REVIEW

Strategic management of livestock to improve biodiversity conservation in African savannahs: a conceptual basis for wildlife–livestock coexistence

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Summary

1. African savannas are complex socio-ecological systems with diverse wild and domestic herbivore assemblages, which adapt spatially to intra- and interannual variation in forage quantity and quality, predation and disease risks.

2. As African savannas become increasingly fragmented by growing human populations and their associated ecological impacts, adaptive foraging options for wild and domestic herbivore populations are correspondingly limited, resulting in declining wildlife populations and impoverished pastoral societies. In addition, competition for grazing by expanding domestic herbivore populations threatens the viability of wild herbivore populations occupying similar grazing niches.

3. Conservation initiatives are further impacted by conflicts between wildlife and local communities of people who often receive little benefit from adjacent protected areas, creating conflict between the livelihood-orientated goals of communities and the conservation-oriented goals of the international community and those with vested interests in wildlife. Conservation strategies facilitating the alignment of these opposing goals of communities and conservationists are needed.

4. *Synthesis and applications.* Key to understanding facilitative and competitive interactions between wild and domestic herbivores are the concepts of niche differentiation and functional resource heterogeneity. Uncontrolled incursions of burgeoning domestic herbivore populations into protected areas (PAs) threaten the conservation of wild herbivore biodiversity. However, domestic herbivores can be managed to minimize competition with wild herbivores and to enhance habitat by maximizing grassland structural heterogeneity (greater adaptive foraging options), creation of nutrient hotspots in the landscape and facilitation of high-quality grazing. Ecosystem service benefits to communities through controlled access to grazing resources in PAs, associated with appropriate disease management, can provide a conservation payment to promote communities' support of conservation of key wildlife migratory ranges and corridors outside PAs.

Key-words: African savanna, disease management, ecosystem engineering, ecosystem services, functional heterogeneity, herbivore coexistence, pastoralism, protected areas, resource partitioning, wildlife–livestock interactions

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Introduction

African savannas support an unparalleled diversity and abundance of large wild and domestic herbivores and their associated predators (Smithers 1983; Homewood 2008; Craigie *et al.* 2010). Combined with some of the last remaining long-range migrations of large wild and domestic herbivores on Earth (Homewood 2008; Harris *et al.* 2009; Fynn *et al.* 2015), these savannas constitute a region of global conservation importance. Ancient pastoral societies and their domestic herbivores (cattle, camels, donkeys, sheep and goats) have for thousands of years interacted with wild herbivores and often followed similar migration routes and seasonal foraging patterns (Homewood 2008; Fynn *et al.* 2015). Domestic herbivores often provide the only viable production alternative to crops in arid and semi-arid areas and play a critical role in cultural practices and in absorbing shocks suffered by households (Homewood 2008).

Shortcomings of conservation strategies in Africa have been exposed in the last decade with the realization that most protected areas (PAs) do not meet the needs of mobile species adapted to coping with strong spatial and temporal variability in resources (Harris *et al.* 2009; Craigie *et al.* 2010; Fynn & Bonyongo 2011). The capacity for large wild and domestic herbivores to move long distances in response to environmental gradients and patchy rainfall and fire events can be an important determinant of domestic herbivore carrying capacity and the long-term sustainability of wild herbivore populations (Owen-Smith 2004; Fryxell *et al.* 2005; Hobbs *et al.* 2008; Augustine 2010; Fynn & Bonyongo 2011).

Ecosystem fragmentation is promoted by development initiatives and agriculture in critical seasonal ranges of wild and domestic herbivores (Serneels, Said & Lambin 2001; Baudron *et al.* 2011), growing human populations and changing land-use policies, such as sedentarization of pastoralists and privatization of pastoral land (loss of mobility and transhumance), leading to overgrazing and dispersed homesteads across landscapes (Ogutu *et al.* 2009; Western, Groom & Worden 2009). As a consequence of these fragmentation effects, many wild herbivore populations across Africa are in decline (Harris *et al.* 2009; Ogutu *et al.* 2009; Western, Groom & Worden 2009; Craigie *et al.* 2010; Fynn & Bonyongo 2011), while pastoral societies become increasingly impoverished (Pamo 1998; Homewood 2008). This raises questions regarding the effective management of broad landscapes that encompass lands with varying management objectives, as illustrated by the varying degree of success met by Transfrontier Conservation Areas (TFCAs) established over the past decade in southern Africa (Andersson *et al.* 2013). In particular, the integrated management of PAs, where the primary objective is conservation of native biodiversity, and adjacent rangelands, where the primary objective is livestock production, can strongly influence whether either of these objectives are met (Western &

Gichohi 1993; Ogutu *et al.* 2009; Homewood & Thompson 2010).

PAs have often displaced local communities of people (hereafter communities) from lands in which they were once able to graze livestock and collect veldt products (Neumann 2001; West, Igoe & Brockington 2006; Andersson & Cumming 2013). These sentiments of disenfranchisement are exacerbated when communities often see little financial benefit from PAs, yet must bear the burden of wildlife conflicts, leading to resistance against conservation activities (Norton-Griffiths & Said 2010). With the recognition of these social deficiencies in conservation follows the recommendation that models for protected area conservation be better aligned with the needs and objectives of communities (Child 2014).

One approach to mitigate conflicts between communities and conservation is to promote access for communities to key ecosystem services and economic benefits within landscapes that encompass one or more PAs (national parks, game reserves and wildlife management areas). These benefits could occur in the form of direct payments to LCs to revise land-use policies or practices to facilitate wildlife use of key habitats and migratory corridors outside PAs (i.e. payments for ecosystem services; Engel, Pagiola & Wunder 2008; Victurine & Curtin 2010), but compensation for such policies or practices could also occur in the form of opportunities to graze livestock in PAs. We argue that management of broad landscapes for both livestock production and conservation objectives may achieve conservation and socio-economic synergies by developing livestock grazing prescriptions from ecological principles of ungulate niche diversity and the ecological processes that generate functional heterogeneity at multiple scales in African savannas. At the same time, competition and conflicts can arise between wild and domestic herbivores that share similar niches, diseases and predators, and these potential problems need to be carefully addressed if landscapes are to be managed for both conservation and livestock production.

Thus, the objectives of this paper are to: (i) synthesize the conceptual basis for competitive and facilitative interactions among different wild and domestic herbivores across seasons and along environmental gradients and (ii) build on these concepts to develop conservation-orientated livestock grazing strategies aimed at improving heterogeneity and maintaining access to large landscapes for wild and domestic herbivores, while improving attitudes of communities to conservation.

Key concepts for coexistence of wild and domestic herbivores in African savannas

FUNCTIONAL HETEROGENEITY

Functional heterogeneity refers to spatial and temporal variation in the grass height (structure), productivity, phenology, composition and chemical attributes of grassland

and savanna plant communities, which determine the abundance, stability, diversity and spatial distribution of large mammalian herbivores in African savannas (see concepts by Owen-Smith 2002, 2004; Hobbs *et al*. 2008; Hopcraft, Olff & Sinclair 2010). Grassland structure is a key variable influencing functional heterogeneity with short-grass patches providing high forage quality for growth and reproduction of herbivore populations, while taller grass patches provide a reserve of forage for the dry season and droughts (Owen-Smith 2002, 2004; Verweij *et al*. 2006; Hopcraft, Olff & Sinclair 2010). Functional heterogeneity may be further enhanced by plant species diversity, which facilitates diet breadth expansion as an adaptive foraging option (Owen-Smith 2002). Thus, herbivore movement among patches of varying structure and quality over the annual cycle can result in greater productivity and stability of their populations than when their foraging is spatially restricted (Owen-Smith 2002, 2004; Hobbs *et al*. 2008). In addition, savanna structural heterogeneity influences herbivores through predation risk. For example, zebra *Equus quagga*, wildebeest *Connochaetes taurinus* and Thomson's gazelle *Eudorcas thomsonii* preferentially forage in open, short-grass (high visibility) habitats and do not conceal calves at birth (Valeix *et al*. 2011), whereas greater kudu *Tragelaphus strepsiceros*, roan antelope *Hippotragus equinus* and sable antelope *Hippotragus niger* conceal themselves from predators in taller grass and wooded areas, and hide calves in tall grass or scrub after birth (Smithers 1983). Oribi *Ourebia ourebi* prefer foraging in short-grass patches but conceal themselves in tall-grass patches while resting (Everett, Perrin & Rowe Rowe 1991). Entire landscapes converted to one dominant savanna structural state will lack the functional diversity necessary to sustain multiple herbivore guilds (Arsenault & Owen-Smith 2008) or resilience during droughts.

Functional heterogeneity arises from multiple abiotic and biotic drivers operating at scales from hectares to thousands of square kilometres and days to years that influence grassland structure, quality and productivity (Owen-Smith 2004; Hopcraft, Olff & Sinclair 2010; Fynn *et al*. 2015). Abiotic drivers at broad (regional) spatial extents (up to several hundred km) include the following: (i) gradients in precipitation amount and seasonality, (ii) variation in geology that influences forage nutrients and productivity and (iii) broad spatial variation in hydrological regimes driving contrasts between woodlands and extensive wetlands and floodplains (Owen-Smith 2004; Hopcraft, Olff & Sinclair 2010; Fynn *et al*. 2015). At smaller landscape scales (up to several kilometres), topographic and edaphic variation often drives soil, hydrological and nutrient regimes leading to similar (but much shorter) productivity and structure gradients observed at regional scales (Bell 1970; Hopcraft, Olff & Sinclair 2010; Fynn *et al*. 2015). At landscape and patch scales, spatial variation created by the distribution of individual precipitation or fire events and patchy grazing can also be an important source of functional heterogeneity by modifying grassland structure and quality (Fryxell *et al*. 2005; Fuhlendorf *et al*. 2009).

Large, mobile herbivores not only respond to functional heterogeneity, but also generate it through their foraging activity (i.e. removal of plant parts consumed, trampling, deposit of faeces and urine), in particular by creating grazing lawns (Arnold, Anderson & Holdo 2014). Large herbivores also modulate fire frequency, distribution and post-fire vegetation dynamics (Fuhlendorf *et al*. 2009) and alter patterns of nutrient cycling (Augustine & McNaughton 2006). Megaherbivores such as hippo *Hippopotamus amphibius* and white rhino *Ceratotherium simum* may play a disproportionately large role in creating grazing lawns, particularly in productive grassland (Verweij *et al*. 2006; Waldram, Bond & Stock 2008; Cromsigt & te Beest 2014). While grazing lawns in many African savannas appear to be generated primarily by herbivore grazing activity (either wild or domestic) and the associated feedbacks to grass regrowth (Arnold, Anderson & Holdo 2014), domestic herbivores provide an additional source of functional heterogeneity through the concentration of excreta in temporary overnight corrals (Fig. 1). Livestock-derived nutrient hotspots (glades) can persist as grazing lawns for decades to centuries (Muchiru, Western & Reid 2008; Augustine *et al*. 2011) and provide key sites with above-maintenance levels of forage nutrients for pregnant and lactating wild herbivores such as impala *Aepyceros melampus*, hartebeest *Alcelaphus buselaphus* and gazelles (Muchiru, Western & Reid 2008; Augustine *et al*. 2011; Porensky & Veblen 2015). In addition to their nutritional benefits, creation of grazing lawns or extensive areas of short-grassland through targeted livestock grazing and corralling may reduce cover for predators, thereby reducing predation risk for wild herbivores (Smuts 1978; Augustine *et al*. 2011), leading to more productive populations (Smuts 1978). However, avoidance of predation risk may compel herbivores to forage in less risky but lower quality habitats (Sinclair & Arcese 1995), which may affect the use of livestock-induced functional heterogeneity by wildlife depending upon each species' perceptions of predation risk.

We argue that: (i) understanding and mapping drivers of functional resource heterogeneity, (ii) overlaying existing socio-political, legal, administrative barriers, disease and land-use boundaries restricting herbivore movements in response to functional heterogeneity and (iii) understanding how livestock management creates functional heterogeneity should provide the basis for the development of mobility-based livestock and wildlife management strategies in African savannas. The goal of such an approach is to incorporate livestock grazing patterns into the landscape to enhance functional heterogeneity within PAs and to overcome the limitations on access to functional heterogeneity in larger landscapes imposed by existing socio-political boundaries.
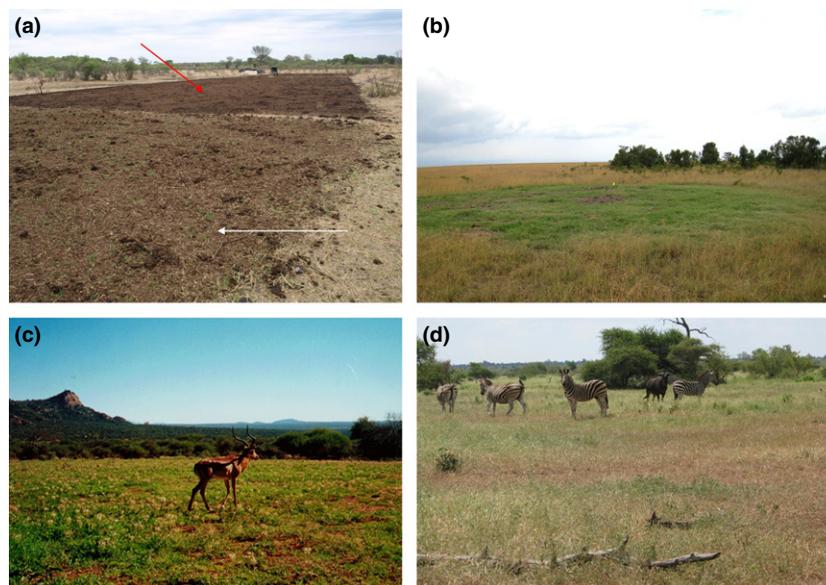
Fig. 1. Examples of abandoned cattle corrals of varying ages in African savannas. (a) Recently abandoned experimental corrals in the Matetsi region of Zimbabwe, showing dense accumulation of dung following several weeks of corralling cattle overnight in the upper portion of the photo (red arrow), and grass emergence in an older abandoned corral site in the lower part of the photo (white arrow) (Photo credit: Mike Peel). (b) Glade development 6 months after corral abandonment in central Kenya (Photo credit: Lauren Porensky). (c) Impala foraging on a glade developed from a corral site abandoned >40 years ago in central Kenya (Photo credit: David Augustine). (d) Heavily grazed glade in central Kruger National Park: South Africa, associated with evidence of ancient human settlement (Photo credit: Richard Fynn).

HERBIVORE SPECIES FORAGE PARTITIONING

Herbivore species achieve coexistence through partitioning of their forage resource base. Body size is one key factor contributing to resource partitioning where the large relative metabolic requirements of small-bodied herbivores constrain them to selection for rarer high-quality forage. By contrast, the larger absolute metabolic requirements of larger-bodied herbivores, combined with their larger less selective mouths, constrain them to a diet of more abundant but lower quality forage – but this lower quality diet may be compensated for by lower relative metabolic requirements (Jarman 1974; Illius & Gordon 1987; Steuer *et al.* 2014). The ability to meet energy requirements on lower quality, high fibre forages, is best achieved by a combination of large body size and a hind gut fermentation system, which reduces mean retention time of forage in the gut, thereby facilitating greater overall forage intake (Steuer *et al.* 2014). Small-bodied herbivores, such as sheep *Ovis aries*, goats *Capra hircus*, impala, Grant's gazelle *Nanger granti* and Thomson's gazelle *Eudorcas thomsonii*, have low absolute food requirements enabling them to meet their maintenance and reproductive resource requirements on short grasslands, whereas large-bodied herbivores with their larger absolute food requirements require taller grassland to optimize bite size and intake rate (Illius & Gordon 1987; Wilmshurst, Fryxell & Bergman 2000).

Mouth anatomy is another key factor contributing to niche diversification in large herbivores (Arsenault &

Owen-Smith 2008; Codron *et al.* 2008). Narrow-mouthed herbivores are better able to select higher quality, green leaves, while avoiding low-quality stems and dead leaves on taller grasses, whereas broad-mouthed herbivores are more efficient at foraging on short, dense swards of grass (Murray & Illius 2000; Arsenault & Owen-Smith 2008; Codron *et al.* 2008). Consequently, narrow-mouthed herbivores such as common reedbuck *Redunca arundinum* (Jungius 1971), sable antelope (Grobler 1981; Codron *et al.* 2008; Hensman *et al.* 2013), roan antelope (Schuette *et al.* 1998; Haveman 2014), hartebeest (Schuette *et al.* 1998) and waterbuck *Kobus ellipsiprymnus* (Kassa, Libois & Sinsin 2007) favour intermediate to tall-grass habitats, generally avoiding higher predation risks associated with large concentrations of other herbivores and their associated predators. By contrast, broader-mouthed herbivores such as wildebeest and white rhino *Ceratotherium simum* favour short-grass habitats (Murray & Illius 2000; Arsenault & Owen-Smith 2008). Wildebeest and Thomson's gazelle favour heavily grazed short grasslands in pastoral areas adjacent to the Masai-Mara Game Reserve in Kenya, whereas buffalo *Syncerus caffer* are restricted to taller grassland occurring mainly within the park (Bhola *et al.* 2012). Buffalo and cattle have relatively wide mouths, but their large body size and the use of a tongue sweep strategy to increase bite size (Illius & Gordon 1987) constrain them to optimal foraging in intermediate grasslands.

Thus, dietary niche partitioning among ungulates can occur through spatiotemporal patterns of habitat use,

specializations to utilize specific plant species and vegetation structural types, and variation in strategies for predator and disease avoidance. As a result, dietary differences among coexisting ungulate species, including differences among domestic and wild species, can be even greater than predicted based on body size and mouth physiology alone (Kartzinel *et al.* 2015), which suggests that plant species diversity may play an important role in facilitating coexistence among herbivore species.

GRAZING FACILITATION VS. COMPETITION

Long-term experiments and observational studies have clearly documented competition between wild and domestic herbivores of similar dietary breadth and body size such as cattle and zebra (Young, Palmer & Gadd 2005; Odadi, Okeyo-Owuor & Young 2009) and cattle and buffalo (Bhola *et al.* 2012). At moderate densities, domestic mesoherbivores, such as sheep and goats, may have positive effects on the abundance and reproductive success of wild mesoherbivores, such as impala, Grant's gazelle and Thomson's gazelle (Bhola *et al.* 2012), but much less so at high densities, which is often associated with greater anthropogenic influence (Georgiadis *et al.* 2007; Bhola *et al.* 2012). Competitive interactions between wild and domestic herbivores are primarily expressed during droughts or dry seasons when forage quantity is limiting (Odadi *et al.* 2011), but will likely occur in all seasons if domestic herbivore numbers are maintained at high levels across large landscapes (Coppolillo *et al.* 2003; Georgiadis *et al.* 2007; Bhola *et al.* 2012).

Narrow-mouthed, intermediate to tall-grass specialist grazers such as roan and sable antelope are particularly vulnerable to competition for grazing by other herbivores. Sable antelope have a minimum acceptance grassland height of around 6 cm (likely also the larger-bodied roan antelope), abandoning high-quality burned grassland (>12% crude protein) for taller low-quality grassland (3% crude protein) once other herbivore species had reduced grass height below 6 cm (Grobler 1981). Reduced competitive interactions between sympatric herbivores species may be achieved by differential selection mechanisms operating at scales ranging from plant parts to habitats, depending on group size, food availability and occurrence of competitors, as illustrated with impala, greater kudu and cattle in Zimbabwe (Fritz, de Garine-Wichatitsky & Letessier 1996). Sable and roan antelope avoid competition and predation by selecting back-country habitats far from water, concentrations of other herbivores, predators and disturbance by people (Hensman *et al.* 2013; Haveman 2014).

Facilitation can be particularly important for small- and medium-bodied short-grass specialists in areas of extensive, productive habitats such as high-rainfall regions, floodplains, swamps and lowlands (Western & Gichohi 1993; Fryxell *et al.* 2005; Verweij *et al.* 2006), where there is potential for grass biomass and height to increase to the point where forage quality limits intake rates for herbivores (Wilmshurst, Fryxell & Bergman 2000; Owen-Smith 2002). Positive interactions among herbivore species (facilitation of nutrient and energy intake) can occur when grazing prevents grassland maturing to less digestible taller grass while stimulating high-quality regrowth (Vesey-FitzGerald 1960; Verweij *et al.* 2006). Thus, the potential for facilitation increases along grassland productivity gradients driven by regional variation in rainfall and topographic effects on soils and hydrology (Augustine & Springer 2013) and during seasonal grass growth periods (Odadi *et al.* 2011). In medium productivity semi-arid regions (excluding wetlands), facilitation is expected during the wet season when grass is actively growing and forage quality may become limiting if allowed to mature. However, competition is expected during the dry season when soil moisture limits forage quantity, as documented for wildlife and cattle (Odadi *et al.* 2011).

In productive habitats such as high-rainfall regions, floodplains, swamps and lowlands, where soils are deep and moisture is generally not limiting to plant growth at any time of the year, resulting in the development of tall less digestible grasses, even greater potential exists for grazing facilitation to occur both in wet and dry seasons. Thus, pastoralists frequently burn floodplains during the dry season to remove the tall hamper of mature grass and stimulate higher quality, fresh regrowth for their livestock (Homewood 2008; Fynn *et al.* 2015), which improves dry season nutrition for wild herbivores (Parrini & Owen-Smith 2009). Clear examples of large herbivores such as elephant, hippo and buffalo facilitating forage quality for smaller ruminants come from multispecies studies on productivity gradients at various scales, such as in Benue National Park in Cameroon (Verweij *et al.* 2006), the Serengeti National Park in Tanzania (Bell 1970), the Rukwa valley in Tanzania (Vesey-FitzGerald 1960), the Amboseli swamps in Kenya (Western 1973) and the Gorongosa floodplains in Mozambique (Tinley 1977). Cattle can also serve this role, as demonstrated by declines in populations of several short-grass grazers following removal of livestock from the high-rainfall Masai-Mara Game Reserve when it was proclaimed (Western & Gichohi 1993).

DISEASES AT THE WILDLIFE–LIVESTOCK INTERFACE

Disease transmission risks threaten wildlife–livestock coexistence in Africa (Bourn & Blench 1999; Bengis, Kock & Fischer 2002). Wild ruminants can maintain diseases that are responsible for significant mortalities and production losses in livestock (Bengis, Kock & Fischer 2002). For instance, where tsetse flies occur, many species of antelope, wild suids, buffalo, rhinoceros and elephant are frequently infected with various *Trypanosoma* species, playing a role of maintenance hosts for *nagana*, a deadly chronic disease of cattle. The African buffalo is a pivotal sylvatic maintenance host for several pathogens of major

concern to veterinary services of the region (Michel & Bengis 2012), such as *Theileria parva* responsible for corridor disease and east-coast fever, and the viruses responsible for foot-and-mouth disease (FMD) in cattle. Although wild ruminants are often asymptomatic carriers of endemic diseases, they may suffer significant morbidity and mortality from exotic livestock diseases, as illustrated by the devastating effects of rinderpest. Bovine tuberculosis, introduced by cattle onto the continent, is spreading in southern and eastern Africa, affecting more than 14 species of wild ruminants, carnivores and primates (de Garine-Wichatitsky *et al.* 2013a). Ironically, a major concern for the development of TFCAs in southern Africa is that bovine tuberculosis may spill back from wildlife to livestock populations (Michel *et al.* 2006; de Garine-Wichatitsky *et al.* 2013b).

Application of key concepts to conservation strategies

Under current scenarios of growing human populations and their ecological footprint, African wildlife is likely to ultimately become restricted to less functional isolated protected patches of larger landscapes unless novel interventions are implemented. One solution is to secure use of large landscapes for wild and domestic herbivores through various incentives to communities. Examples include payments to landowners and communities not to fence or cultivate critical wet season ranges for migratory herbivores in East Africa, such as in the Kitengela corridor outside Nairobi National Park and in the Simanjiro plains outside Tarangire National Park (Victurine & Curtin 2010). However, where insufficient funding exists to pay communities to protect key seasonal ranges in the long term (see Victurine & Curtin 2010), or as an additional incentive to protect these seasonal ranges, communities could be given grazing concessions within non-sensitive parts of PAs. Communities could benefit from grazing concessions within PAs by greater adaptive foraging options for livestock across larger landscapes (as do the wild herbivores), access to forage reserves during the dry season and greater ability to move livestock away from crop fields during the cropping season. Excessive uncontrolled incursions of livestock into PAs would clearly have a negative effect on wild herbivore populations (e.g. Coppolillo *et al.* 2003). However, we suggest that controlled seasonal livestock grazing within non-sensitive parts of PAs (as laid out in Table 1) can actually enhance habitat for wildlife by (i) increasing grassland structural heterogeneity through creation of high-quality, short-grass habitat (especially in key wet season ranges where grazing impact by wild herbivores has declined), while reserving areas as ungrazed taller grass reserves/refuges for dry season habitats and for tall-grass or bulk-feeding grazers (see application by Shamhart, King & Proffitt 2012), (ii) creating nutrient hotspots (glades) through night-time corralling of livestock for predator protection (see application by

Porensky & Veblen 2015; also see Fig. 1); nutrient hotspots originating from corralling of livestock clearly benefit wild herbivore populations (Muchiru, Western & Reid 2008; Augustine *et al.* 2011) and are likely to be especially effective where wild herbivores have been excluded from critical mineral rich, short-grass ranges, as is the case in many East African PAs, (iii) reducing shrub encroachment into important open grassland habitats through targeted goat browsing, and (iv) creation of heavily grazed fire breaks and other conservation objectives requiring reduction of vegetation biomass.

Strategic planning and management of grazing concessions within PAs is clearly a complex process and would require collaboration among a wide range of stakeholders, including ecologists, veterinarians, protected area managers/rangers, livestock owners, village elders and local (e.g. county, district) governments to ensure successful implementation (e.g. Reid *et al.* 2009). We envisage the location of grazing concessions being developed on the basis of spatial data bases (e.g. Lewis 1995) that quantify landscape variation in topography, precipitation, surface water, drainage patterns and soil properties that affect grass nutrient content. These spatial data bases can be used to identify and map key biophysical gradients underlying functional heterogeneity (Hopcraft, Olff & Sinclair 2010), wild herbivore movement patterns, livestock grazing history and the potential for facilitation and competition (Table 1). The viability of grazing concessions as a conservation strategy would also depend upon local contingencies such as political acceptability, cultural approaches to livestock management and livestock densities around PAs. Conservation NGOs or relevant government departments would need to develop effective mechanisms to monitor livestock impacts on vegetation and wild herbivores (positive or negative) and to document that grazing prescriptions (spatial and temporal) agreed to by all stakeholders are followed.

Although disease transmission and predation have historically been obstacles to wildlife and livestock sympatric grazing, new technical and institutional innovations are creating opportunities to promote wildlife–livestock coexistence. In areas with traditional pastoralism and wildlife, where the main income for livestock producers is local consumption and wildlife tourism, opportunities exist for innovative integrated livestock and wildlife health management (Cumming, Dzingirai & de Garine-Wichatitsky 2013). These could involve decentralized health systems with less stringent sanitary mandates (Kock *et al.* 2002), provided with adequate capacities for active surveillance and early control of disease outbreaks. In most situations, strategic prophylactic treatments (acaricides, vaccines), associated with early treatment of individual cases, should maintain the most prevalent tick-borne diseases at acceptable levels. Vaccination against infectious zoonotic diseases could be specifically targeted, including anthrax, rabies and brucellosis, preferably adopting a One Health approach associating veterinary with human public health

Table 1. Selection criteria to determine potential competitive or facilitative effects of livestock grazing on native ungulate herbivores. Potential for facilitation increases with increasing grass height and biomass with associated increased concentrations of indigestible compounds such as cellulose and lignin. Thus, livestock grazing may facilitate intake rates of energy and nutrients by wildlife when grass growth rates are rapid such as during the wet season or in high-rainfall regions or wetlands. Competition is expected under conditions of grass dormancy (dry season) or low productivity (dryland arid regions)

|	Select or avoid	Mechanisms	Citations
Herbivore foraging strategy indicator			
Intermediate to tall-grass specialist home ranges (sable and roan antelope, waterbuck, reedbuck, hartebeest, eland, topi)	Avoid in all seasons	Intermediate to tall-grass specialists favour back-country regions with low herbivore densities and as such are vulnerable to competition for forage as well as direct disturbance effects	Grobler (1981); Schuette *et al.* (1998); Murray & Illius (2000); Hensman *et al.* (2013); Haveman (2014)
Short-grass specialist home ranges (Thomson's gazelle, Grant's gazelle, springbok, wildebeest)	Select in any season	Mesoherbivores favouring short-grass have specialized mouths (and low absolute food requirements) for foraging on short grass (unlike cattle) so are likely to be facilitated by cattle at moderate (but not high)* densities of domestic mesoherbivores (e.g. sheep and goats)	Western & Gichohi (1993); Fryxell *et al.* (2005); Arsenault & Owen-Smith (2008); Bhola *et al.* (2012); Georgiadis *et al.* (2007)*; Bhola *et al.* (2012)*
Bulk grazer home ranges (buffalo and zebra)	Avoid during dry season	Competition for forage by cattle, which have a similar niche	Young, Palmer & Gadd (2005); Odadi, Okeyo-Owuor & Young (2009); Odadi *et al.* (2011); Bhola *et al.* (2012)
Climatic and topoedaphic indicators (Strategic; Long-term)			
Very low productivity short grasslands over large spatial extent (arid regions; shallow or saline, moisture-limited soils)	Avoid in all seasons	Competition for grazing with migratory herbivores that use these short grasslands as key wet season ranges	Derner, Detling & Antolin (2006)
Medium productivity grasslands (semi-arid regions)	Select during wet season, avoid during dry season	Removes low-quality biomass and facilitates high-quality regrowth (or forms grazing lawns) during the wet season but creates competition for forage during the dry season	Arsenault & Owen-Smith (2008); Odadi, Okeyo-Owuor & Young (2009); Odadi *et al.* (2011)
High productivity grasslands such as bottomlands and wetlands (floodplains, swamps, marshes and dambos) or high-rainfall grasslands	Select during dry season, avoid during wet season*	Grazing needed to remove low-quality, productive biomass in patches and stimulate green regrowth over the dry season. *Wetland systems are resilient to heavy dry season grazing impact because they are generally avoided by or inaccessible to grazers during the wet season and store a large proportion of their biomass in rhizomes	Vesey-FitzGerald (1960); Bell (1970); Western (1973); Tinley (1977); Homewood (2008); Verweij *et al.* (2006); Fynn *et al.* (2015) *Observations by Vesey-FitzGerald (1960) and Pamo (1998). *Theoretical foundation in (Fynn 2012)
Weather and disturbance regime indicators (Tactical; Short-term)			
Wet season in average or above-average precipitation years	Select	Remove low-quality biomass and facilitate high-quality regrowth in grazing lawns; increase vegetative heterogeneity through spatially variable grazing. Create long-term nutrient hotspots for wildlife following boma abandonment	Odadi *et al.* (2011); Muchiru, Western & Reid (2008); Augustine *et al.* (2011); Porensky & Veblen (2015)
Recent patchy fire	Select	Maintain patch burns in vegetative state; enhance structural heterogeneity; and facilitate smaller-bodied herbivores	Fuhlendorf *et al.* (2009)
Under-grazed regions with current low densities of bulk-feeding ungulate species	Select	Remove litter, facilitate high-quality grazing	Fryxell *et al.* (2005); Ogutu *et al.* (2009); Bhola *et al.* (2012)
Below-average precipitation years	Avoid where wildlife densities are high	Competition for forage resources	Young, Palmer & Gadd (2005); Odadi, Okeyo-Owuor & Young (2009)
Presence of livestock in either of the previous 2 years	Avoid	Prevent loss of tufted perennial grasses and associated woody invasion* as well as minimize disturbance to sensitive wildlife species†	Fynn (2012)*; Fritz, de Garine-Wichatitsky & Letessier (1996)†
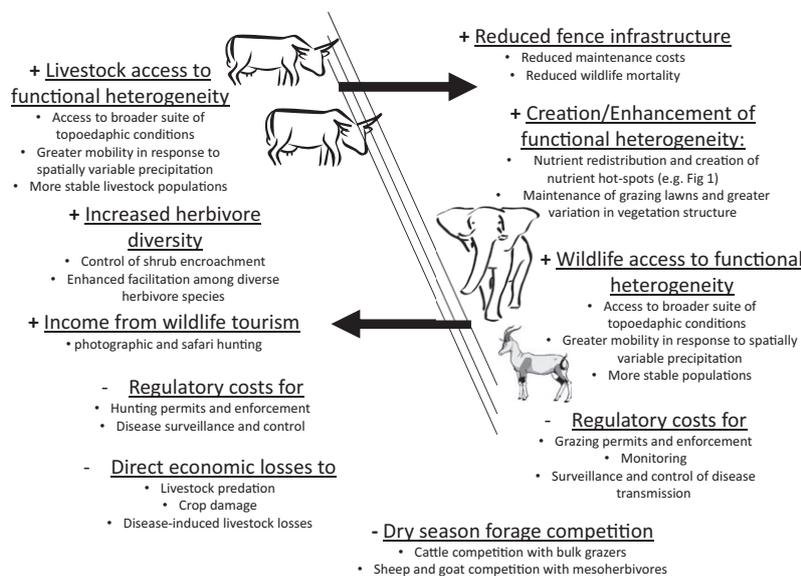
Fig. 2. Summary of the ecological and economic benefits (+) and costs (−) of mobility-based management strategies that allow livestock access into protected areas (right of fence) and facilitate wildlife access into lands managed primarily for livestock (left of fence). Benefits/costs to local communities are listed on the left and benefits/costs to protected areas are listed on the right. Dry season forage competition could affect wildlife or livestock in both areas and would be a key factor to address in livestock grazing plans and hunting regulations.

interventions for increased control efficiency (Zinsstag *et al*. 2007). The efficiency of vaccination against FMD could be improved by incorporating more antigens from strains circulating locally (Jori *et al*. 2014). In some situations, a 'commodity-based trading' approach may provide a more economically viable and ecologically acceptable alternative to the geographic separation of wild and domestic herbivores through veterinary fences (Thomson *et al*. 2013). This approach does not require a geographic separation between wildlife and livestock, as it is based on value-chain-based risk management and mitigation of animal disease hazards, which effectively ensures food safety (Thomson *et al*. 2013). Technological advances also exist to promote livestock–predator coexistence. New designs for livestock corrals constructed from canvas screens or metal panels alleviate the need to use local trees and shrubs for corral construction, can be moved frequently to target livestock grazing and dung deposition into desired locations and have proven highly effective in preventing night-time predation (Frank 2011; Porensky & Veblen 2015). While some losses to predation are inevitable (Kissui 2008), herding of livestock during daytime foraging will be critical for reducing losses to predation, as well as for reducing associated retaliatory killings of predators (combined with regular monitoring by wildlife officers).

In conclusion, we provide a conceptually rigorous conservation management tool guided by our understanding of the drivers of functional heterogeneity and competitive vs. facilitative interactions in African savannas (Table 1; Fig. 2) to design a management approach for protected area complexes and surrounding landscapes that could improve functional heterogeneity within PAs and assist in

maintaining large landscapes for both wild and domestic herbivore adaptive foraging. Such innovations may be especially critical under predicted increased spatial and temporal variability of rainfall with climate change (Ogutu & Owen-Smith 2003), which will require greater spatial adaptive foraging options for herbivore populations to persist (Ogutu & Owen-Smith 2003; Fryxell *et al*. 2005).

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Data accessibility

Data have not been archived because this article does not contain data.

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