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Lines around fragments: effects of fencing on large herbivores

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People construct fences to delineate land ownership and to control access to land. Fences accomplish several purposes, notable among these are containing livestock or wildlife raised for profit or subsistence, excluding use of vegetation within areas to be conserved and reducing conflicts between wildlife and humans. In addition, fences may offer unanticipated benefits such as vegetation within hedgerow fences providing cover to wildlife, or grazing by confined herbivores promoting native flora. However, because fences limit mobility of large herbivores, fenced areas become fragments within the landscape. Fences may entangle or electrocute herbivores, truncate migratory routes, excise important resources needed by large herbivores and allow resident herbivore populations to become too high and damage vegetation. More subtly, fencing parcels may reduce the carrying capacity of a landscape irrespective of habitat loss by eliminating access to heterogeneous forage patches. Normalised difference vegetation indices, derived from satellite images and reflecting green vegetation biomass, are used to suggest effects of fencing upon stocking rates. Ecosystem modeling quantified the decrease in herbivore stocking rate as a 300km² parcel was fragmented. When the parcel was fenced as 10km² sub-parcels, 19% fewer cattle could be supported, compared to the parcel being unfenced.

Keywords: ecosystem modeling, fence design, fragmentation, NDVI, ungulates

Introduction

Fences are constructed for a variety of reasons, but their main purpose is to control access. Fences may improve security from thieves or delineate a boundary. In this paper, we consider effects of fences upon large herbivores, wild and domestic. There are many benefits to fencing. For example, fencing allows range to be subdivided, which can lead to more refined management of livestock and increased productivity. Fencing may also exert harmful effects on ecosystems. Confined herbivores may overpopulate a fenced area, leading to vegetation degradation and starvation. Fences may truncate migratory movements, which may have subtle effects such as animals finding alternative routes, or profound effects causing thousands of deaths as animals concentrate along the break in the migration corridor. Ben-Shahur (1993) posed the question as to whether fences reduce habitat carrying capacity for herbivores irrespective of habitat loss. In short, he asked if elimination of access to heterogeneous forage patches reduces the capability of habitats to support ungulate herbivores.

Here we review existing information on effects of fencing on ungulates and report results of quantitative analyses of satellite images and ecological modeling to demonstrate subtle effects of fragmentation. The scope of fencing, benefits of fencing and some negative consequences are briefly reviewed, using mostly African examples. We then present analyses of remotely sensed data that provide some indication that carrying capacity for herbivores declines as landscapes are fragmented. Finally, ecological modeling is used to quantify the magnitude of declines for a site in southern Africa. We conclude by recommending that fences be properly designed to meet specific needs and note that the recent removal of large-scale fences in Africa provides researchers opportunities to explore herbivore population and range responses.

Scope of fencing

When considering fencing, many in the northern hemisphere would envision a familiar style — five barbed or smooth wires on metal posts 1.3m high bordering individually owned parcels, or sub-parcels. However, such fences are not the norm in Africa, for example, where five strand designs would not impede movements of many large herbivores (Hoare 1992). Instead, fencing materials vary from moats, to cacti, thorn or stone, to barbed fencing with few strands, to poly wire or tape and electrified fencing with 21 high-tensile strands spaced 80–170mm apart (Van Rooyen *et al.* 1989). Fence design varies according to what animals are to be confined, whether they are jumpers (e.g. white-tailed deer (*Odocoileus virginianus*), impala (*Aepyceros melampus*), eland (*Taurotragus oryx*)), crawlers (e.g. gemsbok (*Oryx gazella*), pronghorn (*Antilocapra americana*), tssessbe (*Damaliscus lunatus*)), those that break fences (e.g. elephants (*Loxodonta africana*), giraffes (*Giraffa *camelopardalis*)), animals that do not jump (springbok (*Antidorcas marsupialis*), blesbok (*Damaliscus dorcus*)), or those that are difficult to fence (e.g. warthog (*Phacochoerus aethiopicus*), bushbuck (*Tragelaphus scriptus*), carnivores) (Van Rooyen *et al.* 1989). Some animals, such as carnivores, learn to avoid fences quickly, whereas some, such as giraffes, may take months. Elephants are a special challenge, because of their sheer bulk, so that a fence may be judged 'effective against...even elephants, in the absence of sufficient inducement to break it' (Hoare 1992).

Many in the northern hemisphere would also be surprised by the scale of area enclosed by some fences that do not merely enclose parcels, but rather contain entire regions. Botswana provides an example. There, livestock producers wished to have access to European markets, but to do so required that their livestock products be certified free of foot-and-mouth disease. Fences were constructed beginning about 1950 (Keene-Young 1999) to segregate livestock from wildlife, such as the 100km Nxai Pan Buffalo Fence built in 1968 (Anderson 1998). In 1975 the Tribal Grazing Land Policy stated as a goal of the government the establishment of cordon fences around livestock producing sites (Perkins 1996). Construction surged again in the mid-1990s, when outbreaks of contagious bovine pleural pneumonia were contained. Today, the Setate, Ikofa, Caprivi, Northern Buffalo, Nxia Pan and Phefodiafoka fences sum to thousands of kilometres of sanitary fences fragmenting Botswana (Perkins 1996). The Nxia Pan Buffalo Fence has been decommissioned, meaning it is no longer maintained (Anderson 1998) and 30km of fence were removed (Keene-Young 1999), but in general, the goal of segregating livestock from wildlife remains intact.

Measures to control dingoes (*Canus lupus dingo*) in Australia provide another example. In 1885, dingoes were declared as pests upon sheep; this began bounties, trapping, shooting and poisoning campaigns. Controlling dingoes with these methods was only partially successful. For example, in 1952, an estimated 500 000 sheep were killed by dingoes. In about 1954, construction of a two metre high dingo fence began (Bauer 1964, Allen and Sparkes 2001), and at its peak, 8 614km of dingo fence were in place (Glen and Short 2000). Until 1981, the fence was 5 631km, still the longest fence in the world, and twice the length of the Great Wall of China (Glen and Short 2000). The Queensland section that remains today is 2 560km.

Many conservation areas in Africa have been fenced, including the eastern, southern, and western borders of Kruger National Park that were fenced for decades (flooding prevented fencing the northern border) (De Vos *et al.* 2001). Other conservation areas fenced on a large scale include Addo Elephant National Park, South Africa; Sengwa Wildlife Research Area, Zimbabwe, along the eastern, southern, and western boundaries; Etosha National Park and Skeleton Coast National Park in Namibia; Aberdare National Park, Kenya (Woodley 1965, Rhino Ark 2002); Meru National Park, Kenya, fenced along the northeastern border; Hwange National Park, Zimbabwe; and Gonareszhou National Park, Zimbabwe, soon to merge with Mozambique's Limpopo Park and South Africa's Kruger National Park, to become the Greater Limpopo Transfrontier Park.

Benefits of fencing

The overarching benefit to fencing is to control access, so that livestock or wildlife may be confined, or given exclusive access to landscape patches. Fenced sub-parcels or paddocks allow managers to move livestock between landscape patches, optimising grazing and allowing resting of unused patches, which can increase productivity (Hoare 1992). There is a voluminous literature describing the economic and ecological benefits of grazing systems made possible by using fencing to control the timing and duration of landscape use by large herbivores (e.g. Ratliff and Reppert 1974, Eckert and Spencer 1986, Papadopoulos *et al.* 1995, Werner and Urness 1998, Williams and Hammond 1999, Kie and Lehmkuhl 2001, Halstead *et al.* 2002).

Wildlife may be confined by fences to reduce conflicts with humans, allow exploitation and to protect human life. For example, fencing allows game ranching to occur, an important industry in South Africa where 3 000 ranches exist (Grobler and Van der Bank 1992). Fencing highways is an important tool for reducing vehicle accidents, injuries and deaths (e.g. Clevenger *et al.* 2001). Containing elephants is critically important within their range in Africa. Between 1982 to 1989, 500 people where killed by elephants in Zimbabwe (Riccuiti 1993) and from June 1990 to July 1991, nine Kenyans were killed by elephants (Waithaka 1993). In his surveys in Mbololo, Kenya, Waithaka (1993) found that 97% of local people 'strongly disliked' elephants and 99% of 231 respondents claimed to have lost at least half of their season's crops due to elephant damage. A similar percentage of people voiced similar dislikes in the Aberdare region, until in 1989 an electric fence was installed, eliminating encroachment by elephants and appeasing local people (Waithaka 1993).

Fencing may reduce mixing of wildlife and livestock, decreasing the risk of disease spread and predation. In Botswana, the necessity of preventing disease spread is being debated; critics of the cordon fences say that many of the areas protected for livestock production actually contain few livestock (Anderson 1998). There is also some question about the efficacy of fencing to contain an airborne pathogen such as that causing foot-and-mouth disease (Owen and Owen 1980). Regardless, the overarching goal of meeting the requirements of European markets has been met. In our other example, the Queensland dingo barrier fence has been judged effective in reducing predation by dingoes on sheep (Allen and Sparkes 2001).

Fencing may also exclude herbivores entirely to control erosion, protect streams or water supplies or prevent trampling. For example, Maschinski *et al.* (1996) document how the extinction of sentry milk vetch (*Astragalus cremnophylax* var. *cremnophylax*) from a plot in Arizona was prevented or delayed by fencing-out herbivores. Conversely, heavy grazing by confined herbivores may promote native flora, by suppressing competing exotic species, and can alter the succession of forest due to selectivity in seedlings browsed (Linhart and Whelan 1980). Fencing studies that use enclosures to quantify effects of herbivory or that make cross-fence comparisons are numerous (e.g. Hanson 1929, Bock and Bock 1993, Hiscocks 1999). Studies that investigate vegetation responses in fenced areas where herbivores over-graze are helpful as well (e.g. Guy 1989).

Lastly, the fences themselves may benefit wildlife. The value of hedgerow fencing (or 'living fences') for wildlife has been recognised for decades (e.g. Edminster 1938) and country-wide declines in some avian populations have been documented when hedgerows were removed (O'Connor and Shrubb 1986). The role hedgerows play in connected fragmented landscape patches has become of interest recently (e.g. Demers *et al.* 1995). Lastly, hedgerow and thorn fences can promote landscape diversity by including or sheltering small trees that will escape herbivory (Reid and Ellis 1995).

Negative consequences

Countless fencing projects meet the objectives for which they were built, with little risk to livestock, wildlife, or people (although more subtle declines in carrying capacity may be occurring, as discussed in the next section). It may be that when fencing projects work as intended, their success is muted by calls for action elsewhere, by those complaining of fencing projects that cause harm. Regardless, most fences pose some risk and some fences have become infamous due to the damage caused. Accumulated effects from many small fences may lead to profound changes in animal behaviours (e.g. migrations of pronghorns appear to have been truncated in Texas; Hailey and DeArment 1969), but most are unexplored. Other fences simply do not function well. For example, sheep in California were not protected well by an electric fence (Timm and Connolly 2001) and fencing against predators can be expensive.

Wildlife and livestock attempt to move through fences, with varying degrees of success depending upon the design and species in question. Some bird species, such as swans (e.g. *Cygnus* spp.), owls, and ptarmigan (*Lagopus* spp.) will collide with fences (e.g. Bevanger and Brøseth 2000), but most movements by large herbivores are deliberate attempts to cross. Animals may be attracted to forage or crops on the other side of a fence, attempt to continue a migration or dispersal blocked by a fence, be drawn by their young that have moved under the fence and are calling, or be attempting to escape harassment due to dogs, predators, or poachers (Hoare 1992). Wildlife and livestock can become tangled and die in fences and may be electrocuted (Denney 1964, Hoare 1992). Fences with smooth wire can even provide poachers with material for snares.

Livestock or wildlife confined or excluded from parcels may over-graze the available vegetation. In fenced plots, elephants can severely damage acacias (Hoare 1992). Across a fence in Amboseli National Park that excludes elephants the effects are striking. The fenced forest is dense and green, whereas the acacias outside the fence are broken and stripped of leaves (Ricciuti 1993). Elephants have cleared much of the available browse, so that browsers like giraffes and kudus (*Tragelaphus* spp.) are rare in the park. In general, when elephants are excluded from an area, there is little grass, thick bush develops, and tsetse flies (*Glossina* spp.) may increase (Ricciuti 1993). In Sabi Sand Wildtuin, bordering Kruger National Park, after the fence was taken down the changes in vegetation were profound, mostly due to elephant damage (Hiscocks 1999), but how much of the damage was simply vegetation returning to a more normal state remains a question.

Some concern has been expressed over the potential for inbreeding in fenced conservation areas in Zimbabwe (Ricciuti 1993), but this may be in-part an attempt to deflect some criticism received over their elephant culling programme. The difficulty in maintaining truly impermeable fences (e.g. Van Rooyen *et al.* 1989), and the small number of immigrating animals needed to prevent inbreeding in most species, suggests this is not a pressing problem. In contrast, Grobler and Van der Bank (1992) point out that populations on many South African game farms are very small, with perhaps 10 individuals of the rarer species within a fenced area. Founder effects and inbreeding are distinct concerns, in that case.

Fencing may prevent wildlife or livestock from accessing key resources. For example, in Kajiado District, Kenya, swamps created by water runoff from Mount Kilimanjaro provide a critical dry season forage resource for elephants and other wildlife, as well as Maasai livestock. Namelok Swamp, Kimana Swamp and their associated springs have been fenced to protect water sources and to graze livestock, and fencing and agriculture around other swamps limit access by wildlife and livestock (Boone and Coughenour 2001). Conservationists and cultural anthropologists are concerned that access to the swamps may become so constrained that wildlife and livestock populations will collapse.

In Botswana, fence construction began in the 1950s (Keene-Young 1999), but it was not until the droughts of the 1980s that the international conservation community took note. In the Kalahari, wildebeest only migrate when forage (and water stored within the forage) is too low to sustain the herd. In dry years, wildebeest moved to the northeast to Lake Ngami and the Okavango Delta in search of water, but that migration corridor was severed in 1954 by the Central Ngwato fence (Owen and Owen 1980, Spinage 1992). The fence forced animals to continue to the east, toward Lake Xau, where they accumulated and consumed all available forage. In that year alone, Williamson and Mbano (1988) estimated that 52 000 wildebeest died in the Lake Xau area, and the number may be as high as 80 000 (Parry 1987). A significant migration to the southeast, towards Molopo River was blocked as well. In Botswana, hartebeest (*Alcelaphus buselaphus*) migrate and Spinage (1992) reported 10 000 hartebeest dying against the Ghanzi fences between 1981 and 1987. In the early 1980s, some animals migrated to the north, east, and south as normal, but these could not return because of fences and disturbance from populated areas, so many animals died (Spinage and Matlhare 1992). If animals cannot repopulate areas following droughts, water-independent species such as gemsbok and springbok will be favoured (Spinage and Matlhare 1992). All told, the droughts of the 1980s were estimated to have caused 90% mortality in migratory species (although declines began much earlier (Spinage 1992)), and the populations are unlikely to recover (reviewed in Perkins 1996).

Environmental impact assessments were not required nor were they done when building the veterinary fences of Botswana, nor were communities consulted (Anderson

1998). Local hunters would like some fences to be removed to begin to rebuild wildlife populations (Keene-Young 1999). Small sections have been removed and larger fences decommissioned, but the pace is glacial. Like many African nations, the cause for the declines of wildlife in Botswana are complex: these include hunting, the expansion of livestock production and loss of access to water. Regardless, the losses caused by veterinary fences — and continued fence building — appear to be in conflict with the Botswana National Development Plan that states a desire to make tourism a top contributor to the county's gross domestic product (Perkins 1996).

Fragmentation and carrying capacity

We turn to a more subtle response from fencing a landscape — changes in carrying capacity not related to habitat loss and to quantitative analyses that illustrate effects. Fences can fragment landscape in two ways. Carrying capacity can be reduced if animals are excluded from areas of the landscape because such exclusion compresses the area of usable habitat. Alternatively, even when animals are not excluded from habitats, their movements may be restricted by fences. Here, we discuss effects of fences on carrying capacity resulting from restriction on animal movements, apart from effects due to habitat loss.

Spatially heterogeneous landscapes provide opportunities for vagile herbivores to access forage resources across a range of scales. When these resources are patchily distributed in a random or uniform way, the variety of resources accessible to herbivores increases as a power of the square root of the area accessible to them (e.g. Ritchie and Olff 1999). Thus, herbivores have a range of choices of resources in landscapes that are unfragmented relative to those where movements are more restricted. This is important because when the occupied patch is not providing adequate forage, other more productive patches are available. If fences fragment a landscape, herbivores in low quality or low biomass patches may not be able to access patches that are higher in quality or biomass.

Reports of effects of habitat loss on carrying capacity are common in the literature, but reports of effects of fragmentation alone are rarer; e.g. the question posed by Ben-Shahar in 1993 — *How does fragmentation affect carrying capacity?* This question is a foundation of ongoing research sponsored by the US National Science Foundation. Andrew Ash is leading field trials with cattle in Australian paddocks of differing areas that will provide evidence of effects of fragmentation. Ecological modeling is ongoing as well, assessing effects from fragmentation on large herbivores. Here early progress is reported, using patterns in satellite imagery and ecological modeling to draw inferences.

Inferences from greenness

Data sources

Satellite images provide measures of greenness we may use to infer forage heterogeneity. Advanced Very High Resolution Radiometer (AVHRR) sensors aboard National Oceanic and Atmospheric Administration (NOAA) weather satellites acquire images every day for five bands of the electromagnetic spectrum, for the entire globe, at a resolution of 1.1km, where each pixel in the image represents a square area on Earth, 1.1km on a side. Soils and vegetation reflect near infrared (NIRed, 0.72–1.10μm) and red (Red, 0.58–0.68μm) light differently, so analysts use these bands to calculate normalised difference vegetation indices (NDVI), using: NIRed-Red / NIRed + Red. NDVI indices are correlated with vegetation biomass and condition (an early example includes Tucker *et al.* 1985, with many more recent applications, e.g. Eklundh 1998, Boone *et al.* 2000). Areas with high red reflectance but low NIRed, such as water, receive low NDVIs and areas that reflect NIRed well but not red, such as vegetation, receive high NDVIs. Mathematically, the index spans –1 to 1, but in practice, values range from 0 to about 0.8. Producers scale these values so that they are 8-bit integers, spanning 0 to 255 or a similar range, with some values (e.g. 0 to 5) used to identify water bodies and clouds. The Global Land 1-km AVHRR Program (USGS 1998) used daily satellite images to compile global 1km resolution, 10-day NDVI composites, selecting the maximum NDVI value during the 10-day period, yielding 36 images per year. The images were downloaded for East Africa and South Africa, for April 1992 to May 1996, with several missing periods, including all of 1994. For each of the 36 10-day periods, the images across years were averaged, yielding NDVI images for an average year in the mid-1990s. An annual *greenness profile* may be constructed for each pixel from the 36 images, showing how greenness changed through the year.

A second source for NDVI images is from the SPOT program Earth Observation System, which was designed and developed by Centre National d'Etudes Spatiales of France, with cooperation from the governments of Sweden and Belgium. SPOT satellites are best known for their high resolution (10–20m pixels) images that have been acquired for more than 15 years. However, SPOT4 and the new SPOT5 include a VEGETATION sensor, which has a coarser resolution (1.15km^2 pixels) and acquires images with the same spectral bands as the high resolution sensor. High resolution images and essentially real-time VEGETATION images accompanied by detailed metadata are commercial products sold by Spot Imaging Inc. and the VEGETATION Program. VEGETATION also freely offers full resolution (1km pixel) NDVI images for entire continents, about three months after the images are taken (VITO 2002), with the earliest images from April 1998. These data are 10-day composites, where for each pixel the best NDVI value available (based on sun and sensor angles etc.) is selected from the 10-day period, and a composite similar to those described for AVHRR is created. We acquired the VEGETATION NDVI images for Africa from April 1998 to April 2002 from the VITO server, and retained from them portions for East Africa and South Africa. The images were averaged to yield 36 images of average NDVI from 1998 to 2002, analogous to the AVHRR data.

Fragmentation through land tenure change

Land tenure in Kajiado District, southwestern Kenya, has changed dramatically in the last 30 years. Historically, pastoralists occupied eight Maasai sections grazing their livestock within section boundaries. Sections were large ($\bar{x}$ = 2 731km^2) and contained diverse topography, a variety of habitats, and several water sources. In the 1960s and 1970s, hopes of improving livestock production and land access for Maasai led the World Bank and Kenyan government to subdivide Kajiado into group ranches, now numbering 52 ($\bar{x}$ = 420km^2). Title to group ranches were held by Maasai, with ranch members sharing common ownership. From the beginning of group ranch formation, and increasingly common today, group ranches in southwestern Kenya (e.g. Kajiado District, Narok District ranches adjacent to the Maasai Mara National Reserve) are being subdivided into parcels held by individuals or families.

Many of the goals of group ranch formation have not been met (reviewed in Kimani and Pickard 1998). Land has tended to stay in Maasai ownership (ironically, in some cases because ownership amongst members is contested in court, preventing land sales), but livestock production has not improved, and continued subdivision bodes poorly for the future (Boone and BurnSilver in press). There are many reasons for this, but here we focus upon access to forage. Greenness profiles from NDVI demonstrate effects of fragmentation. In Ilkisongo Maasia Section, in southern Kajiado District, Kenya (Figure 1a), 1km^2 pixels show a broad diversity of profiles — herders that occupied patches with inadequate forage had opportunities to move their livestock to more productive patches. Within Imbirikani Group Ranch (Figure 1b), the diversity of greenness profiles is reduced, reflecting fewer options available to herders to respond to stresses such as drought. Finally, within a single fenced 5km^2 parcel that is individually held (Figure 1c), the profiles essentially overlay each other, and there is little option available to the owner if forage production is low and owners maintain exclusive use of parcels. We have been told that subdivision of group ranches into individual holdings is inevitable. If true, one means of increasing options for herders is for them to join grazing associations (Figure 1d), which increases the diversity of patches available for grazing (Boone and BurnSilver in press). The general reduction in options available to herders suggested in Figure 1 is likely broadly applicable, but in semi-arid and arid areas, loss of access to water may overshadow access to forage. Some owners will receive well-watered, productive parcels. However, most ranch members in southern Kajiado District will gain title to parcels without water and with poor forage production.

Spatial scale and greenness

Oesterheld *et al.* (1998) have demonstrated a strong correlation (e.g. r^2 = 0.90, $P < 0.001$, df = 61) between integrated NDVI values and regional livestock stocking rates in Argentina, and Boone has explained 60% of the variation in cattle stocking rates in rangeland districts of Kenya using integrated NDVI (unpublished data). However, these data were derived from large regions and are for areas where animals can move about relatively freely. The effect of fragmentation shown in Figure 1 suggests that appropriate stocking for landscape patches should include an area measurement, or some other metric reflecting landscape heterogeneity. Developing such metrics is a focus of current research. A promising measure for remotely sensed data is simply the coefficient of variation (CV) of pixel values within a landscape patch. To apply this to annual greenness profiles comprised of 36 images, the CV of the pixels within the area of interest (e.g. group ranch, farm, or parcel) was calculated for each image. The mean value of the 36 CVs represents the vegetative diversity of landscape patches available to large herbivores. We calculated the CVs of pixels for all VEGETATION images for a series of nested parcels within a 300km^2 block of land. For analyses, each 300km^2 block was divided into 1 to 30 parcels (Figure 2). Five locations around each of Maasai Mara National Reserve, Kenya, Ngorongoro Conservation Area and Tarangire National Park, Tanzania, and Kruger National Park, South Africa (maps, Figure 3) were sampled.

As expected, the effect of decreasing parcel area on NDVI diversity was log-linear (Ritchie and Olff 1999) and varied across sites (graphs, Figure 3). Topographically diverse Ngorongoro/Tarangire (Figure 3a) had higher CVs than the flatter Maasai Mara and Kruger regions (Figure 3b and c). Areas with high NDVI values generally have higher herbivore stocking rates (Oesterheld *et al.* 1998), but if NDVI were equal across sites, the higher heterogeneity in Ngorongoro/Tarangire suggests stocking would be higher on those sites than on Maasai Mara or Kruger because animals would have access to forage patches with a greater variety of phenotypic responses. The steeper slope relating parcel area to CV indicates fragmentation would have a relatively greater effect on stocking in Ngorongoro/Tarangire than the other sites (Figure 3). The spread of CVs around the mean CV values was high, however, with area weakly correlated with CVs (Spearman's correlation, Ngorongoro/Tarangire = 0.52, Maasai Mara = 0.49, Kruger = 0.41). This reflects that, even with the smallest parcels, some patches remained heterogeneous, but the tendency was toward homogeneity. How this tendency for fragmentation to reduce vegetation heterogeneity relates to carrying capacity is discussed in the next section.

Ecosystem modeling

SAVANNA modeling system

To begin evaluating the effects of decreasing heterogeneity upon carrying capacity, we used the SAVANNA modeling system. Initial development of SAVANNA began in the Turkana District of Kenya and improvements to the model were made in subsequent applications (e.g. Coughenour and Ellis 1993, Boone *et al.* 2002, reviewed in Ellis and Coughenour 1998). SAVANNA has been used, for example, to: evaluate grazing capacity for livestock and wildlife of Kruger National Park, South Africa (Kiker 1998); address potential management questions in Ngorongoro Conservation Area, Tanzania (Boone *et al.* 2002) and assess the utility of seasonal climate forecasts for livestock owners in the North-West Province of South Africa (Boone *et al.* 2004).

SAVANNA is a series of inter-connected Fortran computer programs that model primary ecosystem interactions in arid and semi-arid landscapes, simulating functional groups for plants and animals. SAVANNA is spatially explicit and represents landscapes by dividing them into a system

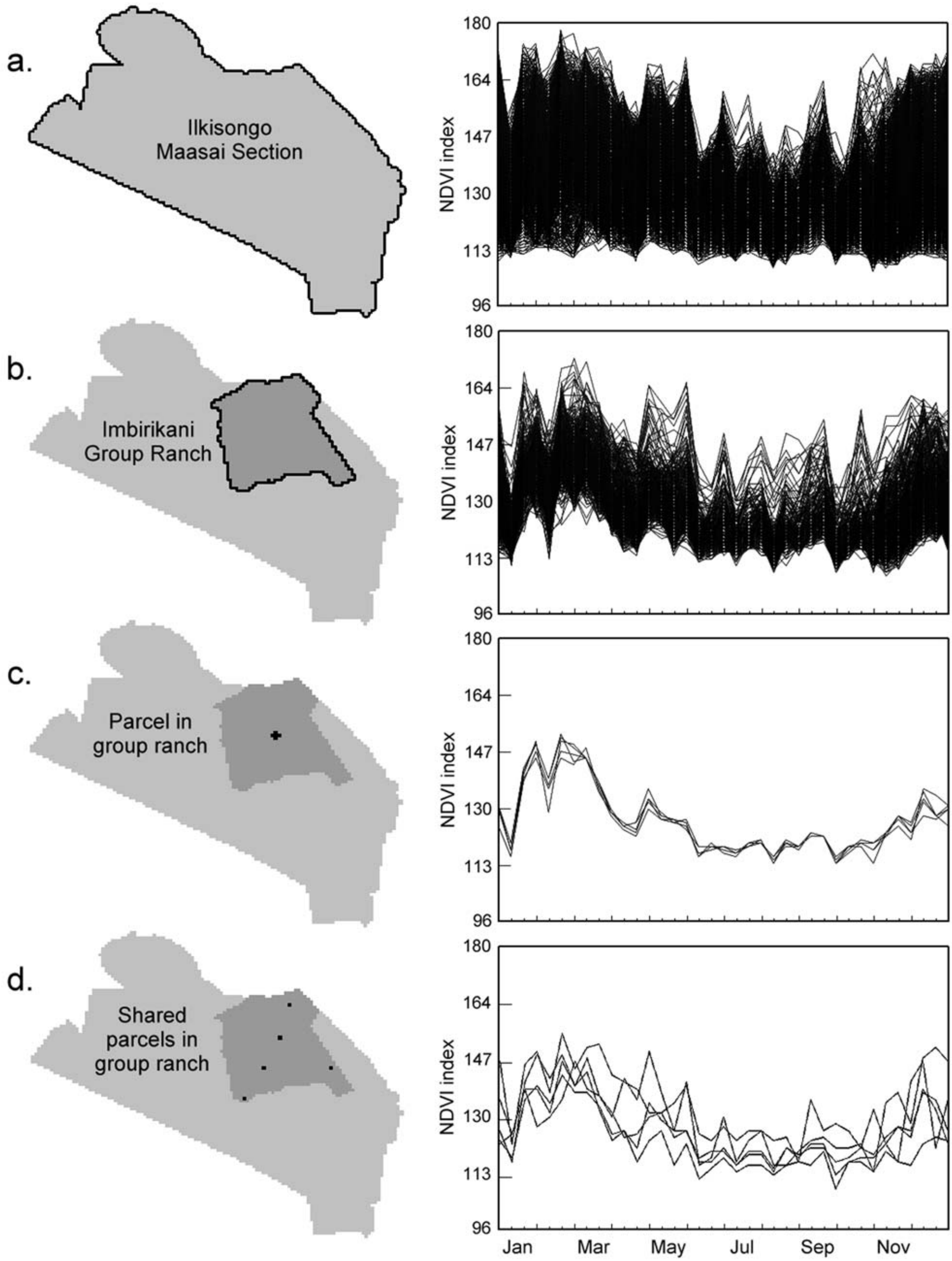

Figure 1: NDVI greenness profiles for each 1km² of a landscape patch, including (a) all of Ilkisongo Maasai Section, (b) Imbirikani Group Ranch, (c) a 5km² parcel within the group ranch, and (d) five shared 1km² parcels representing a grazing association. Ilkisongo Maasai Section is in Kajiado District, in southwestern Kenya

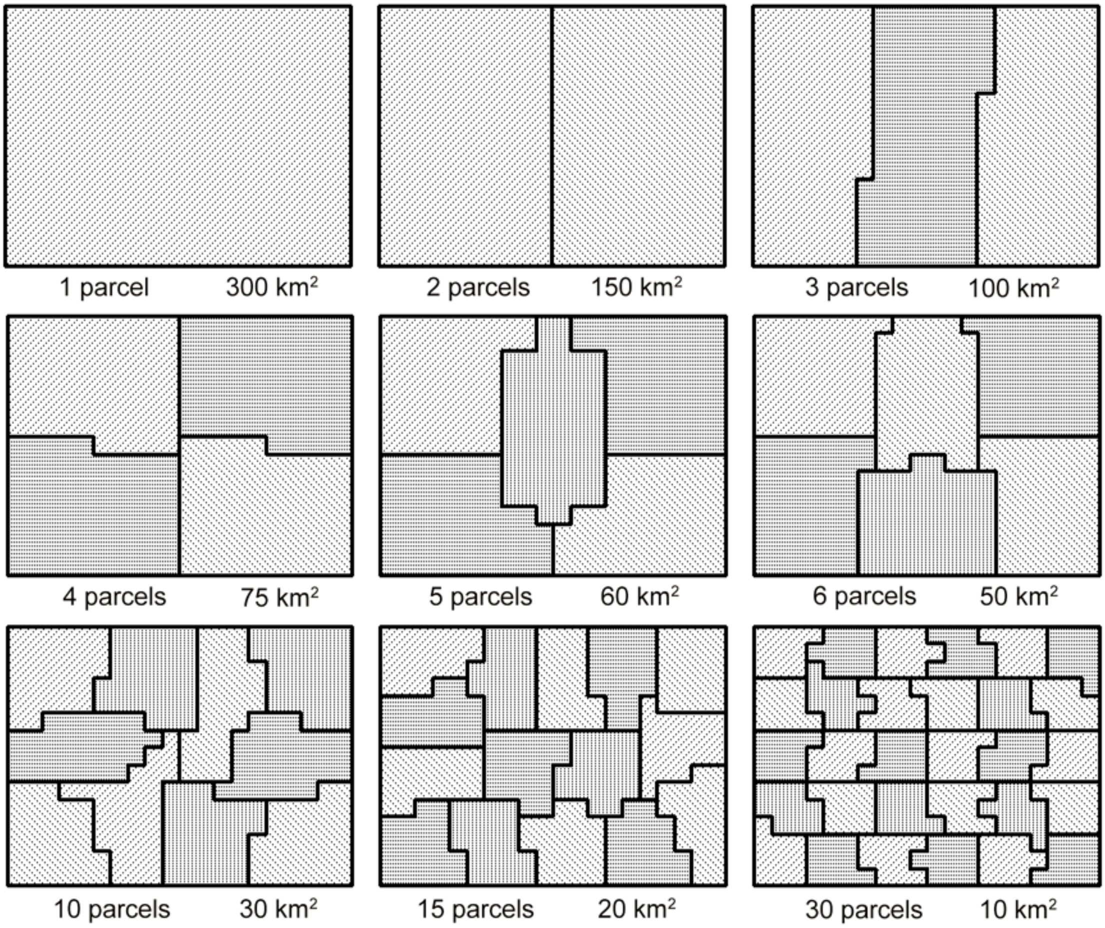

Figure 2: Parcel maps used in spatial analyses, fragmenting a 300km² landscape block that is 20km east-west and 15km north-south. The area of each parcel and the number of parcels are shown below each map

of square cells. SAVANNA reads computerised maps that include, for example, the elevation, aspect and soil type of each cell. The model predicts water and nitrogen availability to plants using rainfall and soil properties for each of the cells. Based upon water, light and nutrient availability, quantities of photosynthate are calculated for plant functional groups using process-based methods (Lambin *et al.* 2000). Photosynthate is distributed to leaves, stems and roots using shoot/root ratios and other plant allometrics, yielding estimates of primary production. Plant populations are calculated from primary production.

A habitat suitability index is calculated for each cell in the landscape, at weekly intervals and for each animal functional group, based upon forage quality and quantity, slope, elevation, cover, water availability and the density of herbivores. Individuals in the population are distributed on the landscape based upon these indices. Animals will feed upon the available vegetation, depending upon dietary preferences and consumption rates. The energy gained is reduced by energy costs associated with basal metabolism, gestation, and lactation. Net energy remaining goes toward weight gain, with weights reflected in condition indices. Summaries of the status of vegetation, herbivores and climate are produced at monthly intervals. For more detail about SAVANNA, see Boone and Coughenour (2001).

Hypothetical application

A hypothetical application was used for these analyses, but it was based upon an existing application of SAVANNA (version 4L) to the Vryburg area in the North-West Province of South Africa (Boone *et al.* 2004). In an application, plant and animal functional groups must be defined, based upon the questions to be addressed, balancing the need for detail in responses and the costs of parameterisation and execution. The application that was modified included seven vegetation functional groups: 1–3) high, moderate, and low palatable grasses, 4) annual grasses, 5) acacia shrubs (e.g. *Acacia mellifera*), 6) camphorbush shrubs (*Tarchonanthus camphoratus*), and 7) acacia trees (e.g. *A. tortilis*). Grasses were grouped into palatability classes reflecting their general acceptance to livestock. Originally, five animal functional groups were defined (i.e. cattle, goats, sheep, horses and donkeys). Herbivore populations show complex compensatory responses, making calculations of standardised metrics (e.g. tropical livestock units) complex and potentially misleading. Here, the hypothetical application was made as

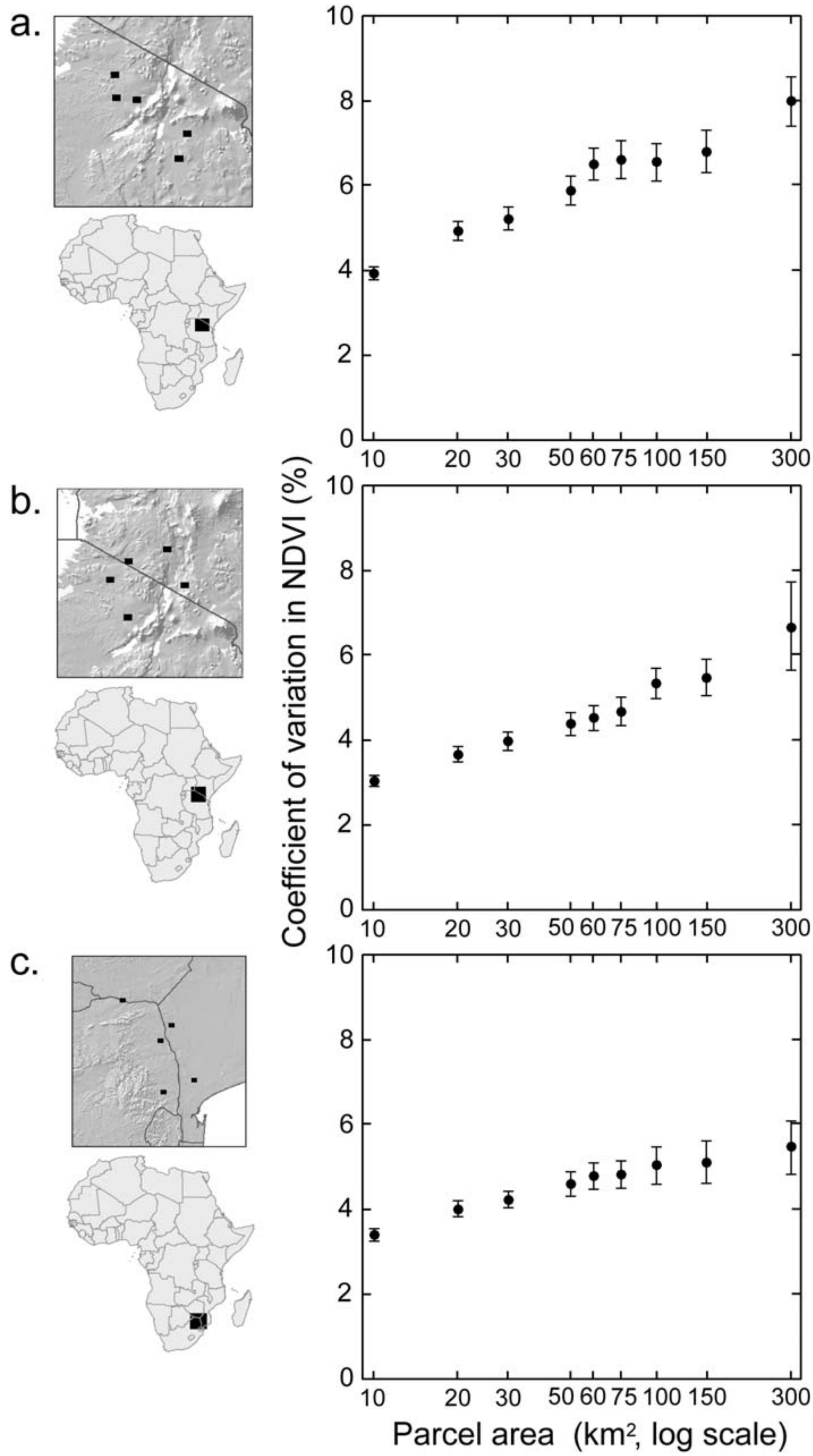

Figure 3: The relationship between parcel area (see Figure 2) and the spatial variation in NDVI, related to habitat heterogeneity, with standard error bars. Five 300km² blocks of land are summarised in each graph, for areas around (a) Ngorongoro Conservation Area and Tarangire National Park, Tanzania, (b) Maasai Mara National Reserve, Kenya, and (c) Kruger National Park, South Africa. Insets show the locations of these blocks, and the region within Africa

straightforward as possible. A single herbivore functional group was parameterised, representing cattle and the seven vegetation functional groups remained as described.

Although this hypothetical application is not intended to link directly to a given landscape and management system, actual spatial data were used in modeling. A 300km² block (20km x 15km) within Vryburg 1 Township was selected. Elevation, slope and aspect were derived from a digital elevation model produced by the US Geological Survey and acquired from the African Data Dissemination Service (ADDS 2001). The block contained a single vegetation type (Low and Robelo 1996), Kalahari Plains Thorn Bushveld. Soil types were taken from the Land Type database available for South Africa and provided to us by the Department of Agriculture, North-West Province. All geographic data were generalised to 1km x 1km resolution cells. Weather data were supplied by the South African Weather Service for 166 weather stations in the region. Records included precipitation and minimum and maximum temperature and spanned the period from 1900 to 1995. Carrying capacity is related to climate history in a complex way that was not the focus of these analyses. We therefore used a method within SAVANNA to generate a random weather history, where weather information for a year is drawn from the weather data randomly. Water sources are typically used in SAVANNA, represented as distance-to-water maps that comprise a component of the habitat suitability index for herbivores. In this hypothetical application, we assumed water was not limiting (i.e. distance-to-water was not included in the suitability measures). This allowed effects of fencing to be explored without being confounded by whether or not a fenced area included a borehole.

Parameters were set in the model based upon an extensive literature review, previous SAVANNA applications (e.g. Coughenour 1992, Kiker 1998, Boone *et al.* 2002), field work, and expert opinion. The numerous parameters may be classified within groups of ecological processes: plant phenology and biomass (e.g. Ndawula-Senyimba 1972, Theunissen 1995), plant allometrics and growth (e.g. Coughenour *et al.* 1990, Tewari 1996), livestock energetics and growth (e.g. Stafford Smith *et al.* 1985, O'Reagain and Owen-Smith 1996), grazing effects and stocking (e.g. Danckwerts and Nel 1989) and effects of rainfall variability (e.g. Donaldson 1967, O'Connor 1994). The initial stocking rate for the block was based on the recommendation from the Department of Agriculture, South Africa (1999). They recommended the site be stocked at 7ha per large stock units (LSUs). Taking each animal to be equal to one LSU, the 300km² would support 4 286 cattle. Parameters were adjusted until the modeled population averaged about 4 286 cattle over a 30 year simulation. However, the population varied by more than 50%, in response to droughts, as seen in the region.

Model performance could not be compared to real-world data in this hypothetical application. However, the overall structure and algorithms of the model have been validated extensively in a variety of contexts (e.g. Kiker 1998, Boone *et al.* 2000, Weisberg and Coughenour 2003). In the application for the North-West Province of South Africa, modeled herbaceous above ground biomass was compared to NDVI (ADDS 2001). We judged that phenology and relative greenness of plants were being represented well by the model, and that livestock losses in drought years were in general agreement with those reported by owners.

Analyses used the spatial arrangement of fenced parcels shown in Figure 2, with parcels ranging from the entire 300km² block modeled, to 30 parcels each 10km². The model was run separately for each of the parcels, with cattle confined to the parcel in question. The initial number of cattle in the model run at 300km² that yielded appropriate stocking was 4 000 animals. For each run with a smaller parcel the initial stocking was adjusted using a simple linear relationship with area (e.g. for 150km², 2 000 cattle, 100km², 1 334 cattle etc.) so that initial stocking rate was proportional to area and the same across simulations. Each simulation was run for 30 years and average stocking in the last 15 years of the simulation was the response of interest, representing carrying capacity after a 15 year period to attain some degree of balance with the environment in the parcel. Stocking rates were summed across parcels so that in each case the measure of interest was the number of cattle that could be supported on 300km². Weather patterns affect stocking strongly in this arid region, so the weather pattern was kept the same for each analysis of the set of parcels (i.e. 300–10km²), but the entire set was modeled 12 times using a different randomly generated weather pattern for each set of analyses.

Results of ecological modeling

The carrying capacity of the 300km² block declined steadily with increasing fragmentation (Figure 4), although capacity varied depending upon weather history, leading to variation in carrying capacity (stocking = 3 583 + 2.858 (parcel area in km²), df = 106, $r^2 = 0.41$, $P < 0.001$). In general, when the 300km² block was fragmented into 10km² parcels, the same 300km² block supported almost 1 000 fewer cattle than when unfragmented. Although this is a single example that frames our future research, rather than an end in itself, the implications of these results are profound. How does vegetation heterogeneity (e.g. Figure 3a vs Figure 3c) affect the relationship in Figure 4? Is the relationship similar for more productive sites? Is topographic complexity more important in determining the slope of the relationship in Figure 4 than vegetation complexity? Is the relationship ameliorated by a larger herbivore community? If the species were migratory and required more diverse resources, would the slope shown in Figure 4 be steeper? These and other questions will be addressed by our ongoing studies.

Discussion

There are clear benefits to fencing parcels, including allowing exclusive access and assignment of title. Governments encourage parcels to be fenced, without considering indirect costs, such as the external inputs that will be required to offset declining livestock productivity. Results such as those in Figure 4 and from ongoing analyses will allow policy makers to better consider costs of fragmentation on herbivore production and balance them against benefits. In some cases the benefits of subdivision may outweigh the need for external

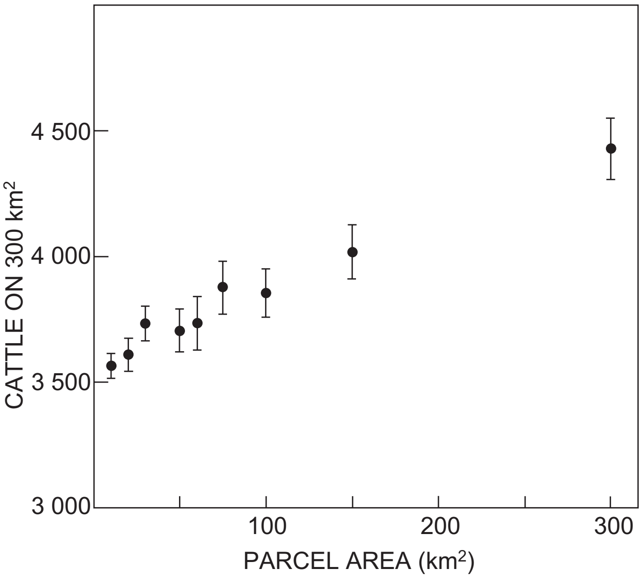

Figure 4: The effect of reducing parcel area on the number of cattle that may be supported on a parcel in an arid South African landscape, with standard error bars and a regression line (see Results). Responses were more variable as parcel area declined, but the larger sample size (e.g. 30 of the smallest parcels versus a single large parcel) led to smaller standard errors

support. In other fragmented areas, it may be most economical to remove fences, reduce fragmentation and allow herbivores to access a greater diversity of landscape patches.

Where fences are used, they should be properly designed, so as to reduce fence mortality and other detrimental effects (e.g. Platt and Temby 1999, Goddard *et al.* 2001). In general, US state governments have designs available that are appropriate for regional wildlife and livestock (e.g. Denney 1964). Fences can be expensive to construct and difficult to maintain, so the fence should only be built to meet an identified need. Creative solutions are possible, especially where semi-permeable fences are adequate. Mirrors, reflectors, repellants, and lights may be used to alert wildlife to rarely traveled roads, for example. Permeable sections may be incorporated into impermeable fences, using gates or underpasses (Putman 1997), with accompanying guide fences to direct wildlife. In cases where fencing is not required year-round, such as in crop production, wire fences may be dropped to the ground or sections opened, to allow animals to pass freely during a portion of the year. If protection of crops was needed, for example, ecosystem integrity may be better served if the cropland were fenced, rather than the conservation area from which wildlife disperse. Fences that are no longer needed should be removed and recycled, a task some non-profit groups will do at no costs. In general, 'fencing should solve the problems, not export them to adjacent areas' (Hoare 1992).

When a fence is removed, often the herbivores return quickly, such as elephants migrating from Kruger National Park into newly opened areas (e.g. Hiscocks 1999). In other cases, effects of fencing are long-lived. Hewson and Wilson (1979) document sheep herds remaining in traditional grazing areas defined by fences that were removed decades before, a pattern stronger than any effect associated with vegetation. Whyte and Joubert (1988) predict that if fences on the western border of the central district of Kruger National Park were removed, the wildebeest population would not rebound, nor would the surviving individuals adopt the migratory ways of their ancestors. Such predictions are testable — those fences are now being removed (De Vos *et al.* 2001). 'What is happening today in Botwana is what happened in, for example, Kenya in the 1920s, when the Rift Valley farms were fenced, preventing the migration of wildebeest and zebra.' (Spinage 1992). We know today that wildebeest populations in the Rift Valley recovered from fencing. We have opportunities to document population responses to fence removal. Quantifying habitat or life history attributes that make some effects of fencing on populations reversible whereas others are not would be helpful to conservation.

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