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The relationship between flooding parameters and grazing herbivores in the south-western Okavango Delta.

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A thesis submitted to the School of Animal, Plant and Environmental Sciences, Faculty of Science, University of the Witwatersrand, Johannesburg, South Africa in fulfillment of the requirements for the degree of Doctor of Philosophy.

Declaration

I declare that this thesis is my own, unaided, original work. It is being submitted for the Doctor of Philosophy degree at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or any other examination at any other university.

Signed: 

28 January 2019

Disclaimer

This thesis consists of a series of chapters that have been prepared for submission to a range of scientific journals for publication. As a result, the styles may vary between chapters in this dissertation and content overlap may occur between the chapters.

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Abstract

Wetlands are ecologically diverse habitats that hold significant local and global value for both people and wildlife. They provide clean water, sequester carbon, provide dry season resources for wildlife and act as important refuges for migratory birds. However, their ecological functioning relies on them remaining intact, and this is severely threatened by anthropogenic water offtake and climate change. Understanding the consequences of such changes are therefore important for successful wetland conservation and the services they provide. The Okavango Delta is a pristine, dynamic wetland system in north-western Botswana. It supports a vast array of wildlife in the middle of the Kalahari Desert, which sustains a highly profitable tourism industry. However, aerial surveys of wildlife abundance have revealed a worrying decline in certain species of herbivores, particularly those in the grazing guild. This coincides with increasing flood levels in the Okavango Delta over the same period. As the unimodal flood pulse influences the quantity and quality of grazing produced as a result of the receding flood at the end of the dry season, I set out to determine how different flood regimes may affect the grazing guild in the Okavango Delta, and whether flood patterns may explain the decline in certain species of grazers. I used a combination of vegetation transects, aerial survey data, satellite imagery and GPS collar data to determine how flooding patterns alter grazing availability, affect the structure of the grazing guild and affect resource selection at different scales. I found that during years of high flood, there is a decrease in the proportion of floodplains which consist of palatable grazing. Within the grazing guild, there was clearer separation in resource use of these floodplains during years of low flood, but in years of high flood, generalist grazers such as zebra and buffalo, converged resource use on areas favoured by specialist grazers, namely red lechwe, wildebeest and tsessebe. When examining resource use more closely in high flood years, I discovered that both generalist and specialist grazers showed increasing selection for floodplain habitat and increasing dependence on flood waters, at the home range scale and in their selection of foraging areas, in the early and late flood season, when grazing resources are otherwise scarce. Based on resource preferences during low flood years, when palatable grazing is more abundant, specialist grazers such as lechwe appeared to be slightly displaced from their favoured foraging areas. This suggests that specialist grazers may face increasing competition for grazing from generalist grazers during years of high flood, which may result in population

decline of selective grazing species. Lessons learnt from this investigation may assist in the management of wetlands elsewhere whose flooding patterns alter the availability of resources at both short- and long-term timescales to ensure the maintenance of species diversity and protect endangered species.

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Motivation

Wetland habitats are some of the most ecologically diverse and productive systems in the world, and provide important ecosystem services at local, regional and global scales (Gopal et al. 2000, Mitsch and Gosselink 2000). Wetlands provide fresh and clean water for drinking and agriculture (Dugan 1990), serve as bridging or key resources for animals during the dry season and in years of drought (Owen-Smith 2002, Fynn et al. 2015), are important habitats for migratory birds (Junk et al. 2006), and sequester significant amounts of carbon (Junk et al. 2013). As a result of being highly productive, wetlands are often over-utilised, and their integrity is threatened by surface water extraction through the construction of reservoirs, dams and dykes, invasion by exotic species, pollution and eutrophication, over-fishing and land reclamation for agriculture (Beilfuss and Barzen 1994, Davies 2000, Junk et al. 2006, Junk et al. 2013). Only recently, however, after a long history of over-utilisation, has it become clear that the continued value of the services provided by wetlands is largely dependent on them remaining relatively intact (Dugan 1990, Nel et al. 2010).

In Africa, wetlands cover approximately 7% of the land surface, and provide important ecosystem services for wildlife and people (Junk et al. 2013, Fynn et al. 2015). A study conducted by the FAO[1] on irrigation potential in Africa, concluded that the economic value of intact wetlands far exceeds the economic gains resulting from irrigation schemes based on damming or upstream water diversion (FAO 1997). Despite this, the main anthropogenic threats to wetland conservation include upstream water offtake for irrigation, upstream damming and overgrazing and deforestation in catchments (Roberts 1988, Davies 2000, Junk et al. 2013, Fynn et al. 2015). Of more recent concern, however, are the effects of climate

[1] Food and Agriculture Organisation of the United Nations (http://fao.org)

change (Milzow et al. 2010, Junk et al. 2013). Climate change models predict that by 2050, temperatures in Africa will climb by between 1 and 2.6°C (Hulme et al. 2005), together with increased rainfall variability and an increase in stochastic events such as droughts and floods (de Wit and Stankiewicz 2006, Junk et al. 2013). These changes are expected to be most amplified in arid areas and have considerable influence on the availability of surface water, which has the potential to decrease the extent of wetlands across the continent (de Wit and Stankiewicz 2006). With a concomitant increase in human density over this period of 2 to 4 billion people (Cohen 2003), demand for fresh water will increase, placing rivers, catchments and wetland habitats under increasing pressure.

The Okavango Delta is arguably one of the continent's most pristine wetlands and has significant importance in Botswana for local consumptive use as well as eco-tourism (McCarthy and Ellery 1998, Gumbricht et al. 2004, Mmopelwa and Blignaut 2014). As a flood-pulsed system, the integrity of the Okavango and its function as a wetland is entirely dependent on hydrological patterns resulting from a combination of local conditions in Botswana, and those in the catchment area along the Okavango River in Angola and Namibia (Gumbricht et al. 2004, Murray-Hudson 2009). In the future, climate change is predicted to have a far more significant effect on the functioning of the Okavango Delta than upstream water abstraction and deforestation (Murray-Hudson et al. 2006). Situated in a semi-arid region with annual rainfall of 490 mm per annum, this region is predicted to experience a 10% decrease in rainfall by 2050, which could result in a potential loss of surface water by up to 50% (de Wit and Stankiewicz 2006, Batisani and Yarnal 2010). These changes could have a significant effect on the extent of the Okavango Delta, affecting water supply to the region as well as the distribution and abundance of local wildlife, heavily impacting on both ecotourism and the regional financial income (Mmopelwa and Blignaut 2014).

Future hydrological changes, such as those predicted from climate change, may result in an increase in dry land and reduction of productive floodplain habitats, which could have significant consequences for the distribution and abundance of wildlife in the region (Murray-Hudson et al. 2006, Fynn et al. 2015). While recent hydrological modelling has proven useful in predicting the changes in flooding under different climate change and offtake scenarios (Murray-Hudson et al. 2006), to have a wider applicability, the use of models should be further linked to resulting changes in vegetation and habitat quality, which allow us to make predictions for species further up the food chain (Milzow et al. 2010). Furthermore, a recent review on the importance of wetlands in Africa for large herbivores and cattle, has revealed that not only vegetation communities, but the species in these communities themselves, resulting from various inundation patterns, are similar in various wetland types across the continent (Fynn et al. 2015). Consequently, lessons learnt from studying pristine wetlands such as the Okavango Delta, regarding the consequences of various flooding conditions for vegetation and wildlife, can be used to inform conservation management plans for large herbivores in all types of wetlands in Africa.

Objectives

The main purpose of this study was to investigate how the flood pulse, as the main driver of ecological change on an inter-annual and multi-decadal scale, influenced resource availability and by extension, the grazing herbivore guild in the Okavango Delta, Botswana. My objectives, therefore, were to:

1. Investigate the relationship between flood regime and the quantity and quality of available grazing produced on floodplains at different flood intensities
2. Investigate the structure of the grazing herbivore guild in the Okavango Delta, and determining whether this changes between periods of high and low flood

3. Examine and compare seasonal resource and habitat use between two generalist herbivores, and one specialist herbivore in flood and non-flood seasons
4. Determine the extent to which generalist and specialist grazers overlap in foraging area selection in the dry season, when flooding most influences resource availability.

Thesis Structure

This thesis is structured into six different chapters. In Chapter 1, I highlight the motivation for the study, and outline the study's objectives. I also review current literature relating to the study's objectives, in order to place the study in context and provide background on which the hypotheses of the study are formulated. I also use this Chapter to introduce the study area and the study species.

In Chapter 2, I investigate the relationship between flooding in seasonal floodplains and vegetation communities, with focus on the changes between grasslands and sedge communities. I focus on the differences in palatability of grass and sedge species which grow under different flood regimes and how this may affect availability of grazing during the late dry season.

In Chapter 3, I use aerial survey data to investigate the relationships between grazers and areas flooded for different durations of time using network analysis. I determine the structure of the relationships between resource and consumer in the network and compare how the structure of the network changes between years of low flood and high flood.

In Chapter 4, I use resource selection functions to look at seasonal resource selection of three of the main grazers in the Okavango Delta, buffalo (*Syncerus caffer*), zebra (*Equus burchelli*) and red lechwe (*Kobus leche*). I also compare seasonal habitat selection by all three species to determine the extent to which seasonal selection diverges or is shared by these grazing herbivores.

In Chapter 5, I use time-selected local-convex hulls (T-LoCoH) to delineate potential foraging areas (based on frequency of use) used by buffalo, zebra and red lechwe respectively. I then use niche overlap analyses to determine the extent of overlap in these foraging areas in each season. I use the results to examine the potential for interspecific competition for resources, particularly in the late dry season, and how this may influence lechwe abundance in the Okavango Delta.

In Chapter 6, I put the study in context, and summarize the findings. I also discuss how the findings contribute to our current knowledge on wetlands and herbivore ecology, and how changes in climate may influence wetland systems and the herbivores they support in the future. I discuss the shortfalls of the study and make suggestions for future studies that will further contribute to our knowledge of wetland systems.

Chapter 1- Introduction

The influence of flooding on vegetation and large herbivores

While some wetland systems may experience stochastic and unpredictable flooding regimes, many experience predictable seasonal flooding patterns, which in turn result in highly productive floodplain ecosystems (Jardine et al. 2015). The productivity of the floodplains, which represent the ecotonal zones between inundated and dry land, is determined by the annual and predictable flood pulse (Junk et al. 1989). However, this seasonal flood pulse is subject to extensive inter-annual variation, resulting in a dynamic and constantly changing environment (Junk et al.1989). The habitat diversity of a flood pulsed wetland ecosystem is primarily characterised by hydrology and, on an extended lifespan, geomorphology, which can play a large role in determining local flood characteristics (Wolski and Murray-Hudson, 2006, Ramberg et al. 2006).

The hydrological characteristics of the flood pulse, such as frequency, duration and depth, are the principal determinants of vegetation zonation in floodplain communities (Blom and Vosenek 1996, Casanova and Brock 2000, Murray-Hudson 2009). The diversity and composition of plant communities in these zones, as well as the abundance of species within these communities, shift with fluctuations in flood characteristics, as well as with the availability of nutrients on a landscape scale (Gentry 1988, Tuomisto et al. 1995, Nuttle et al. 1997). As floodplains alternate between wet and dry conditions, plants may germinate, establish or perish based on the duration of flooding endured each season, the depth of flooding which alters light access, and the frequency of flooding which can alter nutrient contents and oxygen availability in the soil (Mitchell and Rogers 1985, Casanova and Brock 2000). Given the short lifespan of many of these plant species and their rapid reproduction strategies, changes in floodplains can occur over relatively short periods, and as a result, these ecotones are in constant flux (Junk 2000, Murray-Hudson et al. 2014). However, it is the

flooding history, and not the prevailing flooding conditions which will determine vegetation community composition (Tabacchi 1995, Murray-Hudson 2009). Of the various hydrological characteristics, flood depth is least important in determining community composition, while the history of flood duration has proven most predictive in determining community types (Murray-Hudson 2009). During years of high flood, which results in extended inundation, floodplain conditions favour communities dominated by sedges and aquatic plants, while in years of low flood, where inundation periods are shorter, floodplain conditions favour the growth of more palatable, terrestrial and flood-adapted grasses (Murray-Hudson 2009).

The balance between palatable and unpalatable grazing has important implications for herbivore communities which depend on floodplain vegetation. As many wetland flood pulses occur during the dry season, when grazing resources are most limited, receding flood waters stimulate fresh grass growth of higher quality than other drier, more senescent plant material in adjacent habitats (Pamo 1998, Traill 2004, Fynn et al. 2014). For this reason, wetlands are an important dry season resource, and consequently attract considerable numbers of large herbivores (McLachlan 1971, Lindholm et al. 2007, Fynn et al. 2015). As dry season forage is often the limiting factor for large herbivore populations, wetlands therefore function as key resources (Knoop and Owen-Smith 2006), which are resources that ultimately determine the carrying-capacity for large herbivores in the area and maintain herbivore densities at levels where they experience food-related density-dependence (Illius and O'Connor 2000). Additionally, they also act as 'bridging' or 'buffer' resources, which shield large herbivore populations against extreme climatic events such as drought (Owen-Smith 2002). The quantity and quality of forage produced in wetlands, which is innately a function of the flood pulse and its inter-annual variability (Junk et al. 1989, Casanova and Brock 2000), therefore have an important role to play in the stability of functionality of grazing guilds within wetland ecosystems (Fynn et al. 2015).

Foraging ecology of grazing herbivores

Resource partitioning

Co-existence of grazing herbivores can be facilitated by resource partitioning at numerous scales of resource use, both local and regional (Dunning et al. 1992, Bonyongo and Harris 2007). On a regional scale, landscape features such as the size and distribution of resource patches and differences in vegetation structure can largely affect species richness and abundance (Wilson 1974, Dunning et al. 1992). For example, a recent study on the number of grazing species co-existing in several conservation areas indicated that up to 76% of the variation in species packing could be attributed to habitat heterogeneity (Bonyongo and Harris 2007). Locally, resource partitioning can also occur at several scales including grass sward height, relative greenness, as well as nutrient and fibre content of different plants species or even plant parts (Bailey et al. 1996, Wilmshurst et al. 1999, Drescher et al. 2006). Niche separation at these various scales is achieved by numerous mechanisms that have evolved over time to reduce competition between sympatric grazing herbivores, ranging from phenotypic differences in body size and mouth morphology, behavioural, to ecological differences such as habitat specialisation (Bonyongo and Harris 2007, Macandza et al. 2012).

One of the main mechanisms of resource partitioning involves differences in body size, which is directly related to gut retention time and digestion efficiency (Illius and Gordon 1987, Demment and van Soest 1985, Illius and Gordon 1992, Wilmshurst et al. 2000). Larger herbivores, which have longer retention times and lower metabolic requirements per unit body mass, can therefore eat larger quantities of poor-quality grazing, such as longer, mature grass swards with high levels of structural fibre to fulfil the metabolic requirements which match their size (Illius and Gordon 1992, Drescher et al. 2006, Kramer and Prins 2010). Smaller herbivores, however, due to shorter retention times and lower digestive efficiency, require larger quantities of energy relative to their body weight, and must thus continuously select

for high quality forage to meet their metabolic needs (Illius and Gordon 1992, Wilmshurst et al. 2000). After body size, niche separation is further facilitated by secondary mechanisms such as incisor arcade structure, which determines the degree of selectivity grazers can apply when foraging (Jarman 1974, Owen-Smith 1982, Gordon and Illius 1988). Incisor arcade also scales with body size, where smaller grazers have smaller mouths, enabling them to select for higher quality plant parts such as leaves which have lower structural fibre than stems (Gordon and Illius 1988, Drescher et al. 2006). Larger grazers have wider mouths which enables them to maximize intake rate when grazing, particularly in the dry season when shorter, high quality swards are unavailable (Gordon and Illius 1988). Lastly, differences in gut morphology can help to separate similar-sized herbivores in terms of feeding strategy. Hind-gut fermenters, for example, are less efficient in extracting nutrients, but have a faster gut throughput rate, enabling them to extract nutrients faster from lower quality vegetation (Demment and van Soest 1985, Duncan et al. 1990). Ruminants, on the other hand, have a higher gut retention times, conducive to extracting more nutrients. As such, hind-gut fermenters can tolerate much lower quality vegetation than ruminants, and do not require as much high-quality forage during times of food scarcity (Kleynhans et al. 2011). They therefore occupy niches much closer to megaherbivores than to ruminant herbivores of a similar size (Illius and Gordon 1992).

The degree of grazer species-packing (number of co-existing herbivores) is further influenced by the interaction between sympatric grazers. One such interaction is competition, where one species may reduce the quality or quantity of a resource to the extent that it cannot be exploited by other species (Illius and Gordon 1987, de Boer and Prins 1990). For example, on short uniform grazing lawns, reduction in grass sward height by only a few centimetres by wide-mouthed grazers such as wildebeest, might reduce grass height to the extent that larger herbivores can no longer exploit those resources (Murray and Illius 2000). Conversely,

selective feeders may reduce the quality of grass swards by selecting for the most nutritious parts, making grazing unprofitable for other species in terms of remaining energy content (Murray and Illius 2000, Drescher et al. 2006). However, overlap in resource use does not necessarily imply direct competition, as competition would depend on the extent to which the overlapping resource limits population abundance (Arsenault and Owen-Smith 2002). While animals may seek to reduce competition by using different habitats during the non-growing season, the lack of overlap or resource partitioning does not necessarily imply no competition, as competitors may have already been eliminated in the past (Arsenault and Owen-Smith 2002). This is referred to as the "ghost of competition", where in the evolutionary past, strong competition was eliminated by resource partitioning due to the high fitness consequences of competing. This resulted in a guild where grazers overlap in resource use only intermittently or are not strong competitors for the same resource (Connell 1980, Voeten and Prins 1999). While competition is inherently difficult to prove, it can be implied in cases where niche shifts occur (Brew 1982). If animals shift or restrict their niche use away from resources that they would otherwise use, this change in resource utilisation could indicate an attempt by individuals to reduce competition (MacArthur 1969). While this theory argues that niche shifts are a response to changes in the abundance of a competitor, they could also potentially result from a decrease in a shared resource which supports the same number of animals (Brew 1982).

Alternatively, co-existence of grazing herbivores could lead to facilitation, where one species may utilize resources in such a way that they then become suitable for other species in terms of vegetation height or quality (McNaughton 1985, Arsenault and Owen-Smith 2002). In the Serengeti, Tanzania, large migratory herds are sustained by grazing succession, where species follow one another based on a temporal pattern of facilitation (Bell 1971). Plains zebra (*Equus quagga*) graze first, cropping the longer grasses which facilitates short grass grazing species

such as wildebeest (*Connochaetes taurinus*), followed by the more selective Thomson's gazelle (*Eudorcas thomsonii*) which can selectively graze on new shoots stimulated by the grazing of their predecessors (Bell 1971, McNaughton 1976, Cromsigt and Olff 2008). Differences in foraging strategy, or a specific temporal succession of grazing herbivores, could therefore allow a suite of grazing herbivores to utilise the same resource over time.

In wetland systems, larger herbivore species such as buffalo (*Syncerus caffer*) and elephant (*Loxodonta africana*) may facilitate grazing by smaller species such as wildebeest (*Connochaetes taurinus*) later in the dry season by reducing the quantity and height of tall grass and sedge communities (Vesey-Fitzgerald 1960, Western 1973, Tinley 1977). Similar-sized species, such as tsessebe (*Damaliscus lunatus*), lechwe (*Kobus leche*) and wildebeest, are separated by secondary mechanisms such as incisor-breadth arcade (Gordon and Illius 1988), or in the case of lechwe, they are ecologically separated by different niche use owing to specialisation in wetland areas (Bonyongo and Harris 2007). However, during times when resources are scarce, these different species may competitively exclude one another, to the detriment of the inferior competitor (Mishra et al. 2002).

The Okavango Delta: a case study

Study Area

The Okavango Delta is a one of the world's largest alluvial fans, extending over 28 000 km^2 into the lowest lying area of the Kalahari Basin (Ramberg et al. 2006). The Okavango is driven by a unimodal, annual flood pulse, and is fed by the Okavango River which carries seasonal rainfall from the Angolan highlands (McCarthy et al. 2003). This pulse reaches the Okavango basin each year in April, flooding the Okavango Delta in the dry season, and reaching its full extent in July or August (Ramberg et al. 2006). This unimodal pulse creates a diverse array of habitats across a hydrological gradient, which supports significantly elevated levels of biological productivity and mammalian biomass (Junk et al. 2006). The Okavango Delta is

home to an estimated 1300 plant, 71 fish, 33 amphibian, 64 reptile, 444 bird, and 122 mammal species (Ramberg et al. 2006). The average annual rainfall ranges from 460 to 620 mm, and 90% of that rainfall occurs during the summer months from November to March (Mendelsohn and el Obeid 2004). The winter months (May to September) are dry with temperatures averaging 16°C. Temperatures are generally higher during the summer months (October to April) with average temperature of 26°C (Mendelsohn and el Obeid 2004).

The hydrology of the Okavango is extremely variable (Anderson et al. 2003), and as such, the system is in a constant state of flux (Gumbricht et al. 2004). The flood pulse is influenced by a combination of factors, including the size of the annual flood from the catchment area within Angola which feeds into the Okavango river, the local rainfall occurring within the Okavango Delta system itself as well as previous flood conditions (Gumbricht et al. 2004). However, these factors vary on both short (seasonal or annual) and long (decadal) temporal scales, resulting in an array of hydrological conditions to which plant and animal species must continuously adapt (Murray-Hudson et al. 2015).

The flooding patterns result in three main physiographic regions: 1) the upper panhandle, which consists of permanent main channels and swamps, 2) the seasonal floodplains, whose extent depends on the size of the flood, interspersed with smaller islands and 3) the sandveld tongues, which are large high lying islands that never flood, and consist mainly of Chief's Island, Moremi Game Reserve and the Western tongue (Paterson 1976, McCarthy et al. 1993). These regions result in a mosaic of habitat types, each with their own vegetation structure (Ramberg et al. 2006). Smaller islands surrounded by floodplain often contain riparian woodlands on the outer edges, consisting of hydrophilic species such as *Ficus sycamorus*, *Ficus natalensis, Diospyros mespilliformis* and *Garcinia livingstonei* (McCarthy et al. 2005). Island interiors may consist of combination of *Sporobolus spicatus* communities, or grassland

and savanna thickets with Kalahari grasses and large stands of wild sage (*Pechuel-loeschea leubnitziae*). The larger sandveld tongues, which never flood, are often dominated by *Colophospermum mopane, Terminalia sericea, Combretum imberbe* or *Vachellia erioloba*.

Ecologically, the seasonal floodplains are highly productive, and host a higher diversity of large herbivores in the dry season than the surrounding dry habitats (Paterson 1976, Murray-Hudson et al. 2006, Fynn et al. 2015). The seasonal flooding across dry floodplains and savannah mobilizes nutrients from detritus, plant material and animal dung, which in turn results in the deposit of high levels of phosphorous and nitrogen (Høberg et al. 2002, Lindholm et al. 2007). As the floodwaters recede, a 'green flush' of vegetation occurs, which supports a high biomass of grazing ungulates (Lindholm et al. 2007). This green flush of vegetation occurs at the end of the dry season, when grazing resources are typically scarce. This green flush therefore acts as a bridging resource – a critical resource which helps to span the gap between the end of the dry season and the next wet season – which is highly sought-after (Owen-Smith 2002, Fynn et al. 2015).

Characteristics of the flood, such as flood frequency, depth and duration, are what determine the composition of vegetation communities, and thus influence the quantity and quality of grazing produced by the receding flood-line (Murray-Hudson et al. 2014). A recent study on the relationship between floodplain vegetation composition and flooding regime revealed that short term flooding histories, more specifically the length of time an area is flooded in months, averaged over the previous three years, can be used to reliably predict current plant community composition (Murray-Hudson 2009, Murray-Hudson et al. 2014). While successive low floods favour the growth of palatable grasses, successive high floods favour succession to sedge communities, which have higher silica content and are therefore less palatable (Mosimane 2015). As the Okavango Delta alternates between 'wet' and 'dry' cycles at decadal

intervals (Tyson et al. 2002, Murray-Hudson et al. 2014), these changes carry large implications for the carrying capacity of large herbivores (Murray-Hudson et al. 2014). Flooding has an important role to play in influencing vegetation, and therefore has an important 'bottom-up' influence on the trophic cascade.

The study area, which covers approximately 5200 km^2, is located on the south-western edge of the Okavango Delta in the Ngamiland District, south-west of Moremi Game Reserve. (Figure 1:1). This area consists of private concessions NG 25, NG 26, NG 27a, NG 29 and NG 30, which are zoned as wildlife management areas (WMAs) and bound by a veterinary cordon fence along the southern and western boundaries. All the concessions are currently used for low volume photographic tourism but were used for trophy and citizen hunting during of the late 80s and early-mid 90s. The flooding on the western side of the Okavango is highly variable, and as such this area is characterised by large floodplain systems (Wolski and Murray-Hudson 2006). This area has also experienced considerable changes due to increased inflow of water into the area in recent years, proposed to be due to shifting tectonics or blockages caused by vegetation in upper channels, which redistributed large volumes of water down the western side of the Okavango from about 1997 (Wolski and Murray-Hudson 2006). In addition to this, the Okavango Delta has recently gone through a 'wetting' phase – a period of successive high floods – which extends from 1997 to present (Murray-Hudson et al. 2014).

Study species

Lechwe

Red lechwe (*Kobus leche*) are semi-aquatic antelope which are physically adapted to living in wetland habitats (Grimsdell and Bell 1972). Lechwe favour habitat found at the interface between land and water, on the margin of the inundated floodplains (Williamson 1990). Adult female and male lechwe weigh approximately 75 kg and 110 kg respectively, have a narrow

incisor breadth adapted to selectively feeding on vegetation in seasonally flooded floodplains, during both high and low water seasons. A small number of palatable grasses in this habitat make up the majority of the lechwe's diet (O'Shaugnessy 2010). While lechwe tend to avoid the longer grasses in shallow inundated areas, they have been observed to occasionally feed on sedges and forbs, which have a higher fibre and silica content making them more difficult to digest (Williamson 1990). Despite their dependence on the high-quality green flush produced by receding floodwaters, lechwe follow the receding flood waters as shallow water is also an important means of escape from predators (Williamson 1990). As the gait of lechwe is adapted to moving quickly in shallow water, lechwe almost always flee towards water when predators are detected and are vulnerable to predation on dry land (Lent 1969, Williamson 1990). With increasing flood levels, there is a decrease in both preferred habitat and grazing species for lechwe (O'Shaugnessy 2010). As lechwe are forced onto higher ground and outside their favourable habitat, they may become more vulnerable to predation as well as nutritionally stressed, with detrimental effects on lechwe population dynamics.

Tsessebe

Tsessebe prefer open habitat, close to water, with a relatively high abundance of palatable grasses (Joubert 1972). They are often found in ecotonal zones between habitat types, on the edges of grasslands or woodlands where there is ample shade (Child et al. 1972). Adult tsessebe weigh approximately 110 kg (Cumming and Cumming 2003) and have a narrow-incisor breadth which enables them to feed selectively (Gordon and Illius 1988). Tsessebe prefer short grassland habitats, generally where grass height is below 20 cm (often below 10 cm) and grows in rich clay soils, resulting in a high protein content (Gureja and Owen-Smith 2002). Tsessebe foraging strategies are believed to be similar to close relatives such as topi (*Dumascus lunatus jimela*), which occur in East Africa, and select for grasses in the growing phase and with a high leaf to stem ratio (Duncan 1975). Tsessebe thus strongly select for high

quality grasses, regardless of species, often in the growing phase such as grass regrowth in burnt areas, the edges of seasonally flooded floodplains or in drainage lines which retain moisture from the summer rains into the dry season (Child et al. 1972, Biggs 1979, Kingdon 1997, Gureja and Owen-Smith 2002, Dunham et al. 2004). Due to their dependence on high quality grazing, the availability of green grass leaf growth occurring in the dry season appears to be a key resource for tsessebe populations (Dunham et al. 2004). Hence, if grazing by competitors alters the leaf to stem ratio, tsessebe are precluded from selectively grazing (Dunham et al. 2003) or, if dry season green grass growth is limited by poor rainfall or by a reduction in the area of seasonally flooded grassland, tsessebe populations may decline (Rodgers 1982, Dunham et al. 2003, Dunham et al. 2004).

Blue wildebeest

Wildebeest are highly dependent on short to medium grasslands with high-quality, new, green grass growth which is rich in proteins and minerals during the rainy season (Sinclair and Fryxell 1985, McNaughton 1990, Yoganand and Owen-Smith 2014). Adult weight of blue wildebeest is approximately 215 kg for adult females and 250 kg for adult males (Braack 1973). In the Serengeti, large herds of wildebeest migrate in order to follow seasonal availability of green grass, simultaneously stimulating new growth through grazing pressure, creating short grazing lawns that facilitate other grazers such as Thomson's gazelle (Bell 1971). For this reason, ephemeral green flushes resulting from fires or flooding are a sought-after resource for wildebeest, particularly in the dry season (Yoganand and Owen-Smith 2014). If such dry season flushes are not available, wildebeest select for medium height grasses with intermediate greenness that will maximize the intake of dry matter to meet their nutritional requirements (Wilmshurst et al. 1999). Therefore, as their wide incisor-breadth does not allow for selective feeding of plant parts, at a landscape scale, wildebeest select for grazing habitats which offer high quality, green grazing of short to medium height.

(Wilmshurst et al. 1999). Locally, however, grass greenness is more important, indicating that energy requirements are an important driver in resource selection (Wilmshurst et al. 1999).

Zebra

Zebra generally prefer a mosaic of grassland and woodland habitats and are a water-dependent species (Van Soest 1982, Fischoff et al. 2007). Adult plains zebras generally weigh between 300 kg and 320 kg and are large-bodied hind gut fermenters (Smuts 1974). As such, zebra are non-selective, bulk grazers, concentrating on consuming large quantities of roughage (Van Soest 1982). As the retention time for foods in hind-gut fermenters is lower and the digestive system more efficient, grazers such as zebra are capable of extracting higher levels of nutrients from longer, more senescent, poor quality grasses, and so occupy an "ecological refuge" which enables co-existence with other medium-sized grazers (Bell 1971, Janis 1976, Duncan et al. 1990). Although zebra are capable of utilising poor-quality forage, they seasonally select high quality forage to maximise their nutritional intake, and often migrate to follow seasonal rains which result in fresh growth with high protein and mineral content (Sinclair and Arcese 1995, Bartlam-Brooks et al. 2011). Due to their large size and wide incisor breadth, zebra often select for medium-height grasses, and in doing so facilitate grazing for smaller-bodied, short-grass grazers (Bell 1971).

Buffalo

Buffalo are large-bodied, bulk feeders and require not only high-quality forage, but large quantities of forage to fulfil their nutritional requirements (Van Soest 1982, Demment and van Soest 1985). Adult female buffalo can weigh up to 513 kg, and adult males up to 590 kg, and are gregarious, found in large herds of up to several thousand individuals (Patterson 1979, Funston et al. 1994). Depending on the quality of resources available, buffalo may be sedentary or move large distances seasonally in search of suitable forage (Beekman and Prins 1989, Naidoo et al. 2012). During the wet season, buffalo will select open grasslands with

grasses of intermediate height and high quality in terms of greenness. In the dry season however, their movements are primarily limited by the availability of water, and buffalo become less selective, switching to lower quality habitats with a high biomass of grass to fulfil their dietary requirements (Prins 1996).

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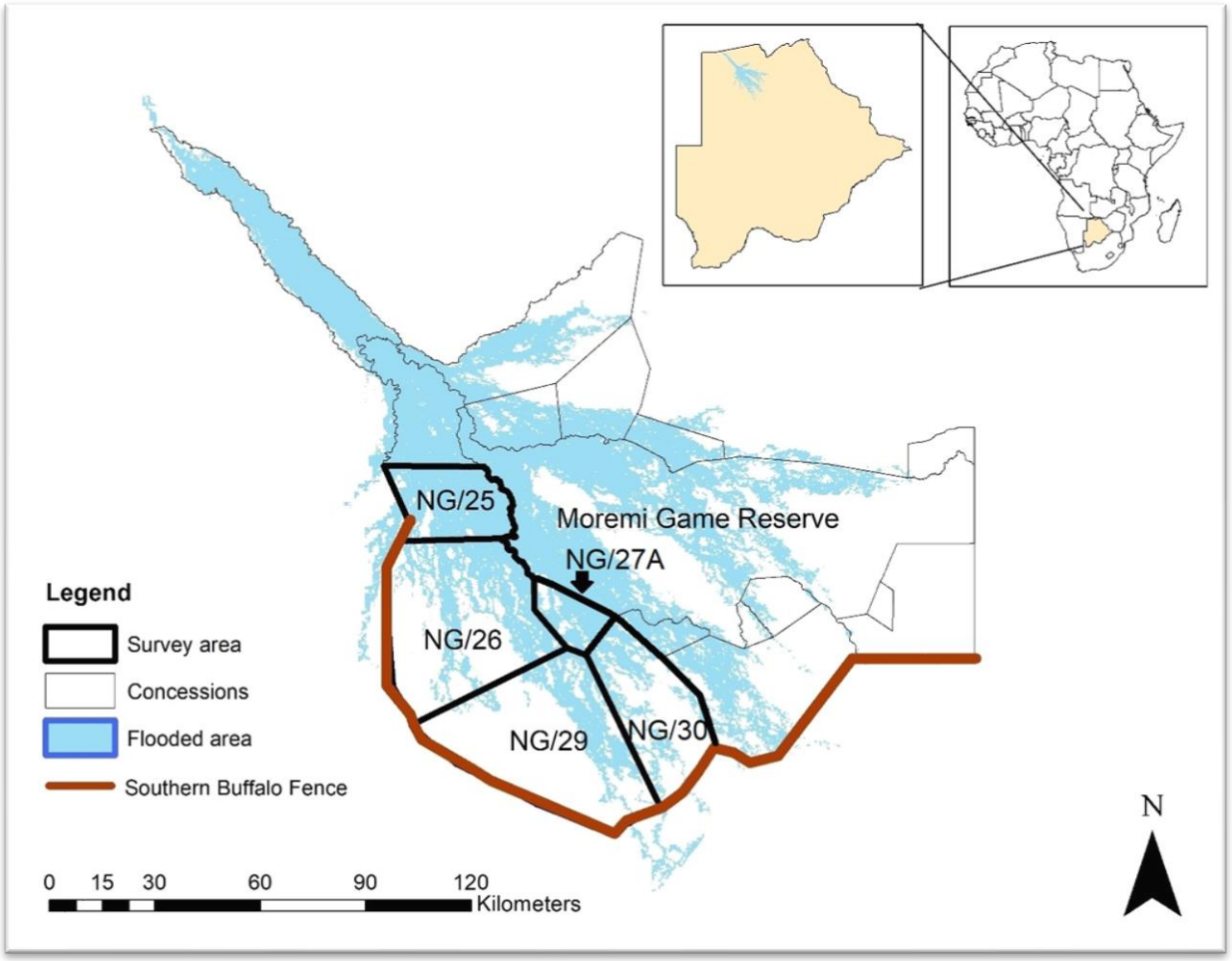


Figure 1:1. The Okavango Delta situated in the north western Botswana. The study area in the southwestern Okavango Delta is outlined in black. This area is characterised by large annual changes in flooding patterns and consists primarily of seasonally flooded areas.

Chapter 2- The relationship between flooding patterns and palatable grazing in a seasonally flooded wetland, the Okavango Delta

Abstract

In seasonally flooded wetlands, the hydrological characteristics of the flood pulse such as duration, frequency and depth, play an important role in determining vegetation communities. Specifically, short-term histories of hydroperiod, defined as the duration of time an area is flooded in a particular year, have been shown to be predictive in determining floodplain vegetation. Generally, during longer hydroperiods, floodplains are dominated by sedges, while shorter hydroperiods encourage grassland communities. This has important implications for grazing herbivores in wetland systems, which depend on the green flush of palatable grasses left as a dry season resource in the wake of receding floodwaters. The main aim of this paper was to quantify the extent to which longer hydroperiods reduced the amount of palatable grazing in floodplain vegetation communities and examine the potential consequences for the grazing guild in the south-western Okavango Delta, Botswana. I used a three-year average flood duration derived from MODIS satellite imagery, which has shown to be highly predictive of wetland vegetation composition, to construct historical maps depicting the three-year average flood duration over a 12-year period from 2003 to 2014. Using vegetation samples from 2007 and 2013, I then examined the relationship between average flood duration in months, averaged over the preceding three years, and the occurrence of palatable and unpalatable species, to determine if the relationship remained consistent between years with different flooding patterns. Lastly, I used generalized linear modelling to determine the flood duration optima for the palatable grasses and unpalatable sedges. Historical flood maps showed that there was a general decrease in the extent of areas flooded between zero and four months, while areas flooded between five and seven months increased in size over the 12-year period. The relationship between three-year average flood duration and the occurrence of palatable and non-palatable species remained consistent in years with different flooding patterns and can thus be used as an indicator of the occurrence of palatable and non-palatable species. I found that areas flooded for longer than five months generally had sedge-dominated communities, while areas flooded for shorter periods were dominated by palatable grasses. Most palatable grasses had flood duration optima of between two and four months, while duration optima of sedges peaked between six and eight months. Increasing hydroperiod in the study area over the twelve-year interval led to the

conversion of large areas of floodplain vegetation from palatable grazing to unpalatable sedges. This reduction in the amount of palatable grazing available may be partially responsible for a historically observed decline in grazing herbivores in this area. Future studies can use this information to predict how shifting inundation patterns caused by climate change or upstream anthropogenic offtake will influence vegetation zoning and biota in higher trophic levels in wetland environments.

Keywords: flooding, Okavango Delta, floodplain vegetation, palatability

Introduction

Freshwater wetlands are highly productive ecosystems (Turner et al. 2000). These systems are driven by temporal flooding caused predominantly by patterns of seasonal rainfall and may thus flood intermittently at the site of the rainfall, or in a single annual pulse if the water is carried by a river or tributaries from elsewhere (Junk 2002, Murray-Hudson 2009). The hydrological characteristics of the flood such as depth, duration and frequency all have an extensive influence on the community composition and biomass of floodplain vegetation (Blom and Vosenek 1996, Scholte 2007, Murray-Hudson 2009, Crase et al. 2013). As these hydrological characteristics change annually as well as cyclically over long time periods, wetlands are highly dynamic ecosystems and drastic changes in vegetation can occur on both short and long-term timescales (Mitsch and Gosselink 2000, Murray-Hudson et al. 2014). These changes in composition result from the constantly changing ecotone between dry and wet land, as various plant species thrive or perish based on plant and seed tolerance to extant and past hydrological characteristics (van der Valk and Welling 1988, Murray-Hudson 2009, Murray-Hudson et al. 2014).

The green grass and shoot growth resulting from the flowing and ebbing of flood levels during the dry season in wetlands makes the seasonal floodplains an important dry season resource, exerting a strong influence on herbivore populations (Illius and O'Connor 2000, Fynn et al. 2015). As a key resource for grazing herbivores in the dry season (Fynn et al. 2015), large

herbivore populations within wetlands are disproportionately dependent on floodplain vegetation (Scoones 1995, Yoganand and Owen-Smith 2014). Shifts in vegetation composition within this habitat type can therefore have significant implications for the availability of suitable grazing, and hence the abundance of large herbivores (Illius and O'Connor 2000, Fynn et al. 2015). Therefore, both the quantity as well as the quality of grazing available in terms of plant species palatability, can shift significantly depending on hydrological characteristics of the flood (Murray-Hudson et al. 2014).

The Okavango Delta is an alluvial floodplain system situated in the arid Kalahari basin (Bonyongo 1999). The flooding consists of a single, annual pulse of water originating from local, seasonal rains in the Angolan highlands (Gumbricht et al. 2000). This water is carried by means of the Okavango River to Botswana and terminates in an alluvial fan to form one of the largest inland deltas in the world (Gumbricht et al. 2004). The water reaches the Okavango Panhandle during the dry season between March and May, and reaches its furthest extent in the south-east in July, before receding once again (McCarthy and Ellery 1998). The flood waters are disseminated through main channels and distributaries, and then overflow into permanent swamps, extensive seasonal floodplains and occasionally, wooded areas (Bonyongo 1999). The floodplains are thus scattered with small, elevated islands, many of which formed as a result of termite mounds, and these islands become larger towards the Delta's periphery (Ramberg et al. 2006).

As the soils are relatively homogenous throughout the Okavango Delta, small changes in elevation can thus have a significant influence on the extent to which an area is flooded, and hence on vegetation zonation (Ellery et al. 1993, Ramberg et al. 2006, van der Valk and Welling 1988). Due to only minor differences in topography in the Okavango Delta, tectonic movements as well as vegetation or sediment build up can drastically alter the distribution of

flood waters (Biggs 1979). Furthermore, flood characteristics vary not only annually, but also cycle through dry and wet periods on a thirty to forty-year cycle (McCarthy et al. 2000, Mazvimavi and Wolski 2006). The consequent changes in hydroperiod, defined as the duration of time for which an area is flooded each year (Crase et al. 2013), result in changes in vegetation communities in floodplain systems (Lenssen et al. 1999, Murray-Hudson et al. 2014). Previous work on the relationship between hydroperiod and vegetation composition in the Okavango Delta has shown that there is in fact a strong relationship between hydroperiod averaged over the previous three years, and current vegetation type (Murray-Hudson et al. 2014). Broadly, during wetter phases in the cycle, extended hydroperiods lead to sedge-dominated communities, while drier hydroperiods favour grassland communities (Murray-Hudson et al. 2014). This has significant implications for population abundance of grazing herbivores, which are often limited by dry season resources.

The main aim of this paper is using the Okavango Delta as a case study, determine the extent to which high floods affect the availability of palatable grass species for grazing herbivores in an alluvial floodplain system. Recent aerial surveys have reflected a significant decline in the abundance of grazing herbivores in the Okavango Delta, which coincides with increasing hydroperiod. Particularly in the western Okavango Delta, flood levels in the Xudum channel, which runs through the centre of the study area, have risen considerably post-1997, most likely due to a tectonic event which redirected water from adjacent tributaries (Wolski and Murray-Hudson 2006). I hypothesize that this has led to a considerable increase in the area flooded and duration of floods over the last 15 years in the western Okavango Delta, and that this has negatively affected the grazing guild through the conversion of vegetation composition from palatable grassland floodplains to unpalatable sedges. The main objective therefore is to determine which flooding conditions have led to the conversion of floodplains from palatable to unpalatable grazing, and to quantify the extent of this change.

Methods

Flood mapping

Moderate Resolution Imaging Spectroradiometer (MODIS) imagery, consisting of 8-day composite images, was obtained from the Okavango Research Institute[2] from the year 2000 to 2014 (no MODIS imagery was available prior to 2000). This imagery had been processed to differentiate between dry and wet pixels (spatial resolution 250 m) in the study area using a threshold identified from band 1 data, and these composite images were then combined into a monthly composite image showing the extent of the flood for each month (refer to Murray-Hudson et al. 2014). For the years 2000 to 2014, monthly images were stacked using ERDAS Imagine 9.1 (Leica-Geosystems 2006) to produce a flood duration map for each year, with each pixel classified according to the number of months in the year for which it remained flooded. Given the relationship between average three-year flood duration and vegetation composition (Murray-Hudson 2009, Murray-Hudson et al. 2014), maps were once again stacked in three-year windows, to generate composite maps depicting the average flood duration in months of each pixel for each year. This produced composite maps for each year of hydroperiod averaged over the previous three years from the year 2003 to 2014.

Vegetation sampling

Vegetation composition data for 2013 were collected at 60 different sites between concessions NG29 and NG30 (Appendix 1). Sites were located along concession roads and located one kilometre apart. At each site, ten one metre square quadrats were sampled on either side perpendicular to the road, at 10 metre intervals. This amounted to 1190 quadrats or approximately 11.9 km of transects. For each quadrat, species composition was recorded, and the percentage cover for each species in the quadrat was estimated. Vegetation sampling was conducted in February 2013, when grasses are in inflorescence to allow for more accurate

[2] Okavango Research Institute, Maun, Republic of Botswana

identification of species. Species were identified in the field, and those species which could not be identified in the field were transported to the Peter Smith Herbarium at the Okavango Research Institute for identification. Vegetation composition data for 2007 were obtained from the Okavango Research Institute for comparison. The methods detailing protocol for data collection are outlined in Murray-Hudson (2009).

Data analysis

Flooding

The total area covered by different average flood durations was calculated by summing the number of pixels for each monthly category of flood duration, and then multiplying the number of pixels by the pixel area (250 m by 250 m). These areas were summed for each year, and then categories compared across 12 years of data from 2003 to 2014, to determine the relative change in flooding patterns over time. Composite flood maps were analysed in ArcMap 10.2 (ESRI 2013).

Vegetation

As 2007 and 2013 data were collected in the same part of the western Delta, the 2007 data were overlaid on the 2013 study area to select quadrats which fell within the 2013 study area for comparison. As there were differences in vegetation composition between the 2007 and 2013 data, both datasets were used to compare whether the average flood duration in months of the previous three years could consistently account for a broader vegetation classification regarding the distribution of species with different palatability. This would enable me to quantify the extent to which flooding affects palatable grazing for herbivores.

The conversion of grasslands to sedges is one of the major consequences of increased flood levels (Murray-Hudson et al. 2009). Sedges are generally deficient in the macronutrients such as nitrogen, phosphorous, calcium and potassium (Stowe and Bonyongo 1993), and have high silica contents, which decrease digestibility (McNaughton et al. 1985, Williamson

1990, Mosimane 2015). While large herbivores may make use of sedges towards the end of a dry season or in drought years, they do not form a substantial proportion of the diets of the study species in most years (Fynn et al. 2015).

Based on this information, for both species data sets, species were thus grouped into three categories of palatability: unpalatable sedges (P1), semi-palatable grasses (P2) and highly palatable grasses (P3). For simplicity, all sedges (family Cyperaceae) were included in the non-palatable group. For the grasses, palatability was defined in terms of the general grazing value of the grass to large herbivores (Russell et al. 1990, Ellery and Ellery 1997, Oudtshoorn 2002). To allow for quantitative analysis, the percentage cover of all species falling within each palatability category was added together, and this quantitative data was then used for further analysis. To determine if the relationship between palatability of species and the previous three years flooding duration remained consistent between the two datasets, a canonical correspondence analysis (CCA) was performed for both data sets using Canoco 5.54 (ter Braak and Smilauer 2006). The results for each year were then evaluated using a Monte Carlo permutation test to determine the significance of the canonical axes.

To determine the optimum flood levels at which the species of the various palatability categories occur, the optimum three-year average flood duration for each species in the various categories was determined using generalised linear modelling (ter Braak and Looman 1986). These were constructed in Canoco 5.54 (ter Braak and Smilauer 2006), using a Poisson error distribution and logarithmic link function (ter Braak and Looman 1986, Murray-Hudson et al. 2009). This modelling approach results in a uni-modal, bell-shaped response curve, with the peak of the bell representing the optimum flood duration at which the species occur, the breadth representing the range of flood duration tolerated, and the amplitude the maximum probability of occurrence at different flood durations (Murray-Hudson 2009). Only species for

which optima could be calculated were used in the analysis (Appendix 1). T-tests were then used to determine whether the mean optimum flood duration for each palatability category did not significantly differ between years. This analysis was performed in R version 3.22 (R Core Team 2014).

Results

Flooding

Patterns of flooding changed substantially between 2003 and 2014. For this period there was a net decrease of approximately 400 km^2 in the amount of dry land available for grazing (Figure 2:1 and Figure 2:2). Most noticeable was the increase in areas flooded for an average of five, six and seven months, with a net increase of 500 km^2 for these flooded areas over the study period (Figure 2:2). Areas flooded for shorter periods of between two and four months fluctuated, reaching their minima in 2007 and 2008 and peaking again around 2011 with a difference of approximately 100 km^2. The inverse occurred for areas flooded for eight months (Figure 2:2). There are few data for areas flooded for longer than eight months, as the study area is focused on the seasonal floodplain areas which exhibit dynamic flooding patterns, away from permanent swamp areas (Figure 2:2).

Vegetation

Both 2007 and 2013 data show similar patterns with regards to the occurrence of palatable species in relation to the average flood duration (Figure 2:3). Unpalatable species such as sedges occur at higher flood durations in relation to medium and highly palatable grass species important for herbivore grazing (Figure 2:3). Both Monte Carlo tests showed a significant relationship with the axis representing three-year average flood duration (2007: F-ratio=59.78, p=0.002; 2013: F-ratio=13.48, p=0.002), although the overall correlation between the palatability categories and average flood duration was greater for 2007 than for 2013 (2007: R^2= 0.488, 2013: R^2=0.158).

The species optima calculations revealed that for 2007 and 2013, there were no significant differences in the mean duration optima for the palatability categories P2 and P3 (P2: t = -0.29645, df = 18, p-value = 0.7703; P3: t = -1.2305, df = 12, p-value = 0.2421). The means for optimum flood duration for species in the P2 category were at 4.95 months for 2007 and at 4.63 months for 2013, and the means for optimum flood duration for species in the P3 category were 4.30 for 2007, and 3.13 for 2013 (Figure 2:4). For the least palatable species, there was a significant difference in means between the two years (t = -2.204, df = 15, p-value = 0.04), with the mean optimum flood duration for species in the P1 category at 6.26 for 2007 and at 4.91 for 2013. There is a consistent pattern of decreasing optimum flood durations from P1 to P3 (Figure 2:4). Median species optima for the three palatability categories as well as the distribution of optima across different flood durations were generally higher for 2007 than for 2013 (Figure 2:4). However, the general pattern indicates that at above five months duration, communities are transitioning from semi-palatable grasses to sedges, and that below five months communities transition to semi-palatable and highly palatable grazing, with many of the highly palatable species occurring at low flood durations of below four months (Figure 2:4).

Discussion

The main findings of this analysis indicate that predictability of patterns of occurrence of palatable versus unpalatable species in relation to flooding patterns remain similar across years with different flooding patterns, and that the three-year average flood duration used by Murray-Hudson (2009) to delineate different vegetation communities is also useful to determine the occurrence of palatable and non-palatable grazing. The flood duration optimum of most of the palatable grass species falls between two and four months, indicating that areas flooded between four and six months are likely the ecotone between sedge and grassland communities. On average, sedge occurrence appears to peak when an area is

flooded for more than five months, while grass occurrence peaks in areas flooded for less than five months, with highest number of palatable species peaking in areas flooded between two and four months on average. A three-year average flood duration of five months thus appears to be the point above which communities become dominated by sedges. The increase in flood extent from 2003 to 2014 indicates that the Okavango Delta has moved into a wetter phase of the flooding cycle. The decrease in dry land was concomitant with an increase in flooded areas, but most notably in areas flooded for an average three-year duration of between five and seven months, when sedge-dominated communities occur. Furthermore, there was a slight decrease in the areas flooded for an average of one and two months – conditions which favour the growth of the most palatable grasses in the floodplain system.

Vegetation zonation in the Okavango Delta, including the occurrence of broad vegetation classifications such as palatable grasses and unpalatable sedges, is largely determined by the tolerance of individual species to various flooding regimes. Recent meta-analyses of wetland systems have revealed that many of the species themselves which dominate different types of flooding frequencies and durations appear to be consistent across different types of wetlands across the continent (Fynn et al. 2015). The pattern of species zonation is therefore similar across swamps, deltas, dambos, broad floodplains in mid- and upper- river catchments, riverine grasslands and grasslands in sumps, pans or drainage areas (Fynn et al. 2015). This study of the pattern emerging between the occurrence of palatable and unpalatable species in the Okavango Delta may thus have wide applicability and can be used to predict changes occurring in other wetlands across Africa. Consequently, Murray-Hudson's three year, backward moving, average flood duration principle (Murray-Hudson 2009) could potentially be used in other ecosystems, using satellite imagery to determine the extent to

which the occurrence of palatable grazing changes with various flood regimes in different wetland systems.

As flooding is the main ecological gradient along which grazing patterns are established in wetland systems (Bonyongo 1999, Fynn et al. 2015), the decrease in available dry land and increase in areas dominated by sedges, has significant implications for the quantity and quality of grazing available for the herbivores in the Okavango Delta. As key resource areas (Illius and O'Connor 2000), wetlands provide dry season palatable grazing for large herbivores, ultimately determining their carrying-capacity, and may have a disproportionate effect on herbivore populations in the Okavango Delta (Illius and O'Connor 2000). Consequently, the conversion of much of this area from dry land or seasonal floodplain grasslands to seasonal sedgelands, and the simple decrease in dry land area available, would likely affect the abundance of grazing herbivore species, and may be a reason for the decline in large herbivores observed in the Okavango Delta over the last decade (Illius and O'Connor 2000, Chase 2011). This is concurrent with studies on other wetlands in southern Africa where declines in floodplain areas have resulted in precipitous declines in large herbivores due to changes in flooding regime. In the Kafue Flats, Zambia, for example, the construction of a dam upriver from the flats, and the resultant change in flooding regime, led to a large decline in Kafue lechwe (*Kobus leche kafuensis*), exacerbated by poaching as well as competition for grazing with local cattle (Chansa and Kampamba 2009). Similarly, the construction of the Cahora Bassa and Kariba Dams on the Zambezi River changed the flooding regimes and thus the grazing vegetation in the Zambezi Delta floodplains, leading to a marked reduction of some of the largest buffalo and waterbuck populations in Africa. These reductions were further exacerbated by civil war (Beilfuss et al. 2010). The evidence of changing flooding regime on floodplain vegetation and in turn large herbivores, as well as the sensitivity of floodplain systems to anthropogenic disturbance is thus irrefutable.

From a conservation perspective, years of high flood cycles in the Okavango Delta result in considerable bottom-up pressure on grazing herbivores due to the conversion of floodplains to sedge-dominated communities. It is during these times that top-down processes such as predation or anthropogenic pressure as a result of bush-meat poaching can have severe additive effects on population declines, which may prevent adequate recovery of populations during lower flood cycles. Future studies should aim to continue the collection of long-term data relating the changes of flooding to changes in vegetation in the Okavango Delta. As this study period took place during a wetting phase, the same kinds of analyses should be repeated over a drying phase, to confirm the conversion of sedge-dominated floodplains to grass-dominated floodplains with palatable grazing during dry phases of the cycle. Additionally, large herbivore populations need to be monitored more intensively during such a period to determine whether the cyclical change in vegetation also results in a cyclical increase in grazing herbivore populations in the Okavango Delta. However, caution should be taken to account for external and anthropogenic influences which may disturb this natural cycle (Bartlam-Brooks et al. 2013). Studies on predator- or anthropogenically-induced mortality of herbivores in this region could serve to disentangle the relative contribution of each factor to herbivore declines. Lastly, the ability of Murray-Hudson's (2009) three-year average flood duration to predict the distribution of palatable and unpalatable grazing in other wetlands should be investigated. The use of satellite imagery to monitor changes in grazing availability relating to flooding patterns in different wetlands would be a valuable and cost-effective tool for monitoring current and future changes to wetlands, as well as predicting the consequences for local large herbivore populations.

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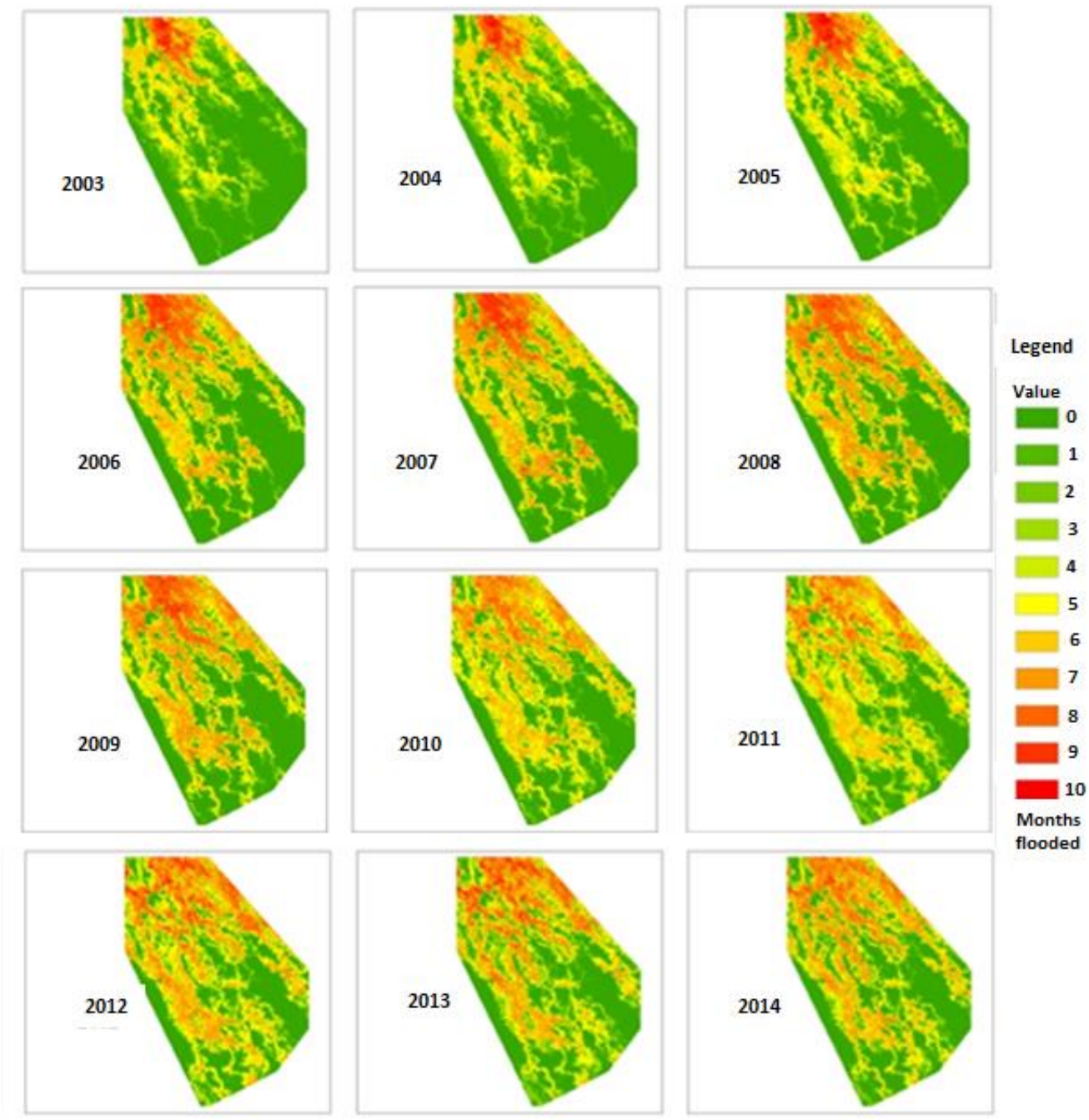
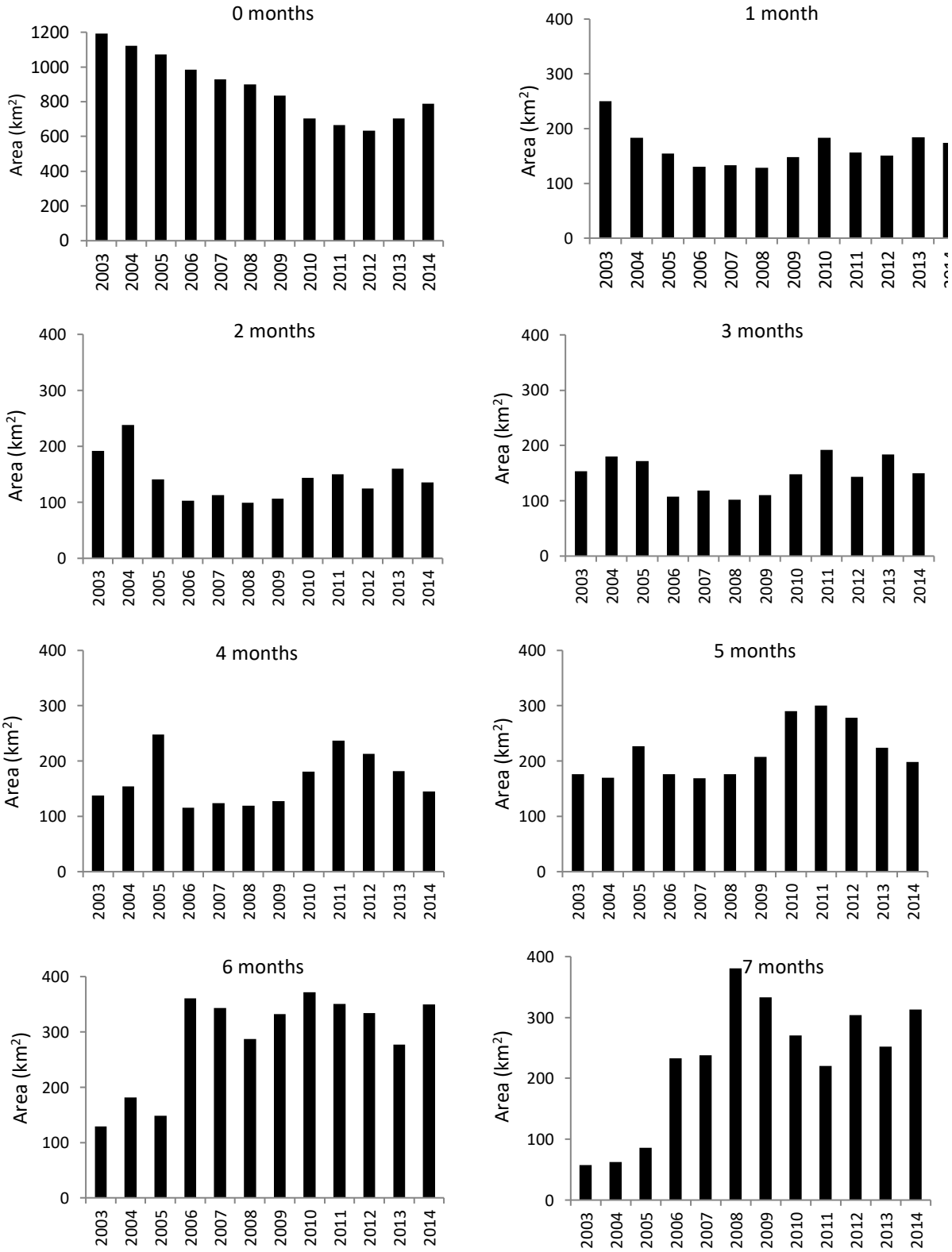


Figure 2:1. MODIS imagery clipping of the study area depicting the changes in flood extent from 2003 to 2014, with pixels classified by colour into flood durations, in months, averaged over the preceding three years


0 months
1 month
2 months
3 months
4 months
5 months
6 months
7 months
Area (km2)
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014

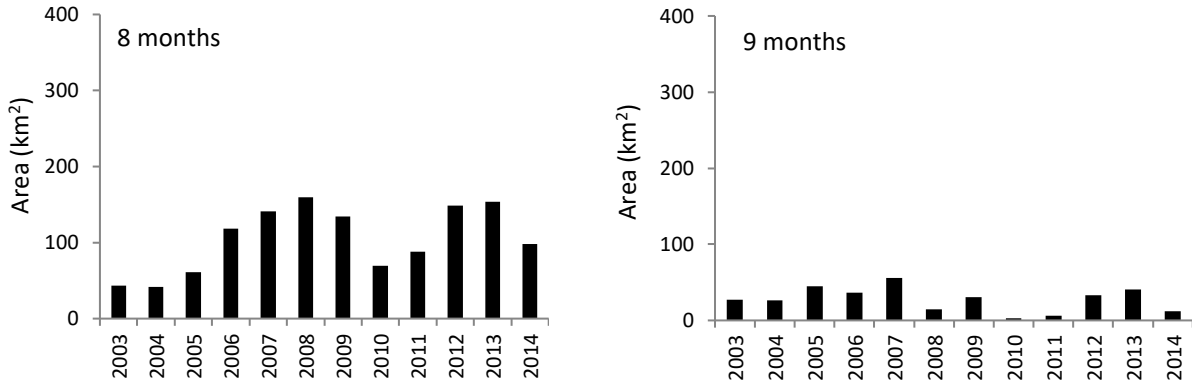


Figure 2:2. Area of land, covered by water for different monthly durations in the study area. Areas covered for ten months are negligible, and areas of permanent swamp that hold water for eleven months or longer fall outside the study area.

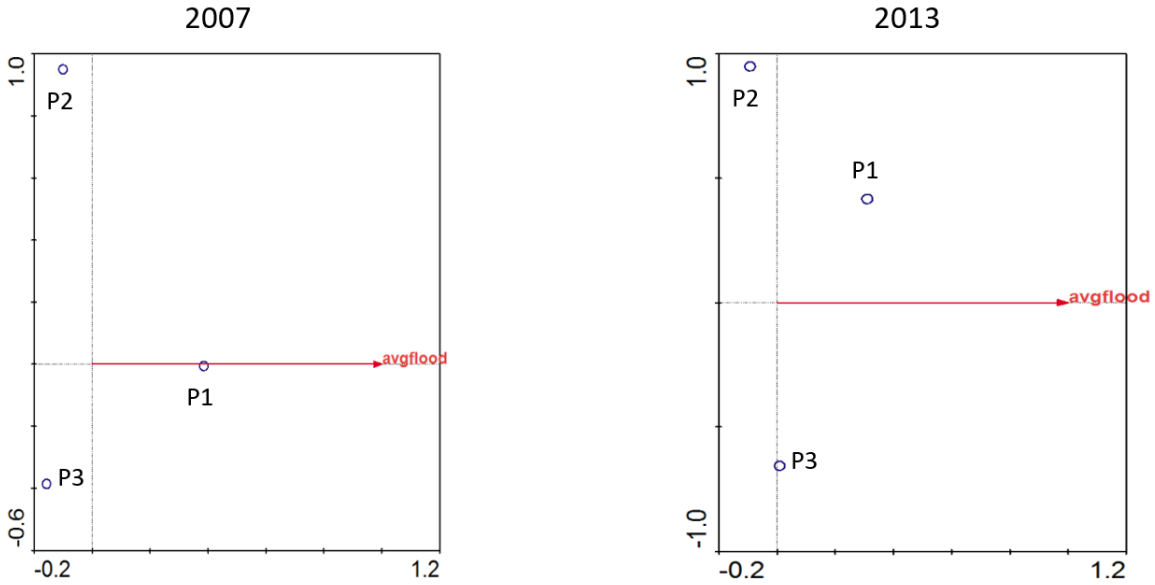


Figure 2:3. CCA ordination plots where species groups of varying palatability are plotted in species space in relation to the average flood duration (avgflood) from the previous three years for 2007 and 2013 data. P1= grasses of poor palatability, P2 = grasses of medium palatability and P3 = grasses of high palatability. Average flood duration from the previous three years increases in the direction of the arrow in both graphs.

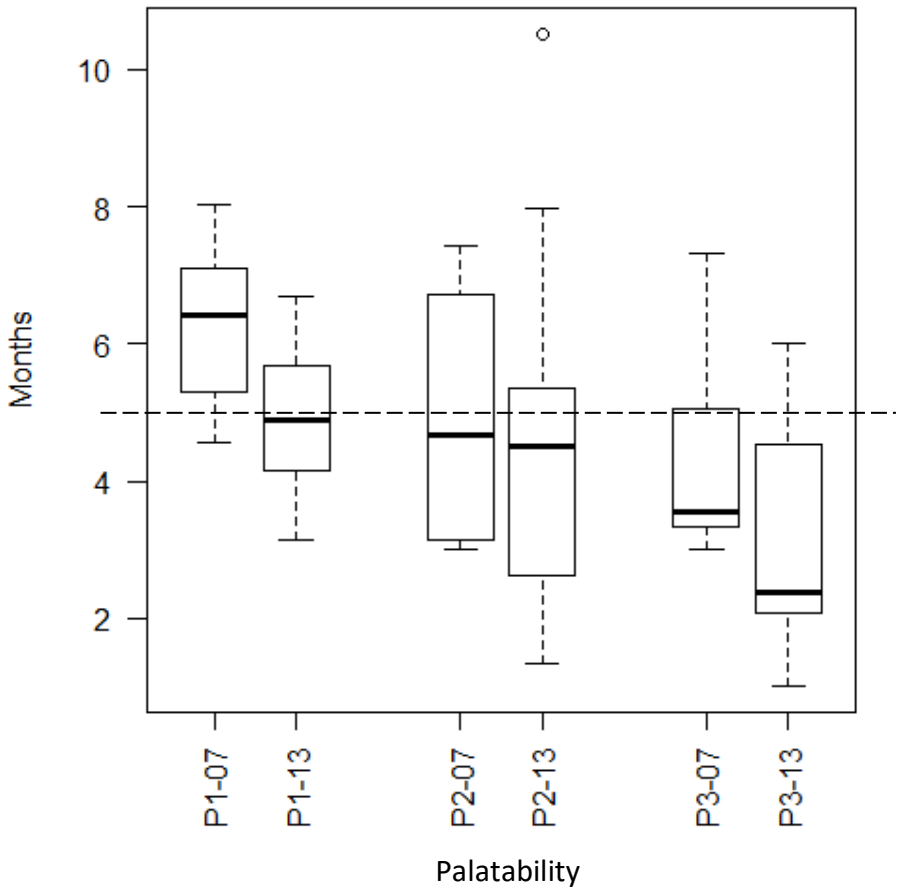


Figure 2:4. The distribution of species optima three-year average flood duration for the various categories of palatable species. P1= non-palatable sedges, P2 = semi-palatable grasses, P3 = palatable grasses, and 07 = 2007 data and 13 = 2013 data. Most palatable species optimally grow in areas flooded for less than five months (dotted line).

Chapter 3 - Patterns of large herbivore resource use in an alluvial floodplain grazing system, the south-western Okavango Delta

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[1]Wrote the manuscript; [2]Provided data and assisted with analysis and interpretation, [3]Supervisor and reviewed the manuscript

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Abstract

In flood-pulsed wetlands, floods drive ecological change in the quantity and quality of vegetation. Seasonally flooded grasslands (areas characterized by grasses tolerant to seasonal flooding) offer important resources for large mammalian herbivores. These areas support densities of herbivores that are seasonally higher than in the surrounding savanna and woodlands. Hence, changes in the extent of these grassland areas, as a consequence of variation in flooding patterns, have implications for the numbers of herbivores, particularly grazers. We used a network analysis approach to quantify the relationship between large mammalian grazers (lechwe, *Kobus leche*; tsessebe, *Damaliscus lunatus*; blue wildebeest, *Connochaetes taurinus*; zebra, *Equus quagga*; and buffalo, *Syncerus caffer*) and areas flooded for different durations in the Okavango Delta, to determine whether assemblages of grazers changed with flooding extent. The small-bodied grazers (tsessebe and blue wildebeest) were associated mostly with dry areas or areas flooded for less than 5 months, and used a subset of the flooding areas used by the large-bodied grazers (buffalo and zebra). Lechwe used areas flooded the longest. In years of high flooding, there was increasing overlap in habitat use within the grazing guild, most likely due to a decrease in the size of preferred grazing areas. Large-bodied grazers like buffalo and zebra are therefore likely to be more resilient to ecological changes in these flood-pulsed systems than other more specialist (i.e., using a narrow spectrum of resources) grazers.

Keywords: *Connochaetes taurinus, Damaliscus lunatus, Equus quagga*, flooding patterns, grazing, *Kobus leche*, modularity, nestedness, network analysis, *Syncerus caffer*

Introduction

Abiotic factors, such as rainfall, temperature, soil, and fire, are important drivers of temporal and spatial variation in vegetation quality and quantity (Venter et al. 2003; Bond and Keeley 2005). These factors may vary seasonally or annually, and ultimately influence herbivore abundance and distribution (Coe et al. 1976; Grant et al. 2011). However, herbivores themselves also may influence their resources, either by facilitating plant growth (i.e., grazing lawns, McNaughton 1984), or by reducing food availability (Mduma et al. 1999).

In flood-pulsed wetlands, frequency, duration, and depth of the flood pulses are the main determinants of vegetation composition and biomass (Scholte 2007; Murray-Hudson et al. 2015). During the dry season, the new, high-quality grass growth resulting from receding flood waters can act as an important food source for grazing herbivores, at a time when vegetation in the surrounding savanna and woodland areas is mostly senescing (Fynn et al. 2015). In such ecosystems, the flood pulses therefore have a significant influence on the population performance of large mammalian herbivores (Wegge et al. 2006).

The Okavango Delta in Botswana (hereafter referred to as the Delta) receives an annual flood pulse as the water from the highlands of Angola reaches and spreads through it. This flood pulse is the main driver of vegetation composition, quality, and quantity (Smith 1976). Seasonal floodplains (areas that are flooded on a seasonal basis) inundated for long periods of the year (up to 8 months) are dominated by facultative wetland sedges (i.e., *Cyperus articulates, Schoenoplectus corymbosus*) and water-tolerant grasses (i.e., *Vossia cuspidate, Leersia hexandra*) that can tolerate short dry periods (Bonyongo et al. 2000). These areas, known as seasonally flooded sedgelands (Murray-Hudson et al. 2015), have low grazing value (Mosimane 2015). Areas flooded less frequently, known as seasonally flooded grasslands (Murray-Hudson et al. 2015), are dominated by grasses such as *Panicum repens, P. coloratum*, and *Cynodon dactylon,* which offer more favourable grazing for herbivores (Fryxell and

Sinclair 1988; Bartlam-Brooks et al. 2011). During high hydroperiods (periods of high flood frequency and duration), many of the seasonally flooded grasslands are converted to seasonally flooded sedgelands (Murray-Hudson et al. 2015), which may result in increased competition for limited resources amongst sympatric grazers (Madhusudan 2004; Cameron and du Toit 2007).

One way to quantify interactions in a resource-consumer system is through network analysis that identifies recurring wiring patterns (network topology) within a network (see Miranda et al. 2014 for a review). These patterns confer important functions to the network, for example two such patterns (nestedness and modularity) confer stability (i.e., allow complex networks to persist; Bascompte et al. 2003; Thébault and Fontaine 2010). Nestedness measures the degree with which consumers that utilize a small range of resources are a subset within the consumers that utilize a wide range of resources (Bascompte et al. 2003). Modularity groups consumers into modules where patterns of resource use are more similar within modules than between modules (compartmentalized network; Bascompte 2010; Thébault 2013). These two patterns have contrasting effects on the stability of the system represented by the network. In a compartmentalized network, the effects of a lost resource are confined to one module (i.e., only the consumers relying on that resource are affected), thereby making that resource-consumer system more resilient (i.e., better able to return to an equilibrium state) to perturbations (Thébault and Fontaine 2010). In a nested network, the loss of a resource may affect the entire network (Thébault and Fontaine 2010).

We examined a consumer-resource system, made of members of the grazing guild (consumers) and areas with varying flood duration (resources), in a flood-pulsed wetland, the Okavango Delta, using a network analysis approach. As the duration and extent of the flooding has steadily increased over the past 12 years (Murray-Hudson et al. 2015), we also

examined whether the network structure changed under different flooding conditions (low hydroperiods versus high hydroperiods). As the diversity of resources and species are largely dependent on flooding in the Delta (Fynn et al. 2015), it is important that we explore how this network functions, to be able to understand, and predict, the effects of changing flooding regimes on large mammalian herbivores in the future. We hypothesised that: 1) grazers would be grouped into modules based on similar physiological and morphological adaptations to grazing, 2) within each module the smaller-bodied grazers would be nested under larger-bodied grazers in terms of use of areas with varying flood duration, and 3) high hydroperiods, which lead to conversion of flooded grasslands to seasonal swamps, would result in increased overlap of resource use within the guild.

Methods

Study area

The Okavango Delta forms one of the world's largest freshwater inland deltas (McCarthy and Ellery 1998). It covers an area of up to 28 000 km^2 in the centre of the Kalahari Basin. The flooding consists of a single, annual pulse of water originating from seasonal rains in the Angolan highlands (Gumbricht et al. 2004). The water moves through Angola via the Okavango River, and spreads into the Delta at the beginning of the dry season (Ramberg et al. 2006). The floodwaters are disseminated through main and secondary channels over the next 4 months, and reach their furthest extent in the south-east in July, before receding (McCarthy and Ellery 1998), largely as a result of evaporation (Gumbricht et al. 2004). Because of the different timing of flooding peaks between the northern and distal ends and small elevation ranges, the Delta is highly heterogeneous. It consists of a network of channels that can vary from one flood to the next, seasonal and permanent floodplains, and islands resulting from sediment accumulation or termite mounds, which grow larger towards the Delta's periphery (McCarthy and Ellery 1998; Ramberg et al. 2006).

Study species

The grazing guild in the Delta consists of 5 principal grazing herbivores: lechwe (*Kobus leche*), blue wildebeest (*Connochates taurinus*), tsessebe (*Damaliscus lunatus*), zebra (*Equus quagga*), and buffalo (*Syncerus caffer*). They are all partial to high-quality green grass but have various morphological and physiological adaptations, that enable them to co-exist and exploit different aspects of the same resource (Demment and van Soest 1985; Illius and Gordon 1987). The small-mouthed grazers, tsessebe and lechwe, prefer the fringe of seasonally flooded grasslands, where the green flush occurs during the dry season, with lechwe being adapted to shallowly-inundated floodplains as well (Skinner et al. 2005). Wildebeest are less selective for high-quality plant parts due to a wider incisor breadth, but often move to short-grass areas on sandy river banks when other resources are heavily overgrazed (Hirst 1975). Zebra, being non-ruminant, are able to feed on longer dry grasses, if necessary, within the dry season (Caro 1999; Bartlam-Brooks et al. 2013). Buffalo, the largest of the grazers, are bulk feeders, and while they select high-quality or new grasses, they can still rely on the longer, more senescent grasses to fulfil their dietary requirements (Illius and Gordon 1992).

Flooding parameters

Moderate Resolution Imaging Spectroradiometer (MODIS) 16-day composite imagery at 250m spatial resolution was used to determine flood duration and frequency, following the procedure outlined in Murray-Hudson et al. (2015). We used the Band 1 (0.62–0.67 µm) threshold method (Murray-Hudson et al. 2015) to classify pixels as wet or dry and generate monthly flood extent maps for the years 2000–2014. MODIS 250 m images were made available by the Okavango Research Institute.

The monthly flood extent maps were then stacked to create a flood duration map (number of months each pixel was flooded) for each year. Average monthly flood duration for the most recent 3 years is most predictive of current vegetation community (Murray-Hudson et al.

2015). As a result, annual flood duration maps for each year corresponding to aerial surveys census data (2003, 2004, 2010, and 2014 – see below) and the preceding 2 years were combined, and the number of months each pixel was flooded was averaged across the 3 years. These 3-yearly flood duration average values were then grouped and associated to broad vegetation communities identified by Murry-Hudson et al. (2015): 0 months = dry grasslands, 1–4 months = seasonally flooded grasslands, 5–8 months = seasonally flooded sedgelands. The amount of area covered by each broadly classified vegetation community was then calculated for each year of the study period, by multiplying the number of pixels in each class by the pixel size.

Fixed-Wing Aerial Surveys

Aerial surveys were conducted in 2003, 2004, 2010, and 2014 in the dry season, to record distribution and abundance of mammalian herbivores. The surveys used the standard methodology for strip-transect sampling (Norton-Griffiths 1978), which is well established for aerial surveys of large African herbivores (Craig and Gibson 2002). The distance between adjacent transects was 2 km for 2010 and 2014, and 3 km for 2003 and 2004, providing a 15 to 20% sampling coverage. Strip widths (combined width of the 2 search strips) were 250 m for 2003 and 2004, and 400 m for 2010 and 2014. The same observers were used throughout each survey, one on each side of the plane. For each sighting, the following was recorded: species, number of individuals in a herd, and GPS position of the herd when the animals were perpendicular to the plane.

Data analysis

GPS positions of animal sightings for buffalo, zebra, tsessebe, blue wildebeest, and lechwe were mapped onto the average monthly flood duration maps for the most recent 3 years (including the year in which the survey took place) in ArcMap 10.2 (ESRI 2013).

To visualize the structure of the network, we constructed quantitative bipartite matrices where 2 types of nodes (species and average monthly flood duration) were linked by the observation frequency of each species (represented by herds) in each flood duration category (strength of interaction). We used the 'plotweb' function in the *bipartite package* (Dormann et al. 2008) in R (R Core Development Team 2014). We chose to use the number of herds instead of the number of individuals for depicting interaction strength to account for differences in social structure between herbivores, thereby preventing a bias towards grazers that congregate in larger numbers, particularly buffalo. We built 4 networks, 1 for each survey year (2003 2004, 2010, and 2014).

To examine modularity within each network, we used a quantitative bipartite modularity algorithm (QuanBiMo, Dormann and Strauss 2014) that produces a modularity index Q ranging from 0 (no separated modules) to 1 (modules perfectly separated into compartments). To assess if the modularity values of our study networks deviated from random patterns, we compared the Q values of our networks to those of 1,000 generated null models constrained to keep marginal totals constant (Dormann et al. 2008; Thébault 2013).

We determined the degree of nestedness within each network by calculating the weighted interaction nestedness estimator (WINE) following the method proposed by Galeano et al. (2009). WINE takes into account the strength of the interactions to determine whether the use of a certain set of resources by a consumer falls within a subset of resources used by other consumers within the network (Joppa et al. 2010). WINE index values range from 0 (random structure, no nested pattern) to 1 (complete nestedness; Galeano et al. 2009). To assess if our study networks were more nested than expected by chance, we compared the nestedness values of our networks to those of 1,000 generated null models. Null models were constructed to ensure that observed values as well as the number of events and distribution

in each interaction remained the same, but marginal totals were not constrained (Dormann et al. 2008; Galeano et al. 2009). To visually represent the patterns of nestedness, matrices were drawn using the 'visweb function' in the *bipartite package* (Dormann et al. 2008).

To further describe the extent to which the use of flood duration categories overlapped within the grazing guild, we calculated Horn Morisita niche overlap indices for each year. We calculated a network-level index by calculating the amount of overlap between each pair of herbivores and then averaging it across all pairs. This index ranges from 0 (no overlap) to 1 (total overlap; Miranda et al. 2014). To determine whether the observed niche overlap values differed from random expectations, we compared them against niche overlap values from 1,000 null models where we had retained the number of interactions and links from the original interaction matrix.

Where degree of modularity, nestedness, and niche overlap within our study networks proved to be significant, we determined whether these indices varied across years. We calculated 1,000 D–values (Manly 1997) by subtracting the value of each observed index (nestedness, modularity, Horn-Morista) from the index values calculated from the 1,000 generated null models (Vazquez and Aizen 2003; Gibson et al. 2011). We considered the difference between years to be significant where the 95% confidence intervals of the D–value distributions for the different years did not overlap (Gibson et al. 2011).

Results

Grazers–flood duration interaction networks showed obvious patterns of preference for many of the herbivores. In 2003 and 2004, lechwe had a high affinity for areas flooded between 4 and 6 months, while in 2010 and 2014 the range of interaction frequencies spread, and there were more interactions with areas flooded for 7 months or more (Figure 3:1). Tsessebe and blue wildebeest showed an affinity for dry areas, and areas flooded on average

for less than 6 months (Figure 3:1). Zebra showed a wider range of use of flooded areas than blue wildebeest and tsessebe, and while in 2003 and 2004 they utilized primarily dry areas and areas flooded for up to 5 months, in 2010 and 2014 they increased their range to include areas flooded for 6 and 7 months (Figure 3:1). Buffalo were associated with all flood duration classes, ranging from non-flooded areas to areas flooded up to 9 months throughout the study period, while showing a preference for areas flooded from 1 to 5 months (Figure 3:1).

All the observed networks showed significant modular patterns, higher than predicted by chance (Table 3:1). In all years, lechwe constituted a single module using flood duration categories mostly not used by the other grazers (Figure 3:2). Modularity between the other 4 grazing species differed each year. In 2003, zebra and blue wildebeest were grouped together in areas of low average flood duration (less than 4 months), while tsessebe were separated into their own module in dry areas and areas flooded for an average of 5 months (Figure 3:2). In 2004, buffalo formed their own module in areas of high average flood duration (8 and 9 months), while the medium-sized grazers were grouped together in areas of even lower average flood duration that the previous year (1 month or less) (Figure 3:2). In 2010, interaction of buffalo with the flood duration categories changed as they changed to areas of medium to low flood duration, being grouped with zebra in dry areas or areas flooded for 5 months or less (Figure 3:2). All 4 species (buffalo, zebra, blue wildebeest, and tsessebe) were grouped together in 2014 in dry areas or areas flooded for less than 4 months (Figure 3:2).

Networks in study years 2004, 2010, and 2014 showed patterns of interaction that were significantly more nested than expected by chance (Table 3:2). Blue wildebeest and tsessebe use of flooded areas were nested within that of zebra and buffalo, and all were nested within lechwe (Figure 3:3). This pattern was most evident in 2014, but nestedness values did not differ significantly between any of the years (Table 3:2).

Niche overlap for the observed networks in the years 2004, 2010, and 2014 was significantly higher than expected based on random matrices (Table 3:3). There was an increasing trend in niche overlap from 2003 to 2014; however, the differences in niche overlap between the years were not significant (Table 3:3).

From low hydroperiods (2003 and 2004) to high hydroperiods (2010 and 2014), there was a decline in areas that were not flooded and areas that were flooded for 4 months or less, hence both dry grassland and seasonally flooded grassland areas decreased in size. At the same time, there was an increase of areas flooded between 6 and 8 months, which indicated an increase in seasonally flooded sedgeland areas (Figure 3:4).

Discussion

In 3 of the 4 study years, which correspond to the drier years in the flood cycle, the networks showed a combination of nestedness patterns, where selective grazers used a subset of the resources used by more generalist grazers, and modularity, where grazers can be separated into different groups based on their patterns of resource selection. While this may seem contradictory, the presence of both patterns within a grazing guild is not unique, and is important in contributing to the stability of the guild (Miranda et al. 2014). The modular pattern, where grazers are separated into discrete groups of similar resource use, may reflect morphological differences (i.e., incisor-breadth areas arcade, Gordon and Illius 1988) or physiological differences (i.e., body size and digestive system, Demment and van Soest 1985, Kramer and Prins 2010).

Species of similar size have similar energy requirements; larger grazers, which have larger gut capacity and slower metabolic rate, require a combination of both high-quality forage and lower quality forage of large quantity to fulfil their nutrient requirements, while smaller grazers with higher metabolic rates require small quantities of high-quality forage (Demment

and van Soest 1985, Kramer and Prins 2010). Similarly, grazers with narrower mouths can be more selective for high quality plant species or parts, while grazers with wider mouths are generally less selective and can ingest larger quantities of food in a shorter amount of time (Gordon and Illius 1998). These two factors interact to ensure that multiple species can exist within the same guild by exploiting different structural, temporal and spatial aspects of grazing resources (Cromsigt et al. 2009, Macandza 2009, Venter et al. 2014). However, in some cases, for example when high quality resources become available at the same time, as is the case with the green flush of grazing after the flood, generalist grazers may be attracted to high-quality grazing generally selected for by smaller specialist grazers, resulting in a 'nesting' of resource use. Therefore, modularity seeks to divide resource use, while nestedness can cause convergence of resource use (Miranda et al. 2014).

Lechwe were highly modular in that they had the ability to make the most use of high flood-duration areas. This reflects the morphological and behavioural adaptations of this species that allow them to use areas with higher levels of water compared to the other grazers (Skinner et al. 2005). Lechwe feed on grasses and sedges in floodplain areas or along the floodplain edges and are seldom found further than 2 or 3 kilometres from permanent water into which they can flee to escape predators (Biggs 1979; Williamson 1990). Their small incisor arcade and lower body size also enables them to select for high quality parts of sedges, and the new flush of grazing to meet higher energy requirements (Williamson 1990, Kramer and Prins 2010). However, when it came to use of areas flooded for different frequencies, most species were 'nested' within lechwe, indicating that lechwe were more generalist in their choice of flooded areas.

The medium–sized grazers, blue wildebeest and tsessebe, were the most specialized in their use of flooded areas (i.e., used only a narrow range of flood-duration categories), mainly

utilizing dry areas and areas flooded for less than 3 months. Both species have low premolars, which allow for intake of short- and medium-sized grasses, and high enamel crowns, which confers resistance to tooth wear that may be caused by ingesting sand particles while feeding close to the ground (Codron et al. 2008). Both species thus favour short to medium grasses of high nutrient quality to fulfil their nutritional requirements (Wilmshurst et al. 1999; Dörgeloh 2006). As floods recede, the short new grass shoots following the receding water is the ideal grazing resource for both species, both in terms of height and nutritional quality. These species occurred in the same module due to similar requirements, but as they were most specialist in their use of flooded areas, their resource use was nested within lechwe as well as the larger-bodied zebra and buffalo.

Zebra were grouped with tsessebe and blue wildebeest during the low-hydroperiods years (2003 and 2004), while being grouped with buffalo during the high-hydroperiods years (2010 and 2014). As large-bodied hind-gut fermenters, zebra have the ability to utilize relatively poor-quality forage to meet their nutritional requirements (Duncan et al. 1990; Kleynhans et al. 2011; Owen-Smith et al. 2015). Although hind gut fermenters are less efficient than ruminants at extracting nutrients, faster throughput rates allow for increased intake of forage to compensate for it (Duncan et al. 1990). As flood levels increased and the availability of seasonally flooded grasslands decreased, zebra were thus able to shift to more-frequently flooded areas, in response to increased competition for the limited short seasonally flooded grasslands. Similarly buffalo, due to their large body mass, wide muzzles, and pronounced premolars, can utilize medium to high grasses of lower quality (Codron et al. 2008) and therefore, during years of high flood, when the extent of seasonally flooded grassland is reduced, they, like zebra, are capable of making use of a wider range of flooded areas than other grazers (Bennitt et al. 2014).

In corroboration of our hypotheses, all grazers showed increasing overlap in resource use, or higher nestedness and lower modularity, during years of high flood. As the seasonally flooded grasslands are the main dry season resource, competitive exclusion is more likely during high flood years when this resource is diminished (Arsenault and Owen-Smith 2002). While generalist grazers, such as buffalo and zebra, were capable of increasing the range of flood duration categories used to compensate for diminishing seasonal grazing, increased competition for floodplain grasslands may have a more detrimental effect on specialized grazers, such as the tsessebe and wildebeest, which due to morphological constraints rely heavily on shorter seasonally flooded grassland grasses (Demment and van Soest 1985, Kramer and Prins 2010). Increased competition from superior competitors, the generalist grazers, may be an explanation for the recent decline of tsessebe and blue wildebeest in the Okavango Delta (Chase 2011, Arsenault and Owen-Smith 2002). Red lechwe, due to their morphological adaptations to swamp and 'generalist' use of flooded areas, would be more capable of coping with higher floods. However, they exhibited a niche shift in modules from areas flooded from medium to long duration, to modules of only long duration during high floods. This could potentially indicate a niche shift to avoid competition (Brew 1982), which may be detrimental to nutrient intake and result in population declines over a longer timescale. Network analysis is thus a useful tool for investigating intra-guild patterns of resource use, determining how these relationships change under different conditions of resource availability, and identifying key resources whose depletion may change system dynamics. In this study, declining availability in short duration flooded areas caused decreasing modularity and increased nestedness across the grazing guild, pointing to increasing levels of competition. Grazers which specialized on this resource responded with population declines and niche shifts, which further points to competitive exclusion by generalist larger-bodied grazers, which appear to be more resilient to ecological change.

This study also points to the fact that decreased heterogeneity of available resources can thus lead to significant changes in grazing guild networks (Cromsigt and Olff 2006; Venter et al. 2014), with negative consequences for some species. The change in flooding in the Delta no doubt exerts a considerable influence on the structure and interactions of the grazing community (Lindholm et al. 2007). Both climate change and anthropogenic water offtake that alter flooding patterns are therefore likely to have a significant influence on the grazing community in the Delta in the future. Upstream anthropogenic offtake, specifically damming in the catchment area in Angola, is likely to result in increased drying, particularly of the productive seasonal floodplains which are important for maintaining herbivore densities and diversity (FAO 1997; Milzow and Kinzelbach 2010). The reversion of these floodplains to woodland communities would result in a decrease in herbivore biomass, and a system that favours browsers over grazers (McCarthy and Ellery 1998; Murray-Hudson et al. 2006). The predicted changes under different climate change scenarios are even more extreme; with higher temperatures and decreased rainfall, all scenarios show that after an initial wetting period, the Delta is likely to undergo significant drying, leading to decreased heterogeneity in floodplain habitat with similar negative effects on seasonal floodplains and grazing herbivores (Cromsigt and Olff 2006; Murray-Hudson et al. 2006).

One way to alleviate density-dependent pressure for grazing herbivores resulting from climate change or water offtake may be through changes to the southern buffalo fence. This fence was erected around the southern and western part of the Delta in the early 1980s, to control the transmission of foot-and-mouth disease from wild buffalo to domestic cattle (Campbell 1976). In systems where resource availability is variable, certain portions of a population may migrate to different areas in search of better grazing, or to avoid predators (McNaughton 1976; Taylor and Norris 2007). In the eastern Delta, portions of the buffalo and zebra populations migrate, particularly those herds that are concentrated on the Delta's

periphery (Bennitt 2012; Bartlam-Brooks et al. 2013). In the western Delta, however, herds of buffalo and zebra are largely impeded by the fence to the south (K. Burger, personal observation), and to the east by large amounts of water, particularly in wetter years. This may exacerbate density-dependent effects of large herds through trampling and over-grazing of resources, which may be particularly detrimental to small species (Fritz et al. 2002; Cassidy et al. 2013). In addition, this confinement may increase vulnerability to predation as well as local bushmeat poaching along the western side of the fence (Rogan et al. 2017). Currently, the cumulative effects of bushmeat hunting and predation may already exceed population growth rates of certain herbivore species, further contributing to their decline (Rogan et al. 2017). Moving the southern buffalo fence to incorporate a larger area, or creating potential corridors for animal movement, may be a necessity for maintaining herbivore densities in the western Delta in the future.

Besides its applicability in the Delta, this study may serve as a baseline for the implications that climate change or water offtake might have on mammalian herbivores in other alluvial floodplain ecosystems. Indeed, evidence of herbivore declines because of damming and consequent drying of floodplains has been observed in both the Zambezi Delta (Beilfuss et al. 2001) and the Kafue floodplains (Chansa and Kampamba 2009). Climate change, particularly changes in rainfall, also may influence lake shore systems such as Lake Manyara, Tanzania, or Matusadona National Park, Zimbabwe, where large herbivores such as buffalo depend on the flush of grasses produced as the lakes shrink in the dry season (Taylor 1985). As these dry season refuges are likely the limiting factor for herbivore abundances in the region, these ecosystems need to be given regional and international conservation priority (Fynn et al. 2015).

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Figure 3:1. Representation of modules for each year in herbivore-flooding interaction networks. Numbers indicate the average flood duration of the previous three years in months. Boxes indicate the modules identified, and squares within the boxes indicate interaction between herbivores and flooded areas. The darker shading indicates higher interaction frequency.

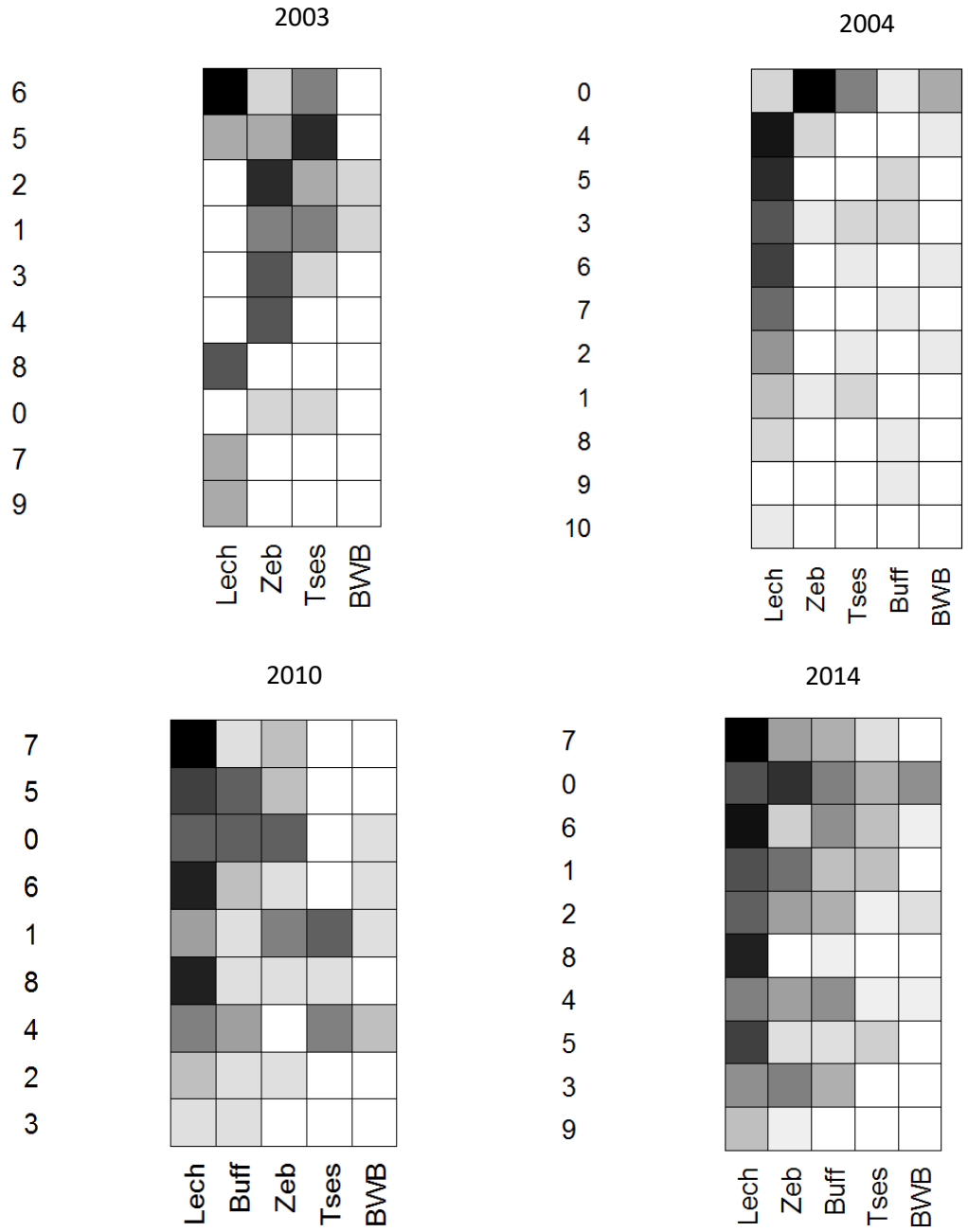


Figure 3:2. Matrices showing the nestedness patterns in each year for herbivore-flooding interaction networks. Matrices are re-arranged where interactions in rows and columns from left to right and top to bottom are arranged in ascending order of interaction frequency. Numbers indicate the average flood duration in months over the last three years. Darker shading indicates higher interaction frequency.

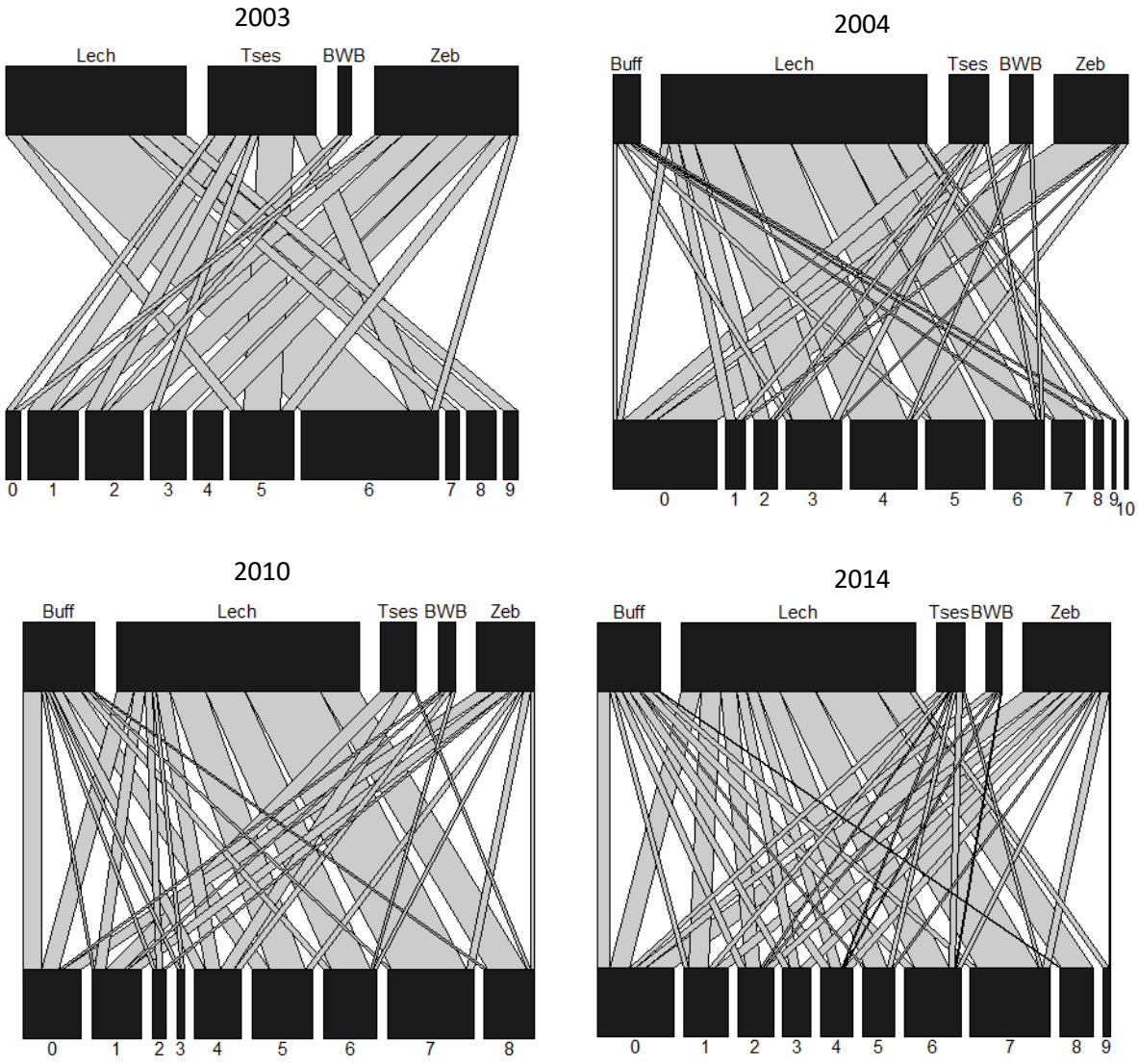


Figure 3:3. Bipartite networks showing the relationship between herds of herbivores (top bars) and flooded areas (bottom bars). The numbers on lower bars represent the average flood duration in months for an area over the last three years. The width of the bars is proportional to the number of interactions between herbivores and different flooded areas, reflecting which species are more generalist or specialist in their use of flooded areas. The width of the joining links is proportional to the frequency of interactions between herbivores and the flooded areas, with the thickest links indicating which flooded areas are preferred by each species.

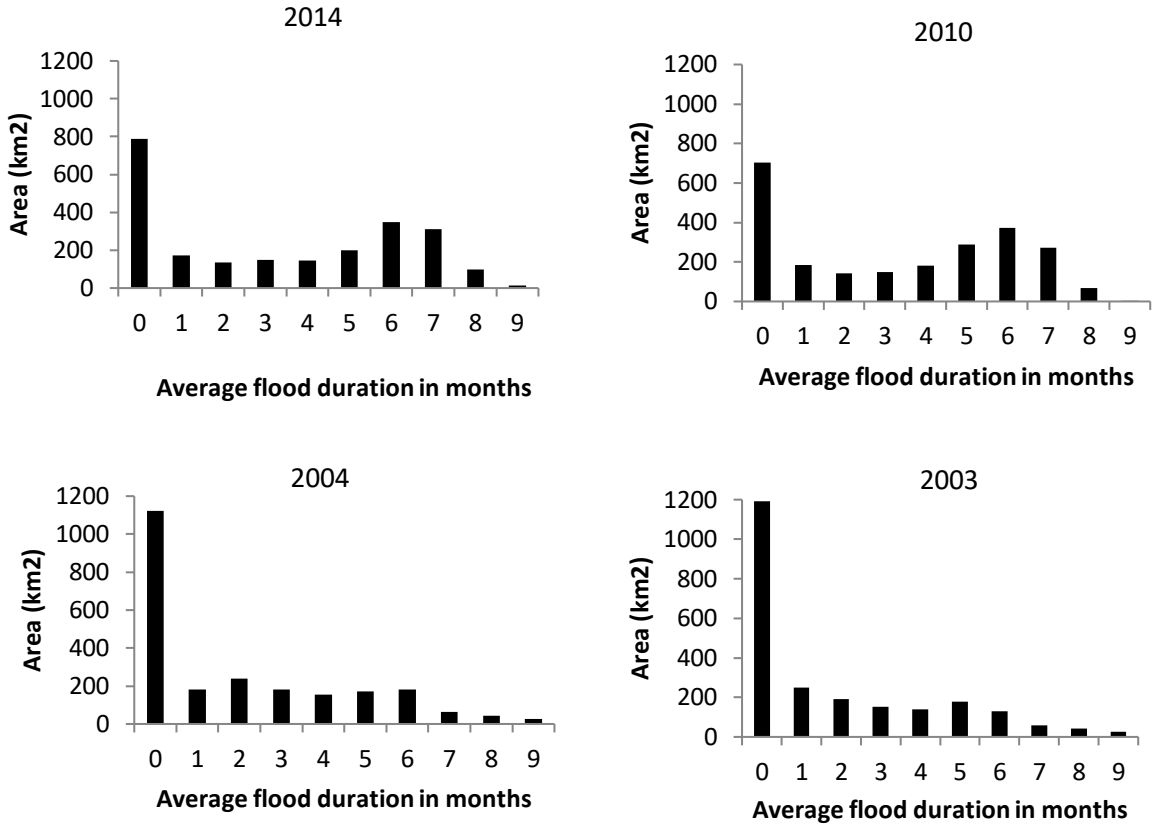


Figure 3:4. Areas, in square kilometres, covered by the flood duration in months averaged over the preceding three years.

Table 3:1. Modularity (Q) index values of observed herbivore flooding networks for each year.

				Confidence limits[3]	
Year	Modularity	z-score[1]	p-value[2]	Lower 95%	Higher 95%
2003	0.402	6.03	<0.001	-0.2786	-0.1344
2004	0.306	8.58	<0.001	-0.2134	-0.1339
2010	0.248	5.32	<0.001	-0.1520	-0.0680
2014	0.200	7.75	<0.001	-0.1386	-0.0833

[1]Z-scores indicate the difference between Q in observed networks and the mean Q from null model distributions

[2]p-values below 0.05 indicate a significant difference in the modularity of observed networks compared to null distributions

[3]The lower and higher 95% confidence intervals represent the distribution of D-values in the difference matrix calculated for each year. Where these intervals overlap, there is no significant difference in the modularity in the networks between years.

Table 3:2. Nestedness (WINE) values of observed herbivore flooding networks for each year.

				Confidence Limits[3]	
Year	WINE	z-score[1]	p-value[2]	Lower 95%	Higher 95%
2003	0.213	1.28	0.1004	-0.1101	0.5361
2004	0.673	4.17	<0.001	0.3445	0.9822
2010	0.559	3.26	<0.001	0.2151	0.8953
2014	0.738	4.59	<0.001	0.4379	1.0629

[1]Z-scores indicate the difference in nestedness between observed networks and the mean nestedness values from null model distributions

[2]p-values below 0.05 indicate a significant difference in the nestedness of observed networks compared to null distributions

[3]The lower and higher 95% confidence intervals represent the distribution of D-values in the difference matrix calculated for each year. Where these intervals overlap, there is no significant difference in the nestedness in the networks between years.

Table 3:3. Horn-Morisita indices of niche overlap in observed and null model herbivore flooding networks for each year. Index values range from zero to one, zero indicating no overlap and one indicating complete overlap. Each year, niche overlaps in observed networks were tested against niche overlap in null model distributions to test for significance.

					Confidence levels[3]	
Year	Observed	Null	z-score[1]	p-value[2]	Lower 95%	Higher 95%
2003	0.379	0.302	0.95	0.1719	-0.2003	0.1208
2004	0.484	0.254	3.17	<0.001	-0.3548	-0.0692
2010	0.512	0.399	1.61	0.054	-0.2282	0.0353
2014	0.672	0.441	3.79	<0.001	-0.3334	-0.0936

[1]Z-scores indicate the difference in niche overlap between observed networks and the mean niche overlap values from null model distributions

[2]p-values below 0.05 indicate a significant in niche overlap of observed networks compared to null distributions

[3]The lower and higher 95% confidence intervals represent the distribution of D-values in the difference matrix calculated for each year. Where these intervals overlap, there is no significant difference in the niche overlap in the networks between years.

Chapter 4 - Seasonal resource selection by sympatric grazers in the Okavango Delta, a flood-pulsed grazing system.

Abstract

Resource selection by grazing herbivores is driven by spatial and temporal variability of available resources such as grass greenness, soil nutrients, rainfall and drinking water. In the Okavango Delta, however, the presence of a unimodal flood pulse during the dry season further influences grazing availability and water distribution. I therefore used resource selection functions to examine resource selection, at the home range scale, by three sympatric grazing herbivores, buffalo (*Syncerus caffer*), zebra (*Equus burchelli*) and red lechwe (*Kobus leche*) in the wet season (December to March), and the dry season, which was split into early flood (April to July) and late flood (August to November) seasons. Results revealed that all grazers were dependent on the flood as a source of water, as well the green flush produced in floodplains and adjacent habitats by receding flood water during the dry season. While grass greenness, measured by Normalized Difference Vegetation Index (NDVI) and used as a proxy for grazing quality, predicted resource selection by buffalo, it did not predict resource selection by zebra and red lechwe. As hind-gut fermenters, I posit that zebra select grazing areas based not only on grass quality, but also quantity, which may not always coincide with peak NDVI values in each season. While zebra and buffalo appeared to be influenced by rainfall during the wet season, lechwe remained in floodplain habitats. The lack of response to rainfall and NDVI values across the landscape for red lechwe are likely due to their adaptations as wetland specialists. Habitat selection varied amongst species in the wet and early flood seasons, but in the late flood seasons, all species showed dependence on floodplains and adjacent habitats, likely as a result of the green flush caused by receding floodwater or higher water table. While differences in body size, gut morphology and feeding strategy allow for divergence in habitat and resource use in the wet and early flood season, the convergence of resource use in the late flood season indicates that this is the limiting season for grazers in the Okavango Delta. Future changes to the Okavango Delta resulting from climate change or anthropogenic water offtake may therefore threaten the balance within the grazing guild during this season in the future.

Keywords: resource selection functions, NDVI, buffalo, zebra, lechwe, Okavango Delta, home range

Introduction

The distribution of large grazing herbivores is influenced by numerous biotic and abiotic factors across the landscape (Senft et al. 1987, Bailey et al. 1996, Cromsigt and Olff 2006). Factors such as climate, topography, forage quality and quantity, availability of surface water, vegetation cover for resting or hiding and the distribution of predators or competitors can all influence the movements of large herbivores (Fritz and Duncan 1994, Bailey et al. 1996, de Leeuw et al. 2001, Redfern et al. 2003, Smit 2011). Furthermore, these resources exhibit considerable spatial and temporal heterogeneity in quantity and distribution, and herbivores must adjust to these changes and select resources accordingly in order to maximize individual fitness (Bailey et al. 1996, Cromsigt and Olff 2006, McLoughlin et al. 2007). In order to account for this heterogeneity, the selection of resources occurs within an assortment of ecological hierarchies which aim to systematically incorporate resources required to rest, breed and meet nutritional requirements (Senft et al. 1987, Johnson 1980, McLoughlin et al. 2007). Resource selection therefore takes place at various scales from a species geographic range (first-order), to selection of home ranges within a landscape (second-order), to the selection of habitats and resources within home ranges (third-order), to the selection of specific foraging patches (fourth-order; Johnson 1980).

The biotic and abiotic factors which influence these scales therefore determine the distribution of animals throughout the landscape, both temporally and spatially (Turchin 1999). In the extant conservation environment, geographic ranges of species are often limited to protected areas, rendering first and second order selection null and void due to natural or manmade barriers which limit movement (Redfern et al. 2003, Boone and Hobbs 2004, Boyce 2006). In these scenarios, selection of resources at the home range scale is most informative for making conservation and management decisions, as the home range is the minimum space required by species in order to survive and reproduce (Burt 1943). For ungulates,

selection of resources at the home range scale is influenced by factors such as habitat type, distance to water, vegetation quantity and quality or risk of predation (Senft et al. 1987, Redfern et al. 2003, Hopcraft et al. 2005). Selection of these resources however, are tempered by a number of influences, including body size constraints which determine food preferences, vulnerability to predation, and thermal tolerances (McLoughlin and Ferguson 2000, Macandza 2009, Owen-Smith and Goodall 2014), diet selection which may influence dependence on water (Redfern et al. 2003) as well as seasonal cycles which introduce temporal variation to resource availability (Boyce 2006).

In wetland environments, annual flood pulses result in a highly dynamic system (Ramberg et al. 2006). Consequently, wetlands experience large seasonal variation in the abundance and distribution of grazing resources (Fynn et al. 2015). In the wet season, rainfall and the resulting distribution of green grass play a large role in habitat selection for various species (Owen-Smith 2008, Bennitt et al. 2014). In the dry season, however, herbivores converge on the floodplains as they make use of the green flush of vegetation resulting from receding flood water (Fynn et al. 2015). This green flush is a critical dry season resource for all grazers and has a large influence on the population densities of various species within the wetland system (Owen-Smith 2002, Fynn et al. 2015). In addition to changes in the quantity and quality of grazing, grazers are limited by the distribution of water (Redfern et al. 2003). While rainfall fills ephemeral pans in the wet season, in the dry season, grazers must rely on the floodwaters, restricting their movement, and by extension, their choice of habitat (Bennitt et al. 2014). Understanding how resources drive herbivore distribution in a particular environment is important for large herbivore management and conservation (Smit 2011).

The aim of this chapter is to determine the seasonal selection of resources of three sympatric grazing herbivores at the home range scale, namely buffalo (*Syncerus caffer*), zebra (*Equus burchelli*) and lechwe (*Kobus leche*) in a protected wetland environment, the Okavango Delta. These analyses were conducted using resource selection functions (RSF), which describe the probability of resources being used in relation to available resources (Boyce et al. 2002, Manly et al. 2002), helping us to pinpoint which features are selected for, or avoided (Koper and Manseau 2012). I expected:

a. Buffalo, zebra and lechwe habitat selection to diverge during the wet season but converge on floodplains and adjacent habitats during the early and late dry season.

b. All grazers to select areas the highest available grazing quality, i.e. areas with the highest greenness (using NDVI as an index), during all seasons.

c. Resource selection of all species to be positively related to rainfall during the wet season.

d. As water-dependent species, buffalo and zebra will be dependent on flood water in the early and late flood season only, while lechwe will be dependent on flood water in all seasons

Methods

To determine resource selection, a "used versus available" design was utilized (Boyce et al. 2002, Manly et al. 2002), and a Design III protocol followed (Manly et al. 2002) using GPS data obtained from collars fitted to individual animals. Resource selection functions were calculated per season in order to account for temporal variability in resource availability (Nielsen et al. 2003). In the Okavango Delta, flooding patterns, along with rainfall, play an important role in the availability of resources for grazing herbivores (Chapter 3; Bartlam-Brooks et al. 2013, Bennitt et al. 2012). Consequently, data was divided into three seasons:

the early flood season (April to July), when flood waters arrive from Angola and fill up the Okavango Delta, the late flood season (August to November), the dry season when flood waters recede and leave a green flush of vegetation, and the rainy season (December to March), when most of the local rainfall occurs resulting in fresh growth (Bennitt 2012). In order to examine third-order resource selection, which analyses the use of resources within the home range (Johnson 1980), for each individual, I constructed 100% minimum convex polygons using the *adehabitatHR* software package (Calenge et al. 2015) in R (R Core Development Team 2014). Minimum convex polygons (MCPs) create a polygon including all used locations, with the shape of the polygon determined by connecting the outlying data points in such a way as to include all data but minimize the size of the polygon. While MCPs have been criticized as being inaccurate for estimating true home range size, and more advanced methods such as kernel density isopleths and local convex hulls are more accurate, the broad classification of home range use afforded by MCPs allows for inclusion of areas in the home range which are present, but not selected for (Manly et al. 2006). To include unused available habitat, a buffer equivalent in size to the average daily distance travelled by each species, was created around each home range (Klar et al. 2008). For individuals whose home ranges bordered the southern buffalo fence, the fence line was used as a cut-off. To represent 'available' habitat points, for each used location, three random locations were generated for within each home range, including the buffer zone, for each individual. These analyses were conducted in ArcMap 10.3 (ESRI 2013). All predictor variables were sampled for both used and random locations.

GPS collars

In order to obtain the geolocation of each species over time, individuals of the sample species were tranquilised using darts and GPS collars attached. GPS collar data was obtained from

the herbivore research programme conducted under Elephants Without Borders [3](EWB). All darting operations by EWB were conducted by a registered veterinarian. All animals were darted from a helicopter during the dry season, in the early morning or late afternoon to minimize thermal stress on animals during capture. A fixed-wing aircraft was used as a spotter to locate suitable breeding herds of each species, after which the helicopter was called in for darting. In each herd, an adult female in good condition, and without young at foot, were chosen to be collared as representatives of the breeding herds. Individuals were all fitted with an Africa Wildlife Tracking [4]GPS enabled satellite tracking collars, which also house a VHF transmitter to ensure retrieval. Collars were manufactured to the specifications of each species and did not exceed the recommended weight for collars (<2% of total body mass). GPS collars recorded the geolocation for each species every 4 hours. In total, 7 adult female buffalo, three adult female red lechwe and three adult zebra were collared during the study, for an average of 18 months each, from the early flood season of 2013 to the wet season of 2015.

Covariates

Normalized Difference Vegetation Index (NDVI)

As an indication of vegetation quality in the area, Normalized Difference Vegetation Index (NDVI) derived from Moderate Resolution Imaging Spectroradiometer (MODIS) imagery were downloaded from NASA's Terra and Aqua satellites (http://glcf.umd.edu/data/ndvi/ and https://earthexplorer.usgs.gov/). This imagery has 250 m spatial resolution and consists 16-day composite images. NDVI is calculated from the red and near infrared bands of satellite imagery and has a linear relationship with the amount of photosynthetically active radiation captured by plants (Arsar et all. 1984, Sellers 1987). NDVI can thus be used as an index of

[3] *Elephants Without Borders, P.O. Box 682, Kasane, Botswana*
[4] (*https://www.awt.co.za)*

vegetation quality and quantity across the landscape, and values range from 0 (low productivity) to 1 (high productivity; Anderson et al. 2010, Ryan et al. 2012). Following calendar dates, two 16-day composite images were selected to represent NDVI values for each month of the year. All pixels which were classified as cloud from NDVI quality files were changed to no data pixels and thus excluded from the analysis. Monthly NDVI values were thus derived from averaging the two composite images for each month. Monthly NDVI values were then averaged across season to obtain seasonal NDVI values.

Rainfall

Rainfall influences herbivore habitat selection in two ways: firstly, by producing spatial and temporal variation in vegetation productivity, and secondly, by determining the distribution of available surface water for drinking (Dunham et al. 2004, Sinclair et al. 2007, Smit 2011). To represent rainfall, Tropical Rainfall Measuring Mission (TRMM3B42 version 7, http://mirador.gsfc.nasa.gov/) daily rainfall data, with a spatial resolution of 27 km, were acquired to generate cumulative monthly rainfall estimates. TRMM3B42 data has been used in previous studies to represent rainfall in the Okavango Delta as well as Makgadikgadi Pans National Park and proved fairly accurate compared to local rain gauges (see Bartlam-Brooks et al. 2013). To get an index of seasonal rainfall, monthly rainfall estimates were then combined to produce an average monthly rainfall per pixel for the season.

Tree cover

Tree cover is an important indicator of habitat use for herbivores, both to provide shelter and as an influence of vulnerability to ambush predators such as lion, *Panthera leo,* (Hopcraft et al. 2005, Valeix et al. 2009). Tree cover was estimated from the Vegetation Continuous Field (VCF) collection, which is derived from MOD44B V006 Moderate Resolution Imaging Spectro-radiometer sensor onboard NASA's Terra Satellite

(https://lpdaac.usgs.gov/). This data has 250 m spatial resolution and provides an estimate for tree cover between 0 and 100%.

Distance to floodwater

While in mesic savannahs, surface water availability in the dry season is determined by rainfall (Redfern et al. 2003, Owen-Smith 2008), the seasonal floods in the Okavango Delta provide surface water at the height of the dry season and may have a large influence on seasonal habitat selection, particularly for water-dependent species (Bennitt et al. 2014). Distance to flood water was used as a covariate in the early and late flood season, when other ephemeral water sources such as pans are likely to dry up. To determine the extent of the flood, MODIS MOD09Q1 (https://lpdaac.usgs.gov/data_access) data was used to distinguish between wet and dry cells using a band 1 threshold classification (see Murray-Hudson et al. 2014), and processed flood maps were acquired from the Okavango Research Institute. This MODIS imagery has a spatial resolution of 250 m and consists of 8-day composite images. These 8-day images were combined for each month, and monthly images combined to produce a seasonal flood extent. Pixels which were flooded for more than half of the season were classified as wet to produce an average flood-line. The distance was then measured from each used location and random location to the centre of the closest flooded pixel to produce distance to flood water values for each used location and random location.

Habitat type

Habitat maps of the area were obtained from the Okavango Research Institute (Ringrose et al. 2003). The habitat raster consisted of 30 metre resolution pixels, each classified as one of seven functional habitat types, namely 1) shrubbed grassland with sage bush, 2) shrubbed woodland with mixed mopane, 3) treed shrubland with *Vachellia,* 4) swamp vegetation with fringing emergents, 5) dry floodplains and island interiors, 6) shrubbed woodland of riparian

zones and 7) shrubbed grassland on former floodplain. Habitat type was sampled as the habitat type present at each used and random location.

Data analysis

A preliminary analysis for habitat selection was conducted for each species in each season using the Manly-Chesson Selectivity Index (Manly et al. 1972, Chesson 1978). This is an index of habitat selection in relation to availability and is calculated by dividing the proportional use by the proportional availability of habitats in each home range. This produces a value of >1 if habitat is selected, a value close to 1 if use is in proportion to availability, and a value of <1 if it is avoided. Resource selection function models were estimated using generalized linear mixed models in R with a binomial error structure, with used points coded as '1' and unused points coded as '0' (R Core Development Team 2014). Mixed models allow the specification of individual animals as random effects, which helps to account for variation in the data as a result of individual behaviour as well as uneven sample sizes between individuals (Gillies et al. 2006). In addition to individual animal, year was also used as a random effect term to account for temporal variance in resource availability in different years (Boyce 2006). A series of nine or 10 candidate models were constructed for each species in each season, depending on what was believed to be most biologically meaningful. Models were compared using Aikaike's information criterion for small sample size (AICCc), and models with the highest model weights were selected as the best models for each animal for each season (Burnham and Anderson 2002). All statistical analyses were conducted in R (R Core Development Team 2014). Mixed models were conducted using the *lme4* software package (Bates et al. 2014) and model comparison using the *MuMIn* software package (Barton 2013).

Results

Buffalo, lechwe and zebra showed clear seasonal habitat preferences between the early flood, late flood and wet seasons (Figure 4:1, Figure 4:2 and Figure 4:3), which was

corroborated by Manly-Chesson selection indices (Figure 4:4). In the early flood season, buffalo selected for shrubland with *Vachellia*, floodplains and dry islands, as well as riparian woodlands. These selection patterns continued into the late flood season, however, there seemed to be an increased selection for treed shrubland with *Vachellia*. In the wet season, buffalo again showed strong selection for treed shrubland with *Vachellia*, but also selected for grassland on former floodplain (Figure 4:4). In the early flood season, zebra selected primarily for mopane and riparian woodlands. In the late flood season, however, zebra moved away from selection for mopane woodland, and selected for floodplains and dry islands in addition to riparian woodland. In the wet season, however, zebra moved away from woodlands and selected primarily grassland habitat on former floodplain (Figure 4:4). Lechwe showed very different patterns of seasonal habitat selection compared to buffalo and zebra. In the early flood season and wet seasons, lechwe showed clear preference for swampland with fringing emergents, and completely avoided the use of shrubbed woodlands and grasslands. In the late flood season however, this selection shifted from swampland with fringing emergents to grassland on former floodplain (Figure 4:4).

Resource selection functions revealed that during the early flood season and late flood season, habitat type, NDVI (vegetation quality) and distance to flood water were important predictors for all three study-species (Table 4:1). Habitat type was an important predictor of used locations for zebra, buffalo and lechwe in both the early and late flood seasons. Distance to flood water had a negative effect on used locations for both seasons, indicating that resource use was concentrated close to the flood water for all three species. For both buffalo and lechwe in the early flood season, resource selection was positively related to high NDVI values, but resource selection for zebra was negatively related to NDVI. In the late flood season, however, only buffalo locations were positively related to NDVI, while both lechwe and zebra locations were negatively related to NDVI.

During the wet season, there was considerably more variation in resource selection by the three grazers. The top model for buffalo resource use included habitat type, as well as a positive relationship with rainfall and NDVI. For zebra in the wet season, used locations were not determined by habitat type, but by rainfall, NDVI and tree cover. Rainfall had a strong positive influence on used locations, and used locations were also positively influenced by tree cover (Table 4:1). NDVI, however, was consistently negatively related to resource use by zebra in the wet season, as it was in the early and late flood seasons. The top model for lechwe resource selection in the wet season included habitat type, distance to flood water and NDVI. Rainfall did not influence lechwe resource selection during the wet season. The number of used locations decreased with an increase in distance to floodwater, indicating that distance to the flood water is an important predictor for lechwe resource selection throughout the year. Resource selection was also negatively related to NDVI values during this period, as it was in the late flood season.

Discussion

Habitat type and water availability in the form of flood water during the early and late flood seasons, and rainfall during the wet seasons, were the most consistent predictors of herbivore resource use across all seasons and across all species. Each species of grazers showed distinct seasonal habitat preferences that were concurrent with body size constraints, water dependence and morphological adaptations (Demment and van Soest 1985, Illius and Gordon 1992, Redfern et al. 2003). All three species consistently selected for floodplain or grassland on former floodplain during late flood season, corroborating our hypothesis that resource use would converge on seasonal floodplains in the dry season. Additionally, during the early flood and wet seasons, the three species showed divergent strategies in habitat and resource selection as expected. Seasonal floodplains are therefore an important bridging resource for grazers during the late flood season (Owen-Smith 2002, Fynn et al. 2015), and the

heterogeneity of habitats in the Okavango Delta is therefore vital in supporting sympatric grazing species (Bonyongo and Harris 2007). It is important to note, that for lechwe and zebra respectively, sample sizes were small (n = 3), and therefore inferences must be interpreted with caution. This study could benefit from follow-up work on these two species within the landscape.

Across all seasons, buffalo habitat selection was positively related to the average seasonal NDVI value, in corroboration with our hypothesis that habitat use would be associated with higher NDVI values. Buffalo are protein limited (Sinclair 1977), and as such require high quality vegetation with high levels of nitrogen. As ruminants, buffalo are able to maximize nutrient extraction from their food through repeated regurgitation and mastication (Fritz et al. 2009). However, as this restricts feeding time, large-bodied animals such as buffalo must compensate by consistently choosing high quality forage in order to meet their energetic requirements (Illius and Gordon 1992). Previous studies on the relationship between faecal nitrogen content, NDVI and buffalo resource selection have shown that there is a strong correlation between higher NDVI values and buffalo resource use, and that peak periods of NDVI translated into peak body condition for buffalo (Ryan et al. 2012). As such, NDVI can thus be used as a fairly consistent predictor of buffalo resource use across the landscape.

However, buffalo are water-dependent, and require large volumes of water on a daily basis (Prins 1996). Buffalo must therefore balance the need for high quality grazing with available water sources. Buffalo movement is restricted to an extent by access to surface water (Redfern et al. 2003), and consequently, buffalo movements followed high rainfall during the wet season, and maintained a short distance to the floodplain edge during the early and late flood season, as expected. However, buffalo selected for a variety of habitats during all seasons. In all seasons, buffalo showed significant selection for *Vachellia* woodlands,

particularly in the wet season. In the rainy season, *Vachellia* woodlands contain grasses with high protein content (Belsky et al. 1994, Dunham 1989), as soil under the canopies naturally have higher concentrations of nitrogen, as well as other macronutrients (Dunham 1989). In similar ecosystems, other large grazers such as elephant (*Loxodonta africana*) also show preference for this habitat during the wet season (Moss et al. 2011). Additionally, shade provided in *Vachellia* woodlands may reduce thermal stress for buffalo, who often rest in the heat of the day (Prins 1996). In the early and late flood seasons, as expected, buffalo select for floodplain habitats and adjacent woodlands. These areas will experience a flush of fresh grass growth resulting from surface flooding, as well as an increase in height of the water table and nutrient deposits that increase vegetation quality (Krah et al. 2005, Ramberg et al. 2006b). Additionally, buffalo are known to feed on sedges and other aquatic species during the late flood season when grasses elsewhere are senescent (Fynn et al. 2015).

Contrary to our expectations, zebra resource-use during all seasons showed an inverse relationship with higher NDVI values. Instead, their movement within the home range was more driven by rainfall in the wet season, and distance to floodplain edge in the early and late dry seasons, which corroborated our expectations for all species. The inverse relationship with NDVI however, concurs with other studies on grazing herbivores, which show that herbivores may 'surf' changing NDVI values (Merkle et al. 2016). This means that instead of selecting for peak NDVI values, zebra follow low to intermediate NDVI values in anticipation of peak greenness (Bischof et al. 2012, Bartlam-Brooks et al. 2013, Merkle et al. 2016). This type of habitat selection, known as the 'green hypothesis', shows that grazers may follow the instantaneous rate of green-up (IRG), a derived NDVI value which peaks at approximately half of the maximum annual NDVI value (Merkle et al. 2016). Previous studies in the Okavango Delta have shown that zebra may either move with this green wave, or at the leading edge of the green wave, anticipating maximum NDVI value by using local rainfall as a cue (Bartlam-

Brookes et al. 2013). Indeed, our RSF models indicate that rainfall was significantly positively related to resource selection during the wet season. In the early flood and late flood seasons, however, the inverse relationship between resource use and high NDVI values may reflect forage selection based on balancing selection for forage quantity as well as quality. As non-ruminants, zebra must spend between 13 and 17 hours a day grazing to prevent a decline in body condition (Duncan et al. 1992). As the peak of the 'green' wave (or IRG) coincides with medium biomass of forage (Merkle et al. 2016), zebra may thus select habitats to maximize their quantity of intake of high-quality grazing. This foraging tactic may apply not only to growth after the rains, but to the green flush produced after receding floods. This is again concurrent with studies on zebra in the Okavango Delta which show that zebra show preference for areas of high forage biomass (Bonyongo 2004). The contrasting response of buffalo and zebra to NDVI may provide some insight into how these two bulk-grazers co-exist, when body weight and incisor-arcade theory predicts that they may be equal competitors (Prins and Olff 1998, Kleynhans et al. 2011). The difference in temporal response to NDVI allows zebras, which are more efficient hind-gut fermenters, to balance intake of vegetation quality and quantity, while immediate response to NDVI allows buffalo to profit from high-protein content of new grass to fulfil higher protein requirements of ruminants (Drescher et al. 2006). In this case divergent digestive strategies allow the two species to make use of different resource patches across the landscape in response to temporal differences in NDVI and rainfall and consequent changes in grass quality and quantity (Fryxell et al. 1991, Cromsigt and Olff 2006, Cromsigt et al. 2009, Venter et al. 2014).

Due to their highly effective gut throughput rate, the selection of areas with high forage biomass appears to carry over into zebra habitat selection during the wet and early flood seasons. In the wet seasons, zebra show strong selection for grassland on former floodplains. Rainfall also shows a strong effect on zebra movement during this period. During the wet

season, grasslands are highly productive, and there is a strong positive relationship between rainfall and above ground net primary productivity (Nippert et al. 2006, Fay et al. 2003, Heisler-White 2008). Indeed, on the eastern side of the Okavango Delta, some zebra migrate away from the Okavango Delta to the grasslands of Makgadikgadi salt pans which have higher mineral and protein content (Brooks 2005, Bartlam-Brooks et al. 2013). In the early flood season, however, zebra appear to select for mopane woodland. While mopane woodland is generally unproductive (Wessels 1999), increase littoral rate after the rainy season can increase productivity and nutrient release in these woodlands (Mlambo and Nyathi 2008), and towards the end of the dry season, biomass in this habitat would have reached a peak. Furthermore, the use of *Vachellia* woodland by large buffalo herds during the wet season may competitively exclude zebra from using this resource during the late rainy season as the floods come in.

Lechwe consistently selected swampland habitat during the early flood and wet seasons. Lechwe are wetland specialists and have developed physical traits such as splayed hooves and large hindquarters which enable them to move easily through the floodplain waters (Kingdon 1997). Additionally, lechwe flee into the water to evade predators (Williamson 1990) and are never found more than a few kilometres from permanent water sources. Contrary to our expectations, and despite their dependence on water, lechwe selected habitats on formerly flooded grassland, further away from the floodplain edge, during the late flood season. This may be a consequence of higher flood levels experienced during the study years as a result of three possible reasons: 1) in high flood years, lechwe may be forced off of smaller islands in the swamps onto the surrounding floodplains (Williamson 1990), 2) increased competition for seasonally flooded grasslands increases after successive years of high flood, and lechwe may be outcompeted by other grazers and forced into adjacent, suboptimal habitats (Chapter 3), or 3) high floods and the lateral water table extends into shrubbed grassland on former

floodplains, resulting in a green flush in this habitat (Ramberg et al. 2006). However, given that buffalo and zebra both select floodplain habitats in the late flood season, the first two scenarios are the most likely explanation.

Given their affinity for water, it is therefore not surprising that distance to flood water is a consistent and strong predictor of used locations throughout all seasons. Interestingly, however, lechwe resource use only showed a positive relationship with NDVI values during the early flood season. This may be as a result of new floodwaters creating a green flush at the ecotone of wet and dry land, and with small incisor breadth, the ability of lechwe to exploit new shoots of vegetation growth while larger grazers such as zebra and buffalo cannot (Illius and Gordon 1992). Contrary to our expectations however, resource use for lechwe was negatively related to NDVI during the late flood season and the wet season, despite expectations that a small-bodied grazer would select for high quality forage (Demment and van Soest 1985, Illius and Gordon 1992). However, as these seasons also coincide with the lowest flood levels, it is likely that resource selection is tempered by vulnerability to predation during these seasons (Radloff and du Toit 2004), and as such distance to the flood water edge is more important. Furthermore, constant access to new shoots at the interface of water and dry land during these seasons, in quantities that may make exploitation by larger species unprofitable, as well as the ability to exploit sedges and other swampland vegetation (Williamson 1990), may allow lechwe to maintain condition during these times.

Understanding the complex interactions between species and the temporal and spatial distribution of their resources is important for conservation planning (Fryxell et al. 2005). This can provide useful information regarding the realized niche of different species within a landscape and help to predict which other areas of the landscape may be important for the conservation of that particular species (Koper and Manseau 2012). Current climate change

scenarios predicted for the Okavango Delta predict drying scenarios which would result in a decrease in the size of seasonal floodplains and the reversion of these floodplains to dryland areas (Murray-Hudson et al. 2006, Milzow et al. 2010). This will have a dramatic effect on the lechwe populations, which select for floodplain and wetland habitats during all seasons. Similarly, there will be increased competition for dry season resources on the floodplains for buffalo and zebra. Previous studies showed that changes in patch size caused by reductions in floodplain size could result in an increase in zebra home range size, and due to the buffalo fence, which constrains further movement, this will result in population decline (Bartlam-Brooks et al. 2013). Future land use and water offtake planning around the Okavango Delta should consider these projected climate change scenarios, to ensure that anthropogenic changes do not exacerbate loss of floodplain habitat, which would have negative consequences for the abundance of local grazing species. As wetland vegetation and succession is deemed to be similar across Africa (Fynn et al. 2015), this information can be used to inform the extent of various wetland habitats required by different grazing species, and how relative changes in the proportions of habitats in wetlands by altered hydrological cycles, caused either by water extraction or climate change, may affect the conservation of these species.

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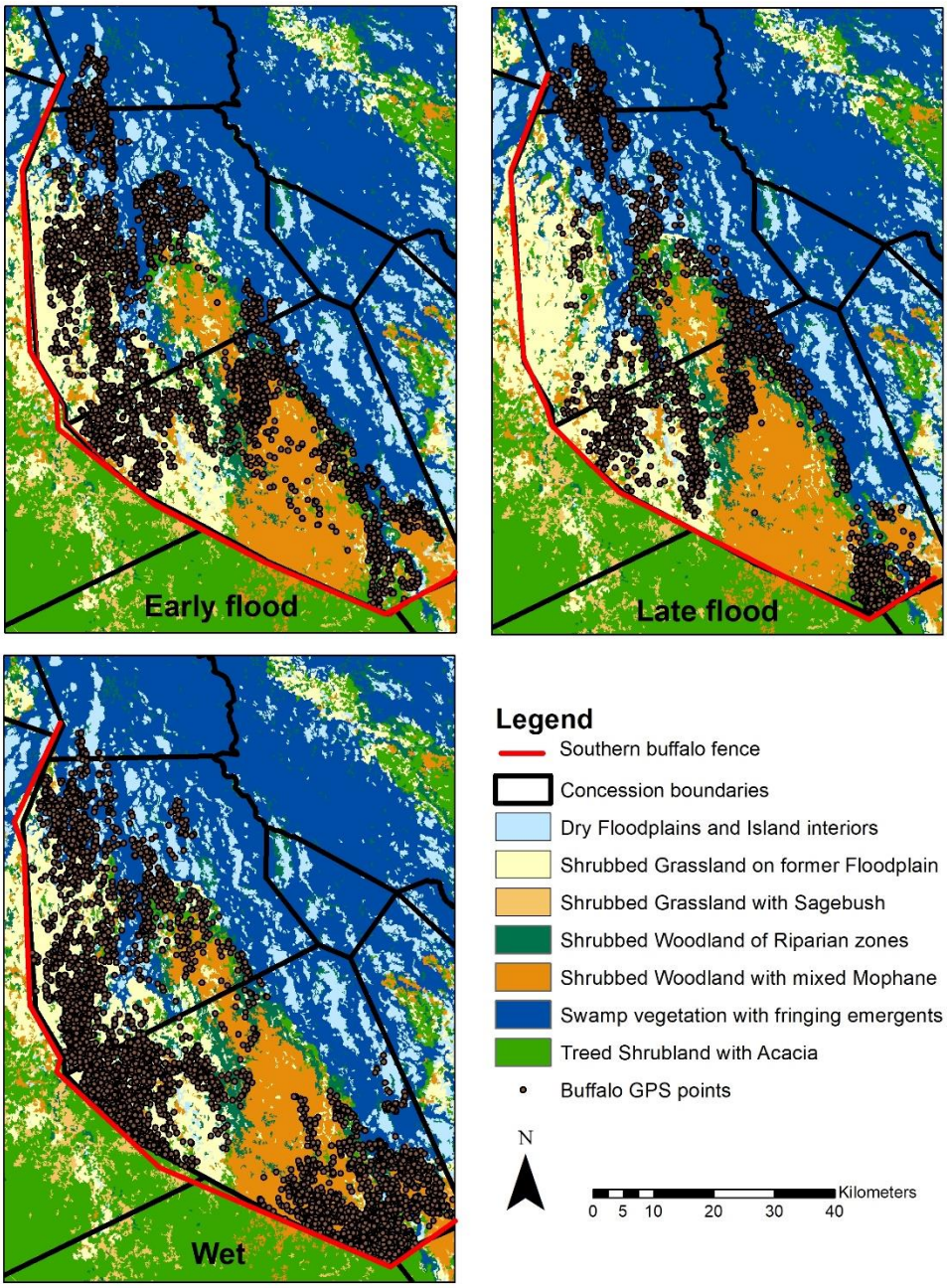


Figure 4:1. Seasonal GPS locations recorded from satellite collars on female buffalo (*Syncerus caffer*) in the western Okavango Delta.

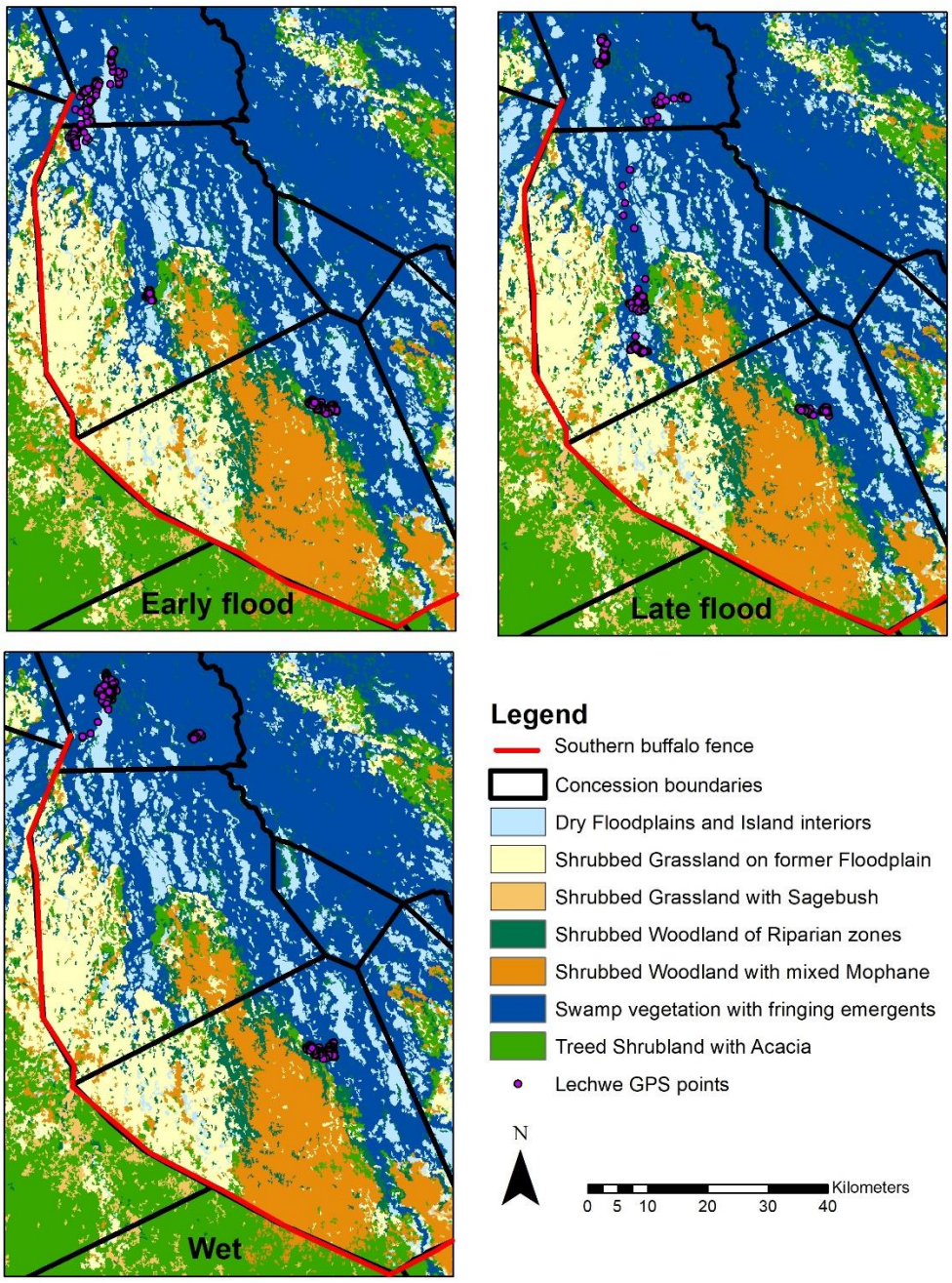


Figure 4:2. Seasonal GPS locations recorded from satellite collars on female lechwe *(Kobus leche*) in the western Okavango Delta.

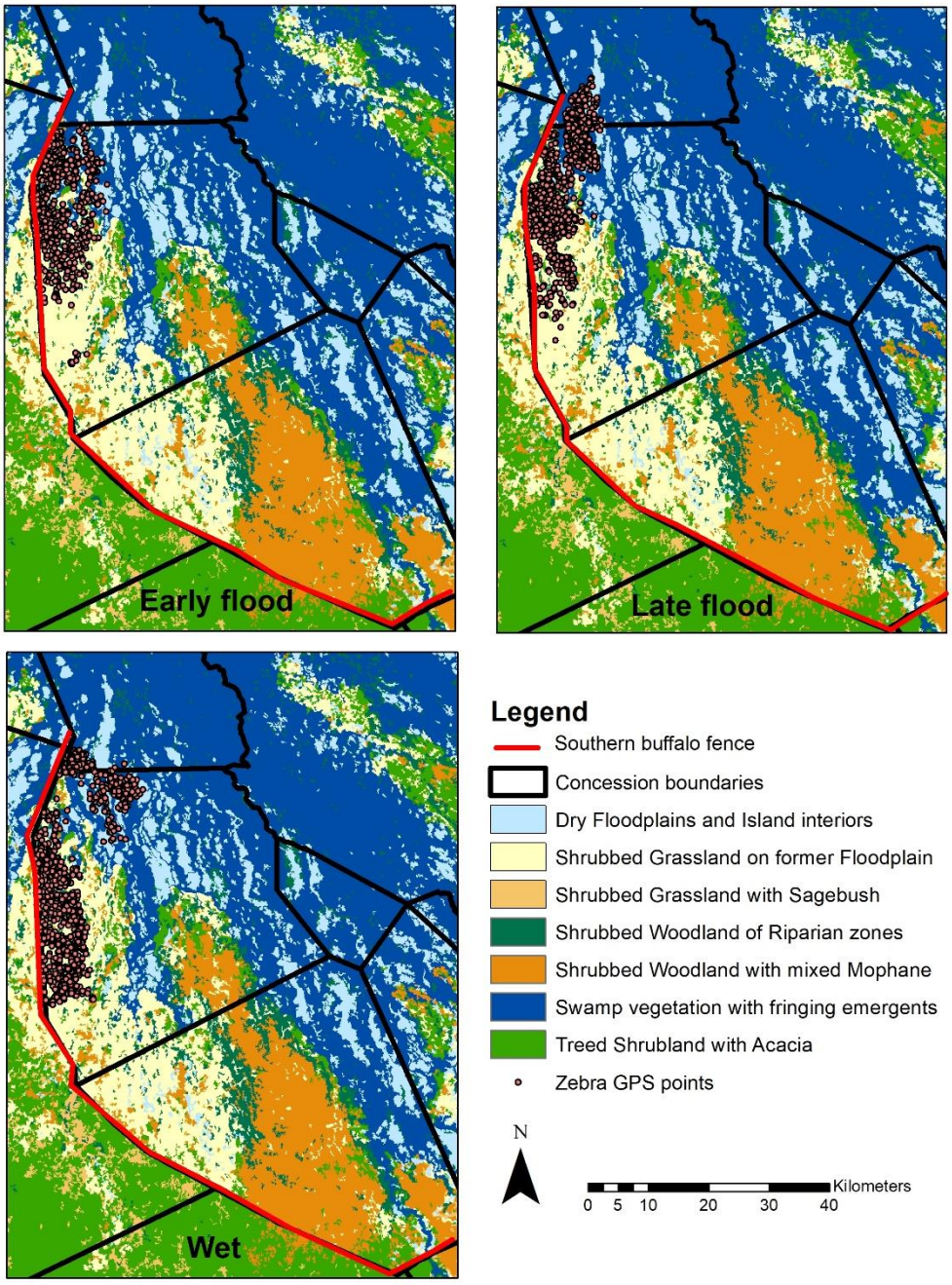
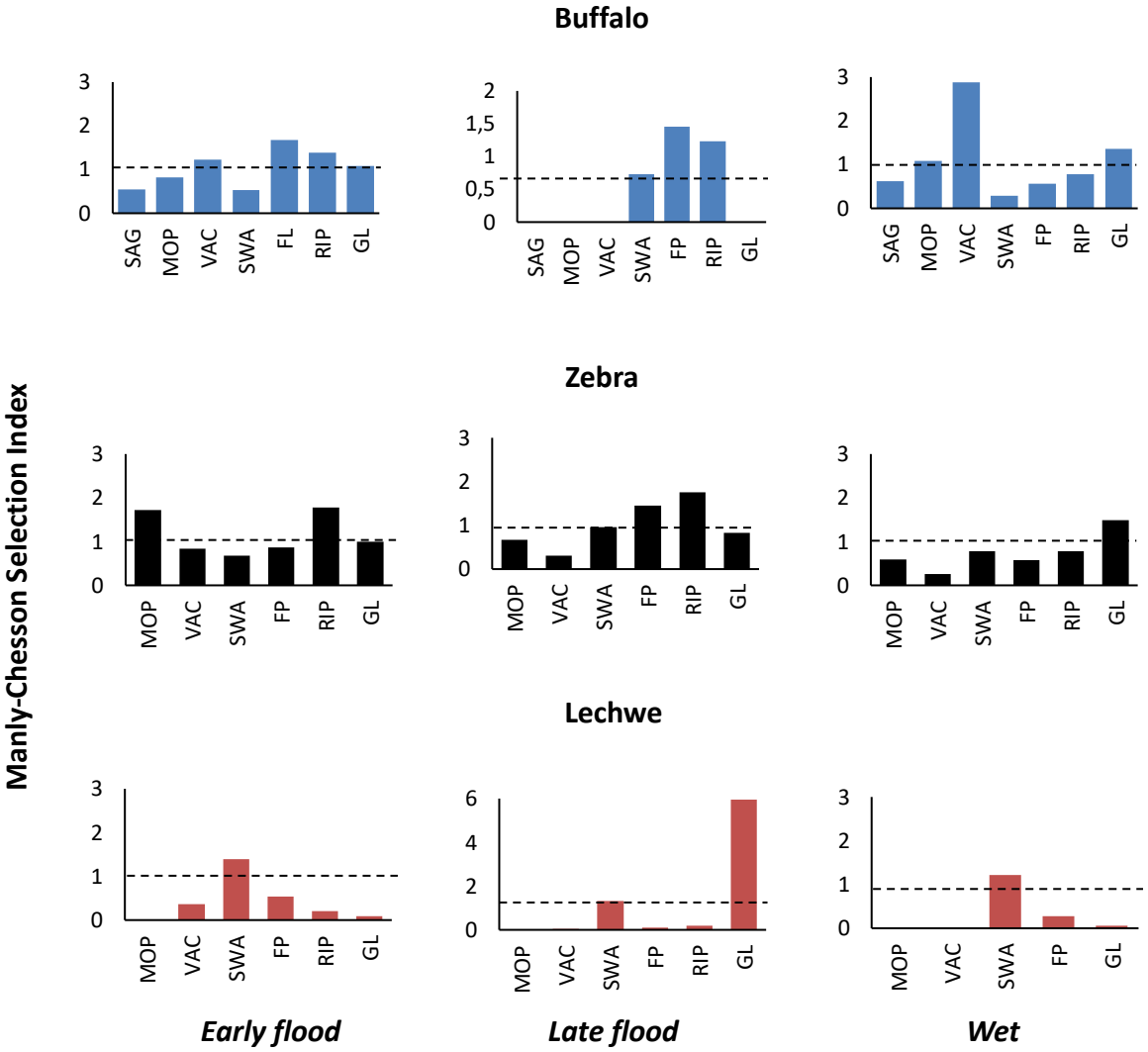


Figure 4:3. Seasonal GPS locations recorded from satellite collars on female zebra (*Equus burchelli*) in the western Okavango Delta.



Habitats
SAG = shrubbed grassland with sage bush,
MOP = shrubbed woodland with mixed mopane (*Colophospermum mopane*),
VAC = treed shrubland with *Vachellia*,
SWA = swamp vegetation with fringing emergents,
FP = dry floodplains and island interiors,
RIP = shrubbed woodland of riparian zones,
GL = shrubbed grassland on former floodplain.

Selection indices
<1 = habitat avoidance,
± 1 = selection in proportion to availability,
>1 = selection.

Figure 4:4. Manly-Chesson habitat selection indices for buffalo (*Syncerus caffer*), zebra (*Equus quagga*) and lechwe (*Kobus leche*), for early flood (April – July), late flood (August – November) and wet (December – March) seasons.

Table 4.1. Top resource selection function (RSF) models selected for each species in each season. Models with the lowest Aikaike's Information Criterion value for small sample sizes (AICc) were considered most parsimonious (ΔAICc<2), and the table represents beta values for each covariate ± standard error (SE). df = degrees of freedom, ΔAICc = change in AICc value between top model and other candidate models, ω = model weight in comparison to other candidate models.

	Intercept	Habitat	NDVI	Distance to flood	Rain	Tree cover	df	ΔAICc	ω
EF									
Buffalo	-1,07	+	0,258 ± 0,025***	-0,111 ± 0,024***			11	0	1
Zebra	-1,12	+	-0,255 ± 0,040***	-0,464 ± 0,046***			10	0	1
Lechwe	-13,15	+	0,447 ± 0,052***	-1,284 ± 0,125***			10	0	1
LF									
Buffalo	-4,37	+	0,400 ± 0,027***	-0,597 ± 0,035 ***			11	0	1
Zebra	-2,46	+	-0,355 ± 0,047***	-0,612 ± 0,056***			10	0	1
Lechwe	-12,38	+	-0,992 ± 0,045***	-1,805 ± 0,126***			10	0	1
WET									
Buffalo	-4,67	+	0,301 ± 0,019***		0,567 ± 0,111***		11	0	0,988
Zebra	-1,54		-0,417 ± 0,047***		3,187 ± 0,500***	0,405 ± 0,046***	6	0	1
Lechwe	-12,60	+	-0,511 ± 0,059***	-2,685 ± 0,109***			8	0	0,999

Seasons: EF = Early flood (April – July), LF= late flood (August to November), WET = wet season (December to March)

Covariates: Habitat = habitat type, NDVI = normalised difference vegetation index, distance to flood = distance from used locations to the edge of the floodwater, Rain = average monthly rainfall in mm, Tree cover = percentage tree cover.

*** = significant value of p<0.001

Chapter 5 - Inferences from flooding patterns and interspecific competition: the decline of red lechwe populations in a seasonally flooded wetland

Abstract

The extent to which sympatric species overlap in the use of certain resources may give insights into the competitive interactions between species, and the potential effects of this interaction on herbivore abundance. Where sympatric grazers depend on the same dry season resources, specialist herbivores may be outcompeted by larger-bodied generalists, who often occur in high densities. I used time-selected adaptive local convex hulls (T-LoCoH) to analyse GPS location data in order to identify core foraging areas of three sympatric grazers in the Okavango Delta: red lechwe (*Kobus leche*), buffalo (*Syncerus caffer*) and zebra (*Equus burchelli*), with the aim of determining whether interspecific competition may be a contributing factor to the observed decline in red lechwe numbers in the Okavango Delta in recent years. In the late flood season, zebra and lechwe showed significant niche overlap in the selection of flooded habitats. When examining these flooded habitats more closely, the analyses revealed that as buffalo and lechwe showed stronger selection for flooded areas, lechwe changed their use of preferred ecotonal floodplain to seasonal sedge communities and more permanent swamp, as well as grassland on former floodplain, which is further from the water line. I suggest that lechwe are thus competitively excluded from their preferred ecotonal habitat at the end of the flood season by high density, generalist species such as zebra and buffalo. This exclusion may thus be a contributing factor to the observed decline in lechwe, particularly in years of high flood where ecotonal habitat and seasonal floodplain grasslands are converted into seasonal sedges and more permanent swamp. High flood periods therefore appear to favour more generalist species, and this should be taken into consideration in conserving the herbivore guild in the Okavango Delta in the face of climate change or upstream water offtake which could significantly affect flooding regimes. Further research could be done with regards to diet selection of lechwe and potential competitors across the landscape to further our understanding of the role of competition in causing lechwe populations declines.

Keywords: foraging area, niche overlap, interspecific competition, Okavango Delta, grazing herbivores

Introduction

The extent to which sympatric species overlap in their foraging areas, particularly when they exist within the same guild, may give us insight into the effects of interspecific competition, which is important for conserving diversity within ecological communities (Schweiger et al. 2015). Due to the high diversity of grazing herbivores in African savannas, niche separation between sympatric grazers has always been of considerable interest in ecological studies (Vesey-Fitzgerald 1960, Bell 1971, Demment and van Soest 1985). Niche differentiation within the grazing guild has often been attributed to differences in allometry; herbivores of varying size have different energy requirements, as well as different incisor arcades, which allow differential utilization of similar resources (Schoener 1974, Gordon and Illius 1988). Smaller-bodied species, and those with narrow incisor arcade, tend to graze selectively on high quality plant species, or parts, to fulfil their energetic needs, whereas large-bodied grazers require larger quantities of food, and compensate by being able to feed on lower quality forage (Jarman 1974, Demment and van Soest 1985, Owen-Smith 1985). These divergences in foraging strategy are often cited as the main reasons for high diversity within grazing guilds, as they allow coexistence by reducing competition for shared resources.

However, environmental factors, such as seasonality, can confound the effects of niche separation through trophic morphology and body size, and influence the extent to which species overlap by producing natural spatial and temporal changes in forage quantity and quality (Pianka 1973, Gordon and Illius 1989, Arsenault and Owen-Smith 2002, Kleynhans et al. 2011). During the abundant season, species tend to utilise a variety of resources, even those outside their strict trophic niches, to take advantage of high-quality forage (Gordon and Illius 1989). As a result, there is often niche overlap during this period (Jarman 1971, Gordon and Illius 1989). In contrast, in the non-growing season, when grasses become dormant and forage quality declines, niche separation is often more pronounced, and herbivores tend to

segregate into different habitats or use different resources (Jarman 1971, Arsenault and Owen-Smith 2002, Kleynhans 2011). However, when new, high quality resources become readily available to sympatric herbivores at the same time, this may result in convergence of resource use, regardless of season (Spowart and Hobbs 1985, Gordon and Illius 1989). For example, sympatric herbivores may converge on burnt areas to take advantage of the growth of young shoots (Spowart and Hobbs 1985, Wilsey 1996), or in wetland areas and river floodplains, where receding flood produces a green flush of vegetation (Fynn et al. 2015).

Resources such as a green flush of vegetation, particularly towards the end of the dry season, are known as bridging resources (Owen-Smith 2002). The availability of high-quality forage during the lean season, when other resources are senescent or depleted, can have a large impact on population densities, particularly for selective grazers (Owen-Smith 2002, Kröger and Rogers 2005). The degree to which more generalist grazers overlap selective grazers in niche use of such a limiting resource may thus give an indication of the degree to which interspecific competition plays a role in shaping communities. However, while studying such interactions, inferences regarding competition need to be drawn with caution (Schweiger et al. 2015). Niche overlap itself may not necessarily indicate competition, but rather separation of resource use at one level or another which enable species to coexist, or facilitation, where the feeding activities of one species increases availability of forage for another (Vesey-Fitzgerald 1960, McNaughton 1976, Arsenault and Owen-Smith 2002). Similarly, lack of overlap does not imply lack of competition; sympatric species may show niche differentiation because other strong competitors were already eliminated in the evolutionary past (Connell 1980), or because feeding by one species may preclude the use of the same resource by another (Rosenzweig 1981). Whether facilitation or competition dominates species interactions depends on consequent changes in population densities (Putman and Putman 1996, Arsenault and Owen-Smith 2002).

In the Okavango Delta, a green flush of grazing is produced by receding flood waters during the dry season, and acts as a bridging resource for grazing herbivores (Fynn et al. 2015). It is during this time that grazing herbivores converge on floodplains, which may lead to increased competition (Spowart and Hobbs 1985). Selective, smaller-bodied grazers, such as red lechwe, depend on the floodplains as a resource throughout the year. However, the number of red lechwe, as well as other selective grazers such as tsessebe (*Damaliscus lunatus*) and blue wildebeest (*Connochaetes taurinus*), have declined in the Okavango Delta in recent years (Chase 2011). One of the hypotheses is that increasing flood levels have reduced the availability of floodplain grasslands, and that the reduction in available forage may have contributed to these declines (Bonyongo 2004, Mendelsohn 2010). Indeed, aerial surveys from the Department of Wildlife and National Parks have shown that red lechwe numbers, which were high in the mid-1990s, declined steadily in the Okavango Delta from the early 1990s to 2012 (DWNP 2013), which also coincided with increasing flood levels. Interestingly, the bulk grazers, zebra (*Equus burchelli)* and buffalo (*Syncerus caffer*) numbers have remained stable over this period.

As competition may occur when grazers overlap in the use of scarce resources (de Boer and Prins 1990), and resource selection can occur at different spatial scales (Johnson 1980), I examined the extent to which resource use areas overlap between red lechwe, a selective grazer, and two high-density generalist grazers, namely buffalo (*Syncerus caffer*) and zebra (*Equus burchelli*), at the scale of selection of core foraging areas, where I assume effects of competition will be most likely. Furthermore, I conducted this study during the dry season of 2013 and 2014, two years of relatively high flood levels, when availability of dry season grazing is lower than in years of low flood level. I examined whether: a) species overlapped by selecting the same habitats for core foraging areas, b) species overlapped by selecting the same vegetation communities (inferred from level of flooding) for core foraging areas in

floodplains. This information will allow us to make more detailed inferences on the potential effects of interspecific competition on the red lechwe, and how changes in the proportions of habitats resulting from changes in the flood regime caused by climate change or upstream water offtake may influence competitive interactions between large herbivores in wetlands in the future. I hypothesize that:

1) the green flush produced on floodplains during the dry season will cause selection of core foraging areas to converge rather than separate, particularly towards the end of the dry season, on floodplain habitats

2) niche overlap between buffalo, zebra and lechwe will be higher in the late dry season than in the early dry season, in selection of floodplain habitat and selection of floodplain grassland

3) red lechwe depend exclusively on floodplain and swampland habitats for foraging throughout the dry season

4) red lechwe may shift resource use to areas flooded for longer in the late dry season to avoid competition with buffalo and zebra

Methods

Animal locations

To examine fine-scale selection of foraging areas, I was provided with locations of red lechwe, buffalo and zebra that had been fitted with Africa Wildlife Tracking[5] GPS enabled satellite tracking collars. Collars were fitted in the dry season, in the early morning or late afternoon, when temperatures were at their lowest and the stress levels of animals minimized. All darting exercises were conducted using a helicopter, and all darting was carried out by a Botswana registered veterinarian. Only adult females were selected from herds of each

[5] (*https://www.awt.co.za)*

species, as they are most representative of general herd behaviour. Collars were set to record GPS positions every four hours. Seven buffalo, three zebra and three red lechwe were collared, and data from the early and late flood seasons for 2013 and 2014 were used for the analysis.

Core forage area delineation

To determine the extent of overlap or separation in resource use between buffalo, zebra and lechwe during the dry season, I identified core resource use areas, which represent areas of intensive use likely related to foraging activity. Using GPS data collected from satellite collars, foraging areas were identified using time-selected local convex hulls (T-LoCoH). T-LoCoH is a local convex hull method of estimating space use that incorporates time into hull estimation, resulting in hulls that are local in both time and space (Lyons et al. 2013). Time units are transformed into units of distance called time-scaled distance (TSD), which enables us to identify certain behaviours from movement data such as time spent in an area, rates of re-visitation and whether movements are directional (indicating searching behaviour) or non-directional (indicating foraging or resting). The balance between time and space in creating hulls, 's', was set to include 60% time-selected hulls for each species and individual to allow comparison between species (Lyons et al. 2013, Schweiger et al. 2015). The number of nearest neighbours to be included in hulls were set using the adaptive or 'a-method', which selects the number of neighbours based on a specified cumulative distance in space and time (Lyons et al. 2013). To balance Type I and Type II errors, a range of cumulative distances were tested against the isopleth's edge to area ratio, and the cumulative distance or 'a' which stabilises this parameter before causing a jump in the isopleth's area was used to select nearest neighbours for each animal (Lyons et al. 2013, Dürr and Ward 2014). This method best suits data from animals where different densities of points can be expected, such as the high density of points in forage areas and the low density of points occurring in habitats with low

resource value (Getz and Wilmers 2004). Once the values of 's' and 'a' have been set, foraging areas were identified using information based on re-visitation rates. To calculate re-visitation rates, the inter-visit gap, which is defined as the time between one visit to a hull and the next consecutive visit to the same hull, was set at 12 hours for all species. This is consistent with activity patterns in buffalo, zebra and lechwe which often show bimodal activity at sunrise and sunset, foraging during these periods and then often resting in the middle of the day (Lent 1969, Winterbach and Bothma 1998, Owen-Smith and Goodall 2014). Hulls were then selected based on the normalized, mean number of separate visits, and merged until a 30% isopleth was obtained. While this small isopleth size might result in Type II errors which exclude used areas, more importantly, it limits the inclusion of areas not used (Type I error) which result in erroneous conclusions regarding the competition for resources (Schweiger et al. 2015). All analyses were conducted using the T-LoCoH package (Lyons and Getz 2014) in R (R Development Core Team 2014).

Classification of habitat

To determine the change in habitat proportions used, I used a habitat map from the Okavango Research Institute [6] created by georeferencing and ground-truthing LANDSAT imagery (Jellema et al. 2002, Ringrose et al. 2003). Core foraging areas calculated for each species were overlaid on a habitat raster, and the proportion of each foraging area constituting each habitat type was calculated in ArcMap 10.2 (ESRI 2014). Six habitat types were identified in core foraging areas, and included Mopane (*Colophospermum mopane*) woodland, *Vachellia* woodland, floodplains and swampland, riparian woodland and grassland on former floodplain.

[6] Okavango Research Institute, Maun, Republic of Botswana

Classification of flooded areas

As the floodplain communities are dynamic and are in constant flux, the three-year flood duration average was used to differentiate between habitats flooded for different periods (see Murray-Hudson 2009 and Chapter 1). To do this, MODIS imagery depicting dry and wet pixels were obtained from the Okavango Research Institute. Monthly flood images were combined in ArcMap 10.3 to form annual flood maps, indicating the number of months each pixel had been flooded throughout the year. Annual flood images from the previous three years were then combined to derive an average flood value. To account for differences in palatability of grasses and sedges with different flood duration optima which may affect resource selection (Chapter 2), flooded areas were divided into palatable floodplain grasslands (flooded between 1-4 months), and ecotonal floodplain grasslands which included a combination of sedges and less palatable grazing (5 to 6 months), and permanent sedge and swamp habitat, which contain primarily sedges and other hydrophilic species (>7 months). Dry areas were considered to be any habitat not flooded for the last three years.

Niche overlap

To determine if the three focal species are competing for the same resources along two niche axes, namely habitat type and flood duration, during the early and late flood seasons, I calculated the average percentage of foraging areas comprised of various habitats and flood histories for each species. To determine the niche overlap in both habitat and flood history for foraging areas for each season, I used Pianka's Niche Overlap formula (Pianka 1973):

$$O_{jk} = O_{kj} = \frac{\sum_i^n P_{ij} P_{ik}}{\sqrt{\sum_i^n {P_{ij}}^2 \sum_i^n {P_{ik}}^2}}$$

Where O_{jk} and O_{kj} is the niche overlap between species *j* and *k,* and P_{ij} and P_{ik} are the proportions of resource *I* used by species *J* and *k* respectively. Values for this niche overlap index range from 0 to 1; 0 indicating no niche overlap and 1 indicating complete niche overlap.

Niche overlap indices were calculated on a pairwise basis, and indices obtained from observed matrices compared to null models to determine significance. Differences between seasons were determined by looking at the overlap in confidence intervals between seasons and considered significant if there was no overlap in confidence intervals. All calculations were conducted using the software package *EcoSimR* (Gotelli et al. 2015) in R (R Core Development Team 2014).

Results

When I examined the proportions of habitat types used in the core foraging areas between the three species, floodplain and swampland habitats as well as grassland on former floodplain form a large proportion of the habitats used by each grazing species in both the early and late dry season (Figure 5:1). Lechwe used floodplains and swampland habitats exclusively during the early dry season, but showed a shift towards grassland on former floodplain in the late dry season. Zebra were fairly consistent in their habitat use between the early and late dry season, while buffalo showed a slight increase in the use of floodplain and swamp habitats towards the end of the dry season, accompanied by a concomitant decrease in the use of mopane and grassland on former floodplain.

During the early flood season, overlap in core foraging areas selected was lowest between buffalo and lechwe, intermediate between zebra and lechwe, and highest between buffalo and zebra (Table 5:1). However, these patterns changed during the late flood season. Niche overlap between zebra and lechwe increased substantially and was significant in comparison to null models. There was a similar increase in overlap in habitat use for core foraging areas between buffalo and lechwe. Conversely, buffalo and zebra showed a decrease in overlap of habitat use during this part of the dry season. There were no significant differences in niche overlap between seasons.

When I examined changes in proportion of flooded habitat used in the foraging areas of all three species, the three grazing herbivores showed increasing dependence on areas flooded for longer as the dry season progressed (Figure 5:2). Comparatively, buffalo and zebra decreased the proportion of their foraging areas in non-flooded habitat, and increased their use evenly across seasonal grasslands, ecotones between sedges and grasses and sedge and swamp vegetation (Figure 5:2). Lechwe, on the other hand, did not use dry areas at all, and while they focused on ecotonal areas during the early flood season, they shifted their resource use in the late dry season to sedge and swamp habitats and seasonally flooded grasslands.

When examining overlap in the proportion of foraging areas composed of different flood histories, in general, observed niche overlap indices did not differ significantly from the null models generated (Table 5:2). However, there were clear species and seasonal patterns of pairwise niche overlap between all three species (Table 5:2). Across both the early flood and late flood seasons, pairwise niche overlap in the use of flooded areas between buffalo and zebra was high compared to niche overlap between buffalo and lechwe, and zebra and lechwe (Table 5:2). When comparing niche overlap between the early flood and late flood seasons, all species pairs showed trends towards increasing niche overlap in the late flood season, particularly between buffalo and lechwe (Table 5:2); however, there was no significant difference between seasons.

Discussion

While in most systems, niche overlap may diverge in the dry season to reduce competition (Schoener 1986, Kleynhans et al. 2011), in a pulsed wetland system such as the Okavango Delta, resource use converges, particularly in the late dry season, on floodplain habitats. The

lower levels of overlap in habitat use observed between the three grazing species during the early dry season may be due to the delay in vegetation growth just after the rains (Zhang et al. 2005), allowing zebra and buffalo to still utilize parts of their wet season ranges into the early flood season (Bennitt et al. 2014). However, as the dry season progressed, both buffalo and zebra showed corresponding increase in the use of floodplain and swampland habitats rather than dry areas, which increased overlap with the core foraging habitats of lechwe, as expected. The division of flooded habitats into areas with varying flooding histories revealed further detail regarding niche use in foraging areas for each species. While all species utilized seasonal floodplain grasslands in the early and late dry season, buffalo and zebra showed similar increases in the use of areas flooded for longer in the late dry season, but lechwe showed a large shift from use of ecotonal areas to seasonal sedge-lands and swamp. The clear distinction between the species in use of floodplain with different flooding histories indicates that flooding patterns and resulting vegetation communities provide further opportunity for niche differentiation in wetlands and shows the importance of examining resource use at different hierarchical levels within habitats (Blix et al. 2014, Schweiger et al. 2015).

As expected, red lechwe depended solely on floodplain and swampland habitat for their core foraging areas. During the early dry season, there is clear preference for the ecotonal areas (flooded between five and six months), which are on the edge of the permanent swamp. Preference for these ecotones has been observed in other studies of red lechwe in the Okavango Delta (Lent 1969) and in the Linyanti System, a seasonally flooded swamp to the north-east of the Okavango Delta (Williamson 1990). As small-bodied ungulates, lechwe are highly selective, and consistently select plants with high protein content (von Richter and Osterberg 1977). Due to the high water-table in the ecotonal areas, there is continuous vegetation growth, and the crude protein content of plants is consistently higher than in adjacent, lower floodplains (Williamson 1990). Furthermore, lechwe depend on shallowly

inundated areas to escape from predators such as lion (*Panthera leo*) and African wild dog (*Lycaon pictus*) (Williamson 1990). Habitat selection is thus strongly influenced by distance to water (See also Chapter 3).

In the late dry season, zebra and buffalo showed increasing overlap with red lechwe in the habitats selected in foraging areas, which was concurrent with our expectations. As we expected, towards the late dry season, lechwe showed a shift in resource use from ecotonal areas towards more permanent swamp, however, contrary to our expectations, they also shifted towards drier habitats. This is consistent with aerial survey data collected on several lechwe herds in 2014 (Chapter 3). The need to include high quality forage in the diet may result in lechwe making use of floodplain grassland habitats (flooded one to four months), which would have experienced a 'green flush' in the wake of receding flood-lines. However, lechwe appeared to also utilize grassland on former floodplain, much farther from the floodplain edges. This may be for two reasons: 1) due to the high flood in the sample years, fresh vegetation growth may also have been stimulated in this habitat, or 2) due to the lower availability of seasonal grasslands during years of high flood (Bennitt et al. 2014), lechwe may have been competitively excluded from the ecotonal and seasonal grassland areas and forced further away from the flood line to fulfil their energy requirements. Given the increased risk to predation associated with foraging so far away from water (Williamson 1990), it is likely that competition with more generalist grazers such as buffalo and zebra, which also occur at higher densities, was the stronger driving force in this niche shift. In addition, species like buffalo and zebra may attract the presence of predators such as lions, exposing lechwe to higher levels of predation than at other times of the year (Owen-Smith and Mills 2008).

As niche shifts away from preferred habitats may indicate competition (Brew 1982), we posit that this is an indication that lechwe are competitively excluded from preferred habitat during

the late dry season, particularly during years of high flood by more generalist, high density grazers such as buffalo and zebra. This confirms our initial hypothesis, and is also supported by the fact that in lower flood years, red lechwe showed stronger preference for floodplain grassland, ecotonal habitat and seasonal sedgelands and swamp and avoided dry areas in the flood season (Chapter 3). As similar studies in the Delta have shown a decline in the availability of forage in seasonal floodplains during high flood years (Bennitt et al. 2014), it is possible that large herds of zebra and buffalo physically displace lechwe from their preferred ecotonal habitat when floodplain grazing is scarce. Shifts in core foraging areas as a result of displacement from larger density species have also been observed in other habitats such as Kruger National Park, where selective grazers like sable antelope (*Hipportragus taurinus*), shifted their core habitat use in response to large buffalo herds (Macandza 2009). Similarly, other selective species such as tsessebe (*Damaliscus lunatus)* and roan (*Hipportragus equinus*) tend to decline with reductions in the availability of their preferred dry season foraging areas (Dunham et al. 2004) or when outcompeted by more generalist grazers in their preferred foraging areas (Kröger and Rogers 2005). While in some places, grazing by bulk herbivores may lead to facilitation for smaller species, bulk grazers in large herds can also reduce grazing availability through trampling, making facilitation for smaller species impossible (Macandza 2009).

Where selective, lower density grazers are competitively excluded from their preferred foraging areas by high density grazers, and shift foraging areas to sub-optimal habitats, population decline is likely to follow (Rosenzweig and Lomolino 1997). I suggest that competitive exclusion by larger bodied, high density grazers may be a contributing factor to the declining red lechwe densities witnessed over longer timescales in the Okavango Delta (DWNP 2013), as well as in recent years (Chase 2011) during high flood regimes, when dry season grazing declines. As selective grazers are particularly vulnerable to interspecific

competition in the dry season, they will be particularly vulnerable to changes in resource availability that may result from climate change (Rosenzweig and Lomolino 1997). Climate change scenarios for the Okavango Delta reveal that both wetting scenarios and drying scenarios will result in decreases in seasonally flooded grasslands, both with negative effects for grazing communities. Furthermore, the veterinary cordon fence, which prevents the migration of buffalo and zebra to adjacent areas likely results in amplified pressure on floodplain systems inside the fence (Bartlam-Brooks et al. 2013), particularly in wet years. In addition, high flood years, which push lechwe towards the fence, may result in increased vulnerability to poaching. The western Delta loses a considerable number of animals to bushmeat poaching each year (Rogan et al. 2017), which can further exacerbate population declines in species like lechwe which already suffer from competition (Rogan et al. 2017). Future conservation efforts for the Okavango Delta may lie in finding ways to extend the extent of this protected area to the full extent of the floodplain system to prevent further loss of herbivore diversity and ameliorate pressure of large generalist herbivores on selective grazers.

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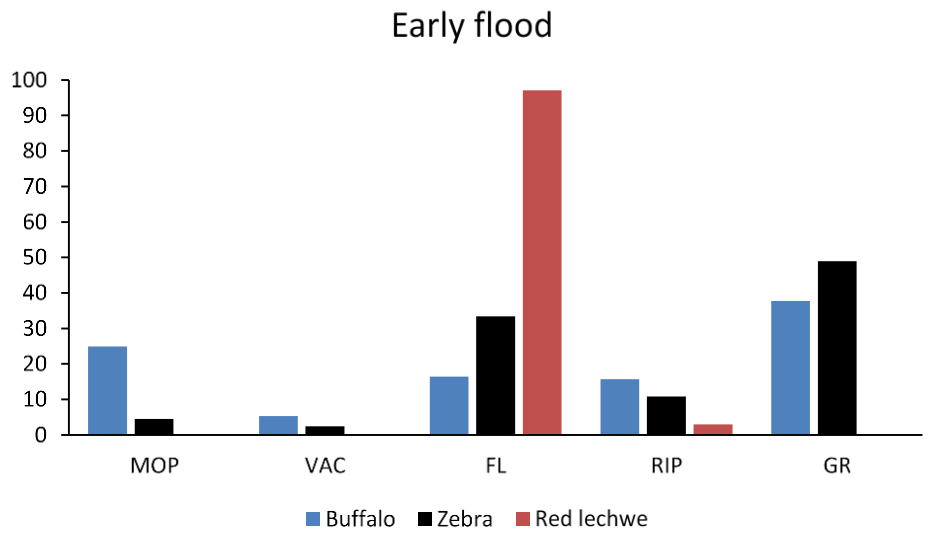
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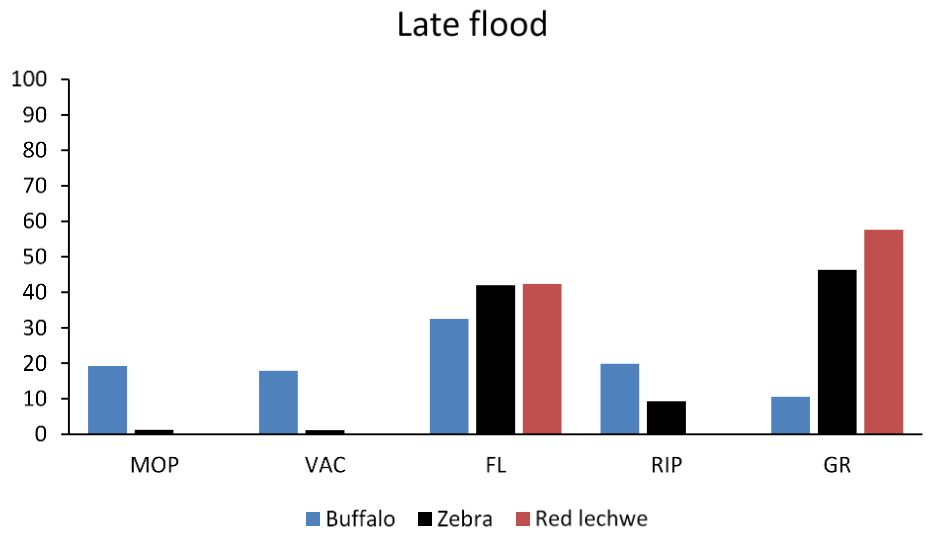
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MOP = Mopane (*Colophospermum mopane*) woodlands,
VAC= Vachellia woodlands,
FL = floodplains and swampland, RIP = riparian woodland,
GR = grassland on former floodplain.

Figure 5:1. Differences in proportions of habitats constituting foraging areas used by buffalo (*Syncerus caffer*), zebra (*Equus burchelli*) and red lechwe (*Kobus leche*) during the early flood (April to July) and late flood (August to November) seasons in the western Okavango Delta, Botswana.

Table 5:1. Pairwise Pianka's niche overlap indices for overlap of habitat use in foraging areas for three grazing species, buffalo (*Syncerus caffer*), zebra (*Equus burchelli*) and red lechwe (*Kobus leche*), in the western Okavango Delta, Botswana. Values of niche overlap range from 0 to 1; 0 indicating no niche overlap and 1 indicating complete niche overlap.

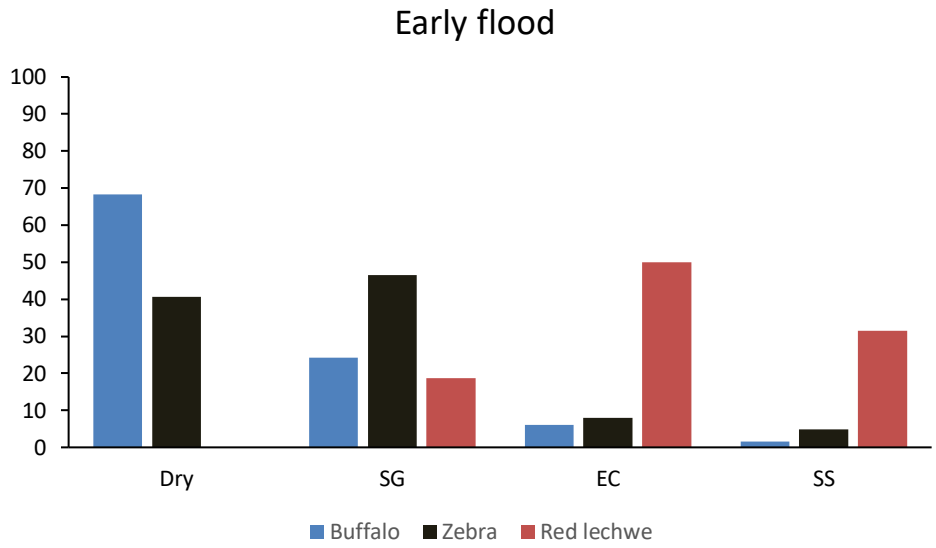
	Obs[1]	Null[2]	*Z*[3]	P[3]	Confidence interval[3]
Early flood					
Buffalo - Lechwe	0.332	0.415	-0.406	0.343	-0.424 - 0.219
Zebra - Lechwe	0.558	0.332	0.754	0.226	-0.268 - 0.516
Buffalo - Zebra	0.874	0.653	1.377	0.084	-0.075 - 0.483
Late flood					
Buffalo - Lechwe	0.585	0.589	-0.033	0.487	-0.215 - 0.181
Zebra - Lechwe	0.984	0.444	1.987	0.023*	0.000 - 0.957 *
Buffalo - Zebra	0.694	0.666	0.234	0.408	-0.149 - 0.198

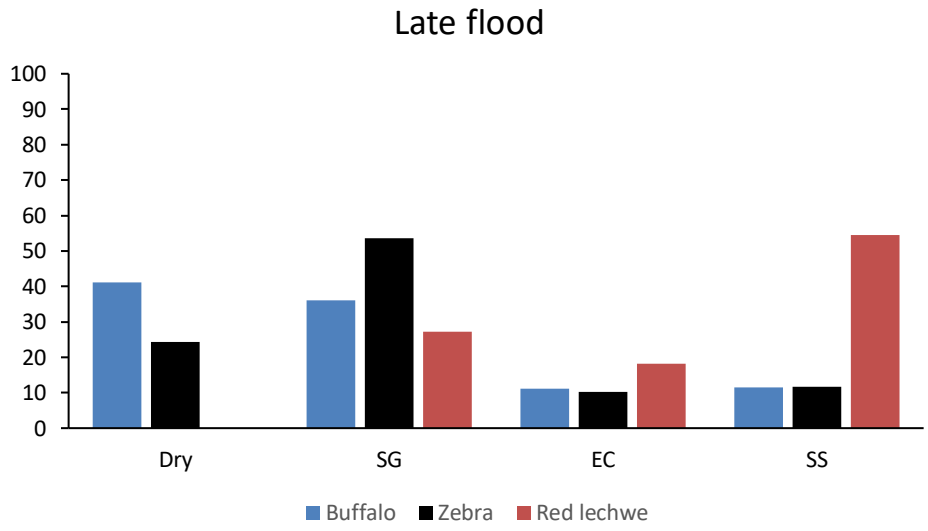
[1]Obs = Pianka's niche overlap index for observed matrix

[2]Null = Pianka's niche overlap index for null matrices generated based on observed matrix patterns.

[3]Values of z and p, and the confidence interval, are based on differences between observed and null matrices generated.

* = value significant ($p<0.05$)





DRY = non-flooded habitat

SG = seasonally flooded grasslands (flooded 1 – 4 months)

EC = ecotone between grass and sedge (flooded 5 – 6 months)

SS = seasonally flooded sedgelands and swamp (flooded >7 months)

Figure 5:2. Change in proportions of use of flooded areas used by buffalo (*Syncerus caffer*), zebra (*Equus burchelli*) and red lechwe (*Kobus leche*) between the early flood (April to July) and late flood seasons (August to November). The change in proportion was calculated for foraging areas used by each species.

Table 5:2. Pairwise Pianka's niche overlap indices for areas with varying flooding histories for three grazing species, buffalo (*Syncerus caffer*), zebra (*Equus burchelli*) and red lechwe (*Kobus leche*), in the western Okavango Delta, Botswana for early and late flood season. Values of niche overlap range from 0 to 1; 0 indicating no niche overlap and 1 indicating complete niche overlap.

	Obs[1]	Null[2]	*Z*[3]	P[3]	Confidence interval[3]
Early flood					
Buffalo - Lechwe	0.178	0.556	-1.546	0.061	-0.774 0.019
Zebra - Lechwe	0.367	0.658	-1.428	0.077	-0.603 0.044
Buffalo - Zebra	0.870	0.546	1.292	0.098	-0.058 0.685
Late flood					
Buffalo - Lechwe	0.500	0.687	-1.085	0.139	-0.447 0.066
Zebra - Lechwe	0.590	0.646	-0.275	0.392	-0.390 0.250
Buffalo - Zebra	0.917	0.719	1.256	0.105	-0.043 0.421

[1]Obs = Pianka's niche overlap index for observed matrix

[2]Null = Pianka's niche overlap index for null matrices generated based on observed matrix patterns.

[3]Values of z and p, and the confidence interval, are based on differences between observed and null matrices generated.

Chapter 6 - Conclusion

Context

As wetland systems are some of the most productive ecosystems on earth, their conservation is important for both people and wildlife (Silvius et al. 2000, Fynn et al. 2015). However, their continued existence is threatened not only by impending climate change, but also by anthropogenic activities which divert water from upland river systems (Poff et al. 2007, Döll and Zhang 2010, Arias et al. 2016). If the primary ecological forces which govern change within the wetlands themselves are not well understood, we cannot hope to preserve wetlands in the future in the face of such change or attempt to restore them to their original functionality (Arias et al. 2016). As the flood pulses of wetland systems are the primary drivers of ecological change for all biota within wetland ecosystems (Junk et al. 1989), it is important to follow the consequences of change in flood pulse up to higher levels of the trophic ladder. Many studies on wetland systems have primarily focused on how changes in flood regime affect vegetation (Bonyongo 1999, Casanova and Brock 2000, Stromberg et al. 2007, Murray-Hudson 2009, Arias et al. 2016). However, besides anecdotal evidence which describes declines in herbivore numbers with changes in flood regime (Chansa and Kampamba 2009, Beilfuss et al. 2010), no study has gone into detail on how flooding can reduce palatable grazing for larger herbivores, and the potential consequences of changing flooding patterns on resource use of grazing herbivores. The aim of this study was to determine how changes in flood pulse affect the availability of suitable grazing and niche overlap of sympatric grazing herbivores.

Synthesis

The Okavango Delta is one of the world's largest inland Deltas, and as land use is primarily devoted to wildlife conservation, was the ideal study site to determine how changes in flood regime affect large herbivores. As flooding regimes change on decadal and inter-annual scales, and these regimes directly influence shifts in vegetation communities (Chapter 1), a

wetland such as the Okavango Delta is the perfect natural system in which to test the selection of resources by herbivores at different temporal as well as spatial scales. The differences in resource selection at different ecological resolutions called for a hierarchical approach to fully unravel the interactions between herbivores and the flooded environment in their entirety (Senft et al. 1987). Herbivores respond to numerous biotic and abiotic cues which affect these hierarchical decisions from the scale of the region (first-order selection), to that of resources within the landscape (second-order selection), to that of the foraging patch within the landscape (third-order selection; Johnson 1980).

I therefore examined how changes in flooding, and associated changes in vegetation communities (Chapter 2), influenced the grazing herbivore community at different scales of temporal and spatial resolution (Chapter 3 to 5). In Chapter 3, I determined how sympatric herbivores adapted their use of flooded areas to different flooding regimes, ranging from low flood to high flood years, using network analysis. In Chapter 4, I used resource selection functions to determine which factors, along with flooding patterns, affected the selection of home range areas by herbivores across each season (second-order selection). In Chapter 5, I look at overlap in foraging areas between three sympatric grazers during the late dry season (third-order selection), where competition for resources is likely at its highest. Finally, I examine how these various scales of resource selection may explain the current observed trends in herbivore populations in the Okavango Delta, and aim to determine how changes in flood patterns as a consequence of climate change and increasing anthropogenic pressures, may shape the future of grazing herbivores not only in the Okavango Delta, but in wetland systems across the world (Chapter 6).

Findings

During the study period, the Okavango Delta transitioned between a dry and wet cycle, resulting not only in an increase in flood extent, but also an increase in flood duration for a

large proportion of the study area (Chapter 2). Consequently, floodplain vegetation communities shifted from palatable grasses to unpalatable sedges, resulting in reduced resource availability for grazing herbivores during high flood regimes in the late dry season (Chapter 2). When examining how the changes in flooding patterns influenced the use of flooded areas by sympatric grazing herbivores, I found that lechwe, although specialist grazers, were able to exploit the largest range of flooded habitat, from dry habitat to habitat flooded for up to 9 months of the year (Chapter 3). While lechwe preferred areas flooded for six or seven months, all other grazing herbivores showed preference for floodplains flooded between one and five months, which also represents areas with the most palatable grazing (Chapter 2 and Chapter 3). Wildebeest and tsessebe were the most specialist in their use of floodplain habitat, concentrating on floodplain grasslands flooded for shorter periods (Chapter 3), and while the larger-bodied species such as buffalo and zebra were more generalist in their use of flooded areas, they showed a clear preference for areas not flooded (Chapter 3). As flooding regime increased however, all grazing species showed increasing overlap in the use of flooded areas, particularly for intermediately flooded areas (Chapter 3). This may result in increased competition between the grazing species for intermediately flooded floodplains during high flooding years, which prove detrimental to species such as wildebeest and tsessebe which rely only on low to intermediate flooding frequency (Chapter 3). Similar patterns in resource overlap between sympatric grazers during high floods occurred in the Kafue Flats in Zambia, resulting in a decline in herbivore abundance most likely linked to high levels of competition (Sheppe and Osborne 1971). I suggest that similar mechanisms may apply in the Okavango Delta.

When selecting home ranges within the landscape, flooded areas were important for lechwe year-round, but were only influential in the selection of home ranges during the early and late flood season for zebra and buffalo (Chapter 4). As expected, due to their physical adaptations

to wetlands, their dependence on water as a means to escape predation (Williamson 1990), and their ability to exploit a range of habitats flooded for different periods, lechwe home range use was most constrained by the distance to water and the selection of swampy and floodplain habitat (Chapter 4). However, in the late dry season, lechwe appeared to select for drier land in high flood years (Chapter 2 and 4), which may indicate displacement as a result of competition from other grazers over these periods. Zebra and buffalo, however, made more use of dry habitats in the rainy and early flood seasons, and responded to changes in rainfall and vegetation greenness as a result of this rainfall (Chapter 4). However, as other ephemeral water sources dry up at the end of the dry season, buffalo and zebra were drawn back towards the flood-line, not only to access water but also to access the green flush of grazing produced in this season (Chapter 4). The premise that buffalo and zebra may displace red lechwe during the late flood season was further investigated in Chapter 5, by examining overlap in foraging areas between these three grazers in the early flood and late flood seasons, which coincides with the season of low rainfall. While it is difficult to prove that shifts in niche space are a direct result of competitive interactions, I posit that the evidence presented in Chapter 3, which indicated that lechwe prefer intermediately flooded areas in low flood years, strongly points to displacement of lechwe by larger-bodied grazers such as buffalo and zebra from preferred swamp habitat during high flood years (Chapter 5). While lechwe can make use of a wide range of flooded areas, their shift towards grassland, away from the flood line and safety of the water, suggests that they are seeking forage outside their preferred niche (Chapter 5). These patterns suggest that during periods of high flood, red lechwe may decline as a result of competition with other large herbivores for preferred grazing (Chapter 5).

Throughout the thesis, differences in body size, digestive strategy and incisor arcade were important in explaining the observed patterns of guild structure and resource selection from

areas flooded with different frequencies, to home ranges, to foraging areas within home ranges. Seasonality also played a large role in resource selection; while zebra, lechwe and buffalo all diverged in habitat selection during the rain and early flood seasons, the convergence of all three species on floodplain habitats, and specifically on intermediately flooded areas during the late dry season, resulted in interspecific competition. In low flood years when intermediately flooded grass communities are abundant, niche separation between sympatric grazers was clearer and in order with predictions based on morphological differences. However, when this resource became scarcer during years of high flood, larger-bodied ungulates appeared to outcompete smaller, more specialist grazers. This may be one of the reasons for the precipitous decline in wildebeest and tsessebe numbers in the Okavango Delta in recent years (Chase 2011), as well as steady declines in red lechwe observed during years of high flood. It is important that such population oscillations, driven by ecological change, are taken into consideration in future management of wetland area and be used as baselines for establishing ecological carrying capacities under varying ecological and anthropogenically induced scenarios.

Study implications

There is growing concern over the decline in large herbivore species on a global scale (Ripple et al. 2015). Large herbivores are vital in maintaining a number of ecosystem services, including the cycling of nutrients (McNaughton et al. 1988, De Mazancourt et al. 1998, Augustine et al. 2003), dispersal of seeds (Janzen 1970, Lamprey et al. 1974), structuring ecosystems by altering vegetation (Waldram et al. 2008, Valeix et al. 2011), increasing biodiversity (Olff and Ritchie 1998, Palmer et al. 2008) as well as providing food for large predators (Ramakrishnan et al. 1999, Treves and Karanth 2003). When such herbivore declines occur on a local or regional scale, it is important to tease apart the factors responsible for declines so that appropriate conservation actions can take place.

As wetlands are important key or 'bridging' resources for wild herbivores during the dry season, and because they play a large role in determining herbivore biomass in the area, it is important to understand the potential consequences of changes in flooding regime for herbivore populations (Owen-Smith 2002, Fynn et al. 2015). Negative responses of herbivore population demographics to declining quantity or quality of dry season resources as a result of changing flood patterns in wetlands have been shown in other areas, such as the decline of buffalo from lake shores of Kariba in Matusadona National Park, Zimbabwe (Taylor 1985), and the decrease in kob (*Kobus kob*) and waterbuck (*Kobus ellipsiprymnus*) from floodplains in Waza National Park after the construction of the Maga Dam in 1979 (Scholte et al. 2007). However, these changes have been related to anthropogenic threats, where wetland changes are primarily driven by anthropogenic upstream changes such as the building of dams or hydro-electric schemes.

The Okavango Delta is one of the most pristine remaining wetlands in the world, and as a result remains largely ecologically intact (Milzow et al. 2010). Recent aerial surveys over the Okavango Delta, however, have highlighted significant herbivore declines, particularly in medium-sized grazing herbivores, over the last few years (Chase 2011). While relationships between hydrology and vegetation community patterns have been studied more extensively in wetlands, the Okavango Delta thus proved to be an ideal place to test ecological theories of how natural, cyclical changes in flooding patterns may affect higher trophic levels (Murray-Hudson et al. 2006). This study suggests that increased flooding patterns may be responsible at least, in part, for the decline in medium-sized herbivores such as tsessebe, wildebeest and red lechwe, as a result of declining dry season resources and increased competition from more generalist, large-bodied grazers such as buffalo and zebra when cycling from years of low to high flood. This corollary, however, also suggests that as flooding cycles result in drier years, these medium-sized herbivore populations should naturally recover.

The recovery of these populations, however, may be suppressed if coupled with other anthropogenic influences such as bush-meat poaching. As highly productive ecosystems, many wetlands have lost large herbivore populations to bush-meat poaching, resulting from increasing anthropogenic pressure and conflict (for example, Busanga Floodplains of Kafue National Park, Zambia – Midlane 2014, Lindsey et al. 2013 and Marromeu Complex Zambezi Delta – Beilfuss et al. 2010). Recent analysis of the bushmeat trade on the western Okavango Delta has revealed increasing trends in anthropogenic offtake, which may exacerbate herbivore population declines (Rogan et al. 2017). Therefore, during wetter cycles, conservation measures should focus on minimising anthropogenic threats such as bush-meat poaching in order to prevent herbivore numbers from being suppressed to levels where population recovery is difficult.

While my study suggests that the reduction in palatable grazing during the dry season with increased flooding could be one of the main causes of herbivore declines in the Okavango Delta, the construction of the veterinary fence in 1982 surrounding the Okavango cannot be ignored as a potential contributing factor (Mbaiwa and Mbaiwa 2006). By cordoning off the populations in the Okavango Delta, the fence could prevent supplementation of the Okavango Delta populations by preventing immigration (Boone and Hobbs 2004). Furthermore, when animals are compressed into an area, their use of suitable forage areas are restricted, particularly when resources are scarce, which could exacerbate the decline in large herbivores during periods of high flood (Boone and Hobbs 2004). Conversely, the fence has prevented degradation of grazing within the Delta by restricting entry of large numbers of cattle, whose effects on local herbivore abundance may have been more detrimental (Ellery and McCarthy 1994).

The relationship identified between flooding parameters and the amount of palatable grazing available also gives an indication of the consequences of changing flooding regimes for the Okavango Delta. While higher flood levels may lead to sedge-dominated communities in floodplains, the cycle back to drier years would result in the reverse. Ultimately, it is the prolonged and predictable flood pulse each year, and the inter-annual variation in this flood pulse, that results in a moving ecotone between dry land and water which promotes nutrient recycling and prevents stagnation, thus leading to higher productivity (Junk et al. 1989). However, if water were diverted from the Okavango River for anthropogenic use, for example, the oscillations in the flooding patterns would be dampened, leading to a decrease in the extent of this ecotone, and ultimately leading to lower productivity in the floodplains in the long term (Poff et al. 2007). As witnessed in other wetlands around Africa, alterations to water supplies in wetland areas can reduce suitable resources and increase incidences of drought, resulting in lower carrying-capacity for local megafauna (Scholte et al. 2007, Belifuss et al. 2010).

Of greater concern, however, are the potential effects of climate change on wetland systems (Burkett and Kussler 2000, Acreman et al. 2009, Milzow et al. 2010). Forecasts for the Okavango Delta indicate that changes caused by climate change present a far greater threat to the functioning of the Okavango Delta than any anthropogenic changes (Murray-Hudson et al. 2006). Worst-case scenario models predict considerable drying of the Okavango Delta, which may lead to a conversion of floodplain into woody habitat, which would result in a significant shift in herbivore assemblage from grazing to browsing species (Milzow et al. 2010). This would not only reduce herbivore diversity but considerably reduce the capacity for large carnivores (Murray-Hudson et al. 2006, Milzow et al. 2010). This study, which uplinks changes in hydrology to higher trophic levels, may thus prove important in future conservation planning regarding climate change mitigation in wetlands. In the Okavango

Delta in particular, greater effort should be made to safeguard the catchment areas in Angola, where the floods originate, to ensure that upstream anthropogenic changes do not negatively impact the current functioning of the Okavango Delta and exacerbate future climate change scenarios. Securing the catchment will help to prevent herbivore declines as already witnessed in other wetlands across Africa (see Beilfuss et al. 2010).

Shortfalls

As with most ecological studies, data analysis would have benefitted from longer-term and larger-scale data. Additional vegetation surveys, or vegetation surveys which match the years and seasons in which aerial surveys took place, would have allowed stronger validation of the link between palatable and non-palatable grazing and herbivore resource use. Furthermore, while all sedges were classified as non-palatable to maintain simplicity, there are some sedge species which form a percentage of the diets of lechwe, as well as the larger grazing species such as buffalo. However, while the analysis between palatable grasses and non-palatable sedges may be an over-simplification of grazing patterns, I feel that the palatable grasses represent the most sought-after resource amongst all the grazing herbivores, as they are of higher nutritional value than sedges which have higher levels of silica and structural compounds which reduce digestibility (Mosimane 2015).

Another consideration which may influence the interpretation of the results is local rainfall. While wetter cycles result from increased rainfall in Angola, local rainfall patterns may also influence the quality of available grazing during the wet season, and hence influence the extent to which herbivores depend on dry season grazing (Yoganand and Owen-Smith 2014). Similarly, the occurrence and frequency of fires, which also influence grazing patterns (Vesey-Fitzgerald 1960, Parrini and Owen-Smith 2010, Yoganand and Owen-Smith 2014) may also influence the dependence of grazing herbivores on floodplains in the dry season. However,

given the trend of increasing overlap in resource use as flooding regimes increase, and that flooding does indeed exert a large landscape scale effect on the availability of suitable dry season grazing, my findings suggest that this pattern cannot be ignored and is likely the over-arching ecological influence in determining the availability of suitable grazing.

As aerial surveys were from multiple sources, and because I only focused on a small area, I was not confident in using estimates of abundance obtained from surveys for each species to determine if there was a direct link between grazing changes and herbivore declines, particularly for large migratory species such as buffalo. Abundance estimates would need to be determined consistently over a larger area to reliably estimate abundance and determine if there is a direct correlation between abundance and flooding patterns. In drawing conclusions from the study, I could only speculate that declines may be linked to the changing flooding regime. Aerial surveys over a small area could also bias results to some extent, by the inclusion of observations of animals occurring in sub-optimal habitat as a result of displacement competition from their own species, which may nullify to an extent our conclusions on competition within the guild from other species. The probability of this occurring would be reduced if aerial surveys occurred over a larger area and included more observations.

While resource selection functions are improving our understanding of how animals utilize their environment, as with all modelling concepts, there may be a few weaknesses. While examining the selection of similar resources across multiple species allows for comparison, there are various species-specific strategies in resource selection which could be missed and result in weaker models. For example, while some grazers follow maximum NDVI values, the resource use of other species may be better explained by other derived NDVI values such as the 'instantaneous rate of green up' (Merkle et al. 2016). Furthermore, different species may

respond to resources at different scales based on size and movement behaviours such as minimum daily distance moved (Boyce 2006). For example, smaller bodied grazers such as lechwe may select local resources at much smaller spatial scales than buffalo, which are capable of moving much larger distances.

Lastly, while foraging areas were inferred based on temporal and spatial aspects of movement behaviour (Bennitt 2012, Lyons et al. 2013, Schweiger et al. 2015), the study could benefit from more accurate examination of foraging behaviour. Hierarchically, a fourth-order selection study such as selection of specific foraging patches or more detailed aspects of foraging areas selected such as nutritional content could allow further insight into niche separation or overlap between species. For example, studies on sympatric herbivores in alpine grasslands revealed that although interspecific competition appeared high based on diet composition analyses revealing similar proportions of plant types in all diets, selection of resources based on other vegetation properties such as biomass and nutritional content revealed significant niche separation (Schweiger et al. 2015). This could be particularly important in highly heterogeneous environments (Schweiger et al. 2015).

Future studies

Future studies should focus on continued long-term data collection regarding the changes in flooding and vegetation composition, particularly when transitioning from a wet to dry cycle. This would confirm whether the amount of palatable grazing would increase as floodplains are flooded for shorter periods of time. Additionally, aerial surveys should continue to monitor whether the grazing herbivores, in particular, undergo population recovery during these periods. It is also important to identify which other factors, such as bush-meat poaching, could possibly be contributing to the decline in all large herbivores in the Okavango Delta. Bush-meat poaching is one of the main causes of decline in large herbivore populations in Africa (Craigie et al. 2010, Lindsey et al. 2013). Investigations into bush meat poaching on the

western border of the Okavango Delta, close to the study area, revealed that individual hunters (n=90) remove on average 163 to 235 kg of bush meat a year, which is equivalent to a medium to large sized herbivore such as wildebeest, tsessebe or zebra (Rogan et al. 2017). This leads to the removal of a substantial amount of bush-meat, with an estimated 1000 hunters operating within the Okavango Delta (Rogan et al. 2017). This study indicates that, when combined with predation, bush-meat poaching has a negative, additive effect on the numbers of large herbivores, resulting in population declines (Rogan et al. 2017). Future studies should focus on mitigation methods to reduce bush-meat poaching and look for alternative livelihoods for hunters who poach commercially.

The veterinary fence, which borders the Okavango Delta, as well as its declaration as a RAMSAR world heritage site, precludes damage to the ecosystem that could be caused by further human encroachment into the Okavango, or damage to grazing caused by the encroachment of cattle. However, the fence may also prevent migration of animals to and from the Okavango, and correspondingly decrease the wet season range available to the members of the grazing guild which may have originally migrated out of the area during the wet season. This is important as wet season range may also contribute to overall carrying-capacity, particularly in wetter years in the Okavango where there is increased pressure on the dry season grazing (Yoganand and Owen-Smith 2014). Therefore, studies on wet season range use for each of the grazing herbivores over various flooding conditions would also prove valuable in determining the effects of the changing environment coupled with space restriction resulting from the veterinary fence.

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Appendix

Table 1. List of species sampled during vegetation sampling conducted in 2007. Species have been divided into palatability categories where 1 = non-palatable sedges (Cyperaceae), 2 = semi-palatable grasses (Poaceae), and 3 = highly palatable species (Poaceae). To maintain simplicity in the division between grass- and sedge-dominated areas, all sedges were classified as non-palatable.

Species name	Abbreviation	Family	Palatability category
Abildgaardia hispidula	Abihis	Cyperaceae	1
Cyperus articulatus	Cypart	Cyperaceae	1
Cyperus compressus	Cypcom	Cyperaceae	1
Cyperus denudatus	Cypden	Cyperaceae	1
Cyperus dives	Cypdiv	Cyperaceae	1
Cyperus esculentus	Cypesc	Cyperaceae	1
Cyperus longus	Cyplon	Cyperaceae	1
Cyperus maculatus	Cypmac	Cyperaceae	1
Cyperus sphaerospermus	Cypsph	Cyperaceae	1
Eleocharis acutangula	Eleacu	Cyperaceae	1
Eleocharis dulcis	Eledul	Cyperaceae	1
Eleocharis variegata	Elevar	Cyperaceae	1
Fimbristylis complanata	Fimcom	Cyperaceae	1
Fuirena pubescens	Fuipub	Cyperaceae	1
Fuirena umbellata	Fuiumb	Cyperaceae	1
Kyllinga erecta	Kylere	Cyperaceae	1
Kyllinga intricata	Kylint	Cyperaceae	1
Mariscus hamulosus	Marham	Cyperaceae	1
Oxycaryum cubense	Oxycub	Cyperaceae	1
Pycreus flavescens	Pycfla	Cyperaceae	1
Pycreus mundtii	Pycmun	Cyperaceae	1
Pycreus nitidus	Pycnit	Cyperaceae	1
Rhynchospora holoschoenoides	Rhyhol	Cyperaceae	1
Schoenoplectus corymbosus	Schcor	Cyperaceae	1

Schoenoplectus erectus	Schere	Cyperaceae	1
Fimbristylis mini	Schroy	Cyperaceae	1
Scleria distans	Scldis	Cyperaceae	1
Scleria dregeana	Scldre	Cyperaceae	1
Andropogon huillensis	Andhui	Poaceae	2
Aristida junciformis	Arijun	Poaceae	2
Aristida meridionalis	Arimer	Poaceae	2
Brachiaria humidicola	Brahum	Poaceae	2
Chloris virgata	Chlvir	Poaceae	2
Cymbopogon excavatus	Cymexc	Poaceae	2
Dactyloctenium aegyptium	Dacaeg	Poaceae	2
Enneapogon cenchroides	Enncen	Poaceae	2
Eragrostis cylindriflora	Eracyl	Poaceae	2
Eragrostis inamoena	Eraina	Poaceae	2
Eragrostis lappula	Eralap	Poaceae	2
Eragrostis viscosa	Eravis	Poaceae	2
Imperata cylindrica	Impcyl	Poaceae	2
Melenis repens	Melrep	Poaceae	2
Miscanthus junceus	Misjun	Poaceae	2
Oryza longistaminata	Orylon	Poaceae	2
Paspalidium obtusifolium	Pasobt	Poaceae	2
Paspalum scrobiculatum	Passcr	Poaceae	2
Phragmites australis	Phraus	Poaceae	2
Pogonarthria squarrosa	Pogsqu	Poaceae	2
Sacciolepis typhura	Sactyp	Poaceae	2
Setaria verticillata	Setver	Poaceae	2
Sorghastrum friesii	Sorfri	Poaceae	2
Sporobolus spicatus	Spospi	Poaceae	2
Stipagrostis uniplumis	Stiuni	Poaceae	2
Tragus berteronianus	Traber	Poaceae	2
Trachypogon spicatus	Traspi	Poaceae	2
Tricholaena monachne	Trimon	Poaceae	2
Acroceras macrum	Acrmac	Poaceae	3
Cenchrus ciliaris	Cencil	Poaceae	3
Chloris gayana	Chlgay	Poaceae	3

Cynodon dactylon	Cyndac	Poaceae	3
Digitaria abyssinica	Digaby	Poaceae	3
Digitaria debilis	Digdeb	Poaceae	3
Digitaria eriantha	Digeri	Poaceae	3
Digitaria eylesii	Digeyl	Poaceae	3
Digitaria maniculata	Digman	Poaceae	3
Echinochloa colona	Echcol	Poaceae	3
Leersia hexandra	Leehex	Poaceae	3
Panicum coloratum	Pancol	Poaceae	3
Panicum dregeanum	Pandre	Poaceae	3
Panicum maximum	Panmax	Poaceae	3
Panicum repens	Panrep	Poaceae	3
Schmidtia pappophoroides	Schpap	Poaceae	3
Setaria sphacelata	Setsph	Poaceae	3
Sporobolus ioclados	Spoioc	Poaceae	3
Urochloa brachyura	Urobra	Poaceae	3
Urochloa mosambicensis	Uromos	Poaceae	3
Vossia cuspidata	Voscus	Poaceae	3

Table 2. List of species sampled during vegetation sampling conducted in 2013 as part of this study. Species have been divided into palatability categories where 1 = non-palatable sedges (Cyperaceae), 2 = semi-palatable grasses (Poaceae), and 3 = highly palatable species (Poaceae). To maintain simplicity in the division between grass- and sedge-dominated areas, all sedges were classified as non-palatable.

Species name	Abbreviation	Family	Palatability category
Bulbostylis hispidula	Bulula	Cyperaceae	1
Cyperus leptocaldus	Cypdus	Cyperaceae	1
Cyperus articulatus	Cypusa	Cyperaceae	1
Cyperus leptocaldus	Cypgus	Cyperaceae	1
Cyperus species	Cypies	Cyperaceae	1
Cyperus leptocaldus	Cyptus	Cyperaceae	1

Cyperus denudatuss	Cypuss	Cyperaceae	1
Eleocharis acutangula	Eleula	Cyperaceae	1
Fimbristylis longiculmis	Fimmis	Cyperaceae	1
Fimbristylis dichotoma	Fimoma	Cyperaceae	1
Fuirena umbellata	Fuiata	Cyperaceae	1
Fuirena pubescens	Fuiens	Cyperaceae	1
Kyllinga intricata	Kylata	Cyperaceae	1
Kyllinga erecta	Kylcta	Cyperaceae	1
Pycreus pelophilus	Pyclus	Cyperaceae	1
Pycreus macrostachyos	Pycyos	Cyperaceae	1
Rhynchospora holoschoenoides	Rhydes	Cyperaceae	1
Schoenoplectus corymbosus	Schsus	Cyperaceae	1
Schoenoplectus erectus	Schtus	Cyperaceae	1
Andropogon eucomus	Andmus	Poaceae	2
Aristida stipitata	Ariata	Poaceae	2
Aristida meridionalis	Arilis	Poaceae	2
Aristida junciformis	Arimis	Poaceae	2
Aristida adscensionis	Arinis	Poaceae	2
Aristida congesta subs congesta	Arista	Poaceae	2
Aristida scabrivalvis	Arivis	Poaceae	2
Brachiaria deflexa	Braexa	Poaceae	2
Brachiaria humidicola	Braola	Poaceae	2
Chloris virgata	Chlata	Poaceae	2
Cymbopogon excavatus	Cymtus	Poaceae	2
Dactlyoctenium aegyptian	Dacian	Poaceae	2
Enneapogon cenchroides	Enndes	Poaceae	2
Eragrostis inamoena	Eraena	Poaceae	2
Eragrosits pallens	Eraens	Poaceae	2
Eragrostis rigidior	Eraior	Poaceae	2
Eragrostis lehmannia	Erania	Poaceae	2
Eragrostis trichophora	Eraora	Poaceae	2
Eragrostis superba	Erarba	Poaceae	2
Heteropogon contortus	Hettus	Poaceae	2
Hyperthelia dissoluta	Hyputa	Poaceae	2
Imperata cylindrica	Impica	Poaceae	2

Melinis repens	Melens	Poaceae	2
Paspalum scrobiculatum	Pastum	Poaceae	2
Pogonarthria squarrosa	Pogosa	Poaceae	2
Sacciolepis typhura	Sacura	Poaceae	2
Schmidtia kalahariensis	Schsis	Poaceae	2
Setaria pumila	Setila	Poaceae	2
Setaria verticillataa	Settaa	Poaceae	2
Sporobolus bechuanicus	Spocus	Poaceae	2
Sporobolus ioclados	Spodos	Poaceae	2
Sporobolus cordofanus	Sponus	Poaceae	2
Sporobolus spicatuss	Spouss	Poaceae	2
Sporobolus festivus	Spovus	Poaceae	2
Stipagrostis uniplumis	Stimis	Poaceae	2
Stipagrostis hirtigluma	Stiuma	Poaceae	2
Trachyopogon spicatus	Tratus	Poaceae	2
Andropogon gayanus	Andnus	Poaceae	3
Brachiaria nigropedata	Braata	Poaceae	3
Cenchrus ciliaris	Cenris	Poaceae	3
Chloris gayana	Chlana	Poaceae	3
Cynodon dactylon	Cynlon	Poaceae	3
Digitaria debilis	Diglis	Poaceae	3
Digitaria eylesii	Digsii	Poaceae	3
Digitaria eriantha	Digtha	Poaceae	3
Enteropogon machrostachyus	Entyus	Poaceae	3
Eragrostis porosa	Eraosa	Poaceae	3
Leersia hexandra	Leedra	Poaceae	3
Panicum subalbidum	Pandum	Poaceae	3
Panicum repens	Panens	Poaceae	3
Panicum maximum	Panmum	Poaceae	3
Panicum fulviicola	Panola	Poaceae	3
Panicum coloratum	Pantum	Poaceae	3
Setaria sphacelata var. Sphacelata	Setata	Poaceae	3
Setaria sphacelata var. Sericea	Setcea	Poaceae	3
Sporobolus fimbriatus	Spotus	Poaceae	3

Urachloa trichopus	Urapus	Poaceae	3

Table 3. Results from generalized linear models used to calculate monthly flood duration optima for species from vegetation transects conducted in 2007. Species which occurred in less than three quadrats were excluded from the analysis. Some excluded species were those whose duration optima were estimated at less than zero (dry land species) or show duration optima that were longer than 12 months. Species with too few occurrences were also excluded as the models did not converge. Palatability refers to the palatability category within which each species was placed, with 1 = unpalatable sedges, 2 = semi-palatable grasses and 3 = palatable grasses. The proportion of original species sampled for which duration optima could be calculated for each palatability category are 0.39, 0.21 and 0.14 for categories 1, 2 and 3 respectively.

Species	Palatability	F	p	Optimum	SE (Optimum)	Tolerance	SE(Tolerance)
Cyperus articulatus	1	0.58	0.4397	4.55	2.33	1.04	2.89
Cyperus denudatus	1	1.75	0.1758	5.24	3.09	1.96	3.09
Cyperus longus	1	3.82	0.0228	6.42	0.84	0.83	1.13
Cyperus sphaerospermus	1	0.10	0.0907	5.53	0.87	0.47	2.17
Eleocharis acutangula	1	1.59	0.2063	5.35	1.57	1.48	1.71
Eleocharis variegata	1	32.53	<1.0e-6	8	1.34	1.52	2.94
Fimbristylis complanata	1	5.45	0.0046	8.02	3.61	1.94	8.57
Fuirena pubescens	1	19.73	<1.0e-6	6.52	0.58	0.87	0.76
Kyllinga erecta	1	9.13	0.0001	6.77	0.63	0.30	1.13

Pycreus nitidus	1	26.57	<1.0e-6	7.42	0.60	0.33	0.35
Schoenoplectus corymbosus	1	28.49	<1.0e-6	5.07	0.25	1.35	0.26
Brachiaria humidicola	2	1.79	0.1678	4.67	1.15	1.31	1.25
Eragrostis inamoena	2	22.86	<1.0e-6	5.3	0.32	1.08	0.37
Eragrostis lappula	2	2.90	0.0562	4.12	1.16	1.74	1.31
Miscanthus junceus	2	7.12	0.0009	7.43	0.68	0.34	0.37
Sacciolepis typhura	2	17.94	<1.0e-6	7.05	0.83	1.36	1.47
Sorghastrum friesii	2	6.21	0.0022	3.13	0.66	1.00	0.85
Leersia hexandra	3	0.03	0.0318	7.31	1.24	0.83	1.59
Panicum repens	3	27.82	<1.0e-6	5.05	0.21	1.36	0.22
Setaria sphacelata	3	5.63	0.0039	3.48	0.47	1.46	0.69

Table 4. Results from generalized linear models used to calculate monthly flood duration optima for species from vegetation transects conducted in 2013. Species which occurred in less than three quadrats were excluded from the analysis. Some excluded species were those whose duration optima were estimated at less than zero (dry land species) or show duration optima that were longer than 12 months. Species with too few occurrences were also excluded as the models did not converge. Palatability refers to the palatability category within which each species was placed, with 1 = unpalatable sedges, 2 = semi-palatable grasses and 3 = palatable grasses. The proportion of original species sampled for which duration optima could be calculated for each palatability category are 0.31, 0.27 and 0.50 for categories 1, 2 and 3 respectively.

Species	Palatability	F	P	Optimum	SE (Optimum)	Tolerance	SE(Tolerance)
Cyperus leptocaldus	1	1.3	0.2726	5.69	7.56	5.29	7.02
Cyperus leptocaldus	1	15.18	<1.0e-6	4.94	0.64	2.17	0.87
Fimbristylis longiculmis	1	4.7	0.0093	6.70	3.14	2.65	6.65
Eleocharis acutangula	1	2.12	0.1207	3.14	0.75	2.03	0.66
Cyperus articulatus	1	4.82	0.0083	4.81	0.93	0.63	0.70
Fimbristylis dichotoma	1	5.43	0.0045	4.15	1.09	0.60	0.71
Sporobolus spicatuss	2	5.72	0.0034	5.51	1.79	4.08	1.95
Sporobolus festivus	2	4.92	0.0074	3.45	0.46	1.67	0.49
Eragrostis inamoena	2	9.78	0.000061	4.51	0.40	1.58	0.55
Imperata cylindrica	2	20.54	<1.0e-6	7.97	1.66	3.60	3.86
Andropogon eucomus	2	5.99	0.0026	10.51	7.56	4.02	24.56
Sacciolepis typhura	2	11.45	0.000012	4.82	0.48	1.21	0.69
Cymbopogon excavatus	2	0.08	0.0767	1.34	22.05	5.24	17.15
Pogonarthria squarrosa	2	0.607	0.4547	4.35	4.16	2.06	3.62
Trachyopogon spicatus	2	9.3	0.000098	5.88	0.90	0.87	0.63
Setaria verticillataa	2	0.067	0.0652	1.55	19.97	4.18	23.16
Cynodon dactylon	3	25.74	<1.0e-6	3.16	0.20	2.71	0.30
Panicum coloratum	3	8.8	0.0002	1.02	1.10	2.60	1.60
Cenchrus ciliaris	3	4.48	0.0116	2.37	0.80	2.68	0.67

Sporobolus fimbriatus	3	1.5	0.2238	2.38	1.05	2.03	1.04
Chloris gayana	3	1.74	0.1758	2.07	1.01	2.18	1.07
Setaria sphacelata var. Sericea	3	12.99	0.000003	5.93	0.20	0.58	0.32
Digitaria debilis	3	24.79	<1.0e-6	3.97	1.90	0.25	0.48
Digitaria eylesii	3	30.25	<1.0e-6	6.00	1.18	0.27	0.32
Enteropogon machrostachyus	3	5.25	0.0054	2.09	0.73	0.57	0.43
Panicum subalbidum	3	20.76	<1.0e-6	6.00	1.29	0.29	0.37