



University of Kentucky
UKnowledge

International Grassland Congress Proceedings

XX International Grassland Congress

Working Within Constraints: Managing African Savannas for Animal Production and Biodiversity

J. T. du Toit
Utah State University

Follow this and additional works at: <https://uknowledge.uky.edu/igc>



Part of the [Agricultural Science Commons](#), [Agronomy and Crop Sciences Commons](#), [Plant Biology Commons](#), [Plant Pathology Commons](#), [Soil Science Commons](#), and the [Weed Science Commons](#)

This document is available at <https://uknowledge.uky.edu/igc/20/satellitesymposium3/12>

The XX International Grassland Congress took place in Ireland and the UK in June-July 2005.

The main congress took place in Dublin from 26 June to 1 July and was followed by post congress satellite workshops in Aberystwyth, Belfast, Cork, Glasgow and Oxford. The meeting was hosted by the Irish Grassland Association and the British Grassland Society.

Proceedings Editor: D. A. McGilloway

Publisher: Wageningen Academic Publishers, The Netherlands

© Wageningen Academic Publishers, The Netherlands, 2005

The copyright holder has granted the permission for posting the proceedings here.

This Event is brought to you for free and open access by the Plant and Soil Sciences at UKnowledge. It has been accepted for inclusion in International Grassland Congress Proceedings by an authorized administrator of UKnowledge. For more information, please contact UKnowledge@lsv.uky.edu.

Working within constraints: managing African savannas for animal production and biodiversity

J.T. du Toit

*Department of Forest, Range and Wildlife Sciences, Utah State University, UT 84322, USA,
E-mail: jtdutoit@zoology.up.ac.za*

Abstract

The mean density of livestock biomass on African rangelands now greatly exceeds that of indigenous large herbivores, although livestock cannot fully substitute for wildlife with respect to co-evolved ecosystem processes involving herbivory. The dominance of livestock in semi-arid rangelands is largely due to water provision, which uncouples livestock population dynamics from the rainfall-driven trajectories followed by indigenous ungulate species in wildlife areas. Ecological sustainability cannot be achieved with a few exotic species maintained at unprecedented biomass densities in savanna ecosystems, which are evolutionarily adapted for species-rich communities of ungulates of a wide range of sizes. Integrating wildlife and livestock in multi-species animal production systems offers a partial solution. Community-based ecotourism can effectively augment pastoralism in semi-arid rangelands but, as rainfall increases, the opportunity costs become too high. Direct payment approaches show promise for offsetting opportunity costs, although major obstacles remain in the form of political corruption and obstructive practices by national governments.

Keywords: rangeland ecology, pastoral systems, tropical conservation, livestock-wildlife interface

Introduction

African pastoralists maintain a tenacious hold on their livestock traditions despite the ravages of droughts, parasites, infectious diseases and predators. With the human population of Africa (presently ~885 million people, of which ~65% conduct rural livelihoods) growing at the world-leading rate of 2.4% per annum (PRB, 2004), it is inevitable that livestock pressure on rangelands must increase even further. Across the pastoral lands of the African savanna biome and its arid ecotones, livestock species already dominate the standing crop of ungulate biomass. In southern African countries the average national ratio of biomass of domestic herbivores:wild herbivores is in excess of 6:1, while the regional ratio of cattle:elephant biomass is about 16:1 (Cumming & Cumming, 2003). The high value of this ratio cannot be simply explained by over-hunting of indigenous species, and is remarkable given that domestic herbivores were introduced to the Horn of Africa some 8,000 years ago and reached southern Africa only about 2,000 years ago (Denbow & Wilmsen, 1986). Without the advantages of ecosystem-specific evolutionary adaptations, as have accumulated in Africa's diverse indigenous ungulate fauna, how did a few introduced livestock species achieve such dominance? Or is this dominance unstable? And what is the future for African rangelands that are becoming increasingly marginal for pastoralism due to combinations of overstocking and global change? These are the main questions that are addressed in this chapter, in which it is also suggested how some current trends in the science and management of tropical conservation might show promise for securing the natural capital of Africa's rangelands as well as the livelihoods of its pastoralists.

Overview of the problem

Subsistence pastoralists in the semi-arid regions of Africa include the world's poorest and most politically marginalized people, who strive to improve their livelihoods under conditions of extreme uncertainty. Widespread and continuous risks of war, forced displacement, social upheaval and institutional, and economic, collapse are compounded by illiteracy, pandemic diseases (especially malaria and AIDS) and climatic unpredictability. Under such conditions it is impossible for pastoralists to adopt the long-term view espoused by advocates of 'sustainable development'. It is also very difficult for aid agencies from the developed world to achieve incremental progress with the management of rangeland ecosystems in such countries because of political corruption and the disintegration of formal structures of governance. Ironically, at present, tropical countries typically have inherently high levels of biodiversity but low governance scores, and indicators of conservation success (or failure) are correlated with national governance scores (Smith *et al.*, 2004). Pastoral systems in African countries will thus continue to lose natural capital as long as pastoralists subsist without the self-organizing institutional structures needed for effective environmental management (du Toit *et al.*, 2004).

Nevertheless, the long-term implications of biodiversity loss have little direct relevance to most subsistence pastoralists in Africa (for reasons already outlined), who are understandably more concerned with how many of their animals they can bring through each drought period. In that respect they are astoundingly successful, to the extent that Oesterheld *et al.* (1992) suggested that extensive pastoral management in African savannas has achieved a similar effect to that in South America, where animal husbandry has increased the overall herbivore carrying capacity of the system at a regional scale. After detailed analysis, however, Fritz & Duncan (1994) refuted this for African savannas where indigenous large herbivore assemblages include mega-herbivores (i.e. with a body mass >1000 kg), which cannot be fully substituted by cattle (Fritz *et al.*, 2002; du Toit & Fritz, 2003). Nevertheless, considering buffaloes (*Syncerus caffer*) as the indigenous African 'equivalent' of cattle, Owen-Smith & Cumming (1993) compared the average metabolic biomass density attained by buffaloes in large protected areas against that for cattle in regions of Africa free of tsetse flies (*Glossina* spp, vectors of *Trypanosoma* parasites). They found that cattle outweigh buffaloes, and indeed any other single species of indigenous grazing ruminant in a protected savanna ecosystem, by a factor of three. This is mostly as a result of water provision; the component of animal husbandry that has provided the greatest boost to livestock carrying capacity in African pastoral systems.

Water provision

Semi-arid grazing systems exhibit high spatial and temporal variability in animal numbers, and this is because density-dependent resource limitation operates episodically in key resource areas where the accessibility of food is restricted during dry seasons and drought periods (Illius & O'Connor, 1999). The crucial factor here is resource accessibility rather than mean resource abundance across the landscape, since grazing ungulates in the dry season are central-place foragers, having to return regularly to a water source. Foraging radius is determined by energetic relationships involving body size and gait, and indigenous ungulates in the 200-500 kg range of live weight can achieve a dry-season foraging radius of ~20 km (Pennycuik, 1979). For cattle the radius is considerably less due to their comparatively slow gait, which is why semi-arid pastoral systems are characterized by discrete concentrations of livestock occurring in overgrazed and trampled piospheres around water points. If, however,

through the construction of dams, wells and boreholes, the mean nearest neighbour distance among water points can be reduced to ~30 km, then virtually all of the standing crop of dry season forage in the landscape becomes accessible to cattle. Given the dependence of animal numbers on dry season food resources in semi-arid pastoral systems (Illius & O'Connor, 1999), it follows that a dramatic increase in the accessibility of these resources will result in a similarly dramatic increase in animal numbers. While pastoralists and politicians celebrate this result, and international development agencies maintain a penchant for introducing water-points, because *inter alia* they are tangible, popular, quick to construct and convenient for media exposure, the long-term ecological implications of a hyper-inflated grazer biomass require more serious thought.

Comparative studies on the processes, by which extensive subsistence pastoralism influences rangeland dynamics, are remarkably scarce, and there is a particular need for controlled experimentation. For example, the ways in which an African savanna landscape changes through time under a regime of subsistence pastoralism should be compared with a set of “control” landscapes with similar vegetation, soils and rainfall but with intact indigenous herbivore communities. From the few comparative studies conducted so far, it appears that the single most important finding concerns the use of groundwater as drinking water, which profoundly influences the dynamics of the plant-herbivore interaction. Walker *et al.* (1987) analyzed demographic data for a range of indigenous large herbivore species in relation to a severe and extended drought in southern Africa during 1982-1984. They found that, although the drought caused widespread declines in wildlife populations, these were particularly catastrophic (80-90% in extreme cases) for grazing ungulates in wildlife areas that had the most closely spaced artificial water points, e.g. Klaserie in South Africa and Tuli in Botswana. In areas where permanent water was more dispersed, e.g. Kruger in South Africa, or where managers had heavily culled the pre-drought populations, e.g. Umfolozi in South Africa, the demographic responses to the drought were much less pronounced. The implication is that where the mean nearest-neighbour distance between water points is artificially reduced, the accessibility to key resources is greatly increased in pre-drought conditions. This causes depletion of “reserve” grazing areas, which lie beyond the normal foraging radius and are not heavily grazed but can be accessed by very hungry animals. If pre-drought grazer densities are allowed to increase in response to the increased accessibility of key resources, then the population crashes caused by droughts are much steeper and deeper than in rangelands with more widely dispersed water points.

Another important finding from Chivi in Zimbabwe was that the number of cattle owned per village in semi-arid communal lands varies widely from decade to decade in response to the cumulative departure of annual rainfall figures from the long-term mean (Sayer & Campbell, 2004). Changes in cumulative rainfall control groundwater, which is abstracted through wells and boreholes at water points, and the collapse of Chivi cattle herds in the 1990s was attributed to water-point failure following a prolonged rainfall deficit from 1981 to 1992. In wildlife areas (e.g. Kruger) it is also apparent that indigenous grazing ungulate populations decline in response to long-term rainfall deficits (Owen-Smith & Ogutu, 2003), but the controlling factor there is availability of green grass in the dry season rather than access to drinking water (Dunham *et al.*, 2004).

Water provision in semi-arid African rangelands has the effect of uncoupling livestock population dynamics from the rainfall-driven trajectories followed by indigenous ungulate populations. In a run of normal or wet years the artificial dispersion of water points allows livestock biomass density to exceed that expected from an indigenous wildlife community.

But during droughts the livestock numbers crash due to both the depletion of “reserve” areas of key resources and the drying of water points, which causes an exponential decline in the accessible food supply. Recovery of livestock herds to pre-drought sizes is slow because the extent of each population crash can be staggering: in Chivi the cattle population in 1993 was just one quarter of what it had been three years earlier (based on data in Sayer & Campbell, 2004). Furthermore, the return of herds to their former grazing areas depends on the resurrection of water points and therefore on the rate of groundwater recharge, but groundwater profiles are ultimately determined by the underlying geology, so recovery time differs widely from one water point to the next. Finally, catchment hydrology can be altered during droughts by changes in land cover, causing unfavorable changes in *inter alia* runoff, infiltration and river sedimentation. The net effect is that livestock numbers in semi-arid pastoral systems tend to oscillate more widely and less predictably than for wildlife in conserved systems. It comes as no surprise, therefore, that in a retrospective analysis of an 11-year data set from Namibia, Burke (2004a) found no statistical relationships between livestock numbers and either annual rainfall or water-point numbers. Quite simply, livestock numbers cannot increase in direct response to rainfall at the end of a dry spell, and counting water points on a map is meaningless without detailed records of which water points were functional over what periods. Moreover, the relationship between livestock density and water point density asymptotes when the mean nearest-neighbour distance (D) between functioning water points is less than twice the foraging radius (R) of the dominant livestock species (i.e. when $D < 2R$).

Ecosystem effects

African savannas are especially heterogeneous at the ungulate habitat scale, and the uniquely high diversity of African ungulates is directly linked to vegetation heterogeneity across multiple spatial and temporal scales (du Toit & Cumming, 1999). The regime of natural herbivory is thus patchily distributed, the species-rich community of indigenous large herbivores (typically ~30 species in any one ecosystem) represents a body size range that spans three orders of magnitude (<10 kg to >1,000 kg), and it includes two main trophic guilds (grazers and browsers), each with a diverse set of co-evolved herbivore-plant interactions: for reviews, see McNaughton & Georgiadis (1986) and du Toit (2003). In sharp contrast, the strategy of extensive livestock production is to remove indigenous large herbivores, and, through water provision, maximize the proportion of rangeland available to livestock, thereby imposing a herbivory regime of high biomass and low diversity (<5 species in any one system). By effectively reducing the heterogeneity of a semi-arid ecosystem in this way, and substituting the indigenous herbivore community for an ecologically mismatched assemblage of livestock, it is inevitable that rangeland degradation will follow, i.e. reduced production of ecological goods and services: see Illius & O'Connor (1999) for a discussion on the definition of rangeland degradation.

To begin with, there are some purely physical implications associated with eradicating a diverse and size-structured indigenous ungulate community and substituting it with a livestock assemblage of much lower species diversity. Across ungulate species of increasing body mass (M), hoof area increases in direct proportion with body mass (αM^1) but stride length increases more gradually ($\alpha M^{0.26}$), which means that in each step taken a cow exerts the same pressure per cm^2 of soil as a gazelle, but in walking the same distance the cow causes greater soil compaction than the gazelle (Cumming & Cumming, 2003). For semi-arid rangelands, the implications become apparent if herbivore biomass density is held constant and the trampling impact of a pastoral system against that of an indigenous wildlife

community is compared. Cattle typically dominate pastoral systems in southern and eastern Africa, while indigenous communities are typically comprised of numerous species of differing size of which only some are water-dependent. The pastoral system has a far greater impact on the soil, not only because of the greater trampling impact per unit animal biomass, but also the extremely high trampling intensity along stock trails that radiate from water points. Trampling causes soil compaction, which impedes water infiltration and seed germination, and some stock trails become the erosion gullies that characterize degraded rangelands.

From the perspective of a savanna ecosystem, removing the indigenous assemblage of large herbivore species implies the termination of multiple co-evolved interactions, especially with indigenous plant species. Some of these interactions, involving seed dispersal, nutrient cycling, mediation of inter-specific plant competition and maintenance of vegetation structure, are taken over by livestock species, which become surrogates for their indigenous counterparts, but the extent to which this occurs requires investigation. It is likely that the greatest losses of co-evolved interactions occur at the extremes of the body size range, with the functional properties of small habitat-specific antelopes from the tribes Antilopini and Neotragini, and mega-herbivores, i.e. hippopotamus, rhinoceros, elephant and giraffe, being particularly non-substitutable (du Toit & Cumming, 1999). Empirical evidence from African savannas on the ecosystem-level effects of the switch from wildlife to cattle is still scarce and equivocal (Richardson-Kageler, 2003). Nevertheless, evidence from rangelands on other continents, e.g. Australia, indicates an association between the introduction of livestock and the local extinction of certain plant species, some of which have functional properties of importance for maintaining ecosystem resilience (Walker *et al.*, 1999).

Global change and unpredictability

Subsistence pastoralists in African savannas depend on traditional knowledge for maintaining their herds but the world is changing faster than traditional knowledge can adapt. Scientific knowledge is not, however, filling the gaps, mainly because of the challenges of maintaining an effective extension service in rural Africa. Furthermore, while scientists seem fairly confident in predicting that global warming will increase the frequency and severity of droughts in African rangelands, there are many other changes that are expected, yet cannot be predicted. For example, the rising atmospheric concentration of CO₂ is expected to influence rangeland plants to the extent that changes should occur in the quantity and quality of food available to livestock. Higher C: N ratios are expected in foliage with increased concentrations of structural tissues and C-based secondary chemicals, which reduce plant digestibility and palatability for large herbivores. Indeed, from experimental studies it is clear that C: N ratios do generally become elevated in plants growing in the CO₂ concentrations predicted for future scenarios but allocations of C to structural tissue and secondary chemistry are unpredictable (Diaz *et al.*, 1998; Penuelas & Estiarte, 1998). It thus remains unclear how such responses might influence large herbivores and translate into ecosystem-level effects at larger spatial and temporal scales.

The inherent problem of unpredictability in African rangelands is likely to become exacerbated by the globalisation of trade, which can exert powerful and unexpected forces on local markets. In this respect a lesson for African savannas can be learned from another biome - the rainforests of West Africa. There the human population uses fish as a primary source of protein, but European fishing fleets operating off the West African coast have reduced oceanic fish stocks and at the same time developed a local dependence on the fishing

industry for food and jobs. Brashares *et al.* (2004) have shown that, with a dramatic decline in the availability of fish in local markets in Ghana, alternative protein sources from animal production are inadequate to meet demands because the dependence on fish had obstructed the development of a local self-organising livestock industry. The protein deficit is now being made up by bush meat, which is extracted from the forest in alarmingly unsustainable quantities. In this example, the global market for one protein source, fish, have prevented, and then unexpectedly presented, opportunities for the local markets of livestock, as a sustainable protein source, at a scale of demand that cannot be met. The price is now being paid, locally, in biodiversity.

In another example, subsistence pastoralists have seized an opportunity presented by the globalization of trade but ironically the outcome of that is also a reduction in natural capital. With the current boom in global markets of organically-grown coffee, pastoralists in and around the village of Hangala, in southern India, are exporting cow dung for use as manure on coffee plantations. This lucrative source of income has caused pastoralists to increase their herds and make greater use of their grazing rights in the adjacent Bandipur National Park, but the intensified herbivory and almost complete removal of dung is posing a serious threat to ecosystem function (Madhusudan, 2005). In short, the preferences of coffee-buying people in the developed world have caused a traditional subsistence pastoral system in India to 'flip' into a commercial nutrient-mining operation of a scale that was completely unexpected by local conservation authorities. A similar transition could occur in pastoral systems within trading distance of the coffee-producing regions of East Africa.

Ways forward?

The preceding review begs two obvious questions. Firstly, are subsistence pastoral systems, as influenced by human population growth, poverty, weak institutional structures, socio-political instability and globalisation, driving the communal rangelands of Africa into scenarios of irretrievable degradation? Secondly, have any new approaches emerged to improve the effectiveness of conservation funds that filter through the hierarchies of international development agencies and non-government organisations, African national governments and traditional pastoral communities? The first question is left for future environmental historians to answer but an attempt is now made at answering the second question. In doing so, it must be pointed out that to prevent any loss of human livelihood options for future generations, a goal of sustainable development, the herbivory regime on African rangelands has to be restored to something resembling the indigenous, naturally selected state. This might be considered idealistic but it is assumed there is adequate interest among decision makers to justify a brief discussion on conserving ecosystem processes while also improving livelihoods in African savannas.

Although animal husbandry can increase livestock biomass densities well above those maintained by any indigenous bovids in conserved ecosystems (Owen-Smith & Cumming, 1993), the advantages of an intact wildlife community, that includes mega-herbivores, will generally outweigh those of any livestock assemblage in the same ecosystem (du Toit & Fritz, 2003). This applies particularly in moist-dystrophic savannas, e.g. in the miombo vegetation type of south-central Africa, where the percentage contribution of elephant biomass to total herbivore biomass reaches ~60% in regions of comparatively low soil nutrient status that receive ~1000 mm of annual rainfall (Fritz *et al.*, 2002). The reason is that the standing crop of plants in such regions is of high abundance but low quality, being fibrous, woody and chemically defended, and elephants, with their voluminous guts and low mass-specific

metabolic demands, tolerate such food better than smaller herbivores can (Bell, 1982). Due to greater efficiency of resource use, therefore, a multi-species animal production system that retains elephants will outperform a livestock-dominated pastoral system in terms of annual meat production per unit area in moist-dystrophic savannas, e.g. in central and north-western Zimbabwe, northern Botswana, western Zambia and eastern Angola. The problem is that subsistence pastoralists cannot manage elephants as they do livestock, and cannot easily harvest and distribute the meat due to logistical constraints and external objections to the killing of elephants. Furthermore, the direct costs of retaining elephants in a settled area, including risks of injury and death to people, damage to crops, granaries and water supplies, adds to the opportunity costs incurred by foregoing land use options that are incompatible with elephants, and these are usually higher than the sustainable elephant-derived benefits that may be relied upon to augment household economies. This problem of managing elephants outside of wildlife reserves exemplifies the general tendency for opportunity costs associated with conserving biodiversity to increase along the arid-to-humid gradient in tropical ecosystems (Burke, 2004b; du Toit, 2004). Quite simply, as rainfall increases so does productivity, and so does the range of opportunities for exploiting it.

In Africa's semi-arid rangelands, however, the opportunity costs associated with retaining wildlife are comparatively low because the alternatives are limited. There is thus considerable scope for developing community-based ecotourism (Kiss, 2004) as an adjunct to pastoralism, and some promising results are emerging from this approach in low-rainfall countries like Namibia (Burke, 2004b). The obvious implication for pastoral systems in rangelands with higher rainfall is that the adoption of a conservation-oriented approach to land use will require financial subsidies to offset the opportunity costs. Deriving these subsidies and channeling them to the communities that need them is a major challenge, especially since political corruption presents a significant obstacle to conservation activities in African countries (Smith *et al.*, 2003). Nevertheless, current thinking within major international funding agencies, such as the World Bank, is tending towards the 'direct payments' approach to funding conservation interventions in developing countries (Ferraro & Kiss, 2002). In principle, direct payments could be provided to semi-arid pastoralists in return for reaching contractually arranged short-term goals, such as destocking village herds, performing reclamation work on erosion gullies, closing water points, removing snares and cutting out alien invading shrubs. In the longer term, negotiated payments in cash or kind could be earned when monitoring surveys detect population increases in key wildlife species, reduced sediment loads in rivers or improved rangeland condition. The financial implications to donors are obviously vast. However, if such payments can indeed be channeled directly to pastoralists living in rangelands of high conservation value, thereby avoiding the costs of corruption and overheads associated with conventionally funded projects that operate through government agencies, then conservation gains per unit cost will be greatly improved.

Conclusions

The livelihoods of Africa's pastoralists depend on the flows of ecosystem goods and services from Africa's rangelands, and so the conservation of savanna ecosystem processes simply has to be the central feature of all major rangeland development interventions. Meat, milk, dung, blood, hides and draught power are all examples of goods and services that rangelands can provide through livestock, while the pastoral lifestyle is a key component of the social-ecological systems of African savannas. However, to achieve a sustainable balance requires an integration of wildlife and livestock management, which in turn requires subsidies in the form of direct payments on a sliding scale based on the opportunity costs associated with

wildlife. Opportunity costs of biodiversity conservation are generally lower in the more arid rangelands, where community-based ecotourism can significantly augment the household economies of traditional pastoralists. In the more humid rangelands, direct payments from global funds are increasingly required for the goals of ecological sustainability to be realistically met. Contractually negotiated direct payments should not be viewed as ‘handouts’, since tropical biodiversity is actually of greater value to the global community than it is to local pastoralists (Balmford & Whitten, 2003). Nevertheless, we cannot delude ourselves over the enormous obstacles presented by political corruption and weak or obstructive governance systems in the countries of which Africa’s pastoralists are citizens. The only way forward is for rangeland ecologists and managers to interact more effectively with economists, sociologists and political scientists to quantify and demonstrate the benefits of sustainable rangelands to everyone, ranging from subsistence pastoralists to government leaders (du Toit *et al.*, 2004).

Acknowledgements

This chapter was written while the author was in the Mammal Research Institute of the University of Pretoria.

References

- Balmford, A. & T. Whitten (2003). Who should pay for tropical conservation, and how should the costs be met? *Oryx*, 37, 238-250.
- Bell, R.H.V. (1982). The effect of soil nutrient availability on community structure in African savannas. In: B.J. Huntley & B.H. Walker (eds) *Ecology of Tropical Savannas*. Springer-Verlag, Berlin, 193-216.
- Brashares, J.S., P. Arcese, M.K. Sam, P.B. Coppolillo, A.R.E. Sinclair & A. Balmford (2004). Bushmeat hunting, wildlife declines, and fish supply in West Africa. *Science*, 306, 1180-1183.
- Burke, A. (2004a). Range management systems in arid Namibia – what can livestock numbers tell us? *Journal of Arid Environments*, 59, 387-408.
- Burke, A. (2004b). Conserving tropical biodiversity: the arid end of the scale. *Trends in Ecology and Evolution*, 19, 225-226.
- Cumming, D.H.M. & G.S. Cumming (2003). Ungulate community structure and ecological processes: body size, hoof area and trampling in African savannas. *Oecologia*, 134, 560-568.
- Denbow, J.R. & E.N. Wilmsen (1986). Advent and cause of pastoralism in the Kalahari. *Science*, 234, 1509-1515.
- Diaz, S., L.H. Fraser, J.P. Grime & V. Falczuk (1998). The impact of elevated CO₂ on plant-herbivore interactions: experimental evidence of moderating effects at the community level. *Oecologia*, 117, 177-186.
- Dunham, K.M., E.F. Robertson & C.C. Grant (2004). Rainfall and the decline of a rare antelope, the tsessebe (*Damaliscus lunatus lunatus*), in Kruger National Park, South Africa. *Biological Conservation*, 117, 83-94.
- du Toit, J.T. (2003). Large herbivores and savanna heterogeneity. In: J.T. du Toit, K.H. Rogers & H.C. Biggs (eds) *The Kruger experience: ecology and management of savanna heterogeneity*. Island Press, Washington, DC, 292-309.
- du Toit, J.T. (2004). Response to Burke. Conserving tropical biodiversity: the arid end of the scale. *Trends in Ecology and Evolution*, 19, 226.
- du Toit, J.T. & D.H.M. Cumming (1999). Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism. *Biodiversity and Conservation*, 8, 1643-1661.
- du Toit, J.T. & H. Fritz (2003). Size matters: body size diversity and resource use efficiency in ungulate guilds. In: N. Allsopp, A.R. Palmer, S.J. Milton, K.P. Kirkman, G.I.H. Kerley, C.R. Hurt & C.J. Brown (eds) *Proceedings of the VIIth International Rangelands Congress, July/August 2003, Durban, South Africa*. Document Transformation Technologies, Irene, 499-501.
- du Toit, J.T., B.H. Walker & B.M. Campbell (2004). Conserving tropical nature: current challenges for ecologists. *Trends in Ecology and Evolution*, 19, 12-17.
- Ferraro, P.J. & A. Kiss (2002). Direct payments to conserve biodiversity. *Science*, 298, 1718-1719.
- Fritz, H. & P. Duncan (1994). On the carrying capacity for large ungulates of African savanna ecosystems. *Proceedings of the Royal Society, London, B*, 256, 77-82.
- Fritz, H., P. Duncan, I.J. Gordon & A.W. Illius (2002). Megaherbivores influence trophic guilds structure in African ungulate communities. *Oecologia*, 131, 620-625.

- Illius, A.W. & T.G. O'Connor (1999). On the relevance of nonequilibrium grazing concepts to arid and semiarid grazing systems. *Ecological Applications*, 9, 798-813
- Kiss, A. (2004). Is community-based ecotourism a good use of biodiversity conservation funds? *Trends in Ecology and Evolution*, 19, 232-237.
- Madhusudan, M.D. (2005). The global village: linkages between international coffee markets and grazing by livestock in a South Indian wildlife reserve. *Conservation Biology*, 19, 411-420.
- McNaughton, S.J. & N.J. Georgiadis (1986). Ecology of African grazing and browsing mammals. *Annual Review of Ecology and Systematics*, 17, 39-65.
- Oosterheld, M., O.E. Sala & S.J. McNaughton (1992). Effect of animal husbandry on herbivore-carrying capacity at a regional scale. *Nature*, 356, 234-236.
- Owen-Smith, N. & D.H.M. Cumming (1993). Comparative foraging strategies of grazing ungulates in African savanna grasslands. *Proceedings of the XVII International Rangelands Congress, New Zealand*, 691-698.
- Owen-Smith, N. & J. Ogotu (2003). Rainfall influences on ungulate population dynamics. In: J.T. du Toit, K.H. Rogers & H.C. Biggs (eds) *The Kruger experience: ecology and management of savanna heterogeneity*. Island Press, Washington, DC, 310-331.
- Pennycuik, C.J. (1979). Energy costs of locomotion and the concept of the "foraging radius". In: A.R.E. Sinclair and M. Norton-Griffiths (eds) *Serengeti - dynamics of an ecosystem*. University of Chicago Press, Chicago, 164-184.
- Penuelas, J. & M. Estiarte (1998). Can elevated CO₂ affect secondary metabolism and ecosystem function? *Trends in Ecology and Evolution*, 13, 20-24.
- PRB (2004). 2004 World Population Data Sheet. Population Reference Bureau, Washington, DC, 16pp.
- Richardson-Kageler, S.J. (2003). Large mammalian herbivores and woody plant species diversity in Zimbabwe. *Biodiversity and Conservation*, 12, 703-715.
- Sayer, J. & B. Campbell (2004). *The science of sustainable development. Local livelihoods and the global environment*. Cambridge University Press, Cambridge, 268pp.
- Smith, R.J., R.D. Muir, M.J. Walpole, A. Balmford & N. Leader-Williams (2004). Governance and the loss of biodiversity. *Nature*, 426, 67-70.
- Walker, B.H., R.H. Emslie, R.N. Owen-Smith & R.J. Scholes (1987). To cull or not to cull: lessons from a southern African drought. *Journal of Applied Ecology*, 24, 381-401.
- Walker, B.H., A. Kinzig & J. Langridgen (1999). Plant attribute diversity, resilience, and ecosystem function: The nature and significance of dominant and minor species. *Ecosystems*, 2, 1-20.