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Review Article

Managing Large Herbivores in Protected Areas

Abstract

By nature of their size, grouping behaviour, and central position within most trophic webs, large terrestrial herbivores -- namely ungulates and elephants -- tend to be both keystone and umbrella species. Their proportionately large impacts on ecosystems extend both top-down (i.e. regulation of vegetation), but also bottom up (regulated their predators). For these reasons, as well as their cultural and economic importance to humans around the world, large herbivores are among the most heavily managed species in any region. Large herbivores have historically been managed by the fact that hunting by humans – or an intentional or forced reduction in that hunting – effectively plays its own top-down role of regulating herbivores. Managing large herbivores in protected areas presents a different set of challenges, however, because where human can no longer hunt large herbivores, the role of humans in the ecosystem is changed dramatically. The necessity of regulating both over and underabundant large herbivore populations remains, however, but we are now challenged to affect this management from outside of our former predator-prey relationships. I reviewed the major approaches to managing large herbivores in protected areas, from a historical perspective, through the development of protected areas and conservation ethics, to more modern methods such as wildlife contraception and behavioural modification. I examine each of these methods from a broader perspective that give further consideration to the impacts on species other than the target species. I synthesize these approaches them from the perspective of holistic ecosystem management, where each method acts to replace a part of ecosystem function that has otherwise been lost by the very fact the herbivore population is in a protected area. As the amount of undisturbed habitat for large herbivores decreases worldwide, these iconic species are increasingly confined only to protected areas, making specific strategies for managing their populations even more important.

Introduction

Protected areas are usually designated to preserve an area in a natural state, free from excessive human disturbance [1]. Because humans and their infrastructure have many negative impacts on natural ecosystem functions, protected areas can be effective conservation tools [2]. Some protected areas may even be designated specifically to protect rare or endangered species, such as the ungulate sambar (*Cervus unicolor*) and the tigers (*Panthera tigris*) that prey on it in Thung Yai Naresuan Wildlife Sanctuary, Thailand [3]. While curtailing global declines in biodiversity is an important objective for protecting natural areas, protected areas also benefit species that are not endangered, and by having optimal sizes of populations of large fauna, overall ecosystem function is enhanced [4]. However, protected areas themselves may result in changes to the role humans play in a naturally functioning ecosystem, and disconnect humans from natural predator-prey relationships with large herbivores. These change relationships with species that may formerly have been prey for humans thus changes the ways we must manage them.

Because of their individual size, overall population biomass, and subsequently large habitat requirements, populations of large animals can have proportionately large positive and negative impacts on the protected area [4]. Most large terrestrial herbivores (here we consider ungulates and elephants, *Loxodonta spp.*) are gregarious [5] and exist in larger population sizes than their predators. This makes large herbivores not only more prone to hyper or hypo abundance when natural population management is insufficient [6], it also magnifies the consequences of inadequate management. Ironically, because of past human interference, maintaining balanced and "natural" ecosystem function within protected areas often requires further human interference. The objective of this review was to examine the different methods humans have employed to manage large herbivore populations, but synthesize them as reactive approaches to replace natural ecosystem process that have been lost. Protected areas have changed our relationship with what essentially is our former prey, but I argue that sustainable management of large herbivores can only be achieved by restoring intactness to ecosystems in which humans are an active part.

Historical large herbivore management

Pre-industrial attitudes and actions: The goal of wildlife management is to decide how best to manipulate ecosystems towards specific ecological but also human goals within that protected area. Humans have managed large herbivores for thousands of years, namely as a continuous and important food source for humans, and particularly as human groups began coalescing in larger groups that could be fed more efficiently with larger prey species [7]. As long as 11,000 years ago opportunistic hunting by natives was "culturally modifying" herbivore populations, and humans were at least partly to blame for the extirpation of mammoths (*Mammuthus primigenius)* and the last horses (*Equus* spp.) native to North America [8]. In North America, large populations of bison (*Bison bison)*, deer (*Odocoileus* spp.), moose *(Alces alces)*, and elk *(Cervus canadensis)* came to be found only the large swaths of "no-man's-land" found between territorial boundaries held by opposing warring tribes [8]. When Lewis and Clark traveled across North America in 1805-06, they found so little wild game outside these neutral zones that they ate their own horses and dogs [8]. While not intended as such, these neutral zones acted as protected areas. While much has been made about the impact European arrival in North America had on bison populations, there may not have been any bison remaining on the Great Plains by the time Europeans arrived, if not for the de facto protected areas created between warring native tribes [9].

Prehistoric humans managed populations of large herbivores more purposefully as well. Non-human predators of large herbivores, such as wolves (*Canis lupus*), bears (*Ursus* spp.), leopards (*Panthera pardus*) and lions (*Panthera leo*) were direct competitors for human food sources, and so were often actively hunted and trapped by humans [10]. When European settlers first arrived in North America they found the local natives used pitfall traps to capture wolves, while other tribes were known to set out poisonous bait [11]. Wolves had been actively hunted across Europe and Asia, but European settlers in North America were particularly committed to predator control, partly out of fear, but partly as management to ensure abundant ungulate populations to feed settlers [11]. In these pre-industrial times humans were still fully-participating components within intact ecosystems, where our predator-prey dynamic with large herbivores was obligate, and competition with other predators necessary for our own survival.

Post-industrial attitudes and actions: With westward expansion across North America by European settlers, treaties were signed between warring native tribes, and hunting again occurred within those former neutral zones [11]. Bison populations began their precipitous decline soon after, no doubt hastened by the spread of firearms that improved our capacity to kill, and to reduce a population at a rate faster than we could control [12]. While the decline of the bison was so dramatic that it began to change people's attitudes towards one more conservation-minded, there remained some strong opposition to protecting these large herbivores at all [13]. In a fascinating – if not disturbing – example of one purpose of ungulate management, many officials in the post-civil war USA government supported a policy of complete bison elimination as a way to finally defeat the last remaining first nations tribes opposing the colonists [14].

From a frontier approach that sought to fight and ultimately conquer nature, attitudes began to shift towards a land ethic that saw value in nature beyond simply resource extraction. Industrialization is thought to have hastened this cultural shift in many nations in Europe and North America, because while it brought many benefits to societies, society began to respond negatively to the loss of wilderness [15]. This eventually resulted in policies where wildlife conservation was seen as a valid end goal of wildlife management [16], eventually to the formation of Yellowstone National Park (NP), USA, in 1872. This park was the first aimed at protected nature – including the extensive populations of large herbivores still roaming the area – for its own sake, rather than just for the maintenance of an abundant food supply [13]. This was a watershed moment in the history of large herbivore management.

Modern purposes of protected areas: The environmental movement that gained footing in Europe and North America through the 1960s and 70s was driven in part by a more modern sense of attachment to nature, and spiritual attachment to wildlife [17,18]. In effect this marked a change from valuing things we might gain from nature, to valuing nature itself. For example, Elk Island NP in Canada was originally designated as a hunting preserve, but now hunting is now banned, and excess bison and elk (*Cervus canadensis*) have become an important source population for re-introduction efforts around the world [19]. Surveys in the United Kingdom found people believed protected areas should have the main goals of protecting nature and conserving natural areas, while maintaining opportunities for low impact human activities like walking and wildlife watching [20]. Local support for conservation in Sariska Tiger Reserve in India recognizes the value of income from tourism, but remains driven by the aesthetic and spiritual value people see in the plants and animals living in the area [21]. A survey conducted in Sierra de Hautla Biosphere Reserve, Mexico found locals understood the purpose of protected areas is to preserve nature with the lowest possible level of human interference [22]. It is important to recognize that this change in attitude reflects a valuation of nature from *outside* of it, where humans are considered apart, or even above nature, and where natural areas are a "thing" for us to value, and *visit*. While this fundamental change benefited nature by giving humans something to protect and preserve, the removal of humans from the ecosystem disrupted ecosystem function within those same protected areas. From this stems most modern management problems in protected areas. We protected the areas, but not the ecological processes within them.

Why large herbivores must be managed

Umbrellas and keystones: Large herbivores have proportionately large impacts on their ecosystem, and are generally defined as keystone species [23]. Beyond the large amount of habitat they require at any one time, many large herbivores also migrate over long distances [24]. These traits further define large herbivores as umbrella species; wherein protecting them requires the preservation of large areas of suitable habitat, and protecting this habitat inevitably protects other resident plants and animals [25]. Large herbivores also hold pivotal positions within ecosystems, where they are subject to "top-down" regulation from keystone predators like lions (*Panthera leo*), while simultaneously acting as keystone predators themselves, as they regulate the vegetation they feed on. These relationships add to the complexity of large herbivore management, because management practices must also consider their effects on predators, vegetation, and even abiotic elements like soil nutrients.

Predator - prey interactions: Ecosystem-based management has moved us past the oversimplified days of protecting "good" animals (large herbivores), and eliminating "bad" animals (predators), and is increasingly recognizing the importance of overall ecological integrity, and the necessity of a holistic approach to ecosystem management [26]. For example, years of persecution and extermination of top predators, such lions, tigers (*Panthera tigris*), wolves, and bears (*Ursus* spp.), either as competitors for our food, or as perceived safety risks, have resulted in global declines in predator populations, which in turn has impacted large herbivore populations. As grizzly bears and wolves were steadily exterminated in the Grand Teton NP, USA area in the mid-20th century, moose populations within the park itself became over abundant [27]. Immediately outside the park there were still no bears or wolves, but hunting by humans was allowed, and had kept the moose populations at a more sustainable level.

Outside of protected areas humans may adopt the role of predator, and thus contribute to the regulation of large herbivores, but inside protected areas where hunting is not allowed, humans not only fail to regulate prey populations, they may disrupt natural predator-prey dynamics. Because prey species more readily adapt to the presence of humans than predators do, once prey learn that humans will not kill them, they will use humans as "shields" from natural predation, and thus limit the ability of natural predation to regulate populations of large herbivores [28]. During calving season, moose have been seen congregating nearer to roads through protected areas, having learned that bears are less likely to follow them there [29]. In both Banff and Jasper national parks, the elk have learned to use the Banff and Jasper town sites as refuges from wolves [30,31].

Herbivore - plant interactions: Excess herbivory is an inevitable consequence of unregulated large herbivores. In the USA the greater Yellowstone ecosystem was absent of wolves for decades, but after wolves were re-introduced in the mid-1990s aspen (*Populus tremuloides,* which had been overbrowsed, was able to recover [32]. Burns et al. [33] compared the responses of entire plant communities to the loss of large herbivores in both South Africa and North America, and found that plant community richness and diversity was higher in single-large herbivore systems, than in systems with no large herbivores at all. A study in east African found that removing large herbivores led to increases in rodent population, and subsequent increases in predatory snake populations [34]. Wolf predation on moose creates soil nutrient hotspots, with corresponding vegetative hotspots of higher diversity and richness [35]. Evidently large herbivores regulate vegetation even after they are dead.

Impacts on humans: Large herbivores are as large, or larger, than humans, and so can hurt people directly by charging at them and knocking the person over, kicking and stomping them with sharp hooves, or goring them with their horns, antlers, or tusks [36]. Aggressive charges often take place during the mating season when males are particularly aggressive and territorial, but just as often during calving seasons when mothers fiercely defend their young [37]. In Banff NP, most aggressive incidents by elk are done by females defending their calves during the spring calving season [38]. Even small herbivores can become dangerous too, such as the increasing problem of white-tailed deer attacks at the Southern University, USA, during deer fawning season [39].

As some ungulates lose their fear of humans, they may habituate [40], and start to aggressively compete with humans for resources [31,41]. Public safety issues tend to be greater in protected areas, as the lack of hunting by humans leads large herbivores to lose their natural fear of humans [11]. While large herbivores may learn to avoid natural predation by moving into areas where there are humans, predators may adapt to this, and also move into these human-disturbed areas [30]. This creates new public safety issues with habituated *predators*, which present an arguably even greater threat than habituated prey.

A lack of predatory regulation in Riding Mountain NP, Manitoba, has led to an overabundant elk population that has spilled out into surrounding agricultural areas, and caused conflicts with farmers over the elk herbivore of crops [42]. When big animals that are attracted to humans and human constructs like roads are wandering around a protected area, wildlife-vehicle collisions are an inevitable result [43]. Property damage resulting from ungulate collisions is estimated to amount to almost $300 million/year in Canada, and over $6 billion/year in the USA, with 90% of DVCs fatal to the ungulate , and 65% injurious to humans [44,45].

Because large herbivores are valued in so many different ways beyond simply ecosystem mechanics or biodiversity, humans can also be impacted by an *under* abundance of large herbivores. Muskox have been a cultural centre piece for many Inuit and Aboriginal groups, for thousands of years, but declining muskox populations have made it more difficult for First Nations groups to retain many cultural traditions [46]. Where hunting is for subsistence, the consequences of large herbivore under abundance can be more severe. Declining ungulate populations in the Hponkanrazi Wildlife Sanctuary, north Myanmar, are forcing villagers to change to less meat-based diets [47].

While public safety issues arising from overabundance are perhaps better known, under abundant large herbivores can also create public safety risks. In Tsavo NP, Kenya, predatory regulation within the park largely keeps large herbivores out of surrounding farmland, but in years of low rainfall – and thus low herbivore abundance – it is the predators themselves that come out of the park and onto farms and ranches [48]. Similarly, lion attacks immediately outside the Gir Forest protected area in India spike when drought conditions reduce prey populations within the park [49]. This can result in further conflicts, such as those with farmers or ranchers whose economic goals are impinged upon by large herbivores competing with stock for resources, or overtly destroying crops. These occurrences are not rare, and create contentious issues that may threaten to derail the goals of the protected area [2].

Strategies for managing large herbivores

Culling: The most straightforward way to reduce a large herbivore population is simply to kill a pre-determined number of individuals. Theoretically this method should closely resemble the natural predator-prey relationship humans have had with large herbivores, but culling is not the same as hunting. Because of the risk to non-target species when using poisonous bait or lethal trapping schemes, culling is usually done by shooting the target species with firearms [11]. Most hyperabundant large herbivore species form herds, enabling quicker and thus more economical population reduction, but typically entailing few mass kills, rather than the sustained but low predation rate of traditional hunting by humans [50]. Some examples of species commonly subject to culling include deer, elk, bison, elephants, caribou and pronghorn antelope (Table 1).

Where terrain, habitat size, or lack of roads, all complicate ground-based culling, shooting will have to be done from a helicopter. Using helicopters for culling, and airplanes for spotting, managers in Australia were able to cull over 800 camels over 5 day span, reducing the targeted population by 50%, at a total cost of $80,000 Australian dollars [51]. The costs and training demands of this method limit the number of parks that can use this method, as managers in poorly funded protected areas may lack access to aircraft or pilots entirely [52]. However, because large herbivore over-populations in protected areas are usually in their highest densities near areas of human disturbance, managers are often able to approach these large and easy targets using roads and trail. The lower costs associated with ground-based culling may compensate for the slightly lower efficiency compared to air-based [53]. An entire herd of ~30 elephants can be culled in a single session of ground-based shooting [54], while sustainable culls of over 1000 elk/year have been estimated for Rocky Mountain NP, USA [55].

Different protected areas will often have different procedures for dealing with the carcasses resulting from lethal management. Banff NP culls up to 20 elk per year, with 1/3 of these being given to indigenous groups residing outside the boundary of the park who had voluntarily given up their ancestral hunting rights within the park boundaries [56]. Elk culled in Rocky Mountain NP, on the other hand, are raffled off to citizens [57]. Similarly, Zimbabwe processes culled elephants for sale to both locals (meat) and tourists (Eg. skins, elephant hair jewellery, bones [58]. Combined with – very controversially – ivory from tusks, a 5% annual elephant cull in Hwange NP would not only reduce the hyperabundant population, it would generate an estimated US$320/ km^2, compared with US$200/ km^2 to manage this protected area [58]. Hwange NP was reluctant to go ahead with this culling program, however, due to negative pressure from the conservation community and its potential to hurt tourist revenue. From a global perspective, public perceptions of wildlife culling programs are overwhelmingly negative [53]. Public pressure led directly to a moratorium on the culling of elephants in Kruger NP, South Africa, despite the inability of park managers to control elephant hyperabundance otherwise (van Aarde et. al, 2009).

Impacts on population & ecosystem: Culling represents a faster rate of population reduction than any natural method seen in even highly stochastic systems. While this makes it appealing for managers concerned with quick solutions, unnaturally rapid population declines can have adverse or unpredictable implications. A prevailing justification for culling large herbivores is that if left to continue their unchecked population growth, their populations would exceed their habitat's carrying capacity and inevitably crash, and so culling is simply pre-empting that crash [59]. However, musk ox and caribou, for example, can experience annual natural die-offs of up to 90% of their population [51]. Culling at their peak population in a misguided attempt to pre-empt this crash, when birth rates are suppressed due to density-dependent effects, could in fact send them past a tipping point towards extirpation [51].

Another risk of culling is that when ungulate populations are severely reduced, density-dependent effects act to increase the species' birth rate [60]. Because of this compensatory fecundity, once a culling program ends, population growth will resume at a rate much more quickly than before the culling began. For example, when a long term elephant cull in Hwange NP was stopped in 1995, the elephant population doubled within 6 years [61]. Culling may also result in changes to dispersal patterns. When elephants were culled in Kruger NP, immigration into the culled areas increased dramatically, quickly restoring population numbers [52]. Culling may therefore need to be perpetual in order for it to have any long-term impact on a population.

While culls immediately reduce herbivore populations, there is a time lag before the remainder of the local ecosystem recovers from excess herbivore [6]. Restoration of over browsed vegetation is limited by plant growth rates, but recovery can often be very fast if the cull reduces the herbivore populations to levels below carrying capacity. The sudden decline in available prey, at the same time, will have immediately negative effects on predators. A major cull of a prey species can replicate a population crash, which could result in extinction events when predator populations are naturally present in low numbers [55]. Predators may also respond by switching to

Table 1: Summary of major strategies for managing large herbivores in protected areas. Top of table describes what natural ecosystem process is being replicated through management intervention, and how this differs from the natural process. Bottom of table describes which species, protected area type, or contexts, each management strategy is best or worst suited for.

Management Strategy	replicated ecosystem process	how different from "natural" process
culling	natural predation, or hunting by humans	more rapid, more extensive, no behavioural modification
contraception	calf mortality and reduced fitness of mothers	influences population structure and breeding behaviour
translocation	immigration/emigration	demographically non-representative, more extreme
physical barriers	small or large scale dispersal	absolute, indescriminate, affects not target species
hunting	natural predation, or hunting by humans	poor replacement for predation by non-humans
behavioural modification	habitat stochasticity, stress from predation	not permanent, may need to be sustained management
Management Strategy	**most suited for**	**least suited for**
culling	musk ox, caribou, species with natural mass die-offs	areas where lethal management is unpopular with public
contraception	disrete populations, species not in guilds	small populations
translocation	bolstering under-abundant populations	moving animals because of problem behaviour
physical barriers	limiting use of unsuitable habitat (eg. a roadway)	migratory species
hunting	protected areas where hunting is allowed on some basis	most protected areas, since hunting is usually banned
behavioural modification	habituated individuals and populations	where non-target species will be influenced negatively

alternate prey and negatively impact those populations [62]. For example, reductions to hyperabundant elk in Jasper National Park, AB may have forced wolf populations to switch to alternate prey that included threatened mountain caribou [63,64].

Contraception: The principle behind contraception is that infertile animals will remain in the population, and so the adverse density-dependent effects of culling animals are not present [65]. The total population is not reduced, only the breeding population, and so while the death rate can remain unchanged, the birth rate is reduced. This means, however, that population reduction via contraception can only be as fast as the natural mortality rate [55]. There are two major approaches to contraception in large mammals: yearly treatment to prevent fertility, or permanent treatment to render a female infertile for the remainder of her life [66]. Mechanical (Eg. intrauterine devices for females) and surgical (eg. vasectomies for males) contraceptive methods are not practical for wild species, and so feasible methods of contraception are all either hormone or immune-system based [66]. While hormone-based contraception using GnRH (gonadotropic releasing hormone) have been effectively on both males (stops spermatogenesis) and females (stops the estrous cycle) of numerous species, they are, curiously, ineffective on male ungulates, and only temporarily effective in female ungulates [66]. The most promising and modern methods use porcine zona pellucida (PZP), a pig tissue extract. Much like a vaccination, this foreign compound elicits an immune response in females that coats ovum with histamines, which blocks sperm entry [66]. PZP has been proven to be up to 100% effective [52].

Delivering contraceptives to wild animals is more costly and complicated than simply killing them. Oral delivery using bait piles is too dangerous, as non-target herbivores may eat bait, with potentially disastrous consequences [66]. This is particularly risky in complex multi-herbivore systems. PZP and GnRH can both be delivered with intramuscular injections, but the amount of GnRH required is so large that individuals must be rounded up and processed through chute systems, as has been done on feral horses in western USA [67]. However, such small amounts of PZP are required that the PZP can be delivered with darts shot from a distance [67]. PZP's greater popularity may be partly due to the reduced labor costs.

The duration of contraception effectiveness is closely associated with the overall time and monetary costs of this method of population control. Yearly contraception costs more than culling, but reaches population targets more slowly: 9 years compared with 7 years [55]. Bradford and Hobbs' computer simulations showed, however, that lifetime contraception required the handling of 1/3 as many elk as either culling or contraception that is done yearly, and so in the long term was proportionately less costly. New PZP formulations have already proven to be effective for several years, and so the theoretical "lifetime infertility" is closer to becoming a reality [52]. This raises further ethical dilemmas. Contraception of wild species is very invasive, and the question of how to sterilize wild species may also need to consider whether heavy-handed management that manipulates birth rates and juggles demographics should be done at all. Management that appears outwardly like animal husbandry may seem anathema to members of the public that believe protected areas should preserve natural processes too [68]. Despite this, and the fact that the public remains mostly poorly informed about what it is and how it is done, support for contraception of hyperabundant animals is increasing, as it is seen as a more palatable alternative to lethal management [68,69].

Impacts on population & ecosystem: The overall population impacts of contraception tend to be more subtle than the effects of culling and hunting. A study on feral horses found that immune contraception did not affect foal survival, sex ratios, and birthing season (Gray et al., 2007). However, contraceptive treatments have been found to produce post-breeding season behavioural changes. While untreated female ungulates and elephants stop having sexual interactions once the breeding season is over, sterilized females remain in oestrous, and so continue mating for many more weeks [52]. This has a cascading effect, where the males are thus compelled to keep fighting for mates and working to gather females in high density "harems" [70]. This makes mating extremely costly for breeding males, as these behaviors also take time away from foraging activities. Females kept in harems for these artificially long periods will also lose condition through increased competition, physical aggression, and decreased forage quality [70]. Changes to breeding behavior can also alter distributions of both males and females, which could have subsequent impacts on local vegetation that may be over browsed, change the distributions of competitor herbivores, and even change the distributions of predators [70].

Population level impacts of contraceptive regimens depend on the sizes of both the population and the protected area. Hobbs et al. [65], found that treating small populations – particularly those in enclosed protected areas – with lifetime contraception magnifies their extinction rate. Conversely, Mackey et al. [71], opined that elephant contraception would only be effective on small populations in enclosed reserves, because their population age structures would be unstable enough for contraception to have an impact. In a large and old reserve like Kruger NP the elephant population is so large and stable that halting its growth rate would require sterilizing 75% of all females; and there are more than *7000* elephants in Kruger NP [52].

Translocations: Ungulate populations normally regulate themselves through emigration and immigration [72]. Because parks and reserves are often surrounded by human-disturbed landscapes, even unfenced protected areas tend to limit animal movements in and out of the protected habitat [52]. Translocation provide managers with a method of controlling emigration and immigration by physically removing animals from one area, and re-introducing them into other areas that are not necessarily even within the same protected area. Often this is done in concert with conservation efforts aimed at re-introducing that same species into areas where none exist, or populations are too low; in effect a transfer of hyperabundant animals from source areas, to sink areas [73].

Large herbivores are a challenge to capture and move, but though large, their herding nature is conducive to live removals on a massive scale, and by 1997 even the largest of the African bull elephants could be moved [74]. Elk Island NP uses corral traps and annual "round-ups" to collect large numbers of elk and bison for live removal from the park [46], but tranquilizer darting may be more effective for smaller numbers of animals. Regardless, translocations are expensive. Veterinarian supervision is essential, and large numbers of trained personal are needed for tracking, herding, trapping, ground-based tranquilizer darting, monitoring, security (from other members of the herd), and so on [75]. Elephants and rhinos are so large that cranes must be available to ensure tranquilized animals are resting in safe positions [76]. Moving the animals is only half of the challenge, however, as much consideration must be given to where the animals are being moved to, such as understanding the carrying capacity of the new habitat [77].

Impacts on Population & Ecosystem: Despite the high costs and other challenges, the benefits of translocations can be extremely high, because two separate populations may benefit. The donor population can benefit from reduced population density, and the translocated group can establish a new population, or bolster a previously hypoabundant herd. A meta-analysis of 22 different large herbivore species found that translocated individuals were 95% successful in surviving until breeding [78]. Van Houtan et al. also noted that when animals were translocated into areas with existing members of the same species (as opposed to colonizing a new area), the population growth rate of the existing population was actually enhanced. Translocations are also clearly more successful when habitat is demonstrably suitable for that species [77].

The donor population is impacted similarly as it is by culling and hunting, because from the perspective of population dynamics, non-lethal removal is the same as lethal removal [52]. Kruger NP was culling 400 elephants a year until 1995, at which point they stopped culling and switched to translocation, and found the impacts (or lack thereof) were virtually indistinguishable from culling [68]. Re-introducing herbivores can also help regulate vegetation in the area. The introduction of elk to a protected area in California increased above the ground biomass of vegetation, while reducing the abundance and biomass of locally problematic and highly invasive exotic grasses [79].

However, some relocations fail. The behaviour of reintroduced animals tends to be more exploratory, and may result in larger than expected home ranges, such as for rhinos reintroduced in Namibia [80]. Animals may struggle to survive when they lack sufficient relevant experience to survive in unique conditions to which they are suddenly exposed, such as predator-naive animals that are moved to high risk habitats [81]. The translocated population may also enter into conflicts with large herbivores already in the area, such as when re-introduced red deer (*Cervus elaphus*) outcompeted then drove down populations of extent Apennine chamois (*Rupicapra pyrenaica*) [82]. When translocated animals are used to bolster an existing population, the risk of disease transmission may threaten either population. Initially inadequate monitoring of tuberculosis, brucellosis, and anthrax in bison transferred to and from Wood Buffalo NP, Canada, resulted in contamination of other herds, and continue to complicated bison management to this day [83]. Despite these challenges, and echoing opinions about contraception, translocations are much more publicly and politically desirable than lethal management [52].

Physical barriers: Fencing remains a coarse method of controlling population movements. Fencing can direct large herbivores towards areas desired by managers, such as funnelling animals away from roads and through road-crossing structures like wildlife over/underpasses [84]. Physical barriers can also be effective at protecting underabundant species from humans or predators [85]. Installing fencing is a straightforward construction project once the decision is made on where the fencing should go. In most cases the area destined for fencing is already clearly delineated, with defined borders dictating where fencing should go, such as the boundaries of the park, or other specific areas warranting the exclusion of large herbivores. The biggest logistical issue of fencing is therefore its cost. Ungulate proof fencing can cost up to $80,000/km [85]. Elephant-proof fencing is even more expensive, particularly if it must be electrified [86].

Impacts on population & ecosystem: Exclusionary fencing directly reduces the amount of habitat available to a population. This may be necessary, such as where overbrowsed vegetation needs to be protected from large herbivores. In the Chang Tang Nature Reserve in Tibet ranchers are allowed to fence off winter grazing areas for their livestock, and while this achieves the goal of preventing competitive grazing by the Tibetan antelope (*Pantholops hodgsonii)*, it has had severe impacts on the population distribution and density of this rare antelope [87]. While in that example exclusionary fencing to manage towards the goals of local ranchers conflicted with the stated conservation goals of the protected area, site specific fencing within a protected areas can sometimes benefit wildlife. After ungulate-proof fencing was installed on both sides of the entire 76km length of the Trans-Canada highway through Banff NP collisions with wildlife were reduced by 80% [85]. Fencing within Hlane National Park, Swaziland, confines predators to a single smaller area within the park, while large herbivores (and tourists) remain in relative safety in the remainder of the park [88]. Ironically, this fencing has kept large predators relatively safe from the vehicle collisions on the highway bisecting the park, while hundreds of large herbivores are killed on the highway each year.

Entire protected areas may be fenced, possible to protect the area from human activities beyond the fence [89]. However, sometimes a protected area is fenced for the benefit of those human activities beyond the fencing, such as to keep elephants and other large herbivores from destroying surrounding crops [42]. Unless there is a buffer zone around the protected area, within which human activities are still at least somewhat regulated, habitat even within the fenced boundary may still suffer from the effects of external activities. For example, Massy et al. [89], found biodiversity within a fenced protected area declined closer to the fenced boundary. Fencing an entire protected area can also have disastrous effects on migratory species. The fencing of the entire perimeter of Pilanesberg National Park, South Africa has been directly linked to declines in the wildebeest population living in the protected area [90]. Fencing compounded the problem by reducing gene flow, prevented wildebeest from following natural routes to optimal foraging patches, and allowed lions to exploit a relatively immobile prey population. Fencing entire protected areas confines animals that often require very large home ranges, and so while smaller protected areas can be fenced more economically, smaller protected areas are more likely to disrupt ecological function if they are fenced [91]. Because most ungulates are at least partly migratory, large herbivore populations may be further impacted by any fencing that essentially fragments their habitat [92].

Hunting by humans: Hunting by humans is closely to related to culling, as they both result in the immediate lethal removal of individual members of the target species, but "hunting" in the present context refers to killing for sport, subsistence, or cultural reasons. Here managers are tasked with deciding the degree of hunting permitted in the protected area. Allowing humans to hunt target species within a protected area remains a viable way to reduce large herbivore populations in some areas [93]. Like culling, hunting by humans can have very precise targeting, which can ensure that underabundant large herbivores are not collateral damage.

With hunting by humans, it is private citizens, rather than professional wildlife managers, that direct action. This significantly reduces the costs of implementing this strategy, and much of the remaining time, labour, and monetary expenditures relate only to the regulating of hunters, and monitoring of the target population. In Hponkanrazi Wildlife Sanctuary, North Myanmar, subsistence hunting is unregulated, and managers merely conduct surveys of hunters in order to monitor trends [47]. In Botswana, areas protected from human settlement and industry are divided into "wildlife sanctuaries" where no hunting is allowed, "wildlife management areas" where hunting and trapping is allowed and mostly unregulated, and "controlled hunting areas", where hunting is allowed but very strictly regulated through licenses and fees [94]. Burkina Faso has a land use designation termed a "local refuge", in which the area is protected from all other activities except subsistence hunting by *locals only*. This latter example limits their opportunity to make money off hunting licenses; a lucrative practice explaining why hunting is allowed in so many Africa protected areas, including national parks [93].

Impacts on population & ecosystem: From a purely numerical perspective, hunting will have the same net reduction in herbivore populations that culling does. Carillo et al. [95], compared two protected areas differing only in the amount of hunting each allowed, and found the difference in ungulate abundance was due almost entirely to hunter harvest. Recent subsistence hunting on tribal reservations in eastern USA was found to keep deer populations regulated, while areas outside the reserve borders were overpopulated [96]. The major differences between culling and hunting, then, are the rate at which the population is reduced, and the demographic selectivity. Where culling is an infrequent series of isolated but very intense population reduction events, hunting is a longer and more gradual process. Thus, the negative effects of abrupt population drops caused by culling are not present with hunting. Hunting by humans may therefore be more compatible with the pace of ecosystem adaptation and evolution.

Because culling is usually non-selective, lethal removal of individuals through hunting is likely to have much greater negative impacts on population dynamics than the same removal through culling. While non-human predators like lions and wolves select old, weak, and smaller individuals because they are easy targets, human predators tend to select the biggest and prime-aged individuals [97]. Hunting by humans may cause adaptive responses towards smaller prey body-sizes and earlier fecundity, which reduced the genetic fitness of the entire population [98].

Where hunting in these protected areas has been historically continuous, the public is more amenable to hunting by indigenous people. A recent survey found that 86% of Canadians thought hunting should never be allowed in National Parks, with another 12% opining that only aboriginal subsistence hunting should be allowed in National parks [99]. Aboriginals still retain hunting rights in many protected areas around the world, such as tribal southern Africa, Amazonia, Central America, and pockets throughout Asia [47,95]. Because subsistence hunting has regulated large herbivore populations in the past, a proposal to reintroduce bison to Banff NP suggested that hunting by First Nations might even be required in order to keep ungulate populations from becoming hyperabundant [56]. These cultural landscapes may also be considered part of the heritage that protected areas are dedicated to preserve [100], and hunting by humans may even be considered a crucial social element that is necessary for us to truly maintain the integrity of natural areas (West et al., 2005). This management method most clearly exposes the conundrum facing protected areas, and forces us to evaluate what elements of human disturbance we truly want to protected large herbivores from.

Population Re-Distribution/Behavioural Modifications: The negative ramifications of large herbivore hyperabundance, which include excess herbivory, out-competition of other herbivores, disrupted predator-prey dynamics, habituation, and public safety, are rarely present throughout an entire protected area, but instead tend to be manifested in localized patches of habitat [11]. In such cases the problem is a spatial matter of hyper-density. Moving animals from the high-density area to a low-density area using translosctions can be effective in the short term, but if the reason(s) those animals had congregated in the high-density area remains, they may simply return to their original habitat [101]. Redistributing a population within a protected area therefore sometimes requires behavioural modification. Moose in Scandinavia have been redistributed by using supplementary feeding sites [102]. Elephants and ungulates in many African game parks have been dispersed or even attracted closer to tourist routes by using artificial water holes [103]. Aversive conditioning has been used to increase elk fear of humans, and thus disperse them from habitats surrounding human settlements [38,104], and even "encouraged" some elk to resume seasonal migratory behaviour [105].

Placing bait stations or supplementary feeder sites is not expensive, particularly during harsh winters when ungulates will be attracted to even poor quality hay [102]. The tropical savannah version of this is using seasonal water holes during droughts and harsh dry seasons, when elephants and ungulates flock to any water they can find (Chamaillé-Jammes et al., 2007) [103]. Water holes are likewise not particularly expensive; the main cost is transporting the water itself [54]. The larger problem is how long such behavioural modification must take place, so that once stopped, the wild population does not simply revert to its original behaviour. Re-distributions only work if conditions are changed such that trade-offs between forage quality and predation risk are re-weighed by the herbivores, and they choose to remain in the new areas they were moved into [106]. A secondary problem is that individual behavioural variation within even single populations can result in management only being effective on a portion of the population [104].

Aversive conditioning techniques include chasing animals with all manner of noisemakers and devices, including those that deliver painful stimuli, as a way to increase the costs to animals choosing a particular habitat [107]. Banff and Waterton NP, in Canada, has used trained dogs, with a professional dog-handler, to conduct predator-resembling aversive conditioning of habituated deer and elk [38]. For comparison purposes, Banff also conducts a very limited annual cull of the elk, which requires two trained staff instead of one dog handler, but accomplishes the desired task in a matter of hours, compared to the few weeks of the calving season over which aversive conditioning is conducted.

Impacts on population & ecosystem: Re-destributing a population mitigates negative density-dependent effects, such as disease-transmission and food shortages. The overall population in the protected area also becomes more genetically robust, with lower rates of inbreeding, once the total population is more dispersed [72]. Population re-distributions can also be used to move underabundant species too. This might be desirable when rare large herbivores are being impacted by areas of particularly high human disturbance [108].

When at appropriate densities, large herbivores improve the growth and health of vegetation, by adding nutrients to the soil once they die, and through seed dispersal through their waste [109]. However, managers must be careful in re-distributing large herbivores into areas that can actually sustain them; otherwise the ecosystem impacts alleviate in one area will simply be moved to a new area. Chamaillé-Jammes et al., found that many African protected areas were placing artificial water holes away from problem areas, to alleviate high densities in those areas, but were placing the holes in areas that were vulnerable to even small increases in herbivory. Predators will also inevitably follow relocated prey species, so managers must consider impacts on other populations of prey species through an influx of predators. In Yellowstone NP, wolves switch back and forth between elk and bison depending on the prey's distribution, but the smaller size of elk make them more vulnerable to wolves [110]. Populations of moose in Jasper NP and eastern slopes buffer regions have been increasing, which has attracted wolves to the area that switch to the easier prey of mountain caribou, and reduce the populations of this already rare ungulate [62].

Conclusions

Challenges for the future

Most management methods described here use human intervention as a proxy for natural population regulators that are no longer present or effective. Ironically, these processes are often not present because of previous human intervention. Culling, hunting by humans, and contraception each decrease population growth that would normally be controlled naturally through disease and natural predation, which includes historical predation by humans. Translocations replicate natural migrations from population sources to sinks, but the dearth of source and sink populations, and reduced capacity for migration, is invariably limited by the forced boundaries of the protected area itself. Even behavioural alterations and population redistributions within protected areas are management substitutes for natural stochastic processes that have been suppressed, such as fire [111-113], and fear responses lost when humans removed natural predators, or made human disturbance a refuge from predators [29].

Large herbivore behaviour is driven individual costs and benefits [104], and it is these that humans have unwittingly changed in protected areas, when we altered our relationship with prey species in order to protect them. Most of the management practices described herein are reactions to the behaviour of large herbivores, where they have responded optimally to costs and benefits in their habitat, but these responses have conflicted with our own human goals for the protected area. It is clear that the public wants populations of large herbivores to be managed, but it is also clear that the public favours reactive management using less invasive and course methods. One survey found 62% of people were in favour of limiting human activities in natural areas if it meant reducing pain and suffering to wildlife, and 63% believed wildlife have a right to live a life free from any pain caused by people [53].

The challenge may thus be convincing the public that even the seemingly benign presence of humans can have a negative influence on our ecosystem goals [28]. Because of this, the only way to truly maintain the ecological integrity of protected areas is either by enforcing the complete absence of humans, or taking the completely opposite tack and integrating humans more fully into the ecosystem dynamics. Thus, management methods that are more dynamic and proactive should be favored. Aversive conditioning is a prime example of this, as it very directly acts to restore a more natural predator-prey relationship with large herbivores. By increasing the costs of associating with humans, we can restore the fear that is the ultimate driver of their behavior. For those species that are threatened by their retained fear of humans, and inability to adapt to human disturbance, the solution may be one of human behavioral modification, and a willingness to abandon habitat in which our use of it threatens the very components in it that we value.

A further challenge to managing large herbivores is climate change that is rapidly modifying existing habitat across the globe [114]. Protected areas are particularly vulnerable to climate change, because paleoecological evidence points out that the primary responses of species to climate change has been range shift, but protected areas have fixed spatial boundaries [115]. The overabundant species of today could become underabundant simply because climate change has rendered their habitat unsuitable [116]. Modeling of populations of Asiatic wild ass (*Equus hemionus),* based on 16 years of previous climate data for Makhtesh Ramon Nature Reserve, Israel, found that in a global change scenario, population fluctuations increased 30%, and extinction rate increased 10 fold [117]. As climate change increases the stochasticity of environmental conditions such as precipitation and fire [113,118], large herbivore management in the future will have to become more proactive and predictive of future change, rather than relying on reactivity to observed changes.

While broad management strategies tend to focus on single populations that are over or under-abundant, in practice ungulate management must consider entire prey guilds, or ideally take a holistic ecosystem approach. Over a 20 year span in Kruger NP several large herbivores (zebra, wildebeest, impala, giraffe) all maintained high abundance, while seven other species (kudu, waterbuck, sable, warthog, sable, tsessebe, roan and eland) all suffered population declines [119]. As an example of multi-ungulate management, because high populations of moose increase wolf populations that also depredate caribou, managing populations of moose is an important component of strategies to recover threatened caribou populations in Ontario, Canada [120].

Large herbivores, as both keystone and umbrella species, are significant ecosystem pieces, and understanding how best to manage them will contribute to efforts to increase biodiversity, and restore ecological integrity [73]. This is not easy, as managing large herbivores requires humans to alter a complex trophic web we do not fully understand, using a multitude of management tools of varying success, with consideration of a myriad of stakeholder values and management goals, and doing it all in a constantly changing world. As challenging as it is, the reward is the conservation of iconic species that have been valued measurably and intangibly for our entire human history.

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