

## FORUM

# Still walking on the wild side? Management actions as steps towards ‘semi-domestication’ of hunted ungulates

Atle Mysterud\*

Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, P.O. Box 1066, Blindern, NO-0316 Oslo, Norway

## Summary

1. Domestication is a process involving adaptations to man and the man-made environment. Semi-domestic animals are those for which humans have only partial control over breeding, mortality, space use and food supply, and that have not been greatly modified by artificial selection. They therefore appear more similar to their wild counterparts.

2. The degree of domestication depends on the level of (i) human control over breeding, mortality, food supply, space use and thereby selection pressures; (ii) how much these differ from original states; and (iii) how strongly the phenotypic traits have been affected.

3. *Synthesis and applications.* Both natural and sexual selection in man-made environments may differ, and some management actions move traits of hunted ungulates closer to those associated with a semi-domestic stage; depending on the harvest pressure and selectivity, fencing, artificial feeding and predator control. There is a trade-off between high productivity of hunted ungulate populations and retaining wild traits.

**Key-words:** artificial feeding, behaviour, bovids, cervids, conservation, demography, fencing, predator control, selective harvesting, sexual selection

## Introduction

The management of wild large herbivores has received a lot of attention lately due to increasing population sizes and their importance to meet economic, conservation and environmental objectives (Gordon, Hester & Festa-Bianchet 2004). Hunters gain from increased opportunities, and hunting right owners can earn more money when populations are dense. On the negative side, traffic accidents, damage to forestry and agriculture and concern for overgrazing and general ecosystem impact increases (Mysterud 2006). Further, the heavy and sometimes highly selective harvesting might have evolutionary impacts on populations (Allendorf *et al.* 2008), and other management actions may have selective effects as well. Extensive feeding programmes are becoming increasingly popular (Putman & Staines 2004). Additional examples of active management are predator control and fencing, and less frequently the addition of individuals to relieve inbreeding, and to initiate stocks, and the use of contraception. Are we in some cases approaching a semi-domestic stage? The theme of ‘wildlife loss through domestication’ has received little attention, with the

notable exception of researchers working with urbanization effects on Florida Key deer *Odocoileus virginianus* Zimmermann, USA (Peterson *et al.* 2005; Harveson *et al.* 2007).

The increasing management of wild ungulates and their reliance on man-made landscapes raises some important questions regarding the potential consequences of selection processes that are more and more under human control. The intention here is to increase awareness of how new, stronger, larger scale and more specific management regimes might bring hunted ungulate populations in a semi-domestic direction. Increased awareness might help us to decide in which direction we want to go – or not to go.

## What is domestic, semi-domestic and wild?

The definition of domestication is not trivial. One definition is: ‘A domestic animal is one that has been bred in captivity for purposes of economic profit to a human community that maintains complete mastery over its breeding, organization of territory and food supply’ (Clutton-Brock 1989, p. 21). Animal domestication is a process involving a change in the phenotype relative to the wild counterparts. The genetic distance to the wild counterpart can be measured using population genetic

\*Correspondence author. E-mail: atle.mysterud@bio.uio.no

tools (Allendorf *et al.* 2008), however, domestication also involves phenotypically plastic responses, i.e. a change in the phenotype due to changes in the environment. The new man-made environmental conditions may vary from extremely contrived in cages to ranging in very large fenced areas, more similar to wild conditions.

A first important stage of domestication is control over breeding, either by separation of males and females, or castration. Clearly, selective breeding has formed the many breeds of 'true domestics' such as livestock. Artificial selection is the part of the domestication process that is best understood (Price 1984), and is often used as the key character of true domestication. However, artificial selection is not the only way genetic changes may influence the development of a domestic phenotype. Importantly, natural and sexual selection may differ in human influenced environments. Small captive populations are also more prone to inbreeding and genetic drift, i.e. a change in the relative frequency of an allele due to random sampling and chance. Indeed, in conservation, there are rules to avoid unintentional breeding effects when wild animals are held in captivity for later reintroductions (Williams & Hoffman 2009).

A separate group, termed 'exploited captives' (Clutton-Brock 1989) or 'semi-domestics', include species such as elephants *Elephas maximus* L. and camels *Camelus* spp. L., for which humans want to retain the original features such as being robust and having the ability to survive harsh conditions. Usually, the morphological traits are largely unaffected by artificial selection in these cases (Clutton-Brock 1989). Hence, a semi-domestic animal can be defined as 'a species (or population) having morphological, behavioural, physiological and/or life-history traits resulting from human management actions involving partial control over its breeding, mortality, space use and food supply to increase potential economic (or other) profit'. A marked distinction from fully domesticated animals is that (lower level) semi-domestication does not require selective breeding (Table 1).

Domestication involves changes in morphological, behavioural, physiological and life-history traits (Table 1). Reduced shyness is an important behavioural trait of domestication. However, captive animals can retain their fear of humans if they are hunted, whilst wild ungulates in many national parks have become habituated to humans. Thus, manifestation of fear of humans is not sufficient for an animal to be considered wild. In the case of the Florida Key deer, changes indicative of domestication were larger group size, higher densities and human control of selective pressure (Peterson *et al.* 2005). Large group sizes typically result from higher densities, which again may result from human control of harvesting. Similarly, high population density may enhance the spread of disease and the level of ecosystem impact. High population density can be seen as a trait of domestic animals. However, ungulate populations can be dense due to other reasons as well.

The degree of domestication depends on (i) the level of human control over breeding, mortality, food supply, space use and thereby selection pressures; (ii) how much these differ

from original states; and (iii) how strongly phenotypic traits have been affected relative to the wild counterpart. Natural and sexual selection in man-made environments may differ, and some management actions such as harvesting, feeding, fencing and predator control, are similar to those used for domestic ungulates. This may cause development of phenotypes with traits closer to a semi-domestic stage (Table 1).

## Game farming and fencing

Even as long ago as in Ancient Egypt, most species of local ungulates were kept in captivity for the purpose of hunting (Clutton-Brock 1989). Today, hunting in South Africa is mainly within game farms (around 2000 of them). The game farms are fenced and managed much like any other farm, except that the harvest is done by client hunters. Fencing, predator control and supplementary feeding are typical management interventions. Some farms have breeding programmes to avoid inbreeding and to increase trophy sizes. In extreme cases, there are even auctions for particular trophy individuals, hunting of feral stocks or animals bred in captivity. Translocations of different species into the same area have also led to hybridization thereby compromising the biological integrity of species (von Brandis & Reilly 2008). Such a management system typifies the extreme case in which all characteristics of being semi-domestic are present, although the animals usually retain their fear of humans due to heavy hunting. Most hunted ungulate populations are clearly quite far from such extreme cases.

Hunting in fenced areas in Europe is common, but involves less extreme management compared with Africa. Management includes fencing to increase population densities, some feeding and predator control, but no breeding programmes. In Austria, the 'winter gatter' tradition is well established and represents an intermediate case. It involves 'trapping' large sectors of the red deer *Cervus elaphus* L. population in fenced areas during winter, feeding them to reduce damage to forestry and also to increase population performance. Fencing is the strictest control over space use and is a strong indicator of the population approaching a semi-domestic stage (Table 1). Fencing can have a major impact on the evolutionary potential of a population (Hayward & Kerley 2009). Genetic drift is unlikely to be important in open, large populations (Hard, Mills & Peek 2007), but can be a major issue for fenced populations.

## Harvesting pressure and selectivity, demographical structure and sexual selection

Hunting can change the genetic make-up of large herbivore populations by processes such as altered gene flow, genetic drift and selectivity for or against specific traits (Allendorf *et al.* 2008). Harvesting regimes, the degree of selectivity and the overall harvest pressure, vary a great deal between different cultures, and are likely to determine selective pressures (Mysterud & Bischof 2010). However, while artificial breeding in the domestic case with full control of individuals can increase the mean values of desired traits, a fundamental difference is that

**Table 1.** An overview of relevant traits and management practices affecting the level of human control over food supply, space use and selection pressure, potentially moving traits of completely wild populations towards those associated with early stages of domestication (semi-domestic)

	Wild	Semi-domestic		Domestic
		Lower level	Higher level	
Management specificity	No control	Mainly indirect control	Direct, partly control	Direct, full control
Origin	Native or natural recolonization		Escaped or released from captive conditions; assisted recolonization; translocation	
Genetics	Native	Mixed with semi-domestic, hybridization	Semi-domestic origin	
Morphology	Normal		Fur coloration, e.g. more white or black morphs	Neonatal traits; special traits
Breeding				
Breeding (life history) – males	Normal	Reduced sexual selection; artificial selection by selective harvest; genetic drift in small populations	Supplement of individuals for active breeding	Artificial selection
Breeding (life history) – females	Normal	Early age of maturity	Contraception	Early age of maturity; large litter size; early ageing
Harvesting				
Harvest level: tagging and handling	None	Trait specific	Partly individual specific; highly trait specific; some handling and marking	Individual specific; handling and marking
Harvest pressure and selectivity	Low	Moderate high, fairly unspecific	High pressure and age; sex specific	High pressure on young animals and males
Resulting density and demographical structure	Density related to other factors; close to even sex ratio; dominance of adults	Density related also to other factors; younger age structure	High density; highly female biased; young male age structure	Very high density; highly female biased; few, but old males
Behaviour				
Shyness	Shy		Reduced shyness	Tame
Space use	Open	Restricted, e.g. due to reliance on artificial feeding sites	Fenced (game farms)	Fenced
Social organization	Natural	Group living, high density	Group living, high density	Group living, high density
Feeding	Natural	Agricultural pastures, urban areas	Outdoor, permanent feeding places	Indoor, or outside inside fences
Temporal dependence		Emergency winter feeding	Regular seasonal feeding	Year round
Type of forage	Natural	Variable	Silage, concentrate	Silage, concentrate
Predation	Natural predator community	Few predators for historical reasons	Aim for low predation levels, active predator control	Aim for eradication

shooting of higher than average quality individuals might yield undesirable evolutionary effects.

#### MALES

Extreme trophy hunting can cause a decline of trophy traits over time due to alterations in the fitness landscape

(Allendorf *et al.* 2008). Compensatory culling of low quality young males, as in the Germanic countries, may counter this theoretically (Mysterud & Bischof 2010). Hunting might also affect the breeding of cervids due to exceptionally skewed sex ratios and a young male age structure. In red deer in Norway, it has been shown that the rutting effort of younger males is more in synchrony with older males now than sex

ratios are skewed, indicating limited intra-male competition for mates and therefore a relaxation of sexual selection processes (Mysterud *et al.* 2008). Similarly on hunted estates in Spain, there was a reversal towards female-biased dispersal in red deer most probably due to lower male-male competition as a result of skewed female sex ratios and a young male age structure (Pérez-González & Carranza 2009). The long-term consequences of this are not known, but lower levels of sexual selection might favour development of lower male body- and trophy sizes. Restoring demographical structure is a major issue in the quest to retain 'normal' selection processes for hunted ungulates. This is fairly simple to achieve by reducing the offtake of males relative to females, but this may decrease the overall production of meat. A more even sex ratio can also have benefits in promoting earlier and more synchronous rutting (Mysterud, Coulson & Stenseth 2002), and there will be more trophy animals to be harvested.

#### FEMALES

Theoretical modelling suggests that adaptive responses towards earlier age at first reproduction are less likely when the increase in mortality due to harvesting occurs either prior to age at first reproduction or late in life (Proaktor, Coulson & Milner-Gulland 2007). For red deer and moose *Alces alces* L. in Scandinavia, often up to two-thirds of the harvest are either calves or yearlings (Milner *et al.* 2006), and there is a reluctance to shoot females with offspring (Ericsson 2001). Breeding early and having offspring at heel may therefore lower the probability of being shot, but the response may depend on the strength of the trade-off between reproduction and survival of both the mother and the offspring (Proaktor, Coulson & Milner-Gulland 2007). The current harvesting regime in Scandinavia with a large proportion of juveniles and yearlings in the harvest is unlikely to induce strong trends towards early maturation in females (Mysterud, Yoccoz & Langvatn 2009). It is not known whether larger litter sizes or early ageing (which are thought to be the life-history cost of early maturation) have been affected in deer populations, but with reduced life expectancy such effects are predicted.

#### Feeding, relaxed natural selection and what else?

Ungulates have been fed to some extent for centuries in Europe (Putman & Staines 2004) and North America (Boyce 1989). Such practices are increasing with the privatization of hunting and a growing emphasis on trophy size and economic return. Extensive winter feeding programmes are developing and many populations have become seasonally dependent on artificial fodder. We are moving from 'emergency feeding to buffer climate extremes' to regular 'seasonal feeding to buffer density effects', which may lead to increasing management problems related to overly dense populations. The crucial point in this context is the extent of the population reliance on feeding in terms of temporal pattern, how large a part of the population

uses artificial fodder, how large a part of their energy they get from this feed, and whether or not this feed is natural to the species.

Emergency feeding is typically employed to buffer extreme climatic conditions (Ouellet *et al.* 2001). This is the least extreme case of feeding, but even this might have an effect on the populations because it takes place during the periods with potentially the strongest selection. For red deer in Austria, winter feeding has been shown to reduce natural selection (for larger body size) among juveniles (Schmidt & Hoi 2002). Evidence from North America on white-tailed deer (Lewis & Rongstad 1998) and mule deer *Odocoileus hemionus* Rafinesque (Bishop *et al.* 2009) also implies that feeding has an effect on performance and thereby is likely to affect selection. There is considerable regional variation in the motivation and development of deer-feeding practices. In many regions, it has been advocated as a way to increase population sizes or to buffer effects of high density in areas where the natural forage has become scarce. Should we compensate for high density by increasing the use of artificial fodder, or should we regulate the population by hunting to a level so they can rely solely on natural forage?

Artificial feeding restricts movements (Guillet, Bergström & Cederlund 1996), alters local distribution patterns (Sahlsten *et al.* 2010), moves habitat selection in the direction of central place foraging (van Beest *et al.* 2010), and might change the mating system of ungulates (Carranza, Garcia-Munoz & Dios Vargas 1995). This can change selection pressure and reduce social learning of, for example, migration routes. For birds, winter feeding was found to select for non-migratory behaviour (Rolshausen *et al.* 2009). However, we know little about the long-term physiological and life-history consequences of such feeding for ungulates. Semi-domestic reindeer made different reproductive decisions depending on the previous feeding regime (artificial feeding vs. natural pastures) (Bårdsen *et al.* 2008). Although these were phenotypically plastic responses, in the long-term reindeer might become dependent on artificial feeding and less able to forage naturally. Small scale changes in spatial genetic structure were documented after a change in artificial feeding regulations in white-tailed deer (Blanchong *et al.* 2006). Physiological effects may depend on the type of forage. The effect of feeding silage to red deer might be less than feeding it to moose, being a browser. Captive browsers have higher rates of tooth wear than their wild relatives, probably due to the change in feeding habits (Kaiser *et al.* 2009).

Management actions other than active feeding can affect habitat and thus feeding conditions of hunted ungulates. Forestry and other land use practises may be very important for forage production. However, there is a distinction as the latter management practice mainly affects production of the natural forage, rather than introducing new dietary items as often is the case with artificial foddering. As such, they are less likely to affect behavioural traits or selection apart from effects on density, and will therefore not come under the 'semi-domestication' umbrella.

## Predator control

Domestication involves removal of predators or strict predator control. Large carnivores have been exterminated from large parts of the world as a consequence, and there is often a continuous battle with meso-predators. Predation may exert strong effects on the selection pressure on most aspects of ungulate behaviour (Caro *et al.* 2004), physiology (Creel *et al.* 2007) and life history. It has been debated whether harvesting can mimic the selection pressure of carnivores (Bischof, Mysterud & Swenson 2008), but the selectivity of human harvesting and predation by large carnivores is likely to differ. Predators are more selective when they are small relative to prey size (Sinclair, Mduma & Brashares 2003). For example, lynx *Lynx lynx* L. killed a random sample of roe deer *Capreolus capreolus* L. compared with what was available, while humans hunted more adult males and less females than expected (Andersen *et al.* 2007). In contrast, wolves *Canis lupus* L. in Yellowstone, USA, killed mainly young and senescent elk *Cervus elaphus canadensis* Erxleben, while hunters shot mainly adult females (Wright *et al.* 2006). Furthermore, predators have an effect year-round, whereas human harvesting is typically seasonal. At present, our understanding of the effects of selection pressures from different predators is very limited.

## Conclusion

Increased levels and specificity of harvesting, fencing, reliance on artificial fodder and predator control can be viewed as steps towards semi-domestication of hunted ungulates, since selection processes become more and more under human control and differ from those acting on the wild counterparts. There is sufficient general knowledge (indirect evidence) and direct empirical evidence documenting the effects of current management practises on various traits to take these issues more seriously (Table S1). However, well-documented cases are surprisingly few considering the wide use of these management practices and the ongoing research on ungulate ecology and evolution. Improved monitoring designs enabling better quantification of such effects are needed to more accurately quantify the long-term consequences for a wider range of phenotypic traits (and its relation to genotype), species and management practices. The aim here is to create awareness of the issue rather than to advocate changes in management to keep hunted ungulates as wild as possible. Clearly, there are many advantages to increasing the level of domesticity so that greater densities of hunted ungulates can be supported thereby creating more hunting opportunities and increasing income in rural economies. However, doing so might negatively affect the phenotype and the perception of hunting in the long-term even without considering the potential negative effects of high density on biodiversity and ecosystem function. Managers should initiate an ethical debate over which direction they should follow, given such a trade-off.

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## Supporting Information

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

**Table S1.** An overview of documented effects of management practises on traits.

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