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# The concept of overgrazing and its role in management of large herbivores


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Mysterud, A. 2006: The concept of overgrazing and its role in management of large herbivores. - Wildl. Biol. 12: 129-141.



Increasing populations of cervids in Europe and North America have made the issue of overgrazing relevant outside areas with domestic or semi-domestic herbivores. Overgrazing is defined depending on management objectives. I focus on challenges related to implementing a 'range ecologist' baseline, defining overgrazing as situations when 'forage species are not able to maintain themselves over time due to an excess of herbivory or related processes'. Herbivores may be naturally regulated at ecological carrying capacity (K) with no overgrazing, but overgrazing may occur below K. Rare, preferred plant species can decline in density due to a 'herbivore pit' created by generalist herbivores, without having much effect on K. The concept of overgrazing is almost meaningless unless the issue of spatial scale is considered, and the extent to which preferred plant species decline in coverage. Herbivore population instability increases with increased population growth rate, but overgrazing depends also on the tolerance to grazing of the forage used by a given herbivore, which is closely related to functional plant traits. Ecosystem factors such as soil quality and slope also affect the likelihood that overgrazing will occur. Currently we can only qualitatively identify some important factors to consider. A better understanding of the sequence of events happening to performance of both animals and plants over time when a herbivore population increases provides a very useful approach until tools are developed to measure overgrazing quantitatively. More detailed knowledge about grazing effects on biodiversity is necessary to implement a broader ecosystem perspective of overgrazing.



*Key words: biodiversity, conservation, herbivory, moose, red deer, reindeer, roe deer*



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*Received 4 March 2003, accepted 26 November 2004*

*Associate Editor: Roger Bergström*


Large herbivores affect vegetation community patterns and ecosystem functioning through processes such as grazing, browsing, trampling, defecation and urination (reviews in Jefferies et al. 1994, Hobbs 1996, Augustine & McNaughton 1998, Bakker 1998, Austrheim & Eriksson 2001). Herbivores graze or browse selectively; they prefer forages with a high content of nutrients and a low level of structural and chemical defences (Hanley 1997).

While herbivory by definition requires removal of plant biomass, grazing may also lead to a decrease or an increase in the coverage of forage plants over longer time frames by affecting processes of competition among plants (Augustine & McNaughton 1998). Preferred grazing plants typically grow fast and are quickly decomposed in the ground, whereas unpalatable chemically defended plants typically grow and decompose slowly. The levels of grazing selectivity and plant tolerance are important in determining vegetation community changes (Augustine & McNaughton 1998).

Overgrazing has been described related to pastoral systems in Africa (Mace 1991), rangelands of the United States (McNaughton 1979) and wetland and riparian areas (van de Koppel et al. 1999). Also famous are examples from Australia (Caughley et al. 1997) and New Zealand (Nugent et al. 2001, Coomes et al. 2003). Severe cases include erosion and subsequent removal of nutrients sometimes causing the ecosystem to reach a stable state with lasting lower productivity (review in van de Koppel et al. 1999). Most cases of overgrazing have been ascribed to grazing by domestic herbivores. Domestic herbivores are often kept at much higher densities than wild herbivores (Oesterheld et al. 1992), because domestic herbivores are supplied with fodder through the lean season which limits wild populations. Whether an area is 'overgrazed' or not is often controversial (Perevolotsky & Seligman 1998). Overgrazing due to introduced cervids was described in New Zealand (Coomes et al. 2003), and the increasing populations of cervids in Europe (Gill 1990) and the US (McShea & Underwood 1997) during the last decades have also raised a debate on whether overgrazing occurs.

In Scandinavia, the most severe cases of overgrazing are related to management of wild and semi-domestic reindeer *Rangifer tarandus* and the devastating effects of trampling on lichen heaths, such as in the Snøhetta reindeer area in Norway in the 1960s (Hansen 1987), Hardangervidda in the early 1980s (Skogland 1983, 1985) and more recently on Finnmarksvidda (Evans 1996). The increasing populations of forest dwelling cervids in Scandinavia during the last decades have also raised a debate on whether these are overgrazing or not (e.g. for moose *Alces alces* in Norway; Mathismoen 2002, Solbraa 2003, Moen 2004). Traditionally, management of the cervid population in Norway has been a question of increasing harvest by selective culling (Langvatn & Loison 1999, Solberg et al. 1999), and to some extent also a question of reducing negative effects such as traffic accidents (Gundersen & Andreassen 1998) and browsing on trees that are economically important to forestry (Sæther et al. 1992). Since grazing may increase or decrease plant species richness, depending on factors such as grazing intensity (Grime 1973, Connell 1978, Hobbs & Huenneke 1992) and nutrient availability (Bjor & Graffer 1963, Proulx & Mazumder 1998), conservation issues related to grazing impact on biodiversity are likely to play an increasingly important role also in cervid management. For example, the Directorate for Nature Management (available at: http://www.naturforvaltning.no/) in Norway state in their report 'Management of cervids towards year 2000' that management should be sustainable and not represent a threat to biological diversity (Direktoratet for naturforvaltning 1995). Today, this issue and goal is still mentioned frequently in cervid management in Norway, while a management framework to deal with such responses is largely absent.

Therefore, explicitly defined terms to indicate (from a management perspective) negative effects of grazing are clearly needed. What is the basis of the different approaches to overgrazing? Are all cases of overgrazing equally deleterious, i.e., how can overgrazing be graded? How can ranges be monitored so that overgrazing can be established and action be taken, i.e., how can overgrazing be determined? I suggest one direction towards the solution to some of the challenges that must be faced in order to achieve sustainable use of grazing systems.

## Definitions (or types) of overgrazing

The term 'overgrazing' (including related processes such as for instance browsing and trampling) is much used and abused in scientific literature (MacNab 1985) and it is usually value-laden as it implies grazing at a higher level than wanted relative to a specific management objective. The term only applies where the excess of herbivory is defined by humans (Coughenour & Singer 2000), but it has been used to describe almost any kind of (from a management perspective) negative impact of grazing. Few use an explicit definition of overgrazing related to a specific ecological pattern or process, which frequently causes unnecessary confusion. Unfortunately, there are often implicitly assumed different definitions of overgrazing in terms of ecological effects, as the objectives are often perceived as different. Extending the classification of different approaches to overgrazing given by Coughenour & Singer (2000), we can use a simplified and idealised view of involved parties to categorise different approaches or views (Table 1):

For 'range ecologists', mainly interested in producing meat, the term may be used to describe some deleterious change of the vegetation caused by wild or domesticated herbivores (Milner et al. 2002), and most often only to the part of the vegetation that is used as forage by herbivores. In an account of overgrazing in Yellowstone

Table 1. A simplistic overview of some of the negative effects of grazing that can be termed 'overgrazing' depending on the personal view, conservation or management objective (partly after Coughenour & Singer 2000). The range manager's view is the most conservative and can serve as a useful starting point, whereas a nature conservationist would most likely term other ecological effects of grazing as overgrazing whenever in conflict with conservation efforts. It is important to note that grazing in many cases may have beneficial effects on other organisms as well, but that is not the topic here. K = carrying capacity; see text for type of overgrazing.

| Type/philosophy of person | Focus | Personal view or objective | (Negative) ecological effect defining overgrazing (type) | Type of overgrazing |
|---|---|---|---|---|
| Population ecologist | One species | Explain population development; not value laden | Grazing above K - natural process necessary before stabilisation at K or 'crashing' under K | 0 |
| Range manager | One herbivore species (or group of herbivores) | Keep plant/animal productivity on range high; value laden | Forage plants do not maintain themselves | Range (A-C) |
| Forest manager | One or several economically important tree species (or crops) | Maintain a high financial income from forestry (or agriculture); value laden | Damage to economically important tree species (or crops) | Crop |
| Wildlife manager | Herbivore vs wildlife (single or groups) | Keep productivity of wildlife high; value laden | Competition with wildlife | Wildlife |
| Nature conservationist | Multiple species | Conserve all species; value laden | Species diversity; abundance of other organisms | Conservation |

National Park, overgrazing was defined "as an excess of herbivory that leads to degradation of plant and soil resources" (Coughenour & Singer 2000). A related definition is often used; overgrazing is when "forage species are not able to maintain themselves over time due to an excess of herbivory or related processes" (adapted from Holechek et al. 1999), linking the concept directly to a decline in carrying capacity (K; Fig. 1). This is similar to the definition of overgrazing given in the Webster Dictionary: "to allow animals to graze (as a pasture) to the point of damaging vegetational cover" (Merriam Webster Dictionary available at http://www.m-w.com/cgi-bin/dictionary). In the following, I will refer to this as the 'range ecology baseline', which provides a fairly classical view of overgrazing.

For 'forest (or crop) managers', interested only in economically important tree species (or crops), overgrazing may be the level at which browsing damage to these trees/crops are above a certain threshold level in serious conflict with forest production aims.

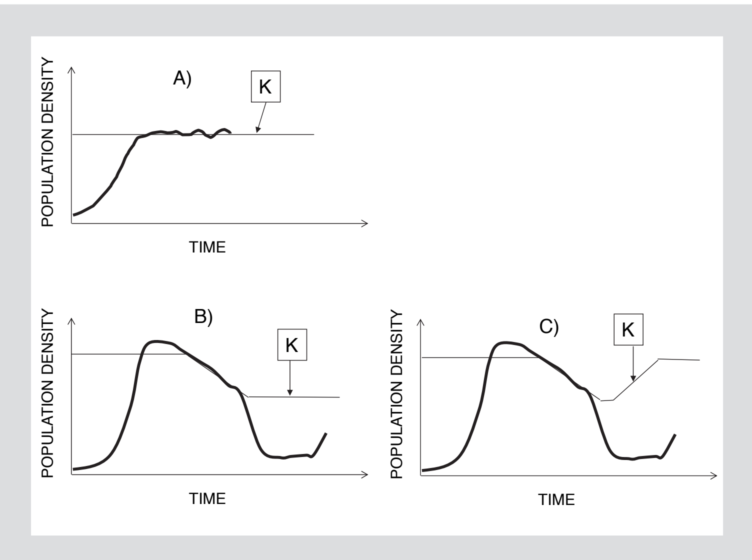


Figure 1. Relationship between carrying capacity (K) and population development over time for A) 'classical (population ecologist) view' with no decline in K, B) an irreversible (very long term) decline in K due to permanent habitat deterioration (e.g. erosion), defined as overgrazing of type A, and C) a reversible decline in K due to (temporary) habitat deterioration, defined as overgrazing of type B or C, depending on the duration of the decline after removal of the herbivores.

For 'wildlife managers', mainly concerned with having as much wildlife as possible, overgrazing is used as a term for grazing above a level where competition between a given herbivore and one or several focal wildlife species occur. Interspecific competition occurs when shared resources are limiting, due to overlap in habitat use and overlap in diets within these habitats (e.g. Tokeshi 1999). Many people involved in hunting management and science use the term overgrazing when density dependence in body weights (or another fitness correlate) is present, i.e., when there is intra-specific competition for forage (indicating that resources are limiting).

For 'nature conservationists', who usually have a multiple species focus and an intention of conserving all species, the term overgrazing implies grazing above a level at which other aspects of biodiversity is threatened, i.e., when grazing is in conflict with conservation efforts. Sometimes nature conservationists have a more narrow focus. For example, an extensive report about grazing and overgrazing in Scotland focuses entirely on birds (Fuller 1996). In this case, overgrazing is implicitly defined as competition or other negative interaction between the grazer (in this case mainly domestic sheep *Ovis aries*) and bird species, leading to lower population sizes of the latter. A 'nature conservationist' would not treat wildlife or economically important tree species any differently than other species, thus definition of overgrazing may also include competition with wildlife or damage to trees. However, the level at which this may be seen as a problem may differ between a wildlife or forest manager and a nature conservationist.

For 'population ecologists', only interested in explaining the population dynamics of a herbivore species, overgrazing is simply the period when a herbivore population is above carrying capacity (K; see Fig. 1A). This differs from the rest of the definitions in that it is not value-laden, but just part of the natural process necessary to stabilise the population around K.

In the following, I will use the definition of what I termed the 'range ecology baseline' (see above). A conservation biologist would likely agree with the range manager that a severe and lasting reduction in carrying capacity is overgrazing, but it is important to realise that range productivity is not the main focus of nature conservationists. For a conservationist, the aim may be a naturally functioning ecosystem, in which overgrazing is not an issue. As the plant species composition may shift to more tolerant or resistant species in response to herbivory, the biomass and production of forage plants may well be lower at K than without herbivores. Whether or not this is desirable depends on conservation objectives; it may be desirable or undesirable depending on whether or not it is part of a natural process (Coughenour & Singer 2000). However, it is possible that even a protected area is not operating naturally due to lack of predators or disruption of herbivore migration routes. Thus an important problem is to determine the extent to which the system has been disrupted by humans (Coughenour & Singer 2000). Biodiversity issues related to grazing are diverse and complicated (see e.g. Miller et al. 1999), and will probably need careful local actions in each specific case. The range ecology baseline can serve as an important starting point that most managers and conservationists can agree upon as negative effects of grazing.

## Relationship between carrying capacity and overgrazing

For population ecologists, (ecological) carrying capacity (K) is the population level above which the population will no longer grow (see Fig. 1A), i.e., the population size at which density dependent processes are so strong that reproduction is balanced by mortality (Begon et al. 1996). A number of other definitions of K exist (e.g. Miller & Wentworth 2000), for example related to soil or vegetation management goals, but will not be dealt with here. A herbivore population may be kept stable for a number of reasons, including food, predators or diseases. In the following, I will use K equivalent to the food-limited K.

As it is linked to K, the concept of overgrazing will mainly be useful if there is some predictability in K. If a system's resource base (i.e. the plant productivity) is primarily driven by stochastic environmental variability, such as climate (e.g. rainfall for African ungulates; Fritz & Duncan 1994), the term K may be less useful in practical management (Mace 1991; see also McLeod 1997). The concepts discussed here will therefore have an easier interpretation in so-called 'equilibrium systems'. Although some variation in K is evident in all systems with variation in climate, the non-equilibrium theory applies mainly to arid and semi-arid environments with highly varying rainfall (Behnke et al. 1993, Tainton et al. 1996). It has been suggested that a threshold is crossed when the coefficient of variation of rainfall exceeds 30% (Stafford Smith 1996; see also Tainton et al. 1996 for a fuller account).

By the range-ecology baseline definition, overgrazing implies that the carrying capacity is decreasing (see Fig. 1B,C). It is whether or not desirable forage plants persist (under competition from other plants) at this high herbivore density that determines whether this is just exceeding K (see Fig. 1A) or overgrazing (see Fig. 1B,C). Exceeding K therefore does not imply overgrazing if plants are able to withstand the grazing pressure. A herbivore population may be stable or unstable living on the same forage resources depending on the demographic traits or the foraging ecology of a species. For given herbivore traits, stability or instability may be a question of plant traits related to tolerance to herbivory. A herbivore population that is unstable due to overgrazing is more likely when forage layers are less tolerant towards herbivory.

## The role of herbivore traits for stability

The best examples of the lack of a direct link between overgrazing and exceeding carrying capacity comes from the famous studies of the red deer *Cervus elaphus* on the

Isle of Rum and Soay sheep in the St. Kilda archipelago, both in Scotland. The Soay sheep population undergoes dramatic fluctuations in size (200-600 individuals in the Village Bay area; Clutton-Brock et al. 1997, Clutton-Brock & Coulson 2002). In contrast, the red deer population on Rum reached a stable density about 10 years after culling stopped, and it has remained stable for > 20 years (200-300 individuals in the North Block; Clutton-Brock et al. 1997, Clutton-Brock & Coulson 2002). Although these grazers affect the plant species composition to some extent (for Rum, see Virtanen et al. 2002), there is no evidence that the habitat is deteriorating (i.e. that carrying capacity declines) neither on Rum nor in St. Kilda (Milner et al. 2002, Virtanen et al. 2002). So, high numbers of large herbivores do not necessarily mean that overgrazing occurs; no severe habitat deterioration is occurring (but see above regarding the dependency of definition).

*Differences in demographic traits hypothesis*

The ecosystems in St. Kilda and on Rum are fairly similar (Clutton-Brock & Coulson 2002). It has been suggested, since a proportion of the Soay ewes mature already as lambs and lamb as yearlings, and since older ewes are twinning, that maximum annual population increase can be 65%, and that they are able to exceed carrying capacity so that an overcompensation in density occurs when a severe winter hits the islands (Clutton-Brock et al. 1997, Clutton-Brock & Coulson 2002). In contrast, red deer hinds never twin and get their first calf at the age of three or four; maximum annual population increase is only 20%, and hence there is good time for density dependence to work, so that carrying capacity is not exceeded by much.

*Differences in foraging ecology hypothesis*

Another explanation of the contrasting dynamics of red deer and Soay sheep was presented by Owen-Smith (2002). Nutrient requirements in ruminants are allometrically related to body size ($W^{0.75}$), whereas rumen volume and gut capacity are isometric with body size. Larger herbivores are therefore able to subsist on a lower quality diet (The Jarman-Bell principle; Bell 1971, Jarman 1974, Demment & Van Soest 1985). Therefore, red deer, being larger, are able to utilise heather *Calluna vulgaris* as a buffer forage at high density (Owen-Smith 2002). Even though they do not grow much when eating the readily available heather, it is sufficient for them to survive. The smaller Soay sheep are not able to survive on heather, and have no buffer when the main forage is in short supply at high population density (Owen-Smith 2002). Therefore we get the contrasting dynamics.

The plant-herbivore system is clearly interactive (Noy-Meir 1975, Caughley 1979, Bayliss & Choquenot 2002). The quick (10 year) increase to reach a stable K as seen in the example of the red deer on Rum is not representative for many other areas. Indeed, cervids introduced into new areas devoid of predators or human management may go through an eruption phase, then a crash, followed by convergence to a stable density, such as that seen in New Zealand (Caughley 1979, Coomes et al. 2003). Examples suggest a 25-30 year eruption phase in mule deer *Odocoileus hemionus* in the Kaibab plateau, moose on Isle Royale and red deer in New Zealand (Caughley 1979). The new stable density is often termed K and is often at a lower level than the initial density during the eruption phase (Caughley 1979) because the plant community has changed.

## The role of the plant traits for herbivore stability

Plants with different morphological and physiological traits, so-called functional plant groups (*sensu* Lavorel et al. 1997), have different ability to either tolerate or resist grazing (Lavorel et al. 1997, McIntyre & Lavorel 2001, Bullock et al. 2001, Díaz et al. 2001). Plants can either avoid being selected (plant resistance) or compensate for loss of plant tissue (plant tolerance). Traits associated with high resistance are either low nutritional value or digestibility or active defenses like structural (e.g. cellulose), mechanical (e.g. spines) or toxic defences (e.g. phenolics) that deter herbivory (Van Soest 1994). Traits associated with high tolerance are, for example, protection of or low placement of growth tissue (such as basal meristem in many grasses), a high root-to-shoot ratio, ability to shuffle nutrients from root to shoot, high photosynthetic activity, and a tufted or matlike growth form (Strauss & Agrawal 1999). On an ecological time scale, the abiotic (climate, light, humidity and nutrient availability) and biotic environments (level of competition, symbionts, grazing frequency and timing of grazing) also affect the possibilities of being tolerant. Grazing frequency will be determined by population density and selectivity of the herbivore. Selectivity of herbivores is reduced when food is in short supply due to a high population density, e.g. during winter or during drought periods in summer. An asynchronous phenology will also lead to less potential for being selective as plants are then not available at the same time. Timing of herbivory may also be important and depends on migration patterns. Ignoring here the large within-group differences, grasses and sedges are the most tolerant. Deciduous browse and trees are less tolerant and more towards the resistance part of the continuum, however, with considerable between-species variability. Lichens are probably the least tolerant.

A possible example of the role of plant traits for overgrazing can be obtained by comparing reindeer and red deer. The dynamics of the red deer on Rum, Scotland, are fairly stable (see above), while the eruption and subsequent crashes of reindeer living on lichens in areas without predation or harvesting are also classic (Klein 1968). The two cervids have a fairly similar demography and feeding ecology; the main difference being that reindeer depend on lichens during winter, while the red deer on Rum rely on grass and heather to a large extent. Also red deer in New Zealand who had a considerable amount of browse in their diet, went through an eruption phase before crashing (Coomes et al. 2003). Overgrazing is most likely more an issue of plant than herbivore traits, but possibly the ratio of annual herbivore population growth relative to plant biomass growth would better predict the chances of getting overgrazing.

## The role of the ecosystem

The likelihood that overgrazing will occur also varies strongly depending on ecosystem characteristics unrelated to herbivore traits, and only partly related to plant traits. Especially vulnerable are wetland areas with unstable soil (van de Koppel et al. 1999), steep slopes in general (Evans 1996) and less productive environments. Arid, semi-arid and alpine regions are generally more likely to experience overgrazing than temperate grasslands. The soil type is part of the explanation. Vegetation on sandy soil is not resilient to herbivore impact, unlike vegetation on clayey soils, due to differences in the water-holding capacity of different soil types (Rietkerk et al. 1997). There has currently been no evaluation of the areas which may be most sensitive to overgrazing in Scandinavia. Clearly, high altitude may also be important.

## Generalist herbivores and 'herbivore pits' - are we safe below the food-limited K?

Herbivore populations may never reach the food-limited K due to, for example, predators or diseases. Will overgrazing be an issue if the herbivore population is regulated at a low density by predation or if frequently occurring severe winters keep the population low? Overgrazing will naturally most often happen at high herbivore densities. The situation in Scandinavia is similar to that in New Zealand, in the sense that it can be seen as a herbivore eruption into areas where they had not been present for a long time. However, cervids in Scandinavia are regulated by human harvest at densities below K, in order to prevent the populations from going through a crash phase to find a stable new density at K. So is overgrazing an issue at all?

The plant community will not 'wait' until K is reached to respond to increasing grazing pressure, and some parts of the plant community may respond to increasing herbivore densities far below K. Large herbivores are generalists. The concept of 'predator pits' related to generalist predators is well known, i.e. that due to diet switching a specific prey species may be kept at a constantly low density (Solberg et al. 2003). The same principles apply to generalist herbivores. If a generalist herbivore has access to rare preferred plants and common less preferred plants that nevertheless are edible, then the rare preferred plants could be held down in a 'herbivore pit' (Coomes et al. 2003).

The plants most sensitive to grazing are often highly preferred forbs, and some of them can be virtually eradicated (for white-tailed deer *Odocoileus virginianus*: Augustine & Frelich 1998; for red deer: Coomes et al. 2003). In Norway, there has been a controversy in major newspapers and outdoor magazines regarding whether moose are overgrazing their habitat (Mathismoen 2002, Solbraa 2003, Moen 2004). In Nord-Trøndelag, the degree of utilisation of preferred deciduous browse such as rowan *Sorbus aucuparia*, aspen *Populus tremula* and willow *Salix caprea* was 80-90%, while the degree of utilisation of Scots pine *Pinus sylvestris* and birch *Betula* spp. was only 40-60% and 10-15%, respectively (Solbraa 2002). Rowan, aspen and willow are regarded as being overgrazed (Solbraa 2002). As these species are highly preferred and possibly kept in a herbivore pit, it is not certain that they will recover even with the suggested management target of a 50% reduction in moose density (Moen 2004).

If the highly preferred plants are not too frequent, this will only lead to a marginal decline in K (and hence very weak overgrazing by the range ecology baseline definition). However, if the preferred plants have conservational values, this is important to consider. In the Lier valley in Norway, there was almost no recruitment of the endangered yew *Taxus baccata* within nature reserves from around 1985 to 1993 (Mysterud & Østbye 2004) due to severe winter browsing by roe deer *Capreolus capreolus* (Mysterud & Østbye 1995). Even though roe deer were fairly abundant during this period, the population was probably well below K, as no density dependence in body weight was evident (Mysterud & Østbye in press). How red-listed species respond to grazing is likely extremely variable, and has not been subject to much research.

Therefore, issues of overgrazing may be relevant without the population reaching K. Obviously, research is needed to evaluate these issues in depth for Scandinavian ecosystems.

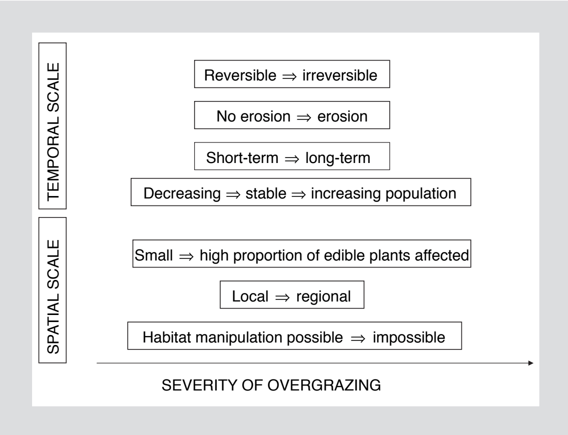


Figure 2. Grading of criteria that should be evaluated when confronted with a possible overgrazing situation. See text for discussion.

## Grading of overgrazing - the range ecology baseline

Accepting an 'overgrazing-paradigm' is not without problems (MacNab 1985). It may be particularly difficult in forest ecosystems in which natural succession towards the climatic-climax vegetation in itself causes large changes in K (MacNab 1985). Herbivores may often change the normal pattern of natural succession, for example by preventing regeneration of trees (Coomes et al. 2003). Measuring K has proven extremely difficult, in particular since we often do not want the population to ever reach K. Relative deer density was introduced as a concept to integrate white-tailed deer management with ecosystem management (deCalesta & Stout 1997). However, as it was based on deer density relative to K, it is not a way to get around the problem. At present, we therefore have no simple, direct way of measuring overgrazing so as to assess its severity. Rather, I suggest that the following aspects should be considered when confronted with what may be an overgrazing situation (Fig. 2):

1) Are effects reversible or irreversible? The most severe cases of overgrazing are when effects are irreversible (on the scale of a century). This can be due to erosion with subsequent permanent loss of nutrient and soil minerals. It can cause 'catastrophic' shifts between alternative stable states, and the ecosystem can stabilise itself at a new equilibrium at a (much) lower level of productivity (Rietkerk et al. 1997, van de Koppel et al. 1999, van de Koppel & Rietkerk 2000).
2) Does erosion occur? The first obvious sign of erosion is when areas of bare ground due to plant mortality are increasing. However, even with no erosion, invasion of chemically defended plants resistant to grazing can be permanent (or at least last for decades; Valone et al. 2002). Local extinction of seed sources, fundamental alterations to successional pathways and shifts in ecosystem processes may also lead to irreversible effects of grazing (see review in Coomes et al. 2003).
3) If effects are reversible, how long will it take to reestablish the original vegetation coverage? The longer it takes to reestablish the original vegetation coverage, the more severe the overgrazing.
4) Are herbivore populations stable, increasing or decreasing? Overgrazing situations will generally occur when population sizes are large. It will be important to know for how long the herbivore population has been this high, in order to tell whether the situation is stable (i.e., that a new equilibrium has already been reached), worsening or improving. However, even if the herbivore population is stable, it does not mean that the level of overgrazing is not increasing unless this has been the situation for a long time.
5) How large a proportion of the edible food plants is overgrazed? A few highly preferred plants may decrease in coverage without this having much effect on the total biomass of plants used by a specific herbivore. When the previously 'averagely preferred plants' or the main forage plants decrease in coverage, this will indicate that overgrazing is more severe. This is equivalent to asking how much the carrying capacity has changed.
6) Have large areas been affected by overgrazing? In virtually any grazing system, small spots of bare ground can be found around water holes, salt licks or along fences (Evans 1996) that may be attributed to trampling and that may be termed local overgrazing, even though they will have no serious effect on the system. Overgrazing is an almost meaningless concept unless the spatial scale is considered. Small patches of bare ground will not decrease carrying capacity by much.
7) Can habitat manipulations alter the situation? In some cases, management can modify the habitat to reduce negative impacts even without reducing herbivore levels. For example, forestry can cut down low quality coniferous trees and burning of chemically defended plants may be an option.

Based on points 1-3, overgrazing can be graded qualitatively into three types, of which type A is the most severe:

Type A: Irreversible effects (scale of century).
Type B: Reversible, long-lasting (decadal) effects.
Type C: Reversible, shorter-lasting (< 10-20 years) effects.

Then, one needs to take into account points 4-7 in order to make a judgement of how much the carrying capacity has changed by considering the spatial extent of the problem and how large a proportion of the edible plants has been affected, and what will happen in the near future (i.e. population development). Based on this, the severity of the situation can be graded between 1 and 5, giving A5 as the most severe, and C1 as the least severe case of overgrazing. The wildlife and forestry manager or nature conservationist may need additional categories (see Table 1).

## Determining overgrazing

Most ranges are not monitored directly with respect to overgrazing. Normally, involved parties more or less subjectively and qualitatively judge whether overgrazing occurs. Some of the most important ways of determining range conditions are given in Figure 3. Ideally, grading of overgrazing should be done directly and quantitatively from the indices. Effects of grazing will first be found on the plants, before any effects of density dependence can be found on animals (Noy-Meir 1975). Determination based on animal performance can be seen as a less conservative management strategy if we regard it as more important to avoid overgrazing than to have maximal production of herbivores. For all indexes, it is important to keep in mind that since alternative stable states are common in grazing systems, it may be impossible to determine overgrazing in hindsight after a new equilibrium has been reached.

## Determining overgrazing from animal performance or density

For centuries, individual or population performance of the herbivore has been used to determine overgrazing (Gudmundsson & Bement 1986). There have been relatively few investigations testing whether the relationship between performance traits such as weight, reproduction or mortality and population density of herbivores are close to linear or threshold-like (McCullough 1999). Fowler (1987) suggested that while body weight was often linearly related to population density, mortality showed more of a threshold relationship. In Norwegian red deer, a close to linear effect of density on body weight was reported (Mysterud et al. 2001). This makes it difficult to define a threshold above which the number of large herbivores should be reduced based on weight measures.

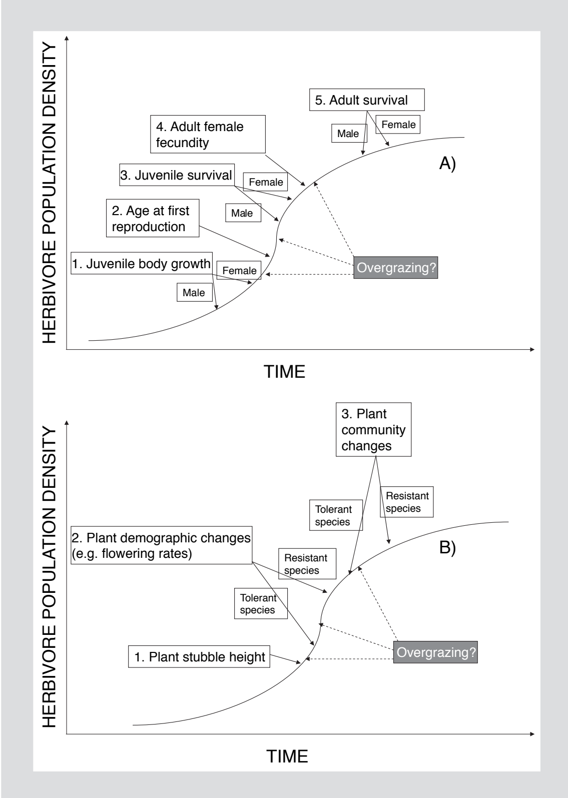


Figure 3. Overgrazing can be assessed based either on the plants directly (A) or on the animals (B). Except when monitoring directly on plant coverage, it requires knowledge about the population level at which a certain plant response or demographic response in animals translates into overgrazing. Different traits/indexes may respond at different density levels, but the specific sequence in Scandinavian ecosystems needs further study.

We have fairly good knowledge of the sequence of effects by which population density affects vital rates such as age-dependent patterns of survival and reproduction (see Fig. 2A; Gaillard et al. 2000, Eberhardt 2002). For cervids, the most sensitive parameter to increasing density is early growth, and therefore it takes longer to reach the body weight acquired to undergo first reproduction. The next vital rate affected by increasing density is juvenile survival, before, finally, adult survival decreases (Gaillard et al. 2000). Furthermore, the influence of density dependence on survival can be seen earlier in males than in females (Clutton-Brock et al. 1997). In some cases, the length of yearling antlers have been used for monitoring condition in cervids both in Europe and USA, as secondary sexual characters may be particularly sensitive to adverse conditions (Schmidt et al. 2001 and references therein).

There may be strong density dependence in vital rates with no overgrazing (*cf.* the Rum and St. Kilda above);

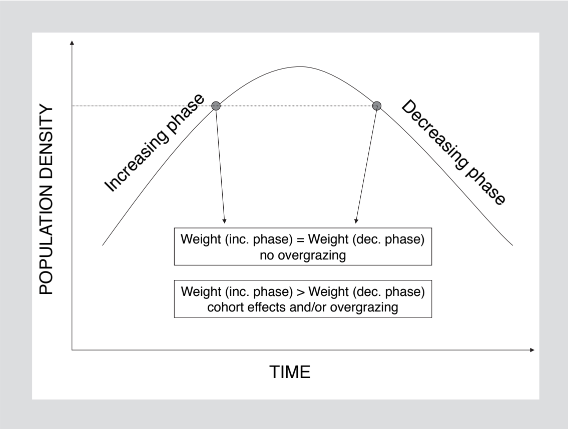


Figure 4. Overgrazing can be assessed directly by comparing performance in the increase and decrease phases of population development. If a population is stable, decreased performance over time will indicate overgrazing. However, it is important to control for cohort effects, i.e., that deer born at high density will have a lower performance as adults, regardless of the overgrazing issue.

therefore, additional ecological insight is required when determining overgrazing. A comparison before and after a population peak can determine if the relationships between density and individual performance has changed, suggesting a decline in carrying capacity (Fig. 4). In such cases, it is urgent (but difficult) to control for cohort effects as animals born at high density will have a lower performance than animals born at low density (Mysterud et al. 2002). Health status of cervids can possibly also be used, but high density is likely necessary for health problems to occur. Density dependence in diet selection (Freeland & Choquenot 1990, Choquenot 1991) is potentially also a way of determining overgrazing. One advantage gained by determining overgrazing based on the performance of herbivores is that good data normally are either available (for domestic species) or are fairly easy to obtain through harvesting (wild species).

An alternative is to directly monitor density of the herbivore population, but this requires knowledge about which density level is appropriate to avoid overgrazing. Population density is relatively simple to define (number of animals per unit area), but the same density may have different effects on performance of populations even in neighbouring areas (Milner-Gulland et al. 2000). However, the main problem is that density can only be estimated directly with extreme difficulty or at very high costs. There are a large number of ways to monitor density of wild herbivores based on indices, which will not be described in detail here.

## Determining overgrazing from plant performance or coverage

Part of the reason for the difficulty in quantifying carrying capacity, is that herbivores are unable to utilise the entire plant community available. Even when dividing plant biomass according to degree of utilisation, management has often failed to find reliable estimates of carrying capacity (Mace 1991). It seems to be better to choose some relevant plant species and monitor their performances.

When using plants to determine overgrazing, a decrease in the availability of palatable species will be an almost direct link to identify overgrazing, as grazed plants will likely decrease in coverage when not able to maintain themselves. Permanent vegetation plots can be used for such monitoring. Fenced controls can be used to separate grazing effects from other factors such as habitat succession. However, the latter will only give information about no grazing and not about grazing due to different density levels of the herbivore. For all monitoring, the spatial heterogeneity should be explicitly quantified (Hirata 2000). One problem related to such monitoring is the different visibility related to flowering and seed banks; clearly, it is more difficult to visually estimate effects on seed banks (Hutchings 1991, Goldsmith 1991).

As plants differ widely in quality to herbivores, a monitoring scheme should use some plants with (initially) low, intermediate and high preference. Likely, the highly preferred forage will respond first to grazing, as was found with dense deer populations in North America (Leopold et al. 1947), unless it is highly tolerant. A single plant species may respond by increasing or decreasing occurrence under heavy grazing pressure, depending on the plant and the ecosystem (Vesk & Westoby 2002), since also competing species such as mosses may be affected. The degree of utilisation may depend on the availability of other vegetation types and plants present, and it is therefore ecosystem dependent. Therefore, a relative preference scale for the area is a preferred choice, but difficult to obtain in practise. Related to this, the degree of utilisation of vegetation types or plants by herbivores can also be an approach to monitor overgrazing. A review of studies from North America concludes that low grazing pressure was 32% utilisation of forage plants, moderate grazing pressure was 43% and heavy grazing pressure (equivalent to defining overgrazing) was 57% utilisation of the most important forage plants (Holechek et al. 1999). There was large variation between the studies, but the authors suggested that this was a very useful approach. The advantages are that specific plants can be chosen to indicate different degrees of overgrazing.

Other ways of determining overgrazing has been to use the height of the vegetation (best for grazers) as severe grazing leads to low mats (Clary & Leininger 2000), but severe climate may have the same impact. A guide to sward monitoring based on vegetation height and related indexes (herbage mass and density and leafiness) are given in Hodgson (1990). The height of certain herbs has been used as an index of browsing pressure by cervids in the USA (Anderson 1994; see also Williams et al. 2000).

Use of vegetation composition or related traditional methods for vegetation monitoring have the disadvantage that they are not always able to detect gradual changes in the structure of vegetation at an early stage (Bühler & Schmid 2001). Time lags are common since individuals of plants are often long-lived, while persistence of a short-lived species requires new colonisation (Miller et al. 1999). This methodological deficiency could be overcome by observing the stage structure of a perennial target species (Bühler & Schmid 2001) or by considering sensitive vital rates of plants such as frequency of flowering. Monitoring the population structure of one or several target species provides important information about the stability of a whole plant community. The target species to use should be frequently occurring species instead of rare or endangered species (Bühler & Schmid 2001). It will therefore obviously be different from overgrazing defined from a conservation perspective (see Table 1).

One problem when monitoring overgrazing will always be stochastic weather variation that will also affect the food supply for the herbivores (see the paragraph on carrying capacity above). In particular, the chances of overgrazing may be larger in years with drought or other factors leading to less forage production. In sensitive areas in the USA, the 'greenness' of the vegetation is used as a warning to identify periods when drought makes the danger of overgrazing particularly high (Hall & Bryant 1995). For domestic animals, this can be used to move the animals when such situations occur, as an alternative to lowering the population density.

## Conclusions

Conservation and management often suffer from a lack of well-articulated objectives (Yoccoz et al. 2001). Monitoring requires that management has clear objectives, formulates explicit hypotheses about patterns and processes, and chooses a design of monitoring reflecting this (Yoccoz et al. 2001). A first step towards a sound management of grazing systems is to realise that there are several different ways of defining overgrazing. Much confusion can be avoided by classifying overgrazing into different types. A range ecology baseline, as outlined here, can serve as a useful starting point when approaching the issue. The range ecology baseline links overgrazing to the (food limited) ecological carrying capacity (K), and we can therefore differentiate the severity of a given overgrazing situation accordingly. However, it is extremely difficult to measure K, and I therefore rather suggest a few important points to consider (see Fig. 2). A better understanding of the sequence of events happening to both animals (see Fig. 3A) and plants (see Fig. 3B) performance over time when a herbivore population increases provide a very useful way to go before we have the tools to measure overgrazing quantitatively. Improved knowledge of grazing effects on biodiversity is a central key, which obviously will also be important in assessing to what extent the range ecology baseline of overgrazing differs from the approach including a broader conservation perspective.

*Acknowledgements* - I gratefully acknowledge very helpful comments by Gunnar Austrheim, Roger Bergström, Rolf Anker Ims, Ivar Mysterud, Harald Steen, Nigel G. Yoccoz and an anonymous referee. I thank the Research Council of Norway that funds my research on impacts of grazers (NFR - program 'Landskap i endring' - project no. 134361/720).

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