Are animals choosing foraging patches according to spatial scaling laws or predator avoidance arguments? A study on grazing ungulates in Hluhluwe Imfolozi

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Abstract

Spatial scaling laws predict that patch choice in animals is determined by body size, with smaller animals utilising smaller patches. However, this theory does not take into consideration the potential impact predator avoidance behaviour may have on patch choice. Smaller animals are more at risk from predation, thus they have to choose grazing patches that meet their nutritional requirements without exposing themselves to an added risk of predation. This paper developed vigilance theory as related to grazer body size and identified different anti-predator strategies. The effects of herd size on patch choice were also considered. Larger herds would enable smaller species to utilise patches that were otherwise considered too risky. The contrasting predictions made by the foraging and predator avoidance hypothesis were then tested by determining animal utilization of different sized patches as determined by dung. It was found that small species appear to be avoiding the smallest patches in opposition to the foraging hypothesis. Warthog, wildebeest and zebra are also shown to discriminate between patches based on the visibility from patches, choosing patches with greater visibility. Animals preferentially grazed the centres of patches which indicates that they may be attempting to maximise their distance from vegetation. This study presents several different arguments that suggest that predator avoidance does influence the patch choice of animals. Future studies could test the theory that was developed through direct observation of animal behaviour on patches that differed in terms of visibility and by determining if patch choice alters once predators have been removed. This paper does suggest that spatial scaling lawns alone inadequately predict the patch choice of herbivores in environments that have both a diversity and abundance of predators.

Introduction

To avoid being eaten or attacked animals scan their surroundings in order to detect a predator's presence. Vigilance represents a fundamental trade-off, as an animal that is scanning (or surveying its surroundings) is not able to graze at the same time, as to do this it has to lower its head. Thus one would assume that vigilance is costly and that an individual would seek to minimise this cost. This can be achieved through a variety of ways.

One way to decrease the costs of vigilance is to form groups. In HluHluwe Imfolozi (HiP) game reserve, most ungulates are found in groups apart from common duiker and steenbok. Animals may form groups for many reasons unrelated to predator avoidance however I will be focusing on vigilance arguments. An individual's predation risk may be influenced by group size in several ways. The first is the "group vigilance effect" or the "many eyes effect" (Pulliam 1973). This idea is that animals benefit from groups as the vigilance of fellow animals leads to an increase in the probability of detecting a predator within the time it would take to attack. An individual can spend less time being vigilant without increasing its predation risk as fellow group mates are sharing the costs of vigilance, and thus can spend more time foraging. A reduction in an individual's vigilance as group size increases is one of the most frequently reported relationships in the study of animal behaviour (Roberts 1996).

Increased group size can have other effects on predation. In larger groups the probability that an individual will be caught is lower (the dilution effect). It may be more difficult for a predator to remain focussed on a single individual throughout a hunt (The confusion effect, Landeau and Terborgh 1986). Peripheral animals may be more at risk (Hamilton, 1971) thus decreasing the risk of animals within the centre of a herd. Groups may also communally defend themselves against predators (Krebs and Davies, 1987; Prins 1996)

Jarman (1973) proposed several possible forms of anti-predator behaviour for African antelope. These are 1) avoidance of detection by, contact with, or exposure to predators 2) flight after detection but before attack 3) flight under attack and 4) threatening or even attacking the predator. I have modified this and related it to body size in the Figure 1 as opposed to Jarman's (1973) system where he had divided antelope into five social classes each with a mix of defensive strategies. It is important to note that antelope have different anti-predator behaviour. If one generalises about vigilance for all antelope, the nuances of the predator avoidance and its impacts may be missed.

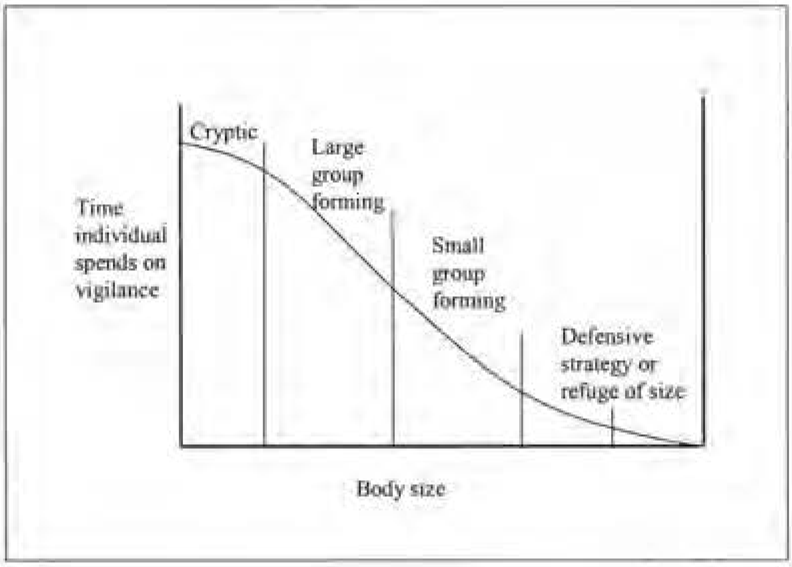


Fig 1. The five strategies that ungulates may be following in order to minimise predation risk.

Body size may also influence the way an animal avoids predation. Due to the increased vulnerability of smaller animals to predation they may avoid feeding in the open, during the day or during bright nights. Medium sized animals may either be more selective about the openness of the environment in which they choose to graze or may form large groups in order to minimise vigilance costs in less open environments. Larger animals may also associate in herd but these may be for defence as well as vigilance. Zebras and Buffalos have both been documented to chase off lions and defend themselves against predators (Prins 1996). Megaherbivores are less prone to predation as their large body size allows them to better defend themselves. Body size can thus affect an animal's predator avoidance strategy (See Fig 1).

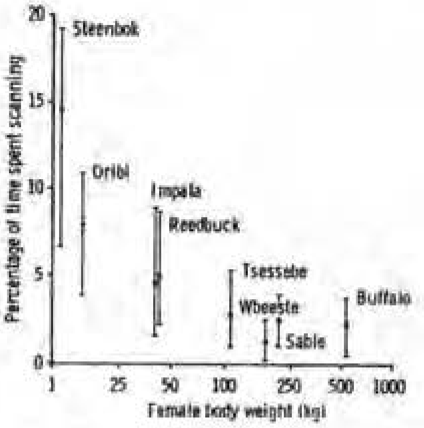
Although there has been a lot of interest in animal vigilance, few studies have highlighted the effects of vegetation structure and cover on vigilance behaviour. There are a few exceptions. A study on desert baboons by Cowlishaw (1997) showed that baboons used refuges in order to decrease predation risk and seldom foraged away from them. If refuges were distant, baboons were more vigilant. Lima (1995) showed that emberizid sparrows were more likely to respond to another bird leaving a feeding site if far from protective cover. There has been in link made with increased rainfall and the resultant increase in cover resulting in the decrease of wildebeest and zebra numbers in the Kruger National Park (Owen-Smith and Ogutu, 2004). Scheel (1993) looked at the scanning rates of eight common ungulate prey species of lion in the Serengeti. He found that cover did not influence the scanning of zebras but that wildebeest scanned more when near cover that could conceal a lion. Warthogs scanned more in short grass habitat and woodlands as opposed to taller grass habitat and dense woodland. This could be due to the futility of scans in tall grass areas as a warthog is so short that it cannot see over the grass anyway.

Underwood (1981) compiled the following table comparing vigilance in open and closed habitats in the Kyle Recreational Park, Zimbabwe

Table 1. Comparison of open and closed habitat vigilance behaviour of antelope in Kyle Recreational Park. From Underwood (1981)

Activity						
	Median rate of looking (looks/minute)			Median % of time looking		
Species	Habitat		P value	Habitat		P value
	Open	Closed		Open	Closed	
Reedbuck	0.7	0.9	0.021	12.15	10.85	0.765
	(43)	(438)		(43)	(429)	
Impala	0.490	1.202	0.000	4.66	7.43	0.000
	(232)	(288)		(232)	(288)	
Tsessebe	0.510	0.687	0.033	0.98	6.43	0.000
	(146)	(467)		(146)	(467)	
Wildebeest	0.132	0.413	0.000	1.36	3.06	0.000
	(193)	(354)		(193)	(354)	
Buffalo	0.384	0.426	0.361	4.47	3.24	0.117
	(201)	(145)		(201)	(145)	
Probabilities from Mann-Whitney U tests						

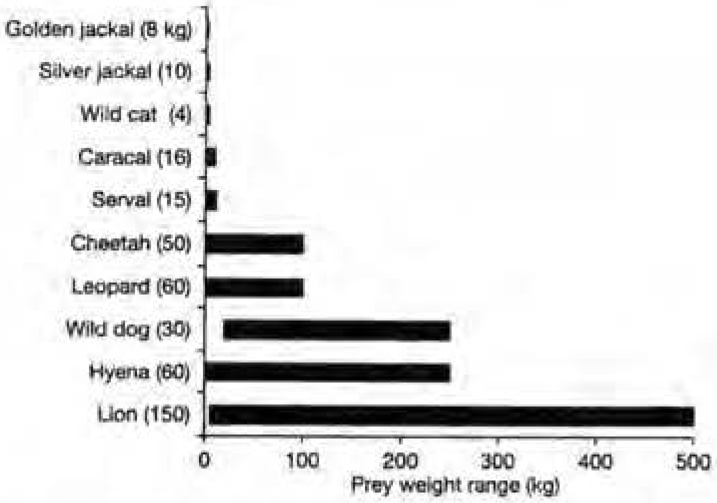
From this table it is clear that Impala, Tsessebe and Wildebeest all spent significantly more time scanning when foraging in closed habitats. Reedbuck was also more vigilant in closed habitats than open ones and was also the most vigilant overall which could explain why there is no significant difference between open and closed habitats for % of time spent looking. Underwood (1982) suggests that the reason there were increased search times in closed habitats in his study was that either screening or the more complex visual environment made a potential predator more difficult to detect, thus increasing scan length. Whatever the reason it is clear that habitat affects the amount of time animals are vigilant and thus could effect the amount of time animals spend grazing in different habitats. As animals spend more time scanning in closed areas it would follow that animals would aim to reduce this by either foraging in closed areas in larger groups or avoiding or minimising the amount of time they spend in these areas. Buffalo do not seem to be affected by habitat openness. This could be due to their defensive strategy or their refuge in large body size to avoid predation (Berger & Cunningham, 1988). Underwood (1982) also made the link with body size and vigilance showing that smaller African ungulates are more vigilant than larger ungulates (see Fig 2).



The relationship between body weight (logarithmic scale) and the amount of time spent looking by antelope grazing on open burnt grassland at K.R.P. Circles indicate medians, upper and lower limits are quartiles.

Figure 2. The relationship between percent of time spent vigilant and body size as reported in Underwood (1982)

All antelope are vulnerable to one or more species of predator e.g. from lions to jackals (See Table 2). Smaller animals are more at risk from predation than larger animals. Jarman (1973) proposed that although maximising the size of a kill for a predator may seem an advantage, the risk of injury from larger prey is greater. Thus there is a physically determined upper limit to the size of prey a predator can attack and a lower limit determined by convenience or efficiency. Hence he believes that smaller antelope are vulnerable to a larger range of predators even if they are not necessarily attacked by them all, while larger antelope are only concerned with the larger predator species. Sinclair (2003) presents a slightly different argument that small ungulates are exposed to a wider size range of predators that could attack them and hence need to be more vigilant. Animals above a threshold of about 150kg have few natural predators and hence are more likely to be inhibited by food limitation (Fig 3). Illius & Fitzgibbon (1994) present the argument that smaller animals are more vigilant as the costs of vigilance are lower for them. Whichever of the three arguments is correct, smaller animals are most vigilant.



The range of weights of mammal prey consumed by carnivores of different sizes in the Serengeti ecosystem. There is a large overlap in diet at small prey sizes. Data are from our unpublished observations and published sources[17-26].

Figure 3. The relationship between the body size of predators in relation to the range in body size of prey. Smaller animals are at risk from many predators. From Sinclair (2003)

All of these factors combined may then affect an animal's choice of which habitat they will graze in. The habitats we observe animals in are habitats they have already selected. It is hard to prove that they are deliberately avoiding other areas. However they may choose to minimise the amount of time they spend in less favourable environments or only graze in these areas if in a large group, or forced to due to severe food constraints. Higher mortality is observed in many species during the dry season. e.g. Buffalo fall prey to lions more often in the dry season in the Kruger National Park (Mills and Funston, 2003). This may be due to several interacting effects. Animals may be in a weakened condition and thus less able to defend themselves or escape. It is possible that as the more dangerous habitats have previously been avoided they still contain forage and thus animals that are resource limited will move into these areas despite the heightened predation risk.

Predation and habitat choice: A hypothesis

Grazing mammals seem to be able to coexist on the same resource within a certain habitat (Sinclair 1985). This is seen in HluHluwe-Umfolozi game reserve where many animals make use of grazing lawns. According to the idea of niche separation one would expect to find animals equally distributed throughout the park. Yet it appears that species are actively choosing to be on lawns even if it means sharing the resource with other species. What is behind the choice of a grazing patch?

The most recent argument put forward is that animals are partitioning what appears to be a similar resource (a grazing lawn) by choosing a lawn of a size that would best suit their size requirements. The theory advanced by Ritchie and Olff (1999) and Olff *et al*(2002) is that species differ in the scale at which they perceive their environment and in their tolerance for low food resources. A smaller species may be able to utilise a patch that may be of the same quality of a larger patch but as the patch is small and thus has low food quantity, it is not efficient for a larger animal to use this patch. Grazer heterogeneity is thus explained, as there is a range of different patch sizes and a range in patch quality. The resource may appear to be similar but is partitioned in terms of quantity and quality so that a range of grazers can coexist.

I propose another mechanism to explain why animals select the grazing patches they do. An animal faces the dilemma of how to obtain enough food for itself without compromising its safety and so becoming food for a predator. Grazing lawns may provide a certain amount of safety to grazing animals as they are open areas and thus a grazer will have a larger distance at which to perceive a threat and hence be able to escape (Pulliam 1973). The open nature of a grazing lawn will allow an animal to spend less time being vigilant and more time maximising its nutrition. There will also be a knock-on effect: as more animals congregate there are more pairs of eyes to be able to scan for predators. A single animal detecting a predator will be able to alert all of the animals on a lawn of whatever species. An individual will thus need to spend less time being vigilant as there are many other animals that can share the burden of vigilance. It has been shown that animals in larger herds are less vigilant (Jarman 1973, Scheel 1993, Roberts 1995, Lima 1995, Treeves 2000).

How would one distinguish between the two different theories? The Ritchie and Olff (1999) argument predicts that smaller animals choose smaller patches because of lower food requirements. In contrast, to a predator avoidance argument predicts that those animals most at risk would be choose larger lawns as this would give them the maximum escape distance. Which animals are most at risk? Sinclair (2003) suggests that smaller animals are most at risk as they are likely to fall prey to the largest range of predators from big to small. Megaherbivores are least likely to be predated as their large size makes them relatively immune from predation from all but the largest species, lion. Thus the minimum preferred patch size would decrease with increasing body size if predator avoidance determines patch choice for feeding. This is useful as it means that the Ritchie and Olff hypothesis for patch selection predicts the opposite from the predator avoidance hypothesis.

The following figure illustrates the two contrasting arguments for patch selection.

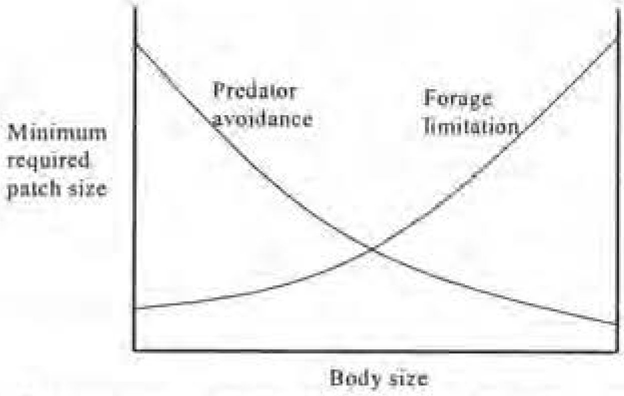


Figure 4. The contrasting predictions of the forage limitation hypothesis and the predator avoidance hypothesis for the relationship between body size and minimum patch size. The predator avoidance arguments predicts smaller animals will require larger lawns.

Herd size and predation avoidance versus forage limitation

Since an individual's vigilance costs are decreased in groups, animals in herds would access patches that would be considered dangerous too for an individual animal. The forage limitation theory does not make predictions about how lawn choice will vary with herd size. However to accommodate the larger number of individuals, larger patches would be needed required to supply sufficient forage. The predator avoidance hypothesis again predicts a different trend. Larger herds result in animals spending less time on vigilance and would thus occupy smaller patches than solitary animals of the same body size. Figure 5 shows how herd size affects patch choice for different sized species.

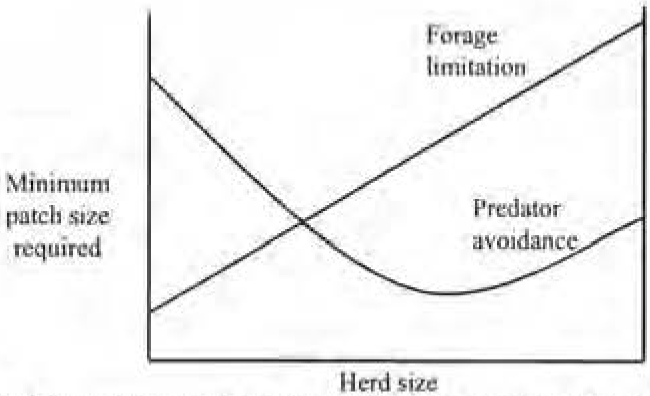


Figure 5. The minimum patch size required for animals of similar body size but herds of different sizes under the forage limitation and the predator avoidance hypotheses. For the predator avoidance hypothesis the minimum patch size required decreases as herd size increases until a threshold is reached. Patch size then increases as larger patches are required to physically accommodate the larger herd sizes.

Given animals of similar body size, minimum patch requirements would be smaller for solitary animals than herds according to the forage limitation hypothesis. In contrast, because herd size decreases individual vigilance, solitary animals would require larger patches than animals of the same species in herds.

I set out to test the opposing predictions of the foraging and predator avoidance hypotheses for patch choice. I did so by comparing species utilization of patches and grazing lawns of different sizes and with different densities of woody plants. As time was a limiting factor, I based my analysis on dung as an indicator of patch utilization. Although dung has drawbacks as a proxy for animal utilization, it would allow me to assess both the presence of different species on different size patches and an indication of their abundance over a relatively long time period (approximately two months). As the range in animal body sizes of potential species that are grazers is limited, it would be difficult to prove that patch choice was influenced by predator avoidance but I hoped to be able to show that it is at least a possibility and deserves greater investigation as a possible agent shaping the choice of patches.

Methods

Study Site

For my study I utilised sites that had been set up for the Gulliver Removal Experiment (GRE). This experiment was set up in 2000 to explore the effect of grazers on grass composition and on rates at which bunch grasslands can be converted to grazing lawns. Gullivers provide a refuge for bunch grasses so their removal is equivalent to "adding grazers" to a patch.

Three sites were chosen. These are Seme, Thiyeni and Crossroads. At each site all gullivers were removed from plots in three different plots sizes of radii 5, 10 and 15m. Three control circles were also marked at each site with a radius of 15m where the gullivers were undisturbed. Thus at each site there were a total of nine cleared plots and three control plots. Each plot was at least 30m from the next and not visible from any other site. All gulliver stumps were treated with Chopper, a non-selective systemic herbicide solution with residual activity. The active ingredient is Imazapyr and gulliver stumps were treated with a 12.5% solution. The sites were periodically checked and re-cleared if necessary.

The centre of each circle was marked with a metal pin. Eight metal pins were also placed around the perimeter of the circle marking up four diameters that were used for permanent transects. As each circle was permanently marked it was possible to determine exactly which circle one was surveying and match up data that had been collected since 2000. When the sites are surveyed the biomass is determined along transects determined by the radii of the circle using a disc pasture meter.

In order to examine grazer activity on patches of different sizes I also surveyed larger grazing lawns. To do this at both the Crossroads and Seme sites I found nearby grazing lawns and repeated the above procedure but on the entire lawn. There were no lawns near the Thiyeni site. I thus surveyed lawns at several sites in the surrounding areas.

This experimental set up served as a convenient test for my project. This is because the circles allowed me to assess grazer response to different patch sizes. I would also assess cover around each patch from the centre of a circle. Since the GRE was set up for another purpose their use removed any bias in sample area selection.

Methods

At each site the entire circle was surveyed and all animal dung was noted (my co-workers in the field were skilled at identifying dung and had been doing it for another project for several years). This was done by inserting a nail in the centre of the circle with a rope attached that had the same length as the radius of the circle. The two dung identifiers held the rope as they moved around the circle. Dung was identified as the rope passed over it. This was to avoid confusion about which dung had been counted and which had not. The species was determined and how fresh the dung was (fresh, medium, old). In addition to this all sites were resurveyed with a 5m-radius inner circle. For the larger grazing lawns dung was recorded and the dimensions of the lawn determined. A sub sample with a radius of 5m was also made in the centre of each lawn.

In additional to the dung surveys, I determined vegetation cover as a measure of the potential for predator concealment. This was done using a vegetation profile method. I stood in the centre of each circle and an assistant carrying a 10x10cm square of white paper walked away from me until only 50% of the square was visible. This was repeated at heights of 50 and 150cm. As my grasp of distances improved I estimated the distance at which I thought the square would no longer be visible. Using a compass I thus determined the vegetation profile in eight cardinal directions.

I also made use of data that had been collected for the GRE from 2000 to 2004. Each year the height of the biomass within each circle and the control sites was measured using a disc pasture meter. The measurements were made at specific distances along fixed transects. This allowed me to compare the grazing intensity on the centres of circles to the perimeters, both between sites, circles and years. If predator avoidance influences patch choice then the GRE might be expected to show different responses in the different sized patches. Grass height might be taller in the smallest circles if all grazers avoid small patches and shortest in the largest circles.

The use of dung as a proxy for animal presence

There are several problems with using dung as a proxy measure of animal presence and lawn utilization. Animals may defecate in an area that they would not consider grazing in. They may just be moving through an area to a more favourable site. Several species are also midden-forming species, the most conspicuous being the white rhino. One would underestimate their presence on a lawn even though it might be their preferred habitat.

It is also not possible to determine how many rhinos have defecated in a midden with any sort of accuracy so that abundance measures from dung are not possible. I recorded rhino middens if they were situated within the confines of the site and also noted any other signs within a site. These included tracks or rubbing stumps. On some of the sites it appeared that wildebeest and impala had formed middens. In this case we made a rough determination of how many animals had used the site as we had a good idea of the volume of dung produced by one animal.

The time period over which the dung accumulated is also difficult to determine as the dung of different species decomposes differently. The rate of decomposition is related to the abundance of dung beetles and the amount of rainfall. Jacobs (2002) showed in her work on dung disappearance in the HiP that for all species the largest loss in dung occurs in the first two days. After that the remaining dung (about 20-35%) remained for the length of the experiment, (64 days), and was still identifiable to a species level

There are also strong seasonal effects in the length of time dung is present and identifiable. Jacobs (2002) did not report on the effects of season on her dung disappearance experiment but one would hypothesize that in the wet season dung would disappear quicker as the higher humidity and temperatures would allow for faster decomposition by microbes or burial by dung beetles and termites. As my study took place in winter, I am confident that if an animal had defecated on a site within the last two months its dung would still be identifiable. Thus my estimates of animal presence and abundance are based on winter/dry season utilization of lawns. This has important consequences for the interpretation of data as several species switch from grazing to browsing in the winter season e.g. impala are predominantly grazers in summer and switch to browse in winter (van Rooyen 1992, Meissner and Pieterse,1996). Thus their abundance in winter on lawns may be less than expected.

Grass length also plays a role in the amount of dung recorded. It is difficult to see dung in longer grass, especially on control sites. As a result we applied extra effort in long grass areas to search for dung and moved grass aside in order to look on the surface. As the dung of smaller species like duiker and hare are also more difficult to spot in long grass, their numbers may be underestimated on control sites. However it will be difficult to tell if there are fewer dung records because they were avoiding the area or because of the difficulty in finding the dung.

The following table shows the range of heights, weights and abundance of various grazing and browsing species found within HiP. Where possible data collected within in the park or in the Natal region was used for animal dimensions. Data was taken from several mammal field guides currently in circulation.

Animal presence and size within HiP

Table 2. Grazing and some browsing species arranged by increasing body mass. Animal numbers are given for 2003 as predicted by a model that also accounted for removals, mortality and introductions. Initial data for the model was gathered using fixed transect game counts in 2002.

Species	Scientific name	Weight (kg)		Height to shoulder (cm)		Number in park (2003 estimates)
		Male	Female	Male	Female	
Hare	*Lepus saxatilis*	1.92	2	50	50	Many
Impala	*Aepyceros melampus*	63	50.4	90	85	26731
Warthog	*Phacochoerus aethiopicus*	80	56	68	60	4223
Nyala	*Tragelaphus angasii*	107	62	112	97	8338
Kudu	*Tragelaphus strepsiceros*	230	157	140	125	1375
Wildebeest	*Connochaetes taurinus*	245	200	140	126	3200
Waterbuck	*Kobus ellipsiprymnus*	270	180	150	110	859
Zebra	*Equus burchelli*	320	260	135	130	3555
Buffalo	*Syncerus caffer*	625	530	145	140	2895
Black rhino	*Diceros bicornis minor*	858	874	150	145	301
Giraffe	*Giraffa camelopardalis*	1200	828	330	280	789
White rhino	*Ceratotherium simum*	2200	1450	180	180	1896
Elephant	*Loxodonta africana*	5000	3200	340	270	360

This table illustrates the range in body sizes found within the park. The species focused on in this study were hare, impala, warthog, nyala, wildebeest, zebra, buffalo and white rhino. Table 3 illustrates the great diversity in predators found within the study site. Lion spoor was found on the Thiyeni study site as well as Hyena droppings. It is reasonable to believe that all species in the table could have been present on the three study sites. There are many smaller predators as well as larger predators thus smaller animals are probably under high predation pressure (Sinclair 2003).

Table 3. Predator species found within Hluhluwe-iMfolozi Park arranged by body mass. Jan A. Graf of the HiP Predator Project provided predator numbers.*data unknown

Species	Scientific name	Weight (kg)		Height to shoulder (cm)		Home range	Number in park
		Male	Female	Male	Female		
Genet large spotted	*Genetta tigrina*	2	1.8	*	*	50-100 ha	Unknown, numerous
African wild cat	*Felis lybica*	5	3.7	*	*	*	Unknown
Jackal black-backed	*Canis adustus*	9.4	8.3	38	*	*	Present in 1860s
Serval	*Felis serval*	11	9.7	58	*	15-30km^2	Not reported
Caracal	*Felis caracal*	13	10	42	*	*	Rare
Wild dog	*Lycaon pictus*	27	*	75	*	*	33
Cheetah	*Acinonyx jubatus*	54	43	87	*	*	40
Leopard	*Panthera pardus*	60	32		*	*	150
Hyena	*Crocuta crocuta*	60	70	80	*	*	300
Lion	*Panthera leo*	190	130	120	90	*	75

Analysis

To test the alternative hypotheses on body size and patch use I used a variety of methods. As a first approach incidence functions were drawn up for the study species for different sized patches. This would determine the minimum patch size a species occurs on. It would also show what patch size a species occurred on most frequently. Here Fig 4 is useful as it contrasts the two arguments. If large animals are found on small as well as large lawns while small animals are only found on large lawns then this is support for the predator avoidance hypothesis. However if large animals are not found on smaller patches and smaller animals are, then this supports the forage limitation hypothesis. The incidence curves were drawn up for species found on the lawns for both the r=5 and the r=x measure (x being the radii of the GRE plot). These curves were drawn up using presence absence data. The data was pooled for all sites according to circle size. A species was then rated on how may sites it was found on out of a total of nine for circles and nine control sites. This is why the Y-axis has a maximum of one if an animal is found on nine out of nine sites. It is thus a probability of finding an animal of that species on a circle of that size. Control sites were included in this analysis to determine if animals preferred long grass on control sites to short grass sites.

The abundance of animals as determined by dung density can be compared between patches of different sizes. Again the predictions from the two hypotheses are contradictory. The predator avoidance hypothesis predicts that the density of dung for small-bodied species would be greater on larger lawns. This differs from the first analysis as one can get a measure of how much time animals spend in different environments as opposed to merely moving through and possibly leaving dung behind. One could compare at which patch size dung density is the highest for different sized species.

The data collected on grass heights for the GRE provides an overall test for the predator avoidance hypothesis as one can compare grazing intensity on the centre of circles as opposed to the perimeters. If predator avoidance influenced habitat choice then one might expect grazers to concentrate grazing in the centre of a circle or patch, furthest from vegetation cover that might conceal a predator. To test if grazing intensity differed between centres and perimeters the height of grass was compared between sites and circle sizes. If predator avoidance influences patch choice then the GRE might show different responses in grass height in the different sized patches. Grass might be taller in the smallest circles if all grazers avoid small patches and shorter in the largest circles.

Results

The following incidence curves were drawn up for species found on the lawns for both the r=5 and the r=x measure.

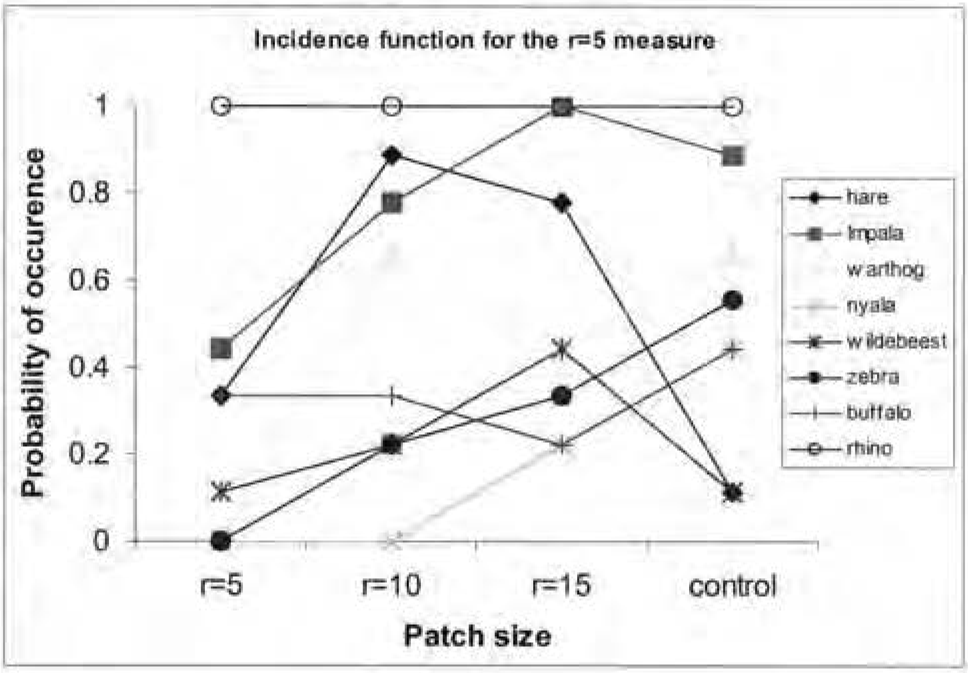


Figure (6). The incidence functions for study species on patches of different sizes using the r=5 measure of dung. Control sites are included. Species are arranged by increasing body size. The data for rhino was collected differently (see Methods, the use of dung as a proxy measure).

From Fig (6) hare were least common on control sites and small circles. They were common on medium and large lawns. Impala were least common on small circles and are more likely to be found as circles size increases. Warthog were not found on small circles and are most likely to be found on medium sized circles. Nyala were rare on all circles and found less than 50% of the time on control sites. Wildebeest were least common on control sites and small circles. They were most common on medium to large circles. Zebra were most common on control sites but the probability of finding them on circles increases as circle size increases. Buffalo were most common on controls but have a similar abundance on all circles. Rhino were present on all size patches.

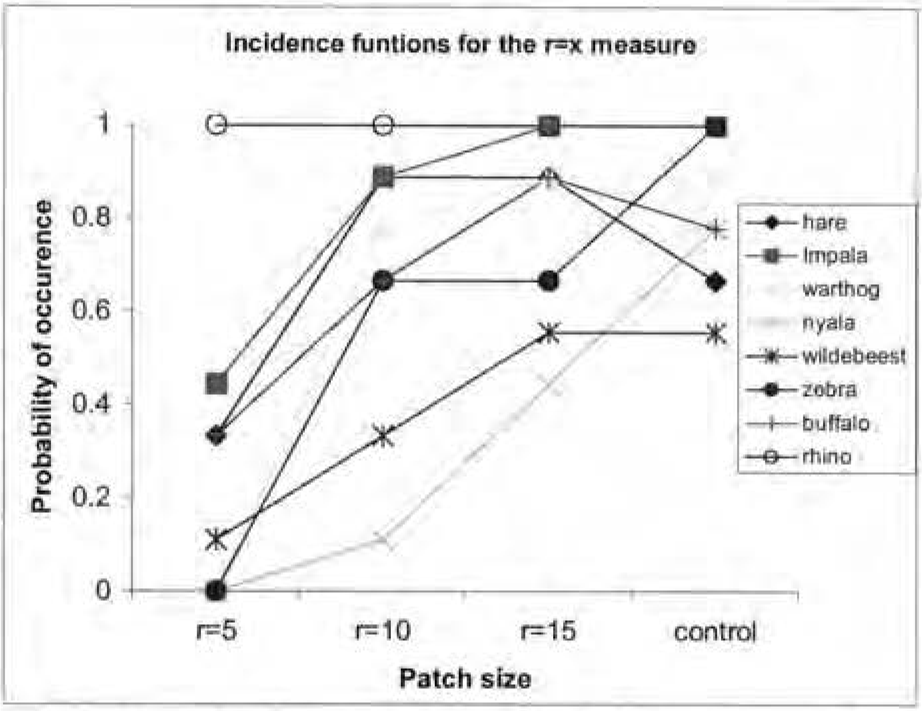


Figure (7). Incidence functions for study species using the r=x measure of dung on patches of different sizes. Control sites are included. Species are arranged by increasing body size. The data for rhino was collected differently (see Methods, the use of dung as a proxy measure).

The same trends for all species are found for this measure with the exception of hare, nyala and wildebeest which were more common on the control using the r=x measure.

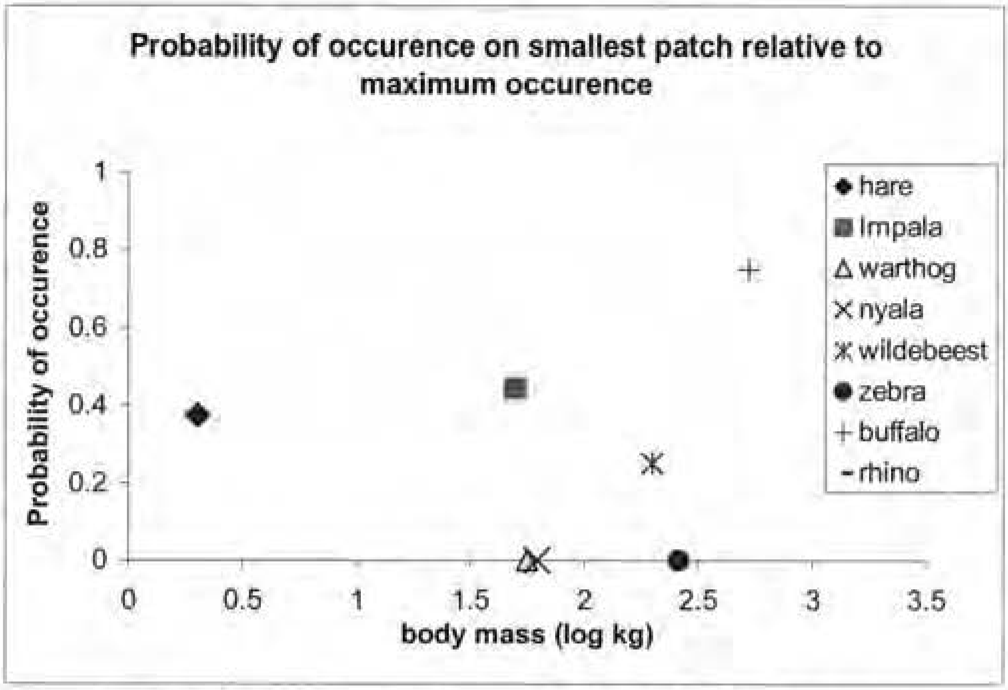


Figure (8). Probability of occurrence on smallest patch relative to maximum occurrence on all patches.

Figure 8 shows the probability of an animal being found on the smallest patch (r=5) relative to its maximum occurrence on all patches. The r=5 measure of dung was used. Probability of occurrence was determined using the incidence functions for species (See Fig 6). The log of the female body size was used (See Table 2).

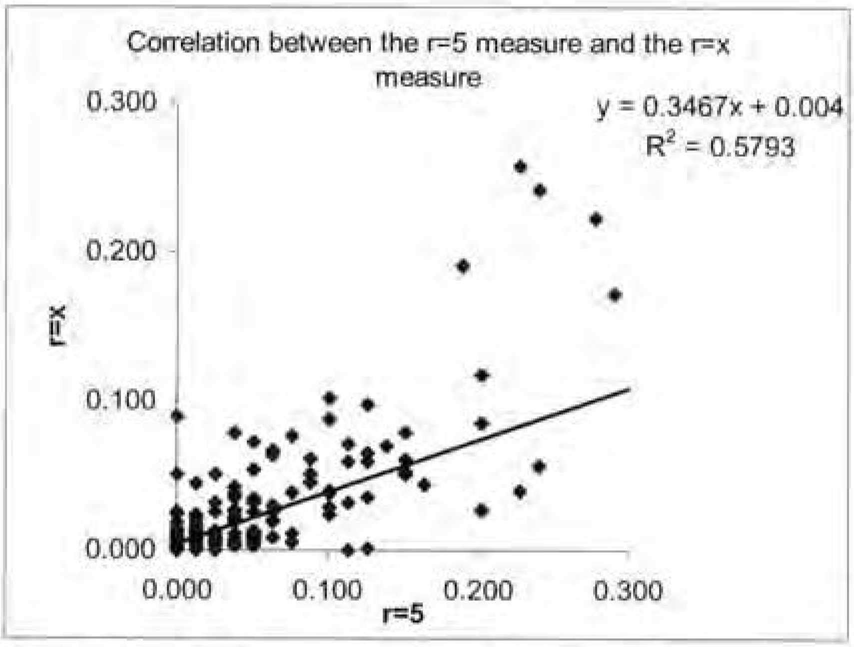


Figure (9). The correlation between the amount of dung found on each circle using the r=5 and the r=x measure.

The overall agreement between the r=5 and r=x measurements is reasonably good (R^2=0.58). The r=5 measure underestimated the amount of dung sites. This is not surprising due to the small area that this measure samples.

Figure 10 is a measure of abundance data for the different circles as opposed to the presence/absence data represented by the incidence curves. The range in size is also greater as the data for lawns is included as well as circle data. Hare are only abundant on small circles; Impala are most abundant on medium sized circles. Warthog are not present on small circles and most common on medium sized circles. Wildebeest are most abundant on lawns and then on small circles. Zebra are not found on small circles, are found almost equally on medium to large circles and most common on lawns. Buffalo are also most common on lawns, then on medium sized circles.

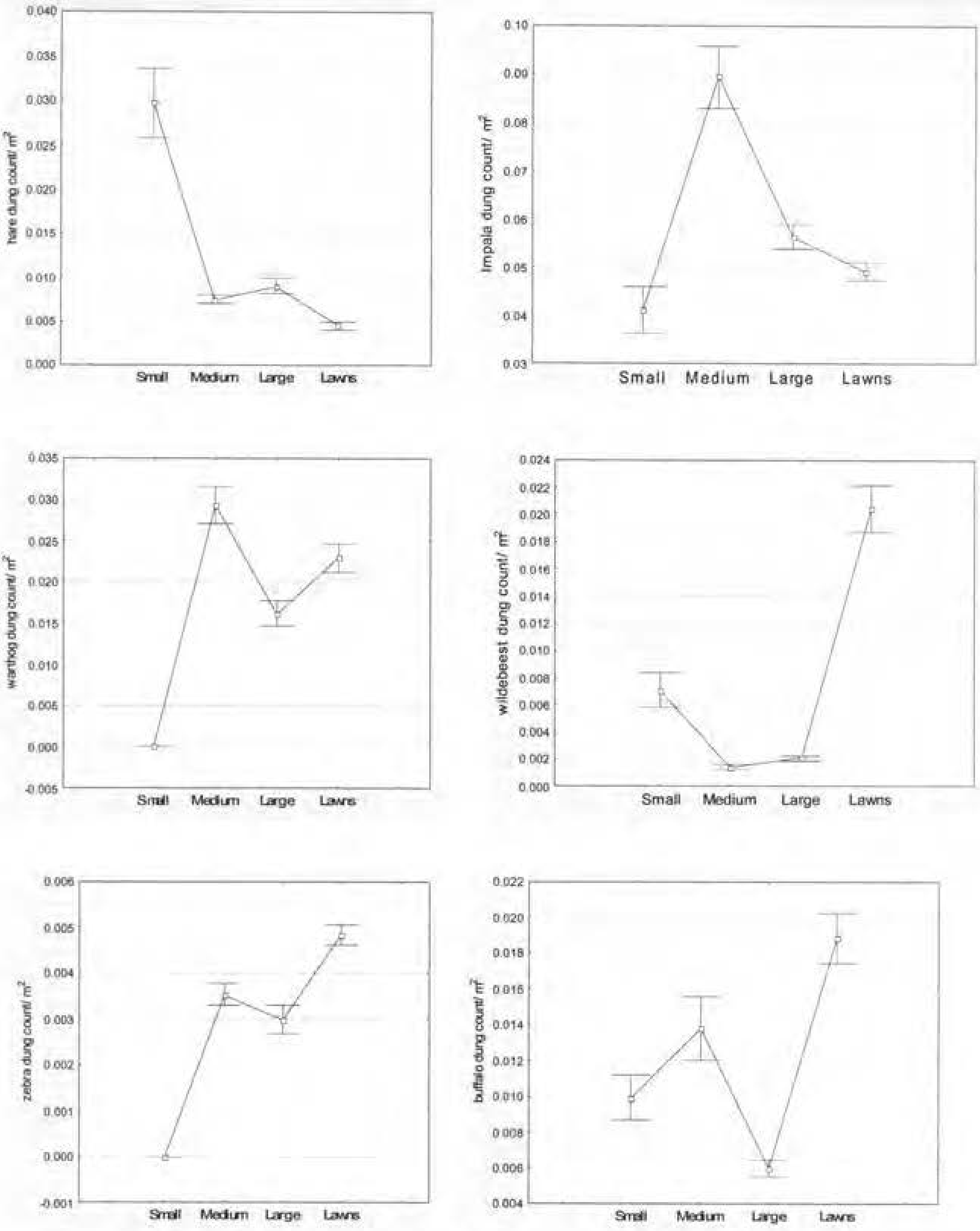


Figure (10). Actual abundance of dung (count/m²) using the r=x method for all focus species. Note that the scale of the Y-axis differs between graphs. The X-axis consists of data for all circle sizes as well as for lawns. Control sites were not included. The centres represent the mean while the error bars represent a 95% confidence interval.

Habitat visibility at different sites

Vegetation density was measured at two heights in 2004. There is a strong trend between the two heights for all sites combined. Distance to cover does increase as circle size increases but the 50cm measure is always smaller than the 150cm measure. There is a significant difference between the two measures (F= 3.49 p<0.02 Fig 10).

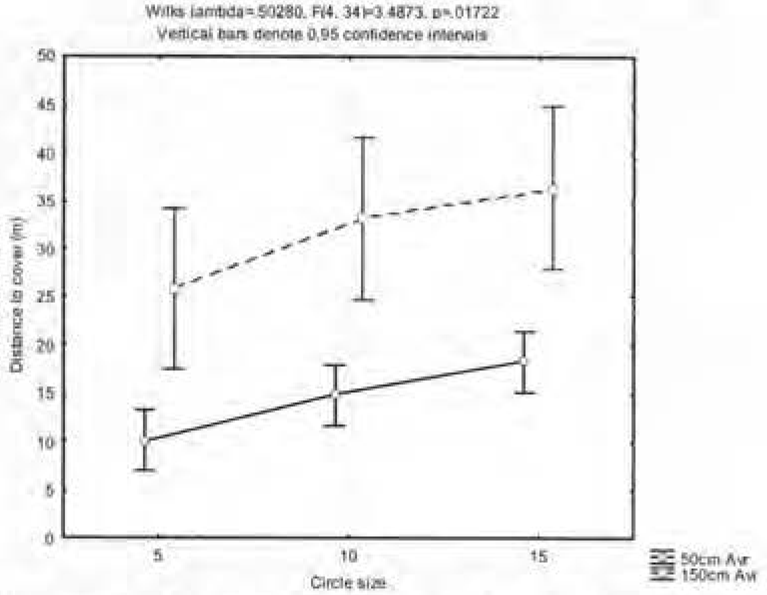


Figure 10. A comparison between the distance to obscuring vegetation cover at 50cm and 150cm around circles of different sizes (r=5,10 and 15).

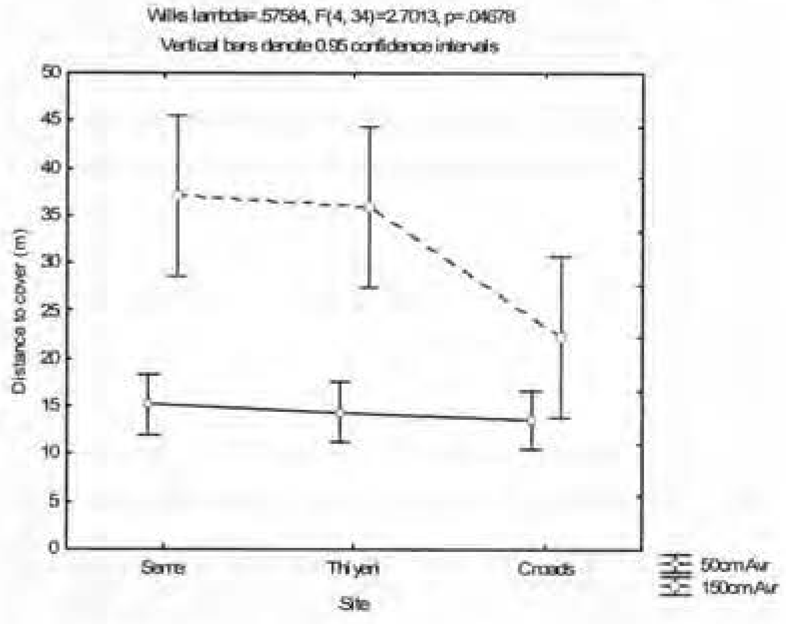


Figure 11. The average visibility at two heights for the three sites for 2004.

There is a significant difference between the two measures of visibility among sites (ANOVA, F=2.70 p<0.05 Fig 11). Sites are all similar at the 50cm height. However, the Crossroads site has a lower visibility at 150cm than the Seme and Thiyeni sites.

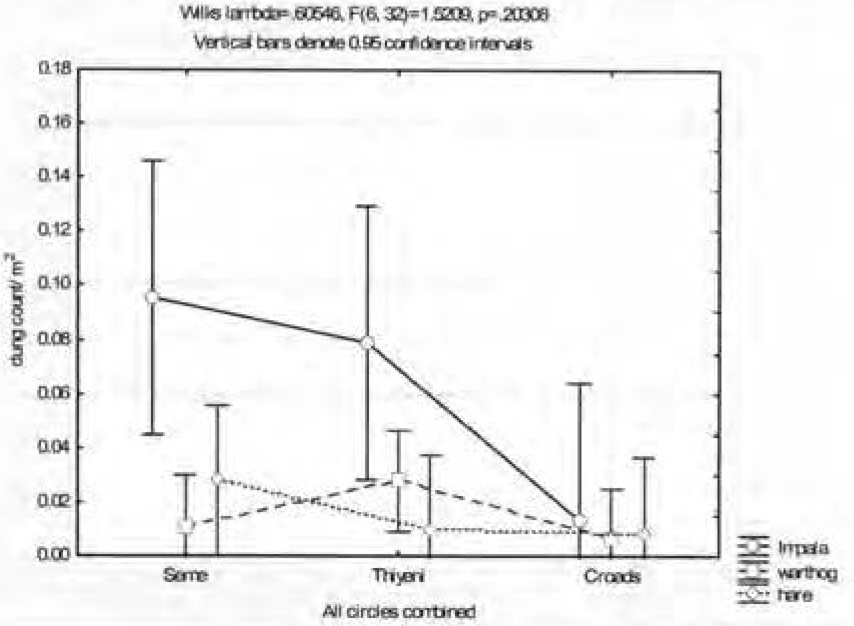
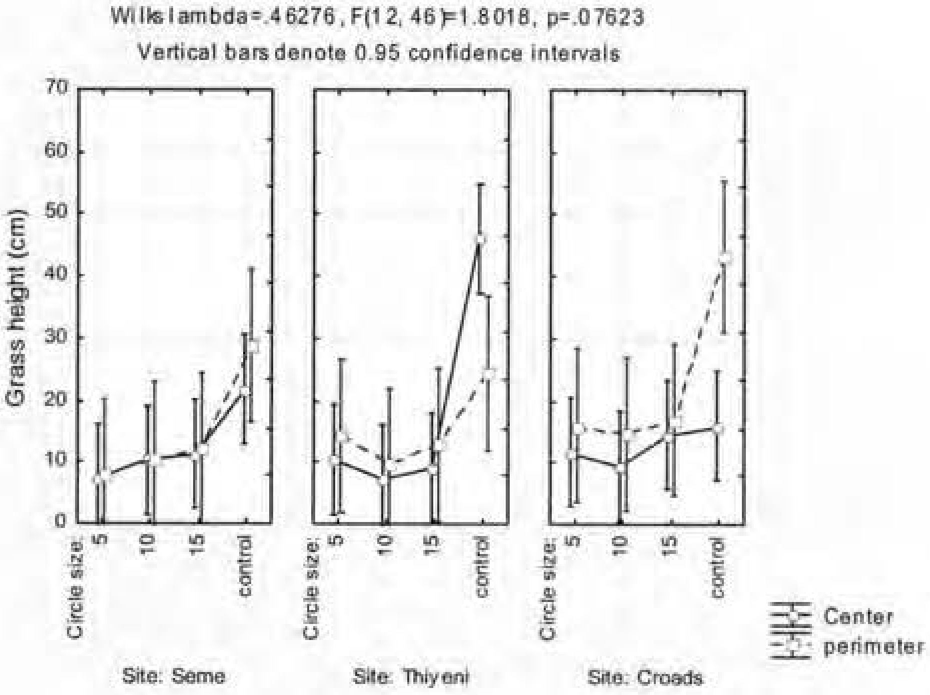


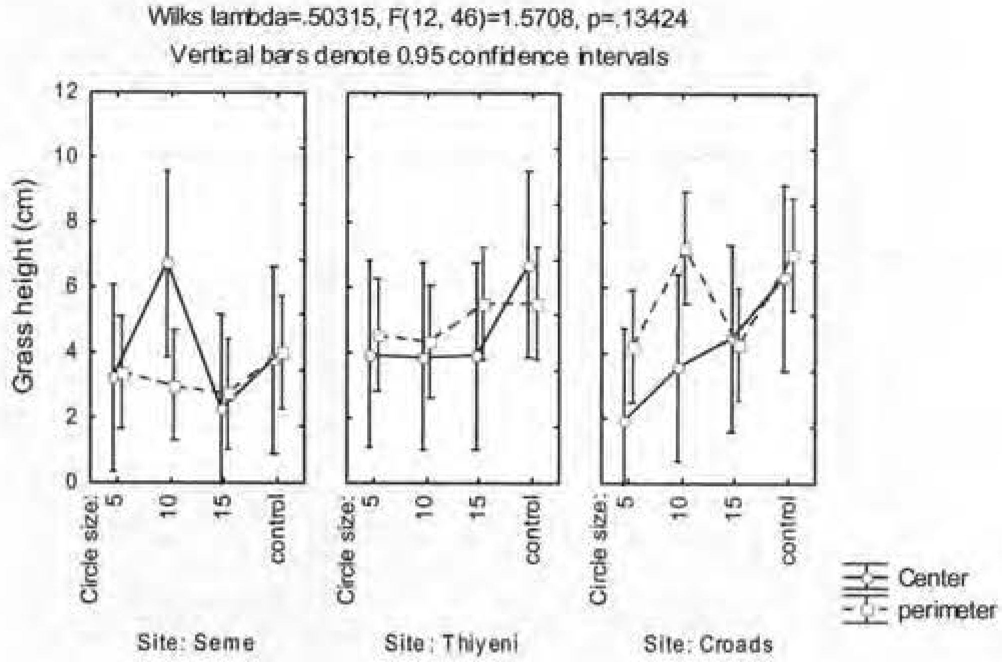
Figure 12. The abundance of dung for the smallest species for all circles combined on a site basis. There is no significant difference between the different species.

Grass height for the three sites for 2000, 2003 and 2004

a) 2000



b) 2003



c) 2004

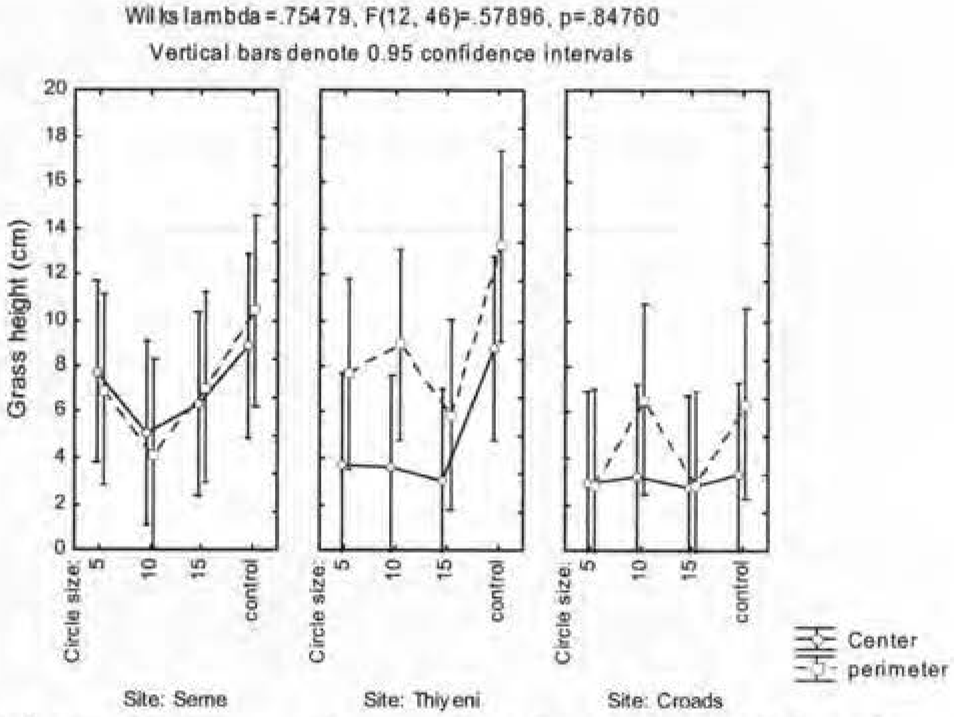


Figure (12) Grass heights on a circle and site basis for a) 2000, b) 2003 and c) 2004 data comparing heights in the centre to the perimeter.

An ANOVA was performed on the pooled data for all three sites for 2000. The circles are significantly different from each other in terms of grass height ($F=10.101$, $p<0.00001$, data not shown) however, this is due to the large difference between the control site and the circles as when the control site is removed the difference is no longer significant ($F=.57$, $p>0.5$, data not shown). The centres of all circles are lower than the perimeter. When the 2000 data is pooled on a site basis, the centres are lower than the perimeters. However there is no significant difference between sites ($F=1.65$, $p<0.2$). Control sites were excluded for this analysis. An ANOVA preformed on both site and circle differences in 2000, was almost significant ($F=1.80$ $p<0.8$, Fig 12a) with control sites included. They account for most of the difference between circles and sites but for all circles at all sites the centre is lower than the perimeter. This is not always the case for the control as at Thiyeni the centre is perimeter, as one would expect to find on a control sites. The grass is also higher overall on control sites.

In 2003, there was a significant difference in the heights of grass between sites ($F=3.22$ $p<0.05$ data not shown). The centre was actually higher than the perimeter in Seme while at Thiyeni and Crossroads it was lower. When control data was included in this analysis, the results were even more significant ($F=4.24$, $p<0.005$, data not shown). This shows that in 2003 Seme was significantly different from other sites in terms of grass height of centre and perimeter. Figure (12b) shows that this variation is due to circles of size $r=10$ in Seme that have centres that are higher than perimeters. At Crossroads for circles of size $r=15$ there is not much difference between centre and perimeter. For all other circles and sizes, the centre is lower than the perimeter, whereas controls vary as to be expected.

For 2004 grass height data, the centres are all lower than the perimeters for circles of all sizes. This is not significantly different between circles of different sizes with controls included ($F=1.69$ $p<0.15$, data not shown). When controls are excluded, the same trend exists with the centres of all circles lower than the perimeters but again no significant differences between circles of different sizes ($F=0.38$ $p<0.9$, data not shown). When the data for all sites for 2004 is pooled including controls, there is a significant difference between sites ($F=4.42$ $p<0.005$ data not shown). At the Thiyeni site the centre is lower than the perimeter at all circle sizes. At Crossroads this is also the case but at circles of size r=5 and r=15 there is almost no difference between the centre and the perimeter. Seme is again different as the centre is higher than the perimeter at circles of size r=5 and r=10. When controls are excluded, this relationship is still significant (F=3.27 p<0.05 data not shown). An ANOVA between the effects of sites and circle sizes showed no significant differences (F=0.58 p<0.9, Fig 12c). When control sites were excluded, there was still no significant difference (F=0.59 p<0.8, data not shown). Controls overall have longer grass than circles.

The correlation between animal dung and visibility measures

Animal dung abundance at each site was related to vegetation profiles. These profiles were taken at both 50 and 150cm. The data was then analysed for a variety of measurements for each circle; average visibility, minimum visibility, maximum visibility and modal distance to obscuring vegetation where possible. This was determined at both heights. A correlation between the abundance of animal dung and each measurement at each height was then made. The r=5 measurement was used in an attempt to standardise the patch size analysed and thus only compare differences in visibility between sites. Although this is not ideal as circles were a range of sizes, a standard area of each (r=5) was measured for dung abundance. The effects of circle size on visibility are ignored for this analysis and one must assume that all visibilities are due to individual differences in visibility between patches rather than the size of the circle the patch is situated in. Species not found in the table did not have a significant correlation between dung abundance and vegetation measures.

Table 4. A summary of the results for which site and visibility factors best explain the variance observed in the abundance of dung found on circles of different sizes.

Species	Factors	Correlation co-efficient	P values for factor
Warthog	150cm mode	R=0.7128	P<0.0001
Wildebeest	50 cm minimum	R=0.5808	P<0.001
	150cm minimum	R=0.4463	P<0.02
Zebra	50 cm minimum	R=0.4211	P=0.02
	150cm minimum	R=0.3830	P=0.03

The following figures (Fig 14, 15 and 16) graphically display some of the relationships reported in Table 4.

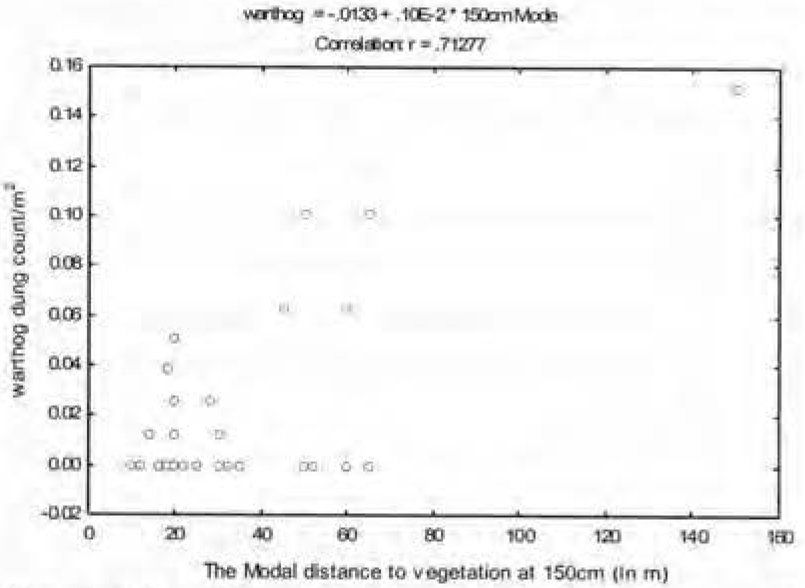


Figure 14. The correlation of the modal distance to vegetation (as measured at 150cm) with warthog dung for all circles using a standard patch size (the r=5 measure). Dung is measured as a count per m².

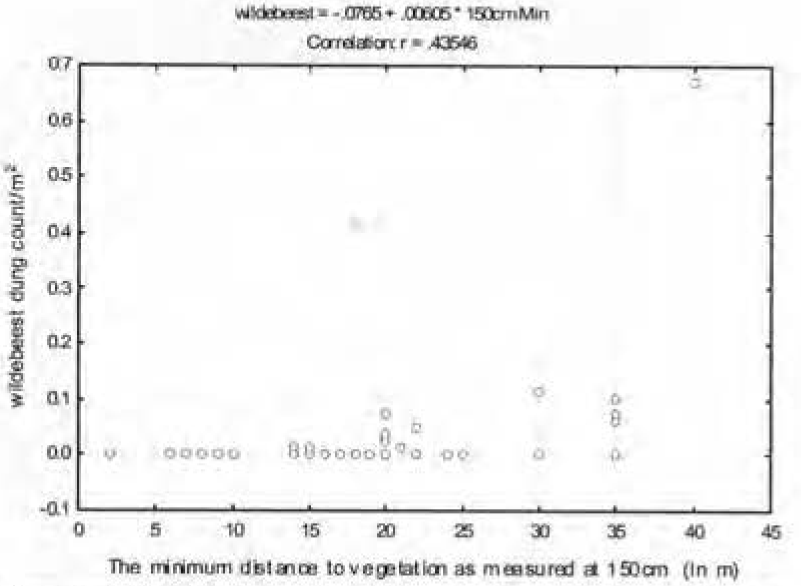


Figure 15. The correlation between the minimum distance to vegetation (measured at 150cm) and the abundance of wildebeest dung for a standard size patch (the r=5 measure) for all circles.

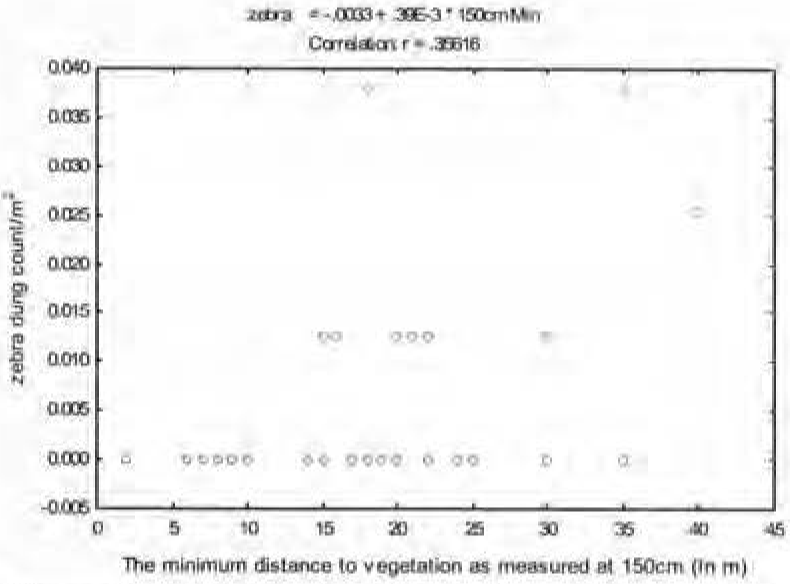


Figure 16. The correlation between the minimum distance to vegetation (measured at 150cm) and the abundance of zebra dung for a standard size patch (the r=5 measure) for all circles.

All three figures (Fig 14, 15 and 16) display a triangular relationship between the two variables, however the correlation for all three is significant. All three figures have a positive slope as well indicating increased animal utilization with increasing visibility.

Discussion

Testing determinants of patch choice

The forage limitation hypothesis predicts a relationship between body size and forage patch size and quality. To simplify tests of the opposing prediction, I defined a foraging patch as a short grass sward (or "grazing lawn" where grasses have been grazed short enough for long enough to switch species composition to predominantly lawn grasses). I then tested several predicted patterns of animal distribution in relation to lawn size. Very small mammals e.g. rats and mice are exposed to both aerial and ground-based predators. I restricted my study to grazers too larger for aerial predators with the exception of hares. I assumed that predator avoidance was primarily by visual cues and not due to olfactory or auditory cues.

Circles as a test of the patch choice

The gulliver removal experiment (GRE) provided an opportunity to test the patch choice hypothesis as it created grazing lawns of different sizes on three different sites that animals could choose between. Animals could be choosing to graze on a lawn due to several criteria. At one site, one would expect that all circles have grass on them of the same quality no matter what the circle size. Animals could be choosing to graze on patches that maximise food intake for their body size (Ritchie and Olff 1999, Olff *et al* 2002). Alternatively, animals could be choosing a site that best suits their predator avoidance strategy to minimise their predation risk. Since small animals are more at risk from a larger range of predators (Sinclair 2003) and are more vigilant (Underwood 1982, see Fig 2), one would expect that their strategy would be different to larger animals.

Presence/Absence data

From Figure 6 and 7 appears that impala are not as common on smaller circles as on larger ones. This is in opposition to the forage choice hypothesis that predicts impala would forage on small patches due to their small body size. This trend is also apparent for warthogs (Fig 6 and 7). No warthogs were found on the smallest lawns (r=5) while they are readily found on larger circles. The avoidance of small lawns by both of these species supports the predator avoidance hypothesis since both species have a high risk of predation. Rhino were present at all sites and rhino middens were situated near all circles. Thus, they are considered present for all sized circles on all sites, consistent with the predator avoidance hypothesis for large grazers.

Nyala were included even though they are mixed feeders with a relatively high browse intake, since they were found on circles and sometimes graze. In summer, their intake of monocotyledons is estimated to be 82% of their diet, dropping to less than 18% in winter (van Rooyen, 1992). They were rarely found on any circles and only on the larger circles (Fig 6 and 7). They are most common on control sites. This is in agreement with a more cryptic strategy this species may be following in order to minimise predation pressure.

The pattern for buffalo differs according to whether one uses the r=5 or the r=x measure of dung. Using the r=5 measure it appears that buffalo are found equally on all circle sizes regardless of size (Fig 6). Under the foraging hypothesis, it would be predicted that buffalo would only be found on the larger lawns. The r=x data supports this hypothesis as buffalo were more abundant on larger circles according to this measure (see Fig 7). Buffalo are also found in larger numbers on the control sight. This could mean they prefer denser vegetation, or that they are not trying to minimise their predation risk, as they have a predation refuge in their large body size and therefore are found in areas that have denser vegetation. They are also tall grass feeders and may thus prefer control sites where the grass is longer.

Wildebeest were present less often on smaller circles than larger circles (Fig 6 and 7). It appears that they are selecting for larger circles. This would be in line with the foraging hypothesis. The two measures of abundance however show a different result for control sites. The data for hares for the r=5 and the r=x measure is similar (see Fig 6 and 7). Hares were present most often on larger circles. Zebra were least often encountered on the smallest lawns and most often encountered on control sites when presence/absence data is considered (see Fig 6 and 7). This would seem in line with the foraging hypothesis that larger animals would select larger grazing patches

Figure 8 considers the probability of animals occurring on the smallest patches relative to their total presence on all patches. If animals were selecting patches according to the foraging hypothesis then one would expect only small animals to be present on small patches. Rhino are present on small patches in opposition to the foraging hypothesis. Buffalo are also present on small patches in accordance with a predator avoidance argument and in opposition to the foraging hypothesis as they could be on these patches without endangering themselves. The next most abundant animal is impala. There is a contrast between impala and animals of a similar body mass (warthog and nyala), which are not present on the smallest patches as would be predicted by the foraging hypothesis. Herd size and the predator avoidance hypothesis could explain this phenomenon. Impalas are present in larger herds than either warthog or nyala. Due to the effects of herd size on vigilance, it appears that this data best supports the predator avoidance argument as related to herd size (see Fig 5) for impala.

Hares are most likely to be found on small patches after impala. This appears to support the foraging hypothesis as small animals are found on small patches. However, I believe that this pattern for hares could also be in support of the predator avoidance hypothesis as hares are small enough to fall prey to aerial predators. Thus, patch size is also another way at looking at distance to cover for small species. If patches are small, a hare can quickly dash to the protective cover offered by the surrounding vegetation. The larger the patch the further the distance to cover, the less likely a hare will be found on a patch. It is difficult to disentangle this effect from the foraging hypothesis predictions though.

Figure 9 shows the overall correlation between the r=5 and the r-x measure of dung on circles and control sites. The amount of dung found on circles of r=5 does explain 58% of the dung found on the entire circles. The smaller area being sampled does affect the amount of dung recorded and probably the number of species that may be encountered. Thus where possible both measures are used or just the r=x measure is used in order to avoid the under sampling of the r=5 measure. The measure of dung in dung piles per m^2 using the broadest measure made of dung abundance, the r=x measure is used in Figure 10 to get the maximum counts for all species to avoid under sampling (see Fig 9). Hare, the smallest study species, are most abundant on small circles. This appears to support the foraging hypothesis However, predator avoidance arguments for this species might also be relevant as previously mentioned.

Impala are not present on the smallest patches (Fig 10). This can be interpreted as support for the predator avoidance argument as they are avoiding the smallest circles where their risk of predation would be highest. They are not however as abundant on large circles as one would expect. It is possible that the larger circles are used by several species and much of the forage has already been removed. Due to the winter drop in food availability, impala may be grazing on smaller circles where the risk of predation is higher but food resources are still available. In order to counter the increased predation risk they graze in these environments in larger herds as predicted by Fig (5) and thus the abundance of dung is the highest on intermediate sized circles.

Warthog have a similar trend to impala and are most abundant on medium sized circles. However, they are still quite abundant on large circles whereas impala are not.

This could again be a herd size effect (Fig 5) as warthog generally form smaller herds than impala. The difference in visibility between medium and large patches and lawns is also probably of little consequence for warthogs as they have quite poor eyesight. Wildebeest do not seem to be abundant on any circles and seem to prefer lawns. This trend can be interpreted as support for either patch choice argument. Zebra are not present on the smallest patches. Their abundance is similar on medium and large patches but they are most abundant on lawns. This could be interpreted as supporting the foraging hypothesis as zebra are selecting larger patches. Zebras are also quite vulnerable to predation. The avoidance of small patches by zebra may thus be interpreted as support for the foraging hypothesis as well as support for the predator avoidance hypothesis.

The animal least likely to be affected by predation according to body size arguments in this study would be buffalo. Thus, one would expect their choice of patch size to be mostly due to the foraging argument or to be random. Buffalo are most common on lawns and almost absent on large circles. One would also expect them on large circles if they were choosing patches purely on size. They are also relatively abundant on small and medium sized lawns. This is in contradiction to the foraging hypothesis that would predict them only selecting the largest patch sizes. Thus, the data for buffalo does not contradict the prediction made by the predator avoidance hypothesis and does not fully support the forage choice hypothesis.

The patterns for all species abundance on different patch sizes can be interpreted in different ways. However, several species openly contradict the foraging hypothesis prediction on patch size, notably the smallest species (warthog and impala) while several of the larger species are not only found on the largest patches (buffalo). Thus, there is some support that predator avoidance may be affecting the patch choice of smaller animals as predicted by the predator avoidance arguments and that the foraging hypothesis does not explain all of the variability in patch choice displayed by larger animals.

Habitat visibility at different heights and different sites

Figure 10 supports the assumption that increased circle size does increase the distance to vegetation cover. Figure 11 shows that there are site differences in distance to cover. This indicates that the Crossroads site is a more wooded or scrubby site than the Seme or Thiyeni site. One would predict that patches in an overall more enclosed site would be avoided to an even greater degree. If patch choice were not influenced by predator avoidance arguments then one would expect no difference between the circles on different sites. Figure 12 shows the results for the smallest animals alone as one would expect these would be the most influenced by distance to vegetation cover according to the predator avoidance hypothesis. All species appear to be less common at Crossroads that at either Seme or Thiyeni. This suggests that the overall visibility of sites does affect patch choice of smaller species.

Comparing the height of grass in the centre of circles to the perimeter

If the predator avoidance argument holds then one would expect animals to graze in the centre of circles to maximise their viewing distance to potential predators that could be concealed in the surrounding cover. Thus one would expect the grass in the centres of circles to be lower than the grass on the perimeter. The foraging hypothesis makes no prediction about where an animal will graze in a patch but as the argument is based on food quantity and quality I would expect an animal to graze the perimeter and the centre equally as the quality would be uniform across a circle. Figure 12 a) b) and c) presents the data by site and circles for 2000, 2003 and 2004.

For the data for 2000, 2003 and 2004 most circles have perimeters that are higher than centres. Seme is an exception for most years as perimeters and controls are usually similar in height. Controls vary in whether the perimeter or the centre is higher as to be expected as these plots were laid out in tall grass areas. This is in support of the predator avoidance argument, as it can be interpreted that animals prefer to graze in the centre of circles, where their distance to vegetation cover is maximised, as opposed to the perimeter where they are closer to vegetation that may be hiding a predator. Seme does not conform to this trend, which may be due to the action of rhinos, its general openness or due to some other unforeseen site difference.

The correlation between animal dung and visibility measures

In order to compare the abundance of animal dung under different visibility conditions with the only variable being the visibility from each patch, a standard size patch within each circle was chosen; the r=5 measure of dung abundance. The size of the circle has been shown to influence the distance to obscuring vegetation (Fig 10) but the average increase in visibility from a circle of size r=5 to r=15 is about 10m at the 150cm measure of visibility. Thus, this assumption should not influence the results greatly as differences between different circles are usually much greater than this. Several different measures of visibility were used from the vegetation profile data, as animals may be discriminating between patches using different criteria than we might. Correlations for three species were significant between dung abundance and visibility measures (see Table 4). A single significant relationship for each species is illustrated (Fig 14, 15 and 16).

The correlation between warthog abundance and the modal value of distance to vegetation at 150cm is the most significant of the relationships in Table 4. The modal distance to vegetation could be interpreted as the overall openness around a patch or the uniformity of vegetation around a patch as warthog may avoid patches where a single large bush may provide an ambush site for a predator. It is possible that warthogs are selecting patches that are generally quite open or uniform in their openness. This is support for the predator avoidance hypothesis, as one would not predict any relationship between patch choice and patch openness based on the foraging hypothesis. Figure 14 presents this relationship. Warthog can either be present at certain measures of openness or not. This indicates that there may be other factors that affect warthog patch choice.

Wildebeest and Zebra also have significant correlations between the abundance of dung and the minimum distance to vegetation for the 50 and 150cm measures (Table 4). This suggests that for both species the presence of small bushes or tall grass (the 50cm measure) and presence of larger shrubs and trees the 150cm measure) affects their choice of patch. Figure 15 and 16 show that wildebeest and zebra can either be present at certain measure of visibility or not, indicating that factors other than the minimum distance to vegetation at 150cm are affecting patch choice. The herd size effect on patch choice as predicted by the predator avoidance hypothesis (Fig 5) could explain the higher than expected abundances for certain visibility measures.

Although the correlations between dung abundance and visibility measures did not account for all of the variability in the data it is worth noting that all correlations were positive and that the slopes of all correlations were positive, thus dung abundance increased with increasing visibility. This again suggests that predator avoidance may be influencing the patch choice of animals. This correlation was not found for buffalo, thus supporting the predator avoidance argument, as one would predict that buffalo patch choice would not be affected by patch size, as they are not as sensitive to predation due to their large body size. Different species may also be discriminating between patches based on different measures of patch openness.

Conclusion

Many of the different analyses suggest that smaller animals are not found on the smallest patches as predicted by the foraging hypothesis. It is possible that animals are selecting patches that meet several criteria. It is difficult to directly contrast the foraging hypothesis and the predator avoidance hypothesis because they do not have a comparable currency. As Underwood (1981) first explained, the major difficulty in analysing vigilance behaviour is that an animal finding food by sight (or according to the foraging hypothesis selecting an appropriate size patch for a certain body size), receives immediate feedback on the success of its search behaviour. However by scanning for predators it is investing time in detecting a much rarer event and it may have little direct feedback of how effective its scanning is.

Ritchie & Olffs' scaling laws (1999, Olff *et al* 2002) are an attempt to find common simplifying relationships in ecology that can explain biological diversity and habitat partitioning. However, they have overlooked predation and predator avoidance, which are especially important in African game reserves where we still have a high density and diversity of predators. Even if it is difficult to quantify the effects of predator avoidance on patch choice, it is important to recognise that it may be taking place. Their model might work well in environments where predators are rare or absent and food choice may purely be based on quantity, quality and body-size arguments. However for animals in environments that contain predators I believe the primary concern is how to obtain food without becoming food.

The interface between animal behaviour, foraging theory and vegetation structure is important and deserves more attention. The implications of these relationships are exciting and potentially powerful as one could manipulate the natural environment to the benefit of target species, or to better observe how environmental change affects species. This is especially relevant with vegetation change in most game parks leading to bush encroachment. The impacts of a thicker vegetation cover on grazing species may result in greater mortality because the vegetation provides enhanced cover for predators. The loss of grazing lawns in HiP may affect grazers directly through a diminished food resource and indirectly due to diminished visibility on lawns. The change in vegetation observed in HiP provides an opportunity to test these ideas.

This study has provided several arguments that animal choice of grazing patch may be influenced by predator avoidance. This finding could be incorporated with current patch choice arguments in order to better explain the patterns observed in biological systems with a diversity of predators and prey and their interactions with their environment.

Further Study

The theory developed in this study remains to be directly tested. Visual observation of animal vigilance in different habitats to determine the actual impacts of vegetation on vigilance behaviour would be a first step. The effects of vegetation are complex as plants provide both food and cover. Cover can again be a shelter from predators as well as a potential ambush position. One would need to be able to be able to keep all factors the same and experimentally manipulate one factor in order to see what its singular effects are. Hunter & Skinner (1997) had such an experimental set-up and showed that animals were more vigilant when predators were present and that vigilance behaviour increased over time after the introduction of predators. Experimental manipulations of vegetation density and visibility distance would help clarify the effects of vegetation on patch choice. Removing large predators from an area and seeing if patch choice changed over time would also provide support for the predator avoidance argument of patch choice.

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