# Functional conservation areas and the future of Africa's wildlife

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## Abstract

Ungulate populations in African conservation areas (CAs) are in widespread decline, which can largely be attributed to a lack of functionality of the area encompassed by the CAs themselves. We present evidence from a wide range of African CAs showing that they do not encompass both the functional wet- and dry-season resources that ungulates traditionally migrated between. Before human populations and economic development had grown to levels where they interfered with migrations outside the CAs, ungulates were able to make use of their traditional seasonal resources but this is becoming increasingly difficult and we are now seeing the effects of this restriction of movement on ungulate population numbers. New innovative strategies are required for the conservation of African wildlife. An urgent Africa-wide survey is needed to establish past and present functional resources in and around CAs and to prioritize conservation regions that are most functional. In addition, innovative attempts need to be made to reconsolidate functional seasonal resources within revised expanded protected areas.

*Key words*: ecological gradients, habitat fragmentation, Kgalagadi, Kruger National Park, migration, predation limitation, resource limitation, seasonal resources

## Résumé

Les populations d'ongulés dans les aires de conservation africaines (AC) sont largement en déclin, ce que l'on peut en grande partie attribuer au manque de fonctionnalité de la superficie englobée par les AC elles-mêmes. Nous présentons des preuves tirées d'une large gamme d'AC africaines qui montrent qu'elles ne comprennent pas l'ensemble des ressources fonctionnelles de saison des pluies et de saison sèche entre lesquelles les ongulés ont l'habitude de migrer. Avant que les populations humaines et le développement économique n'aient atteint des niveaux où ils interfèrent avec les migrations qui se font en dehors des AC, les ongulés étaient à même d'utiliser leurs ressources saisonnières traditionnelles, mais ceci est devenu de plus en plus difficile, et nous voyons désormais les effets de cette restriction des déplacements sur les chiffres des populations d'ongulés. Il est urgent de réaliser une étude à l'échelle du continent pour établir quelles sont les ressources fonctionnelles passées et présentes dans et autour des AC et pour prioriser les régions de conservation qui sont les plus fonctionnelles. De plus, il faut innover pour consolider les ressources fonctionnelles saisonnières au sein d'aires protégées révisées et élargies.

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## Introduction

Many of Africa's conservation areas (CAs) are experiencing large declines in the size and diversity of their ungulate populations (Whyte & Joubert, 1988; Ben-Shahar, 1993; Williamson, 2002; Owen-Smith & Mills, 2006; Caro & Scholte, 2007; Bolger *et al.*, 2008; Newmark, 2008; Harris *et al.*, 2009; Ogutu *et al.*, 2009; Western, Russell & Cuthill, 2009). We provide evidence from a wide range of African CAs showing that the major reason for these declines appears to be because many of Africa's CAs do not encompass the full range of functional resource gradients, migratory corridors and seasonal habitats critical for the maintenance of a diverse array of productive ungulate populations.

Forage quantity and quality in the savannas of Africa are highly variable both spatially and temporally (Vesey-Fitzgerald, 1960; Breman & De Wit, 1983; Ellis & Swift, 1988; Illius & O'Connor, 2000; Fryxell *et al.*, 2005; Owen-Smith, 2007). The stability and productivity of ungulate populations is dependent upon them being able to pursue

an optimal energy-maximizing foraging strategy by tracking this spatial and temporal variability in forage quantity and quality (Albon & Langvatn, 1992; Rettie & Messier, 2000; Owen-Smith, 2002, 2004; Fryxell *et al.*, 2005; Holdo, Holt & Fryxell, 2009; Parker, Barboza & Gillingham, 2009; Hopcraft, Olff & Sinclair, 2010).

Forage quality is generally at its highest in lower productivity regions such as on shallow, upland soils and in low-rainfall regions because minerals, protein and energy become more diluted and digestibility decreases as grass biomass increases (Jarrell & Beverly, 1981; Breman & De Wit, 1983; McNaughton & Banyikwa, 1995; Murray, 1995). Thus, except for a few species such as sable antelope (*Hippotragus niger*) and topi (*Damaliscus korrigum*), which have mouth parts adapted to selecting green leaves on taller grasses (Murray & Illius, 2000), the predominance of short grasses in these less productive areas results in greater rates of nutrient and energy intake by most ungulate species (Wilmshurst, Fryxell & Bergman, 2000; Owen-Smith, 2002). Low productivity areas are, therefore, critical for supplying sufficient protein, energy and minerals in forage during the period of lactation and for building up body stores before the dry season (McNaughton & Banyikwa, 1995; Parker, Barboza & Gillingham, 2009; Hopcraft, Olff & Sinclair, 2010). By contrast, more productive, high-rainfall regions or floodplains, although supporting grasses generally lower in quality during the wet season than grasses in less productive regions, often provide some form of green forage in the late dry season (Vesey-Fitzgerald, 1960; McNaughton, 1985; Fryxell, 1987; Fryxell & Sinclair, 1988a), when forage quality is severely limiting (Ellis & Swift, 1988; Mduma, Sinclair & Hilborn, 1999; Illius & O'Connor, 2000).

In addition to the advantages of better adaptive foraging capability for migratory populations, migration also allows ungulate populations to break free from predation limitation (Fryxell, Greever & Sinclair, 1988; Mills & Schenk, 1992; Heard, Williams & Melton, 1996; Rettie & Messier, 2000; Fryxell *et al.*, 2007), which limits the size of nonmigratory ungulate populations well below the ecological carrying capacity (Smuts, 1978; Gasaway, Gasaway & Berry, 1996; Hopcraft, Olff & Sinclair, 2010). In addition, as human population densities adjacent to CAs increase (e.g. Newmark, 2008; Ogutu *et al.*, 2009), ungulates having to migrate to seasonal grazing grounds outside of CAs often experience greatly elevated levels of poaching and human interference in these unprotected areas (Whyte & Joubert, 1988;

Williamson, Williamson & Ngwamotsoko, 1988; Newmark, 2008; Ogutu *et al.*, 2009).

Thus almost all of the world's extant large, stable ungulate populations are in unfragmented migratory systems consisting of a high-forage-quality, wet-season resource (low-rainfall regions or high-altitude regions), a dry season and drought-refuge resource (high-rainfall regions or floodplains and wetlands) and a transitional foraging area acting as a corridor between the wet- and dry-season resources (e.g. Fryxell & Sinclair, 1988a; Bolger *et al.*, 2008; Harris *et al.*, 2009). Unrestricted access to all these resources enables ungulates to follow an optimal adaptive foraging strategy, reduce predation risk and minimize human interference and poaching (McNaughton, 1985; Fryxell & Sinclair, 1988a; Heard, Williams & Melton, 1996; Bolger *et al.*, 2008; Harris *et al.*, 2009; Parker, Barboza & Gillingham, 2009; Hopcraft, Olff & Sinclair, 2010). Thus for the purposes of this paper, we define as 'dysfunctional' or 'not fully functional', CAs that no longer allow ungulates full protected access to all the critical seasonal foraging regions that they once regularly utilized on a seasonal basis.

## Layout of African conservation areas (CAs) in relation to critical ecological gradients

### The Kruger National Park

The Kruger National Park (KNP) has surprisingly low ungulate densities relative to other CAs such as Serengeti National Park (SNP) in Tanzania, Hluhluwe-Imfolozi Park (HIP) in South Africa and the Okavango Delta in Botswana. In 1993, herbivore biomass for KNP, HIP and SNP were 3185, 8949 and 12365 kg km$^{-2}$, respectively (Norman Owen-Smith, unpublished data), while herbivore biomass in the Okavango Delta is 11888 kg km$^{-2}$ (Bonyongo, 2004). An intriguing question is: has KNP always had such low herbivore biomass? Historical records from KNP (Stevenson-Hamilton, 1947; Wolhuter, 1948), more recent examples from KNP (Whyte & Joubert, 1988; Ben-Shahar, 1993) as well as other recent examples from other CAs (Gasaway, Gasaway & Berry, 1996; Serneels & Lambin, 2001; Williamson, 2002; Newmark, 2008; Harris *et al.*, 2009) suggest that the reason for these low densities is because natural migratory routes along functional environmental gradients have been cut off rendering the system dysfunctional in terms of the ability of ungulates to follow optimal adaptive foraging strategies and minimize

predation risk. The KNP occurs dominantly in the low-rainfall region (400- to 600-mm zone) of the Lowveld ecosystem (LE). However, just west of KNP, along the entire length of the Park, are zones within the LE receiving between 800 and 1200 mm of rainfall per annum (Fig. 1). Writings of previous KNP wardens and rangers provide evidence that (i) migrations on this once intact rainfall gradient in the LE were common and (ii) these migrations were critical for the maintenance of a large ungulate population within the LE.

Colonel James Stevenson-Hamilton, the first warden of KNP, had this to say:

*'Most of the purely grass-eaters are, at least locally, migratory in habit, and, though wildebeest, for instance, appear to be able to thrive on a larger assortment and coarser types of grasses than some of the others, they, for the most part, regularly change their grazing grounds annually, and in the Park migrate in winter often as much as fifty miles to the west of their summer haunts'* (Stevenson-Hamilton, 1947). Stevenson-Hamilton continues (bold emphasis ours):

*'Between 1925 and 1936 occurred a long period of drought, hardly uninterrupted by a rainfall during three of the intervening years, which, though reasonable in actual amount, fell at the wrong times, and usually in the shape of heavy storms*



Fig 1 Rainfall map of the Lowveld ecosystem (LE) of South Africa. It is clear that the Kruger National Park (KNP) lies dominantly within the 400- to 600-mm rainfall zones of the LE. Just west of KNP, however, along the entire length of the Park, are zones within the LE receiving between 800 and 1200 mm of rainfall per annum. The >1200-mm zone represents the LE escarpment or LE boundary (delineated by the thick black line) and represents a barrier to further westward migration by ungulates. Rainfall map data sourced from Schulze et al. (1997). Blue arrow, recently blocked wildebeest migration between the Sabi-Sand reserve and KNP (Whyte & Joubert, 1988; Ben-Shahar, 1993); Red arrows, Stevenson-Hamilton's descriptions of ungulate migrations prior to interference by agriculture and human settlement in the high-rainfall regions (Stevenson-Hamilton, 1947); Black arrows, predicted migrations (no records)
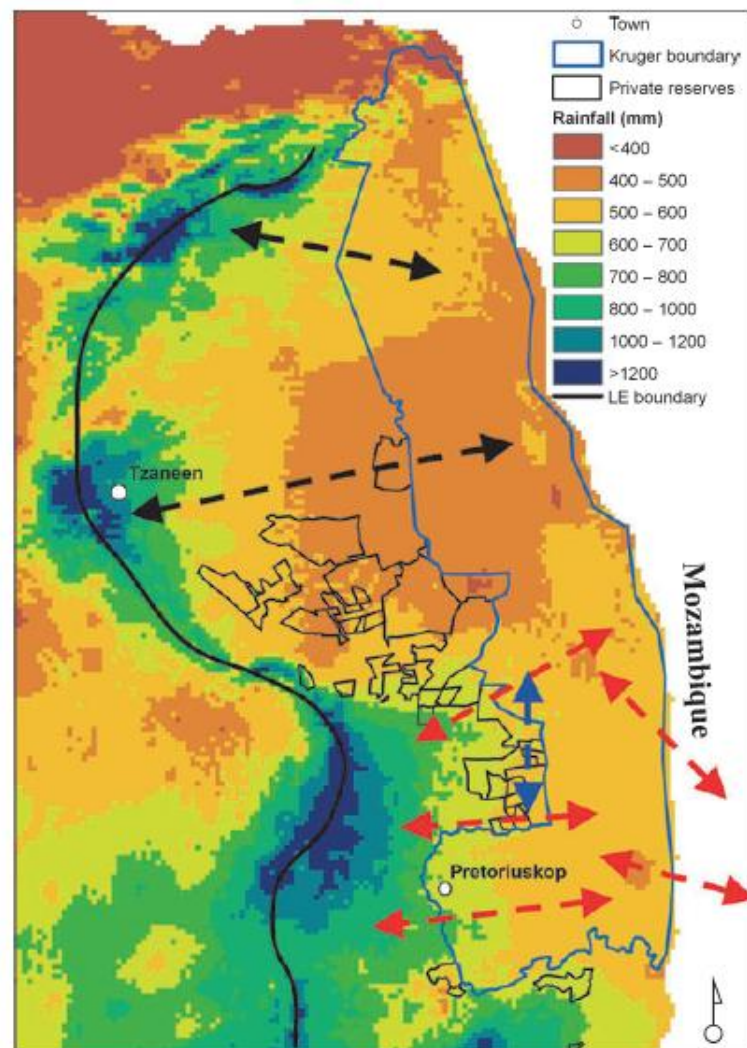
*instead of light soaking rain. The result was a general exodus of the more migratory species from the already overgrazed portions of the Park in the east, towards the more fertile and better-watered foothills of the Drakensberg and eastwards into Portugese territory. **Some such exodus had always taken place annually in the past, with a backward trek at the first rains**, but owing to persistently arid conditions from year to year, culminating in 1934–5, there was less and less tendency for the herds to return to their former grazing grounds, and finally they became largely settled in the new localities. **Had there been no natural migrating space available, or had the Park been enclosed by some unsurmountable obstacles, as some think it ought to be, no doubt there would have been wholesale death from starvation and disease among all the ungulate fauna.**'*

From Colonel Stevenson-Hamilton's observations, it is clear that many of the species in the LE, especially wildebeest (*Connochaetes taurinus*), migrated east – west along the rainfall gradient, using the eastern, low-rainfall regions in the wet season and the western, high-rainfall regions in the dry season (Fig. 1). Similarly, the eastward migration into Mozambique or Portugese territory in Stevenson–Hamilton's time (Fig. 1) is also on a strong rainfall gradient increasing to an 800- to 1000-mm zone within 100 km of southern KNP (Nhantumbo, Ledin & Du Preez, 2009), which is well within the distance of most African ungulate migrations (Jarman & Sinclair, 1979; Williamson, Williamson & Ngwamotsoko, 1988; Bartlam-Brooks, Bonyongo & Harris, in press). These migration patterns on rainfall gradients east and west of KNP are in accordance with SNP ungulate migration patterns in the Serengeti Ecosystem (SE) where ungulates use the low-rainfall (400–600 mm), short-grass Serengeti plains during the wet season and the high-rainfall (>1000 mm), taller grasslands on the Tanzania-Kenya border during the late dry season (Jarman & Sinclair, 1979; McNaughton, 1985; Holdo, Holt & Fryxell, 2009). Similarly, the high-rainfall (>1000 mm), Masai-Mara Game Reserve (MMGR) forms the dry-season range and the low-rainfall (500 mm), short grasslands of the Loita plains the wet-season range for ungulate migration in the Masai-Mara ecosystem (MME) (Serneels & Lambin, 2001; Serneels, Said & Lambin, 2001) while the high-rainfall (850 mm) Nairobi National Park (NNP) forms the dry-season range and the low-rainfall (400 mm) grasslands of the Athi-Kapiti plains the wet-season range for ungulate migration in the Athi-Kapiti ecosystem (AKE) (Hillman & Hillman, 1977; Gichohi, 2000). In addition, the migration of pastoralists and their

cattle in the Sahel Transhumance ecosystem (STE) follows similar seasonal patterns on a strong rainfall gradient (200–900 mm) (Breman & De Wit, 1983; Fryxell & Sinclair, 1988a). The short, nutritious grasses in the low-rainfall regions of SE and STE have been shown to have a higher concentration of protein and minerals than grasses at the high-rainfall end of the gradient (Breman & De Wit, 1983; McNaughton & Banyikwa, 1995; Murray, 1995). It appears that lower leaching at low-rainfall combined with fertile, volcanic ash soils result in more nutritious grasses than those growing on the poorer, granitic soils in the high-rainfall regions of the SE (McNaughton, 1983; Anderson *et al.*, 2010). Similarly, the low-rainfall regions of the eastern LE support more nutritious grasses on fertile volcanic clay soils than the granitic and sedimentary derived soils further west (Skidmore *et al.*, 2010). In addition, the low-rainfall KNP allows the development of saline/-sodic soils supporting short, nutritious grasses (Grant & Scholes, 2006; for effect of rainfall see Anderson *et al.*, 2010). This explains why ungulates preferably use these low-rainfall regions of the STE, SE, LE, MME and AKE during the wet season (Stevenson-Hamilton, 1947; Hillman & Hillman, 1977; Breman & De Wit, 1983; McNaughton, 1985; Fryxell & Sinclair, 1988a; Serneels & Lambin, 2001).

Dry-season movement of ungulates to the high-rainfall foothills of the LE escarpment and the high-rainfall regions of the STE, SE, MME and AKE appears to be because these high-rainfall regions provide dependable green grass in the late dry season. A key feature of the high-rainfall grasslands in SE and MME is that sufficient dry-season rainfall provides some degree of green grazing in the late dry season: '*Because of their extended growing season those tall grasslands were the last reservoir of green forage available at the end of the dry season*' (McNaughton, 1985; also see Holdo, Holt & Fryxell, 2009). Similarly, Harry Wolhuter, the first ranger in KNP, noted that a key feature of the foothills of the LE escarpment was their dependable green grazing in the late dry season (early summer):

'*In 1926, when the Sabi and Shingwedzi Game Reserves were united in the Kruger National Park, certain areas along the western boundary of the old Sabi Reserve were excised. In my own section, the Pretorius Kop area of the park, much of the area excised at the time of its removal from the park's territory it was literally packed with game. In fact it is sad to relate that this portion covered some of our best game country, as it was well watered, and, with big vleis in most parts, **there was always early summer grazing**'* (Wolhuter, 1948). These

excised areas west of Pretoriouskop were clearly in very high-rainfall areas (Fig. 1). Rainfall averaged over four sites in the high-rainfall foothills (White river, Hazyview, Bushbuck ridge and Tzaneen) was 31, 66 and 109 mm for September, October and November (late dry season), respectively. By contrast, rainfall averaged for four sites in the lower-rainfall, eastern LE (Shingwedzi, Letaba, Satara and Lower Sabi) was 18, 37 and 62 mm for September, October and November, respectively (Zucchini & Nenadic, 2006). Consequently, dependable green grazing can be expected 1–2 months earlier in summer in the western than eastern regions of the LE. Thus, these high-rainfall grasslands of the LE appear to be functionally similar to the high-rainfall SE grasslands, providing dependable green grazing in the late dry season. Thus, the search for green leaf appears to be one of the major drivers of ungulate migrations to floodplains and high-rainfall regions during the dry season (Vesey-Fitzgerald, 1960; Fryxell and Sinclair, 1988a,b; Holdo, Holt & Fryxell, 2009).

Currently, ungulates can migrate no further than the western fence of KNP and its associated private CAs (the fence between KNP and the private CAs has been removed) and fencing of the southern KNP-Mozambique border on the east of KNP prevents movement into Mozambique (Fig. 1). Even if the western fence was removed, dense human settlement and intensive agriculture in the high-rainfall regions (800–1200 mm) of the LE would make it impossible for ungulates to reach their traditional dry-season and drought-refuge grazing areas in these high-rainfall regions (Fig. 1). Thus, the area encompassed by KNP and its associated private CAs is not a fully functional grazing ecosystem because ungulates are now only able to select traditional wet-season and corridor grazing areas within the low- and medium-rainfall areas of the LE (up to and including the 700-mm zone but no further). Similar to the example of the AKE where the true dry-season range of the ecosystem in the high-rainfall Ngong hills region was lost to settlement and agriculture (Gichohi, 2000), a fully functional KNP would have to extend all the way westwards to the LE escarpment, thereby including the very high-rainfall regions between KNP and the escarpment and include the high-rainfall regions east of KNP in southern Mozambique (Fig. 1). As a consequence of the loss of migrations in KNP, ungulate population size is now severely limited by predation (Smuts, 1978; Mills & Schenk, 1992). Functional regional-scale selection of habitat for resources and predation avoidance (both wet- and dry-season regions) has been recognized as the most important determinant of productive ungulate populations (Fryxell, Greever & Sinclair, 1988; Fryxell & Sinclair, 1988a; Rettie & Messier, 2000; Parker, Barboza & Gillingham, 2009; Hopcraft, Olff & Sinclair, 2010), but ungulates in KNP are no longer able to select at a functional regional scale.

Data on ungulate numbers in the LE before the massive die offs in the Rinderpest epizootic of 1896/97 (Wolhuter, 1948) is lacking and it is therefore not possible to determine what effects the loss of access to the drought-refuge and dry-season grazing of the high-rainfall regions has had on ungulate population size in the LE. However, a more recent restricted wildebeest migration occurred between wet-season grazing on fertile Gabbro-derived soils of the Orpen region of KNP and dry-season grazing along the Sand river in the adjacent private CAs directly west of KNP (see blue arrow in Fig. 1). Erection of the western boundary fence of KNP in 1961 severed this migration resulting in an 85% reduction in their population size from around 6000 in 1965 to around 900 by 1978, whereas two other wildebeest sub-populations further east, whose movements were not affected by the fence, have not declined in size over time (Whyte & Joubert, 1988; also see Ben-Shahar, 1993). It is, therefore, reasonable to assume that disruption of far more extensive migrations between the low-rainfall, wet-season range and the high-rainfall dry-season range (Fig. 1; Stevenson-Hamilton, 1947; Wolhuter, 1948) is likely to have resulted in a large overall decline in the size of ungulate populations of the LE as observed for other disrupted migrations on rainfall gradients (e.g. AKE and MME).

This decline following the removal of a seasonal resource is predicted by ecological models (Owen-Smith, 2004; Fryxell et al., 2005). Similar to the KNP example (Whyte & Joubert, 1988; Ben-Shahar, 1993), a major crash in the SE wildebeest population is expected should either the high- or low-rainfall areas of SE be removed from the Park (Owen-Smith, 2004; Fryxell et al., 2005). Far higher herbivore biomass levels in HIP (8949 kg km$^{-2}$) relative to the 21 times larger KNP (3185 kg km$^{-2}$) appears to be because of the strong rainfall gradient within HIP (635–990 mm), which combined with great variability in elevation and topography (60–600 m) creates a high degree of functional habitat heterogeneity in this small CA. How much greater, however, could ungulate biomass in HIP be if it encompassed the full range, diversity and area of ecological gradients within the Zululand ecosystem, which is far greater than that currently encompassed by this small CA?

A major population crash of several ungulate species following the fragmentation of key seasonal resources was observed in the Kgalagadi ecosystem (KE) in Botswana. The KE contains various CAs such as the Kgalagadi Transfrontier Park (KTP) in the south west extending northwards to relatively higher rainfall areas of the Central Kalahari Game Reserve (CKGR) and the Makgadikgadi Pans Game Reserve (MPGR) to the north east of the CKGR, while north of the CKGR the Okavango Delta outflows of Lake Ngami and the Boteti river provided dry-season water and grazing (Fig. 2).

During the wet season, the bulk of the KE wildebeest, red hartebeest (*Alcelaphus buselaphus*) and springbok (*Antidorcas marsupialis*) populations concentrated in the 250- to 350-mm rainfall zone in the region of the southern KE known as 'The Schwelle' where nutritious grazing could be found on saline pan grasslands (Williamson, Williamson & Ngwamotsoko, 1988; Williamson, 2002). Ungulates tracked green grazing associated with patchy rainfall events across the Schwelle and CKGR (Verlinden, 1997; Verlinden & Masogo, 1997). Radio collaring, as well as observational studies, showed that during severe drought years wildebeest migrated between 300 and 500 km straight-line distance up the rainfall gradient from the southern KE and CKGR to Lake Ngami, the Boteti river

and possibly even the floodplains of the Delta itself (Owen & Owen, 1980; Williamson, Williamson & Ngwamotsoko, 1988; Williamson, 2002; Fig. 2). It appears that during these very dry years, the moisture of grasses had fallen to levels too low to meet the needs of the wildebeest and they were forced to move to the permanent surface water provided by the Boteti river (Williamson, Williamson & Ngwamotsoko, 1988).

Since the late 1950s rapidly increasing cattle posts and veterinary cordon fences have interfered with ungulate movements across the KE (Cooke, 1985; Verlinden, 1997; Mbaiwa & Mbaiwa, 2006). Human settlement and cattle posts are making it increasingly difficult for wildlife to utilize the Schwelle and to move between the Schwelle and the CKGR (Verlinden, 1997) and the critical drought-refuge resources of the Okavango Delta, Lake Ngami and the Boteti river have been cut off from KE ungulates by veterinary fences, settlements and cattle ranching (Owen & Owen, 1980; Williamson, Williamson & Ngwamotsoko, 1988; Fig. 2). During the severe droughts of 1979–1985, massive mortalities of wildebeest were recorded as wildebeest massed against the Kuke fence in their attempts to reach the Boteti river (Owen & Owen, 1980; Williamson, 2002) and ungulate populations in general in the KE (including MPGR) have declined to a mere fraction of their former numbers (Fig. 3). From the data presented in Fig. 3, it is apparent that the isolated CAs of the KTP and CKGR,
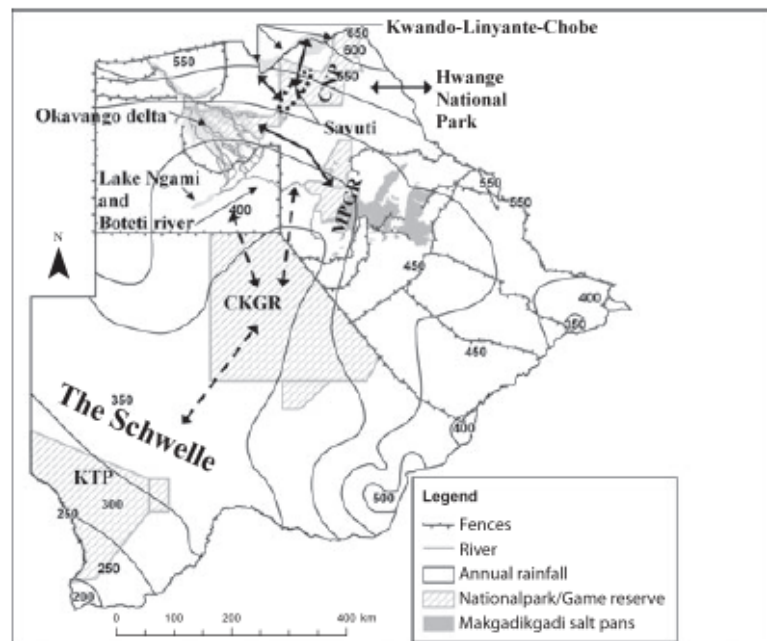


Fig 2 Map of Botswana showing important migratory pathways between key seasonal habitats in the Kgalagadi ecosystem (KE) as well as the complex of national parks and game reserves in northern Botswana/Zimbabwe (OMSCH complex). CNP, Chobe National Park; MPGR, Makgadikgadi Pans Game Reserve; KTP, Kgalagadi Transfrontier Park; CKGR, Central Kalahari Game Reserve. Broken double-headed arrows, disrupted migrations; Unbroken double-headed arrows, extant migrations
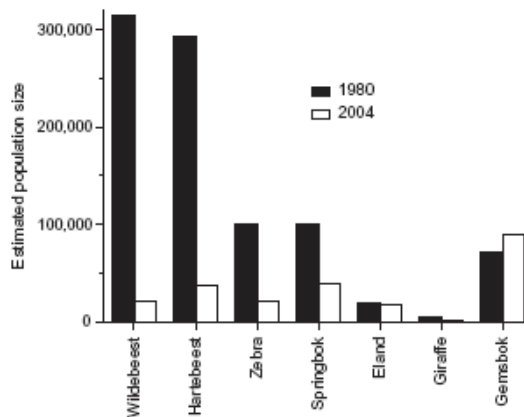
Fig 3 Estimated ungulate numbers in the Kgalagadi ecosystem (including Makgadikgadi/Nxai pans) in 1980 and 2004. Data sourced from Cooke (1985) and DWNP (2004)

despite their vast size, contribute very little to the conservation of most ungulates in the KE any longer because they do not allow connectivity between high-quality, wet-season grazing in the saline grasslands of the Schwelle and MPGR, dry-season grazing in the CKGR and the drought-refuge water and grazing of the Okavango outflows of Lake Ngami and the Boteti river (Fig. 2).

Similarly, Etosha National Parks' (ENP) wildebeest population declined from a peak of about 30,000 in 1965 to 2000 by 1993 and Burchell's zebra (*Equus burchelli*) from a peak of 23,000 in 1955 to less than 4000 by 1990, while springbok have undergone a less dramatic decline (Gasaway, Gasaway & Berry, 1996). The wildebeest

population decline appears to be because of the erection of a fence that cut off their migrations outside of the Park to dry-season grazing (Berry, 1982; Gasaway, Gasaway & Berry, 1996). The major wet-season grazing area of the Etosha ecosystem (EE) was short, nutritious 'sweet' grassland on lime (Berry, 1982) to the west of the main Etosha Pan (Fig. 4) while ungulates migrated north for the dry season to the regions around Lake Oponono and the Oshana wetlands of the Cuvelai drainage system originating in Angola (H. Berry, *pers. com.*) (Fig. 4). The Cuvelai drainage system is an inverted delta consisting of a savanna matrix between open grass-covered drainages dominated by wetland grasses such as *Echinochloa* (P. Beauv.) and *Elytrophorus* (P. Beauv.) sp. (WWF/TNC, 2008). Thus, this grazing ecosystem appears to have operated in a very similar manner to the adjacent KE, which also had a wet-season resource in low-rainfall pan grasslands and a dry-season resource in the drainages originating in Angola (Figs 2 and 4).

In east Africa, human population growth, private ranching and agriculture have increasingly prevented ungulates reaching their wet-season range outside of Tarangire National Park (TNP) in the Tarangire ecosystem (TE), NNP in the AKE and MMGR in the MME (Kahurananga & Silkiluwasha, 1997; Gichohi, 2000; Serneels & Lambin, 2001; Serneels, Said & Lambin, 2001; Bolger et al., 2008; Ogutu et al., 2009). As with the southern African examples of the LE, KE and ENP, disruption of migration in these three East African ecosystems has resulted in a collapse of their wildebeest populations (Fig. 5). Several other ungulates such as topi, kongoni (*Alcelaphus buselaphus cokei*), zebra and hartebeest have

Fig 4 Map showing the major wet- and dry-season grazing regions of the Etosha ecosystem. A veterinary fence along the northern Border of Etosha National Park (ENP) has severed the traditional ungulate migrations between high-quality wet-season grazing adjacent to Etosha Pan and water and dry-season grazing north of the Park in the Cuvelai drainage system. The broken, double-headed arrow indicates the severed migration. Map and information on ungulate movements courtesy of H. Berry
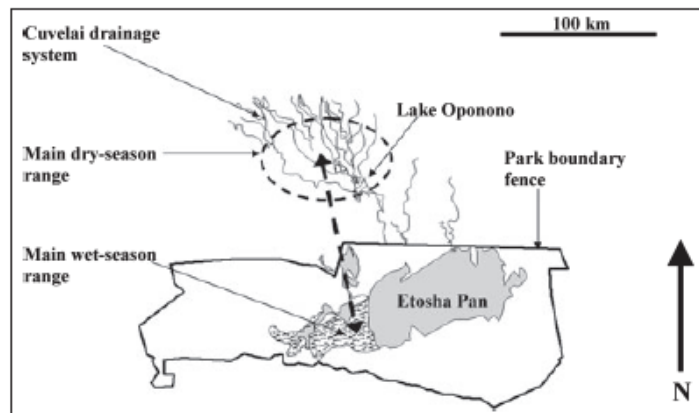
also declined, but similar to the southern African examples, the response has been more variable compared to the ubiquitous dramatic wildebeest declines (Bolger *et al.*, 2008; Imbahale *et al.*, 2008; Ogutu *et al.*, 2009; Western, Russell & Cuthill, 2009). The examples of MME, AKE and TE demonstrate that it is not only the dry-season range that is important but also the wet-season range (see Voeten *et al.*, 2009).

## Functional conservation areas (CAs) remaining in Africa

Several CAs in Africa still provide relatively unfragmented functional wet- and dry-season habitats capable of supporting large viable ungulate populations. Perhaps the most functional and productive wildlife system on earth is the famous SE with its millions of wildebeest, zebra and Thomsons gazelles (*Eudorcas thomsonii*), which migrate between the low-rainfall, short-grass plains where they spend the wet season and the high-rainfall woodlands on the Kenyan border where they spend the dry season (Jarman & Sinclair, 1979; McNaughton, 1985; Holdo, Holt & Fryxell, 2009). The unparalleled size of the ungulate
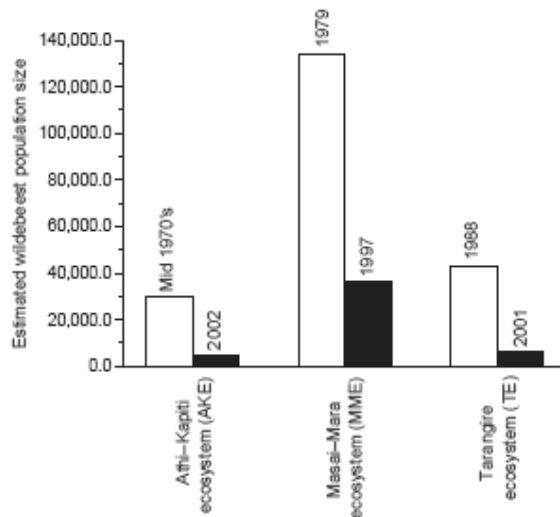


Fig 5 Changes in wildebeest population size in three east African grazing ecosystems. Nairobi National Park (NNP), Masai-Mara Game Reserve (MMGR) and Tarangire National Park (TNP) do not encompass the critical nutritious short grasslands of the Athi-Kapiti ecosystem (AKE), Masai-Mara ecosystem (MME) and Tarangire ecosystem (TE), respectively. Data from Serneels & Lambin (2001); Bolger *et al.* (2008); Imbahale *et al.* (2008)

populations of SE is because the SNP and its associated wildlife management areas encompass almost all of the highly nutritious, short grasslands, productive high-rainfall grasslands and transitional mid-grasslands of the SE (McNaughton, 1985). This great grazing ecosystem is without doubt Africa's flagship CA.

The Selous-Niassa complex on the Tanzania-Mozambique border is a vast wildlife region comprising the Selous Game Reserve in Tanzania (47,000 km$^2$), the Niassa National Reserve in Mozambique (42,000 km$^2$) and the Selous-Niassa wildlife corridor (8000 km$^2$) as a link between the two reserves. The complex is made up of a mix of open wooded grasslands and miombo woodlands with riverine vegetation, swamps and floodplains of the Ruaha, Rufiji, Lugenda and Rovuma rivers (Baldus *et al.*, 2003; SRN, 2003; UNEP-WCMC, 2008). The region has the largest populations of wild dog (>1000) and sable antelope (>13,000) in Africa, populations of buffalo (*Syncerus caffer*) and elephant (*Loxodonta africana*) exceeding 100,000 each, endemic species of wildebeest (*C. taurinus johnstoni*), zebra (*Equus burchelli boehmi*) and impala (*Aepyceros melampus johnstoni*) and many other antelope species, including large populations of Burchell's zebra, Lichtensteins hartebeest (*Alcelaphus lichtensteinii*) and kongoni (Baldus *et al.*, 2003; TOEB, 2004; Hahn, 2008; UNEP-WCMC, 2008). Despite being one of Africa's greatest and most important CAs, there is very little published research on ungulate migration and ecology in this complex. Laying claim to both the SE and 60% of the Selous-Niassa complex, Tanzania should be rewarded for conserving the greatest wildlife populations on earth.

The Boma ecosystem (BE) of Sudan supported nearly one million white-eared kob (*Kobus kob leucotis*) that migrate between the floodplains of the Oboth and Neubari rivers where they spend the dry season and the outlying lightly wooded grasslands south of the Kangen river where they spend the wet season (Fryxell, 1987; Fryxell & Sinclair, 1988b). Although numbers of white-eared kob appeared to have declined to about 200,000 in 2001, the area still supports large increasing or stable populations of eland (*Taurotragus oryx*) (21000), roan antelope (*Hippotragus equinus*) (2000), reedbuck (*Redunca arundinum*) (29000) and Lelwel hartebeest (*Alcelaphus buselaphus lewel*) (5600) as well as several other ungulate species (USAID/USDA PASA, 2001). An aerial survey in 2007, however, suggests that there has been no decline in white-eared kob numbers from their 1980 levels (National Geographic Society) – http://press.nationalgeographic.com/pressroom/

index.jsp?pageID=pressReleases_detail&siteID=1&cid=1181653239588.

The BE of Sudan, the TE (Kahurananga & Silkiluwasha, 1997; Gereta *et al.*, 2004), the Rukwa valley ecosystem (RVE) (Vesey-Fitzgerald, 1960), the Kilombero valley ecosystem (KVE) (Jenkins *et al.*, 2002), ENP, as well as the Southern Darfur transhumance ecosystem (SDTE) of Sudan (Wilson, 1977) function in a similar manner to the Okavango Delta-Makgadikgadi-Savuti-Chobe-Hwange complex (OMSCH complex) of Botswana, which has migrations between dry-season grazing on the Okavango Delta and Kwando-Linyante-Chobe floodplains and wet-season grazing in the outlying woodlands and the saline pan grasslands of Savuti and MPGR (Table 1; Fig. 2). The OMSCH complex is a vast wildlife region that extends to the MPGR 240 km to the south and hundreds of km eastwards across into Hwange National Park in Zimbabwe as well as into parts of the Caprivi strip in Namibia (Kwando-Linyante-Chobe region) and north of the Caprivi strip into CAs along the Zambezi river in southern Angola and Zambia (Fig. 2). This region supports the largest population of elephant in Africa (*c.* 150,000) and large populations of Burchell's zebra, wildebeest, buffalo and red lechwe (*Kobus leche*) as well as some of Africa's last-remaining healthy populations of eland, tsessebe (*Damaliscus lunatus*), sable and roan antelope (Bonyongo, 2004). Some zebra populations have recently been found to be migrating 240 km, spending the dry season on the floodplains of the Okavango Delta and the wet season on the nutritious short saline grasslands of MPGR (Bartlam-Brooks, Bonyongo & Harris, in press). Other populations of wildebeest and zebra also use the saline grasslands of MPGR during the wet season and migrate to the Boteti river where they spend the dry season (Kgati & Kalikawe, 1993; Brooks, 2005). A large zebra migration also occurs between the wet-season grazing areas of the Mababe-Savuti depression and dry-season grazing on the Kwando-Linyante-Chobe floodplains 70 km to the north (Fig. 2; Vandewalle, 2000; Owen-Smith, 2002). Both the Savuti and MPGR grasslands are short, saline grasslands as indicated by a high proportion of *Sporobolus ioclados* (Trin.) Nees in the sward (Venter, Scholes & Eckhardt, 2003; Naz *et al.*, 2010). An important pattern is that *S. ioclados* and other saline-grasses such as *S. spicatus* (Vahl) Kunth are key dominants of the wet-season grazing areas of SE (McNaughton, 1983), KNP (Khomo, 2003; Venter, Scholes & Eckhardt, 2003), ENP (WWF/TNC, 2008) and OMSCH (Brooks, 2005). Sodium and phosphorus are important minerals for lactation (Murray, 1995), and it appears that elevated concentrations of these minerals in grasses growing in these saline grasslands (McNaughton & Banyikwa, 1995; Murray, 1995; Grant & Scholes, 2006) makes them sought-after wet-season grazing habitats for ungulates throughout east and southern Africa (see Anderson *et al.*, 2010).

In the light of the issues discussed in this paper, these functional unfragmented CAs (BE, SE, Selous-Niassa and OMSCH complexes) are now critical areas of conservation importance in Africa. Fragmentation of key seasonal habitats within these four great CAs must be prevented at all costs; they are all that remain of the fully functional wildlife areas that once characterized Africa. They, therefore, all warrant priority in future international conservation efforts (e.g. research focus, world heritage conservation status, international support).

## Conclusion and the way forward

A pattern that emerges from the examples presented in this paper is that low-rainfall regions, where leaching of minerals and nutrients is low, often support short, nutritious (often saline) grasslands (see Anderson *et al.*, 2010), which form the key wet-season range of many large

Table 1 Seasonal wet- and dry-season ranges of various African ungulate populations

| Seasonal resource | Habitat description | Grazing ecosystem |
| --- | --- | --- |
| Wet season range | Woodland | BE, RVE, KVE, OMSCH, LE |
| | Low-rainfall grasslands (often saline) | OMSCH, KE, EE, SE, LE, MME, AKE, STE, SDTE |
| Dry season range | High-rainfall grasslands | SE, LE, MME, AKE, STE |
| | Floodplains and wetlands | RVE, KVE, KE, OMSCH, BE, TE, SDTE, EE |

AKE, Athi-Kapiti ecosystem; BE, Boma ecosystem; EE, Etosha ecosystem; KE, Kgalagadi ecosystem; KVE, Kilombero valley ecosystem; LE, Lowveld ecosystem; MME, Masai-Mara ecosystem; RVE, Rukwa valley ecosystem; SDTE, Southern Darfur transhumance ecosystem; SE, Serengeti Ecosystem; STE, Sahel transhumance ecosystem.

African ungulate populations (Table 1). Exclusion of these nutritious grazing regions from the home ranges of ungulate populations is likely to negatively impact the productivity and sustainability of these populations (White, 1983; Cote & Festa-Bianchet, 2001; Cook et al., 2004; Bolger et al., 2008; Parker, Barboza & Gillingham, 2009; Hopcraft, Olff & Sinclair, 2010), as observed in the examples of MME, AKE and TE. Similarly, when the concentrations of protein and energy in forage have fallen well below maintenance levels by the late dry season (Ellis & Swift, 1988; Owen-Smith, 2007), ungulates seek to reduce the rate of decline in body stores by moving to regions supporting forage of adequate quality (Owen-Smith, 2002; Parker, Barboza & Gillingham, 2009). Thus, high-rainfall regions and floodplains, which provide some green grazing in the late dry season (Vesey-Fitzgerald, 1960; Fryxell, 1987; McNaughton, 1985), form important dry-season ranges for many African ungulate populations (Table 1). Large population crashes are often observed (especially during droughts) when these dry-season ranges are excluded from the home ranges of ungulates (Owen & Owen, 1980; Whyte & Joubert, 1988; Williamson, Williamson & Ngwamotsoko, 1988; Gasaway, Gasaway & Berry, 1996). It is clear, therefore, that a large, stable ungulate biomass in African CAs is dependent upon access to short, nutritious grassland in the wet season as well as access to high-rainfall or floodplain grasslands during the dry season, especially during droughts (Table 1).

With the highly fragmented distribution of African CAs (e.g. Vanderpost, 2007) and the large areas required to encompass the critical wet- and dry-season resources together with the corridors between them (e.g. the KE), it is rare that all the seasonal resources in an ecosystem are fully (or even partially) encompassed by CAs (see Bolger et al., 2008; Nelson, 2008; Newmark, 2008). Despite this, Africa's CAs were generally able to sustain large ungulate populations in the past because human population densities were low enough to allow ungulates to migrate outside the CAs to their wet- or dry-season ranges, but human populations have grown rapidly over the last 20 years (Newmark, 2008; Ogutu et al., 2009) and migration outside CAs is becoming increasingly restricted, and in many cases impossible (e.g. Cooke, 1985; Verlinden, 1997; Gichohi, 2000; Serneels, Said & Lambin, 2001; Newmark, 2008; Ogutu et al., 2009; Voeten et al., 2009; Western, Russell & Cuthill, 2009).

Consequently, we can expect that, except for the few remaining fully-functional CAs in Africa, most of Africa's

CAs will exhibit declines to a new low-biomass, species-poor equilibrium governed by small-scale, nonmigratory dynamics (Fryxell, Greever & Sinclair, 1988; Rettie & Messier, 2000; Owen-Smith, 2004; Fryxell et al., 2005; Holdo, Holt & Fryxell, 2009; Parker, Barboza & Gillingham, 2009; Hopcraft, Olff & Sinclair, 2010). Moreover, loss of large migratory herds is predicted to have additional undesirable feedback effects on ecosystem functioning such as reduced rates of nutrient cycling, compositional changes to less palatable species and reduced grassland productivity (Augustine & McNaughton, 1998; Frank, McNaughton & Tracy, 1998). In turn, changes in these ecosystem properties (grassland structure and productivity, Allee effect of herd size on grazing behaviour, trampling, nutrient cycling and predation risk) may result in tree invasion (Rogues, O'Connor & Watkinson, 2001; Mills & Fey, 2005; Estes, Raghunathan & Van Vleck, 2008; Riginos, 2009) and an ecosystem shift to a new low-forage-quality, high-predation-risk stable state (Augustine & McNaughton, 1998; Frank, McNaughton & Tracy, 1998; Fryxell et al., 2007; Hopcraft, Olff & Sinclair, 2010) not suitable for wildlife conservation or ecotourism (Treydte, Edwards & Suter, 2005).

The examples of KNP, CKGR, ENP, NNP, MMGR and TNP discussed in this paper exposes severe flaws in African conservation strategy inherited from the colonial era; merely proclaiming large areas of land as CAs without thought given to critical seasonal habitats and corridors may do little to conserve the ungulate ecology and ecosystem structure and functioning of that region. It is now unequivocally clear that most formal CA's in Africa are completely inadequate for conserving large productive ungulate populations and that the future of wildlife in Africa is critically dependent on landuse policies outside the CA's (see also Nelson, 2008). Thus, current conservation strategies for Africa need to be revised. Wildlife conservation strategies must now adopt a socio-economic-ecological framework (Nelson, 2008; Reid et al., 2009). Failure to adequately address socio-economic issues will ultimately lead to habitat fragmentation and ecological collapse in the region. A major internationally funded initiative is urgently needed to conduct an in-depth analysis of Africa's CAs that identifies critical migratory corridors and key wet- and dry-season resources of ungulates, current and potential threats to ungulate movement between key habitats and the degree of fragmentation of habitats. This data can be used by conservationists to prioritize unfragmented CAs and look to identify other wildlife regions in Africa where loss of

functionality through habitat fragmentation can still be reversed.

Three practical, socially and politically acceptable ways of reconnecting key habitats of ungulates in Africa could be explored by conservationists: (i) Identify nonpriority CAs, where there is no possibility of restoring functionality, which could be deproclaimed and exchanged for land in crucial linkage/corridor areas in more functional CAs; (ii) Local communities living in corridor areas could be encouraged to convert their region to community-based natural resource management areas (CBNRM) where they derive income from tourism and hunting (see Nelson, 2008). This has been successfully achieved in areas linking CAs in northern Botswana (Mbaiwa, 2004, 2005) and is critical for the future of African wildlife conservation (Nelson, 2008); (iii) Sedentary cattle ranching in migratory corridors or seasonal resources must be avoided because sedentary (but not mobile) pastoralism has a destructive impact on ungulate populations (e.g. Wallgren *et al.*, 2009; Western, Groom & Worden, 2009). Grouping all the cattle in a region into fewer larger herds that track spatial and temporal variability of resources (transhumance) has been demonstrated to be beneficial to livestock production and rangeland condition (Breman & De Wit, 1983; Fryxell & Sinclair, 1988a; McAllister *et al.*, 2006) as well as to wildlife populations (Wallgren *et al.*, 2009; Western, Groom & Worden, 2009).

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