Journal of Applied Ecology 2004
41, 1021–1031

REVIEW

The management of wild large herbivores to meet economic, conservation and environmental objectives

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Summary

1. Wild large herbivores provide goods and income to rural communities, have major impacts on land use and habitats of conservation importance and, in some cases, face local or global extinction. As a result, substantial effort is applied to their management across the globe. To be effective, however, management has to be science-based. We reviewed recent fundamental and applied studies of large herbivores with particular emphasis on the relationship between the spatial and temporal scales of ecosystem response, management decision and implementation.

2. Long-term population dynamics research has revealed fundamental differences in how sex/age classes are affected by changes in density and weather. Consequently, management must be tailored to the age and sex structure of the population, rather than to simple population counts.

3. Herbivory by large ungulates shapes the structure, diversity and functioning of most terrestrial ecosystems. Recent research has shown that fundamental herbivore/vegetation interactions driving landscape change are localized, often at scales of a few metres. For example, sheep and deer will selectively browse heather *Calluna vulgaris* at the edge of preferred grass patches in heather moorland. As heather is vulnerable to heavy defoliation, in the long term this can lead to loss of heather cover despite the average utilization rate of heather in a management area being low. Therefore, while herbivore population management requires a large-scale approach, management of herbivore impacts on vegetation may require a much more flexible and site-specific approach.

4. Localized impacts on vegetation have cascading effects on biodiversity, because changes in vegetation structure and composition, induced by large herbivores affect habitat suitability for many other species. As such, grazing should be considered as a tool for broader biodiversity management requiring a more sophisticated approach than just, for example, eliminating grazing from conservation areas through the use of exclosures.

5. *Synthesis and applications*. The management of wild large herbivores must consider different spatial scales, from small patches of vegetation to boundaries of an animal population. It also requires long-term planning based on a deep understanding of how population processes, such a birth rate, death rate and age structure, are affected by changes in land use and climate and how these affect localized herbivore impacts. Because wild herbivores do not observe administrative or political boundaries, adjusting their management to socio-political realities can present a challenge. Many developing countries have established co-operative management groups that allow all interested parties to be involved in the development of management plans; developed countries have a lot to learn from the developing world's example.

Key-words: bighorn sheep, conservation, habitat management, impala, population dynamics, red deer, saiga antelope, ungulates

Journal of Applied Ecology (2004) **41**, 1021–1031

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Introduction

In many parts of the world, populations of wild large herbivores provide a substantial resource supplying local and regional communities with goods and economic income (Conover 1997; Barnes, Schier & van Rooy 1999; Loibooki *et al*. 2002; Ogutu 2002). They also have a major impact on land use and habitats of conservation importance (Hobbs 1996; Kirby 2001). Some species are the targets of policies to conserve dwindling populations (Stanley Price 1989; IUCN 2002) while others are increasing in number and need to be controlled, for example deer in UK woodlands (Putman & Moore 1998). In this review, we highlight how recent ecological research has investigated the relationships between large herbivores and their resources, yielding insights into the dynamics of the herbivores and the vegetation upon which they subsist. We emphasize the role of spatial and temporal variation in herbivore and vegetation abundance, giving examples of how this information could provide guidance to those responsible for devising and implementing the conservation, harvesting and culling of large herbivores across the globe.

Historically, the vast populations of large herbivores that roamed the plains of Africa, the steppes of Asia and the prairies of America appeared to offer a vast, bountiful resource for humans to exploit (Roosevelt 1910). However, overexploitation, predation, disease and changes in climate and land use have reduced many large herbivore species to levels at which they now need to be actively conserved (Beard 1988; Teer *et al*. 1996; Danz 1997). On the other hand, in the developed world some species have benefited from climate and land-use changes, reduced human off-take and the removal of predators, and now require management to ensure that their numbers do not affect other land-use objectives, including agriculture, forestry and habitat requirements for other species (Gill 1990; McShea, Underwood & Rappole 1997).

For well over half a century, one of the prime justifications of applied ecological research has been to provide objective information for ecosystem managers who wish to meet environmental and economic objectives (Elton 1924; Sheail 1985, 1987). For example, since the mid-1950s information derived from large game counts has been used to set harvest quotas for many ungulates in Africa, North America and Europe, either for sport hunting (Caughley & Sinclair 1994) or to reduce impacts on, for example, commercial timber stocks (Putman & Moore 1998; Terry, Mclellan & Watts 2000). While this long history of linking ecological research with management advice has been valuable to both parties (Sheail 1987; Sutherland 2000), ecologists are now expected to link their science more closely with the needs of the public if scarce public funds are to be channelled into research rather than competing uses such as education, health, transport and the military (Dale *et al*. 2000). Furthermore, natural resource managers are seeking increasingly sophisticated advice, for example the escalating costs of both surveying and culling large herbivores means that more precise information is needed for managers regarding how many animals to cull or which sections of the population (e.g. age/sex classes and geographical location) are damaging natural resources (Gill 1992; Georgiadis, Hack & Turpin 2003).

Recently, both the research and management communities have been questioned about the extent to which advances in the understanding of the ecology of natural resources have been used to guide management (Stinchcombe *et al*. 2002). In an effort to address this issue we present recent developments in large herbivore ecology that are most likely to guide the development of management planning to meet economic, conservation and environmental objectives. For these developments to be taken up by managers, ecologists must collaborate with researchers in the humanities to develop methodologies by which ecological science-based management is adopted by managers and policy makers.

Why does large herbivore management matter?

First, large herbivores have high economic value; they are often an important source of revenue through sport hunting (Williamson & Doster 1981; van der Waal & Dekker 2000; Leader-Williams, Smith & Walpole 2001) and ecotourism (Barnes, Schier & van Rooy 1999; Ogutu 2002). They can also be major pests to agriculture, forestry and conservation areas, and they may present serious traffic hazards (Ratcliffe 1987; McShea, Underwood & Rappole 1997; Ramsay 1997; Malo, Suárez & Díez 2004). For example, at present a trophy value of approximately US$10500 is placed on a male elephant *Loxodonta africana* in Zimbabwe (http://safariconsultants.com/zornframespage.htm), with much of this revenue returning to natural resource management organizations and local communities (Murphree 2001). In Scotland, the cull of more than 70000 red deer *Cervus elaphus* per year generates more than £5 million per annum, and 300 permanent and 450 part-time jobs for the rural economy (Reynolds & Staines 1997). The latter value is likely to be substantially higher when ancillary activities such as accommodation, transport, craft and food and drink purchases are taken into account (K. Thomson, W. Slea & D. Macmillan, personal communication). As long ago as 1975, deer hunters in the USA were estimated to spend more than $1 billion annually on pursuing their sport (Williamson & Doster 1981) and this is likely to be substantially higher today.

Secondly, some large mammalian herbivores are priorities for conservation because their populations are critically low as a consequence of habitat loss, persecution and overhunting. Of the approximately 175 species of ungulates in the world, 84 are listed as critically endangered, endangered or vulnerable in the 2002 *Red Data Book* of the International Union for the Conservation of Nature (IUCN) (IUCN 2002; http://www.redlist.org/). Large herbivores are often used as flagship species for conservation management planning because of their high public profile (Stanley Price 1989; Bowen-Jones & Entwistle 2002) and because they are keystone species in many ecosystems (Danell *et al*. in press).

Finally, across the globe, large areas are grazed by wild herbivores that drive the structure, composition and functioning of these ecosystems (Miles 1985; Martin 1993; Thompson, Hester & Usher 1995; Pickup, Bastin & Chewings 1998; Wallis de Vries, Bakker & van Wieren 1998). High densities of large herbivores can impact upon the agricultural, conservation and environmental value of the landscape (McShea, Underwood & Rappole 1997).

Successful large herbivore management, be it driven by economic goals or by the desire to conserve and expand specific habitats or species, requires a clear understanding of the processes involved in plant–herbivore interactions and their consequences for the dynamics of both plants and herbivores; in this context applied ecological research is crucial. The following sections address key areas of importance to managers to demonstrate the value of ecological research in understanding the population dynamics of large herbivores and their impacts on natural resources.

Density-dependent and density-independent drivers of large herbivore population dynamics

An understanding of what factors cause animal populations to increase, decrease or remain stable is fundamental to the provision of advice on how to manage them. While it is advocated that species restoration and conservation plans should be based upon sound studies of the species' population ecology and habitat requirements (Bodmer, Fang & Ibanez 1988; Stanley Price 1989), there are still many cases where the fundamental data required to inform the process are lacking (Stinchcombe *et al*. 2002) or where developments in theoretical ecology are not incorporated into management plans.

Long-term ecological studies of population dynamics in large mammalian herbivores provide a detailed understanding of the effects of intrinsic and extrinsic factors in determining population size and composition (Saether 1997; Gaillard, Festa-Bianchet & Yoccoz 1998; Gaillard *et al*. 2000). These fundamental studies have focused on the relationships between population density, weather and individual survival rates of different sex/age classes (Gaillard, Festa-Bianchet & Yoccoz 1998; Gaillard *et al*. 2000). Density-independent effects (Milner-Gulland 1997; Smith & Anderson 1998; Coulson *et al*. 2001) also impact upon large mammal populations. There are often interactions between density-dependent and density-independent effects, because malnourished animals are more likely to succumb to severe climatic events at high than at low population densities (e.g. roe deer *Capreolus capreolus*, Gaillard *et al*. 1997; moose *Alces alces*, Crete & Courtois 1997; bighorn sheep *Ovis canadensis*, Portier *et al*. 1998; alpine ibex *Capra ibex*, Jacobson *et al*. 2004). More importantly, it has become evident that the impacts of both density-dependent and density-independent effects vary substantially according to a population's sex/age structure. This is because the survival of different sex/age classes is not equally affected by resource abundance and inclement weather. In general, adults are relatively impervious to density and weather effects, while juveniles (and possibly senescent individuals) are highly susceptible to both (Gaillard, Festa-Bianchet & Yoccoz 1998; Gaillard *et al*. 2000; Coulson *et al*. 2001). This finding has crucial relevance to management strategies, first because it underlines that population projection forecasts must take sex/age structure into account (Gaillard, Loison & Toïgo 2003), and secondly because it suggests possible fundamental differences in how exploited and unexploited populations will react to changes in density and weather. The proportion of juveniles and yearlings (the age classes most sensitive to both weather and density) tends to be much greater in harvested than in unharvested populations, while the proportion of senescent individuals (with higher mortality and sometimes lower fecundity; Gaillard *et al*. 2000) is much lower (Langvatn & Loison 1999; Apollino, Bassano & Mustoni 2003; Festa-Bianchet 2003; Festa-Bianchet, Gaillard & Côté 2003). It therefore seems reasonable to predict that the growth rate of heavily harvested populations may vary more than that of unharvested or lightly harvested populations in response to changes in weather and density. This idea merits further consideration, because much of our current understanding of population dynamics in ungulates comes from long-term monitoring of unharvested populations (Gaillard *et al*. 2000). In particular, ungulate populations subject to heavy harvest should show steep declines following seasonally harsh weather (because of the high proportion of juveniles) and possibly rapid increases following either mild weather or a relaxation of harvest (because of the sudden influx of young reproducing females, and the very high adult survival given the young age structure). If those predictions are correct, sport hunting, as currently practised in many areas, may increase population variability, the opposite of the often-stated goal of management programmes (Fryxell *et al*. 1991; Langvatn & Loison 1999). Management programmes that target young of the year for a substantial proportion of the harvest should be less likely to increase the amplitude of weather-related population fluctuations and more likely to maintain an age structure not radically different from that in naturally regulated populations.

Recent research on population dynamics of herbivores has also underlined the importance of time lags in both weather effects and density-dependence, because of a combination of delays in the recovery of overgrazed vegetation and the effects of changes in the age structure of the population (Saether 1997; Post & Stenseth 1998). An important applied consequence of time lags in the population response of herbivores is that if managers determine harvest quotas based on current population estimates, they risk overharvesting declining populations and underharvesting recovering ones, amplifying rather than dampening fluctuations in population density. This has been reported for white-tailed deer *Odocoileus virginianus* in Canada and moose *Alces alces* in Scandinavia (Fryxell *et al*. 1991; Solberg *et al*. 1999).

The saiga antelope *Saiga tartarica* L. demonstrates the interaction between density-dependent and density-independent effects on a species for which management is critical for both the economy of local communities and for saiga conservation. The saiga occupies the semi-arid steppes of Kazakstan, Russia and Mongolia (Bekenov, Grachev & Milner-Gulland 1998). Historically, the species was exploited for its meat in a regulated fashion. However, with the opening of the Chinese medicine market in the 1990s, there has been increasing pressure on male saiga, the horns of which fetch a high price (Chan, Maksimuk & Zhirnov 1995; Milner-Gulland 1997), leading to a dramatic decline in numbers (Sharp 2002). The species was listed under Appendix II of the Convention on the International Trade in Endangered Species of Wild Fauna and Flora (CITES) in 1995 (Baillie & Groombridge 1996) and was assessed as critically endangered by IUCN in 2002 (IUCN 2002; http://www.redlist.org/). Saiga antelope populations are characterized by large fluctuations in size, primarily attributed to density-independent factors (Milner-Gulland 1997; Coulson *et al*. 2001). Summer droughts and severe winters affect birth rates of adult and yearling females, and mortality of both young and old animals. Recent modelling has suggested that sustainable legal harvests of saiga can be achieved through risk-averse management (Milner-Gulland 1997), with quotas set that account for vulnerability to severe weather. This example demonstrates how an increased understanding of density-independent and density-dependent effects could be incorporated into future models, which could then provide more realistic predictions of population dynamics. However, as has been demonstrated for saiga antelope over the past 2 years, no amount of ecologically based advice will save a species from decimation if legal frameworks are not implemented to reduce poaching. This requires an understanding of proximate causes of poaching that include local poverty, lack of law enforcement and open trade across national boarders (Milner-Gulland *et al*. 2001; Sharp 2002). Currently, saiga antelope cannot sustain any harvest (Milner-Gulland *et al*. 2003).

To date most studies on large mammalian herbivores have concentrated on temperate species (reviewed by Gaillard *et al*. 2000) and have focused on long-term monitoring programmes of a few populations, mostly in the northern hemisphere and mostly unexploited (Clutton-Brock, Guiness & Albon 1982; Festa-Bianchet, Gaillard & Côté 2003). These populations may behave differently from those in other environmental contexts, or those subject to controlled harvests. As such there are limits to the generalizations and extrapolations that can be made from these studies. We encourage more research to further our understanding of the impact of intrinsic and extrinsic processes on population dynamics in tropical ungulates, including predation (Messier 1994) and the effects of harvests on sex/age structure and on age-specific vital rates (Sinclair 1977; Owen-Smith 1993; Mduma, Sinclair & Hilborn 1999).

Population response to age- and sex-specific culling

Many management schemes prescribe sex-specific levels of culling. Ecological research has demonstrated how culling different sexes has very different impacts on population dynamics (Mysterud, Coulson & Stenseth 2002). A failure to take this into account can lead to unexpected and often undesirable consequences (Gaillard, Loison & Toïgo 2003).

Many African antelope species have been put forward as possible candidates for sustainable wildlife harvesting schemes (Darling 1960), to the extent that attempts were made in the 1970s to domesticate some species (e.g. Lewis 1975). The impala *Aerycerus melampus* is a medium-sized antelope, ubiquitous in the semi-arid bush savannas of southern Africa (Kingdon 1972; Smithers 1983). It is a highly social species in which the females range in medium to large groups, with each group accompanied by an adult male (Murray 1982). As is common in many polygynous antelope species (Jarman 1974), the males carry horns whereas the females are hornless. Historically, the hunting pressure on impala was very heavily male-biased as the species was hunted for its trophy value (Fairall 1985). It was suggested that male-biased hunting pressure may limit population size because female fecundity may be reduced when trophy males are removed (Fairall 1985; Ginsberg & Milner-Gulland 1994). This was disputed by other authors because young males can fertilize females in the absence of trophy males (Mysterud, Coulson & Stenseth 2002). In saiga antelope, however, the sex-biased harvest is thought to have led to reproductive collapse (Milner-Gulland *et al*. 2003).

Modelling, using parameters derived from autecological studies of impala, suggests that, under certain circumstances, strongly sex- and age-biased hunting (as occurs in game ranches and under trophy hunting) can lead to population collapse in ungulates (Fairall 1985; Mysterud, Coulson & Stenseth 2002). This may also be true in other species where males represent a greater economic resource than females (e.g. elephant *Loxodonta africana*, Milner-Gulland & Mace 1991; moose *Alces alces*, Solberg *et al*. 2002; but see Laurian *et al*. 2000; saiga *Saiga tartarica*, Milner-Gulland *et al*. 2003). For example, many hunted populations of wapiti *Cervus elaphus canadensis* have post-hunt ratios of five or fewer males per 100 females (Bender *et al*. 2002) and few males survive past 4 years of age (Biederbeck, Boulay & Jackson 2001), possibly affecting the timing of conceptions (Noyes *et al*. 1996). Most of the evidence, however, currently suggests that extreme sex ratio biases (less than five males per 100 females) are required to affect population productivity.

More recently, concerns have been raised about how sport hunting mortality leads to sex- and age-specific mortality rates that are radically different from those in unhunted populations. Sport harvest may have evolutionary consequences such as changes in life-history parameters, as have been recorded in commercially exploited fish, including changes in size and age at maturity and possibly in reproductive effort (Jennings, Reynolds & Mills 1998; Law 2001; Harris, Wall & Allendorf 2002; Festa-Bianchet 2003; Olsen *et al*. 2004). Recent evidence strongly suggests that high levels of trophy hunting, whereby males with the largest horns are targeted, can select for small-horned males over a few generations (Coltman *et al*. 2003). It is becoming evident that managers should consider evolution, as well as population dynamics, in deciding which animals to cull. Moving towards 'evolutionarily enlightened management' (Ashley *et al*. 2003) will be a major challenge facing the management of large herbivores over the next few years.

The link between sex-specific culling programmes and trophy harvest opportunities is clearly demonstrated in red deer, where recent research has concluded that emigration of male red deer from natal areas increased with female density (Clutton-Brock *et al*. 2002). The authors incorporated this information into an economic model to assess optimal culling strategies on Scottish estates, taking account of deer numbers on neighbouring estates. They advocated that to maximize economic returns from hunting stags, estate managers should reduce female densities to around 50% of the ecological carrying capacity. This will reduce male emigration and possibly encourage immigration from neighbouring populations. However, this does not account for the fact that stags may move large distances in search of hinds during the mating season (mating commutes; *sensu* Hogg 2000). As the mating season coincides with the hunting season in Scotland, stags are likely to be shot on land holdings (estates) other than those where they spend most of their lives (Sibbald, Hooper & Gordon 2001). In bighorn sheep, ram movements during the rut are affected by both social rank and the relative availability of ewes in neighbouring populations. Middle-ranking rams are more likely to move to ewe groups up to 50 km away in years when there are few breeding opportunities in their natal population (Hogg 2000). There is clearly a need to understand the role of both short-term movement (mating commutes) and long-term dispersal among hunted populations (McCullouch 1996) and between hunted populations and protected areas (Hogg 2000), if managers are to more effectively account for metapopulation responses to management strategies. Large-scale male movements during the rut also demonstrate that biological processes often occur at a much larger scale than that affected by individual management plans, hence there is great value in co-operation between different resource managers to ensure that their management targets are not jeopardized by the activities of others (see below, Managing large herbivores to meet multiple objectives: the future).

Herbivore impacts on vegetation: local to landscape

Herbivore distribution and associated impacts on vegetation are scale-dependent (Senft *et al*. 1987; Bailey *et al*. 1996; Roguet, Dumont & Prache 1998; Rietkerk *et al*. 2000). It is, therefore, fundamentally important to understand the scales of impact driving vegetation or landscape change in large herbivore dominated ecosystems. For example, at the landscape scale heavy grazing may lead to increasing dominance of grazing-tolerant or unpreferred plant species that may reduce diversity, whereas at local scales heavy pressure on preferred vegetation might locally increase diversity through the provision of new germination niches by trampling or improved nutrient cycling (Crawley 1997). Large herbivores generally have extensive ranges, and therefore their management tends to be focused at a large scale, which may not be the most appropriate scale of management for the resources themselves (Palmer *et al*. 2003). Much work has been done to define desirable densities of different herbivores for particular aims, and to explore how culling or other management regimes should be employed to achieve those aims (Welch 1984; Beaumont *et al*. 1994). Other studies have focused on the vegetation responses to grazing pressure (utilization rates) rather than on management through fixed herbivore densities, particularly in grass–shrub systems (Archer 1996; Armstrong *et al*. 1997). Without a full understanding of what drives herbivores to distribute themselves across the landscape, however, all these 'large-scale' approaches have their limitations.

Ecological research has shown how key resources, such as vegetation, water and shelter, together with aspects of herbivore sociability and gregariousness, all drive the distribution of herbivores and thus their impacts on resources at a range of scales (Hunter 1962; Kolasa & Pickett 1991; Milchunas & Lauenroth 1993; Schaefer & Messier 1995; Bailey, Dumont & Wallis de Vries 1998; Pastor *et al*. 1998; Illius & O'Connor 2000; Apps *et al*. 2001). Much of this research suggests that the distribution of herbivores is primarily determined by abiotic factors, such as terrain or distance to shelter/water, and herbivore responses to vegetation heterogeneity operate within these higher level constraints (Bailey *et al*. 1996; Tainton, Morris & Hardy 1996; Adler, Raff & Lauenroth 2001; Landsberg *et al*. 2003). The effects of vegetation heterogeneity on herbivore distribution are complex. Herbivores are generally attracted to preferred vegetation, but the spatial relationship between preferred and non-preferred vegetation is of paramount importance in driving the system dynamics

(Reichman, Benedix & Seastedt 1993; Archer 1996; Hester *et al*. 1999; Illius & O'Connor 2000; Palmer *et al*. 2003). Recent research has clearly shown that different spatial patterns of vegetation types can change herbivore behaviour and their concomitant impacts on the dynamics of the vegetation itself (Clarke, Welch & Gordon 1995; Wallis de Vries 1996; Illius & O'Connor 2000; Oom *et al*. 2002). For example, Palmer *et al*. (2003) examined the impacts of red deer on heather *Calluna vulgaris* moorland. As predicted from previous studies (Clarke, Welch & Gordon 1995; Hester & Baillie 1998), patterns of impact on heather were strongly linked with its location relative to preferred grass patches (at a 1-km^2 scale or less), demonstrating that it was impossible to predict the severity and pattern of heather utilization from only management-scale (> 100 km^2) parameters such as herbivore density and total area of grassland (Stohlgren, Schell & van den Heuvel 1999; Ryerson & Parmenter 2001). Thus, it appears as though the impacts of large herbivores on non-preferred resources are most strongly driven by the position of these resources relative to preferred resources (Ball, Danell & Sunesson 2000). The success of large-scale herbivore management to control impacts on vegetation is unpredictable, because of the weakness of the relationship between herbivore density and distribution of foraging impact in large, heterogeneous areas. These studies demonstrate that, before accurate predictions can be made about the consequences of different natural resource management scenarios, there has to be a shift of focus from simple consideration of the relative abundance of different resources and/or species (Archer 1996), to a consideration of their spatial distribution within the landscape. Refinements to management might include 'artificial' manipulation of localized vegetation composition (e.g. through targeted grazing by domestic stock), with the aim of manipulating the distribution of other, free-ranging herbivores in the area (Gordon 1989). For example, if herbivore use of a vulnerable, highly preferred area of vegetation is 'unacceptably' high even after major reductions in overall herbivore densities, manipulation of the vegetation elsewhere could alter herbivore distributions and consequently their impact (Rea 2003). When linked to spatially explicit process models (Boone *et al*. 2002), new technology, such as remote sensing, GPS and GIS, will be able to provide valuable information at the appropriate spatial scale for informing management decisions (Sibbald & Gordon 2001; Danks & Klein 2002; Johnson *et al*. 2002; Stalmans, Witkowski & Balkwill 2002).

Implications for biodiversity conservation

With increasing concern for biodiversity and conservation internationally, many countries have now signed agreements targeted at specific plant or animal species and habitats designated as of international or national importance (Department of the Environment 1994; CITES, http://www.cites.org/). These obligations require strong, underpinning ecological knowledge upon which to devise appropriate management regimes to achieve the agreed targets. However, in many cases these obligations highlighted a widespread lack of understanding of what drives the impacts of free-ranging large herbivores on biodiversity (Wallis de Vries 1996).

Notwithstanding the fundamentally important effects of abiotic factors, maximization of vegetation diversity in a landscape is widely hypothesized to require intermediate levels of herbivory (Grime 1973; Crawley 1997; Olff & Ritchie 1998; Ritchie & Olff 1999; Bullock *et al*. 2001), although definitions of 'intermediate' are not always easy. To integrate the management of large herbivores with biodiversity/environmental objectives, the relationships between grazing and biodiversity must be understood. A recurring problem, however, has been that many experimental treatments of ecosystems have tended to be either grazing 'on' (unknown grazing species' contribution to grazing pressure, unknown herbivore density, unknown seasonality of grazing) or grazing 'off' (using exclosures) (Hester *et al*. 2000). 'Exclosure' use as a management tool has already highlighted the inappropriateness or short-term nature of the 'benefits' of simple removal of herbivores, rather than manipulation of their densities. But managers are unlikely to develop management plans based on varying wild herbivore densities until qualitative theoretical hypotheses about desirable herbivore impacts can be expressed as recommendations for actual densities under a range of different conditions. This problem is gradually being redressed (Bullock 1996; Bullock *et al*. 2001) but generally requires complex or costly experimental designs and careful measurement of all key driving factors in different systems, before widespread practical generalizations can be made.

One example of the widespread use of grazing removal, to conserve or expand a vulnerable habitat, as opposed to the manipulation of herbivore density, is the case of woodland regeneration in Scotland. Native woodland and scrub now covers less than 4% of Scotland's land area (Mackenzie 1999), yet theoretically it could cover more than 50% (Towers *et al*. 2004). Many woodland communities and some of their associated plant and animal species have now been designated for protection and/or expansion under the UK Habitats and Species Directive. Grazing is thought to have played a major role in woodland decline across the whole of the UK (Birks 1988; Milne *et al*. 1998), and the impacts of both red deer and sheep in suppressing regeneration have been clearly demonstrated (Beaumont *et al*. 1994; Hester, Mitchell & Kirby 1996; Miller, Cummins & Hester 1998). Elsewhere in Europe, widespread deforestation and suppression of regeneration by large herbivores is also a major problem (Humphrey, Gill & Claridge 1998; Hester *et al*. 2004), with several European countries having designations to protect and expand such habitats. The knock-on effects of forest declines of such magnitude on other aspects of biodiversity are relatively poorly understood (Hester *et al*. 2000). One exclosure study, for example, found higher densities of invertebrate species in ungrazed Scottish native pinewoods than in grazed pinewoods (Baines, Sage & Baines 1994). To date, where woodland cover is now greatly restricted, fencing has been widely used as a 'quick fix' in protecting woodland sites and encouraging regeneration. However, problems associated with fencing include deaths of protected species such as woodland grouse (e.g. capercaillie *Tetrao urogallus*), high cost, frequent snow damage, adverse landscape impact and problems associated with higher densities of wild herbivores in the surrounding areas due to loss of land within their range (Hester *et al*. 2000).

Managing large herbivores to meet multiple objectives: the future

The future management of wild large herbivores will require ecologists to co-operate with sociologists, economists, politicians and the public. As shown by the severe decline of the saiga (Milner-Gulland *et al*. 2003) and the reintroduced Arabian oryx *Oryx leucoryx* (Spalton, Lawrence & Brend 1999), it is irrelevant how much information from ecological research is provided to policy makers for the conservation of target species if other factors are not taken into account. For example, if herbivore populations are being decimated by poaching because of local poverty, lack of law enforcement and open illegal trade across national borders, then these sociological issues must be addressed. If they are not brought under control, extinction is a real likelihood for many large herbivore species (Ludwig, Hilborn & Walters 1993). The management of large herbivores must undergo a sea-change, where the ecological understanding of population dynamics and habitat relationships is linked with socio-economic studies that address the issues relating to human–wildlife interactions (du Toit, Walker & Campbell 2004).

In many countries, wildlife (usually referring only to large mammals) belongs to the state and the right to hunt wildlife is regulated by a government, as is the protection of wildlife within national parks and reserves (Geist 1994). Over the past two decades, particularly in developing countries, there has been a shift in government policy towards handing over the right to use, if not the ownership of, wildlife outside protected areas to local communities (Harris & Shilai 1997; Hulme & Murphree 2001; but see Prins, Grootenhuis & Dolan 2000). This change in approach is derived from the philosophy that, in order to conserve wildlife outside protected areas, local people must derive some benefit (usually financial) that outweighs the costs of co-existing with that wildlife (Murphree 1998). Much research has been concentrated on the benefits of the community conservation approach to rural economies and people's attitude to wildlife (Hulme & Murphree 2001). Ecological research is now required to help local communities determine the most effective ways of managing wildlife in their area (Féron *et al*. 1998; De Garine & de Garine-Wichatitsky 1999) and to provide cost-effective means of population assessment. Costly aerial surveys (Jolly 1969; du Toit 2002; Jachmann 2002) are inappropriate in this context but low-cost methods could be employed, such as dung surveys (Laing *et al*. 2003), bicycle surveys (Gaidet, Fritz & Nyahuma 2003) or by using information from culls and harvests (e.g. age structure and fecundity rates). Over time, indices of population responses to environmental conditions and management decisions should become available. While there are arguments as to the value of this approach to wildlife conservation (Hulme & Murphree 2001; du Toit, Walker & Campbell 2004), the philosophy is still valid and should be adopted in developed countries, where local communities could be encouraged to have a more positive attitude towards wildlife in their local area.

The home range of wild herbivores often extends over land held under more than one ownership, providing an additional challenge to management. To date, the management of ungulate populations has tended to focus on the management of single populations within defined management units, for example estates, community lands and nature reserves/national parks. Ecological research needs to develop a more detailed understanding of the interactions between subpopulations (e.g. immigration and emigration rates) and the consequences of management of one population on neighbouring populations, especially where the management units have very different goals (e.g. hunting and conservation). The outcomes of this research should be coupled with policy and management instruments that facilitate the co-operative management of large herbivore populations. Management units must more closely reflect the biology of the populations rather than the human-defined ownership and jurisdictional boundaries. In many respects, the developing world is leading the way in approaches to public involvement in management and co-operative management, and the developed world would do well to learn from the relative success or otherwise of different attempts to manage large herbivore populations more holistically, as part of a socio-ecological system rather than in isolation.

Acknowledgements

Thanks go to Jean-Michel Gaillard, Glenn Iason, Norman Owen Smith, Robin Pakeman and an anonymous referee for their valuable comments on the manuscript. I.J.G. and A.J.H. acknowledge the support of the Scottish Executive Environment and Rural Affairs Department. In addition, I.J.G. was supported by CSIRO.

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Received 14 March 2003; final copy received 7 September 2004