range size be explained using remotesensing estimates of environmental productivity? *Ecoscience* **12**:68–75.

Noyes, J. H., B. K. Johnson, L. D. Bryant, S. L. Findholt, and J.W. Thomas. 1996. Effects of bull age on conception dates and pregnancy rates of cow elk. *Journal of Wildlife Management* **60**:508–517.

Ozoga, J. J., and L. J. Verme. 1985. Comparative breeding behavior and performance of yearling vs. prime-age white-tailed bucks. *Journal of Wildlife Management* **49**:364–372.

Packer, C., and A. E. Pusey. 1987. Intrasexual cooperation and the sex ratio in African lions. *The American Naturalist* **130**:636–642.

Pluhacek, J., and L. Bartos. 2005. Further evidence for male infanticide and feticide in captive plains zebra, *Equus burchelli*. *Folia Zoologica* **54**:258–262.

Preston, B. T., I. R. Stevenson, J. M. Pemberton, and K. Wilson. 2001. Dominant rams lose out by sperm depletion. *Nature* **409**:681–682.

Pusey, A. E., and C. Packer. 1994. Infanticide in lions: consequences and counterstrategies. Pages 277–299 in S. Parmigiani, and F. S. vom Saal, editors. Infanticide & parental care. Harwood Academic, London.

Robinson, J. R., and E. L. Bennett 2000. Hunting for sustainability in tropical forests. Columbia University Press, New York.

Rogers, L. L. 1987. Effects of food-supply and kinship on social behavior, movements, and population growth of black bears in Northeastern Minnesota. *Wildlife Monographs* **97**:1–72.

Rubenstein, D. I. 1986. Ecology and sociality in Horses and Zebras. Pages 282–302 in D. I. Rubenstein and R. W. Wrangham, editors. Ecological aspects of social evolution. Princeton University Press, Princeton, New Jersey.

Sæther, B.-E., E. J. Solberg, and M. Heim. 2003. Effects of altering sex ratio structure on the demography of an isolated moose population. *Journal of Wildlife Management* **67**:455–466.

Sæther, B. E., S. Engen, R. Lande, A. P. Moller, S. Bensch, D. Hasselquist, J. Beier, and B. Leisler. 2004a. Time to extinction in relation to mating system and type of density regulation in populations with two sexes. *Journal of Animal Ecology* **73**:925–934.

Sæther, B.-E., E. J. Solberg, M. Heim, J. E. Stacy, K. S. Jakobsen, and R. Olstad. 2004b. Offspring sex ratio in moose *Alces alces* in relation to paternal age: an experiment. *Wildlife Biology* **10**:51–57.

Schwartz, C. C., and E. F. Becker. 1994. Growth of moose calves conceived during the first versus second estrus. *Alces* **30**:91–100.

- Shackleton, D. M. 1991. Social maturation and productivity in bighorn sheep: are young males incompetent? *Applied Animal Behaviour Science* **29**:173–184.
- Sheldon, B. C. and S. A. West. 2004. Maternal dominance, maternal condition, and offspring sex ratio in ungulate mammals. *The American Naturalist* **163**:40–54.
- Sinclair, A. R. E., S. A. R. Mduma, and P. Arcese. 2000. What determines phenology and synchrony of ungulate breeding in Serengeti? *Ecology* **81**:2100–2111.
- Singer, F. J., and L. C. Zeigenfuss. 2002. Influence of trophy hunting and horn size on mating behavior and survivorship of mountain sheep. *Journal of Mammalogy* **83**:682–698.
- Smuts, G. L. 1978. Effects of population reduction on the travels and reproduction of lions in Kruger National Park. *Carnivore* **1**:61–72.
- Solberg, E. J., and B.-E. Sæther. 1994. Male traits as life-history variables: annual variation in body mass and antler size in moose (*Alces alces*). *Journal of Mammalogy* **75**:1069–1079.
- Solberg, E. J., B.-E. Sæther, O. Strand, and A. Loison. 1999. Dynamics of a harvested moose population in a variable environment. *Journal of Animal Ecology* **68**:186–204.
- Solberg, E. J., A. Loison, B.-E. Sæther, and O. Strand. 2000. Age-specific harvest mortality in a Norwegian moose *Alces alces* population. *Wildlife Biology* **6**:41–52.
- Solberg, E. J., A. Loison, T. H. Ringsby, B.-E. Sæther, and M. Heim. 2002. Biased adult sex ratio can affect fecundity in primiparous moose *Alces alces*. *Wildlife Biology* **8**:117–128.
- Squibb, R. C. 1985. Mating success of yearling and older bull elk. *Journal of Wildlife Management* **49**:744–750.
- Stalling, D. H., G. J. Wolfe, and D. K. Crockett. 2002. Regulating the hunt. Pages 749–791 in D. E. Toweill and J. W. Thomas, editors. *North American elk. Ecology and management*. Smithsonian Institution Press, Washington, D.C.
- Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press, Oxford, United Kingdom.
- Stevenson, I. R., and D. R. Bancroft. 1995. Fluctuating trade-offs favour precocial maturity in male Soay sheep. *Proceedings of the Royal Society B* **262**:267–275.
- Stringham, S. F. 1983. Roles of adult males in grizzly bear populations. *International Conference on Bear Research and Management* **5**:140–151.
- Swenson, J. E. 2003. Implications of sexually selected infanticide for the hunting of large carnivores. Pages 171–189 in M. Festa-Bianchet and M. Apollonio, editors. *Animal behavior and wildlife conservation*. Island Press, Washington, D.C.
- Swenson, J. E., F. Sandegren, A. Söderberg, A. Björvall, R. Franzén, and P. Wabakken. 1997. Infanticide caused by hunting of male bears. *Nature* **386**:450–451.
- Taquet, M., J.-P. Ouellet, R. Courtois, and C. Laurian. 1999. Does unbalanced sex ratio in adult moose affect calf size in the fall? *Alces* **35**:203–211.
- Trivers, R. L., and D. E. Willard. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science* **179**:90–92.
- White, G. C., D. J. Freddy, R. B. Gill, and J. H. Ellenberger. 2001. Effect of adult sex ratio on mule deer and elk productivity in Colorado. *Journal of Wildlife Management* **65**:543–551.
- Whitman, K., A. M. Starfield, H. S. Quadling, and C. Packer. 2004. Sustainable trophy hunting of African lions. *Nature* **428**:175–178.
- Wielgus, R. B., and F. L. Bunnell. 2000. Possible negative effects of adult male mortality on female grizzly bear reproduction. *Biological Conservation* **93**:145–154.
- Wielgus, R. B., F. Sarrazin, R. Ferriere, and J. Clobert. 2001. Estimating effects of adult male mortality on grizzly bear population growth and persistence using matrix models. *Biological Conservation* **98**:293–303.