Large herbivores in space

Resource partitioning among savanna grazers in a heterogeneous environment

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Joris Petrus Gerardus Marinus Cromsigt

geboren op 27 december 1975
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Promotores:	Prof. Dr. H. Olff Prof. Dr. H. H. T. Prins
Beoordelingscommissie:	Prof. Dr. N. Owen-Smith Prof. Dr. H. De Kroon Prof. Dr. M. Klaassen

In memory of Xolani Mthiyane

Ik kwam als vreemdeling hier
Lang geleden aan
Jij hebt met mij gepraat
Ik heb jou leren verstaan
Ik ken jouw schaduw-kant
Ik weet hoe jij kan wees
Zo innemend en zo gesloten
Soms zo koud als die Weskus zee

Maar jij hebt mij altijd weer ontvangen
Met open armen op mij gewacht
Jij was mijn uitweg uit het donker
Jij was het daglicht na die nacht

Jy vir my Suid Afrika

Dus trek jouw grijze mantel uit
Van koude trots en zelfverwijt
Want de plek die zijn onschuld heeft verloren
Is ook de plek waar de liefde wordt geboren

(Stef Bos, Jy vir My, Donker en Licht)

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Voorwoord

Het is natuurlijk onmogelijk om precies te weten waar het ooit begon. Voor mijn gevoel spelen twee situaties echter een centrale rol. Ons pap, die met me rondstruinde door gebieden als de Kampinasche heide en me wijs wist te maken dat mars repen niet uit Veghel komen maar uit het rulle Brabantse zand, terwijl ik me inprentte dat de wolven ons op de hielen zaten met de ondergaande zon. Maar eigenlijk toch vooral ook opa Braam, die ik volgde in 't veld tijdens z'n inspectierondes. De trots en warmte die ik voelde als hij over z'n land en gewas heen keek heeft me onbewust de liefde voor 't veld bijgebracht. Nu nog, als ik m'n veldexperimenten 'inspecteer', denk ik terug aan die uren met hem. Op de een of andere manier hebben Daktari en de fotogids van safaripark Beekse Bergen me op een gegeven moment ingeprent dat het Brabantse veld toch echt ooit eens het Afrikaanse veld moest worden. In die wolven tussen Boxtel en Oisterwijk geloofde ik al lang niet meer, dus die spanning moest nu van elders komen…

Dit kreeg een vervolg tijdens een open dag aan de Landbouwuniversiteit Wageningen in 1993 waar ik, gedesillusioneerd door de verhalen van Bosbouw en Tropisch Landgebruik, opeens tegen een student aanliep die net terug was van onderzoek aan olifanten in Afrika. Dat was het einde van mijn twijfel en omdat hij biologie studeerde was die keuze dus gemaakt. Ironisch genoeg bestond mijn hele studie vervolgens uit kasstudies en theoretisch modelleerwerk. Toen ik dacht eindelijk het Afrikaanse veld in te kunnen voor een onderwerp aan Zwarte Neushoorn bleek bij aankomst in Pietermaritzburg, Zuid-Afrika, dat ik de neushoorns maar moest simuleren in een stoffig kantoor omdat m'n veldwerk niet te regelen viel. Daar zat ik, eindelijk onder de Afrikaanse zon, in een airconditioned hok! Vreemd genoeg was dit wel de aanleiding voor dit proefschrift. Halverwege mijn tijd in PMB kreeg ik het verzoek uit Nederland om Han Olff gezelschap te houden tijdens zijn zoektocht naar veldsites voor nieuw op te zetten onderzoek. Dit bracht me dan toch eindelijk waar ik wilde zijn, de Afrikaanse wildernis. Deze trip met Han naar Hluhluwe-iMfolozi en Mkuze Game Reserves leidden er later toe dat ik solliciteerde op een promotieproject bij hem, een sollicitatie die uiteindelijk heeft geleid tot dit proefschrift.

Dit proefschrift ligt er niet zomaar en naast mijn eigen bloed en zweet van de afgelopen maanden ben ik vele mensen erg dankbaar voor hun steun gedurende het traject van de afgelopen 4 en half jaar. I start with thanking the people that I am most grateful to because they from the basis of the work presented in this thesis, our SABRE field team. Thanks to Xolani Mthiyane, Nonhlahla Mbatha, Khanyi Mpandza, Sinenhlahla Mhlongo, Johan Ngobese, Sipho Khumalo, Emmanuel Buthelezi, Thobile Shelembe and Russell Xaba I was able to collect the enormous amount of data presented in the following chapters, and more… Next to being invaluable in the field, you all made my stay in South Africa an unforgettable journey. Ngiyabonga kakhulu! Salani kahle!! Xolani boet, may you be resting in peace, your enthusiasm and joy of life will keep on encouraging many.

Verschillende studenten hebben met een afstudeeronderwerp in Hluhluwe-iMfolozi bijgedragen aan dit proefschrift. Mijn dank gaat met name uit naar Eelke Folmer, Hilco Jansma en Margreet Drijfhout. Jullie hebben allemaal een belangrijke bijdrage geleverd wat ook blijkt uit het feit dat veel van dit opgenomen is in dit proefschrift. Bedankt vooral ook voor de goeie tijd in het veld.

Dank gaat uiteraard ook uit naar mijn beide promotores, Prof. Dr. Han Olff en Prof. Dr. Herbert H.T. Prins. Han, voor mijn gevoel is dit ooit begonnen toen we achter een neushoorn vast zaten in Mkuze Game Reserve. Het bewijs hiervan staat nog steeds ergens op video. De vrijheid en het vertrouwen die je me gegeven hebt de afgelopen jaren hebben me een zelfstandig onderzoeker gemaakt en bovendien geleerd hoe ik een veldproject moet organiseren en leiding geven in de tropen. Bedankt ook voor je bijdrage aan mijn stukken. Herbert bedankt voor het snelle doorlezen van het manuscript en voor het steunen van mijn overgang van Wageningen Universiteit naar Rijksuniversiteit Groningen. Bovendien bedankt voor het faciliteren van de aanvraag waaruit dit proefschrift is voortgekomen, ook dank aan anderen die aan deze aanvraag hebben bijgedragen.

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Dungbeetle, the research centre, is a place that does not let itself easily be explained. It received its name from an Australian research team that studied dung beetles and funded some accommodation that eventually led to the beautiful research station it is now. Besides all the fantastic facilities, it is the people who make it such a special (though sometimes weird) place. From naked dinners to quiet tea breaks on the 'stoep', all in all one can't wish for a better place to do your field work. Some people I have to specifically mention. First of all, Tamalina, you are the secret (though not quiet) driver of Dungbeetle! Thanks for being a second mom to all of us… And of course the dungbeetle gang thanks for being a second family, specifically Jan, Matt, Luca, Bernie, Wendy, Nicole, Cleo, Nikki, Liz, Krissie, Thadaigh, Michaela, Glenn, Helena, Anna, Alice, Max, Cathy… Finally, I want to mention our mammalian brothers and sisters that lived with us in the camp. The usual zebra and nyala, a grumpy old warthog male that was shot because it chased some school children (in memoriam), our 3 elephant boys that frequented the pond behind the wooden garden hut we lived in (for some reason they pushed over all the trees in the camp without hitting our hut, though I didn't believe this the first night I heard an elephant stomach rumbling on the other side of a 1 cm wooden wall), and the ghost leopard we regularly heard but saw only once.

En dan blijven daar de mensen die ik telkens achter moest laten als ik weer eens naar het zuiden vloog. Mensen die elke keer weer daar waren bij terugkomst, vrienden en familie. Bedankt, voor zoveel meer dan een week wandelen in de vrieskou, nachten lang doortrekken met discovery en rembo & rembo, het in de voetsporen treden van Rooks en Theunisse, fijne kroeggesprekken, 'n gedeeld verleden; Igor, Peter, Ties, Esther, Jorit, Rik, Kees, Robert, Jelle, Steve en Sabine, Wendy, Jan and Cleo, Roos. En m'n familie, thuiskomen blijft de heerlijkste remedie om weken van gevechten met figuren en schrijfblokkades van je af te laten glijden. Dit gevoel, dat ik krijg als ik bij Den Bosch de Maas over ga, daar zijn jullie verantwoordelijk voor; ons pap en mam, Yvonne en Ferry, de cromsigten en bramen. Dat het voorbij Doetinchem in het uiterste oosten van het land ook goed toeven is dank ik aan Johanna, Dick, Dennis en Frank!

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maart 2006, Drakensberge, Republic of South Africa

1

General introduction

Joris P. G. M. Cromsigt

Xolani, you were the first SABRE team member, working with us from 2000-2003, and jointly responsible for setting up many successful studies, including the one in chapter 5 and 6 of this thesis… After 2003 you started a successful career within the tourism department of Ezemvelo KZN Wildlife. In 2004 a tragic car accident took you from our midst…

Setting the scene

Large mammalian herbivores are among the most diverse and conspicuous species groups of the animal kingdom. They can be found all over the world inhabiting an enormous range of habitats from the desert-adapted scimitar-horned oryx *Oryx damma* to the recently discovered saola *Pseudoryx ngetinhenisis* of the lush tropical forests of Laos and Vietnam. They exhibit an extraordinary plasticity in size ranging from the tiny Royal antelope *Neotragus pygmaeus* (24-26 cm) to the enormous giraffe *Giraffa camelopardalis* (up to 5 meters tall). Some species are widely distributed and occur in large numbers, such as the red deer *Cervus elaphus* (ranging all over the northern hemisphere south of the polar), while others are extremely rare, e.g. the Przewalski's gazelle *Procapra przewalskii* from the Qinghai region in China for which the latest estimate fluctuates around 300 individuals.

The richest assemblages of large herbivores can be found on the African continent. Close to a hundred plant-eating large mammals have been described for this continent (Kingdon 2001) and assemblages of locally coexisting species exceed a total of 20 in places such as the Serengeti plains. Africa, however, has not always been so unique in terms of its large herbivore species richness. Up to the late Pleistocene (ca. 30,000 BP) rich assemblages of large plant eating mammals (larger than 5 kg) dominated ecosystems worldwide (e.g. Owen-Smith 1987, Johnson 2002). However, during the late Pleistocene (30,000-10,000 BP) massive extinctions depleted the worlds herbivore populations; 75 % of the genera went extinct in the Americas and around 45% in Australia and Eurasia (Owen-Smith 1987). Africa was left relatively untouched and lost 'only' 13.5% of its large herbivore genera. Debate on the ultimate cause of these extinctions is still fiery, with climate change adherents (Trueman et al. 2005) versus human overkill supporters (Surovell et al. 2005). In general, however, there seems to be a consensus that humans played a significant role in most of the Pleistocene extinctions (Barnovsky et al. 2004, Esty 2005). One would think this ancient legacy is motivating enough to be concerned about conserving the last remaining strongholds of large herbivore dominated systems in Africa.

Diverse large herbivore assemblages and the grazing systems they live in have been ascribed great socio-economic as well as ecological value (Frank et al. 1998, Gordon et al. 2004). The impact of these large herbivores on humans has been enormous throughout the evolutionary history of mankind (Diamond 1996). Wild herbivores have been (and for some still are) a main source of protein and they were the first animals after the dog to be domesticated, going back as far as 8,000-10,000 years ago in the near-East (Gautier, 1998). These domesticated forms have taken over most of the socio-economic role of wild ungulates in industrialized societies (though their role in tourism industry can still be significant) but in many African countries, where domesticated animals were introduced relatively late, the socio-economic impact of wild ungulates is still

strong (Prins et al. 2000; Gordon et al. 2004). In many cases they still form a main source of protein (Loibooki et al. 2002, Milner-Gulland and Bennett 2003) and in other situations, especially in Southern and Eastern Africa, they drive the fast-growing tourism industry (Barnes et al. 1999, Prins et al. 2000). The potential socio-economic impact of large herbivores is also huge because they can strongly influence terrestrial ecosystems (McNaughton 1993, Hobbs 1996, Detling 1998, Danell et al. 2006). This ecological impact of large herbivores ranges from driving large-scale changes in vegetation structure (e.g., Prins and Van der Jeugd 2003) to influencing system nutrient cycling (McNaughton et al. 1997, Augustine et al. 2003) and vegetation species composition (Augustine and McNaughton 1998) and production (McNaughton 1976). By shaping the systems they inhabit, large herbivores influence communities of many other taxa that depend on these systems (from arthropods (Gonzalez-Megias et al. 2004), to birds (Milchunas et al. 1998) and large carnivores (Sinclair et al. 2003)). Several studies, moreover, discuss the importance of species-diverse herbivore systems for the functioning of grazing systems because species differ in the way they shape their environment (Bakker et al. 2004, Bakker et al. in press, Cumming and Cumming 2003, Hobbs and Searle 2005). Du Toit and Cumming (1999) emphasize the risk of the replacement of diverse, wild herbivore assemblages with species-poor livestock systems in African savanna systems for the functioning of these systems.

Alarmingly, these diverse herbivore communities and their ecological and socio-economic role are increasingly threatened. Free-roaming large herbivores have disappeared from large parts of Africa and are increasingly replaced by livestock (Prins 1992, Lamprey and Reid 2004) as elsewhere in the world and wild African herbivores more and more depend on confined (often fenced) protected areas (Newmark 1996). Moreover, areas with the highest species richness seem to coincide with regions that have the highest human population growth (Cincotta et al. 2000, Balmford et al. 2001). Therefore, the conflict between the conservation of Africa's rich large herbivore assemblages and increasing human populations is due to increase. To conserve these diverse assemblages we need to understand what factors shape the large herbivore communities in time and space. In other words we need to understand how these different large herbivore species can locally coexist.

The generally accepted ideas that explain large herbivore coexistence start from the competitive exclusion principle (Gause 1934, Hardin 1960); i.e. potentially competing species can only coexist if they occupy different realized niches. Though other aspects such as differences in predation pressure (Sinclair 1985, Sinclair et al. 2003) and disease susceptibility (Dobson and Hudson 1986) have been mentioned to be important in structuring these niches, partitioning of the food resource is generally accepted to be the basis of large herbivore niche differentiation and ultimately coexistence. Hofmann and Stewart (1972) tried to explain resource partitioning of large African herbivores based on differences in the digestive physiology, dividing them into grazers (diet dominated by graminoids), browsers

(diet dominated by dicotyledons) and intermediate feeders (diet composed of both resources). This division in diet amongst African herbivores was already noted earlier by Lamprey (1963). Hofmann (1989) clearly stated that these digestive adaptations were principally independent of body size. Later authors showed that this probably does not hold (Gordon and Illius 1994, Gordon and Illius 1996). These studies emphasized the importance of body size to explain the separation of feeding niches amongst large herbivores along resource quality and quantity axes.

These body-size based explanations on large herbivore resource partitioning go back to the early 1930s when Kleiber (1932) published a paper where he plotted the log of basal metabolic rate against the log of body mass of a range of mammals (see also Smil 2000). This publication started the discussion on one of the few, reasonably accepted, universal laws in biology, the now-called Kleiber's law, stating that an organism's basal metabolic rate increases proportionally with its body mass with a factor 0.75. Though Kleiber only started with a very limited number of mammal species, several studies have since shown that his relationship holds for an enormous range of endothermic as well as ectothermic species across 18 orders of magnitude (Peters 1983, Smil 2000, Gillooly et al. 2001, Savage et al. 2004). Several mechanisms have since been proposed to explain the 0.75 factor (Smil 2000), of which the best elaborated one is based on the properties of fractal-like resource transport systems, such as blood vessels in mammals and vascular systems in plants (West et al. 1997, Brown et al. 2004). Several studies have since used Kleiber's law to introduce body mass into theories on resource partitioning amongst herbivore species by combining it with the observation that rumen volume is isometric with body size (Demment 1982). The combination of these relationships leads to the now generally accepted hypothesis that larger herbivores can tolerate a lower-quality diet than smaller ones, also known as the Jarman-Bell principle (Bell 1970, Geist 1974, Jarman 1974, Demment and Van Soest 1985). These studies defined quality in terms of food digestibility as the ratio between easily digestible cell constituents (like proteins) and poorly digestible cell wall components (fiber: cellulose, lignin); i.e. low quality food has a low protein-fiber ratio. Moreover, because in tropical savanna systems protein is normally the limiting factor relative to carbon (Demment and Van Soest 1985), N content is often measured as an estimate of food quality (where crude protein content equals 6.25 times N content, Robbins 1993).

The Jarman-Bell principle has subsequently been the basis of a range of studies that tried to explain the coexistence of different-sized herbivore species (McNaughton and Georgiadis 1986, Owen-Smith 1988, Du Toit and Owen-Smith 1989, Bugalho 1995, Belovsky 1997, Prins and Olff 1998, Ritchie and Olff 1999, Wilmshurst et al. 2000, Olff et al. 2002). The basis of these studies is that there is sufficient variation in food quality and quantity (i.e. resource heterogeneity) available to large herbivore species to be able to coexist. Up to now, in the African context resource heterogeneity has mostly been defined in terms of variation in plant species (Jarman 1971, Hansen et al. 1985, Perrin and Brereton 1999) and in

vegetation structure, such as grass or browse height or leaf-stem ratio (Du Toit 1990, Murray and Brown 1993, Perrin and Brereton 1999, Voeten and Prins 1999, Murray and Illius 2000, Woolnough and Du Toit 2001, Farnsworth et al. 2002). Furthermore, studies from East Africa showed that different-sized grazers partition resources over time, where species use the same areas and plant species but at different moments in time exploiting different vegetation growth stages that vary in resource quality and quantity (Vesey-Fitzgerald 1960, Bell 1970, McNaughton and Georgiadis 1986).

In many areas, however, large scale migrations as observed in East Africa do not (or no longer) occur. Still these same areas sustain species rich and abundant herbivore assemblages without clear evidence of competition for resources. In general we can say that, despite our increased knowledge on resource partitioning amongst African herbivores, clear empirical evidence proving that competitive exclusion shapes large herbivore communities is still lacking (Arsenault and Owen-Smith 2002). As Ritchie and Olff (1999) and Arsenault and Owen-Smith (2002) conclude this is partly due to the fact that the spatial dimension has not been well incorporated into our thinking on large herbivore resource partitioning. This recognition coincides with the shift towards a new paradigm in the management of grazing systems. This so-called heterogeneity paradigm states that management should promote grassland heterogeneity to maintain biologically diverse communities in these systems (Du Toit and Cumming 1999, Fuhlendorf and Engle 2003, Du Toit et al. 2003, Owen-Smith 2004). It is essential that we get a better understanding of how spatial variation in resource quality and quantity might contribute to the resource partitioning and coexistence of African herbivores.

Past studies have linked spatial variation in resource quality and quantity to individual species distributions (Wilmshurst et al. 1999, Fryxell et al. 2004, 2005), foraging behavior (Hester et al. 1999, Wallis de Vries et al. 1999) and stability of herbivore population numbers (Illius and O'Connor 2000, Owen-Smith 2004, Fryxell et al. 2005). We, however, lack studies that specifically relate resource heterogeneity to spatial resource partitioning and ultimately coexistence patterns in species rich systems. Some studies are available on a continental to global scale that relate large herbivore species richness patterns to spatial variation in the main drivers of resource heterogeneity, rainfall and soil fertility (East 1984, Fritz and Duncan 1994, Olff et al. 2002). At finer scales habitat quality has been related to spatial partitioning amongst different-sized herbivores (Du Toit and Owen-Smith 1989), but generally empirical evidence for spatial resource partitioning in species rich African herbivore assemblages is still poor.

Thesis outline

In this thesis I explore how naturally coexisting large African herbivores might spatially partition resources by defining variation in resource quality and quantity on different spatial scales using experimental as well as observational techniques. I limited my study to species of the grazer guild; i.e. the group of herbivore species that have grass as the major part of their diet. I believe this group is especially interesting because diverse species groups are regularly seen grazing together in the same grasslands, while at first sight grass seems to be a fairly homogeneous resource. Moreover, up to now studies have mainly focused on partitioning of grass height or grass species and this did not satisfactory explain resource partitioning among different species. In chapter 2 to 6 I define heterogeneity as spatial variation in grass quality and quantity at different scales (Fig. 1) and study how this heterogeneity might promote the coexistence and ultimately diversity of large grazer species in Hluhluwe-iMfolozi Park, South Africa. I start with discussing the effect that spatial scale has on the basis of all studies of large herbivore ecology, i.e. the monitoring of their presence and spatial distribution (chapter 2). Using park-scale dung count data I then describe how different-sized large grazer species partition the landscape and how this distribution is linked to landscape variation in habitat type and quality (chapter 3, Fig. 1A). At a much finer scale (within different park regions) different soil types cause spatial variation in grassland types (Fig. 1B1 and B2). Chapter 4 describes how grazer species partition these grassland types that differ in resource quality and availability and how fire interacts with grassland type to affect grazer community composition. At an even finer scale, most grassland in Hluhluwe-

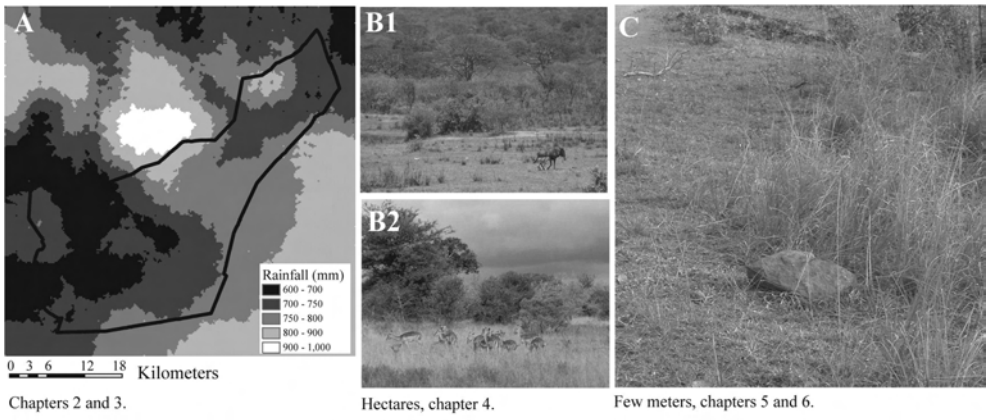

Figure 1 - Different spatial scales at which grazer resources are distributed, from a landscape scale rainfall gradient (A) to regional differences in grassland types (B) and within grassland variation in tall and short grass (C).

iMfolozi is characterized by a high spatial heterogeneity at the patch level (few meters), with alternating patches of short and tall grass (Fig. 1C). I studied how within-grassland variation in short grass patch size and resource quality might increase opportunities for resource partitioning amongst savanna grazers and ultimately mediate their coexistence (chapter 5). At this scale herbivores do not only respond to heterogeneity, but they can also shape vegetation heterogeneity. In chapter 6 I experimentally test a scale-dependent mechanism that might drive short-tall patch dynamics in savanna grasslands. In the last chapter I combine the former chapters and discuss how resource partitioning among large grazers might be nested across different spatial scales. Furthermore, I discuss how future research might benefit from newly available techniques that allow us to better integrate observed patterns of spatial resource use across these scales.

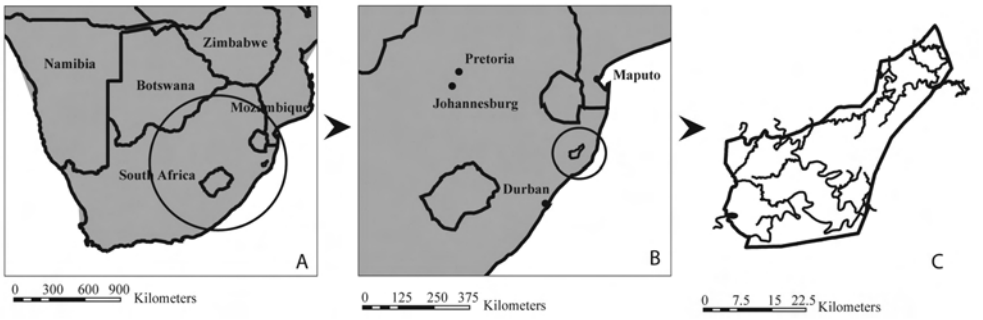

Figure 2 - A. Southern Africa with the position of Hluhluwe-iMfolozi Park (HiP) encircled. B. Northeastern part of South Africa with the position of HiP encircled. C. Hluhluwe-iMfolozi Park with its outer boundary and the main rivers.

The study site

All the studies described in this thesis were carried out in Hluhluwe-iMfolozi Park, Kwazulu-Natal province, South Africa (Fig. 2). This reserve resulted from the integration of Hluhluwe Game Reserve, Umfolozi Game Reserve and the so-called Corridor area. Hluhluwe and Umfolozi game reserves were first proclaimed in 1895 (Brooks and MacDonald 1983, Brooks 2005), making them the oldest reserves of 'colonial Africa'. These two reserves were connected by the so-called Corridor area that was part of the colonial crown lands (areas reserved for future use by settler farmers). Zulu communities lived and farmed in this area until the 1940s when they were removed as part of an anti Tsetse fly campaign (Brooks 2005). In practice from this moment on the corridor was seen as protected land that connected Umfolozi and Hluhluwe game reserves, but it took until 1989 until the corridor was formally incorporated into Hluhluwe-Umfolozi Park, recently renamed as Hluhluwe-iMfolozi Park (HiP) and currently covering close to 90,000 ha.

HiP is situated in a coastally modified climate zone and receives relatively high amounts of rain, mainly falling during a wet season from October to March. Large parts of the park, especially in the north, are strongly undulating, with altitudes ranging from 50 meters close to the main rivers to above 500 meters on the highest peaks (Fig. 3B). Though there is a regional rainfall trend from the southeast to the northwest (Fig. 3A), rainfall is locally modified by altitude. Mean annual rainfall varies from close to a 1000 mm in the high altitude areas to 650 mm in the valley bottoms in the south (Fig. 3C). Most of the park is situated on sand- and mudstone derived soils, but there are also significant proportions of granite and basalt in the high altitude areas and alluvium derived soils near the main rivers (King 1970). Due to the strong variation in altitude and rainfall one can find a large variation in vegetation types, from evergreen gallery forests on the highest hills to savanna woodland and open grassland (Whateley and Porter 1983). The park is inhabited by a very diverse large mammal community, including most indigenous large herbivore and carnivore species (Brooks and MacDonald 1983). Since its proclamation HiP has had a very dynamic history, especially regarding its management of the large herbivore populations (Brooks and MacDonald 1983). During two periods large herbivore populations have been significantly culled. First of all during the 1930s and 1940s a major part of all herbivores, except White Rhino, was culled in Umfolozi Game Reserve as part of an anti-Tsetse fly campaign (Brooks 1995). Secondly during the 1950s and 1960s populations of especially the grazer species were heavily controlled, especially in Hluhluwe Game Reserve, to prevent overgrazing during a long period of drought and allow the vegetation to recover (Brooks and MacDonald 1983). Since the 1970s interventions in herbivore populations have been relatively limited and currently very high densities of all indigenous herbivore species occur in the park. As mentioned this thesis specifically focuses on grazer species. Six grazer species occur in large numbers in

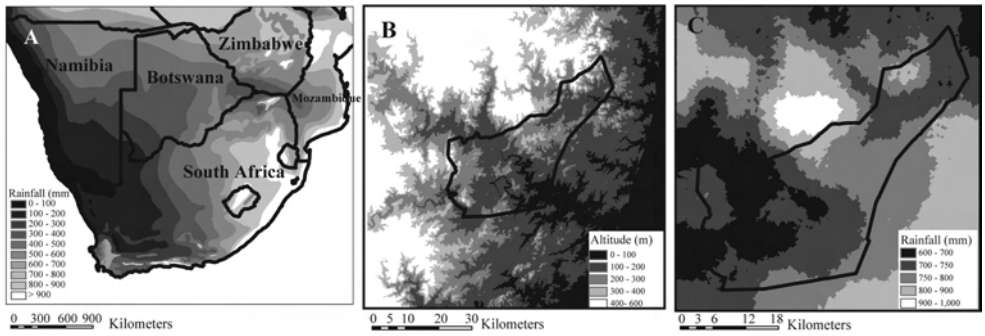

Figure 3 - A. Mean annual rainfall gradient (mm) in southern Africa (data originates from the FAO/UNEP desertification and mapping project, as rasterized by UNEP-GRID (http://geodata.grid.unep.ch)). B. Elevation map of Hluhluwe-iMfolozi Park and surroundings. C. Mean annual rainfall in Hluhluwe-iMfolozi Park, modified by local altitudinal variation, with higher annual rainfall in the high altitude areas. The rainfall data for Hluhluwe-iMfolozi Park originates from Schulze (1997), and represents a long-term annual average.

HiP and can be frequently observed grazing close to each other; these species are impala *Aepyceros melampus*, common warthog *Phacochoerus africanus*, blue wildebeest *Connochaetes taurinus*, common zebra *Equus burchellii*, African buffalo *Syncerus caffer* and white rhino *Ceratotherium simum* (Table 1).

Table 1 - List of the large grazers (larger than 5 kg) that occur in Hluhluwe-iMfolozi Park and that are the central study species in this thesis. Body mass data are from Owen-Smith (1988). Population numbers are based on a 2004 game census that was organized by Ezemvelo KZN Wildlife, the managing authority of HiP (see chapter 2 for methods, personal comments, S. van Rensburg).

Common name	Scientific name	Body mass (kg)	Digestive strategy	Population number	Population density (no. km^{-2})
Impala	*Aepyceros melampus*	40-63	Ruminant	25.563	26.9
Warthog	*Phacochoerus africanus*	58-80	Non-ruminant	3.284	3.5
Wildebeest	*Connochaetes taurinus*	163-252	Ruminant	3.179	3.3
Zebra	*Equus burchellii*	220-320	Non-ruminant	3.408	3.6
Buffalo	*Syncerus caffer*	520-650	Ruminant	3.151	3.3
White Rhino	*Ceratotherium simum*	1600-2200	Non-ruminant	1.793	1.9

HiP is characterized by a high spatial variation in grass quality and quantity at different spatial scales (Owen-Smith 2004). First of all, the strong rainfall gradient in the park, the dryer southern part versus the wetter north (Fig. 3C), potentially results in higher resource quality areas in the south. At a finer, regional scale in the park (Fig. 1B) variation in soil types and altitude create variation in grassland types. In contrast to the well-described large-scale (tens of square kilometers) short or tall grassland systems of the Serengeti, these grassland types (Fig. 1B1 and 1B2) can alternate in HiP every few 100 meters. Moreover, at an even finer scale, most of the grassland in HiP is characterized by patches of tall and short grass alternating every few meters (Fig. 1C). The fact that HiP exhibits such a high spatial variation in factors that potentially control resource quality and quantity for large grazers makes it an ideal location to study how spatial heterogeneity influences large grazer coexistence and diversity patterns.

2

Evaluating large mammal monitoring methods at different scales: implications for diversity indicators

Joris P.G.M. Cromsigt, Sue van Rensburg, Rampal S. Etienne and Han Olff

Khanyi, you started working with us in 2002 and are still with our project at the moment of printing this thesis. Thanks for doing this with a smile! I will especially remember your hearty laugh…

Abstract

Monitoring of large herbivores is central to research and management activities in protected areas. Monitoring programs were originally developed to estimate (trends in) population sizes of individual species. However, emphasis is shifting more and more towards conservation of diversity and communities instead of individual species, as there is a growing literature showing the importance of herbivore diversity for ecosystem functioning. We argue that the design of monitoring programs has not yet been adapted well to this new emphasis. Using large herbivore census data from Hluhluwe-iMfolozi Park, South Africa, we studied how monitoring methodology (observational counts versus dung counts) and spatial scale interact in influencing estimates of large herbivore species richness and diversity. Dung counts resulted in higher herbivore species richness and diversity estimates than direct observational counts, especially at finer monitoring resolutions (grid cells smaller than 25 km^2). At monitoring resolutions coarser than 25 km^2 both methods gave comparable diversity estimates. The methods also yielded different spatial diversity estimates, especially at finer resolutions. Grid cells with high diversity according to the dung count data did not necessarily have high diversity according to the observational counts, as shown by low correlation of grid cell values of both methods. We combined these results with estimates of the sampling effort of each method in a cost-benefit analysis for both methods. We discuss new monitoring designs that are better suitable for tracking temporal and spatial trends in large herbivore diversity and community composition.

Introduction

Large herbivore species characterize ecosystems around the African continent and have important ecological (Bell 1971, McNaughton 1985, Owen-Smith 1988) as well as economic value (Prins et al. 2000, Gordon et al. 2004). Their populations, however, are increasingly threatened by human activities (Prins 1992, Cincotta et al. 2000, Olff et al. 2002). A unique aspect of African large herbivore groups is the high diversity of species (Olff et al. 2002), ranging from small forest-dwelling duikers to massive savanna elephants (Kingdon 2001). An increasing number of studies illustrate the importance of herbivore species diversity in structuring ecosystems because different-sized species have different effects (Du Toit and Cumming 1999, Bakker et al. 2004, Bakker et al. in press, Cumming and Cumming 2003, Hobbs and Searle 2005). This growing acknowledgement of the ecological importance of herbivore diversity coincides with a shifting paradigm in the management of savanna systems from a focus on single target species towards conserving complete and diverse herbivore communities (Du Toit and Cumming 1999, Stalmans et al. 2001, Du Toit et al. 2003). As a result diversity targets are increasingly incorporated in reserve management plans (e.g., Conway et al. 2001).

Monitoring programs are essential for the evaluation of these targets. Large herbivore population management and monitoring programs have long focused on determining population numbers of certain target species (especially the largest species). These programs are possibly not well designed for monitoring species diversity. A wide range of methods has been used in the past to monitor African mammals, ranging from direct observational counts (aerial, drive, waterhole and foot counts) to indirect counts based on signs left behind by the animal (dung counts, track counts or a combination of indirect signs, such as dung, tracks, hairs and feeding signs) (see Wilson et al. 1996). Several studies compared these methods based on species abundance estimates (Caughley et al. 1976, Norton-Griffiths 1978, Bothma et al. 1990, Peel and Bothma, 1995, Reilly and Haskins 1999). However, hardly any studies looked at the effect of monitoring methodology on large herbivore diversity estimates. Gaidet et al (2005) showed that methodology can influence estimates of mammal species richness, but they did not look at the impact on species diversity indicators that include relative abundances of species. Species richness estimates give little information on the structure and composition of species communities. Diversity indicators that include data on species proportional abundance give more insight in the response of communities to environmental change due to unwanted anthropogenic processes or changes in management regime (Magurran 1988, 2004). To our knowledge there are no studies that evaluated the impact of monitoring methodology on large herbivore diversity indicators that include species abundance data.

Diversity can be monitored at the park level but this does not help management authorities to understand changes in diversity as a response to e.g.

environmental change. It is necessary to monitor at finer resolutions to get insight in the processes that determine herbivore diversity patterns, including the effect of management practices such as prescribed burning. The scale at which monitoring results should be evaluated depends on the scale of the processes that determine herbivore diversity. Spatial scale, however, can influence monitoring results (Condit et al 1996, Magurran 2004). Therefore, it is important to include spatial scale in evaluations of monitoring methodology. Monitoring methods might result in perfectly interchangeable diversity estimates but only above a certain spatial scale. It is unclear how scale interacts with the methodology of monitoring diversity of large diversity.

We used large herbivore census data from a protected savanna site in South Africa to analyze how monitoring methodology affects estimates of species diversity and how this depends on the spatial resolution at which the monitoring scheme is evaluated. We evaluated a direct versus an indirect method and determined sample effort and intensity for each method to be able to evaluate their effectiveness in measuring herbivore diversity.

Methods

The study was performed in the Hluhluwe-iMfolozi Park, an 89,665 ha reserve in Kwazulu-Natal, South Africa. This reserve is situated in the southern African savanna biome, with vegetation types ranging from open grasslands to closed *Acacia* and broad-leaved woodlands. It has a coastally modified climate with a strongly seasonal annual rainfall, most rainfall falling between October and March. The mean annual rainfall mostly depends on altitude, ranging from 985 mm in the high altitude regions to 650 mm in the lower areas. Annual daily maximum temperatures range from 13 ºC to 35 ºC. The park is inhabited by a diverse set of indigenous large herbivores and carnivores (Brooks & MacDonald 1983).

In 2004 we monitored large herbivore distribution (species richness and abundance) on line transects that were evenly distributed over the park (Fig. 1). We used a direct (observational counts) and indirect (dung counts) method and compared the methods on the basis of commonly used species richness and diversity estimates. Every two years since 1986 observation teams walked a total of 26 fixed line transects that vary between 3.9 and 10.4 km (7.9 km on average, Table 1) to monitor the abundance of all large herbivore species that are present in the park. We used the data from the 2004 census to compare with the results from a dung counting method. Transects were evenly distributed over the reserve, covering all vegetation types and topography. The most southern part of the park is managed according to a wilderness concept, which limits management and research practices, and was, therefore, not covered by any line transects. Different teams of two observers walked transects just after sunrise during a period of about 3 months in the dry season (end of July up to beginning of October). Teams walked each transect 14 times on average with a speed of 2-3 km per hour (Table 1). All

herbivore observations (of species larger than hare) were recorded that were sighted within 500m of both sides of the transect. For each observation the species and number of individuals was recorded. Furthermore, the position of each observation was recorded in decimal degrees using a handheld gps, as the position of the observer at the time of the observation. Because visibility was generally lower than 500 meters, we estimated visibility every 100 meters on both sides of each transect according to three classes: up to 50 meter visibility, up to 250 meter visibility and up to 500 meter visibility.

During the 2004 observational census period we conducted dung counts on the same line transects as used for the observational counts. The transects were walked with a team of two well-trained observers that continuously counted the number of dung pellet groups for all large herbivore species (larger than hare) on and within 1 meter on each side of the transect. Instead of recording the spatial position of each pellet group, we summed the number of pellet groups per species for every 5 meter on the transect and recorded the spatial position of these 5 meter plots in decimal degrees.

Data analysis

Sampling effort and intensity

For the observational counts we averaged transect walk time, walk speed and visibility per transect and calculated an overall average over the 24 transects (Table 1). We compared both methods on the basis of their sampling effort and sampling intensity. We defined sampling effort as the number of man hours that it took to perform a complete census. For the observational counts we summed the total walk times of all transects (Table 1). For the dung counts we used an average walk time per transect of 5 hours and multiplied this with 24 (number of transects).

We estimated sampling intensity as a measure for the number of hours that an area is sampled by each method. We defined sampling intensity, I as

$$I = (t \times f) / A$$

where t is sample period, f sample frequency and A the sample area. The sample area, A, was the actual area that was sampled by both methods. The dung counts were sampled 1 meter on both sides of the transect, so the dung count sampling area was 2 meter times the total length of transects (190.6 km, Table 1). For the observational counts we multiplied the total length of transects with twice the average transect visibility to estimate the sample area (74.6 m, Table 1). We defined the sample period, t, as the period (in hours) that a certain point on the transect was observed. For the dung counts this period depends on the dung decay rate. In a study in Hluhluwe-iMfolozi GR, Jacobs (2002) showed that in the dry season dung from a range of herbivore species was still perfectly recognizable at the end of her two month study period. We used this period of 2 months (=1464 hours) as our minimum sample period for the dung counts. For the observational counts we

divided average overall transect visibility by the average overall walk speed (Table 1) to estimate the sample period, assuming that the point is not visible as soon as the point is passed. The sample frequency, *f*, equaled the number of times a transect was sampled per year. For the observational counts we used the average number of times a transect was walked (Table 1). For the dung counts the transects were sampled once.

Table 1 - Transect characteristics of observational counts. Transect duration, walk speed and visibility are transect averages(*N* and *SE* given between brackets). The last two rows of the table give overall transect average and sum for the different characteristics. These overall values were used to determine method sampling intensity and effort.

Transect number	Transect frequency (y^{-1})	Transect length (km)	Transect duration (h)	Walk speed (km/h)	Visibility (m)
1	14	3.9	2.3 (14; 0.24)	2.1 (14; 0.38)	79 (77; 6.7)
2	13	8.2	4.8 (13; 0.27)	1.8 (13; 0.09)	61 (81; 3.4)
3	12	8.4	3.6 (12; 0.16)	2.4 (12; 0.11)	92 (82; 8.0)
4	13	5.4	2.2 (13; 0.10)	2.6 (13; 0.10)	64 (54; 6.3)
5	14	8.5	3.1 (14; 0.11)	2.8 (14; 0.09)	61 (83; 3.3)
6	14	8.5	4.4 (14; 0.27)	2.1 (14; 0.15)	54 (84; 1.6)
7	13	8.7	3.3 (13; 0.15)	2.7 (13; 0.12)	57 (87; 2.3)
8	12	9.6	4.1 (12; 0.21)	2.4 (12; 0.11)	78 (97; 4.9)
9	15	8.3	3.8 (15; 0.17)	2.2 (15; 0.09)	115 (82; 9.5)
10	15	6.2	2.3 (15; 0.10)	2.8 (15; 0.13)	54 (61; 2.7)
11	14	9.2	3.9 (14; 0.15)	2.4 (14; 0.10)	88 (92; 6.3)
12	16	6.1	2.8 (16; 0.27)	2.4 (16; 0.14)	102 (62; 7.9)
13	16	8.7	4.1 (16; 0.22)	2.2 (16; 0.12)	106 (89; 7.3)
14	16	7.7	3.8 (16; 0.18)	2.1 (16; 0.10)	82 (78; 5.2)
15	16	6.9	3.0 (16; 0.17)	2.4 (16; 0.17)	74 (70; 5.1)
16	13	8.7	3.6 (13; 0.19)	2.5 (13; 0.13)	77 (88; 5.3)
17	15	6.4	2.9 (15; 0.09)	2.3 (15; 0.08)	65 (65; 4.9)
18	16	6.9	3.3 (16; 0.16)	2.1 (16; 0.10)	94 (70; 7.2)
21	13	9.4	4.0 (13; 0.12)	2.4 (13; 0.07)	55 (95; 2.0)
22	17	10.4	4.3(17; 0.14)	2.5 (17; 0.09)	96 (104; 6.8)
23	13	9.6	3.3 (13; 0.17)	3.0 (13; 0.14)	53 (97; 1.3)
24	18	8.2	2.8 (18; 0.11)	3.0 (18; 0.13)	63 (84; 4.8)
25	15	9.1	3.3 (15; 0.08)	2.7 (15; 0.07)	61 (92; 3.2)
26	11	7.6	3.1 (11; 0.20)	2.6 (11; 0.16)	60 (77; 2.5)
Average	14.3 (24; 0.4)	7.9 (24; 0.3)	3.4 (24; 0.1)	2.4 (24; 0.06)	74.6 (24; 3.8)
Sum	344	190.6	835.5	-	-

Diversity measures

We overlaid our dung and observational count data with grids of different spatial resolutions using ArcView 8.3 (ESRI 2003). The spatial resolution increased from 0.01 km², 0.25 km², 1 km², 6.25 km², 25 km², 56.25 km² to 100 km². We joined the dung and observation count data with each of these grids, summing the number (*n*) of dung pellet groups and individuals per species per grid cell (Fig. 1). We also summed the total number (*N*) of dung pellet groups and individuals over all species per grid cell for all resolutions, giving a sample size for both methods per grid cell.

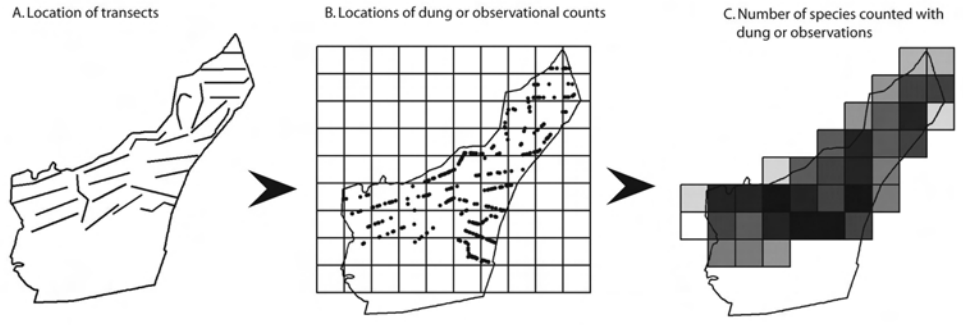

Figure 1 - Process of joining a 5 by 5 km grid with the dung and observational count data using ArcMap 9.0 (ESRI 2003). A. Outline of Hluhluwe-iMfolozi Park showing the position of the 24 transects. B. Locations of dung or observational counts of a species, overlaid with a grid of 5 by 5 km cells. C. Values of species diversity per grid cell, based on the join of the overlay grid with the dung or observational count data, for example the number of species counted per grid cell.

For both methods and for all 7 resolutions we determined three commonly used indices of species richness and diversity: species richness (*S*), the Shannon-Wiener diversity index (*H'*) and Fisher's α. We calculated *S* as the number of species that we counted per grid cell. The Shannon-Wiener diversity index is defined as:

$$H' = -\sum p_i x \ln(p_i)$$

where p_i is the relative abundance (n_i/N) of species *i* (Pielou, 1975).

We determined Fisher's α from:

$$S = \alpha \ln\left(1 + \frac{N}{\alpha}\right)$$

where α is the sole parameter (Fisher et al. 1943; Condit et al. 1996).

We used the Wilcoxon signed rank method to test if the effect of monitoring methodology on the diversity indices was significant. This method accounts for the fact that diversity indices from the same grid cell, but resulting from different monitoring methods, were paired samples. For each diversity index and all monitoring resolutions we calculated Pearson correlation coefficients (r) between the estimates of the two monitoring methods per grid cell. A high Pearson r would indicate that both methods measure the same relative differences in herbivore diversity between grid cells, regardless of the absolute estimate of each method (which could be significantly different as shown with the Wilcoxon test).

Results

Sampling effort and intensity

Sampling effort was 7 times higher for the observational method than for the dung counts (Table 2).

Table 2 - Estimated sampling intensity and effort of the two monitoring methods. Sampling intensity, I, is calculated as $(t * f)/ A$, where t is sample period, f sample frequency and A the sample area.

Method	A (km^2)	t (h)	f (y^{-1})	I ($h\ km^{-2}\ y^{-1}$)	Sample effort ($h\ y^{-1}$)
Dung counts	0.3812	1464	1	3840.5	120
Observational counts	28.44	0.031	14.3	0.016	835.5

While the average walk time was lower for the observational counts than for the dung counts (3 and half hours instead of 5 hours), the sampling frequency for the observational counts was much higher. Sampling intensity was 45 times higher for the dung count methodology compared with the observational counts. This means that on average each point on the transects was sampled 45 times longer using dung counts than using observational counts (Table 2). This difference was caused by the large difference in observation period. The high sampling frequency of the observational counts only partly made up for the low observation period.

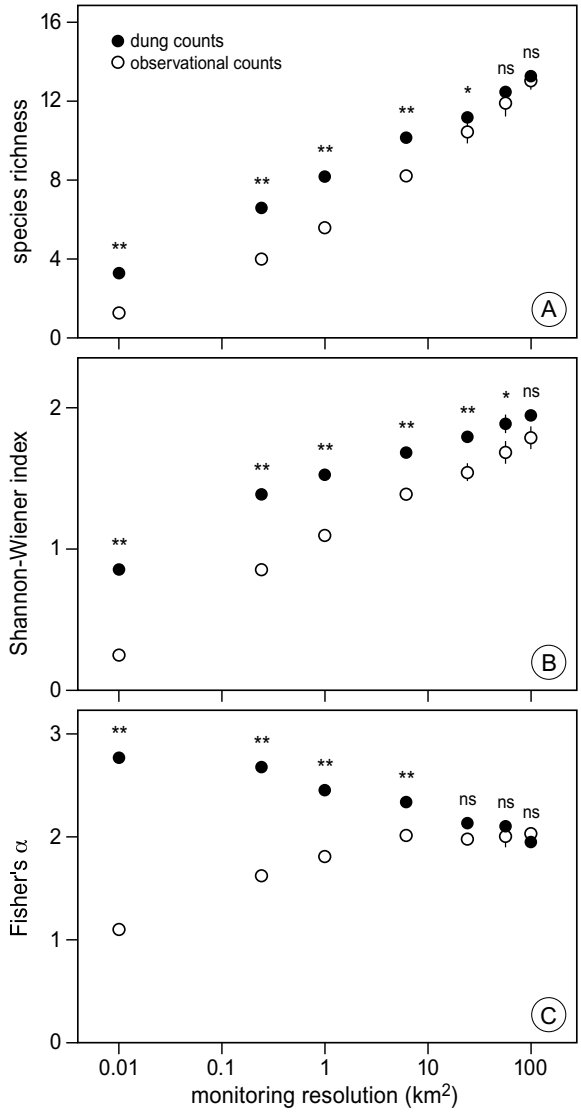

Figure 2 - Estimates of three species richness and diversity indices versus monitoring resolution (km²) for two different counting methods, dung counts (solid circles) and observational counts (open circles); A. Species richness (*S*), B. Shannon-Wiener index (*H'*), C. Fisher's α. The asterisks indicate that diversity estimates were significantly different between counting methods for that monitoring resolution (Wilcoxon signed rank test, **: $P < 0.01$, *: $P < 0.05$). ns indicates that diversity estimates did not differ significantly between methods ($P > 0.05$).

Diversity measures

Average species richness per grid cell was higher using the dung count method than with the observational counts, except for the 56.25 and 100 km² resolutions (Fig. 2A). For the 25 km² resolution the difference was significant, but smaller than 1 species (0.8). At the finer resolutions species richness was substantially higher using the dung counts, ranging from 20 to 166% higher going towards higher resolution. The Shannon-Wiener index also increased with decreasing resolution (Fig. 2B). *H′* dung count based estimates were higher than using observational counts even at the coarser resolutions, though at 100 km2 this difference was just short of significant (Z = -1.9, P = 0.06). The proportional difference in value of *H′* between methods increased with increasing resolution to as large as 240% for the 0.01 km² grid cells. Fisher's α showed a different trend than the other two indices (Fig. 2C). Again the proportional difference between dung counts and observational counts increased with increasing monitoring resolution, where diversity was higher when we used dung counts. Fisher's α, however, decreased towards coarser resolution for the dung counts, while it

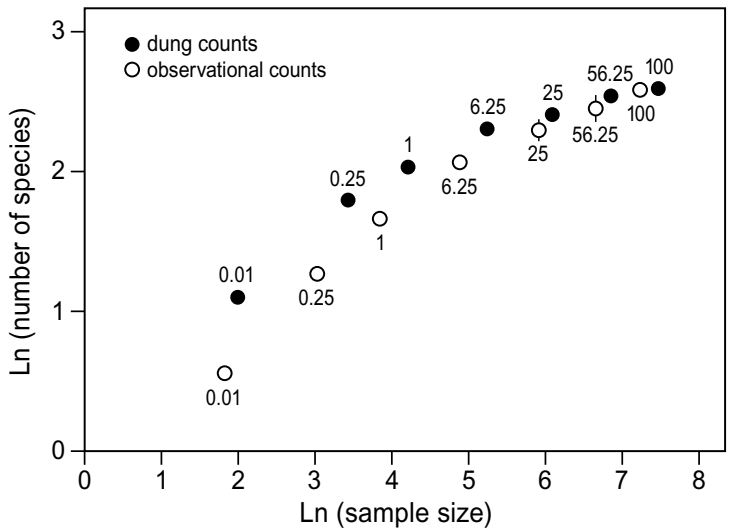

Figure 3 - Relation between the natural log of the average number of species and the natural log of the average sample size per grid cell for two different counting methods, dung counts (solid circles) and observational counts (open circles). Error bars show the standard error of the mean of the number of species. Samples sizes and number of species were averaged over all grid cells per monitoring resolution. This monitoring resolution is illustrated as a foot note next to each circle in the graph.

increased for the observational counts. Fisher's α directly reflects the nature of the relation between S and sample size N. To illustrate this behavior we calculated average sample size per grid cell for each monitoring resolution and compared this with the number of species present in that sample size (Fig. 3). As indicated by the behavior of α, more species were found with dung counts than with observational counts, especially in smaller sample sizes. Furthermore, on average, sample size was larger for the dung counts than for the observational counts, especially at the higher resolutions (Fig. 3, 4).

Both methods resulted in potentially very different spatial estimates of species richness and diversity, especially at finer resolutions (Fig. 5). This was especially true for the diversity estimates, Fisher's α and H'. Pearson r for these indicators did not exceed 0.5 and for α it even remained below 0.1 at all but one resolution. Species richness estimates from both methods were better comparable spatially, especially at resolutions coarser than 1 km². At these resolutions correlation between grid cells was 0.8 or higher, indicating that both methods resulted in the same relative differences in number of species between grid cells.

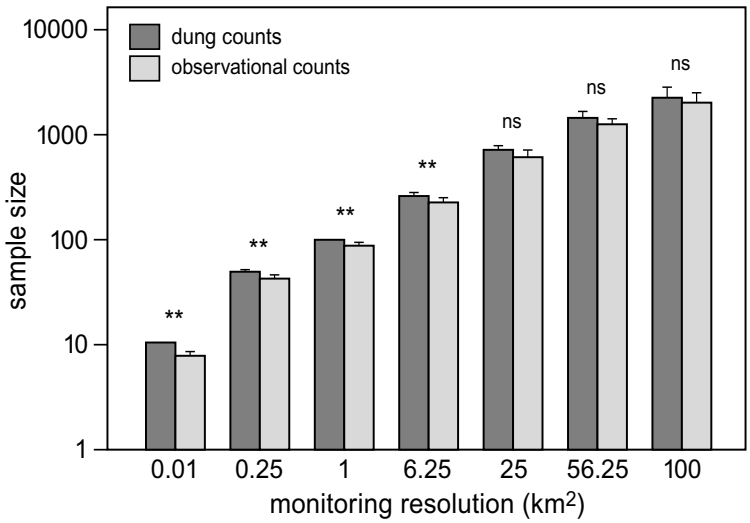

Figure 4 - Average sample size per grid cell per monitoring resolution for two different counting methods, dung counts (solid bars) and observational counts (open bars). Error bars show the standard error of the mean of the sample sizes. The asterisks indicate that sample sizes were significantly different between counting methods for that monitoring resolution (Wilcoxon signed rank test, **: $P < 0.01$, *: $P < 0.05$). ns indicates that sampling sizes did not differ significantly between methods ($P > 0.05$).

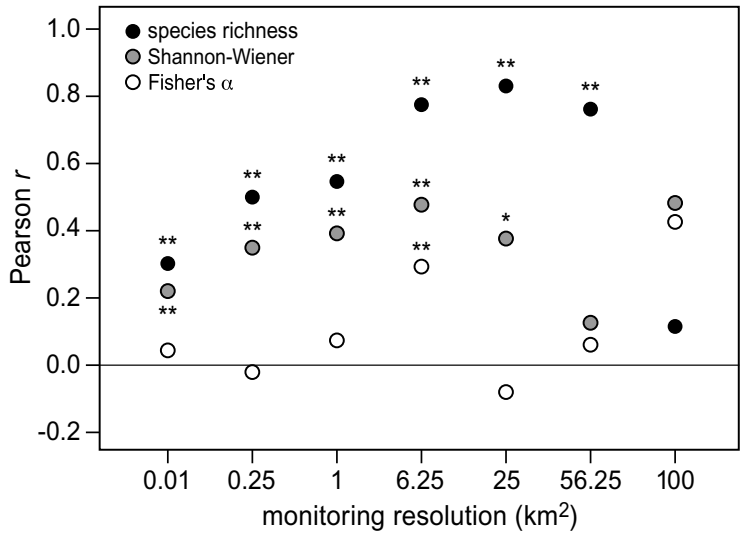

Figure 5 - Pearson correlation coefficients for the estimates of three species richness and diversity indices, Fisher's α (open circles), Shannon-Wiender index H' (shaded circles) and species richness S (solid circles), between two different counting methods (dung counts and observational counts), over a range of monitoring resolutions (km^2). High correlation illustrates that the two counting methods estimate the same changes of herbivore diversity in space. The asterisks indicate that the correlation was significant for that monitoring resolution (**: $P < 0.01$, *: $P < 0.05$), no asterisk shows that the correlation was not significant ($P > 0.05$).

Discussion

We showed that monitoring methodology can strongly influence estimates of large herbivore species richness and diversity and that this effect interacts with the scale of monitoring. Dung counts resulted in higher herbivore species richness and diversity estimates than direct observational counts, especially at finer monitoring resolutions (grid cells smaller than 25 km^2). This effect was the same for all three, commonly used, indicators; species richness, Fisher's α, and the Shannon-Wiener index. At monitoring resolutions coarser than 25 km^2 observational diversity estimates were comparable with dung count estimates. Methodology did not only affect absolute values of diversity estimates but estimates of herbivore diversity also differed spatially. Especially at finer resolutions, correlation between grid cell values for richness and diversity estimates from both

methods was very low (Fig. 5). This effect was stronger for the diversity estimates than for the richness estimate, indicating that methods especially differed spatially in their estimates of relative abundance.

The differences between the monitoring methods were caused by a sample size effect and, when sample size was constant, by differences in sighting probabilities. The dung counts resulted in a larger sample size than the observational counts per grid cell, especially at the finer resolutions (Fig. 4). Several studies have shown that an increase in sample size results in increasing species richness (see Magurran 2004 for a recent overview). The larger average sample size that we found per grid cell with dung counts can be directly related to the higher sampling intensity of dung counts, which is mostly caused by the much longer sample period of dung counts (Table 2). Secondly, even with an equal sample size for both methods we found more species with dung counts than with observational counts, especially in small samples (Fig. 3, samples smaller than 500 pellet groups or individuals). The much higher Fisher's alpha for dung counts, especially at finer resolution (Fig. 2C) also indicates that the dung counts resulted in relatively many rare species, while the small samples of observational counts consisted of fewer, but more abundant, species. This difference is probably due to the fact that the sample sizes of the observational counts were influenced by observations of herds of common species, while the dung counts have a higher sighting probability for rare species (low-density species and species that are difficult to observe directly, e.g. night-active species and species that are sensitive to disturbance). According to Gaidet et al (2005) a high sampling effort is required to observe species that occur at low densities. Though this is true for direct observational methods, we showed that indirect dung counts have a relatively low sampling effort and high probability of observing rare species.

The sampling effort of our indirect dung counting method was much lower than of the observational counts, while it resulted in a much higher sampling intensity (observation hours per km^2) due to the much longer sample period. Most studies that compare monitoring methods do not mention sampling effort (Magurran, 2004). The few studies that we found that did estimate sampling effort of large mammal monitoring methods confirmed our finding. Jachmann (1991) also showed that his dung count method was much less labor-intensive than foot counts, though he compared methods in terms of costs. Gaidet et al. (2005) recently presented sampling effort data for a range of observational methods for a wooded savanna (comparable to our study site) and their sampling effort of the observational foot counts was very comparable to our study. They, however, did not evaluate indirect methods.

In many large African reserves, like the Kruger NP and Serengeti NP, aerial observational counts are the preferred monitoring method, because ground-counts are too labor-intensive when covering such a large sample extent. Aerial counts have indeed been shown to have an equally low sampling effort as dung counts (Jachmann 1991). Several studies, however, pointed out that aerial censuses hugely

underestimate abundance and are strongly biased towards the largest species especially in forest or woodland habitat (Caughley 1974, Caro 1999, Barnes 2001, Jachmann 2002, Gaidet et al. 2005). Since the major part of African reserves is covered by these habitats we argue that aerial censuses are unsuitable to monitor mammal species diversity. Therefore, we suggest that even in these very large reserves the use of indirect dung counts should be considered. Instead of monitoring the whole reserve, one should consider setting up a monitoring network of fixed sampling units (line transects or blocks) that reflects a representative part of the reserve (such as the line transect network discussed in this study). Using a method with a relatively low sampling effort, like dung counts, this network could be sampled on a regular basis (e.g. yearly or even seasonally) and equally as important, especially in large reserves, one could create a spatially more comprehensive sampling scheme (Brashares and Sam 2005). To illustrate this; in our study we could have carried out 7 dung count programs with the same effort as 1 program based on observational counts (Table 2). More replication of monitoring in time and space would offer more insight in mammal diversity response to environmental change and management practices, making it much more suitable for adaptive management schemes. Moreover, because of its simplicity and low sampling effort, dung counts can be relatively easily incorporated in community-based conservation initiatives and management programs (such as patrols) in general (Danielsen et al. 2005).

We realize that there is a potential conflict between the monitoring of diversity and the monitoring of abundance of certain target species. For certain species it might be important to get very accurate population abundance estimates (e.g. when estimating off take for translocation programs of endangered species). Direct observational counts might be better suitable to estimate accurate abundance of these species (using distance sampling techniques, Buckland et al. 1993). However, especially in systems with low visibility like tropical rain forests, this is contested and Barnes (2001) concluded that dung counts result in equal or even better estimates of population abundance in these systems. Since visibility in many savanna systems is often equally low (as shown in this study) dung counts might provide an underestimated alternative in these systems as well.

Concluding, monitoring methodology can strongly influence species diversity estimates. While conservation is more and more orientated at managing diverse herbivore communities, our results suggest that current monitoring programs that are based on direct observational counts are not the most optimal method to monitor diversity. Dung counts seem to better represent diversity (including rare species) and are less labor-intensive.

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