Chapter 6

Effects of Selective Harvesting on Ungulate Populations

Atle Mysterud

Selective harvesting of ungulate populations is an old management tradition. Most commonly it is driven by either a desire to shoot males with large ‘trophies’ such as antlers and horns (Geist, 1986) or avoiding shooting females with offspring to enhance population growth (Milner et al., 2011). Such intentional selective harvesting practices arising from hunter preferences are clearly very important for offtake, and also modified or strengthened by management requirements such as quotas and economic incentives (Mysterud, 2011). Selectivity can also arise due to non-intentional selection due to differences in behaviour among animals making them more or less prone to being harvested. Any level of harvesting of an animal population clearly has an impact on population dynamics by removing individuals and, when selective, it can greatly affect the remaining age and sex structure of the population (Beddington, 1974; Ginsberg and Milner-Gulland, 1994; Langvatn and Loison, 1999). This will obviously again affect population growth, but also a range of other processes.

That some animals are more important than others for population growth has likely been known to humans since prehistoric times. Clearly, only females produce new young and how many depends on their age (Gaillard et al., 2000). This is formalised into the concept of reproductive value describing the extent to which individuals of different age contribute to future population growth (Fisher, 1930; Engen et al., 2007, 2009). There is a huge theoretical literature, using in particular matrix models, to investigate how age-specific harvesting may affect population growth. For a long period of time, studies of the effects of selective harvesting were mainly linked to such direct effects of individual removal on population growth. I will term these the direct demographic effects (Figure 6.1). However, indirect demographic effects may arise due to such age-specific harvesting that also affects dynamics through changes in age structure and sex ratio of the remaining population.
Ungulates are typically polygynous to differing degrees (Loison et al., 1999a). As only female ungulates give birth and alone raise the young, most of these population models, when applied to ungulates, only consider the female population. Males are not regarded as limiting for population growth, and it is presumed that skewing the population sex ratio towards females will largely enhance population growth. However, it is quite clear that at some point sex ratios may become so skewed that males may become limiting, or need longer time periods to inseminate all females, as was first convincingly shown in an influential theoretical paper by Ginsberg and Milner-Gulland (1994). Despite the fact that some form of selective harvesting is nearly universal in the management of ungulate populations, it is only until quite recently that such more indirect effects of selective harvesting became a topical issue (Mysterud et al., 2002).

For a long time, most studies of ungulates and their life history were deliberately focused on populations without harvesting, such as the red deer on Rum (Clutton-Brock et al., 1982) and the Soay sheep of St Kilda (Clutton-Brock and Pemberton, 2003). There has been a renewed interest in studies of the effects of harvesting during the last decade. The patterns of age- and size-specific mortality induced by human harvesting differ markedly from those seen in populations both without harvesting and predation (Gaillard et al., 1998). In theory, such differing mortality patterns will yield markedly different selective pressures from those impinging on populations without harvesting (Proaktor et al., 2007) or with large
predators (Bischof et al., 2008). There is indeed huge current interest in how selective harvesting might affect evolutionary responses (Harris et al., 2002; Allendorf et al., 2008; Allendorf and Hard, 2009). For terrestrial systems, this was sparked by an influential study of the genetic consequences of trophy hunting of bighorn (Ovis canadensis) rams in Canada (Colman et al., 2003).

The aim of this chapter is to review how hunter selectivity might affect ungulate populations beyond direct demographic effects, i.e. indirect demographic effects related to changes in age structure and sex ratio and evolutionary effects. I will consider general mechanisms, but a key issue is to review the empirical evidence for its importance relative to other factors with an emphasis on European ungulate populations.

6.1 Harvesting selectivity

Harvesting or hunter selection can be defined as any non-random offtake of individuals from the population. Hunter selection will thus by definition yield a shift in the structure of the remaining population. The three main categories of harvesting selectivity are those related to selectivity for sex, age and body (or antler/horn) size. For population dynamics, clearly those related to offtake depending on age and sex is the most critical, while body (or antler/horn) size (relative to cohort average) is the more important for directional selection and potential evolutionary effects (more below).

6.1.1 Intentional and non-intentional factors

Some selectivity of harvest may result from both direct and intentional factors such as the influence of hunter preferences (e.g. trophy-hunting), quotas and economic costs, etc., but also as the result of indirect and non-intentional factors through more general impacts on animal behaviour and abundance. Direct effects are likely by far the more important, though the indirect effects are currently little studied. That there is clear selection for age and sex is well established, and most often imposed as the result of quotas set for harvest by regulatory authorities who may determine a required cull of a particular number of males or females and/or may determine a particular age-structure within that cull. The way of giving quotas differs substantially across Europe (Apollonio et al., 2010), and the proportion of different sex and age classes in the harvest differ accordingly. As an example of this, when comparing red deer (Cervus elaphus) harvest statistics across 11 European countries (Milner et al., 2006), the proportion of calves in the harvest varied from 10–40%, while males typically accounted for 40–60% of the remainder. Cultural traditions setting management aims are likely a main driver of such variability (Milner et al., 2006).

After quotas are established, the intentional factors causing harvesting selection are those related to hunter preferences and the opportunities given for being selective. Hunters’ preferences differ depending on hunter motivation, whether
they are aiming for meat, recreation or trophy; clearly, trophy hunters are the most selective. It has been suggested that several factors causing selection are related to the opportunity to be selective (Mysterud, 2011): animal trait variation, animal behaviour, animal abundance, population structure (sex ratio and age structure) and habitat openness. Hunters have time limitation, and we expect hunters to be less selective if the chance of not getting anything is a worse alternative. Therefore, selectivity will be reduced where there is low population density (Tenhumberg et al., 2004), a skewed sex ratio leading to low density of one sex (Nielsen and Solberg, 2006), a high quota relative to population size (Solberg et al., 2000), a short duration of hunting season or small estate size (Mysterud, 2011). It is less well documented how the level of knowledge and skill (use of guides), cultural background, religion (taboos) and individual ethics affect selectivity, but it is likely to play a role. In Alaska, the largest moose (Alces alces) were shot by client hunters where guides were able to find better areas with higher availability of large moose (Schmidt et al., 2007). Competition among hunters can also decrease selectivity if passing a chance increases the risk that the animal may be shot by another hunter. In some cases, quotas are given not to single hunters or teams, but to larger areas. No such case is reported for ungulates, but such a quota system is commonly used for large carnivores (brown bears Ursus arctos: Bischof et al., 2009; lynx Lynx lynx: Nielsen et al., 2012).

Lastly, it might not be possible to achieve the level of selectivity that would be the optimal choice, due to practical management or implementation constraints (Milner et al., 2011). For example in Scandinavia, it is a management goal for moose populations to harvest a high proportion of yearlings, and the aim is to shoot as many female as male yearlings. It is quite easy to separate a yearling male from other classes of moose, while it is difficult to separate a yearling female from an adult female. Therefore, when given quotas of yearlings, hunters end up shooting 1:4 female:male yearlings and then skewing sex ratio towards females to an undesired degree (Haagenrud and Lordahl, 1974). Similarly, it might be difficult to separate male from female chamois in some cases. Therefore, empirical analysis of what has been actually harvested is important, but there are currently few such studies.

6.1.2 Empirical evidence for hunter selection

Ideally, evidence of hunter selection should compare the composition of the harvest relative to the structure of the remaining or overall population, or be based on individually marked animals so that selectivity can be determined relative to other marked individuals (Bischof et al., 2009). Unfortunately, most studies of harvest selection are not designed this way due to data limitation. Rather, the majority of published studies available have compared the composition of offtake among hunting methods (drive versus stalking) or different groups of hunters (trophy stalker versus local hunter) to identify differences. Typically, this assumes that since they hunt from the same population, differences will reflect variation in selectivity, which is likely a fair assumption within a given hunting season with low levels of
other mortality. Also, several studies compare the harvests taken by human hunters with off-take of natural predators, following the same logic (moose–wolf *Canis lupus*; Sand *et al*., 2012; roe deer *Capreolus capreolus*–lynx: Andersen *et al*., 2007; wild boar–wolf: Nores *et al*., 2008). A recurrent problem with many studies is the lack of separation with selection for age and size (Mysterud, 2011); older males are also larger, but separating these effects has rarely been done.

A very common pattern of selectivity is to avoid harvesting females with offspring. Female moose 5–10 years old which were without a calf had a 3.2 times larger risk of being harvested (Ericsson, 2001). No selection for size or between single and twin moose calves was found (Moe *et al*., 2009). For chamois, too, survival was higher for females with offspring due to hunting (Rugghetti and Festa-Bianchet, 2011). In some areas, wild boar females with piglets are not allowed to be shot (Keuling *et al*., 2010). [In such a context, it has been demonstrated that orphaned red deer calves do indeed have lower body growth and survival even after weaning (Andres *et al*., 2013).]

Studies have shown that for red deer in Spain, larger males, overall, were shot during trophy stalking than during management hunting and monteira, a particular way of drive hunting in Spain using chasing dogs (Martínez *et al*., 2005). A special kind of selective monteira, with the aim of removing inferior males, showed that smaller males were shot compared to during commercial trophy hunting even after correcting for age (Torres-Porras *et al*., 2009). For red deer harvesting in Hungary, local hunters shot younger and on average smaller stags than foreign, trophy stalkers (Rivrud *et al*., 2013). Similarly, local roe deer hunters in Poland aimed more for meat and shot smaller males, while foreign hunters aiming for trophies naturally shot larger bucks (Mysterud *et al*., 2006). Part of this was due to the fact that late in the season, fewer large males may be around due to depletion (Mysterud *et al*., 2006). Selectivity for larger and older males among moose hunters in Norway decreased when the opportunity to select was limited due to a female-biased sex ratio and a young male age structure (Nilsen and Solberg, 2006).

Selection may decrease if trait size is similar among groups of animals due to low body size dimorphism or lack of visual secondary sexual characters. If so, we would expect reduced hunter selectivity for monomorphic species like roe deer. However, a study from Italy showed that hunters were surprisingly capable of targeting the larger males even for roe deer with fairly small trophies compared to larger species (Ramanzin and Sturaro, 2013). In this specific case, this may be partly achieved due to the openness of the habitat; habitat openness, which also often promotes gregariousness, is likely a very important factor in increasing the potential for accurate selection, but documentation of this is lacking. Selectivity is also affected by habitat *quality*, as this affects the overall size of antlers (Ramanzin and Sturaro, 2013).

In Portugal, nocturnal hunts by single hunters for wild boar at bait (called ‘espera’) were highly selective for larger males and avoiding piglets compared to drive (‘montaria’) hunting (Braga *et al*., 2010). No evidence of sex-biased hunting of marked piglets was found for wild boar in Germany, where the dominant
Effects of Selective Harvesting on Ungulate Populations

hunting method was from hides, with some drive hunting (Keuling et al., 2010). For wild boar with drive hunting, the mere size of the animal may be important, due to the difficulty of hitting smaller targets, but data are currently lacking.

Few studies quantify how much animal behaviour affects harvest-related selection. For wapiti in Rocky Mountains, USA, the probability of a female surviving during the hunting season decreased with age, year, extent of space use, cover and human tracks (Webb et al., 2011). Clearly, it is possible that animals with higher energy requirements, for example hinds with male offspring, are more frequently using pastures or ranging over larger areas and hence have an increased likelihood of being shot. Slightly higher selection for male brown bear likely resulted from the fact of their larger home ranges (Bischof et al., 2009). Despite the intuitive logic of some of these relationships, a study of red deer harvesting in Norway found limited support for the notion that behavioural differences were important for the resulting offtake (Rivrud et al., 2014). There is currently no study to document specifically whether the use of dogs might affect selectivity. The use of dogs on a leash or barking in Fennoscandia (Ruusila and Pesonen, 2004) or during drive hunting in continental Europe (Apollonio et al., 2010) is common. Drive hunts with or without dogs are typically less selective, but the role of dogs in affecting this pattern remains unclear. Though some effect of non-intentional selectivity is likely, this is clearly less important than intentional selection.

6.2 Demographic consequences of selective harvesting

Individuals differ greatly in their contribution to population growth rate (Sæther et al., 2007). Hence selective harvesting may have a huge impact on the population growth rate depending on whether actively reproductive individuals are being targeted. Female ungulates raise offspring alone without any help from males. They start reproducing at ages between 2 and 5 years and continue to do so every year or every other year, depending on species, habitat, climate and population density, until they reach a senescent stage (Gaillard et al., 2000). The most obvious link between selective harvesting and population growth rate is thus the number and proportion of adult females in the harvest (e.g. Nilsen et al., 2005); harvesting the adult female population will have the largest impact on future population growth and this is also confirmed empirically for red deer (Milner et al., 2006). It is quite clear that indiscriminate hunting of all age and sex classes is much more detrimental to population growth than selective trophy hunting (Caro et al., 2009). In theory, it is ‘easy’ to find the optimal way to harvest populations given an explicit and clear aim. In reality, aims are often not so clear; often there are multiple aims and there is a strong cultural component involved in harvest regimes. In addition, selectivity might be difficult to achieve due to practical problems of separating animals of different age and sex, or due to limitations of time as explained above.

Indirect demographic consequences of selective harvesting can be defined as those not linked to the removal of individuals (simply in terms of numbers) or the reproductive value of those remaining in the population. Mainly, indirect effects
are linked to how mating is affected by changes in the sex and age structure of the population. Population models only consider the female part of the population, assuming there are always a sufficient number of males. This assumption may not hold for populations with severely skewed sex ratio, and it may depend on the mating system of the species in question (Caro et al., 2009; Schindler et al., 2013). Selective harvesting might skew sex ratios and age structure up to a limit where the role of males might be important (Ginsberg and Milner-Gulland, 1994; review in Mysterud et al., 2002). Such models can be termed behaviourally sensitive models, and there has now long been an aim to link individual behaviour to population dynamics (Sutherland, 1996).

It is clear that without any males, no offspring will be produced. Equally true for polygynous ungulates, a few males can sire many offspring. The interesting question is exactly how skewed sex ratios need to be before male limitation becomes an issue causing reduced productivity, and whether this differs depending on the level of polygyny. Simulations suggest that male capacity to inseminate females can be limiting when the adult sex ratio is severely skewed (Gruver et al., 1984; Ginsberg and Milner-Gulland, 1994), especially for monogamous mating systems (Caro et al., 2009). We can divide effects into several demographic or life history variables, mainly reduced reproductive rate and later, and less synchronous, breeding as a result of changes in sex ratio and age structure of males (review in Mysterud et al., 2002). Note also that hunting during the breeding season in itself might affect populations (Apollonio et al., 2011). Less attention has been paid to the fact that sexual selection processes will change with sex ratio and male age structure. Reduced male competition at skewed sex ratio may affect mass loss in males (Mysterud et al., 2005, 2008) and in consequence reduce mortality. With lower male harassment of females, there might be less mass loss also in females.

What is the evidence there are simply too few males to inseminate all females? Is there evidence that fewer males take longer to inseminate all females? Are females more reluctant to mate younger males? Can the presence of males induce ovulation (the male effect)? Does male harassment affect mass loss or female distribution?

### 6.3 Potential indirect effects of population age and sex structure on demography

Ungulates in Europe face a strongly seasonal environment. Short growing seasons impose a severe constraint on the life histories of ungulates, as, especially in higher latitudes, there is only a comparatively short time to raise an offspring that will be of a sufficiently large size to survive the winter. Plant quality and quantity often peak early in the season (Bunnell, 1982; Côté and Fest-Auban, 2001). Therefore timing of mating is important. If mating is delayed, it will normally affect the birth dates, as duration of gestation is flexible only within relatively narrow limits (Klitic, 1982, 1988; Clutton-Brock et al., 1982). A late ovulation provides the next year's offspring with a poor start in life, as they will have less time to grow before winter and may also be born after peak protein levels (Hogg et al., 1992).
Late-born offspring are more likely to die (bighorn sheep: Festa-Bianchet, 1988) and have lower social status later in life (American bison Bison bison: Green and Rothstein, 1993). Small body mass in autumn is known to cause higher overwinter mortality (red deer: Loison et al., 1999b) and it may take an additional year to reach the size required to mature for females (Langvatn et al., 1996, 2004).

Despite the fact that gestation periods are comparatively inflexible, earlier mated females, being typically older and larger, have somewhat longer gestation period than females mated later in the season (bison: Berger, 1992; semi-domestic reindeer Rangifer tarandus: Mysterud et al., 2009a). In a manipulative study using vasectomised males to ‘trick’ females into reovulation, the late conceiving females had 10 days shorter gestation times (Holand et al., 2006a). Late-breeding females gave birth to offspring of lower mass, and they were substantially smaller in autumn. However, a late calving may also affect the females next reproductive cycle (Hogg et al., 1992; Langvatn et al., 2004), reducing future fertility. In red deer, a 1% reduction in fertility was reported for every day past the date of median conception in previous year (Clutton-Brock et al., 1987; see also for caribou: Cameron et al., 1993).

There is no study reporting how much the reduced synchrony in birth, due to more variable breeding induced by selective harvesting, may affect calf survival. Many calves are taken by predators during the first few week of life (Linnell et al., 1995; Aanes and Andersen, 1996; Jarnemo et al., 2004; Panzacchi et al., 2008) and, in general, synchrony of birth is considered an important strategy to reduce predation rates through a swamping effect (Estes, 1976; Leuthold, 1977). In bighorn sheep, no difference was found between birth dates and synchrony in two founder populations with either sex ratio 1:7.5 adult male (≥2-year olds):female (≥3.5-year olds) and in a group with 0:12, but with 1.5 year old males (Whiting et al., 2008).

Time limitation leading to later mating can potentially be linked to several processes: (1) if prime-age males are few, it may take them longer to inseminate all females, either due to the requirement for courtship or simply because they become exhausted (courtship), (2) females may be reluctant to mate if there are only young males around early in the rut (female choice), (3) presence of (prime-aged) males may itself stimulate oestrous directly (male effect), and (4) female distribution may differ (mate search). There may be sperm depletion during late rut, even for feral sheep with comparatively large testicles (Preston et al., 2001), but currently there is no evidence that this is a severe limitation for breeding in selectivity harvested populations.

6.3.1 Female choice, search and competition
In general, female ungulates clearly compete more for resources needed for successful reproduction rather than for mating opportunities (Clutton-Brock, 2009).

1In contrast, female condition was similar among the groups, providing evidence of the conservative reproductive tactics used by ungulates (Gaillard and Yoccoz, 2003).
However, among topi, females were shown to compete actively for preferred males (Bro-Jørgensen, 2002, 2007). Female red deer prefer the roars of larger males (Charlton et al., 2007) and selected males with a high roaring frequency (McComb, 1991). In bison, too, it was shown that females in groups with large males (25-year-olds) were more likely to copulate (Bowyer et al., 2007). A reluctance of females to mate with younger males was reported in fallow deer (Komers et al., 1999). A considerable energy cost of mate sampling was also documented in female pronghorn (Byers et al., 2005). That this was a costly behavior was also suggested since effort for mate search was reduced in a dry summer when there was less forage available (Byers et al., 2006). Such mate search may be to obtain better genes (Byers and Waits, 2006) or act as fertility insurance (fallow deer: Briefer et al., 2013). And in evidence that a reduction in availability of mature males may have a significant effect on reproductive behavior and dynamics, Milner-Gulland et al. (2003) suggested that increased female aggression and competition for the remaining few males was an important factor driving the reproductive collapse observed in saiga antelope, although such assertion is largely based on anecdotal evidence.

6.3.2 Male effect

That the presence of a male may stimulate female reproduction is well documented in animal husbandry and termed the male effect (see more generally in Mc Clintock, 1983). Presence of rams stimulates ewes to oestrus with an elevation in plasma luteal hormone (LH) secretion (Rosa et al., 2006). The pre-ovulatory pulse of LH was 7 hours earlier in ewes housed in the same pen as a ram, and thus able to interact directly, compared to those with a ram housed in a separate pen situated between every two ewes (Abecia et al., 2002). A longer exposure to rams increased the chances of ewe lambs starting breeding (Kenyon et al., 2008). In goats, it was shown that higher ranked females responded first to males (Alvarez et al., 2003, 2009).

There is also some evidence from cervids. In reindeer, when males were introduced to groups of females late, this resulted in a 10-day later onset of ovarian activity (Shipka et al., 2002). Females are stimulated by both sound and smell of males. Recorded roaring by red deer stags induced oestrus in females, but smell and/or vision seemed also to play a role (McComb, 1987). Male urine contains odiferous compounds that may induce oestrus (Whittle et al., 2000). Cow moose aggressively compete for access to bull urine (Miquelle, 1991). The concentration of some of these compounds is related to male age (Miller et al., 1998), and therefore not only male presence, but also to age of available males (fallow deer: Komers et al., 1999).

6.3.3 Male search and female distribution

Distribution patterns of females during the rut may also vary with sex ratio and male age structure and hence affect the likelihood of a synchronous calving
Effects of Selective Harvesting on Ungulate Populations

season. Recent studies documented variation in female spatial organisation during the peak of the rut depending on the availability of males. In a manipulated herd of semi-domestic reindeer with an even sex ratio and male age structure, the female distribution was best described as one large floating harem (L’Italien et al., 2012). Most of the females were easily accessible for the males and vice versa during the main rut. With a skewed sex ratio, females gathered in several distinct harems throughout the main rut and quite a few females were always in transit between harems although the frequency decreased during peak rut. In fallow deer, a switch to lekking was found with a high density of mature males (Schaal and Bradbury, 1987; Langbein and Thirgood, 1989; Thirgood et al., 1999). Therefore, the presence of high quality, prime-aged males, may lead to females being less dispersed and hence increasing the probability of a more synchronous rut. Reindeer males with higher rank control larger and more stable groups; however, mating group size and stability decreased with more male-based sex ratio (L’Italien et al., 2012). Prime-aged male reindeer devoted more and young males less energy with more females in the mating group (Tennenhouse et al., 2011). Under conditions of high female aggregation in red deer, males were unable to monopolise whole female groups (Pérez-González and Carranza, 2011), but mainly when the population sex ratio and male age structure was even so the proportion of competitive males was high.

6.3.4 Male harassment

Females may have energetic costs related to mate search, but may also incur additional costs by being harassed by males (Clutton-Brock et al., 1982). Therefore, change in rutting activity related to changes in sex ratio and age structure of males imposed by selectivity harvesting may also affect female body condition. An excess of males may lead to more aggression towards adult females (Le Galliard et al., 2005). Male harassment of females may be exacerbated or reduced by selective harvesting; female biased sex ratios might be expected to cause less intense mate competition and harassment. By contrast, in populations where there are few mature males and the population is dominated by an excess of younger males, these may have a less well-developed social structure and heightened levels of harassment of females (Valdez et al., 1991; Komer et al., 1999; but see Shackleton, 1991).

The strongest evidence for a high cost of rutting comes from studies of feral sheep in Kerguelen sub-Antarctic archipelago, where male harassment caused direct mortality of females at a very male-biased sex ratio (Réale et al., 1996). Female fallow deer in captivity confined with young males lost more weight than when confined with older males during rut (Komer et al., 1999). In semi-domestic reindeer, female mass loss was highest where both young and old males were present (Holand et al., 2006b), suggesting again that more female-biased sex ratios may relieve such costs. In all these studies, the loss of body mass of females was linked to the harassment frequency and resulted in reduced time for feeding.
Females in larger herds were less frequently harassed (red deer: Clutton-Brock et al., 1982; McComb and Clutton-Brock, 1994).

6.3.5 Sex ratio adjustments

A controversial theory in life-history evolution is the possibility of adaptive sex ratio adjustment (Hewison and Gaillard, 1999). There are two manipulative studies simulating effects of selective harvesting on offspring sex ratio producing largely the same results. In moose, when skewing population structure towards females and with young males, offspring sex ratio was skewed towards females (Sæther et al., 2004). Similarly in studies of semi-domestic reindeer, offspring sex ratio was markedly skewed towards females when fewer and younger males were present (Roed et al., 2007). For Scandinavian populations of red deer (Mysterud et al., 2000) and moose (Sæther et al., 2004), there are quite marked effects in offspring sex ratios observed in the harvest statistics, and such an increasing production of female offspring will positively affect population productivity.

6.4 Actual effects of selective harvesting on demography

Most studies reporting the number of females a male can inseminate come from animal production, and must be seen as upper thresholds for what is possible. At highly skewed sex ratios, there is often also a younger male age structure (Ginsberg and Milner-Gulland, 1994). Younger males do not have the same capacity to inseminate a large number of females as prime-aged males (Haigh and Hudson, 1993). For Scandinavia, a lower proportion of primiparous females were found to be breeding in moose when sex ratios were skewed and male age structure was young (Solberg et al., 2002). Reduced fertility was registered at approximately 1:3 male:female, and currently management of moose in Norway often aims to keep sex ratios no more extreme than 1:2.5. In the wild, the only reported case of a dramatic decline in reproductive rates of females is for the saiga antelope at 1:50 male:female (Milner-Gulland et al., 2003; above). Though reproductive rates may be compromised in extreme cases, it is rather an exception that females are not mated at all. Much more common is that rutting is delayed (Mysterud et al., 2002).

There are still comparatively few studies providing evidence for how skewed sex ratios need to be before there may be an effect on reproductive success or how important this is for actual population growth. The only quantified study of the effects of unintentional selective harvesting for population dynamics is for red grouse (and thus an example outside of ungulates; Bunnefeld et al., 2011). With integral projection models (Coulson, 2012), it should be possible to model the population effect of reduced body growth and so forth, but before such modelling studies are done, we cannot really determine how important changes in timing of mating on offspring survival and future reproduction really are in terms of their effects on overall population dynamics.
6.5 Evolutionary consequences

Strong directional selection for specific phenotypic traits, such as is typical of trophy hunting, can potentially lead to long-term evolutionary consequences (Harris et al., 2002; Festa-Bianchet, 2003; Allendorf et al., 2008; Colman, 2008; Allendorf and Hard, 2009; Darimot et al., 2009). There is little doubt trophy hunting is directionally selective. However, in such analysis it is important to remember that many populations are often not only harvested by trophy hunters and that in practice trophy males usually make up a very small proportion of the total harvest from any population. Moreover, management regulations often restrict hunters from following their preferences.

The level of directional selection for hunters targeting meat, subsistence, recreation or population control rather than trophies is not well documented. Reported evidence of directional selection acting on size is weak, as most such analyses only compare age classes differing in size (Mysterud, 2011), while the age-specific size within a population (the unit for evolution) remain uncertain. The degree of size selection may strongly differ between the age classes that are targeted in both males (Mysterud and Bischof, 2010) and females (Proaktor et al., 2007). Directional selection is sometimes reduced by counter selection pressure on small, young males (Mysterud and Bischof, 2010). In addition, trophy males are often shot at the age of trophy culmination, so that they have done most of their breeding before getting shot (Apollonio et al., 2010). It therefore cannot be taken for granted that the mere presence of trophy hunting always induces strong directional selection as a result of hunter preferences for large trophies. A lower level of selection will affect the expected rate of evolutionary response.

Further, we must recognise that any selection in harvest will always operate alongside forces of natural selection working either in the same or opposite direction (Ratner and Lande, 2001). It is also clear that increasing knowledge on how genetic architecture may limit evolutionary responses and of contrasting selection pressures in males and females (Johnston et al., 2013) will move our understanding forward in years to come. A critical point, in particular, is the extent to which antler size is heritable from father to son (Kruuk et al., 2002) and consistent from young to late age in deer during ontogeny, which remains debated (Bartos et al., 2007; Koerth and Kroll, 2008, 2010; Demarais and Strickland, 2010). The latter assumption is more likely to hold for horns that are not shed every year.

For small populations there might be other challenges related to selective harvesting (Hard et al., 2007; Steenkamp et al., 2007). Effective population size may become lower (Sæther et al., 2009). Similarly, under such conditions, it has been shown that it is the combination of mating system and sex ratio that is a driver of the variation in population growth (Lee et al., 2011). In small populations of highly polygynous species, there are only a few males to inseminate a large number of females. Any random event that affects the males ability to do their job may markedly affect population productivity (Lee et al., 2011). This may be the case, for example, in small alpine populations of boids being target of trophy hunting.
Indeed, harvesting may remove particularly important individuals from the population. For example in elephants, old mothers know migration routes (McComb et al., 2001). There are limited studies of how removal of top ranking males might affect the social structure, but anecdotal evidence from red deer in low density populations suggest removal of the top stag may lead to local redistribution of females. For large populations, regions with limited harvesting might buffer selective effects of harvesting through migration (Tenhumberg et al., 2004).

6.5.1 Empirical evidence of trends in trophy size

For mouflon in Massif Central, France, a decline in overall size and width of horns could be related to trophy hunting (Garel et al., 2007). In alpine chamois, horn length appeared to have a limited role in male reproductive success and hunter selection was regarded as unlikely to yield an evolutionary response in males (Rughetti and Festa-Bianchet, 2010) or females (Rughetti and Festa-Bianchet, 2011). In red deer in Hungary, based on data from trophy exhibitions from 1880–2008, there was no clear overall trend in trophy size (Rivrud et al., 2013; Figure 6.2). Note that trophy sizes from Hungary were not age-corrected and variation in trophy sizes among periods was most likely related to overharvesting connected to the World Wars.

Figure 6.2a Trophy trends of red deer in Hungary (from Rivrud et al., 2013). Figure is reproduced from the Journal of Applied Ecology by kind permission of John Wiley and Sons (Wiley-Blackwell Publishers) and shows number of antler tines per trophy through time.
Analysing the trophy scoring of North American ungulates also showed that age structure seems to be the main driver of size (Monteith et al., 2013). For Iberian wild goat (Iberian ibex) and the aoudad or Barbary sheep in south-eastern Spain, an observed decline in horn length over an 18-year period was suggested to be due in part to effects of density, but also to removal of large males by trophy hunters (Pérez et al., 2011). Clearly, temporal variation in phenotypic traits is not very strong evidence of evolutionary change, as it may reflect phenotypic plasticity. In three populations in Vosges in eastern France, however, changes in allele frequency coding for the number of tines on the antler in red deer was linked to the level of selective hunting (Hartl et al., 1991).

The limited empirical evidence should not be taken as argument that trophy hunting cannot generate evolutionary effects. Rather, one might consider taking a precautionary principle and apply either spatial and temporal refuges, compensatory culling, saving stags until prime age culmination and demanding higher prices for larger trophies (Rivrud et al., 2013). Due to the economic incentives and demands for larger trophies, there is a risk that supplementary feeding, selective breeding through introduction of males with specific, desired characteristics, and other management actions for hunted populations of ungulates become so interventive that they take animals close to a semi-domestic stage (Mysterud, 2010). I will argue this latter development might be important to consider in conservation.

Figure 6.2b Trophy trends of red deer in Hungary (from Rivrud et al., 2013). Figure is reproduced by kind permission of John Wiley and Sons (Wiley-Blackwell Publishers) and shows changes in average beam length (cm) through time.
6.5.2 Reduced sexual selection among males

Growth patterns of male moose suggested that in populations where there is a strong bias towards females, males may show lower body and trophy sizes, presumably as a consequence of lower levels of sexual selection (Mysterud et al., 2005; Tiilikainen et al., 2010). In red deer it is clearly documented that such changes in sex ratio and age structure affect the degree of polygyny (Pérez-González and Carranza, 2011). Also in red deer, male-biased dispersal is the most common pattern of dispersal. However, a transition to female-biased dispersal was found in areas with selective harvesting, causing sex ratios strongly biased towards females and with a high proportion of young males (Pérez-González and Carranza, 2009). Under these conditions, male–male competition for mating opportunities was lower, and this reduction of competition made it possible for young males to remain, which in turn may have meant that females were more likely to disperse as a response to male philopatry. In Spain, selective harvesting of red deer documented lower genetic diversity in hunting estates than within a national park without hunting, arguably due to fewer males and limited competition among males (Martínez et al., 2002). It is clear from such examples that selective hunting might affect social dynamics within a harvested population, but compared to the extent of such hunting, studies are still few.

6.5.3 Female life history and hunting

Theoretical models for red deer females suggest that under heavy harvest pressure, individuals that begin reproduction at a young age and at a light weight have a greater chance of reproducing at least once compared with those that begin reproduction at heavier weights later in life (Proctor et al., 2007). This will be a trade-off against the cost of early reproduction, which is often substantial. No trend towards earlier maturation was found for red deer in populations where a high proportion of non-breeding juveniles are harvested (Mysterud et al., 2009b). This can be seen as support of the theoretical model for how selective harvesting might affect life history (Proctor et al., 2007), as hunting is mainly expected to affect life history if hunting pressure is most heavy after the animals reach reproductive maturity. Differences in harvesting pressure among populations of wild boar correlated with the proportion of juveniles reproducing; generation time was 3.5 years in a lightly hunted population and 2.3 years when heavily hunted (Servanty et al., 2009). Wild boar started to reproduce at an earlier age under heavy hunting pressure (Gamelon et al., 2011). Hunting might thus lead to evolution for earlier age of first reproduction in ungulates. The tradition of saving females with offspring might in theory also lead to evolution for more frequent reproduction (Ericsson, 2001).

6.6 Conclusion

Hunting is usually selective for age, sex or size. Selectivity is driven mainly by intentional factors such as harvest quota and hunter preferences, though cases of

...
non-intentional selection occur. Theoretical models give clear motivation and directions on how to harvest populations given clear management aims, but they have often ignored that a certain proportion of males are needed. Effects of selective harvesting may be difficult to predict as there might be multiple goals, such as both aiming for high quality trophy males as well as controlling the population size and using the meat.

From a management perspective, there are many positive effects of being selective. Selective harvesting can increase productivity when saving adult females. However, there is a limit to how low the proportion of males within the populations can be without affecting productivity and, in particular, delaying breeding. Further, skewed sex ratios and age structure in harvested populations may lead to a relaxation of sexual selection processes. These processes are currently understudied. Still, there is limited empirical evidence to demonstrate convincingly how important such evolutionary processes are for trait development among European ungulates.

References


Mysterud


Effects of Selective Harvesting on Ungulate Populations


Effects of Selective Harvesting on Ungulate Populations


Mysterud


