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Abstract. The African savanna biome supports a higher diversity of ungulate species than is found in any other biome or continent. This exceptional faunal diversity and herbivore biomass density is directly linked to the high spatial heterogeneity of African savanna ecosystems. The dependence of herbivore dietary tolerance on body size translates into important size-related differences between savanna ungulate species in terms of habitat specificity, geographical range, and the share of community resources exploited. Intact savanna ungulate communities, with species distributed across body size classes and feeding guilds (grazer/browser), have strong regulatory influences on savanna ecosystem structure and function. Replacement with livestock systems of low diversity and high biomass density within a narrow body size range has occurred through the removal of competitors, pathogens, and predators, and the widespread provisioning of water. Overgrazing by livestock, coupled with episodic droughts, has caused widespread rangeland degradation and loss of floristic and faunal diversity which, by current models, is unlikely to recover to 'climax' conditions even with destocking. In selected regions where potential still exists, African savanna biodiversity and human economic development will both be best served by the integration of sustainable wildlife utilization into multispecies animal production systems.

Key words: African savannas, biodiversity, conservation, multispecies animal production

Introduction

The African savanna biome carries the earth's greatest diversity of ungulates and has sustained multispecies animal production systems for millenia. By contrast, modern attempts to impose single species systems, or monocultures of animal production, have been unsuccessful as development initiatives within the biome (e.g. Dyson-Hudson 1985). Here we examine the roots of the ungulate diversity in African savannas, explore the functional significance of this diversity, and consider its implications for sustainable use and conservation. While focusing on the biodiversity/management interface in African savannas we hope to draw out lessons that may be widely applicable to savannas and grasslands across other continents.

The African savanna biome includes those tropical ecosystems that are characterized by a continuous grass layer occurring together with trees under a climatic regime of distinct wet and dry seasons (Walter 1971; Walker and Noy Meir 1982; Justice et al. 1994). These diverse ecosystems, which together cover about half of sub-Saharan Africa (Figure 1), are broadly grouped into two categories called either moist-dystrophic and arid-eutrophic savannas (Huntley 1982) or broad-leafed and fine-leafed savannas (Justice et al. 1994) respectively. The moist- dystrophic/broad-leafed savannas occur on the African plateaux where the soils, derived mainly from igneous rocks of the basement complex, are relatively infertile and leached under annual rainfall regimes above 600 mm. The arid-eutrophic/fine-leafed savannas occur in lower-lying areas on heavier-textured nutrient rich soils, under an annual rainfall regime of 400–800 mm. The broad-leafed savannas in southern/central Africa are typified by *Brachystegia/Julbernadia* woodland interspersed with grassland along drainage lines, i.e. miombo woodland. The fine-leafed savannas are typified by the drier Acacia studded plains that merge into the steppes of the Sahel in the north and Karoo and Kalahari in the south.

The African savanna environment is where *Homo sapiens* evolved, about a million years ago, as a generalist predator/scavenger and gatherer of fruits, seeds and tubers. Human populations in Africa sustained themselves exclusively in this way until the introduction of livestock and cropping from the Arabian peninsula some 7000–8000 years ago. Livestock then spread across the Sahelian zone into West Africa about 6000 years ago, and into southern Africa about 2000 years ago (Cumming 1982; Denbow and Wilmsen 1986). Livestock now dominates the ungulate biomass of
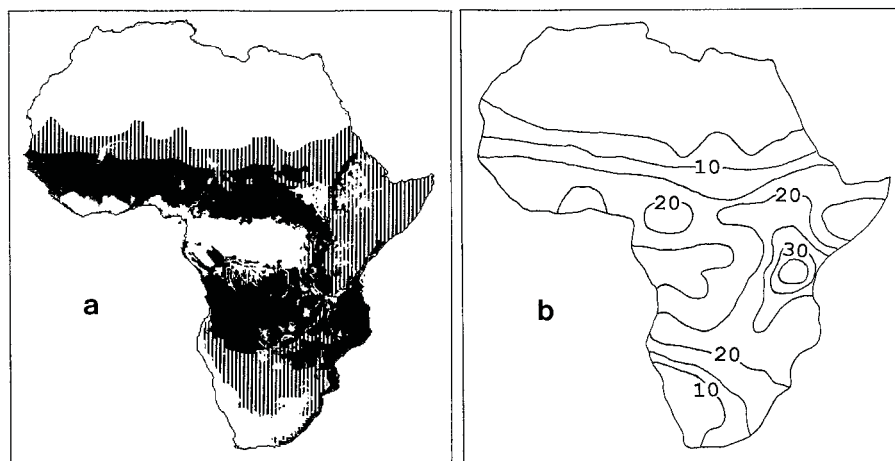

Figure 1. Distribution of savannas (a) and ungulate species richness (b) across Africa. In (a) the broad-leafed/moist-dystrophic savannas are in black and the fine-leafed/arid-eutrophic savannas are hatched. Map (a) is reproduced with permission from Justice et al. (1994); isolines in (b) are redrawn from Turpie and Crowe (1994).

Africa, with indigenous ungulates presently contributing less than 10% of the standing crop (Cumming 1982).

Functional significance of ungulate diversity

Rainfall, fire and herbivory are the prime driving variables in African savannas with frost also being important in some areas (Bourliere and Hadley 1970; Walker and Noy-Meir 1982; Frost et al. 1986). Large mammalian herbivores consume about half of plant production, with insects, particularly orthopterans, accounting for a large part of the rest (Phillipson 1973; Sinclair 1975; Gandar 1982; Tshuma et al. 1988). Hence, we are placing particular emphasis here on the functional significance of the large herbivore component of African savanna biodiversity.

Links between savanna heterogeneity and ungulate diversity

A particularly high diversity of indigenous large mammals (> 5 kg) is a natural feature of African savannas (Huxley 1961; Bourliere and Hadley 1970; Huntley 1982). While large mammal biomass varies considerably across the biome, largely in response to variations in mean annual rainfall and soil nutrient status (Coe et al. 1976; Bell 1982; East 1984), the biomass densities of herbivores in certain protected savanna ecosystems account for some of the highest levels of herbivory ever quantified in terrestrial ecosystems (Botkin et al. 1981; McNaughton and Georgiadis 1986).

Extant ungulates endemic to the savanna biome of Africa number some 46 species, of which about 80% belong to one family along, the Bovidae. This diversity of ungulates exceeds that of any other continent, even if for Eurasia and the Americas we include those species that went extinct in the late Pleistocene (Owen-Smith and Cumming 1993). The origin of this ungulate diversity appears to lie in a significant species turn-over pulse about 2.5 million years ago, which was probably triggered by an episode of rapid climatic change that caused widespread aridification and transition from forest to savanna (Vrba 1992). The present distribution of ungulate diversity across the African continent is clearly associated with the distribution of the savanna biome (Figure 1), with a particular concentration of species in the topographically diverse Rift Valley region of the East African savanna (Turpie and Crowe 1994). Interestingly, this is where the earliest definitive fossils our own genus *Homo* appear, dated at shortly after the radiation of the ungulates (Vrba 1992).

The high ungulate diversity in African savannas is directly linked to the spatial heterogeneity inherent in the savanna biome. At a coarse scale (e.g. that of ungulate species geographical ranges) the two broad classes of savanna ecosystem interdigitate (Figure 1), such as along the major valley systems of Central/East Africa. At a finer scale (e.g. that of ungulate habitats) marked seasonality and spatial variation in plant

available moisture and soil nutrients create patchiness in the quality and quantity of savanna vegetation (Bell 1986).

Scaling of habitat specificity

The interaction between spatial heterogeneity in savanna vegetation and ungulate species diversity occurs by virtue of ungulate habitat specificity, which varies with ungulate body size. Due to the ways in which herbivore gut capacity and metabolic rate scale with body mass (Bell 1971; Jarman 1974; Demment and van Soest 1985), the smaller-bodied ungulate species have narrower dietary tolerances than the larger species and tend to specialize on habitats that provide high quality forage throughout the year (Jarman 1974; du Toit and Owen-Smith 1989). In savannas, such habitats (riverine thickets, rocky outcrops, etc.) tend to be spatially discrete and scattered to a greater or lesser degree within a landscape mosaic. The larger-bodied ungulates, with their wider feeding tolerances, are able to feed in a wider range of habitats and are thus more evenly spread through the ecosystem. This could explain why it is that among African savanna ungulates there is a significant positive scaling relationship between population metabolism (energy use per species population) and species body mass (du Toit and Owen-Smith 1989). In other words larger ungulates metabolize a disproportionately larger share of local resources. This is a significant departure from the Energetic Equivalence Rule (Damuth 1981, 1987), by which it was widely accepted until recently that population density and energy use per individual scale with mean body mass across species with almost exactly opposite slopes. They should thus cancel each other out (i.e. large species use of lot of energy per individual but they occur at low densities), so population metabolism should generally be independent of species body mass. A number of other recent analyses have questioned the generality of the Energetic Equivalence Rule (Marquet et al. 1995; Silva and Downing 1995) and it does appear that the large mammal communities of African savannas include unusually high population densities of large-bodied species. A likely reason for this is that the smaller-bodied species, being more habitat-specific, are more constrained in their distribution through savanna ecosystems by virtue of disjunctions in forage quality at habitat edges.

Two predictions of the above hypothesis are (1) that large bodied African savanna ungulates should have larger species geographic ranges than smaller-bodied species, and (2) that the body size frequency distribution of species within a large and mainly savanna-adapted taxonomic group of African ungulates, such as the antelopes, should be biased towards more species in the smaller size classes. This would be due to the greater probability of allopatry associated with habitat specialization in an environment that is spatially heterogeneous, or patchy, at the ungulate habitat scale.

Scaling of species geographical range

We plotted the geographical ranges of ungulate species ($n = 74$) endemic to the African continent and occurring in forest, savanna, desert biomes using the distribution maps of Dorst and Dandelot (1970), Smithers (1983), and East (1988, 1989, 1990). Range areas were measured with planimetry. Body mass estimates of adult females for each species were extracted from the above sources as well as Macdonald (1984) and Owen-Smith (1988). A positive relationship between the logarithms of body mass and geographical range was clearly found to apply, as expected, for savanna and desert species (Figure 2) but not for forest species (Figure 3). The hypothesis advanced here is that these results reflect a difference between patterns of habitat use by ungulate species in the African forest biome, which is spatially and temporally relatively homogeneous at the ungulate habitat scale, and the savanna and desert biomes, which are more heterogeneous (Turpie and Crowe 1994).

Large body size will only confer an advantage to ungulates in terms of ability to feed in a wide range of habitats, and hence disperse over larger geographic ranges than smaller species, if there is a wide range of habitats available (du Toit and Owen-Smith 1989). The savanna ecosystems of Africa provide this range of ungulate habitats. The scatter in geographical range sizes among the smaller (< 100 kg) savanna ungulate species (Figure 2) is an artefact resulting from the use (by necessity) of 'crude' distributions to measure range areas. If 'ecological' distributions (i.e. the areas of habitat actually occupied, isolated from the intervening unoccupied habitats) were used then the estimates of range area for the smaller species would be much reduced, resulting in a more linear relationship betweenthe logarithms of species area and body mass.
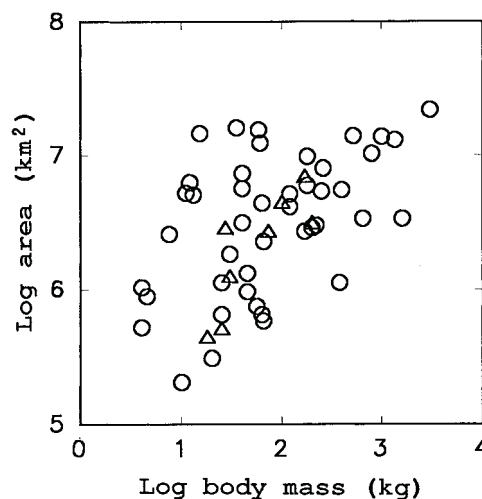

Figure 2. Scaling of species geographical range (area) with body mass for ungulates endemic to African savanna (circles) and desert (triangles) biomes ($r = 0.445$, $n = 52$, $P < 0.001$).
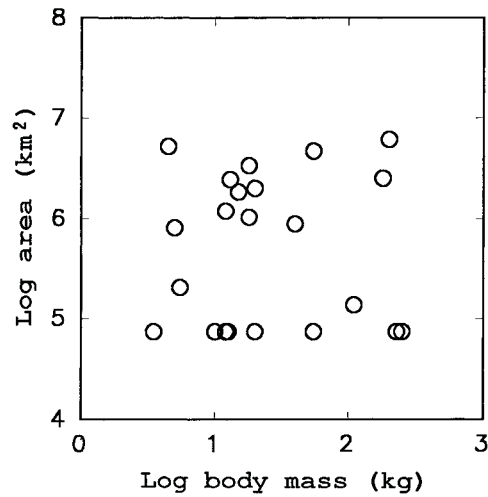
Figure 3. Scaling of species geographical range (area) with body mass for ungulates endemic to the African forest biome (*n* = 22).

The difference between crude and ecological distributions diminishes as body size increases, since the larger species are (or at least were until recently) spread more evenly through the habitats within their ranges.

Size frequency distribution of antelope species

For African antelopes the frequency distribution of species body masses (Figure 4) is highly modal and skewed, revealing a predominance of speciesin the lower half of the
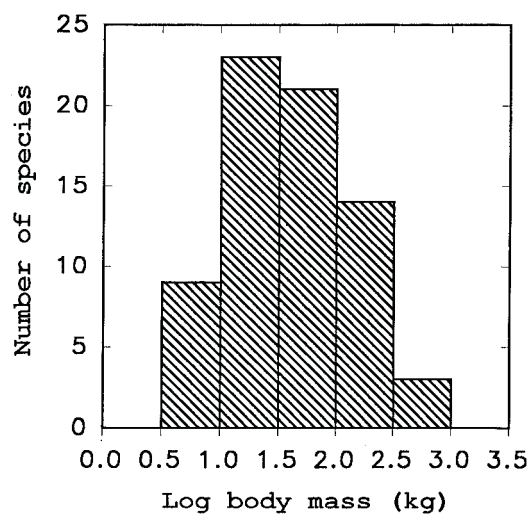

Figure 4. Size frequency distribution of African antelope species (*n* = 70) with size classes expressed in body mass on a $\log_{10}$ scale.

body mass range. This conforms with the pattern that generally applies, with some variations, across taxa at regional, continental and global scales (Caughley 1987; Blackburn and Gaston 1994). Nevertheless from Brown and Nicoletto's (1991) data-set for North American land mammals the shape of the distribution varies between biomes and is flattest in those biomes (e.g. prairie and taiga) that are relatively mono-tonous at the spatial scale of mammalian habitats. Conversely, the patchy distri-bution of ungulate habitats across African savanna landscapes is associated with frequent species turnover (high beta diversity) among the smaller-bodied ungulates. An apparent anomaly among African antelopes is the radiation of the duikers (Genus *Cephalophus*), which are small forest species. This can, however, be explained by Vrba's (1992) 'habitat hypothesis'. Cyclical climatic changes resulted in periodic expansions and contractions of the forest biome, and hence significant back-and-forth geographic movements of the forest/savanna ecotone, during the evolution of the present assemblage of African antelopes. Populations of the smaller, more habitat-specific species (such as duikers) would have become isolated in remnant forest fragments in topographically diverse areas within the savanna biome during each retreat of the forest/savanna ecotone. Allopatric speciation could then have occurred during the period (up to 100,000 years) of each 'Milankovitch' climatic cycle (Vrba 1992) before the next advance of the forest/savanna ecotone.

Significance of evolutionary links

The purpose of the above evolutionary case-study to the thrust of this paper is to illustrate that the unique diversity of the African ungulate fauna is directly linked to a salient feature of African savanna biodiversity, which is high spatial heterogeneity, or patchiness, at the ungulate habitat scale. Indeed, the degree of heterogeneity in vegetation types (= ungulate habitat types) accounts for a statistically significant proportion of the regional variation in ungulate diversity (and consequently large carnivore diversity) across the African continent (Turpie and Crowe 1994).

The heterogeneity in the plant component of African savanna ecosystems is de-rived from two sources. Firstly, plant species richness in the savannas approaches that of the equatorial rainforests with an average aerial density (species per $10,000 \, \text{km}^2$) of about 1750 species for savannas and 2020 species for rainforests (Menaut 1983). The core of the African savanna biome, in terms of plant species richness, is the Somalia-Maasai region with about 2500 species of which 50% are endemics, representing what is probably the world's richest grassland zone (World Conservation Monitoring Centre, 1992). Secondly, the spatial and temporal patterning of savanna plant species and communities in a vegetation mosaic, across a vast distribution, distinguishes sa-vanna biodiversity in terms of its functional significance for diversity and biomass in animal production (reviewed by du Toit 1995).

Feedback to savanna ecosystem structure

Just as the diversity of the large herbivore fauna is a product of the spatial, temporal and taxonomic diversity of the savanna vegetation, the structure and function of savanna ecosystems are regulated by a multitude of feedback loops from large herbivores to plants. The balance between grass and woody biomass can depend on the densities of elephants (*Loxodonta africana*) impacting on the mature canopy and opening woodlands for invasion by fire (Laws et al. 1975; Owen-Smith 1988; Dublin et al. 1990), giraffes (*Giraffa camelopardalis*), preventing medium-sized trees from growing out of fire-susceptible size classes (Pellew 1983), and/or small ruminants like impala (*Aepyceros melampus*) and steenbok (*Raphicerus campestris*) constraining tree recruitment through browsing on seedlings and saplings (Belsky 1984; du Toit 1990a). Perturbations of the large herbivore fauna, such as by panzootics, can result in dramatic changes in savanna vegetation that may persist in alternative stable states, or else in disequilibrium, for decades (Dublin 1995; Sinclair 1995). Evidence includes apparent anomalies like even-aged (and now senescing) stands of *Acacia* trees at various locations in eastern and southern Africa, which trace back to pulses of seedling establishment when browsing ruminants were decimated by rinderpest a century ago (Walker 1989; Prins and van der Jeugd 1993). Conversely, local eruptions of grazing ungulate populations, triggered by predator release or water provisioning, can weaken the grass layer to the advantage of herbivory-adapted woody plants (e.g. *Dichrostachys* and *Acacia* spp.) leading to bush encroachment (reviewed by O'Connor 1985).

Hence the large herbivore component of a savanna ecosystem, by virtue of the balance between grazer and browser metabolic biomass and the distribution of species body sizes within each guild, is an important regulator of the proportions of primary production contributed by the woody and herbaceous components of the system. Further complexity is added by mixed feeders, like impala, which oscillate seasonally between browsing and grazing guilds, and fire, which interacts strongly with herbivory. Additional herbivore-plant feedback loops include the dispersal by browsing ungulates of seeds (Coe and Coe 1987; Miller 1994) and probably pollen (du Toit 1990b) of certain savanna trees, mainly *Acacia* spp. In each case, interactions between the plant and ungulate species involved are fairly specific.

Feedback to savanna ecosystem function

At a more complex level savanna nutrient cycling and plant nutrition are intricately linked with, and mediated by, large herbivores. These linkages have been best elucidated for grazing systems, especially that of the Serengeti (McNaughton 1985; McNaughton et al. 1988). Grazing herds continually convert grass into dung, urine and carrion, all of which release their nutrients quickly back through the decom-

position subsystem to the plant-available nutrient pool. Nutrient uptake by grasses is stimulated by grazing (McNaughton and Chapin 1985) and so the result is a fast, tight nutrient cycle close to the soil surface. The grazing guild is essential to the maintenance of nutrient cycling in savanna grazing systems, since unless nutrients are cycled quickly in the growing season (which is also the wet season) they will steadily leach away from the rhizosphere (Botkin et al. 1981). Such cycles are particularly well developed in patches, or grazing lawns (McNaughton 1984), where concentrated grazing maintains a high productivity of high quality vegetation. The spatial distribution of grazing lawns also contributes to structural diversity in grasslands, with the edges of the lawns often being quite pronounced. Examples include the scatter of finely grazed lawns maintained by white rhinos (*Ceratotherium simum*) within medium to tall grassland, especially around termitaria (Owen-Smith 1988), and by hippos (*Hippopotamus amphibius*) near the shores of major rivers and lakes (O'Connor and Campbell 1984).

The influence of the browsing guild on savanna nutrient cycles is much less understood and is likely to be more complex due to the involvement of plant secondary compounds, which are prevalent in woody plants (Bryant et al. 1991). Nevertheless, interactions between browsers (giraffe and impala in combination) and *Acacia* trees are broadly analogous to those between grazers and grazing lawns (du Toit et al. 1990). Also, preliminary evidence from a southern African savanna on Kalahari sands indicates that browsing by elephants may accelerate nutrient cycling through the woody component of the ecosystem (du Toit, Bryant and Ruess, unpub. data). Removal of elephants with their key megaherbivore effect (Owen-Smith 1988) and artificial inflation of the selective feeding component of the browsing guild (i.e. with goats) could, in theory, significantly reduce rates of nutrient cycling through the browsing system (Pastor et al. 1988; Bryant et al. 1991).

There are weaknesses in our understanding and quantification of processes operating through soils, plants, grazing and browsing herbivore guilds and decomposers in African savanna ecosystems. An important point, however, is that while many of these savanna processes might equally be facilitated by domestic herbivores, there are certainly examples where this could not apply. These include the grazing succession of the Serengeti (Vesey Fitzgerald 1960; Bell 1971), the megaherbivore effect of elephants (Owen-Smith 1988), *Acacia* pruning by giraffes (Pellew 1983; du Toit et al. 1990) and the creation of discrete grazing lawns by white rhinos (Owen-Smith 1988). Most indigenous large herbivore communities in African savannas are dominated by four or five large species (together contributing up to 95% of total biomass; Cumming 1982), which are most susceptible to hunting (Figure 5) and least matched for substitution by domesticated species. Also, a high diversity of large herbivores and their predators, by virtue of their very presence and actions, maintains an even higher diversity of niches for other species, both vertebrate (e.g. birds) and invertebrate (especially detritivores). Consequently we can predict for African savannas that a substantial reduction in large herbivore diversity will feed back to substantial and
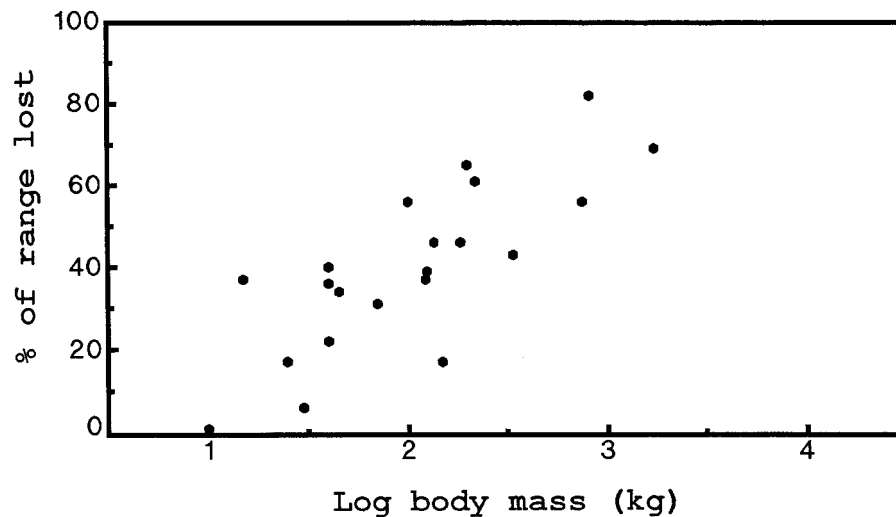
Figure 5. Percentage of ungulate species range lost over historical time in East Africa, plotted against species body mass (data from Parker 1989).

long-term changes in ecosystem structure and function as well as a cascading decline in savanna biodiversity.

Impacts of pastoralism on African savanna biodiversity

Only a couple of large herbivore species have become extinct in Africa in historical times, and these (the quagga, *Equus quagga*, and the blue antelope, *Hippotragus leucophaeus*) had small distributions that were peripheral to the savanna biome. There have, however, been drastic reductions in geographical distribution (Figure 5), population size and genetic diversity among large herbivore species throughout the African savannas. The eruption of human populations (Figure 6) is obviously the root cause. A direct impact on animal communities was the replacement of indigenous herbivore biomass with domestic livestock, largely with the assistance of programmes for the eradication of tsetse flies (*Glossina* spp.), which were (and still are) mostly foreign-funded and of questionable development value (Matzke 1983). A direct impact on savanna vegetation and soils was the loss of spatial heterogeneity and plant cover, with land transformation occurring through subsistence cropping and desertification.

Interventions to ameliorate habitat conditions for livestock

The shift from wildlife to livestock has resulted in dramatic imbalances in standing crop biomass (Figure 7), and in some cases inflation of livestock metabolic biomass
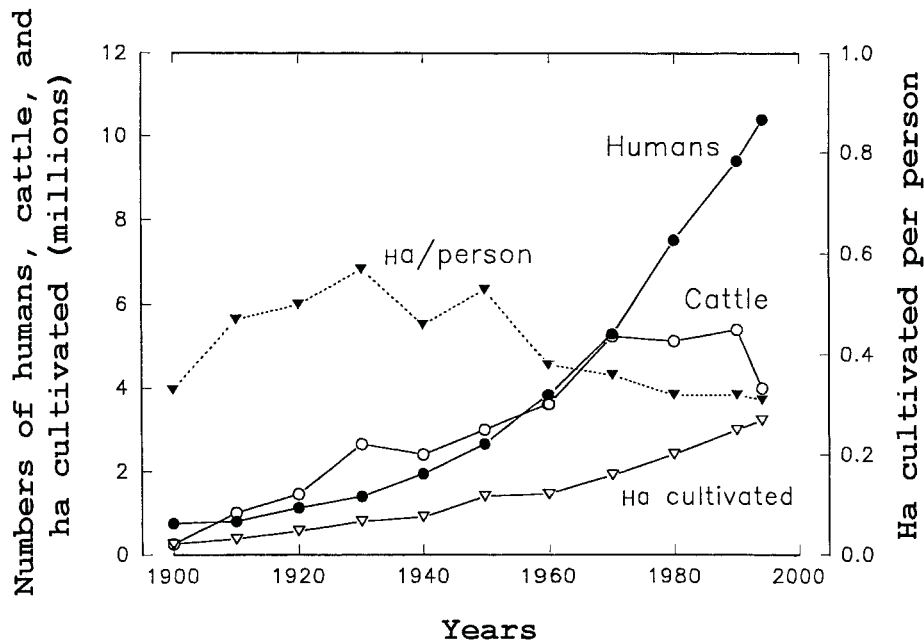
Figure 6. Human population growth and associated changes in cattle and cultivated land in Zimbabwe during this century (from Cumming 1994).

well above that predicted for wildlife. This has been achieved through interventions to ameliorate savanna habitats for livestock (see also Oesterheld et al. 1992). The average metabolic biomass density of cattle across tsetse-free regions of Africa is about triple that of buffalo (*Syncerus caffer*) or any other indigenous grazing ruminant species in protected ecosystems, which means that cattle are using more of available habitats than their indigenous counterparts would (Owen-Smith and Cumming 1993). Apart from controlling predators and pathogens the major intervention has been artificial provisioning of water (boreholes, dams, wells, etc.), resulting in reduced seasonal variation and increased spatial distribution of surface water availability. The standard strategy of extensive livestock management is to maximize the proporiton of available rangeland that is accessible to livestock, which is effectively to reduce rangeland heterogeneity under a herbivory regime of high biomass and low diversity. This is clearly an ecological mismatch when viewed against the evolutionary background of large herbivores and vegetation in African savannas.

Overstocking

Impacts of livestock management on savanna rangelands vary depending on stocking rate and its interactions with rainfall regime, soil properties, topography, and the occurrence of stochastic and extreme events such as drought (Walker 1993).
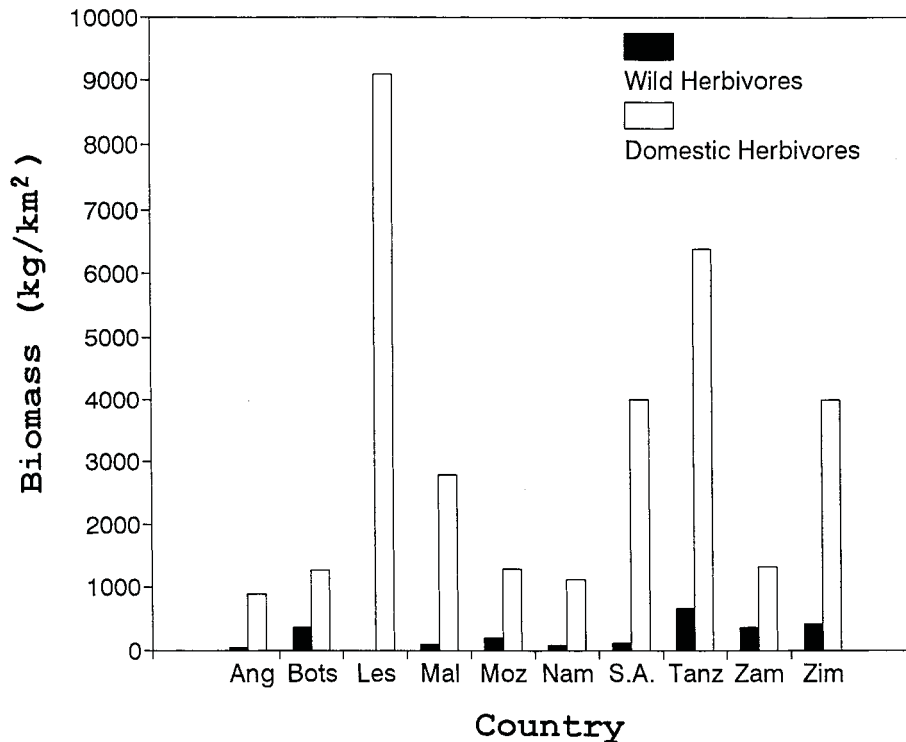
Figure 7. Standing crop biomass of wild and domestic herbivores in southern African countries (from left: Angola, Botswana, Lesotho, Malawi, Mozambique, Namibia, South Africa, Tanzania, Zambia, Zimbabwe). Reproduced with permission from WWF.

Such complexity evades the meaningful application of blanket national policies to match stocking rates with rangeland carrying capacities, and fuels debate about links between livestock and rangeland degradation (e.g. Abel and Blaikie 1989). Nevertheless, heavily grazed rangelands do exhibit symptoms of progressive degradation (reviewed by Skarpe 1991; Milton et al. 1994). These include spiralling demographic trends among perennial grass species (O'Connor 1991), increases in spinescent and chemically defended woody species, increases in frequency and area of denuded soil patches and piospheres around waterpoints (Andrew 1988), increased runoff and reduced rain-use efficiency. After reviewing 126 field experiments on the grass layer in southern African savannas, O'Connor (1985) concluded that grazing (and fire, where fuel loads permit) exaggerates the effects of rainfall variability by indirectly reducing the availability of soil moisture to grass roots. This applies particularly in the drier savannas and on the heavier textured soils. Negative feedback to livestock productivity was investigated by Dean and MacDonald (1994), who analyzed a long-term data-set (1911–1981) on commercial livestock production in arid and semi-arid karoo and savanna ecotone districts in South Africa. They found consistent declines

in stocking rates in the latter part of that period, which were unrelated to market forces or state policies, but instead indicated a progressive decline in the secondary productivity of those rangelands.

The proximate cause of rangeland degradation in African savannas is essentially an ecologically unrealistic concentration of metabolic biomass lumped into one species in each large herbivore guild (cattle and goats) and distributed more widely across habitats (by water provisioning) than would occur in indigenous herbivore communities. The ultimate cause is human perception, by which stocking rates achieved in a series of above-average rainfall years are upheld by pastoralists as 'good' and 'right' for that system. Water provisioning extends grazing pressure into areas not previously accessible from natural water sources. Then when droughts occur, population crashes of both livestock and wildlife are steeper and deeper than in unmanaged systems due to attrition of 'reserve' grazing areas (Walker et al. 1987). Grassland biodiversity is periodically knocked back by rare and extreme droughts even in the absence of heavy grazing (Tilman and El Haddi 1992). When coupled with artificially elevated grazing and trampling and reduced 'reserve' areas, which are also important in maintaining source-sink seed flows, we can expect – despite a dearth of research results at present – that the combined impacts on the herbaceous component of savanna biodiversity will be severe and cumulative. This expectation is reinforced by the currently accepted scenarios of global climate change, which for African savannas portray an increased frequency of extreme droughts (Allen-Diaz 1996).

Savanna states and transitions

Throughout the world's rangelands the problem of degradation and declining productivity has caused range scientists to reconsider the principles by which rangelands are assumed to respond to, and recover from, overgrazing and drought. There is now a growing acceptance that rangelands will not always return to some pristine 'climax' state if destocked and allowed to rest, but could remain locked in one of a number of possible states even if the original agent of disturbance (e.g. overgrazing) is removed (Westoby et al. 1989; Walker 1993). The obvious implication of this for African savanna biodiversity is that even with massive injections of foreign aid for environmental mitigation and improved animal husbandry, we cannot expect the impact of pastoralism to be absorbed within the human time-frame.

Implications for development and conservation

On a continental scale the overbearing conservation problem in African savannas is the ever-increasing human demand for resources (see Figure 6). There is a widespread and irreversible replacement of nomadic pastoral systems with sedentary agro-
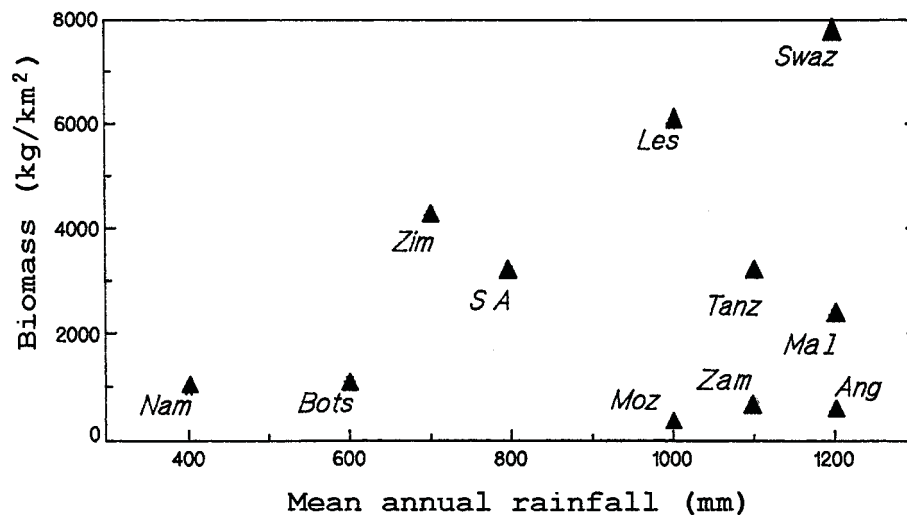
Figure 8. Biomass of livestock plotted against mean annual rainfall for southern African countries. The countries are the same as in Figure 7, with the inclusion of Swaziland (Swaz). Reproduced with permission from WWF.

pastoral systems (Young and Solbrig 1993). Rangelands are being eaten into by cultivation and stocking rates are being maximized on non-arable land. Nevertheless, there are extensive areas in African savannas, mainly in the more mesic regions, where livestock biomass is still well below potential levels (Figure 8) due largely to the persistence of tsetse flies. In semi-arid savannas the livestock potential is stretched to the limit in most areas but cannot meet human needs for protein since there are already more people than there are livestock units. There is thus a real need for animal production systems to diversify to increase returns and at the same time to halt, and hopefully reverse to some extent, the erosion of biodiversity in African savannas. This requires African governments and NGOs to promote multispecies animal production systems that incorporate sustainable wildlife utilization.

Livestock species outperform indigenous ungulates in converting forage into animal protein (meat, milk, blood) and traction. This reality dampened early hopes of bountiful meat production from wildlife (e.g. Huxley 1961). However, in Botswana for example, over 50 species of wild animal provide an average of 90 kg of protein per person per year (Stuart and Adams 1990). Taking into account the economic value of wildlife and its products (meat, hides, curios, hunting and photographic safaris) when utilized to its full sustainable potential, annual returns from wildlife in parts of Mozambique could reach US$ 1000 per household (Cumming 1994). The challenge to progressive conservation and development agencies is to achieve the national and regional political and institutional reforms and incentives to allow rural people to realize the full benefits of wildlife utilization as an adjunct or alternative to livestock production. This involves altering a pervasive mindset – that livestock

production should dominate landuse in semi-arid (non-arable) areas as a pre-requisite for economic development. This mindset is manifest in what McNeely (1993) calls 'perverse incentives', which include government subsidies to elevate national cattle herds (e.g. in Botswana) without due consideration of social equity and environmental cost.

Considerable progress has nevertheless been achieved in some southern African countries (Zimbabwe, South Africa, Namibia) where shifts in the international market forces governing beef exports and wildlife enterprises, combined with a series of extreme droughts and easing of regional political tensions, have seen the emergence of a trend towards multispecies animal production systems involving wildlife. Various indigenous large herbivores (including megaherbivores) have been reintroduced to parts of their former range, while managers of protected wildlife areas are starting to involve neighbouring human communities in integrated wildlife utilization schemes. At present 17% of the SADC region is under some form of wildlife utilization and there is potential for this to extend, as an economically viable and sustainable landuse, to over 30% of the region (Cumming 1994).

The use-it-or-lose-it principle (Janzen 1992) of biodiversity is the only hope for stemming the tide of biodiversity erosion in African savannas. On a continental scale the unrelenting problem of human population growth outpacing the growth of national economies provides a reality check on how much can be achieved on average. But with cooperation between international conservation and development agencies on the one hand, and African government agencies, NGOs and local communities on the other, specific areas can be identified as having high existing potential for the integration of sustainable wildlife utilization into regional landuse planning (see Cumming 1993). This approach has every ingredient for success, especially if it includes a fully interdisciplinary commitment to applied research, extension and monitoring at the interface between human needs and the supply of resources and services from savanna ecosystems.

Acknowledgements

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