



# **Niche partitioning: African savanna species coexistence reviewed**

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African savanna species coexistence reviewed**

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**Table of contents**

<b>Abstract.....</b>	<b>4</b>
<b>Introduction.....</b>	<b>5</b>
<b>Niche partitioning mechanisms.....</b>	<b>8</b>
Mouth morphology.....	9
Ruminants and non-ruminants.....	9
Grazers and browsers.....	12
Seasonality.....	13
GPS tracking.....	15
DNA metabarcoding.....	15
Heterogeneity.....	16
Predators.....	17
<b>Conclusions.....</b>	<b>18</b>
<b>References cited.....</b>	<b>20</b>

## Abstract

The incredible high biodiversity of Africa has been a subject of much discussion. The assemblages of large mammalian herbivores on this continent are usually comprised of about 10-25 species, coexisting on a limited range of resource types. A much-asked question is thus, how can so many species coexist without competitively excluding each other? A compelling explanation emerges through the differing body sizes of the species, that span three orders of magnitude. The Jarman-Bell principle states that large endotherms can consume low quality forage, provided there is sufficient quantity, while smaller species consume high quality forage in smaller quantities. This is a much-studied principle, however there is still much debate and uncertainty on the precise mechanisms involved in niche partitioning amongst African savanna herbivores.

This paper provides a comprehensive review of the most relevant literature existent on niche partitioning, giving a good overview of what should be taken into account in future studies. Novel methods, such as GPS collaring and DNA metabarcoding, are discussed and gaps in the research pointed out. A reminder is given on the importance of ecosystem heterogeneity, that is under threat due to human impacts.

Found was that the diet quality of the species is important in niche partitioning as there is a negative relationship between diet quality and body mass. However, this pattern differs according to the digestive adaptation of the species. Non-ruminants, compared to similar sized ruminants, can consume lower quality food leading them to occupy a more diverse habitat. Additionally, body size has no clear influence on niche partitioning in non-ruminants. Body size is also not related to diet type (browser/grazer). Furthermore, sometimes there is more diet similarity across grazer and browser guilds than within them. Larger species generally have larger mouths, allowing them to consume higher quantities of the lower quality forage they need to meet their nutritional requirements, with exception of the megaherbivores. Additionally, studies should encompass both the dry and the wet season, as competition is reduced in the wet season, making niche partitioning less apparent. Next to resource limitation, predation pressure also plays a vital role, which is widely ignored. New methods such as GPS collaring allow for conclusions at a finer habitat scale, while DNA metabarcoding permits identification of the vegetation being consumed at the species-level. Future research should take all of these mechanisms into account to get a clear picture of niche partitioning.

The increasing human population and its impacts bring these delicate interactions into danger, reducing ecosystem heterogeneity and consequently biodiversity. Understanding the mechanisms of niche partitioning, and how humans impact them, should be a priority in African savanna research.

## Introduction

As Hutchison asked in 1959, why are there so many kinds of animals? In 2011 the number of species was estimated at around 8 million (Mora et al, 2011). How can they all coexist within the limited space available on earth?

The competitive exclusion principle states that two competing species cannot coexist at constant population values (Volterra 1928). Therefore, for species to coexist they should have mechanisms that allow them to reduce the level of competition between them (Levin 1970).

Niche theory is the main theory used to explain this species coexistence. An ecological niche is a concept that expresses the functional outcomes of the anatomy, behavior and physiology of a species for its distribution and abundance (Hardin 1960). These phenotypic attributes predict how organisms obtain shelter from the environment, encounter and cull food sources, assimilate the food, procure water and avoid predators (Hardin 1960). Niche theory then forebodes that species can coexist by purposing the environment in different ways (Hutchinson 1959, Hardin 1960). Species can partition their niche through several proposed mechanisms. Firstly, the species in the niche can be preyed upon by different predators. This way each prey is constrained by a distinctive natural enemy and will be able to coexist (Kotler 1984). Additionally, species can differentiate their niche via a competition-predation trade-off if one species is a better competitor when predators are absent, and the other is better when predators are present. Defenses against predators are often costly, and therefore, these species are generally poor competitors when predators are absent. Here coexistence is possible if predators are more abundant when the less defended species is common, and less abundant when the defended species is

common (Holt et al 1994). Another way species can partition their niche is by differing in competitive abilities based on varying environmental conditions. For instance, one species can survive better in dry conditions and the other when the environment is wetter (Angert et al 2009). Finally, species can coexist when they use different resources. This is illustrated by the Galapagos finches. The larger beaked birds consume the larger seeds, while the smaller beaked birds feed on the smaller seeds (Lack 1947). This way they exist in the same niche and reduce competition by partitioning the resources available.

Of the many faunas in which this mechanism is thought to be important, few have led to as much research and debate as the assemblages of large mammalian herbivores in Africa, that are usually comprised of about 10-25 species that coexist on a limited range of resource types (McNaughton & Georgiadis 1986). Local landscapes differ greatly in geological properties and therefore elevations, resulting in steep gradients of precipitation. Consequent habitat fragmentation, high diversity of vegetation and climatic conditions, led to major adaptive radiations of the mammal fauna (Mcnaughton & Georgiadis 1986). Therefore, we can assume that the high heterogeneity of the African savanna ecosystem allowed the evolution of the great biodiversity of herbivores (Mcnaughton & Georgiadis 1986). However, how so many apparently generalist consumer species coexist has been subject of much debate and has been intensively studied both theoretically and observationally (Cromsigt & Olff 2006). Nevertheless, the mechanisms of resource partitioning are often unclear. It is crucial to understand these mechanisms, however, as large African grazer assemblages are important both ecologically (Bell 1971) and economically (Prins et al 2000). Moreover, in Africa 50% of the land area is made up of savanna ecosystems. They

support a large fraction of the human population, rangelands and livestock. Furthermore, they contain one the last remaining high densities of wild herbivores and carnivores in the world (Scholes & Archer 1997), next to those found in boreal forests for example, where White-tailed deer (*Odocoileus Virginianus*) reach densities of  $>15$  deer/km<sup>2</sup> (Cote et al 2006). Unfortunately, these ecosystems are increasingly threatened by human activities. The human population is predicted to increase at a very rapid rate, leading to more livestock and consequent overgrazing of the ecosystem (Sinclair et al 2008). Climate change is also expected to negatively affect these ecosystems, increasing drought events (Olf et al 2002). We need to know what these threats will do to the ecosystem in order to make informed conservation decisions.

A lot of research has therefore been done on this question, and niche partitioning has been considered in terms of how body size influences diet quality requirements (Jarman 1974), how distinctions in digestive adaptations affect the ability to cope with vegetation with high fiber contents (Hofmann 1989), how differing mouth morphologies affect the ability to consume grasses of different heights (Bell 1970) and finally, how the group size influences predation risk (Jarman 1974).

African mammalian herbivores are largely influenced by bottom-up factors (resource based) and their body masses span three orders of magnitude (du Toit & Olf 2014). The body size of mammalian herbivores dictates the minimum quality of food necessary for survival and hence for the feeding niche selected. This hypothesis was first proposed by Bell (1970) and Jarman (1974), who performed two independent studies on the feeding ecology of grazing guilds and on the behavioral ecology of browsing and grazing antelope,

respectively. The hypothesis is based on the fact that gut volume is a constant proportion of body weight (Demment 1982), while maintenance metabolism (a prime determinant of intake) is a fractional power of body weight (Kleiber 1975). Since these two factors influence how long the food particles are retained and therefore the digestion extent of the diet, body size has been considered as a mechanism through which species differ in diet and can therefore occupy the same niche (Bell 1970, Van Soest 1982). In other words, by extending the retention time, large ruminants allow for additional fermentation and therefore extract more energy from forage. This means that larger species have a wider food tolerance that allows them to use a larger proportion of the landscape and a higher diversity of habitats, which include habitats too poor in quality (fibrous forage) for smaller species. Smaller species require higher quality, but sustain on lower bulk intake diets (du Toit & Owen-Smith 1989). This implies that there will be a negative relationship between diet quality and body mass. Gordon and Illius (1996) term this the diet-quality assumption or model, and argue that diet quality is the primary determinant of niche diversity. Megaherbivores (defined as herbivores weighing more than 1000 kg) seem to be an exception to this pattern. Allometric relations would predict that megaherbivores should be bulk feeders capable of utilizing the very lowest quality forage when compared to smaller species. However, Owen-Smith (1988) shows that even during the dry season, megaherbivores exhibit protein levels in their stomach contents comparable to those of much smaller grazers.

The fact that the vegetation quality and quantity linked to body size is a compelling explanation for niche partitioning amongst African herbivores, also led people to look at mouth morphology. A larger herbivore has a larger mouth and can therefore consume

higher quantity of forage, while a smaller herbivore has a smaller specialized mouth that allows selective foraging of high quality food (Arsenault & Owen-Smith 2008, Gordon & Illius 1988). For example, the wildebeest (*Connochaetes taurinus*) has a wider mouth, permitting it to ingest more forage at a faster rate, meeting its nutritional needs on a short pasture. The topi (*Damaliscus lunatus jimela*) has smaller mouth and therefore, bite area, needing higher quality forage in smaller quantities (Figure 1).



**Figure 1.** The wildebeest has a wider mouth than the topi, giving it a bigger bite area and can therefore gain more energy from the shorter grass, despite having a lower bite depth.

Next to body and mouth morphology, diet type has also been considered when looking into niche partitioning. Herbivores can be grazers or browsers. Grazers eat foliage of grasses and sedges, while browsers eat foliage of forbs and woody plants (du Toit & Olff 2014). Some mammals are represented in both guilds, such as bovids, cervids and rhinos, while others are exclusive to either one. Additionally, some are known as “mixed feeders”. Grazing when grass is available, and otherwise browsing, such as elephants (*Loxodonta Africana*). Hofmann & Stewart (1972) and Hofmann (1973) suggested that the major ecological dichotomy separating species of ruminants is their adaptation to consuming a bulk diet of primarily grasses (grazers) or a concentrate diet of primarily browse or forbs (browsers). The idea is that, relative to their size, browsers have a lower

rumen volume with a higher passage rate and energy assimilation capacity than grazers. Gordon and Illius (1996) term this the diet type assumption, later used as diet type model by Codron et al (2007). However, a comparative allometric analysis of the digestive function of African ruminants (Gordon & Illius 1994) showed that there was little difference in many of these parameters between browsers and grazers. Nevertheless, they are recognized as behaviorally and functionally distinct within their ecosystems (Gordon & Prins 2008) and many niche partitioning studies have focused on this diet type model.

Studies on resource partitioning have greatly focused on ruminants (for example, du Toit & Owen-Smith 1989). Ruminants are able to ferment the ingesta in a specialized stomach. However, the ruminant browsers investigated are only a small subset of the functional diversity found in savanna herbivores. Non-ruminants do not ferment and are therefore less efficient at extracting nutrients from forage, but compensate for this by having higher throughput rates (Duncan et al. 1990). These increased throughput rates enable non-ruminants to be more effective at processing very low quality forage than a similar size ruminant (Demment & Van Soest 1985, Owen-Smith 1988, Duncan et al 1990). Consequently, a non-ruminant of a certain size is expected to overlap in diet more with bigger ruminants than with ruminants of the same size (Illius & Gordon 1992). Hind-gut fermenters can also use taller and more fibrous grass as symbiotic bacteria aid in digestion in a single-chambered stomach (Ditchkoff 2000). Therefore, one must take the digestive strategy of the herbivores into account when investigating the mechanisms involved in niche partitioning. The type of digestive strategy dictates the quality of food that the species is able to digest, and therefore the relationship between body-size and diet quality.



The larger body of research on niche partitioning has focused on resource partitioning as an explanation for species coexistence. However top-down factors are potentially also playing a role. Predation risk can dictate spatial patterns of herbivores, as they will try to avoid predation by staying in groups and by avoiding high risk areas (Hopcraft, Sinclair & Packer 2005). Additionally, body-size affects rates at which it is predated (Cohen et al 1993).

Many studies on niche partitioning only look at one of the possible explanations, while it is highly likely that they are not mutually exclusive (Kleynhans et al 2011). Therefore, here we review the most important work that has been done on this question, linking the studies and providing insights into the next steps that need to be taken. I focus on the main mechanisms proposed for niche partitioning, namely, body-size, mouth morphology and digestive strategy. I discuss the effects of the dry and wet season on competition and niche partitioning. Additionally, new methods that allow more insights are explained. Furthermore, gaps in the research are presented, such as the lack of focus on top-down mechanisms. Finally, future directions for research are provided as human impacts intensify.

## Niche partitioning mechanisms

Ritchie and Olff (1999) use principles of fractal geometry to show, theoretically, that heterogeneity of the environment is an important factor facilitating the coexistence of species. They suggest that larger species should perceive and use less spatial detail (coarser grain) of heterogeneously distributed resources. This is in agreement with one of the main theories that tries to explain niche partitioning, namely that distinct species sizes

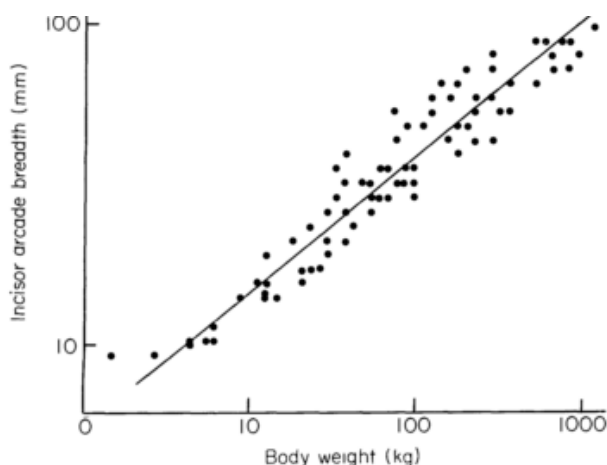
lead to differential resource use (Bell 1970, Jarman 1974, Geist 1974). Large endotherms can consume low quality forage, provided there is sufficient quantity, while smaller species consume high quality forage in smaller quantities (du Toit & Owen-Smith 1989) (Figure 3). A whole body of research has been done on this theory and has provided some compelling evidence. Demment and Soest (1985) provide first evidence for this theory, and indeed show that allometric relations between body size and metabolic rate, and body size and gut capacity lead to this pattern. There has been some divide as to what is the most important vegetation property in order to maximize nutritional gain. Some argue that grass height greatly impacts bite size, and hence the amount of food intake (Laca et al 1992, Farnsworth et al 2002). They state that the larger species require longer grass in order to meet their nutritional needs, while the smaller species can still have an adequate food intake rate on short grasses. This would mean that smaller species would have a competitive advantage over bigger species for being able to utilize short grasses too low in biomass for the bigger species. A study by Arsenault and Owen-Smith (2008) test this idea and found that grass height is inadequate to explain species coexistence and call into question the competitive superiority of smaller species on sparser vegetation. The problem with this study is that it doesn't take the quality of the vegetation into account. Tall vegetation does not imply higher nutritional value. In fact, smaller grasses are generally more leafy and of higher quality (Bell 1971, Geist 1974, Jarman 1974). They found that the white rhinoceros (*Ceratotherium simum*) concentrated on the smaller grass, while being the biggest species. Food quantity in relation to body size alone does not suffice to explain niche partitioning. Illius and Gordon (1992) did look at food quality however, and found that the longer



retention time of forage in larger animals was equal to better digestive ability and where therefore able to use lower quality forage. They were at a disadvantage when food was limited however, because they need much larger quantities of food. Thus, food quantity and quality should both be included in niche partitioning studies looking at body-size. However, next to body size, other factors are contributing to niche partitioning and species coexistence, which are discussed next.

### Mouth morphology

Next to body size, mouth morphology has also been included in studies looking into the Jarman-Bell principle. According to the principle small animals must be more selective in their choice of food. Therefore, small species would be expected to have a feeding apparatus which allows a greater degree of selectivity than that of larger animals. This is exactly what Gordon and Illius (1998) looked at. Larger species have a greater incisor arcade breadth (Figure 2).



**Figure 2.** The relationship between log incisor breadth and log, body weight (Gordon & Illius 1998).

A wider mouth increases bite area which allows larger species to ingest high quantities of low quality forage. Smaller species have specialized mouths that allow them to reach

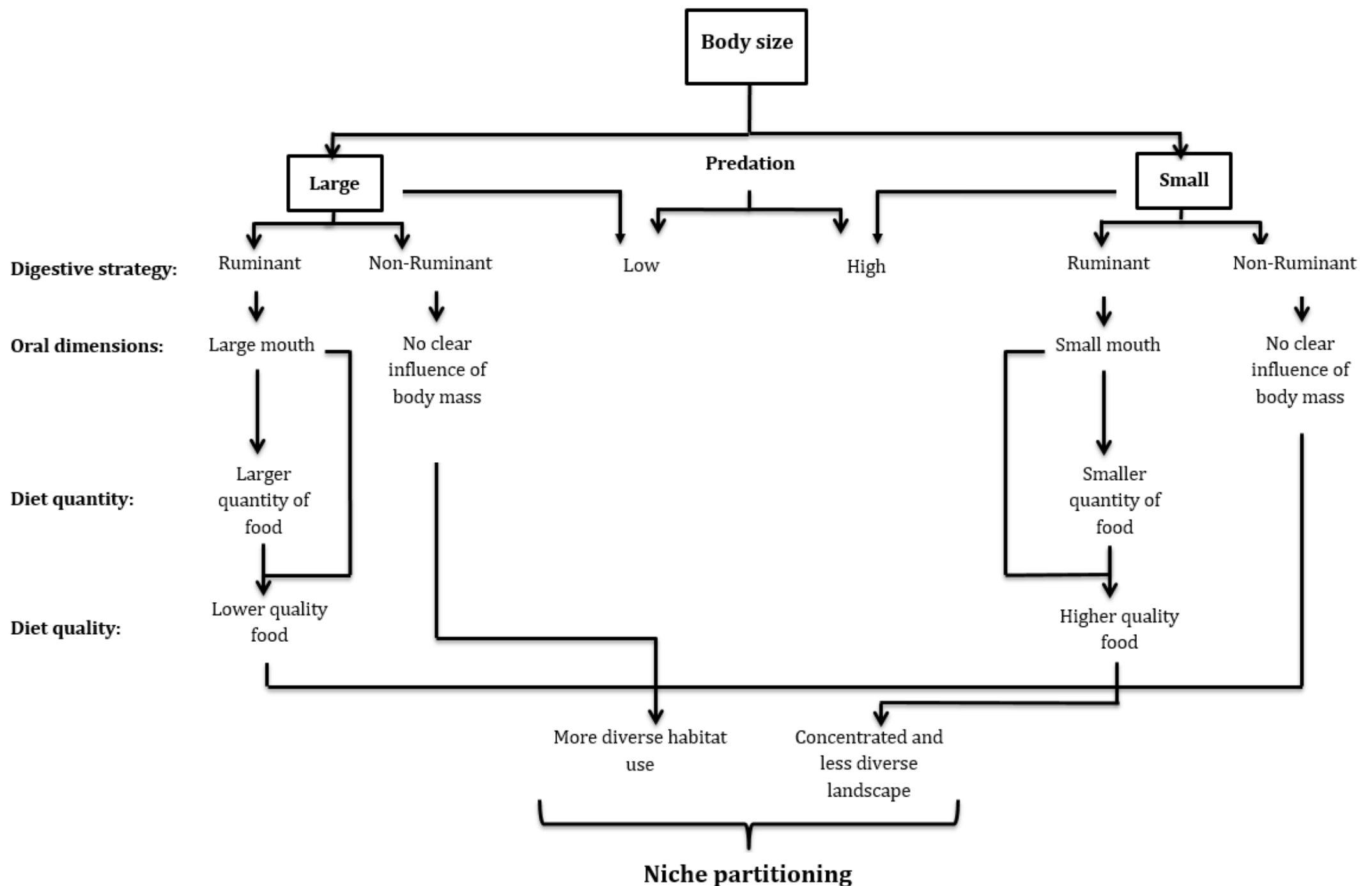
the high-quality forage that is available in lower quantities (Gordon & Illius 1998). Mouth morphology is therefore important in determining what quantity and quality the herbivore can consume, which in turn leads to different habitat use and niche partitioning (Figure 3). Two of the largest grazers, the hippopotamus (*Hippopotamus amphibious*) and the white rhinoceros have an exceptionally wide mouth. According to the Jarman-Bell principle one would expect them to forage on very big amounts of the lowest quality forage. This does not happen however, since their lips allow them to pluck the grass and gain sufficient nutrition on the grazing lawns they maintain, which are of high quality. This is probably why Arsenault and Owen-Smith (2008) found the rhinoceros feeding on low grass patches. However, due to their size and therefore reduced metabolic requirements, can also exploit lower nutritious vegetation (Owen-Smith 1988). Bonnet et al (2010) argue that the rhino exploits both high quality and low quality vegetation as this is needed for the metabolic maintenance of such a large body (Bonnet et al 2010). These species are generally distinguished as megaherbivores and have been shown to not fit the theory (Kleynhans et al 2011, Owen-Smith 1988). Thus, studies looking at niche partitioning should take mouth morphology into account, however not forgetting that megaherbivores show a different pattern than that predicted by the principle due to their ability to consume both low and high quality forage.

### Ruminants and non-ruminants

There are various studies showing that body size and consequently mouth width lead to niche partitioning through differential resource use. Nevertheless, in 2011 de Jongh and colleagues performed a study in Northern Cameroon investigating the importance of diet composition and diet quality on resource

partitioning among eight species of savanna herbivores, with different body masses. They concluded that the species did not segregate in food quality or diet composition along a body mass axis. The lack of a body mass–diet quality relationship was in sharp contrast to the Jarman–Bell hypothesis. The interesting thing about this study is that they looked at the individual grass species level. This is rarely done even though this seems a logical step. However, the authors do argue that the range of food plants found in the diet is not informative about the quality of the food that is consumed. So, the data was distinguished into diet composition and diet quality (by measuring phosphorus and nitrogen levels in dung). One might argue that by looking at the species level, contrary evidence to the Jarman–Bell principle emerges and that perhaps herbivores do not have such partitioned niches after all, offering the potential for competition. However, this study was conducted in a tropical area where resources are plentiful and herbivore densities low. The authors conclude that the lack of partitioning actually shows a lack of competition, and that niche partitioning would become more apparent with increasing resource scarcity (Iongh et al 2011). This study is important as it provides indirect evidence for competition in the areas where niche partitioning was found and shows that climatic conditions can influence the conclusions taken. In the same year, Kleynhans and colleagues performed a very complete study on niche partitioning. While other studies normally looked at mechanisms separately, this study investigates resource partitioning among ruminants, non-ruminants and a megaherbivore in South Africa, taking individual grass species into account, in the dry and wet season. Their conclusion was that savanna herbivores in this system coexist mostly through body size-driven resource partitioning in the dry-season (with exception

of the megaherbivore). This study provides very compelling evidence for the Jarman–Bell principle as it encompasses a lot of covariables, including digestive adaptations, such as ruminant and non-ruminant digestion. As shown by Foose (1982), relatively high digestibility is a typical strategy found in ruminants, while the other extreme is found in non-ruminants. It should not be forgotten that the hindgut fermentation system can also allow a strategy of food intake closer to ruminants, as evident in rhinos (Foose 1982, Steuer et al 2011). Duncan (1990) showed that non-ruminants of a similar size to ruminants have a higher food intake rate that more than compensates for their reduced digestibility. Therefore, they extract more nutrients per day from a wider range of forage, including that used by ruminants (figure 3). An experimental study by Crooms and colleagues (2009) confirms this by showing that non-ruminant grazers were more evenly distributed than similar-sized ruminants and that body mass did not clearly influence their diversity of habitat use and use of low quality habitat (Figure 3). For example, warthogs (*Phacochoerus africanus*), zebras (*Equus quagga*), and the white rhino, all non-ruminants, select for high quality forage regardless of their increasing body mass. The small sized ruminant grazers (impala (*Aepyceros melampus*) and wildebeest were more concentrated in the landscape and used a less diverse habitat (Figure 3). Therefore, non-ruminants differ from ruminants as evidence does not show a clear influence of body mass on partitioning for non-ruminants, and they occupy a wider range of habitats (figure 3). Small ruminants do show evidence of body size effect and are more concentrated in certain habitat types. This difference serves as a way to niche partitioning (Figure3).



**Figure 3.** Generalized outline of the conclusions taken by research on niche partitioning amongst African herbivores.

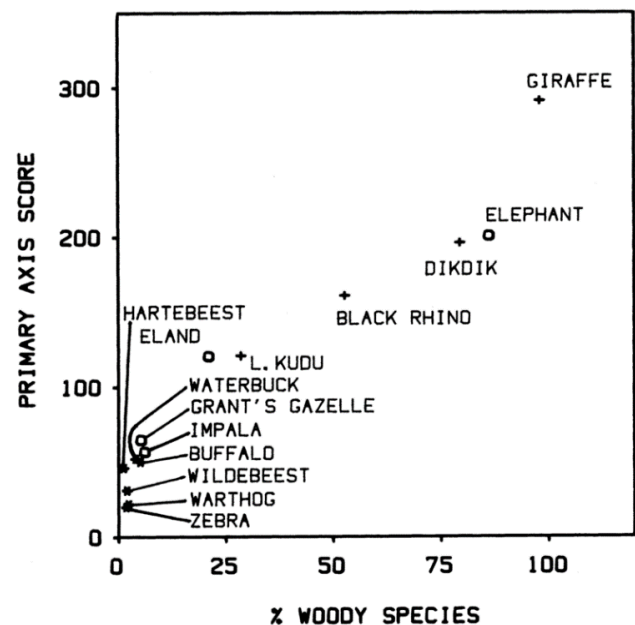
There is thus a negative relationship between diet quality and body mass (diet quality model), when controlling for the digestive adaptation (Table 1), as in non-ruminants, body-size does not clearly influence habitat use.

**Table 1.** Table showing the digestive adaptation, diet type and habitat use for a variety of African savanna species. Small ruminant grazers, such as the impala and wildebeest use the habitat in a more concentrated manner. Non-ruminant grazers have a more diverse habitat use, and body size does not influence this distribution (Cromsigt et al 2009).

Species	Digestive adaptation	Diet type	Habitat use
<i>Impala</i>	Ruminant	Grazer	Concentrated
<i>Wildebeest</i>	Ruminant	Grazer	Concentrated
<i>Warthog</i>	Non-ruminant	Grazer	Diverse
<i>Zebra</i>	Non-ruminant	Grazer	Diverse
<i>Rhino</i>	Non-ruminant	Grazer	Diverse

### Grazers and browsers

Herbivores are also classified as either a grazer or a browser (Lamprey 1963). McNaughton and Georgiadis (1986) review that dietary studies showed that the gut anatomy of ruminant species from East Africa are closely associated with feeding strategy and gut morphology. The proportion of different plant parts (leaf, stem, sheath, fruit) in the ingesta indicated trophic distinctions between grazing species (Figure 4). Grazers are capable of prolonged digestion, while browsers have a faster turnover of lower cellulose containing vegetation and can absorb nutrients faster (McNaughton & Georgiadis 1986). Hofmann and Stewart (1972) state that the classification into grazer or browser is too broad as there is huge variety of structural plans within each guild, like ruminant and non-ruminant digestive strategies (Table 1).



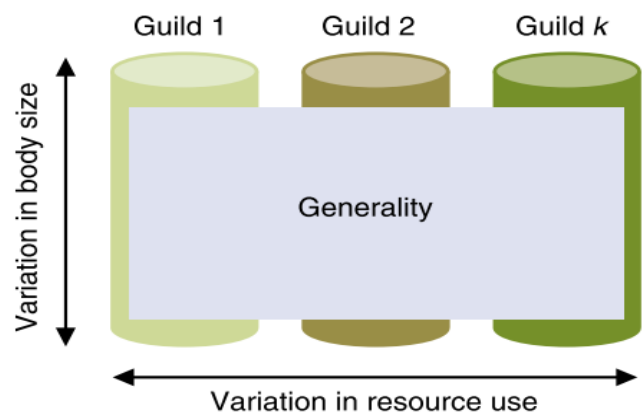
**Figure 4.** Results of correspondence analysis of Lamprey's (1963) herbivore food preference data: the relationship between primary axis scores and number of woody plant species in the diet of grazers (\*), mixed feeders (0) and browsers (+) (McNaughton & Georgiadis 1986).

Furthermore, Gordon and Illius (1996) show that there is no difference in the predicted potential digestibility or net energy yield from the diet of browsing and grazing species after controlling for body mass. Therefore, even though the species had different diets, it had little effect on the nutritional ecology of the animals. They argue that the activity of the gut microbes affect the energy obtained from the diet. Hence, food properties, rather than anatomical adaptations, have the greater significance for nutritional ecology. Dietary classification of niche cannot be generalized beyond botanical terms, further proving that looking at the species level of forage consumed is highly important in studies of niche partitioning. Additionally, Codron and colleagues (2007) show that the assumption that browse is of higher nutritional quality is misleading. They conclude that the more efficient fiber digestibility recorded in grazers compared to browsers cannot be treated as an adaptation to poor quality diets, but rather to

maximize benefits of higher fiber digestibility of grass. Therefore, there is no difference in diet quality between grazers and browsers. Furthermore, Redfern and colleagues (2006) show that small species do not avoid larger species, in both browsers and grazers. Finally, Codron et al (2007) find that body mass and diet type are not related, but confirm predictions that diet quality decreases with increasing body size.

There is thus compelling evidence that the diet type does not alter the relationship between diet quality and body mass. Therefore, the grazer and browser distinction is not included in figure 3. The Jarman-Bell principle will hold across both guilds. It must be stated however, that most of these studies only include ruminants, and as we saw, non-ruminants show different patterns (Table 1). Nevertheless, I do not expect that non-ruminant grazers and browsers differ significantly, and therefore comparing the patterns across these guilds is possible.

From the body of research that has been done it has become clear that resource partitioning occurs through differential body sizes that need different quantities and qualities of forage. Moreover, the considerable amount of studies in different locations and across different guilds support the notion that the Jarman-Bell principle is not a contingency (du Toit & Olff 2014) (Figure 5). Figure 5 shows a conceptual framework for identifying generalities applicable to vertebrates at the community level. Differing resource use, allows for the classification of African species into a grazing and browsing guild, within each of which there is variation in body size. Comparing the patterns across these guilds lead to the emergence of patterns that are applicable across all variations in resource use and body size, despite differences in digestive morphology (ruminant vs. non-ruminant) complicating the pattern among grazers.



**Figure 5.** The Jarman-Bell principle is a community-level generality as it is free from contingency across guilds. Body size emerges as the primary axis along which resources are partitioned among coexisting species in all guilds (du Toit & Olff 2014).

A contingency is a constraint on a generality and occurs when a pattern is only applicable within one subset of potential conditions. A community-level generality is free of contingencies across guilds, which is the case for the Jarman-Bell principle, as it is found across grazers and browsers.

### Seasonality

One aspect that has been ignored in past studies is the effect of seasonality. The mechanisms involved in niche partitioning can change according to season, as food is limiting in the dry season but not in the wet season (Sinclair et al 2008).

This seasonal variation means that the way in which resources are partitioned and the scale at which they are partitioned (i.e. habitat or diet) may change seasonally (Owen-Smith 2002). Clearly, grass is not a homogeneous resource. Rather, the nutritional quality of its major structural components (leaf, sheath, and stem) differs with season. Furthermore, the herbivores also migrate according to the season to capitalize on the high protein content of the short green sward. When the food resource is abundant, facilitation can explain

the movement of smaller grazers onto swards that have been coarsely grazed and trampled by larger species (Van de Koppel & Prins 1998). However, it is to be expected that feeding efficiency declines for the facilitating species when resources become limited (Arsenault & Owen-Smith 2002). Therefore, niche partitioning will be more paramount in the dry season as competition increases. In the wet season resources are abundant and competition will not play a major role. It is therefore imperative that, when looking into niche partitioning, to take all seasons into account. Originally proposed by Bell, it is thought that the larger species, that can ingest a wider range of forage, including the more fibrous components, prepare the grazing patch for the next species. Larger herbivores can enhance the amount of food available within the quality range required by smaller herbivores by reducing grass height and by encouraging grass regrowth (McNaughton 1976). Bell looked at the zebra, wildebeest, and Thomson's gazelle (*Eudorcas thomsonii*). With the zebra being the biggest and the gazelle the smallest, they grazed on the same patch in order of size, each separated by two months. This concept has been widely questioned, however (du Toit & Olff 2014). Nevertheless, du Toit and Olff (2014) argue that, since competition is evident in both grazing and browsing guilds, smaller species do directionally displace the larger ones and conclude that competition has a stronger influence than facilitation in structuring large herbivore assemblages under conditions of resource limitation (du Toit & Olff 2014). The patterns do differ between the grazing and browsing guilds however, in that one is temporal and the other spatial. Browser stratification occurs with the giraffe (*Giraffa Camelopardalis*) for instance. It's very long neck is thought to be an evolutionary adaptation in response to competition with

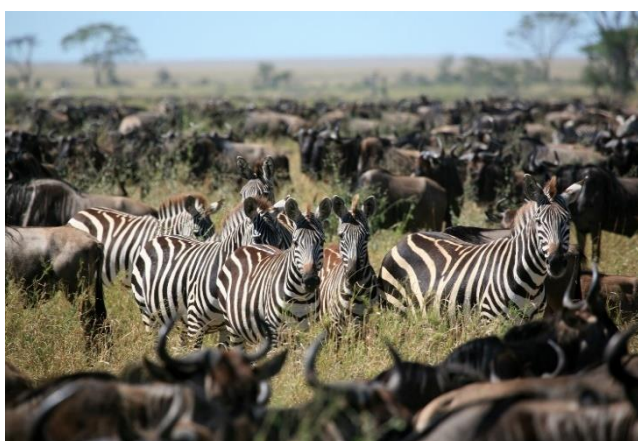
smaller browsing species (Camerson & du Toit 2007). Giraffes can feed up and down a wide height range, but by feeding above reach of other browsers they derive an advantage in leaf mass gained per bite from the canopy (Woolnough & du Toit 2001). The smaller-bodied guild members, feed on the high quality food, have narrower muzzels and have lower intake requirements which allows them to pick the most palatable leaves and shoots within their reach. Giraffes benefit from their necks as they can reach the palatable browse out of reach of the other species. du Toit and Olff (2014) argue that this process is driven the same way as the grazing succession described by Bell, but then vertically. Coming back to the study by Kleyhans and colleagues (2011), that provided evidence for the Jarman-Bell principle that encompassed a lot of covariables, including the wet and the dry season. The conclusion was that savanna herbivores coexist mostly through body size-driven resource partitioning, but only in the dry-season. This is likely due to the fact that competition between the species is highest in the dry season, when resources are limited. It is therefore arguable that the studies that did not find evidence for the Jarman-Bell principle did not take the season or the resource availability into account. For example, the study by de Jongh (2011) only had very wet conditions that probably led to competition being reduced and niche partitioning less apparent. However, Hansen et al (1985) found very low dietary dissimilarities among species in the Northern Serengeti and they were not frequently higher in the dry season than in the wet season. This was caused by a very wet dry season, which led to no apparent food shortage. Spatial movements, such as migration also reduce competition due to food shortage, as the animals follow food availability.

We can therefore conclude that in niche partitioning studies one must include seasonal

variation and spatial movements, which lead to variations in resource availability and therefore competition.

### GPS tracking

Some studies find that there is a higher niche overlap than expected (du Toit 1990, Prins et al 2006, Redfern et al 2006). There is substantial overlap among grazing ungulates in habitat conditions occupied and grass species and height ranges exploited (Owen-Smith et al 2015). Within the geographic distribution range of the species, individual animals or groups commonly restrict their movements to bounded home ranges, and selectively occupy distinct habitats within these ranges. It is possible that spatial partitioning dependent on body size may operate at a larger scale than readily addressed experimentally. Owen-Smith et al (2015) looked at a generalist grazer with hindgut fermentation (zebra) with a similar-sized grazing ruminant (wildebeest) in west-central Kruger National Park, South Africa. These two herbivores are especially intriguing as they are commonly found as mixed-species herds (Figure 6).



**Figure 6.** Zebra and wildebeest both migrate together. They often do this in a mixed-species herd, with overlapping grass consumption. They show a more behavioural distinction in niche exploitation than through habitat separation.

While the hindgut digestion of zebra enables them to utilize taller and more fibrous grass than is generally selected by wildebeest, zebra also exploit short grass within the height and quality range favored by wildebeest (Arsenault & Owen-Smith 2008). Despite occurring together in the Serengeti ecosystem, zebra numbers have remained unaffected by the five-fold increase in the migratory wildebeest population that followed elimination of the rinderpest virus (Sinclair et al 2007). It is thought that zebra improve the grazing conditions of the wildebeest by removing the taller and more unpalatable grass (Bell 1970). Using GPS telemetry, Owen-Smith et al (2015) investigated the spatial patterns of these herds. They found that herds of the two species overlapped substantially in the home ranges that they occupied. However, they exploited spatially distinct foraging arenas. Furthermore, they differed in exploitation time and movement rates within the arenas. In particular, wildebeest herds concentrated within small areas for prolonged periods, while zebra herds used more foraging arenas but exploited them for briefer periods. Hence, these herds show a more behavioral distinction in niche exploitation than through habitat separation.

Thus, the new GPS tracking technologies can provide very important insights into niche partitioning mechanisms. Distinctions in patterns of exploitation at this finer scale may partially negate the competitive interaction that might otherwise be expected between species with overlapping resource needs (Owen-Smith et al 2015).

### DNA metabarcoding

Browse and grass encompass enormous taxonomic, phylogenetic, and trait diversity, yet, as discussed earlier, few studies have evaluated resource partitioning at the plant-



species level. This lack is mainly because of the difficulties that come with trying to identify the taxonomic levels of the forage consumed. Diet profiles are highly mobile, hard to observe at close range in the field and herbivores often feed on inconspicuous plant species (Kartzinel et al 2015). Two methods have been used to look at the diet type and quality in niche partitioning. Firstly, by direct observations of foraging animals and secondly, through microhistology, in which plant parts from feces are visually identified. Direct observations require advanced knowledge of the plant species present and is prone to omission, during foraging at night time or in uncommon locations. Microhistology is work intensive and is often inadequate and unprecise as there is limited availability of reliable identification libraries, that would permit comparative studies.

During new developments DNA metabarcoding has become readily available and more affordable (still at a much higher cost than the other methods). Fecal samples of the species are collected and sequenced with a broad spectrum DNA metabarcode marker. In 2015 Kartzinel et al performed DNA metabarcoding to quantify diet breadth, composition, and overlap for seven abundant species in a semiarid African savanna. These species ranged from almost-exclusive grazers to almost-exclusive browsers in order to analyze if species vary along a grazer–browser continuum, and their position on this continuum. Furthermore, they wanted to test if dietary dissimilarity increased with the size disparity between species. Found was that dietary overlap was greatest between species of similar size, providing some evidence for the Jarman-Bell principle. Nonetheless, diet composition differed between all species, and dietary similarity was sometimes greater across grazing and browsing guilds than within them. Further proving that the division in these

two guilds is misleading. They do demonstrate that African herbivore diversity may be more tightly linked to plant diversity than is currently recognized. DNA metabarcoding is thought to have a limited ability to reveal relative amounts of foods consumed due to variation in DNA content across plant species and tissues. Laboratory procedures include the possibility of primer mismatch inhibiting the amplification of some plant species. Another issue with this method is that you are looking at the plant material that is undigested and discarded by the herbivores. It is therefore, arguable that it is not a clear representation of the vegetation actually used by the species. Furthermore, the samples for the analysis were collected in the wet season, when dietary segregation is not as pronounced as in the dry season. Assumedly, the niche partitioning documented would be clearer in the dry season.

The novel method of using DNA metabarcoding has some potential in the sense that it allows a species-level accounting of food plants, offering a more precise way of integrating diet type with the plant traits, which in term determine diet quality (Kartzinel et al 2015). However, it is a work intensive and expensive method that does not offer significantly more answers than the methods already being used.

## Heterogeneity

Ruminants and non-ruminants in grazers and browser guilds use the landscape in different ways to avoid competition, allowing niche partitioning. The landscape should therefore be heterogeneous enough with sufficient vegetation diversity to permit such coexistence. Representatively, mean annual rainfall varies from 400 mm to 1100 mm across the Serengeti, with vegetation species and biomass ( $9 \text{ Mg ha}^{-1}$  to  $27 \text{ Mg ha}^{-1}$ ) varying accordingly (McNaughton 1983). Much of the animal

diversity and the carrying capacity for herbivorous animals of the Serengeti ecosystem is intimately related to the heterogeneity in the landscape (McNaughton & Georgiadis 1986). It is becoming more apparent that this heterogeneity is in a delicate balance and that one organism can be an agent in creating a more diverse ecosystem. Exemplifying this are studies done on macrodetritivores. Howison et al (2016) found that soil conditions, water infiltration and therefore grass bunch, were significantly increased by activity of dung beetles. macrodetritivores interact with large herbivores to maintain the structural heterogeneity in the vegetation. Furthermore, the large amount of defecation produced by the white rhinoceros, which is hereafter used by the dung beetles, contribute to this increase in heterogeneity. Increased heterogeneity allows for more species to coexist in the ecosystem (Howison et al 2016). Removal of these keystone species could lead to large ecological changes, with cascading impacts on local vegetation heterogeneity, biodiversity, and associated ecosystem functions and services. Termites have also been shown to increase heterogeneity (Bonachela et al 2015). Termites alter soil properties, thereby enhancing plant growth benefiting the African savanna herbivores (Bonachela et al 2015).

Heterogeneity of the ecosystem, which can be increased even by the smallest macrodetritivores, allows species coexistence, preventing competitive exclusion. This is an important concept for conservation efforts in the ecosystem.

## Predators

Next to bottom-up factors influencing niche partitioning, top-down factors can also play a role. It is poorly understood when one or the other predominates (Sinclair et al 2003).

Sinclair et al (2003) found that two factors influence an adult's mortality. Firstly, the species diversity of both the predators and prey, and secondly the body size of that prey species relative to other prey and predators.

Small species are exposed to more predators (Figure 3) due to opportunistic predation. Furthermore, smaller species also suffer higher predation rates and strong predation pressure. Large adult herbivores are more challenging for predators to prey upon due to their speed and size (Figure 3). It is therefore hypothesized that the megaherbivores are their size due to an arms race with the predators (Owen-smith 1988). It is still unsure how the prey base is partitioned among the predators. Small herbivores are predated upon by small carnivores, but also by larger carnivores. However, there is evidence that large carnivores specialize on large herbivores and small carnivores on small herbivores. Predation levels also depend on features of the landscape. Ambush predators like lions rely on tall grasses to remain hidden, for instance (Figure 7) (Hopcraft et al 2012). Therefore, the degree to which an herbivore is predator-regulated depends on its body size, on the body size of its predators, on how predators partition prey and on landscape features (Hopcraft et al 2012). Species larger than 150 kg have limited natural enemies, and become food limited. Thus, biodiversity allows both predation (top-down) and resource limitation (bottom-up) to act simultaneously to affect herbivore populations (Sinclair et al 2003). Predation can therefore be a mechanism leading to niche partitioning. Distinct responses to the risk of predation can lead to differences in habitat occupation between species with similar resource requirements. Additionally, these distinct responses also have indirect consequences for habitat structure. This is commonly known as the ecology fear. A well-known example are wolves that change

the relative configuration of grasslands and woodlands due to their influence on the behavior of their prey (Estes et al. 2001). Hopcraft et al (2012) analyzed the spatial distribution of five grazer species of different body size in relation to gradients of food availability and predation risk. They found that the distribution of small grazers was indeed constrained by food quality, but also by predation, whereas the distribution of large grazers was relatively unconstrained by predation. For example, the distribution of the largest grazer (African buffalo (*Syncerus caffer*)) is primarily associated with forage abundance but not predation risk, while the distributions of the smallest grazers (Thomson's gazelle and Grant's gazelle (*Nanger granti*)) are associated with high grass quality and negatively with the risk of predation. The distributions of intermediate sized grazers (Coke's hartebeest (*Alcelaphus buselaphus cokii*) and topi) suggest they optimize access to grass biomass of sufficient quality in relatively predator-safe areas. This shows that diverse grazing assemblages are composed of herbivores of many body sizes, because these herbivores best exploit the resources of different habitat types.

Not enough attention has been paid to this top-down mechanism of niche partitioning, even though there is enough evidence that it is also important. For example, wildebeest and zebra populations both show negative growth responses to annual variation in rainfall, apparently responding to changes in cover for their major predator rather than resource production (Hopcraft et al 2012). Different habitat features may be favored for different activities, meaning that the location where one animal is secure, for example in locations with less vegetation biomass, may differ from where it has the most resources (Figure 7).

Therefore, predation can contribute to niche partitioning among species differing in body

size, which otherwise appear similar in their resource needs (Figure 3) (Ritchie 2009).



**Figure 7.** A wildebeest can find the most forage somewhere with high biomass, however, here there is a higher risk of predation due to the lion's ability to hide in the high vegetation, making it prefer lower biomass patches. Bigger species are not influenced by predators, and can therefore make use of the high biomass locations. This way there is niche partitioning and increased species coexistence.

## Conclusions

It is rather clear that the Jarman-Bell principle is a great explanation for the coexistence of the great biodiversity in the African savanna ecosystem. The divergent body sizes of the herbivores in the ecosystem allow them to use different resources, due to their distinct digestion capabilities and metabolic needs (Bell 1971, Geist 1974, Jarman 1974). There is compelling evidence across different African savanna ecosystems, seasons, and guilds and therefore the Jarman-Bell principle can be considered a generality (du Toit & Olf 2014). Larger species have bigger mouths, allowing them to consume the larger quantities of lower quality food they need to reach their nutritional requirements (Figure 3) (Arsenault & Owen-Smith 2008, Gordon and illius 1988). There are however important exceptions to this principle. Megaherbivores, are able to eat a wider range of vegetation types in relation to their immense mouth width (Kleynhans et al 2011, Owen-Smith 1988). They jointly consume lower quantities of high quality forage with bulk of lower quality forage, in order to maintain such a large body.

The exceptional diversity of ungulates has been described from a grazer/browser model of differentiation, based on differences in the types of foods these herbivores consume (diet type model). Research shows us however, that there is no difference in the quality of food between grazers and browsers. Furthermore, body size was not related to diet type. The Jarman-Bell principle can therefore not be explained in terms of diet type, but instead by diet quality. Larger species can consume lower quality forage, allowing them to use a more diverse landscape. There is thus a negative relationship between diet quality and body mass (diet quality model). However, this pattern differs according to the digestive adaptation of the species (Table 1). Non-ruminants, compared to similar sized ruminants, can consume lower quality food leading them to occupy a more diverse habitat (Figure 3). These differences in habitat use lead to niche partitioning and species coexistence. One must thus differentiate between these when studying niche partitioning mechanisms. Additionally, in non-ruminants, body-size does not clearly influence habitat use.

When looking into the mechanisms of niche partitioning, the season can have a great impact on the conclusions taken. In the wet season competition is reduced, making niche partitioning less apparent, whereas in the dry season, resources are limited leading to their partitioning allowing the species to coexist (McNaughton 1976). There is some evidence that the larger species can facilitate the smaller species by reducing grass height, however, competition has a stronger influence than facilitation in structuring large herbivore assemblages under conditions of resource limitation, as it is evident across the guilds (du Toit & Olff 2014).

Little research has focused on the species level of the vegetation utilized by the herbivores, even though this could provide more insights

into the quality of the vegetation consumed. New technical developments are allowing insights at a finer scale. GPS collaring showed that behavioral distinctions can reduce the competition between species that seem to overlap in resource use (Owen-Smith et al 2015). DNA metabarcoding is promising in the sense that it allows a species-level accounting of food plants, offering a more precise way of integrating diet type with the plant traits, which in turn determine diet quality, however it is a costly method that does not allow significantly more insights than the cheaper methods currently being used (Kartzinel et al 2015).

Heterogeneity of the ecosystem is the main way through which species can coexist through niche partitioning (Mcnaughton & Georgiadis 1986). Ecosystem heterogeneity is a delicate balance where even the smallest species can engineer heterogeneous soil conditions thus promoting growing conditions for structurally different plant species. The dung beetle and the termite are examples of macrodetritivores that play an important role in allowing biodiversity in African savannas (Bonachela et al 2015, Howison et al 2016).

Resource partitioning is thus important (bottom-up), however little research has focused on predator pressures on herbivores (top-down) (Figure 3), even though smaller herbivore distribution is mainly determined by predator pressure. Larger species are primarily influenced by resource availability however. The combination of both resource availability and predator pressures lead to differential habitat use and thus niche partitioning (Ritchie 2009).

Research on niche partitioning should thus look at ruminants and non-ruminants, throughout the year, to include all seasons. Additionally, the species level of the vegetation foraged should be included and finer scales of habitat use analyzed through movement

tracking. Finally, predation pressures should also be included to get the full picture of the mechanisms driving niche partitioning. Heterogeneity of the ecosystem is imperative for biodiversity and coexistence and should be prioritized in conservation efforts.

The impact of the ever-increasing human population in savanna ecosystems is already having detrimental effects in the shape of overgrazing by the paralleled increasing livestock (Sinclair et al 2008). Competition between humans and wildlife, and livestock and wildlife increases. During food shortage overgrazing becomes a serious issue for the high diversity and density of herbivores, as competition for the limiting resources intensifies. Little is known on how livestock grazing overlaps with the niches of wild herbivores. More research on this should be a priority. What will the consequences be for niche partitioning as human impacts continue and intensify? The climate is also changing, with an increase in extreme weather conditions (Olff et al 2002). How will this alter the ecosystem and the vegetation composition? Next to increased livestock grazing, land use also intensifies, further leading to reduction in resources available for the wildlife. Whole niches could disappear, leading to reduced species coexistence and consequent reduction of the species diversity. Awareness on this is imperative, as African savannas have one of the last high densities of herbivores. These herbivores, and associated carnivores, attract big numbers of tourists that are an important income for the developing countries associated with African savannas. These ecosystems seem to be highly specialized, with the interactions between herbivores, resources and predators in a delicate balance. All the aforementioned disturbances have the potential to reduce the heterogeneity of the ecosystem reducing niche partitioning. Furthermore, the loss of one key stone species can already lead to a steep

decrease in ecosystem heterogeneity. Understanding the mechanisms of niche partitioning, and how human impacts can affect them, are therefore important research questions that need further investigation.

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