

## FORUM

# Selective harvesting of large mammals: how often does it result in directional selection?

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## Summary

1. Harvesting of large mammals is usually not random, and directional selection has been identified as the main cause of rapid evolution. However, selective harvesting in meat and recreational hunting cultures does not automatically imply directional selection for trait size.

2. Harvesting selectivity is more than a matter of hunter preference. Selection is influenced by management regulations, hunting methods, animal trait variance, behaviour and abundance. Most studies of hunter selection only report age- or sex-specific selection, or differences in trait size selection among hunting methods or groups of hunters, rather than trait size relative to the age-specific means required for directional selection.

3. *Synthesis and applications.* Managers aiming to avoid rapid evolution should not only consider directional selection and trophy hunting but also mitigate other important evolutionary forces such as harvesting intensity *per se*, and sexual selection processes that are affected by skewed sex ratios and age structures.

**Key-words:** conservation, evolution, evolutionary enlightened management, hunting, large mammals, management, sustainability

## Introduction

There is increasing concern about the possible long-term evolutionary consequences of heavy human harvesting (Harris, Wall & Allendorf 2002; Festa-Bianchet 2003; Allendorf *et al.* 2008; Allendorf & Hard 2009; Darimot *et al.* 2009). Such effects have been linked to strong directional selection for specific phenotypic traits, such as against large fish because of mesh sizes of closing nets (Jørgensen *et al.* 2007) or against large trophy males because of hunter preference (Coltman *et al.* 2003; Garel *et al.* 2007). Directional selection effects of trophy hunting on size are well documented for bighorn sheep *Ovis canadensis* Shaw in Canada (Coltman *et al.* 2003). Trophy hunting is widespread (Courchamp *et al.* 2006; Johnson *et al.* 2010), so these results should be taken seriously.

However, most harvesting of large mammals is not a result of trophy hunting. Moreover, management regulations often restrict large mammal hunters from following their preferences. When comparing red deer *Cervus elaphus* L. harvest statistics across 11 European countries (Milner *et al.* 2006), the proportion of calves in the harvest varied from 10% to 40%,

while males typically accounted for 40–60% of the remainder, i.e. male and female harvests were of similar magnitude. Trophy bulls usually make up a very small proportion of the harvest. Directional selection are sometimes reduced by counter selection pressure on small, young males (Mysterud & Bischof 2010), and trophy males are often shot at the age of trophy culmination (Apollonio, Andersen & Putman 2010). The degree of size selection may strongly differ between the age classes that are targeted in both males (Mysterud & Bischof 2010) and females (Proaktor, Coulson & Milner-Gulland 2007). Different selection pressures arise from harvesting aimed at meat provisioning, subsistence, recreation or population control. It therefore cannot be taken for granted that harvesting always induces strong directional selection as a result of hunter preferences for large sized individuals.

Identifying the level and pattern of selection is crucial for predicting expected rates of evolutionary responses to large mammal hunting. Here, it is argued that: (i) there are currently few studies documenting directional selection for body or trophy size despite claims on the contrary (Tenhumberg *et al.* 2004; Allendorf & Hard 2009) and (ii) that in many cultures, large mammal harvesting is not expected to induce strong directional selection in trait size. Harvest selectivity in mammals is complex because of highly variable environments,

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management culture and regulations. We also need to broaden our focus beyond trophy harvesting when considering evolutionary effects.

### The mechanisms of harvest selectivity

The factors affecting patterns of harvest selectivity in terrestrial ecosystems can be broadly organized into: (i) hunter preferences and (ii) opportunities to be selective via (a) management regulations (quotas; economic costs etc.), (b) hunting methods (stalking vs. drives etc.), (c) animal trait variation (strength of hunter cues, appearance), (d) animal behaviour, (e) animal abundance, (f) population structure (sex ratio and age structure) and (g) habitat openness. Table 1 gives an overview of common traits targeted by hunters in terrestrial ecosystems and the cues the hunters use to separate individuals at the within-species level most relevant for directional selection. The hunters' preferences are likely to differ depending on hunter motivation (i.e. meat, recreation or trophy), level of knowledge and skill (use of guides), cultural background, religion (taboos), individual ethics and animal trait variation. For example, trophy hunters using guides shot larger moose *Alces alces* L. in Alaska, because guides took client hunters to areas with lower population densities and therefore larger moose (Schmidt, Ver Hoef & Bowyer 2007). More importantly, strong directional selection for size is often unlikely because of

limited (or redirected) opportunities for hunter selection because of both direct and intentional factors such as quotas or economic costs of high pricing and also time limitations, cost of lost opportunity, and indirect and non-intentional factors through animal behaviour and abundance (Table 2).

If there is little opportunity for choice, for instance because of a low population density (Tenhumberg *et al.* 2004), a skewed sex ratio leading to low density of one sex (Nilsen & Solberg 2006), a high quota relative to population size (Solberg *et al.* 2000), a short duration of hunting season, or small estate size, selectivity will be reduced. For example, moose hunters did not select for male age (older being larger), in a situation where a female-biased sex ratio and a young male age structure limited the opportunities to select (Nilsen & Solberg 2006). High competition among hunters is likely to produce the same effect. For example, for large carnivores in Scandinavia, quotas are given for large regions rather than to an individual hunter. Low selectivity was found for brown bears *Ursus arctos* L. under such management regulations (Bischof *et al.* 2009). A given hunter might prefer to shoot a very large male, but might not risk passing up a small bear because the quota for the area might be filled before the hunter encountered a large bear, and furthermore, the hunter has nothing to lose by shooting the small bear as there is no individual quota. Similar effects result as a consequence of team hunting on the same estate.

**Table 1.** Traits used for direct hunter preference or selection

Trait targeted	Hunter cue	Examples	References
Age: juvenile vs. yearling/subad.	Juvenile traits (short jaw), small body size, overall appearance (fur colour etc.)	Cervids	
Age: yearling/subad. vs. adult	Body size, antler or horn size	Cervids	
Sex: male vs. female	Sexual traits (presence of penis) Secondary sexual traits (presence, size or form of horns, antlers, tusks; colour of mane) Sexual body size dimorphism	Cervids Elephants, lions <i>Panthera leo</i> L., cervids Chamois	Kurt, Hartl & Tiedemann 1995; Whitman <i>et al.</i> 2004
Females: reproductive status	Offspring vs. no offspring at heel	Moose Brown bear Chamois	Ericsson 2001 Bischof <i>et al.</i> 2009 Rughetti & Festa-Bianchet 2011
Female size	Body size	Cervids	
Male size	Trophy or body size	Cervids, bovids	Coltman <i>et al.</i> 2003
Special trophies – 'oddities'	Parück vs. normal	Roe deer <i>Capreolus capreolus</i> L.	
Colour morphs	Black morphs vs. normal	Springbok <i>Antidorcas marsupialis</i> Sundevall, roe deer	
	White morphs vs. normal	Springbok	
	Silver morphs vs. normal	Fox <i>Vulpes v. fulvus</i> Desmarest	Haldane 1942

**Table 2.** Mechanisms affecting the level of hunter selection beyond hunter preferences

Factor	Effect on selectivity	Mechanism	Type of selection
<b>Management</b>			
Quota: size	More selective if small quota	Law enforcement and time limitation	Direct
Quota: specificity	Less selective the more specific the quota	Law enforcement	Direct
Quota: scale	Less selective if quota for a region or team rather than for individual	Competition among hunters	Direct
Duration of hunting season	More selective the longer the hunting season	Time limitation, but depletion may reduce selectivity	Opportunity for direct
Size of hunting estate	Less selective on smaller estates	Fewer to choose from	Opportunity for direct
Price	Less selection the more costly to shoot the larger one	Not all hunters have endless amount of money	Direct
<b>Hunting implementation</b>			
Hunting method	Stalking more selective than drive hunt	More time to assess differences when animals are calm	Indirect, and opportunity for direct
Use of guides	Use of guides increase selectivity	Guides assess size better; know where largest animals are living	Direct, opportunity for direct
Use of dogs	Use of dogs may lower selectivity	Preference of dogs might differ from preference of hunter	Indirect, and opportunity for direct
Trapping	Use of traps may change selectivity	Traps differ in specificity due to variation in catchability	Indirect
<b>Animal</b>			
Trait variation (Table 1)	More opportunities to select if animals differ in traits	Hunters ability to select differ, and differences can affect chances of being observed	Indirect, and opportunity for direct
Animal population density (and skewed sex ratio)	More selective the more to choose from	Time limitation to find animals at low density	Opportunity for direct
Grouping behaviour	More opportunities to select if animals in herds	Easier to assess differences in size when individuals are close	Indirect, and opportunity for direct
Mother-offspring bond	More selective if strong bond	If offspring do not follow mothers closely, more difficult to separate mothers from non-mothers	Indirect, and opportunity for direct
Sexual segregation	More (or less) selection if sex groups spatially segregate	Spatial search of hunter increase likelihood of shooting a given sex (but may decrease selection in some cases)	Indirect, and opportunity for direct
Home range size	More selection for animals with large home ranges	More exposed if large home range size	Indirect
Activity levels	More selection for animals that are more active	More active more exposed	Indirect
Habitat use	More selective harvest in open habitat (or farmland)	More vulnerable if using open areas (or farmland)	Indirect, and opportunity for direct
Individual personality	More selection for animals that expose themselves more	Animals may differ in their propensity to take risk	Indirect
<b>Landscape factors</b>			
Habitat	More open habitat increase selection	Easier to see what is available	Opportunity for direct

Table 3. Studies of harvesting selection of mammals in terrestrial ecosystems. Dir. Sel. = evidence of direct selection on trait size (or character)

Species	Trait	Assumed mechanism	Selectivity comparison	Population average or availability known	Dir. sel.	Reference
Ungulates						
Bighorn sheep	Male trophy size	Hunter preference	Rams of different sizes	Yes	Yes	Coltman <i>et al.</i> 2003
Chamois	Female reproductive status	Management	Populations with different management	No	Yes?	Rughetti & Festa-Bianchet 2011
	Female horn size	Hunter preference	No selection found	No	No	Rughetti & Festa-Bianchet 2011
Red deer	Age and sex	Management	Mortality of marked individuals	Yes	No	Langvatn & Loison 1999
	Male body mass	Hunter method	Montería vs. trophy-stalking vs. management catch vs. bycatch	No	No	Martinez <i>et al.</i> 2005
	Male body and trophy size	Hunter method	Commercial vs. selective montería	No	No	Torres-Porras, Carranza & Pérez-González 2009
Roe deer	Male body mass	Management	Local vs. client hunters; early vs. late season; habitat openness	No	No	Mysterud, Tryjanowski & Panek 2006
	Age and sex		Hunter vs. lynx <i>Lynx lynx</i> L.	No	No	Andersen <i>et al.</i> 2007
Moose	Female reproductive status	Management	Survival with or without reproduction (marginally sign.)	Yes	Yes?	Ericsson 2001
	Age and sex	Hunter preference (females, none found for males)	Age groups; within season decline	No	No	Nilsen & Solberg 2006
	Age and sex	Management	Sex-specific age groups; years with low and high quota relative to population size	No	No	Solberg <i>et al.</i> 2000
	Male trophy size	Hunter preference; implementation	With or without aid of guides	No	No	Schmidt, Ver Hoef & Bowyer 2007
	Calf size	None found	Male vs. female calves	No	No	Moe <i>et al.</i> 2009
Elk <i>Cervus elaphus</i> L.	Age and sex	Hunter preference	Hunters vs. wolves <i>Canis lupus</i> L.	No	No	Wright <i>et al.</i> 2006
White-tailed deer <i>Odocoileus virginianus</i> Zimmermann	Age and sex	Trapability	Trapability of marked individuals	Yes	No	Hiller <i>et al.</i> 2010

Table 3. Continued

Species	Trait	Assumed mechanism	Selectivity comparison	Population average or availability known	Dir. sel.	Reference
	Age and sex	Hunter method	Archery vs. firearm	No	No	Mattson & Moritz 2008
	Male age	Management	Mortality of marked individuals	Yes	No	Webb, Hewitt & Hellickson 2007
	Age	Hunter preference(?)	Mortality of marked individuals	Yes	No	Pac & White 2007
	Disease prevalence (CWD = Chronic Wasting Disease)	None found (animal behaviour hypothesized)	Periods of different harvesting methods	No	No	Grear <i>et al.</i> 2006
Mule deer <i>Odocoileus hemionus</i> Rafinesque	Age and condition	Assumed none	Hunter vs. mountain lions <i>Puma concolor</i> L.	No	No	Krumm <i>et al.</i> 2010
Wild boar	Age and sex	Hunter method	Espera vs. Monteria hunt	No	No	Braga <i>et al.</i> 2010
	Age	Hunter preference(?)	Hunters vs. wolves vs. estimated population	Yes	No	Nores, Llana & Alvarez 2008
	Age and sex	Hunter preference(?)	Mortality of marked individuals	Yes	No	Toigo <i>et al.</i> 2008
	Age and sex	None found	Mortality of marked individuals	Yes	No	Keuling <i>et al.</i> 2010
Large carnivores	Body mass	Hunter method	Moose vs. bear specialist hunters	No	No	Bischof <i>et al.</i> 2008
Brown bear	Age and sex	Animal behaviour	Mortality of marked individuals	Yes	No	Bischof <i>et al.</i> 2009
Mountain lion	Age and sex	Hunter preference(?)	Mortality of marked individuals	Yes	No	Cooley <i>et al.</i> 2009

Clearly, a lack of appropriate cues may in many cases limit the hunters' ability to select. Selection may decrease when there is low sexual body size dimorphism or lack of visual secondary sexual characters. By contrast, habitat openness promotes gregariousness, which can increase the likelihood of selection. Climate affects movement such as the timing of migration and can also affect opportunities for selection. We currently have rather limited knowledge of how much animal behaviour affects harvest-related selection in mammals, but it is likely to be an important factor. For example, young birds were more prone to being shot than adult birds because of difference in behaviour (Bunnefeld *et al.* 2009). Furthermore, selection on bold personality with fast growth has been found in fisheries (Biro & Post 2008).

In Fennoscandia, hunting of cervids is often carried out with the aid of dogs (either on a leash or barking), which is known to increase moose harvesting success by up to 56% (Ruusila & Pesonen 2004). Drive hunting in Europe is carried out both with and without the aid of dogs (Apollonio, Andersen & Putman 2010). In Nicaragua, dogs sometimes selected non-target prey species (Koster 2008), and it is possible dogs can be selective of scent from, e.g. rutting males, affecting selectivity. The spatial hunting behaviour of humans may also influence the selective pressures exerted (Schmidt, Ver Hoef & Bowyer 2007).

### Limited empirical evidence of directional selection

In a recent review of terrestrial ecosystems, Allendorf & Hard (2009) pointed out that selection is important for trait evolution. This conclusion was based on theoretical modelling which indicated that size-selective harvesting can cause shifts in trait values. However, the few empirical cases that were listed consisted of different kinds of hunters shooting different kinds of animals without any evidence that the total harvest differed in terms of trait mean from what was available in the population. There was thus no clear link from theory (directional selection → evolution) to data (non-random harvest). A broader review undertaken here (Table 3) reveals that there are no clear-cut examples of directional selection apart from the case study of bighorn sheep arising from trophy hunting. The most common documentation of selective harvesting comes from comparing different groups of hunters or using different hunting strategies or methods, or comparisons of age or sex classes rather than size directly (Table 3). That hunters select adults over calves is not evidence of directional selection acting on size, this would require comparison with age-specific mean size within a population (the unit for evolution). The population mean or availability in the population is known only rarely, and these studies therefore cannot say with confidence that selection is directional.

There is little doubt trophy hunting is directionally selective, but the level of directional selection for hunters targeting meat, subsistence, recreation or population control rather than trophies is not well documented. We do know that foreign trophy stalkers select differently than local hunters (Martínez *et al.* 2005; Mysterud, Tryjanowski & Panek 2006) and in some

cases, selection is based on size. A lower level of selection will strongly affect the expected rate of evolutionary response. Harvesting selection will always work against forces of natural selection (Ratner & Lande 2001). It is not known when selection pressure from harvesting is strong enough to alter the fitness landscape. The level of trait heritability is clearly also critical, but not the focus here.

In the bighorn sheep case (Coltman *et al.* 2003), the smaller males became the more successful breeders, which is a quite extreme example of harvest-driven directional selection. However, for elephants *Loxodonta africana* L. in Tarangire National Park, Tanzania, the larger males retained a higher mating success even under poaching pressure (Ishengoma *et al.* 2008), suggesting that the fitness landscape did not change qualitatively. In Alpine chamois *Rupicapra rupicapra* L., horn length appears to have a limited role in male reproductive success, and hunter selection was regarded as unlikely to yield an evolutionary response in males (Rughetti & Festa-Bianchet 2010) or females (Rughetti & Festa-Bianchet 2011). Harvesting effects are expected to be stronger in small populations (Hard, Mills & Peek 2007; Steenkamp, Ferreira & Bester 2007), and effective population size might become an issue (Sæther, Engen & Solberg 2009). For large populations, there is less likely to be uniform harvest pressure, and regions with limited harvesting might buffer selective effects of harvesting through migration (Tenhumberg *et al.* 2004).

### Harvesting intensity is itself important

A mild preference for large quarry size, for example in cultures where animals are hunted for meat, does not imply an absence of evolutionary effects but we need to consider other mechanisms. Even non-selective harvesting may theoretically affect trait evolution (Bischof, Mysterud & Swenson 2008).

The intensity of harvesting *per se* and the timing of the harvest relative to the age of first reproduction may be important in this context because life expectancy is a crucial fitness component in large mammals. The same harvest pressure is thus more important for males than females, because of lower life expectancy of males (Toïgo & Gaillard 2003). 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 (Proaktor, Coulson & Milner-Gulland 2007). However, we do not know how strong harvest pressures need to be to outweigh the (high) cost of early reproduction. Population differences in harvesting pressure have been shown to correlate with the proportion of juveniles reproducing in wild boar *Sus scrofa* L. (Servanty *et al.* 2009) but no trend towards earlier maturation was found for red deer in populations where a high proportion of non-breeding juveniles are harvested (Mysterud, Yoccoz & Langvatn 2009). Hunter preference for non-reproducing females is common (Table 1).

Furthermore, skewed sex ratios and age structure in harvested populations may lead to a relaxation of sexual selection processes. Limited intra-male competition for mates in

harvested populations with skewed population structure is suggested by observations of younger males rutting more in synchrony with older males (Mysterud *et al.* 2008) and a reversal towards female-biased dispersal (Pérez-González & Carranza 2009) in red deer. Lower levels of sexual selection might favour development of lower male body- and trophy sizes, as suggested by growth patterns of moose (Mysterud, Solberg & Yoccoz 2005; Tiilikainen *et al.* 2010).

## Conclusion

Understanding the mechanisms by which harvesting might affect trait evolution is crucial for management to select efficient mitigative efforts. It is emphasized here that harvesting, although selective, is not always expected to be strongly directional as a result of hunter preferences for large-sized individuals. In meat and recreational harvesting cultures, harvesting pressure, skews in population structure and timing of harvest relative to age at maturity are potentially more important drivers. Although the empirical basis for advice is currently weak, managers aiming to avoid artificial selection should also maintain a 'natural' population structure and target a high proportion of individuals that have not reached the age of maturity.

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