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Water and wildlife in the Serengeti-Mara ecosystem

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Water and wildlife in the Serengeti-Mara ecosystem

Emilian S. Kihwele

The research reported in this thesis was carried out at the conservation ecology group of Groningen Institute for Evolutionary Life Sciences (GELIFES) in the Faculty of Mathematics and Engineering of University of Groningen according to the requirements of the Graduate School of Science.

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Water and wildlife in the Serengeti-Mara ecosystem

PhD thesis

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on the authority of the
Rector Magnificus Prof. C. Wijmenga
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the decision by the College of Deans.

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Friday 16 April 2021 at 12.45 hours

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A photo of elephant herd wallowing into mud for thermoregulation (Source: Emilian Kihwele)

Chapter 1

General introduction

Emilian S. Kihwele

Surface water availability for herbivores in savannah ecosystems is progressively under threat through changes in land-uses, deforestation, increased irrigation (Mati et al. 2008; Gereta et al. 2009; Kipampi et al. 2017) and climate change (Tramblay et al. 2018; Nikam et al. 2018); More importantly, this unprecedented continual decline in surface water is expected to have devastating consequences on herbivore distributions and ecosystem processes (Gereta et al. 2009). Alterations in surface water availability can affect species interactions and disrupt ecosystem functioning through restricting herbivore populations from accessing and utilizing their seasonal home ranges (Weeber et al. 2020). If migratory species are confined to a delimited localized area and unable to disperse to more suitable habitats, populations might face severe decline and some species may undergo local extinction. Conservationists are concerned with potential loss of ecosystem services because of failure to understand and manage accordingly the effects of surface water availability on herbivore distributions. Understanding surface water dependence of African savannah herbivores to increase our predictive ability of ecosystem response to changes in surface water availability is critical to the success of protected area conservation and management.

Surface water is a key resource for wildlife conservation and its spatial and temporal distribution is important in understanding the distribution and composition of large herbivore assemblages across savannah ecosystems (Weeber et al. 2020). Ongoing human population growth and associated land use changes are placing high pressure on surface water distributions that are essential for maintaining savannah ecosystems. Particularly susceptible are the migratory species for which homogenization (more even distribution across landscape) of surface water availability through water points would result into disconnecting them from utilizing crucial home ranges (Redfern et al. 2005; Valeix et al. 2008; Valeix 2011; Weeber et al. 2020). Most ungulates in drylands and savannah ecosystems require a regular and adequate access to surface water to maintain body water balance (Maloiy 1973). Given the rate of land use and climate changes, situations where populations are prevented from accessing water are expected and would result into disrupted landscape use with ultimate effects on ecosystem processes. Surface water facilitates predation and its homogenisation will result into favouring water-dependent species, subsequently promoting forage competition and habitat degradation while subjecting water independent species into high predation risk (Hopcraft et al. 2010). Equally important, the lack of surface water would have opposite effects on predators and water requirements for large herbivores. Therefore, changes in surface water in either direction will change how herbivores utilize the landscape and thereby shift the dynamics of African savannah ecosystems.

In savannah ecosystems, maintaining surface water availability for herbivores is particularly critical for sustaining ecosystem processes (Gereta and Wolanski 1998; Gereta et al. 2009; Sinclair et al. 2018). Various studies have related distance to water distribution of herbivores with their water dependence (Western 1975; Gaylard et al.

2003; Redfern et al. 2003; Smit 2011; Owen-Smith 2012). But the spatial distribution of large herbivores across the landscape is also confounded by other factors such as predation risk and food requirements. In this thesis I explore the causes and consequences of hydrological changes on African savannah herbivores and how ungulates interact with variation in surface water availability across the Serengeti-Mara ecosystem.

Study area

This study was carried out within the Serengeti-Mara Ecosystem (SME) which is an important trans-boundary ecosystem shared between Tanzania and Kenya. This extensive ecosystem is located within 34° to 36° E and 1° to 3° 30' S, in North Western Tanzania and South Western Kenya. About 85% of the ecosystem is legally protected through a network of protected areas under different management authorities. In the context of this study this ecosystem is defined based on the annual home range used by migrating ungulate (wildebeest migration) and systems of major river basins that drain the landscapes.

The Serengeti-Mara ecosystem, thus defined by the wildebeest migration, is a landscape of ecological importance with the highest levels of species diversity and biomass of large herbivores in the world (LVBC and WWF-ESARPO, 2010). It is home to the last large mammal migration of ungulates (Harris et al. 2009) composing an estimated 1.2 million wildebeest, the keystone species and 0.25 million zebra, which all together support the lives of about 2500 lion and 7000 hyena (Hopcraft, 2010). The ecosystem covers an area of about 33,000 square kilometers characterised by the range used by the migrating ungulates in an annual cycle in search of water and forage (Figure 1.1).

Administratively and as shown in figure 1.1, the Serengeti-Mara ecosystem comprises of core ecological units of the Serengeti National Park (14,763 km²) and the Masai Mara National Reserve (1,510 km²) surrounded by other protected area systems of Ngorongoro Conservation Area (8,288 km²), Maswa Game Reserve (2,200 km²), Ikorongo and Grumet Game Reserves (979 km²), Kijereshi Game Reserve (46 km²), Speke Game Controlled Area (50 km²), Loliondo Game Controlled Areas (4,000 km²), IKONA Wildlife Management Area (242 km²) and MAKAO Wildlife Management Areas (769 km²). Furthermore, this ecosystem is an important water catchment area that is not only important for Lake Victoria but also for maintaining the integrity and the sustainability of wildlife in it.

Hydrologically the SME is composed of three catchment basins, the Mara River (10,300 km²); the Grumeti River (11,600 km²) and the Mbalageti (2680 km²) River catchments, all flowing westward to Lake Victoria (Gereta and Wolanski, 1998). The Mara River, a trans-boundary resource shared between Kenya (65%) and Tanzania (35%) drains the Maasai Mara National Reserve and far northern part of Serengeti

Figure 1.1: Map of the study area, indicating lakes, rivers, rainfall (CHIRPS, average 1981–2018), protected areas and the annual wildebeest migration.

National Park. The Grumeti and Mbalageti Rivers drain much of the wooded savannah, treeless grasslands and hills in the central, northern and southern areas, much of which fall within the Serengeti National Park.

The Mara River which is 395 km long, originates from the Napuiyapui swamp on the Mau Escarpment in the highlands of Kenya with two main perennial tributaries, the Amala and Nyangores Rivers (Mati et al. 2008). It is the only permanent source of drinking waters for migrating animals, especially during the dry season and in drought years (Wolanski and Gereta, 2001; Gereta and Wolanski, 2008). The sustainable use by the people and wildlife of this river is however, under severe threat as its water quality is progressively changing, with increased contribution from groundwater, with higher pH and visibility and varying salinity (Gereta et al. 2009). The flow rate of the river during drought has decreased by 68% mainly due to deforestation of the Mau catchment forest and increased abstraction of water to meet irrigation demand in Kenya (Gereta et al. 2009; Mnaya et al. 2017).

Outline of this thesis

Chapter 2: Large herbivore assemblages in a changing climate: incorporating water dependence and thermoregulation

In this chapter, we review literature on how herbivore's body size relates with water dependence and thermoregulation in savannah and semi-arid ecosystems which are often water constrained especially in the dry season. We further developed testable hypotheses about expected changes in large herbivores community composition following changes in surface water availability. Surface water availability may explain a large scale spatial distribution of herbivores across the landscape; traditionally the distance to water has been used as a proxy for species water dependence because the species' spatial distribution over the landscape has been well established to depend on species' sensitivity to water, predation risk and food requirements (Hopcraft et al. 2012; Owen-Smith et al. 2015).

In this chapter we propose two main dimensions of niche partition in savannah herbivores, related to forage and surface water availability. Thus the inadequacy of distance to water distribution to be used as a reliable generalized index of surface water dependence compromises the capacity of conservationists to predict effects of surface water on the spatial distribution of herbivores given both human impacts on water availability and climate change impacts. The addition of surface water availability allows ecologists and conservationists to understand how similar sized herbivores can co-exist in the same ecosystem by using habitats that are characterised by different distance to surface water. This leads to four hypotheses related to water requirement. We predict that increased spatial homogeneity in surface water availability reduces the number of ungulate species that can coexist (H1). Furthermore, we expect that increased extreme droughts will have the most negative impact on the largest grazers that depend most on surface water (H2). We also hypothesize that species that prefer to occupy areas close to permanent surface water are expected to have fewer problems with increasing temperatures as they can increase water intake and use it to compensate (H3). In addition, because surface water increases predation risk, we expect that water dependent herbivores generally experience higher exposure to predation because predator densities are higher around surface water (H4).

Chapter 3: Upstream land-use negatively affects river flow dynamics in the Serengeti National Park

Landscape use by wildlife in space and time has been shown to depend on surface water availability (Western 1975; Gereta et al. 2009; Veldhuis et al. 2019) and in turn has consequences for herbivore population regulation and ecosystem processes (Hopcraft et al. 2010; Owen-Smith and Traill 2017). In this chapter, I study how upstream land-use affect river flow (water availability) in the Serengeti National park, and subse-

quently wildlife community diversity and composition. I quantify the effects of different land management regimes (fire and livestock grazing) through continuous monitoring stream flow dynamics in small watersheds under intensive livestock grazing and fire treatments and compared this effect with the control watersheds. To elucidate the effects of land use between human dominated landscape and protected area, I further monitored river flow levels in four major watersheds that were further compared with historical flow levels. In this study, I show that between 1972 and 2018, human activities upstream and outside protected area has changed the recession time scale of the Mara River while the lack of human activities in the Serengeti National Park has maintained the hydrological properties of the Mbalageti River.

Chapter 4: Quantifying water requirements of African ungulates through a combination of functional traits

In this chapter, we investigate how African ungulates differ in water requirement using functional traits related to dung, urine and evaporation and how changes in water availability will affect the community composition of savannah ungulates. We quantified water dependence of 48 African large mammalian herbivore species using six functional traits. We combined data on dung in Serengeti and Gorongosa National Parks with data from published studies. We further subsequently investigated how predicted water requirement relate with herbivores feeding type, phylogeny and classifications of surface water dependence based on literatures. We showed strong correlations between traits related to water loss through dung, urine and evaporation, indicating that herbivore species conserve body water through multiple pathways simultaneously. Furthermore, we described that browsers and grazers, despite having similar water requirement can coexist because browsers reduce dependence on drinking from surface water by compensating with water obtained through food. This is because herbivores have developed different physiological, ecological and behavioral adaptation that allow them survive periods of water shortage. Thus, we propose that heterogeneity in surface water across savannah ecosystems increases species diversity and allows coexistence of diverse herbivore assemblages.

Chapter 5: Variation in water requirements allow spatial niche partitioning among savannah grazers

In this chapter, we investigated drivers of spatial niche differentiation among savannah herbivores in relation to distance to permanent surface water through dung and visual counts across Serengeti National Park. Here, we tested how mean distance to water, dry season dung moisture and body size might determine the water requirements of herbivore species. We identified water requirements as an additional dimension of spatial niche partitioning for grazing herbivores along distance to surface water gradient. Conversely, we showed that the distribution of browsers coincided with highest tree basal area suggesting that their distribution might be driven by food availability.

A photo of herbivore community assemblage in northern Serengeti (Source: Musa Mandia)

Large herbivore assemblages in a changing climate: incorporating water dependence and thermoregulation

Michiel P. Veldhuis, Emilian S. Kihwele, Joris P.G.M. Cromsigt
Joseph O. Ogutu, Grant C. Hopcraft, Norman Owen-Smith & Han Olff

Abstract

The coexistence of different species of large herbivores (ungulates) in grasslands and savannah has fascinated ecologists for decades. However, changes in climate, land-use and trophic structure of ecosystems increasingly jeopardize the persistence of such diverse assemblages. Body size has been used successfully to explain ungulate niche differentiation with regard to food requirements and predation sensitivity. But this single trait axis insufficiently captures interspecific differences in water requirements and thermoregulatory capacity and thus sensitivity to climate change. Here, we develop a two-dimensional trait space of body size and minimum dung moisture content that characterizes the combined food and water requirements of large herbivores. From this we predict that increased spatial homogeneity in water availability in drylands reduces the number of ungulate species that will coexist. But we also predict that extreme droughts will cause the larger, water-dependent grazers as wildebeest, zebra and buffalo – dominant species in savannah ecosystems – to be replaced by smaller, less water-dependent species. Subsequently, we explore how other constraints such as predation risk and thermoregulation are connected to this two-dimensional framework. Our novel framework integrates multiple simultaneous stressors for herbivores and yields an extensive set of testable hypotheses about the expected changes in large herbivore community composition following climate change.

Introduction

Predicting how climate change will affect ungulate communities is now urgent (Speakman and Król 2010; Fuller et al. 2014; Shrestha et al. 2014; Fuller et al. 2016; Pigeon et al. 2016) because increasing land temperatures, changing rainfall regimes (Niang et al. 2014) and habitat fragmentation increase the risk of regional extinctions (Ripple et al. 2015). Herbivores thus face rapid changes in the availability of food and water simultaneously. Furthermore, the capacity of species to adapt to these changing resource availabilities will interact with changes in other constraints, such as temperature and predation risk. For effective conservation strategies we need integrated predictive frameworks that incorporate all of these key determinants of herbivore assemblages. Here, we propose to integrate these constraints for ungulates in grasslands and savannah through a limited set of key functional traits (see Glossary) using the large herbivore assemblages in African savannah ecosystems as a generalizable example. This trait-based approach aims to capture the main axes of variation with regard to physiology, ecology and evolutionary history (Cadotte et al. 2013) into a broader framework. This yields five testable hypotheses (H1-H5) about changes in ungulate assemblages in response to climate change or management interventions, such as protected area enlargement (including longer landscape gradients), homogenization of landscape water availability through establishment of artificial water points (e.g., dams for watering livestock), or extirpation or reintroduction of predators.

Niche partitioning among ungulates: the role of body size

The diversity of mammals in African savannah has intrigued ecologists for decades, particularly the coexistence of so many ungulates that apparently eat similar food. Multiple key insights on dietary niche partitioning have followed since. First, predictable dietary variation is found along the grazer-browser continuum (Lamprey 1963), a separation which has recently been studied in greater detail using differences in isotopic signals of C4 grasses and C3 trees and forbs (Ambrose and Deniro 1986; Cerling et al. 2003; Codron et al. 2007), or even to the species level using DNA-barcoding techniques (Kartzin et al. 2015). Second, digestive strategy (ruminant vs non-ruminant) and body size capture the trade-off between foraging on large amounts of low-quality food (such as including a high proportion of stems and twigs) vs small amounts of high-quality food such as young leaves (Illius and Gordon 1992; Wilmshurst et al. 2000). Body size variation is therefore commonly used to explain niche differentiation and coexistence along major landscape gradients of plant available moisture and nutrients, that together determine the availability and digestive quality of plant biomass (Olf et al. 2002; Hopcraft et al. 2010). In addition, body size predicts how vulnerable animals are to predation (larger species are generally less vulnerable) (Sinclair et al. 2003). This has yielded an established framework for explaining resource partition-

ing based on interspecific differences in body size and feeding style (grazer-browser continuum) (Olf et al. 2002; Gordon and Prins 2008; Hopcraft et al. 2010). Based on this framework we expect larger herbivores to be more affected by drought through reduced availability of forage (Olf et al. 2002; Hopcraft et al. 2010). Furthermore, grazers are expected to be more susceptible to droughts than browsers (Kay 1997; Gordon and Prins 2008). This is because shallow-rooting grasses dry out much faster with the onset of the dry season than deeper-rooting woody species. However, this framework is incomplete, as it does not incorporate key components of physiological tolerance of the ecological niche: thermoregulation capacity and water requirements. Given the current rate of climate change, we need to understand if important interspecific differences in adaptations to drought and high temperatures can also be explained by variation in body size, or whether other (independent) functional traits are required to predict species responses to landscape gradients and climate change scenarios. Such an integrated framework will be useful for the design of novel experiments to test underlying mechanisms and to improve predictions of future changes in large herbivores community assembly.

Thermal tolerance of different-sized species

Below-optimal body temperatures potentially restrict the metabolic rate and activity of animals (Gillooly et al. 2001; Savage et al. 2004). Endotherms can generally maintain high metabolic rates and associated activity despite low external temperatures through homeostasis of body temperature. However, much less known and studied are the negative effects of above-optimal temperatures in endotherms that can potentially lead to hyperthermia (Speakman and Król 2010; Payne and Bro-Jørgensen 2016). Body mass is an important determinant of heat balance in endotherms, because larger species have less surface area per unit volume or weight (Porter and Kearney 2009). This causes large animals to more easily retain heat under cold conditions but also to more difficulty lose heat under warm conditions. Problems with losing heat may thus limit the activity of large ungulate species, as buffalo (*Syncerus caffer*), hippo (*Hippopotamus amphibius*) or elephant (*Loxodonta africana*), under very hot conditions (blue arrows Figure 2.1A). Current evidence confirms these predictions and shows that larger ungulates indeed limit their activity more strongly at high temperatures (Du Toit and Yetman 2005; Aublet et al. 2009; Gardner et al. 2011; Owen-Smith and Goodall 2014). Moreover, there is evidence that larger animals rely more on sweating and wallowing than small species as a way of losing heat (Robertshaw and Taylor 1969; Parker and Robbins 1984). Lastly, smaller animals also can better create or access burrows, holes, caves and shaded habitats under taller grass, shrubs and trees, all cool microhabitats that allow them to temporarily escape hot times with high solar radiation (Fuller et al. 2016). Therefore, body size is a key functional trait for understanding not only the food requirements and predation risk of savannah ungulates, but also for understanding their thermoregulatory constraints.

Capturing surface water dependence in a key trait

Weak dependence on surface water is beneficial for savannah ungulates as it reduces various costs associated with drinking (Cain et al. 2012). For example, it opens up additional foraging areas far away from water, reduces energy costs associated with travel to and from water, enables spatial partitioning with other (more water-dependent) ungulates for food and reduces exposure to predation (see below). Increasing availability of census data and technical and statistical methodologies have therefore produced a range of new results on how ungulate behaviour is driven by spatio-temporal availability of surface water, using distance to surface water as a proxy for surface water dependence (Redfern et al. 2003; Smit 2007; Ogutu et al. 2010; Smit 2011; Owen-Smith 2012; Ogutu et al. 2014). However, it is still difficult to draw clear general conclusions from these studies due to confounding of water requirements, food requirements and predation risk sensitivity as a key driver. A more reliable, and more easy to measure, indicator of surface water dependence may instead be found in specific functional traits related to water balance adaptations (Kihwele et al. 2020).

Water scarcity in savannah has led to specific morphological, physiological and behavioral adaptations in ungulates, allowing them to survive through the dry season (McNab 2002; Cain et al. 2006; Fuller et al. 2016; Abraham et al. 2019). Reduced dependence on surface water has evolved in ungulates through different adaptations: i) increasing dietary water intake, ii) higher water storage in the body (also in carbohydrates, proteins or fat for later release as metabolic water), or iii) by reducing water losses ((Rymer et al. 2016); Figure 2.1B).

Figure 2.1: Overview of the primary components of the thermoregulation (A) and water balance (B) of terrestrial endothermic ungulates. Red arrows represent routes of heat gain and loss over a time interval while blue arrows represent water loss and gain (affected by morphology, physiology and behavior). (A) Heat gain can be reduced by either avoiding direct sunlight or decreased activity, while heat loss can be increased through transpiration, direct contact with cool substrates or increased air flow across the skin. (B) Regular dependence on surface water is lower in species with less water losses or higher dietary water content. Intervals between water intake (surface or dietary) are higher in species with higher internal storage.

During the dry season, the leaf water content of grasses that die off aboveground is generally lower than that of woody plants that remain green. The resulting higher dietary water intake makes browsers generally less surface water-dependent than grazers (Kay 1997). This dietary water intake can even yield sufficient water for some species to survive for long periods without drinking. Metabolic water production (e.g. through metabolizing carbohydrates, fat or proteins that were stored in the body in the wet season) is crucial for dryland granivorous birds and small mammals (Schmidt-Nielsen 1964; Degen 1997), but seems to play only a small role in the water balance of dryland ungulates (Taylor 1968).

Ungulates lose water through five routes: pulmonary evaporation, cutaneous evaporation, faeces, urine and lactation ((Rymer et al. 2016); Figure 2.1B). Faecal and urinary water losses have been studied most extensively in dehydration experiments (Taylor 1968; Brobst and Bayly 1982) and dissections to study internal organs (Clemens and Maloij 1982; Woodall and Skinner 1993). These studies show that ungulates exhibit two main physiological adaptations for reducing water loss. Arid adapted species have 1) a relatively long large intestine and smaller circumference of the spiral colon that allows them to resorb more moisture from their faeces (Woodall and Skinner 1993; Woodall 1995) and 2) increased length of the loop of Henlé in the kidney nephron that makes them capable of producing more concentrated urine (Louw and Seely 1982; McNab 2002; Ouajd and Kamel 2009). These traits are phylogenetically correlated: species that typically produce dry dung can also produce highly concentrated urine (Louw and Seely 1982; Kihwele et al. 2020) (Figure 2.2A; LM: $F_{1,5} = 128$, $R^2 = 0.96$, $P < 0.001$). Selective pressures for one mode of water conservation will also likely favor the other. It can therefore be expected that across species, traits that restrict pulmonary and cutaneous water losses are correlated with traits that restrict faecal and urinary water loss (Kihwele et al. 2020). For example, species that need to obtain most water from drinking surface water produce relatively wet dung. In contrast, very dry dung pellets are produced by species that obtain a substantial proportion of their water from leaves, as demonstrated through oxygen isotope enrichment (Kohn 1996; Blumenthal et al. 2017) (Figure 2.2B; Linear model: $F_{1,14} = 20.7$, $R^2 = 0.71$, $P < 0.001$). The strong correlations between these three traits (dung moisture, urine osmolality, isotopic oxygen enrichment) likely reflect physiological niche differentiation among species along landscape aridity gradients. Overall, this strongly suggests that the capacity to resorb water from dung (minimum dung moisture) and urine (maximum urine osmolality) are reliable indicators of the water requirements of ungulates (Kihwele et al. 2020).

The interplay of food and water requirements

To study the interdependence between food and water constraints we explore the relation between body mass (capturing food requirements) and minimum dung moisture content (capturing water requirements) using published datasets. Minimum dung

Figure 2.2: Relationships between key functional traits related to water requirements of savanna ungulates. A) Negative correlation between minimum dung moisture content and maximum urine osmolality for 6 ungulate species (Linear model: $F_{1,5} = 128$, $R^2 = 0.96$, $P < 0.001$). B) Negative correlation between minimum dung moisture content and isotopic oxygen enrichment for African folivorous ungulates (excluding species with high percentage fruit in their diet because fruits are not enriched in oxygen isotopes) (Linear model: $F_{1,14} = 20.7$, $R^2 = 0.60$, $P < 0.001$). Higher levels of enrichment indicate a higher percentage of water derived from food. Abbreviations: BRHI = black rhino, BUF = buffalo, BUS = bushbuck, BWIL = black wildebeest, CAM = camel, CAT = zebu cattle, CELA = common eland, DON = donkey, ELE = elephant, GIR = giraffe, GOA = goat, HAR = hartebeest, HIP = hippopotamus, IMP = impala, KDD = Kirk's dikdik, MREE = mountain reedbeek, PZEB = plains zebra, SHE = sheep, WAR = common warthog, WAT = waterbuck, WIL = common wildebeest. Dung moisture data obtained from (Clemens and Maloiy 1982; King 1983; Maloiy et al. 1988; Edwards 1991; Woodall and Skinner 1993; Woodall et al. 1999; De Leeuw et al. 2001; Sitters et al. 2014). Isotopic oxygen enrichment data from (Blumenthal et al. 2017). Urine osmolality data from (King 1983). See Online Supplemental Information Table S1 for the scientific names of the species.

moisture increases with body size (Linear model: $F_{1,33} = 17.2$, $R^2 = 0.34$, $P < 0.001$; Figure 2.3) but this relation is especially determined by the largest and smallest species. Megaherbivores (>1000 kg) have high dung moisture contents of 70 – 90%. In contrast, small ungulates (<20 kg) have low dung moisture contents. Excluding these largest and smallest species, the relationship between body mass and dung moisture content disappears (Linear model: $F_{1,22} = 0.003$, $R^2 = 0.0001$, $P = 0.95$; dashed square Figure 2.3). Surprisingly, grazers and browsers do not have different minimum dung moisture content (ANOVA: $F_{2,19} = 1.59$, $R^2 = 0.05$, $P = 0.22$), suggesting that water requirements do not differ between grazers and browsers (in contrast to surface water dependence due to differences in dietary water intake), but this remains to be tested through quantifying minimum fundamental frequency of drinking (Owen-Smith 2012). Dung moisture was higher for non-ruminants (ANOVA: $F_{1,21} = 12.2$, $R^2 = 0.37$, $P = 0.002$), suggesting decreased water dependence for ruminants which is in agreement with the finding that

artiodactyls evolved and speciated under arid conditions (Strauss et al. 2017). Species generally classified as surface water-independent (Western 1975; Woodall and Skinner 1993; Kingdon et al. 2013) such as (from small to large), springbok (*Antidorcas marsupialis*), hartebeest (*Alcelaphus buselaphus*), gemsbok (*Oryx gazella*), camel (*Camelus dromedarius*) and giraffe all have low dung moisture contents while species classified as water-bound like southern reedbuck (*Redunca arundinum*), common warthog (*Phacochoerus africanus*), common wildebeest (*Connochaetes taurinus*), plains zebra (*Equus quagga*) and African buffalo have high dung moisture contents (Western 1975;

Figure 2.3: Predicted consequences of environmental change (temperatures, rainfall, predator abundance) for savannah ungulates across the food and water requirements dimensions, based on the outlined interactions between food quantity and quality and water requirements of different species. Within the intermediate range of 20–1000 kilograms of body size there is a full occupation of niche space in both dimensions. Global change is expected to affect larger ungulates more strongly but increasing temperatures and droughts have opposing effects between water-dependent and independent species. The addition of a second dimension suggests a trade-off between thermal stress and exposure to predation. In addition to abbreviations in figure 2.2: BADUI = bay duiker, BLE = blesbok, BUDUI = blue duiker, CDUI = common duiker, GEM = gemsbok, GKUD = greater kudu, KLI = klipspringer, MDUI = Maxwell's duiker, NDUI = natal duiker, NYA = nyala, SPR = springbok, SREE = southern reedbuck, STE = steenbok. Livestock species are shown in red. Mean female body mass data from (Smith et al. 2003; Kingdon et al. 2013). Dung moisture data obtained from (Clemens and Maloiy 1982; King 1983; Maloiy et al. 1988; Edwards 1991; Woodall and Skinner 1993; Woodall et al. 1999; De Leeuw et al. 2001; Sitters et al. 2014). See Online Supplemental Information Table S1 for the scientific names of the species and their body sizes.

Woodall and Skinner 1993; Kingdon et al. 2013). This large range in body size for both water-dependent and water-independent species, as also shown in figure 2.3, suggests the existence of an additional axis of niche differentiation that is independent of body size. We therefore suggest two main dimensions for niche differentiation in savannah ungulates, related to forage (Box 1) and surface water availability (Box 2), respectively. The addition of this second dimension allows us to understand how similar-sized grazers or browsers can co-exist in the same ecosystem by using habitats characterized by different distance to surface water. From this, we predict that increased spatial homogeneity in surface water availability (water sources everywhere in the landscape, such as artificial water points or dams for watering livestock that increase everywhere across arid Africa) reduces the number of ungulate species that can coexist (**H1**). Furthermore, we expect that extreme droughts will have the most negative impact on the largest grazers that depend most on surface water (**H2**; Figure 2.3). We now continue to discuss how other constraints, such as thermoregulation and predation risk might play out across this two-dimensional framework.

Box 1: Changes in livestock species composition

Rangelands in semi-arid parts of Africa are often degraded, as indicated by reduced herbaceous vegetation cover, increased exposure of bare soil and loss of productivity (Milton et al. 1994). This degradation results from multiple causes, including climatic extremes (Cai et al. 2014) and livestock overgrazing (Ayoub 1998). As such, rangeland degradation in recent decades could be viewed as representing an extreme ecosystem state that protected areas could approach under climate change, where elevated stress (both abiotic and biotic) has resulted in landscapes with limited forage and water retention capacity (Snyman 2005), i.e. drought. Recent studies show significant decreases in cattle (*Bos taurus indicus*) population size in Kenya's rangelands of approximately 25% between 1977–1980 and 2011–2013 (Ogutu et al. 2016). Cattle are slowly being replaced by sheep (*Ovis aries*) and goats (*Capra hircus*) that increased by 76.3% in the same period and, to a lesser extent, by camel (*Camelus dromedarius*, 13.1%) and donkey (*Equus asinus*, 6.7%). This pattern is consistent with the prediction that the ratio of cattle to sheep and goats should decrease with increasing aridity in Kenya's rangelands (Peden 1987). The increasing species are better able to survive extended periods of drought and can graze shorter grass better than cattle or switch to browsing so that they are still able to forage in dry areas or periods. Also, these species (sheep, goats and camel) have generally drier dung (Figure 2.3), suggesting that they are better able to resorb water from their dung. We thus expect a shift towards species with low minimum dung moisture in wild ungulate assemblages with increasing droughts and generally more mixed-feeders and/or browsers. Increased rainfall variability could amplify such shifts because rainfall is the most critical climatic component for ungulates in savannas. Rainfall governs ungulate biomass, population dynamics and distribution through its controlling influence on surface water distribution, forage production and quality (Western 1975; East 1984). Greater rainfall variability would thus exert stronger controls on ungulate population dynamics in savannas, through its influence on calving rates and deaths during severe droughts, especially of breeding females and immature animals (Angassa and Oba 2007).

Box 2: Niche differentiation along the water requirements dimension: surface water-predation interactions in Kruger National Park.

Kruger National Park encompasses a gradient in mean annual rainfall from 750 mm in the south-west to 450 mm in the north-east (Venter et al. 2003). Between the four perennial rivers that traverse the park, surface water persisted through the dry season only in pools in some of the seasonal rivers and in a few long-lasting pans or springs. Ungulates concentrate around these water sources and heavily graze in their vicinity, so that much vegetation remains unutilized remote from water. To spread animals more widely and alleviate the intense local forage depletion, the park authority constructed numerous dams, weirs and boreholes in areas that lacked perennial water sources (Smit 2013). Subsequently, zebra (*Equus quagga*) moved from the central region where most grass got consumed into the northern region during the extreme 1982-3 drought, where more food remained because of low ungulate numbers, formerly constrained by lack of water but now provisioned with artificial water points (Harrington et al. 1999). With greater prey availability, lion (*Panthera leo*) numbers also increased in the north. When the next drought occurred in 1986-7, the rarer antelope species found mostly in the north had to contend with abundant predators as well as little food. Populations of sable antelope (*Hippotragus niger*), roan antelope (*Hippotragus equinus*), tsessebe (*Damaliscus lunatus*) and eland (*Tragelaphus oryx*) crashed (Ogutu and Owen 2003). The increased surface water availability thus benefited especially zebra, with their greater water dependency, to the detriment of overall ungulate diversity in the park. The rare antelope species affected all produce very dry dung pellets, enabling them to survive in areas remote from water, unlike the more common grazers like zebra, buffalo (*Syncerus caffer*) and wildebeest (*Connochaetes taurinus*) (Figure 2.3; (Woodall and Skinner 1993)). The effect of excessive surface water provision has been to occlude the spatial heterogeneity that allowed both highly water-dependent and less water-dependent ungulates to coexist. The latter benefit especially through occupying areas where predation pressure is reduced because of the lack of the abundant grazers that form the primary prey of lions (Owen-Smith and Mills 2008).

Trade-offs between thermoregulatory and food requirements

Ungulates not only need to balance foraging and drinking but simultaneously face thermoregulatory challenges. Too low or too high temperatures can force them to seek shelter to prevent hypo- or hyperthermia, respectively. Ungulate species at high-latitudes select for thermal shelters against cold winds at the cost of forage quality during warmer times (van Beest et al. 2012; Street et al. 2016; Mason et al. 2017). European (van Beest et al. 2012) and North American moose (Street et al. 2016) prefer mature coniferous forests as thermal shelters over nutritionally more favorable deciduous and open forest habitat. Savannah ungulates seek shade during hot moments of the day thereby reducing foraging time, a reduction that is strongest for larger species (Du Toit and Yetman 2005). However, whether thermoregulatory constraints outweigh foraging constraints or vice versa is context-dependent. For example, the habitat selection of North American elk (*Cervus elaphus*) in a high-elevation desert environment was driven

more by thermoregulation than food, while in a forest environment, where thermal costs were generally lower, access to food of sufficient quality was the main limiting factor (Long et al. 2014). The same study also highlighted within population differences, with individuals that showed the poorest condition at the end of winter selecting more strongly for thermal shelters during spring and summer. Interestingly, these individuals did not increase selection for habitats with higher food quality. This supports the idea that thermoregulatory constraints can be a stronger determinant of fitness differences among individuals than limited food quality (Speakman and Król 2010; Long et al. 2016).

The interplay of surface water dependence and thermoregulation

As outlined previously, body mass is a key trait governing sensitivity to hyperthermia for savannah ungulates (Figure 2.4C). However, larger savannah ungulates can compensate for this by accessing water more frequently to cool themselves down (Figure 2.4D) suggesting an interplay between surface water dependence and thermoregulation needs. Evaporative cooling can be an important way of losing heat (Tattersall et al. 2012) but strongly increases water requirements and is thus extremely costly when drinking water availability is limited. Some extreme drought-adapted species such as the Arabian oryx (*Oryx leucoryx*) have in fact been found to prioritize the restriction of water loss over maintaining body temperature homeostasis; they tolerate increased body temperature to preserve water (Hetem et al. 2016). Furthermore, bathing or wallowing is an important behaviour to cool down but requires the presence of sufficient surface water. *Species that prefer to stay close to permanent rivers or lakes during the dry season (species with high water requirements) are therefore expected to have fewer problems with increasing temperatures as they can increase water intake and use it to compensate* (H3; Figure 2.3). Indeed, large water-independent species have specific adaptations to cope with high temperatures such as feeding nocturnally, an elongated shape with large surface area to volume ratio (Mitchell et al. 2004) and long legs so that the body is far away from the hot boundary layer close to the ground (Clarke 2017). However, these species would face greater difficulties if droughts and climate warming cause the permanent water bodies or wetlands to substantially shrink or dry out (Crafter et al. 1992).

The interplay of surface water dependence and predation risk

Emerging evidence shows that spatial niche differentiation of species with different water requirements can be mediated by predation risk (Box 2; (Ogutu et al. 2014)). This is because concentrations of ungulates near water attract predators that might also benefit from increased cover in catching their prey. Lions (*Panthera leo*) are more commonly found close to water sources (Ogutu and Dublin 2004; Valeix et al. 2010) and kill more prey near surface water sources than expected by chance (Hopcraft et al.

2005; de Boer et al. 2010; Davidson et al. 2013). Plains zebras (*Equus quagga*) move away from water sources during night time reducing their exposure to hunting lions (Courbin et al. 2018). Although still few, these studies suggest that water-dependent species generally experience higher exposure to predation, especially close to surface water (see also Box 2). Altogether, this suggests that *water-dependent ungulate species*

Figure 2.4: Predation risk and thermoregulation in relation to body size and water availability. A) Small prey are exposed to more predator species and become increasingly predator regulated. Abbreviations: B = buffalo; E = elephant; G = giraffe; H = hippo; I = impala; O = oribi; R = black rhino; T = topi; W = common wildebeest; Z = plains zebra. B) Lions select areas that are closer to rivers for hunting more often than expected (red bars), based on the availability of these resources across the landscape (blue bars). C) Decrease in activity on hot days (max 35+ °C) compared to cool days (max 20–24 °C) in terms of percent diurnal time allocated to feeding plotted against body mass for steenbok, impala, greater kudu and giraffe respectively ($R^2 = 0.98$; $P < 0.001$) and D) body temperature of a captive oryx exposed to the same environmental heat but with water (blue line) and a free-living oryx without water (brown line). Thus, predation risk decreases with increasing body size and distance to river and cooling down is more problematic for larger ungulates with restricted access to water. Reprinted and adapted with permission from (Du Toit and Yetman 2005; Hopcraft et al. 2010; Fuller et al. 2014).

(high minimum dung moisture) generally experience higher exposure to predation because predator densities are higher close to surface water (H4A). Since potential mortality from predation is also inversely related to body size (Figure 2.4A), it is expected that *the smaller water-dependent species are particularly at risk (H4B, Figure 2.3).* It is now time to upscale species-specific studies of carnivore-ungulate interactions to community wide investigations (Montgomery et al. 2019).

Trade-off between predation risk and thermoregulation

Our integrated framework also suggests a trade-off between exposure to predation risk and thermal stress that stretches across the two dimensions (food and water requirement) of Figure 2.3. As far as we know, this trade-off has not yet been investigated. Animals temporally adjust their activities to variation in temperature and, during hot periods, become less active or shift from diurnal to nocturnal or crepuscular activity (Du Toit and Yetman 2005; Hetem et al. 2012; Owen-Smith and Goodall 2014). This may increase the risk of being killed by nocturnal predators.

Ungulates can also behaviourally adjust their habitat use by selecting cooler parts of the landscape to prevent heat stress, such as shady and/or breezy areas (Hetem et al. 2007; Kinahan et al. 2007). Spatial variation in ambient temperature may thus be a strong driver of landscape use by ungulates (Kinahan et al. 2007; Bowyer and Kie 2009; van Beest et al. 2012; Wiemers et al. 2014). In other words, ungulates perceive a 'landscape of heat' "thermal landscape" (Sears et al. 2016) and in savannah are expected to avoid very hot places, especially when water is limiting. This 'landscape of heat' phenomenon as a driver of landscape use is conceptually similar to that of a 'landscape of fear' in response to heterogeneity in predation risk (Laundré et al. 2010). Importantly, woody vegetation (shrubs, trees) shapes both the landscapes of heat and fear. Although it may reduce predation risk for some species (Atkins et al. 2019), dense woody vegetation generally seems to increase perceived and actual predation risk (Hopcraft et al. 2005; Valeix et al. 2009; Ford et al. 2014; Riginos 2015) and reduces effective heat loads by providing shade from solar radiation (Bader et al. 2007; van Beest et al. 2012). As outlined above, exposure to predation declines with body mass (Hopcraft et al. 2010) and theory predicts that vulnerability to heat stress increases with body mass (Porter and Kearney 2009; Riek and Geiser 2013). While some work on this trade-off has been done in rodents (Bozinovic et al. 2000), empirical data for ungulates showing how different species trade-off thermal against fear landscapes are largely lacking (Wiemers et al. 2014).

Overall, this suggests the existence of an ecological trade-off between predation and thermal tolerance that remains to be tested (Figure 2.3) through investigating how ungulates behaviorally adapt to increased temperatures in both the presence and absence of carnivores. We thus predict that *predation risk compromises the behavioral capacity for thermoregulation of especially smaller water-dependent ungulates by*

jeopardizing their options to nocturnal activity and to remain in areas near water (H5). The largest species should thus adjust their spatio-temporal patterns more strongly to minimize the effects of high temperatures (while still meeting their high food requirements) (Kinahan et al. 2007; Shrestha et al. 2014) but can afford to be active at cooler but potentially riskier times (night) and areas (high cover).

Concluding remarks and future perspectives

The integration of food and water requirements, predation risk and thermoregulatory constraints yields a two-dimensional framework that generates testable predictions (H1-H5) on the consequences of climate change for community assembly of Africa's ungulates (Figure 2.3). They need to negotiate simultaneously a "landscapes of fear", a "landscape of food", a "landscape of heat" and a "landscape of water", where body size and minimal dung moisture content capture important trait dimensions that explain their niche differentiation and coexistence opportunities in such landscapes. This conceptual framework has important implications for biodiversity conservation. For example, previous work predicts highest potential diversity (most coexistence of small to large species) of ungulates at intermediate rainfall and high soil fertility at the regional scale (Olf et al. 2002). Our new framework in addition predicts regional ungulate diversity to increase with landscape heterogeneity in distance to water by enabling water-dependent and water-independent species to coexist through spatial partitioning of food. Local wildlife and livestock managers cannot change rainfall, but they can influence the distribution of surface water through dams and boreholes. Ecotourism interests often motivate an increase in the number of water points in protected areas, but our framework suggests that this may come at the cost of species diversity, depending on the landscape setting (see Box 2). Also, predation risk is not only expected to mediate niche differentiation along the surface water-dependence dimension, but also to influence daily activity patterns, so the loss or reintroduction of large carnivores will not affect all ungulate species evenly.

We suggest that future research tests the predictions in Figure 2.3 and the hypotheses outlined throughout the text (H1-H5). We recommend that investigations of food partitioning between African ungulates include the effects of surface water dependence and trade-offs between thermoregulation and exposure to predation. So far, physiological investigations of the mechanisms of water balance and thermoregulation are often restricted to a few species. But our framework allows generalizable predictions for ungulate species that lack such detailed investigations. Studies investigating the combined effects of food, water, temperature and predation are highly needed, as these factors concurrently affect the ecological interactions of savannah ungulates.

In summary, we propose that gradients in both food availability and distance to surface water set the scene for niche differentiation among savannah ungulates and that thermoregulation and predation risk are related to both niche axes but in opposing

ways. We identified key functional traits that integrate constraints from food (body size) and water requirements (minimum dung moisture content) that are easy to measure. It is now time to study the interactions between different constraints and upscale from species specific to community wide investigations. The framework we present here assists in the design of such studies of which the results will aid the anticipation of the consequences to large ungulates of human-induced global change.

Glossary

Allometry: the study of the relation of body size to physiology, morphology and behaviour

Ecological niche: an "n-dimensional hypervolume", where the dimensions are environmental conditions and resources, that define the requirements of an individual or a species to practice its way of life, more particularly, for its population to persist.

(Functional) traits: qualities of organisms that define species in terms of their ecological roles

Hyperthermia: an abnormally high body temperature due to failed thermoregulation that occurs when a body produces or absorbs more heat than it dissipates.

Loop of Henlé: a long, U-shaped portion of the tubule that conducts urine within each nephron in the kidney

Metabolic water: water created inside living organisms through metabolism, by oxidizing energy-containing substances in their food

Nephrons: the microscopic structural and functional units of the kidney.

Niche differentiation: the process by which natural selection drives competing species into different patterns of resource use.

Spiral colon: in contrast to humans, where the descending colon is short and straight, the descending colon of ungulates coils down in a long spiral.

Ungulates: hooved mammals of the orders Perissodactyla, Artiodactyla, Hyracoidea and Proboscidea.

Urine osmolality: the number of dissolved particles per unit of water in the urine

A photo of livestock grazing in the Loliondo Game Controlled Area, an important water catchment for Grumeti River (Source: Emilian Kihwele).

Upstream land-use negatively affects river flow dynamics in the Serengeti National Park

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Abstract

In the Greater Serengeti-Mara ecosystem, with the Serengeti National Park (SNP) at its core, people and wildlife are strongly dependent on water supply that has a strong seasonal and inter-annual variability. The Mara River, the only perennial river in SNP, and a number of small streams originate from outside SNP before flowing through it. In those watersheds increasing grazing pressure from livestock, deforestation, irrigation and other land uses affect river flows in SNP that subsequently have impacts on wildlife. We quantified the changes since the 1970s of river discharge dynamics. We found that the baseflow recession period for the Mbalageti River has remained unchanged at 70 days, which is a natural system inside SNP. By contrast it has decreased from 100 days in the 1970s to 16 days at present for the Mara River, coinciding with increased commercial-scale irrigation in Kenya that extract Mara River water before it reaches SNP. This irrigation will result in zero flow in the river in SNP if the proposed dams in the river in Kenya are built. We observed high flash floods and prolonged periods of zero flows in streams draining livestock grazed watersheds, where severe major erosion prevails that results in gully formation. This eroded sediment is expected to silt and dry out the scattered dry season water holes in SNP, which are an important source of drinkable water for wildlife during the dry season. It appears likely that the future water supply of SNP is at risk, and this has major consequences for its people and wildlife. Ecohydrology-based solutions at the catchment scale are urgently needed to reduce catchment degradation while ensuring sustainable water provision.

Introduction

Semi-arid and savannah ecosystems of East Africa are home to most diverse wildlife communities and important in tourism-driven economy. However, these communities face changes in surface water availability that is predicted to affect their abundance and composition (Veldhuis et al. 2019; Kihwele et al. 2020). Surface water connects human-dominated landscape and natural ecosystems, with upstream-downstream effects. Natural ecosystems are capable of sustaining the provision of freshwater to downstream dependants and though the water supply in the dry season may be limited in arid areas, this benefits ecosystem processes and people's livelihoods. In contrast, human activities upstream affect catchment quality through decreased low-flow periods and destruction of flow pathways (Nugroho et al. 2013; Lin et al. 2015; Jacobs et al. 2018; Lee et al. 2018). Such cause-and-effects relationship from declines of river flows have been documented for a number of rivers in East Africa, including the Ruaha River (Mtahiko et al. 2006; Kihwele et al. 2018), the Mara river (Gereta et al. 2009; Mango et al. 2011), the Wami River (Kiwango et al. 2015) and the Katuma River (Elisa et al. 2010). Sustainable supply of water depends on the condition of watersheds, which is driven by human activities (Nugroho et al. 2013; Welde and Gebremariam 2017; Guzha et al. 2018; Jacobs et al. 2018; Lee et al. 2018). Furthermore, the IPCC predicted that climate change in East Africa may affect rainfall and thus river flows with consequences for livelihoods and wildlife. However, the rainfall data from the Masai Mara National Reserve in Kenya, adjoining the Serengeti National Park (SNP), do not support that prediction so far (Bartzke et al. 2018).

In the Serengeti-Mara ecosystem, with SNP at its core (Figure 3.1A), land use changes and catchment degradation are the key factors driving the progressive decline of the flows of the Mara River, the only perennial river in SNP (Figure 3.1B; Mati et al. 2008; Gereta et al. 2009; Mnaya et al. 2017). Between 1973 and 2000, for the Mara watershed upstream of SNP, there has been a decline in natural forest by 31%, an increase in agricultural land by 204%, and savannah and rangelands reduced from 79% to 52% of the basin land (Mati et al. 2008; Kipampi et al. 2017), and all these have significantly impacted the river flow dynamics. In addition, there is commercial-scale irrigation in Kenya using Mara River water (Figure 3.1C); in 2005 it extracted Mara River water at a rate of $0.5 \text{ m}^3 \text{ s}^{-1}$ in the dry season (Hoffman et al., 2011), which is larger than the measured minimum Mara River flow of $0.3 \text{ m}^3 \text{ s}^{-1}$ in SNP in 2005 (Gereta et al. 2009). Thus in 2005 irrigation farmers in Kenya took out about 62% of the Mara River water during the dry season.

Water availability determines habitat use and the seasonal distribution of large herbivores during the dry season (Hopcraft et al. 2012; Owen-Smith 2015). Thus human activities that change water availability is expected to affect large herbivores, particularly water dependent species (Kihwele et al. 2020). The annual animal migration in

Figure 3.1: (A) Map of Serengeti Mara ecosystem showing SNP, its surrounding protected areas and its large rivers. (B) Map of the Mara River watershed in Kenya; the Mara River is formed by the confluence of the perennial Amala and Nyangores Rivers that start in the Mau forest; the Mara River is the only perennial river in the Serengeti Mara ecosystem. (C) GoogleEarth view of one of the two large-scale commercial irrigated farms and the thousands of small artisanal farms in Kenya, all use Mara River water.

SNP depends on water from the Mara River in the dry season and several scattered water holes in the other, otherwise dry, rivers in SNP (Wolanski et al. 1999; Mati et al. 2008; Gereta et al. 2009; Mnaya et al. 2017). Hydrologically, the Serengeti-Mara ecosystem is made up of four different watersheds, namely the transboundary Mara River (shared between Kenya and Tanzania), the Grumeti River, the Mbalageti River, and the Simiyu/Duma River in the far southwest of SNP, all flowing westwards to Lake Victoria (Wolanski et al. 1999). Despite of the ecological importance of surface water, the availability of water in the ecosystem has not been monitored, nor has the threat to this water been quantified from the increased use of river water for irrigation, the increased use of fires, and the increased overgrazing by cattle in watersheds originating from upstream SNP but draining into SNP mainly through the Grumeti River. If these flow dynamics are not quantified and monitored, their consequences for people and wildlife cannot be predicted and mitigated.

Thus, we collected field data on the effects of land use regimes on the flow properties of streams draining small watersheds inside and outside SNP, and simultaneously we collected data on rainfall and the flows in the large rivers in SNP. Using these data, we quantified the cause-and effects processes affecting these life supporting components of the ecosystem in SNP. We suggest that these processes are significant enough that they need to be taken into account by decision makers for the sustainable management of SNP and its surrounding areas to ensure sustainable biodiversity conservation and flows of benefits to people. Our study does that by answering four hydrological questions of importance to the ecosystem, namely: (1) What are effects of livestock grazing in the Loliondo Game Controlled Area (LGCA; Figure 3.1) outside SNP on the flow characteristics of small streams draining into SNP?; (2) What are the effects of fire inside SNP on the flow characteristics of small streams?; (3) Is the hydrology regime stable inside SNP?; (4) Is the Mara River likely to dry out in SNP in the future due to human activities in Kenya?

Material and Methods

The study area

The study area covered the Serengeti National Park (SNP) and the LGCA. The climate of the area follows the classical bimodal rainfall pattern of East Africa, mainly restricted to November-May, peaking in December and in March/April. The long rain generally occurs from late February through May while short rain occurs between October and December. There is a pronounced rainfall gradient with rainfall increasing from the south-east (500 mm) to the far-north (1200 mm). The altitude varies from 3000 m in the Ngorongoro highlands to about 920 m in the west near the shore of Lake Victoria. The physical boundary of the ecosystem is formed by the Great Rift Valley and the Ngorongoro highlands in the east, and Lake Victoria in the west.

Study design

We studied the flow dynamics by establishing gauging sites in both large rivers (Figure 3.2) and small streams (Figure 3.3). The watershed areas of both large rivers and small streams at each gauging site were delineated from digital elevation model (DEM) using

Figure 3.2: Map showing the hydrology network of the large rivers (shown in thick coloured lines) in SNP. The numbers indicate the gauging sites described in Table 3.1. The watershed boundaries are shown as thin black lines.

Rainfall data

We acquired rainfall data for the period 2016 to 2018 from Climate Hazards Center InfraRed Precipitation with Station data (CHIRPS) through the web browser <https://www.chc.ucsb.edu/data>.

Measurement of the discharge of large rivers

River flow dynamics in the large rivers were monitored from July 2016 to October 2018 at the stations shown in Figure 3.2. The headwaters of the watersheds varied in their land use. The Bologonja, Mbalageti, Seronera and Duma watersheds are natural, entirely protected ecosystems. The headwaters of the Mara, Grumeti, Banagi and Warangi Rivers are located in human-dominated ecosystems upstream of SNP (Figures 3.1 and 3.2). The loggers logged data at 30 min interval. For each of the river, we developed a rating curve from typically 8–10 measurements of the flow rates and the water level following Chaudry (2008):

$$Q = C h^m \quad (1)$$

where Q is the water discharge ($\text{m}^3 \text{s}^{-1}$), C is the discharge when the effective depth of flow h is equal to 1 m, and m is the coefficient that typically has a value between 2 and 4 according to the watershed. We then used the rating curve for each station to calculate the discharge rate for the entire period of observation from the half-hourly collected water level data.

Measurement of the discharge of the streams draining the small experimental watersheds

To quantify how land use affects the watersheds' hydrological processes, we monitored the streamflows in small (1 km^2) watersheds in SNP subject to fire and wildlife grazing (fire), livestock grazing in LGCA (livestock), and wildlife grazing without cattle and fire in SNP (control) (Figure 3.3). Data on streamflow were measured by water pressure loggers (ReefNet's third generation dive data loggers Sensus Ultra) from March 2017 to November 2017. The loggers were deployed at the pour point of each delineated watershed to measure the pattern of water levels following rainfall events. The loggers logged data at 15 min interval, so that all flow events were captured. To convert these water level data into discharge data, we used the Manning equation for open channel hydraulics (Chaudry, 2008):

$$Q = V A \quad (2)$$

$$V = (k/n) (A/P)^{2/3} S^{1/2} \quad (3)$$

where Q is the discharge, n is the Manning coefficient that depends on the stream bed

sediment and roughness characteristics and vegetation in the stream, A is the cross-sectional area (m^2) of the stream, P is the wetted perimeter (m), S is the slope of the stream, V is the velocity of water (m s^{-1}) of the flowing water, and $k \sim 1$. These small watersheds are all very close to each other in the same landscape with visual similar features, suggesting that they have similar physical environmental properties such as soil texture, soil heat and water retention properties.

Measurement of grass biomass in small watersheds

The grass biomass of each small watershed was measured along three transects perpendicular to the river bank of 200 m length at 0, 100 and 200 meters from the river bank. At each such site, a 20 m sub-transect was laid down where grass biomass was measured by dropping a Rising Plate Meter/Pasture Meter at ten points, 2 m apart, and measuring the grass height as a proxy for grass biomass. The data on grass biomass were analysed in a mixed model analysis of variance, with treatment (livestock grazing, fire, and control) as fixed effects, and transect nested with watershed, and watershed as random effects. The model was fitted using the `lme` function of the `nlme` library in R version 4.0.2 (R Core Team 2020) as `lme(Biomass~Treatment*Distance,random=~1|Watershed/Transect,method="REML",data=data.grass)`. The significance of the differences between the treatments was calculated using a Tukey HSD test, using the transect-average biomass as replication.

Measurement of the infiltration rate in small watersheds

Data on infiltration rate were obtained using a single ring infiltrometer (15 cm diameter). In each experimental watershed, we installed the infiltrometer by driving it about eight centimetres into the soil. We then filled the ring with water. We monitored the

Table 3.1: Large river gauging stations, river name and measurement site.

Gauging station	River name and measurement site
1	Mara River at Kogatende
2	Bologonja River at Makutano bridge
3	Grumeti River at Klein's bridge
4	Warangi River at Mbuzi mawe bridge
5	Banagi River at Banagi bridge
6	Seronera River at Morcas bridge
7	Grumeti River at Dala bridge
8	Mbalageti River at Sopa bridge
9	Mbalageti River at Handajega bridge
10	Duma River at Duma ranger post/Duma bridge

Figure 3.4: Recession curve for the discharge after rainfall of the Seronera River (site 6 in Figure 3.2) in SNP from our data, showing the method used to estimate the flow recession time scale. This method was used for both large rivers and small streams.

infiltration of water into the soil by manually recording the depth of the water in the infiltrometer every 5 min for an hour. We calculated the average infiltration rate for each infiltration sequence as the slope of the linear regression of the remaining water level versus time. Visual inspection of the infiltration graphs showed that a linear model was appropriate. We then tested the effect of treatment (livestock grazing, fire, and control) using one-way analysis of variance, followed by Tukey contrasts.

Estimating the recession time scale for both large rivers and small streams

The large rivers and the small stream in SNP and LGCA have a classical hydrological behaviour at recession, comprising of an exponential decrease of surface runoff after rain, followed by a slower exponential decrease of the flow sustained by the drainage of the shallow aquifer, and finally followed by an even slower exponential decrease of the flow sustained by the drainage of the deep aquifer (Brown et al. 1981). An example from our data for the Seronera River is shown in Figure 3.4. Thus we could estimate the baseflow recession time scale, which is the time required for the base flow to decrease to 1.8% of its original value, by using Eq. (4):

$$Q = Q_0 \exp(-kt) \quad (4)$$

where t is the time in days, k is the recession coefficient (it has units of day^{-1} ; it is the slope of the flow recession curve in a log plot), Q is the discharge ($\text{m}^3 \text{s}^{-1}$) and Q_0 is the discharge at time 0 after rainfall.

Results

Visual observations

The rivers with headwaters entirely within SNP generally showed no sign of bank erosion as their banks were covered by vegetation (Figures 3.5A-C). The streams originating from intensively cattle-grazed areas outside of SNP in Loliondo Game Controlled Area (LGCA) were mostly erosion gullies with intense erosion during high flows (Figure 3.5D) and this gully formation propagated downstream in SNP (Figure 3.5E).

Flow characteristics of streams in small watersheds

The flows in the small streams draining watersheds originating from cattle-treated areas in LGCA varied rapidly with short-lived flash floods and flow recessions lasting a few hours only (Figure 3.6, Table 3.2). By contrast the flows in the small streams draining the fire-treated and the control watersheds were less 'spikey' with smaller floods and with flows lasting much longer after rainfall. Indeed, the mean flow recession period in the control watersheds was 2.53 days (± 1.72 , $n = 4$), which is not significantly different from that (2.46 days; ± 1.49 , $n = 4$) in the fire treated watersheds, and this is significantly larger than that of 0.106 days, (± 0.066 , $n = 4$) in the livestock treated watersheds. As a result, the streams in the control small watersheds had no flow for 63.98 %

Figure 3.5: Pictures illustrating the contrast between the stable river banks facilitated by stabilising vegetation within SNP (A: Warangi River; B: Mbalageti River; C: Seronera River), (D) a stream degrading into a gully in the cattle-overgrazed LGCA just outside SNP, and (E) an eroding stream in SNP affected by cattle in LGCA.

Figure 3.6: Time-series plot of the discharge in the small streams draining the 12 experimental watersheds, 4 in each treatment. Left column: 4 watersheds located in SNP used as control that were only grazed by wildlife with no fire; Middle column: 4 watersheds subjected to intensive livestock grazing in LGCA; Right column: 4 watersheds subjected to fire and wildlife grazing inside SNP. The numbers in red bold are the percentage of the time that the stream had no flow.

(± 16.83 , $n = 4$) of the time on the average, in the fire treated small watersheds for 73.70 % (± 5.12 ; $n = 4$) of the time, and in the livestock treated small watersheds for 83.98 % (± 9.13 , $n = 4$) of the time (Figure 3.6).

Grass biomass and infiltration rate in the experimental watersheds

The mixed model analysis of variance for the grass biomass showed a significant effect of treatment ($F_{2,12} = 4.23$, $P < 0.041$) and distance ($F_{1,2652} = 18.22$, $P < 0.001$), while their interaction was not significant ($F_{1,2652} = 2.36$, $P = 0.09$). A subsequent Tukey HSD test showed that the grass biomass was not significantly different between control and fire treated watersheds ($P > 0.05$) while the watersheds with livestock present had a significantly lower biomass than both these treatments (Figure 3.7). In general, there was inter-specific variation in grass biomass within and between watersheds with similar treatments (Figure S1).

Table 3.2: The baseflow recession time scales (days) of stream draining 12 small watersheds treated with livestock grazing, fire, and control.

Watershed number	Treatment	Recession time scale (days)
1	Livestock grazing	0.15
2	Livestock grazing	0.08
3	Livestock grazing	1.68
5	Livestock grazing	0.02
6	Control	6.65
7	Control	2.97
9	Control	0.54
15	Control	1.97
8	Fire	1.35
11	Fire	3.62
12	Fire	1.00
13	Fire	3.88

Figure 3.7: Variation of the grass biomass (indexed as Disc Pasture Meter [DPM] settling height; mean $\pm$ SE) in the experimental watersheds as a function of the three treatments, shown as boxplots. Means with the same letter are not significantly different (Tukex HSD test after mixed-model analysis of variance, with transect and watershed as random effects).

Figure 3.8: Variation in the infiltration rate in the experimental watersheds as a function of the three treatments, shown as boxplots. The effect of treatment was not significant ($P > 0.05$).

The infiltration rate data suggest that the control watersheds had higher infiltration rates than the fire and livestock grazing treatment (Figure 3.8), but this treatment effect was not significant in a one-way ANOVA ($F_{2,12} = 2.08$, $P = 0.17$).

Flow characteristics of large rivers

The large rivers within SNP each had different flow recession rate, so that some rivers had longer-lasting flows than others, but nevertheless the flows all varied slowly with time scales of days to weeks (Figure 3.9A-C, Table 3.3). The discharges varied from river to river, and so did the water yield (i.e. the discharge divided by the watershed area) and this can be attributed not just to the geology but also to the rainfall that varied spatially (Figure 3.9D-F). The mean baseflow recession time scale was 27.63 days (± 23.3 , $n = 8$). Most importantly for the ecology, excepting the Mara River, which is perennial, and the Bolongonja River, which is sustained by a perennial spring with the small flow of $\sim 0.02 \text{ m}^3 \text{ s}^{-1}$, all the other rivers dried out during the dry season. The average number of days with zero flow in each river was 67.1 days per year (± 44 , $n = 5$; Minimum = 3.5 days; maximum = 130 days). Substantial differences in the flow recession time scale occurred between rivers, that time scale ranging between a maximum of 70 days for the Mbalageti River at Sopa bridge and a minimum of 5.4 days for the Grumeti River at Klein's bridge (Table 3.3). This implies that after rain, the rivers differed significantly in the way their base flows decreased exponentially to 1.8% of the original flow (Figure 3.9A-C). The peak recorded discharge (i.e. during floods) for the Mara and Mbalageti rivers was, respectively, $623.3 \text{ m}^3 \text{ s}^{-1}$ on 17 April 2018 and $193.8 \text{ m}^3 \text{ s}^{-1}$ on 2 December 2017 (Figure S2). However, these high flow data are based on an extrapolation of the rating curve to levels for which no data exist; hence these data during floods are indicative only. The peak observed flood flows for the Bologonja, Warangi, Grumeti, Banagi and Seronera rivers were, respectively, $0.17 \text{ m}^3 \text{ s}^{-1}$ on 28 March 2017; $27.7 \text{ m}^3 \text{ s}^{-1}$ on 16 March 2018; $11.6 \text{ m}^3 \text{ s}^{-1}$ on 20 April 2018; $132.3 \text{ m}^3 \text{ s}^{-1}$ on 5 January 2018; and $10.4 \text{ m}^3 \text{ s}^{-1}$ on 27 April 2018 (Figure S2).

Historical changes to river flows

The World Meteorological study of the White Nile basin in 1970–1974 gauged the Mara River at Mara Mines and the Mbalageti River near its outlet in Lake Victoria (SMEC, 1977; Brown et al., 1981). Both of these historical gauging sites are very close to our gauging sites. The Mbalageti River watershed is entirely within SNP, thus in a natural state. The Mara River watershed is mostly in Kenya with extensive deforestation and increasing use of Mara River for irrigation occurring in Kenya since the 1970s. As shown in Table 3.3, the baseflow recession time scale of the Mbalageti River was 70 days in the 1970s and this has not changed, i.e. the hydrological characteristics have not changed in SNP. By comparison the baseflow recession time scale of the Mara River has decreased by a factor of about 6 from 100 days in the 1970s to 16.4 days at present.

Figure 3.9: Time-series plot of (A-C) the daily water yield of the large rivers and (D-F) the weekly rainfall over their watersheds.

Table 3.3: Comparative recession time scales for discharge levels in river in the 1970–1974 study of SMEC (1977) and Brown et al. (1981) and this study (2016–2018). Also shown are, for this study period, the maximum, minimum and mean discharge and the number of days with zero flow.

Gauging station no.	Watershed area (km ²)	Recession time scale (days) in 1970–1974	Recession time scale (days) in 2016–2018	Maximum discharge (m ³ s ⁻¹)	Minimum discharge (m ³ s ⁻¹)	Mean discharge (m ³ s ⁻¹)	Number of days with zero flow
1	8,881	100	16.4	623.3	0.1	41.5	0
5	1,423		38.5	132.3	0	2.6	94.5
3	467.5		5.4	11.6	0	0.2	na
6	447.1		29.2	10.4	0	0.4	3.5
2	295.9		8	0.17	0.01	0.02	0
8	1,341	70	70	193.8	0	2.24	na
4	2,492		47.6	27.7	0	1.3	70.9
9	2,810			63.1	0	4.4	130
10	735.0		6	147.0	0	0.4	36.6

Sedimentation-induced historical changes to rivers inside SNP

The Seronera River (site number 6 in Figure 3.2) is located entirely inside SNP and it is now being modified by long-term sedimentation that likely results from wet-season erosion from dirt roads in the southern grasslands of SNP. This is illustrated by sequential photos dating back to 1996 (Figure 3.10).

Discussion

Cattle grazing

We investigated how livestock grazing and fire affect the condition of small watersheds and their streamflow yields. The livestock grazing treated watersheds in LGCA had a smaller grass biomass and a smaller water infiltration rate than that in the control watersheds in SNP. The flow recession period was the same (~ 2.53 days) in the control watersheds and in the fire treated watersheds. However, the flow recession period was much shorter (~ 0.11 days) in the livestock grazing treated watersheds where, therefore, flash floods were common during rainfall and the flows were short-lived after rainfall. In addition, our visual field observations and photographic evidence revealed intense gully erosion in the small streams originating outside SNP in the LGCA where there is intensive livestock grazing, a clear indication of deteriorating watersheds. These small streams are the tributaries of large rivers of SNP, such as the Grumeti River, which is seasonal. In the dry season these rivers do not flow but they hold water through a network of water holes along the river. The spikey floods in the small streams in LGCA

Figure 3.10: Sequential photographs from 1996 to 2016, in the dry season, of the same waterhole in the Seronera River. The water hole is silting and this affects the dry season water availability for wildlife.

bring this sediment to SNP and this sediment silts these water holes and shortens the time that these water holes retain water in the dry season. Evidence for the silting of water holes from soil erosion upstream is found in water holes in the Seronera River that are silting from erosion from dirt roads in the southern grasslands of SNP. The sedimentation of the dry season water holes is expected to have a severe impact on the ecosystem because water from these water holes allows for spatial niche partitioning and co-existence of diverse grazing herbivores in the dry season (Kihwele et al., in prep.). Thus, cattle grazing in the buffer zones, especially the LGCA, is likely to dry out these water holes in the future and thus this will alter the whole ecosystem processes and functioning. In summary, the hydrology has remained stable for watersheds within SNP but river flows have become much more ‘spikey’ and fast drying for the watersheds outside SNP but draining into SNP.

Irrigation in Kenya

The baseflow recession period of the Mbalageti River has not changed (= 70 days; Table 3.3) since the 1970s. Its watershed is entirely within SNP, thus it is in a natural state because of total protection of resources in SNP. Thus the hydrology of rivers entirely within SNP appears stable over the last 45 years.

By contrast, the baseflow recession time scale of the Mara River in SNP has decreased from 100 days in the early 1970s to 16.4 days at present. This change means that for Mara River water to reach SNP, in the early 1970s in the dry season a rainfall event was needed every 3–4 months in the Mau forest in Kenya, now this is needed every 2–3 weeks. This suggests that a future drought is likely to stop the Mara River flow entering SNP. The main reason for that appears to be commercial irrigation in Kenya. Indeed, Google-Earth images show that there are two commercial-scale irrigation areas using Mara River water in Kenya; one area is that shown in Figure 1c and it appears slightly changed in surface area since 2005; the other area is located a few km downstream and it appears to have substantially grown by 40 % since 2005, indicating that the total irrigation area may have increased by about 20 %. In 2005 the water extracted from the Mara River for commercial scale irrigation in Kenya was $\sim 0.5 \text{ m}^3 \text{ s}^{-1}$ during the dry season (Hoffman et al., 2011). In the same year the low flow discharge of the Mara River in SNP was $0.3 \text{ m}^3 \text{ s}^{-1}$ (Gereta et al. 2009), implying that in 2005 the commercial irrigators were withdrawing 62% of Mara River water before it reached the Serengeti-Mara ecosystem. In November 2016 we measured a Mara River discharge of $0.16 \text{ m}^3 \text{ s}^{-1}$, i.e. the commercial irrigators in Kenya were extracting $\sim 75\text{--}79\%$ of the Mara River water before it reached SNP.

The threat of Kenya withdrawing water from the Serengeti ecosystem is even worse because there are proposed dams on the Mara River and its tributary, the Nyangores River, also in Kenya, as well as a proposal for a dam in the Mau forest in Kenya to divert Amala River water to another watershed to the east; all these dams are located upstream of the irrigation areas. The minimum proposed flow at the outlet of the dams would be $0.1 \text{ m}^3 \text{ s}^{-1}$ (Mnaya et al. 2017). However, the irrigators in Kenya are located downstream of these dams and to maintain their crops they need to extract all that water and thus they will completely dry out the Mara River. This will likely destroy the annual migration of wildebeest and zebras for which SNP is famous (Mnaya et al. 2017). The ecosystem may then change to one supporting a population of resident animals, with no annual migration, around water holes in rivers, at least those that are not silting from overgrazing in LGCA (Mnaya et al. 2011; Weeber et al. 2020). Indeed, there is no other sufficient source of freshwater beside the Mara River in SNP in the dry season because, as shown in Table 3.3, all the other rivers dry out in the dry season except for the very small flow of $\sim 0.014 \text{ m}^3 \text{ s}^{-1}$ in the Bologonja River that is fed by a perennial spring. There is no drinkable water either in the southern plains of SNP in the dry season because of high salinity levels (Gereta and Wolanski 1998; Wolanski et al. 1999; Gereta et al. 2009).

This paper is a plea for a strict control of commercial and artisanal irrigation in Kenya and for improved livestock husbandry through increasing control of grazing in watersheds draining into SNP, with urgent action needed in LGCA. Furthermore, the use of fire as a management tool needs to proceed with caution and careful monitoring. Ecohydrology-based solutions are urgently needed.

Supplementary information

Figure S1: Grass biomass in the small watersheds at three distances from the stream with different treatments. Watersheds 1-5 are watersheds in LGCA treated with intensive livestock grazing. Watersheds 6-7, 9-10 and 15 are control watersheds in SNP with no fire. Watersheds 8, 11-14 are watersheds in SNP treated with fire.

Figure S2: Time-series plot of the discharge of the large rivers in SNP from July 2016 to November 2018 (the thick black bar). The numbers are the gauging stations described in Table 3.1.

A photo of the Mara River, the only perennial and thus vital water source for migrating ungulates in the dry season (Source: Musa Mandia).

Quantifying water requirements of African ungulates through a combination of functional traits

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Abstract

Climate and land use change modify surface water availability in African savannas. Surface water is a key resource for both wildlife and livestock and its spatial and temporal distribution is important for understanding the composition of large herbivore assemblages in savannas. Yet, the extent to which ungulate species differ in their water requirements remains poorly quantified. Here, we infer the water requirements of 48 African ungulates by combining six different functional traits related to physiological adaptations to reduce water loss, namely minimum dung moisture, relative dung pellet size, relative surface area of the distal colon, urine osmolality, relative medullary thickness and evaporation rate. In addition, we investigated how these differences in water requirements relate to differences in dietary water intake. We observed strong correlations between traits related to water loss through dung, urine and evaporation, suggesting that ungulates minimize water loss through multiple pathways simultaneously, which suggests that each trait can thus be used independently to predict water requirements. Furthermore, we found that browsers and grazers had similar water requirements, but browsers are expected to be less dependent on surface water because they acquire more water through their diet. We conclude that these key functional traits are a useful way to determine differences in water requirements and an important tool for predicting changes in herbivore community assembly resulting from changes in surface water availability.

Introduction

Variability in temperature and rainfall patterns is increasing, with consequent effects on resource availability for herbivores across Africa. For arid and semi-arid regions throughout Africa, a reduction in the amount of precipitation received during the dry season is expected, which will likely trigger more recurrent and severe droughts (Engelbrecht et al. 2015, Bartzke et al. 2018). Droughts will not only influence herbivores indirectly through changes in food availability, but also directly through decreased surface water availability (Gaylard et al. 2003). Most ungulates in drylands and savanna ecosystems require access to surface water to maintain body fluid homeostasis. However, we lack a general understanding of how ungulate species differ in their water requirements and whether and how changes in surface water availability will affect the community composition of savanna ungulates.

During the dry season, water-dependent herbivores are constrained by their minimum fundamental frequency of drinking (Western 1975, Smit 2011, Valeix 2011, Cain et al. 2012). Dry season distributions of herbivores in relation to surface water (distance to water) are therefore commonly used as a measure of their surface water dependence (Smit et al. 2007, Gereta et al. 2009, Smit 2011, Owen-Smith 2015, Kihwele et al. 2018). However, herbivore distributions are confounded by other factors such as predation risk and food availability, so that distance to water is not a reliable indicator of water dependency. It is now possible to measure drinking frequency from higher resolution GPS data to quantify the degree of surface water dependence (Cain et al. 2012, Curtin et al. 2018), but it is logistically not feasible to collar many individuals and species across broad geographic areas. Therefore, we propose to use a combination of functional traits to quantify herbivore water requirements as an alternative approach.

In order to deal with periods of water shortage, ungulates have developed a suite of ecological, physiological and behavioral adaptations to conserve body water (Cain et al. 2006, Turner et al. 2010, Cadotte et al. 2013). These adaptations allow water loss to be reduced through different channels (Figure 4.1) to cope with changes in water availability (Cain et al. 2006). For example, some arid-adapted species exhibit a relatively large surface area to volume ratio of the spiral and distal colon that allows them to reabsorb more water from their dung (Taylor 1968a, Maloiy and Hopcraft 1971, Maloiy 1973). Similarly, a relative thick kidney medulla supports juxtamedullary nephrons with long loops of Henle to concentrate urine and enable arid-adapted species to reduce urinal water loss (Maloiy et al. 1988). However, it remains to be investigated whether different water conservation traits are associated.

Here, we quantified water requirements for 48 African large mammalian herbivore species using six functional traits. We combine data on dung properties collected in Serengeti National Park and Gorongosa National Park with physiological and ecological traits from published studies. We then explore the relations between minimum dung

moisture, dung pellet size, distal colon area, urine osmolality, medullary thickness and evaporation rate to find the best indicator(s) for water requirements of mammalian herbivores. Subsequently, we investigate the relationships between our predicted water requirements with herbivore feeding types, phylogeny and classifications of surface water dependence based on literature assessment. Last, we investigated whether species water requirements relate to the amount of water obtained through their diet by comparing our predicted water requirements to dietary water intake using published data on oxygen isotopic enrichment.

Methods

We quantified water dependence of 48 herbivore species through combining data obtained from previously published studies with data measured in the field. We used 6 functional traits as indicators of water dependence: minimum dung moisture content, relative dung pellet size, relative distal colon area, urine osmolality, relative medullary thickness and evaporation rates. We subsequently tested our predictions for a subset of 11 ungulates using experimentally quantified water requirements (percentage weight loss in response to water deprivation). We surveyed the literature for data using the Web of Science, Google Scholar and cross-referencing to search for each attribute. We extended our dataset with data on dung moisture and fresh pellet size in Serengeti National Park and Gorongosa National Park that allowed us to study seasonal variation

Figure 4.1: Overview of the primary components of the water balance of ungulates. Red arrows represent routes of water loss over a time interval while blue arrows represent water gain (affected by morphology, physiology and behaviour). Some species have specific adaptations to store water (blue circle) like for example fat storage in the camel's hump. Water requirements are lower in species with reduced water loss. Species with higher water requirements are generally more dependent on surface water, but can (partially) decrease this dependence through the intake of water through their diet. Figure adapted from Veldhuis et al (2019).

in dung moisture. Furthermore, we used isotopic oxygen enrichment (see below) as a measure of dietary water intake to investigate which species could decrease their dependence on surface water by using alternative sources of water.

Field data collection

Data were collected in 2018 in both wet (Mar-May) and dry season (Aug-Oct) in Serengeti National Park (SNP), Tanzania, and supplemented with dry season (Oct) data from Gorongosa National Park (GNP), Mozambique. Samples of 13 herbivore species (impala (*Aepyceros melampus*), hartebeest (*Alcelaphus buselaphus*), wildebeest (*Connochaetes taurinus*), topi (*Damaliscus lunatus*), plains zebra (*Equus quagga*), Thompson's gazelle (*Eudorcas thomsonii*), giraffe (*Giraffa camelopardalis*), waterbuck (*Kobus ellipsiprymnus*), elephant (*Loxodonta africana*), Grant's gazelle (*Nanger granti*), common warthog (*Phacochoerus africanus*), buffalo (*Syncerus caffer*) and eland (*Tragelaphus oryx*)) were collected for dung moisture content and, of these, 11 species for dung pellet size (buffalo did not produce pellets, elephant pellets are highly variable between individuals) in Serengeti National Park. In Gorongosa National Park, we collected data on both dung moisture and pellet size from seven species: sable antelope (*Hippotragus niger*), oribi (*Ourebia ourebi*), bush pig (*Potamochoerus larvatus*), southern reedbuck (*Redunca arundinum*), nyala (*Tragelaphus angasii*), bushbuck (*Tragelaphus scriptus*), and greater kudu (*Tragelaphus strepsiceros*). In both parks, drinking water is abundant during the wet season and becomes scarce as the dry season reaches its peak.

Dung pellets were collected between 07:00 and 18:00 and stored in a plastic ziplock bag in a cooler box for transport to the laboratory. Pellets were only sampled from observed defecating individuals to be sure that the samples were fresh (collected directly after defecation). In the lab, the length (L), width (W) and height (H) of 3 to 9 individual pellets were measured for each sample using Vernier calliper. Dung moisture content was calculated as the percentage of mass loss between fresh samples and samples dried in an oven until no further mass loss (GNP: 10 days at 60°C) or air-dried (SNP: 14 days).

Dung moisture content

In addition to our dung moisture data from SNP and GNP, we obtained dung moisture data for the dry season and captive animals through our literature search. When multiple sources presented such data, we chose for the minimum value for dry season dung moisture. In our final database, dry season dung moisture originated from our own field sampling, Woodall and Skinner (1993), King (1983), De Leeuw et al. (2001), Woodall et al. (1999); Sitters et al. (2014); Clemens and Maloiy (1982), Maloiy et al. (1988); and unpublished data for Grevy's zebra (*Equus grevyi*) from Mpala Research Centre and Conservancy. Dung moisture data of captive individuals with *ad libitum* water was obtained from Clauss et al. (2004) and Taylor (1968a). We then correlated the dung

moisture data from the wet season (sufficient water) against the dry season (water limited) collected in Serengeti and the dung moisture of captive individuals (*ad libitum*) against the dry season dung moisture (water limited) data of our overall database and fitted linear regressions to investigate the plasticity of this trait (Figure S1B,C). Dry season dung moisture was lower than wet season moisture for free-ranging individuals and lower than captive individuals, and this difference was larger for species with low dry season dung moisture (slope < 1). We thus used minimum dry season dung moisture in the subsequent analyses as this best represents the species capacity to reabsorb water from dung.

Relative pellet volume

Pellet volume (V) was calculated from the three dimensions (L×W×H) assuming an ellipsoid shape: $V = 4/3 \times \pi \times 0.5L \times 0.5W \times 0.5H$. Pellet volume did not differ between seasons (Fig. S1A) suggesting that pellet volume is a stable trait within species. We thus grouped dung volume estimates from both seasons for further analyses. To correct for species body size, we divided pellet volume by the body mass of each species, because arid-adapted species have smaller pellets than predicted for their body mass (Coe and Carr 1983). Pellet volume is determined by the cross-sectional area of the rectum so that pellet volume is expected to scale allometrically with body mass with an exponent of 0.67. A linear model of the logarithms of pellet volume and body mass for ruminants had a slope of 0.69 (Figure S2) which is very close to our assumed relationship of 0.67. Ecosystem and sex-specific body mass data for SNP was obtained from Sachs (1967), except for migrating wildebeest that were taken from Hopcraft et al. (2013). Body mass of bushbuck (n = 29) and nyala (n = 16) for GNP are unpublished estimates.

Relative distal colon area

Data on the dimensions of the intestines for 15 ruminant ungulates were acquired from Woodall & Skinner (1993). The surface area of the distal colon, where most of the water reabsorption takes place (Woodall and Skinner 1993), divided by the total surface area of both small and large intestine, to correct for body size, was calculated and used as an indicator of the capacity to reabsorb water from dung. This indicator has not previously been used but is analogous to the relative medullary thickness used for the ability to reabsorb water from nephrons.

Urine osmolality

Urine osmolality data was obtained from Beuchat (1990, 1996), Penzhorn (1988), King (1983) and Cloete and Kok (1986), which all represent maximum urine osmolality values. The maximum was taken when multiple sources presented osmolality measures of the same species as this best represent the maximum capacity of the species to concentrate urine.

Relative medullary thickness

Data on the relative thickness of the medulla (RMT) was taken from Beuchat (1990, 1996) and Cloete and Kok (1986) and calculated from published values on medullary thickness (MT) and kidney volume (KS) (Maluf 1991, 1995, 2002) following: $RMT = MT / KS * 10$, where KS is computed as cube root of the product of the three size dimension: $(L \times W \times H)^{0.33}$ (Greenwald 1989, Beuchat 1990). Hippo's (*Hippopotamus amphibius*) lack central medulla and thus have little capacity to concentrate urine (Beuchat 1996).

Evaporation

Data on evaporation rates are scarce, as they require controlled experiments in climate rooms. Maloiy (1973) summarizes data from three studies (Taylor 1970, Maloiy and Hopcraft 1971, Maloiy and Taylor 1971) that executed such experiments for 12 ungulate species under two temperature regimes: 1) constant temperature of 22°C and 2) alternating between temperatures of 22°C and 40°C every 12 hours, both under conditions with limited water availability (dehydration). Evaporation was higher under the alternating regime for all species, as expected, but the qualitative patterns between evaporation and body mass were similar (Figure S3). We used the evaporation rates from the constant temperature regime for our study, because 22°C is quite close to the average dry season temperatures in most of Africa's savannas. Furthermore, this included waterbuck (*Kobus ellipsiprymnus*) which lacked measurements in the alternating treatment because it lost 12% of its body mass within the first 12 hours, suggesting it would not survive long under that temperature regime. We corrected for body mass through dividing evaporation rates by body mass^{0.67} which is the relationship between changes in surface area and volume. Deviations from this general relationship (relative evaporation), were used as a measure of adaption to reduce water loss through evaporation.

Water requirements

The same experiments also yielded unique data on water requirements (Taylor 1968a, Maloiy and Hopcraft 1971, Maloiy and Taylor 1971) through gradually reducing drinking water to a point where animals were able just to maintain their weight at about 85% of the initial levels, which was then presented as the minimum water requirements of those species. Also here, we used the water requirement under stable 22°C conditions divided by metabolic weight ($\text{kg}^{0.75}$) to compare animals differing greatly in size (Taylor 1968a). Deviations from this general trend are presented as the relative water requirements.

Predicting water requirements based on the functional traits

We then used the six different traits to predict the water requirements of 48 ungulates for which we had at least data for one of the traits. To obtain a single currency for water requirements, we predicted the dung moisture from the regressions between dung

moisture and the other functional traits. These estimates of inferred dung moisture from different traits were then averaged for each of the three different pathways: dung (dung moisture, relative dung volume, relative distal colon areas), urine (urine osmolality, relative medullary thickness) and evaporation (relative evaporation) and rescaled between 0 and 100, representing a scale from deficient to excessive water requirements. An overall ranking is then presented using the mean of the three predictions linked to the three channels.

Dietary water intake

Isotopic oxygen enrichment was used as an indicator of the amount of water obtained through diet relative to drinking surface water (Kohn 1996). $\delta^{18}\text{O}$ values in plant leaves are higher because evaporation enriches the remaining water in the heavy isotope ^{18}O relative to source water (Blumenthal et al. 2017) and $\delta^{18}\text{O}$ values in large herbivores can thus be used as an indicator of the source of water (surface water vs diet). We used the dataset from Blumenthal et al. (2017) where we selected data from sites with a water deficit > 0 , which is the annual difference (in mm/y) between water loss (evaporation and transpiration) and water gain (precipitation), so that we only included areas with low water availability where animals are challenged to meet their water requirements. To increase the robustness of our analyses, we only included species with at least three data points in this final dataset.

Feeding type

Feeding types were distilled from Owen-Smith (1997), Kingdon et al. (2013) and Gagnon and Chew (2000), yielding 6 feeding type categories: obligate grazers (GRO), variable grazers (GRV), variable browsers (BRV), obligate browsers (BRO), frugivores (FRU) and generalists (GEN). Livestock species were not included in the analyses of feeding types.

Water dependence classification

Classification of surface water dependence was taken from Hempson et al. (2015), which aggregated data from Kingdon et al. (2013) and Wilson and Mittermeier (2011). They classified water dependence into three categories: 1) obtains all water from forage or has physiological adaptations allowing the species to go for long periods without requiring access to surface water (None), 2) requires access to drinking water irregularly but do not display specific physiological adaptations to survive without water for long periods (Low), and 3) requires almost daily access to drinking water placing constraints on daily foraging ranges (High).

Data analysis

All statistics were performed in R software version 3.5.1 (R 2018). Basic ANOVAs and linear regressions were used for all analyses.

Results

Comparison between different indicators of water loss through dung

All three indicators of water loss through dung were highly correlated (Figure 4.2). Dung moisture represents the actual water loss but varies based on water availability (Figure S1), while relative pellet size and distal colon area are constant throughout the seasons and provide secondary indices for the capacity to prevent water loss through dung. Herbivore species differed significantly in these physiological and ecological traits related to water loss through dung. Minimum dung moisture content showed strong correlations with relative distal colon area (corrected for total intestine area, Figure 4.2A; $y = 73.6 - 128.0x$) and with relative pellet volume (corrected for body mass, Figure 4.2B; $y = 145.5 + 58.8x$). However, the non-ruminant ungulates common warthog (*Phacochoerus africanus*) and plains zebra (*Equus quagga*) did not follow the general trends with relative pellet volume and had relatively larger pellets than the ruminants. We did not have data on distal colon area for non-ruminants so we could not investigate whether they follow the trends we found for the ruminants. No significant differences were found between feeding types for minimum dung moisture content (ANOVA: $F_{6,36} = 2.0$, $P = 0.08$), relative pellet volume (ANOVA: $F_{3,10} = 1.2$, $P = 0.34$) or relative distal colon area (ANOVA: $F_{4,11} = 1.1$, $P = 0.37$).

Figure 4.2: The relationships between different indicators of water loss through dung. Correlation of minimum dung moisture against relative distal colon area (A) and relative dung pellet volume (B). Dashed black lines represent linear regression models that only represent ruminants (excluding EqQa and PhAf in (B)). Colors identify feeding types. Abbreviations represent the two first letters of the genus and species names (see Table S1).

Relationships between indicators of the different pathway of water loss

We observed strong correlations between indicators of the three different channels of water loss (dung, urine and evaporation), with the most robust relationship between dung moisture and urine osmolality. Our results indicate that animals with dry dung have concentrated urine (Figure 4.3A ; $y = 218.4 - 49.4\log_{10}(x)$), greater relative medullary thickness ($\text{corrected for kidney size, Figure 4.3B}$; $y = 80.4 - 35.2\log_{10}(x)$) and low relative evaporation rates ($\text{corrected for body mass, Figure 4.3C}$; $y = 69.3 + 61.8x$),

Figure 4.3: Relationships between indicators of water loss through dung, urine and evaporation. Correlation of minimum dung moisture against urine osmolality (A), relative medullary thickness (B) and relative evaporation rate (C). Dashed black lines represent linear regression models. Colors identify feeding type of wild herbivores. Livestock species are presented in black. Abbreviations represent the two first letters of the genus and species names (see Table S1).

so that arid-adapted herbivores prevent water loss through all pathways simultaneously. Urine osmolality (ANOVA: $F_{4,15} = 1.8$, $P = 0.18$), relative medullary thickness (ANOVA: $F_{4,10} = 2.9$, $P = 0.08$) and evaporation rates (ANOVA: $F_{3,8} = 0.2$, $P = 0.87$) did not differ between feeding types.

Figure 4.4: Relationship between measured water requirements of 11 ungulates and their predicted water requirements based on composite indicators of water loss through dung (A), urine (B), evaporation (C) or a combination of them (D). Dashed black lines represent linear regression models. Colors identify feeding type of wild herbivores. Livestock species are presented in black. Abbreviations represent the two first letters of the genus and species names (see Table S1).

Relating water loss indicators to water requirements

Composite indices of water loss through dung (combining dung moisture, relative pellet size and distal colon area into a single indicator), urine (combining urine osmolality and relative medullary thickness) and evaporation all predicted the experimentally measured water requirements of large herbivores well (Figure 4.4), with evaporation explaining most variation. Combining these indices into a single indicator had similar predictive ability of the experimentally measured water requirements (Figure 4.4D).

Predicting water requirements for the African ungulate guild

Our predicted water requirements based on combined indicators of water loss through dung, urine and evaporation show a wide variety of water requirements among 48 African ungulates, with Kirk's dik-dik (*Madoqua kirkii*) having the smallest and hippo (*Hippopotamus amphibius*) the largest water requirements (Figure 4.5). The variation of our prediction for water requirements is in general agreement with the categories of surface water dependence classifications (ANOVA: $F_{3,44} = 6.9$, $P < 0.001$). Water requirements did not differ between feeding types (ANOVA: $F_{5,42} = 1.5$, $P = 0.20$), even when we excluded non-ruminants (ANOVA: $F_{5,33} = 1.1$, $P = 0.36$). However, we did find a strong phylogenetic signal of water requirements (ANOVA: $F_{15,35} = 7.3$, $P < 0.001$). Non-ruminants, Bovinae (Bovini and Tragelaphini) and Reduncini showed higher water requirements in general, while the gazelles (Antilopini), horse-like antelopes (Hippotragini) and dwarf antelopes (Neotragini) are predicted to exhibit low water requirements.

Relationships between dietary water intake and water requirements

Water obtained through food relative to drinking generally decreased with an increase in our predicted water requirements (Figure 4.6; $y = 44.1 - 0.12x$), suggesting that species adapted to arid conditions do not only reduce water loss, but also increase dietary water intake, thereby reducing their dependence on surface water. Feeding type did not significantly affect dietary water intake across all ungulates (ANOVA: $F_{4,15} = 1.69$, $P = 0.20$). However, there were significant differences when we limited the analyses to ruminants only (ANOVA: $F_{3,9} = 9.4$, $P < 0.01$). Obligate browsers (BRO) obtained more water from their diet than obligate grazers (GRO; $P < 0.01$), while variable grazers (GRV) and variable browsers (BRV) showed intermediate dietary water intake but marginally insignificant from obligate browsers ($P = 0.06$ and $P = 0.09$ respectively), probably due to their low sample size. Greater kudu (*Tragelaphus strepsiceros*) and Grevy's zebra (*Equus grevyi*) showed significantly higher oxygen isotope enrichment than would be expected based on their predicted water requirements, suggesting that these species can compensate for their relatively high water requirements through dietary water acquisition making them less dependent on surface water than expected.

Figure 4.5: Predicted water requirements of 48 African ungulates based on composite indicators of water loss through dung (D), urine (U) and evaporation (E). Colors represent water dependence classifications based on literature assessment with three classes: none (red), low (green) or high (blue). Livestock species are presented in black. Insets display the variation of water-dependent classification (top), feeding type (middle) and phylogenetic group (bottom). Data availability of the 6 indicators per species are presented in the columns on the left with dung moisture content (M), relative pellet size (S) and relative colon area (C) as indicators of water loss through dung (D); urine osmolality (O) and relative medullary thickness (M) as indicators of water loss through urine (U) as well as water loss through evaporation (E).

Figure 4.6: Amount of water obtained through food relative to drinking as a function of the predicted water requirements of African ungulates. The dashed black line represent linear regression models. Colors identify feeding type of wild herbivores. Abbreviations represent the two first letters of the genus and species names (see Table S1).

Discussion

We quantified water requirements for 48 species of African ungulates by combining six functional traits related to water loss. We found these traits to be highly correlated and accurately predicted the experimentally measured water requirements of a selection of ungulate species, suggesting each single trait is a valuable indicator of ungulate water requirements. African ungulates varied widely in their water requirements and in general, water-independent species obtain more water through their food relative to drinking thereby reducing their dependence on surface water. In general, our predicted water requirements were in line with classifications based on literature assessments. Furthermore, our results suggest higher water requirements for non-ruminants, which is in agreement with the finding that artiodactyls evolved and speciated under arid conditions (Strauss et al. 2017). Altogether, our results show great potential for using functional traits to predict ungulate water requirements, specifically for large herbivore species assemblages.

The strong correlations between minimum dung moisture and all other indicators of water loss provide evidence that herbivore species reduce water loss through multiple pathways simultaneously, such that species producing dry dung also produce highly concentrated urine (Maloij 1973). However, some of these traits are more plastic than others. Dung moisture was higher in the wet season than dry season and a higher mois-

ture content was observed in captive individuals provided with free access to drinking water than free-ranging individuals, which is in agreement with previous work (Maloiy 1973, Edwards 1991, Rymer et al. 2016). Not surprisingly, urine osmolality also varies with water availability and evaporation varies with both water availability and ambient temperature (Taylor 1968b, Maloiy 1973). The flexibility of these traits appear to be an important physiological and ecological adaptation to (seasonal) changes in water availability (Woodall and Skinner 1993) and thus provide a more sensitive and plastic variable to assess water requirements in temporally and spatially heterogeneous landscapes. In contrast, anatomical adaptations such as the dimensions of the kidney and intestine, and consequently dung size, are likely to be more constant and may thus provide a better indication of the capacity to conserve water. We therefore suggest that dung moisture is an easy-to-measure (flexible) index of the hydration state of African ungulate species, while relative dung size is an easy-to-measure (static) index of the species' capacity to conserve water.

Our interpretation of the data must be tempered by some limitations. First, we do not have a complete list of traits measured for all species under the same environmental conditions. Our predicted water requirements for some species are based on a single trait measure, which make those predictions less reliable. Second, our data is biased towards ruminant herbivores. Although non-ruminants followed the general patterns for the correlations between minimum dung moisture, urine osmolality and relative medullary thickness, we do not have data on intestine dimensions or evaporation rates for these species. Furthermore, plains zebra and warthog (non-ruminants) were strong outliers to the general trend between minimum dung moisture and relative dung pellet volume (Figure 4.2B). Zebra and warthog have relatively large dung pellets which provide a small surface area for water resorption through the colon (Woodall et al. 1999). Future work should thus aim to augment the trait dataset, specifically for non-ruminants, to improve the accuracy of the predictions and the robustness of our conclusions about the generality of the observed patterns. Third, the isotopic oxygen enrichment that we used in our analysis is a valuable tool but has important limitations. For example, fruits do not exhibit oxygen enrichment (Kohn 1996) thereby reducing the reliability of the method for species with a high percentage of succulent fruit in their diet. This calls for further research to investigate the proportional contribution of each food component on the overall water budget of the species. Despite these limitations, our study shows great potential for using functional traits to predict ungulate water requirements.

While our predicted water requirements generally were in line with classifications based on literature assessments, there were some intriguing inconsistencies between the two. We predicted relatively lower water requirements for some species (beisa oryx, Thompson's gazelle, impala and hartebeest) and higher water requirements for others (eland, Grevy zebra, bushpig and bushbuck). Deviations towards lower predicted water requirement could result from species using habitats closer to water for other

reasons than water requirements that led observers to believe the species was water dependent. For example, impala are generally found close to water and are therefore often classified as water dependent even though their water requirements have been shown to be low (Maloiy 1973). Water dependence classifications of hartebeest are ambiguous; some authors place them in the water-bound group (Western 1975) whereas others classify them as water independent (Woodall and Skinner 1993). Our prediction is based on functional traits and thus is less confounded by ecological factors such as food availability or predation risk. Our deviating predictions towards higher water requirements likely result from the difference between water requirements and surface water dependence. Species with higher water requirements can reduce their dependence on surface water through increased intake of preformed water. For example, eland are generally classified as water-independent (Western 1975, Woodall and Skinner 1993), even though experiments have shown they have about the same water requirements as buffalo (Taylor 1968b). Eland could increase independence of surface water by means other than water conservation such as the selection of succulent food (Taylor 1969). Increased intake of preformed water could thus decrease surface water dependence regardless of their basic water requirements and might be of particular importance for species that are closely related to more water-dependent lineages (Bovinae, Equidae, Suidae).

In general, there was a negative correlation between isotopic oxygen enrichment and water requirements, with those species relying on preformed water in their diet scoring lower on our predicted water requirements based on functional traits. Overall, species with lower water requirements are thus also less dependent on acquiring water through drinking. Nevertheless, specific species such as greater kudu and Grevy's zebra, recognized for occupying drier areas, are predicted to have relatively high water requirements but reduce surface water dependence through behavioral adaptation such as increased dietary water intake and thus can decrease surface water dependence if sufficiently high moisture forage is available. Also, ruminant browsers showed significantly higher dietary water intake than ruminant grazers, even though feeding type did not affect their water requirements, suggesting that browsers are less dependent on acquiring water through drinking than grazers. This is in agreement with the suggestion that browsers acquire a substantial amount of water from their diet, potentially making them less dependent on surface water (Western 1975). Altogether, our results suggest that the reduction of surface water dependence through increased intake of preformed water can be very important, is difficult to quantify and very species specific. Detailed investigations of the proportional contribution of each food component to the overall water budget of each species are required.

Conclusions

The expected changes in climate and land use, compounded by an increase in the fre-

quency and intensity of drought, will further exacerbate the limited water supply in savanna ecosystems, especially during the late dry season. As such, the quantification of herbivore water requirements is vital to guide management and conservation of herbivores. We conclude that functional traits are a great tool to predict ungulate water requirements. Each of these traits provide specific information about ungulate water balance and their combination provides a convenient estimate of water requirements. Expanding this approach to a more complete dataset and a greater range of species will further elucidate the role of water requirements in structuring African ungulate communities.

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Supplementary information

Table S1: Species characteristics. Water dependence classifications are based on a literature assessment following Hempson et al. (2015). Feeding types were distilled from Owen-Smith (1997), Kingdon et al. (2013) and Gagnon and Chew (2000).

Scientific name	Common name	Abbreviation	Phylogeny	Feeding type	Digestive strategy	Water dependence
<i>Aepyceros melampus</i>	Impala	AeMe	Alcelaphini	GRV	Ruminant	High
<i>Alcelaphus buselaphus</i>	Hartebeest	AlBu	Alcelaphini	GRO	Ruminant	High
<i>Antidorcas marsupialis</i>	Springbok	AnMa	Antidorcini	BRV	Ruminant	Low
<i>Bos indicus</i>	Zebu Cattle	BoIn	NA	NA	NA	NA
<i>Camelus dromedarius</i>	Camel	CaDr	NA	NA	NA	NA
<i>Capra hircus</i>	Turkana Goat	CaHi	NA	NA	NA	NA
<i>Cephalophus dorsalis</i>	Bay Duiker	CeDo	Cephalophini	FRG	Ruminant	None
<i>Cephalophus natalensis</i>	Natal Red Duiker	CeNa	Cephalophini	FRG	Ruminant	None
<i>Cephalophus silvicultor</i>	Yellow-backed Duiker	CeSc	Cephalophini	FRG	Ruminant	None
<i>Connochaetes gnou</i>	Black wildebeest	CoGn	Alcelaphini	GRO	Ruminant	High
<i>Connochaetes taurinus</i>	Common Wildebeest	CoTa	Alcelaphini	GRO	Ruminant	High
<i>Damaliscus lunatus</i>	Topi	DaLu	Alcelaphini	GRO	Ruminant	Low
<i>Damaliscus pygargus</i>	Blesbok	DaPy	Alcelaphini	GRO	Ruminant	High
<i>Diceros bicornis</i>	Black rhinoceros	DiBi	Non ruminant	BRO	Hind-gut	High
<i>Equus africanus</i>	African wild ass	EqAf	Non ruminant	GRO	Hind-gut	Low
<i>Equus asinus</i>	Donkey	EqAs	NA	NA	NA	NA
<i>Equus grevyi</i>	Grevy's zebra	EqGr	Non ruminant	GRO	Hind-gut	Low
<i>Equus quagga</i>	Plains zebra	EqQu	Non ruminant	GRO	Hind-gut	High
<i>Equus zebra</i>	Mountain zebra	EqZe	Non ruminant	GRO	Hind-gut	High
<i>Eudorcas thomsonii</i>	Thomson's gazelle	EuTh	Antilopini	GRV	Ruminant	Low
<i>Giraffa camelopardalis</i>	Giraffe	GiCa	Giraffidae	BRO	Ruminant	Low
<i>Hippopotamus amphibius</i>	Hippopotamus	HiAm	Non ruminant	GRO	Fore-gut	High
<i>Hippotragus niger</i>	Sable antelope	HiNi	Hippotragini	GRO	Ruminant	High
<i>Hyemoschus aquaticus</i>	Water chevrotain	HyAq	Tragulina	GEN	Ruminant	None
<i>Kobus ellipsiprymnus</i>	Waterbuck	KoEl	Reduncini	GRO	Ruminant	High
<i>Kobus kob</i>	Kob	KoKo	Reduncini	GRO	Ruminant	High
<i>Litocranius walleri</i>	Gerenuk	LiWa	Antilopini	BRO	Ruminant	None
<i>Loxodonta africana</i>	African elephant	LoAf	Non ruminant	GEN	Non-ruminant	High
<i>Madoqua kirkii</i>	Kirk's dik-dik	MaKi	Neotragini	BRO	Ruminant	None
<i>Nanger granti</i>	Grant's gazelle	NaGr	Antilopini	BRV	Ruminant	None
<i>Oreotragus oreotragus</i>	Klipspringer	OrOr	Neotragini	BRO	Ruminant	None
<i>Oryx beisa</i>	Beisa oryx	OrBe	Hippotragini	GRO	Ruminant	Low
<i>Oryx gazella</i>	Gemsbok	OrGa	Hippotragini	GRO	Ruminant	None
<i>Ourebia ourebi</i>	Oribi	OuOu	Neotragini	GRV	Ruminant	None
<i>Ovis aries</i>	Fat-tailed Sheep	OvAr	NA	NA	NA	NA
<i>Phacochoerus africanus</i>	Common warthog	PhAf	Non ruminant	GRO	hind-gut	High
<i>Philantomba maxwellii</i>	Maxwell's Duiker	PhMa	Cephalophini	FRG	Ruminant	None
<i>Philantomba monticola</i>	Blue Duiker	PhMo	Cephalophini	FRG	Ruminant	None
<i>Potamochoerus larvatus</i>	Bush pig	PoLa	Non ruminant	GEN	Non-ruminant	Low
<i>Raphicerus campestris</i>	Steenbok	RaCa	Neotragini	BRV	Ruminant	None
<i>Redunca arundinum</i>	Southern Reedbuck	ReAr	Reduncini	GRO	Ruminant	High
<i>Redunca fulvorufula</i>	Mountain Reedbuck	ReFu	Reduncini	GRO	Ruminant	High
<i>Sylvicapra grimmia</i>	Common Duiker	SyGr	Cephalophini	GEN	Ruminant	None
<i>Syncerus caffer</i>	African Buffalo	SyCa	Bovini	GRO	Ruminant	High
<i>Tragelaphus angasii</i>	Nyala	TrAn	Tragelaphini	BRV	Ruminant	Low
<i>Tragelaphus oryx</i>	Common Eland	TrOr	Tragelaphini	BRV	Ruminant	None
<i>Tragelaphus scriptus</i>	Bushbuck	TrSc	Tragelaphini	BRO	Ruminant	Low
<i>Tragelaphus strepsiceros</i>	Greater Kudu	TrSt	Tragelaphini	BRO	Ruminant	Low

Figure S1: Plasticity of the dung moisture and pellet size under varying conditions of water availability. A) Pellet size of 11 herbivore species in the dry and wet season in Serengeti National Park ($\log_{10}(y) = 0.16 + 0.95\log_{10}(x)$). B) Dung moisture of 13 herbivore species in the dry and wet season in Serengeti National Park ($y = 31.1 + 0.65x$). C) Dry season dung moisture of free-ranging individuals and captive individuals that have *ad libitum* access to water ($y = 12.1 + 0.90x$). Grey solid lines represent $x = y$ and dashed black lines represent linear regression models. Colors identify feeding type of wild herbivores. Livestock are presented in black. Abbreviations represent the two first letters of the genus and species names (see Table S1).

Figure S2: Pellet volume as a function of body mass. The black dashed line is the expected allometric relationship between body mass and pellet volume with exponent $2/3$ ($y = 3 + x^{0.67}$) based on the area to volume ratio resulting from the cross-sectional area of the distal colon (determining pellet volume). Residuals from this trend are used as a measure of adaptation to reduce water loss through dung, where water can be reabsorbed more efficiently from smaller pellets. Intercept is chosen in such a way that all species have negative residuals. Colors identify feeding type of wild herbivores. Abbreviations represent the two first letters of the genus and species names (see Table S1).

Figure S3: Evaporation rate as a function of body mass under conditions of water deprivation. Black species abbreviation represents evaporation rates under constant conditions of 22°C , while red species abbreviations are evaporation rates when temperatures alternated between 22 and 40°C every 12 hours. The black dashed line presents the expected increase in evaporation rates with body mass based on the surface area to volume ratio ($y = 0.1 + x^{0.67}$). Residuals from this expected general trend were used as a measure of adaptation to prevent water loss through evaporation (see Figure S4). Abbreviations represent the two first letters of the genus and species names (see Table S1).

Figure S4: The relationship between water loss through dung and evaporation. Black species abbreviations represent evaporation rates under constant conditions of 22°C ($y = 69.2 + 61.8x$). Red species abbreviations represent evaporation rates under circumstances where temperatures alternate between 22 and 40°C every 12 hours ($y = 51.6 + 43.2x$). Under both conditions, there is a strong relationship between the two indicators of water requirements where species that prevent water loss through dung (dry dung) have the lowest relative evaporation rates (corrected for body mass). Abbreviations represent the two first letters of the genus and species names (see Table S1).

A photo of elephant family drinking water in water holes in the Grumeti River during the dry season
(Source: Musa Mandia)

Variation in water requirements allow spatial niche partitioning among savannah grazers

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Abstract

Body mass and feeding type (grazer vs browser) have been identified as key dimensions of dietary niche partitioning that allow coexistence of diverse herbivore assemblages in African savannah ecosystems. Recently, it has been suggested that differences in herbivore water requirements might add an additional dimension through spatial partitioning along a distance to surface water gradient, but whether and how variability in water requirements affect the spatial distribution of herbivores has inadequately been quantified. Here, we investigated the drivers of spatial niche partitioning among 16 herbivore species in relation to surface water through large herbivore dung counts and visual counts along transects with varying distances to permanent water points across Serengeti National Park. Our results show strong variation in the distribution of grazing herbivore species in relation to permanent water sources, but not for browsers. Dry season dung moisture content, an index of water requirements, best explained the variation in mean distance to surface water between grazers, suggesting differences in water requirements lead to spatial niche partitioning among grazers. Furthermore, tree basal area was highest closer to surface water and coincided with mean distance to water distributions of browsers suggesting that browsers congregation around water might be driven by food availability. Our results suggest that herbivore water requirements can serve as an additional axis of spatial niche partitioning among grazing herbivores. We conclude that it is crucial to consider water requirements as a driver of niche partitioning among savannah herbivores and should be incorporated by managers into water provision policies in protected areas.

Introduction

The mechanisms explaining the coexistence of diverse herbivore assemblages in African savannah ecosystems in relation to forage resources have been intensively investigated (Sinclair et al. 2003; Anderson et al. 2010; Hopcraft et al. 2010; Owen-Smith 2015). Various studies have shown that variation in nutritional quantity and quality of forage allows coexistence along a body size dimension, with small-sized grazing mammalian herbivores showing strong associations with areas of high quality grasses while large grazing herbivores preferring using areas with low quality but abundant grass biomass (Anderson et al. 2007; Anderson et al. 2010; Hopcraft et al. 2012; Owen-Smith 2015). More importantly, existence of an incredible high diversity of plant communities provides an enabling environment that allows for herbivores of different feeding type (browser vs grazer) and digestive physiology (ruminant vs non-ruminant) to occupy same habitat because they are able to partition forage resources, i.e. dietary niche partitioning (Zolho et al. 2013; Owen-Smith et al. 2015; Murray and Brown 2016; Pansu et al. 2019). But, recently, it has been suggested that variation in water requirements among herbivores might contribute to an additional axis of spatial niche partitioning along a distance to surface water gradient (Veldhuis et al. 2019; Kihwele et al. 2020). However, how variability in water requirements spatially position different herbivores across the landscape has inadequately been quantified.

Surface water are progressively in decline in drylands and savannah ecosystems affecting landscape use pattern for herbivores. To maintain body water balance, dryland and savannah herbivores require regular access to surface water, which, its availability particularly in droughts and dry seasons is incredibly scarce in time and space. Limited surface water availability has profound constraints to herbivores, such that it is used to predict herbivore's seasonal movements, which ultimately result into partitioning the landscape into different seasonal used compartments (Gereta et al. 2009). A well-established pattern of wet season dispersal and a dry season congregations of herbivores around water sources has been strongly associated with changes in the availability of surface water (Western 1975; Wolanski and Gereta 2001). Availability of surface water for example has been linked with the wildebeest migration in the Serengeti National Park (Gereta and Wolanski 1998; Wolanski et al. 1999). Furthermore, studies have suggested that the dry season distribution of herbivores in relation to distance to water to indicate species' water dependence (Western 1975; Redfern et al. 2005; Smit 2007; Ogutu et al. 2014). Although, the existence of savannah herbivores is water dependent, but still how spatial and temporal availability of surface water will affect herbivore community assemblages needs to be quantified.

Variations in water requirements among herbivores may have important ecological implications on diverse ungulates assemblages; thus, allowing their coexistence and spatial niche partitioning. Distinctions in the position in relation to distance to water

across the landscape has been used to group species into water dependent and water independent species. For instance, based on water requirements, grazers and browsers have different responses against droughts (Abraham et al. 2019), such that they exploit different forage with different moisture content. Existing evidences suggest that the browse may have a higher water content than the grass, so that in the dry season, browsers rely on water from the food rather than drinking (Western 1975). Proving this additional axes of niche differentiation among savannah herbivores is important in the light of human-induced changes to the hydrology and climate change.

The increasing availability of census data and technological development such as the use of satellite GPS collars, have recently improved our understanding on how herbivore movements and distributions are related to surface water availability at different spatial and temporal scales. These quantifications generally yielded substantial knowledge on the distance to water as a proxy for surface water dependence (Redfern et al. 2003; Redfern et al. 2005; Valeix 2011; Cain et al. 2012). Additionally, herbivore distributions along the landscape are confounded by other factors such as nutritional requirements (Smit 2011; Hopcraft et al. 2012; Owen-Smith et al. 2015), sensitivity to predation (Hopcraft et al. 2012; Grant et al. 2014; Owen-Smith 2015) and landscape features (Hopcraft et al. 2010; Owen-Smith and Traill 2017). Lately, a new approach of quantifying water requirements of African herbivores using functional traits has provided evidences on a wide range of surface water requirements among African large herbivores. This, therefore, calls for investigation on whether water requirements can allow for spatial niche partitioning and thus add an additional dimension that is independent to body mass and feeding type.

While distance to surface water and concentration of ungulates in the immediate vicinity of water during the dry season is a well-established pattern, it remains unclear whether variation in water requirements between herbivores represents an additional dimension of niche partitioning that is independent of body size and feeding type. In this study, we investigated how surface water distributions affect the distributions of large mammalian herbivore species across the Serengeti National Park at both spatial and temporal scales. Furthermore, we subsequently aimed to explain these distributions through variation in water requirements, body size and feeding type to unravel whether variation in water requirements allows for spatial niche partitioning between herbivores. We combine data on dung count transects, road transects, grass biomass, total tree basal area and dry season dung moisture content collected in the Serengeti National Park. We used these data to quantify how different herbivores position themselves and use the landscape along surface water gradients.

Materials and Methods

Study area

This study was conducted in the Serengeti National Park, covering an area of 14,763 square kilometers within Serengeti Mara ecosystem which is defined by areas used by annual migration of wildebeest and zebra across rainfall gradients. The park is heterogeneous in vegetation types, soil and grass nutrients which partition the area into seasonally used compartments (Wolanski et al. 1999). This area exhibits diverse habitats ranging from open grasslands in the southeast to Acacia dominated woodlands in the central and western Serengeti to Miombo dominated vegetation in the north (Anderson et al. 2003; Reed et al. 2009). Moreover, the park is featured by bi-modal rainfall pattern with two distinct rainfall seasons, the short rains falling during November – December and long rain occurring between March and May with a dry season occurring in July – October. Mean annual rainfall ranges from about 500 mm in the southeast to more than 1200 mm in the northwest. Four major rivers intersect the park, the Mara, Grumeti, Mbalageti and Duma all flowing westwards to Lake Victoria (Gereta and Wolanski 1998). The Mara River becoming the only permanent river and the life support for the migrating herbivores that drains the northern part of the park (Gereta et al. 2002; Gereta et al. 2009)

Mapping permanent surface water sources

In August 2016, we conducted an intensive survey to locate and map all the dry season permanent water sources in the Serengeti National Park that are used by wildlife for drinking considering a salinity threshold of 4 ppt (Wolanski and Gereta 2001). The survey was guided by a long served and experienced park ranger whereby GPS coordinates were taken at each water source. We used ArcGIS 10.4 (ESRI) to produce a distribution map of permanent water sources that were later used to locate transects for dung counts.

Herbivore distribution: dung counts

Data on the distribution of herbivores in relation to distance to permanent surface water across the Serengeti National Park were collected from systematic dung counts along 9 transects of 10 km long located at the northern, central and southern part of the Park (Figure 1) over a two-year period. For northern and central areas, we did dung count (presence/absence) in both wet (March 2017 and April 2018) and dry (July and September 2017; and September 2018) seasons along 100 meters sub-transect laid down at 0.2 km, 1 km, 4 km, 7 km and 10 km from permanent water sources (Figure 5.1) running perpendicular from the main transect following methodology used by (Cromsigt et al. 2009; Veldhuis et al. 2016). Using ArcGIS, we created buffers of 10 km and based on the buffers, we then located 10 km transects so that we were confident

Figure 5.1: Map of Serengeti National Park showing nine transects used for dung count and the permanent water sources that were used to locate the transects. The rectangular box shows how the dung was spatially sampled along the distance to water gradients.

that the sub-transects were not located close to any other permanent water sources. To further increase gradient in distance to water, we included areas even further away from permanent water sources by locating three transects on the southern plain, the driest part of the park. At this area, we laid out 100 meters-long sub-transects at 9.2 km, 9.97 km, 12.45 km, 12.62 km and 15.29 km for the Barafu transect; 19.5 km, 20.2 km, 22.87 km, 24.97 km, and 29.73 km for Gol and 18.95 km, 19.65 km, 22.32 km, 24.81 km and 27.91 km for Naabi from the closest permanent water source (Figure 5.1). The 100 meter transects were further subdivided into 50, 2 meter segments and determined the presence or absence of dung within two meters. Dung pellets were tallied to herbivore species by a team of four observers. The observers were two park ecologists and two experienced park rangers. Their experience provided a reliable identification of a species based on the dung pellet morphological features. However, due to difficulties in distinguishing the dung pellets of topi (*Damaliscus lunatus*) from that of hartebeest (*Alcelaphus buselaphus*), we were not able to individually assess these two species and we decided to group them.

Herbivores distributions: animal counts

The Serengeti Biodiversity Research Program has been monitoring large herbivore population dynamics using road count (ground survey) from nine permanent transects since 2014. We acquired data from road counts for the period between February 2014 and November 2018. These data were used to increase the robustness of our results by using a different method and to be able to separate topi and hartebeest. We selected visual count data from April 2015, 2016 and 2018 to investigate the wet season herbivore distributions and data from August and September 2015 to investigate dry season distributions because July and August were particularly dry in 2015 when compared to other months that are usually dry. Observers recorded odometer reading at each observation point after sighting wildlife along each transect. Road transects were geo-referenced with GPS coordinates which were taken after every one kilometre distance along the road transect. The odometer readings were also categorised to 1 km increments and then translated to GPS coordinates, whereby all odometer readings falling within 0–1 km were assigned a GPS coordinate of 0 km and those between 1–2 km were assigned a GPS coordinate of 1 km and so on. We then estimated the distance of all encountered observations to the nearest permanent water source (Figure 5.1) using the nearest neighbour distance in the spatial analyst tool of ArcGIS 10.4.

Water requirements

Dry season dung moisture content has been shown to indicate the water requirements of African ungulates (Kihwele et al. 2020). Data on dung moisture were collected in 2018 between August and October in Serengeti National Park (SNP). Samples of 13 herbivore species (impala (*Aepyceros melampus*), hartebeest, wildebeest (*Connochaetes taurinus*), topi, plains zebra (*Equus quagga*), Thompson's gazelle (*Eudorcas thomsonii*), giraffe (*Giraffa camelopardalis*), waterbuck (*Kobus ellipsiprymnus*), elephant (*Loxodonta africana*), Grant's gazelle (*Nanger granti*), common warthog (*Phacochoerus africanus*), buffalo (*Syncerus caffer*) and eland (*Tragelaphus oryx*)) were collected for dung moisture content. Dung pellets were collected between 07:00 and 18:00 h and stored in a plastic ziplock bag in a cooler box for transport to the laboratory. Pellets were only sampled from observed defecating individuals to be sure that the samples were fresh (collected directly after defecation). In the laboratory, fresh dung was weighed to get fresh dung weight and then allowed to air dry for fourteen days. Dung moisture content was calculated as the percentage of mass loss between fresh samples and samples dried until no further mass loss.

Body mass and feeding type

Data on body mass was obtained from Owen-Smith (1988) and Kingdon et al (2013) while those for feeding types were distilled from Owen-Smith (1997), Kingdon et al. (2013) and Gagnon and Chew (2000). Body mass was significantly related to dry

season dung moisture content for species in Serengeti for both grazers and browsers (Figure S1).

Grass biomass and tree basal area

To investigate how food availability could confound the relationship between herbivore distributions and water, we estimated the above ground standing grass biomass layer using a disc pasture meter and extracted tree basal area (TBA) data from vegetation map of Serengeti Mara ecosystem produced by Howison et al. (unpublished). We used tree basal area as an estimate of food availability for browsers. To account for variability in foraging availability and a better representation of differences in herbivore distribution, we estimated grass biomass for both wet and dry seasons at a total of 45 sub-transects along the nine dung count transects as a measure of food availability for grazers. At each 100 meter long sub-transect, the grass biomass measurement was determined by dropping a disk pasture meter at ten sampling units at an interval of ten meters to compress the grass vegetation and record the biomass as height. TBA was extracted using ArcGIS 10.4 (Environmental System Research Institute) by creating buffers of 300 m from a point of observation for both methods. Based on the established buffers, we then through geometry calculator, calculated TBA in square meters.

Data Analysis

A logistic regression model was used to estimate the probability of occurrence of herbivore species in relation to distance to water using both the dung count and animal count datasets. We tested for nonlinear correlation by also including a quadratic function to predict the optimum distribution of herbivore relative to distance to water. The result of the logistic regression was then considered as the observed distribution of species along the gradients where from this, we then calculated the weighted average across all transects to determine the average distance to water for each species for both dry and wet season. Subsequently we explored to what extent water requirements, body size and feeding type could explain this variation in mean distance to water constructing separate linear regression for both dung count and visual count datasets, both seasons and both feeding types. Mean distance to water was the response variable and dry season dung moisture content and body size were explanatory variables in separate models. To investigate the relationships between water and food availability, we constructed linear regression models with distance to water as the independent variable and either grass biomass or tree basal area as the response variables.

Results

Average distance to water of different herbivores

We found a strong spatial variation in the distribution of grazers in relation to distance to water but not between browsers (Figure 5.2). In general, we observed three groups of grazer species distribution relative to distance to permanent water: 1) species that are always located far from water; 2) species that occur at intermediate distance from water and generally move away from permanent water sources in the wet season and then move closer to water in the dry season, including migratory wildebeest and zebra, and 3) species which are always located close to water.

Figure 5.2: Seasonal distribution of herbivores in relation to the distance to the surface water sources using dung counts (A) and visual counts (B) in the Serengeti National Park. Points represent mean distances of herbivores during the dry (black dots) and wet (grey dots) season. Bars indicate the standard error. See Table S1 for logistic regression models results.

The greatest mean distance to water were evident for wildebeest and zebra in the wet season, and Thomson's gazelle and Grant's gazelle in both seasons (Figure 5.2), supported by mostly significant positive trends in the logistic regression models (Figure S2; Table S1). Hippopotamus, waterbuck and buffalo were consistently located closer to water in both seasons (Figure 5.2), and showed significant negative associations with distance to water, except waterbuck which showed no significant relationship (Figure S2). Topi, hartebeest, warthog, oribi, zebra and wildebeest all showed a significant optimum at intermediate distance from water during the dry season. The migratory species, wildebeest and zebra, showed largest differences in mean distance to water between seasons, occupying areas far from permanent water during the wet season (Serengeti Plains) and moving closer to water during the dry season (Figures 5.2, S2). Eland occurred at intermediate distance from water in the dung count dataset but at large distances from permanent water in the visual count dataset, which was the only qualitative difference between the two datasets. Browsers were all positioned relatively close to water (Figure 5.2) and either showed negative (impala, elephant, giraffe dry season) or no significant (dik-dik, giraffe wet season) relationship with distance to water (Figure S2).

Summarizing, we found that grazers were spatially separated relative to surface water especially during dry season, but browsers congregated closer to water.

Relationship between the mean distance to water, dry season dung moisture content and body mass

Dry season dung moisture content (an index of water requirements) was strongly negatively correlated with mean distance to water during the dry season for grazers in both datasets (Figure 3A,C). Grazer body mass also explained significant dry season variation in mean distance to water for the dung count dataset (Figure 3B), but was not significant in the visual count dataset (Figure 3D). Wet season patterns between dry season dung moisture content and distance to water were qualitative similar to dry season patterns, although less variation was explained (Figure S3A,C). Body mass did not have significant relationship with mean distance to water for the wet season for dung count dataset, mostly because oribi, a small species, occurred close to water (Figure S3B). For the wet season visual count dataset, we did find a strong correlation between body mass and distance to water (Figure S3D). Altogether, dry season dung moisture consistently better predicted the variation in mean distance to water than body mass for grazers and these relationships were stronger during the dry season. For browsers, we found consistent weak and insignificant relationships with dry season dung moisture and body mass in both datasets.

Figure 5.3: Dry season dung moisture (A,C) and body mass (B,D) explain variation in mean distance to water for grazers in the dung count dataset (A,B) and visual count dataset (C,D) during the dry season. Grazer (red triangles) and browser (black dots) species are identified by the first two letters of their genus and species name. Lines represent linear regressions for grazers (red dashed) and browsers (black solid).

Above ground grass biomass and tree basal area

Grass biomass significantly decreased with distance to water in the wet season but not during the dry season (Figure 5.4). Furthermore, grass biomass was higher during the wet season than dry season (ANCOVA: $F_{1,173} = 6.29$, $P = 0.01$) and this difference decreased with distance to permanent water (Figure 5.5; ANCOVA: $F_{1,173} = 29.6$, $P < 0.001$). Woody vegetation was mostly clustered around permanent water source for both datasets (Figure 5.5).

Discussion

Grazers showed a clear spatial habitat separation in relation to surface water especially during dry season but browsers congregated closer to surface water. In this, we found a

Figure 5.4: Relationship between mean grass biomass (DPM) and distance to water for the wet season (black circles) and dry season (grey triangles). Lines represent linear regressions for the wet season (black solid) and dry season (grey dashed).

Figure 5.5: Tree basal area as a function of distance to water for the dung count dataset (A) and the visual count dataset (B). Black dashed lines represent the linear regression models.

strong spatial variation in the distribution of grazers relative to water. In addition, greatest mean distances to water were evidently to wildebeest and zebra in the wet season and Thomson’s gazelle and Grant’s gazelle in both seasons. Furthermore, we found a strong negative correlation between dry season dung moisture content (an index for water requirements) and mean distance to water during dry season for grazers. Similarly, Grazer’s body mass also did show significant effect on dry season variation in mean distance to water. The ability of functional traits of dung moisture and

body mass to explain grazers distribution relative to water confirm our earlier work that these traits are useful indexes of interspecific differences in water requirements. In summary, we found that dry season dung moisture content consistently, better predicted variation in mean distance to water than body mass for grazer and that relationships were stronger in the dry season. Our results support the hypothesis that the distribution of savannah large herbivores across landscape gradients is driven by resource partitioning through interspecific differences in food and water requirements as two interacting niche axes. Moreover, we showed that browser and grazers were both affected by density of woody biomass, which may have a confound effects on forage availability for browsers and predation risk for both groups.

The effects that surface water exerts in grazers depict important ecological choices herbivores make in-order to enable them balance the trade-off between water constraints and nutrition requirements. Our result shows a clear pattern of habitat separation relative to species' water requirement between seasons, with some species moving closer to water and few species remaining in areas far away from water in the dry season. For instance, during wet season, wildebeest, zebra, Thomson's gazelle and Grant's gazelle occupied areas within the southern plains, the most drier party of the landscape and during the dry season, zebra and wildebeest substantially moved to areas closer to water while Thomson's gazelle and Grant gazelle maintained their position by occupying areas away from surface water coinciding with their water dependence. Nevertheless, there was a clear movement of grazers to water suggesting that migration behaviour can also be explained by species' water requirement (Fryxell and Sinclair 1988; Frank et al. 1998). In comparison, grazers are more vulnerable to surface water constraints than browsers so that grazing herbivores are comparative more capable of travelling long distances than browsers (Abraham et al. 2019). Greatest mean distances to water observed for wildebeest and zebra in wet season explain their dry season movements to areas with available water (Wolanski et al. 1999; Gereta et al. 2009). This exceptionally large differences of mean distance to water distribution of zebra and wildebeest in response to surface water variation collaborates their higher water dependence (Redfern et al. 2003b; Valeix 2011). Accordingly, we found a relatively higher strong association of mean distance to water with minimum dung moisture content than body mass, which indicates that the need for herbivore species to occupy position in the landscape is better explained by its water requirement. Our findings are in agreements with other studies (Gereta and Wolanski 1998; Wolanski et al. 1999; Wolanski and Gereta 2001) that also indicated ungulates distribution across the landscape is driven by surface water availability. Therefore, differences in water requirements among grazers allow spatial separations of habitats given surface water constraints and while observing critical threshold for forage requirements. Therefore, we suggest that water requirements provide an additional dimension of spatial niche partitioning among grazer across the landscape.

Water and forage availability play a fundamentally key role in shaping large herbivore community assemblages along minimum dung moisture content and body size dimensions. We showed difference responses to distances to water between grazers and browsers, coinciding with the well-established differences in water dependences between the two feeding groups (Western 1975; Smit 2011; Kihwele, et al. 2020). While grazers did change their position on the landscape in response to surface water, browsers on the other hand persistently maintained their habitat use closer to water, coinciding with highest wood vegetation (TBA) which provides the required foraging ground. Thus, the lower mean distance distributions of browsers is independent of surface water, supporting existing evidences of being less dependent on drinking water (Western 1975; Smit 2007; Veldhuis et al 2019; Kihwele et al. 2020). The preferential affinity of browsers to rivers suggest that rivers are capable of simultaneously acting as habitat, source of water and food, thus driving the preferential selection by browsers. Although grazers are known to be more water dependent, there were species specific variation in mean distance distribution to water with a clear pattern of associations. Given similarity in water requirements between the two feeding groups, it is believed that grazers differ from browsers in the frequency of drinking, suggesting that in the dry season and drought years, surface water constraints thresholds are more critical to grazers than browsers. This is also confounded by relative low water content of a graze than that of a browse in the dry season, thus imposing a more need for regular access to drinking water for grazers. It is further expected to be critical during drought when both grasses and water become reduced (Abraham et al. 2019). Given the distinct variation in water requirement between grazers and browsers, the water independent species (browsers) largely maintain their water balance through forage relative to drinking (Kihwele et al. 2020). Importantly, and in-line with water requirements, it is imperatively important to understand how spatial habitat partitioning in grazers and the spatial distribution of wood vegetation will affect the population structure of browsers and the ecology of the riparian habitats.

Surface water availability is potentially important ecological factor influencing the landscape-scale distribution of herbivores across savannah ecosystems. For savannah ungulates, body size has been shown to influence habitat selection and facilitate species co-existence (Cromsigt et al. 2009), based on food requirements thresholds (Olff et al. 2002; Hopcraft et al. 2012; Owen-Smith et al. 2015), and water requirement tolerances (Redfern et al. 2005; Kihwele et al. 2020). Thus both dimension determine the species' choice and occupancy of a preferred habitat in the landscape. We found that grazers preferentially divide habitats across the landscape following seasonal changes in surface water while browsers respond to forage availability. This indicates that surface water is more important for grazers than browsers. Our analysis showed strong associations between mean distance distribution with both dry season dung moisture content and body mass, with both functional traits decreasing with distance to water. Thus,

these strong correlations infer that large herbivore water requirement can serve as an additional axis of spatial niche partitioning among herbivores as long as there is a penalty in occupying habitats close to water. This could be low forage quality and quantity (Anderson et al. 2010; Hopcraft et al. 2012) but also other constraints such as predation (Mduma et al. 2007) or disease transmission that impose a limitation for a species selecting different optimum distance from water to balance these different constraints.

Heterogeneity in resources across the landscape is an important ecological factor that provides for abundant and diverse herbivore community assemblages. The observed variation in both grass abundance and tree basal area provide an enabling environment for different species to coexist given that they can partition the food resources and thus reduce competition. Variation in resources both in time and space impose a constraint to herbivore allowing them to respond by either shifting to alternative resource or moving to seasonal ranges with available and accessible resources. For instance, a strong spatial association of total basal area with distance to water indicates a considerable potential contribution of surface water on soil moisture that has a strong effect on vegetation community and composition (Reed et al. 2009).

However, the rate of human population growth around protected areas (Veldhuis et al. 2019), increased land use changes (Mati et al. 2008; Mwangi et al. 2017) and climate change (Bartzke et al. 2018) will compromise ecological processes by limiting herbivores from accessing and utilizing historical ranges (Bolger et al. 2008; Harris et al. 2009). Our result shows water requirements to be fundamentally critical for allowing spatial niche separation for grazing herbivore and the co-existence of diverse community assemblages. Therefore, sustaining heterogeneity in surface water distribution in space and time will have a profound effects on improving the diversity and composition of herbivore species in savannah and arid ecosystems (Veldhuis et al. 2019). Thus, based from our result, we suggest that drought imposed constraints are going to be more critical to grazers than browsers while mixed feeders are going to shift diets whereby large grazers will move to areas with available water (Abraham et al. 2019). The current management intervention through water points provision, though controversial, must be limited to maintain the historical heterogeneity of water availability and avoid homogenizing of water availability across the landscape. This is because the homogenisation of surface water distribution can result into altering ecosystem processes through changes in local movement patterns and dietary shifts while facilitating predation risk (Harrington et al. 1999; Redfern et al. 2003; Abraham et al. 2019).

Surface water availability is increasingly becoming a major environmental concern in the Serengeti Mara ecosystem with adverse effects on wildlife conservation in core protected areas. Continuous decline in the flow level of the Mara River, the lifeline of the ecosystem caused by land use/land cover changes (Mati et al. 2008; Mango et al. 2011), deforestation of the catchments (Kipampi et al. 2017), growing irrigation

demand (Wolanski et al. 1999; Gereta et al. 2009; Mnaya et al. 2017) and population growth (Veldhuis et al 2019) is further compromising ecosystem health and functioning. Given the additional likely impact of climate change, the drying of the Mara River in the dry season is inevitable and is predicted to affect grazers more than browsers (Kihwele et al. 2020), and from model prediction by (Wolanski et al. 2002), the drying of the river will result into the collapse of the ecosystem. Because of existing threats on surface water, wildlife managers are foreseeing intervention of planning for artificial water provision through water points. The focus is to improve water provision such that water can be manipulated for dry season wildlife use across the landscape geared towards improving population numbers and tourism satisfactions. Considering water provision based on our observed mean distance distribution and species water requirements (Kihwele et al. 2020) might be challenging and misleading. Therefore, any water provision policy will need critical assessment and evaluation, in particular to avoid homogenisation of the habitat in relation to surface water availability.

Conclusion

The current study shows that grazers are spatially partitioned following species-specific water requirement, and that the distribution of browsers also depends on water but in addition is confounded by other ecological processes and habitat features including TBA. This implies that, the dry season distribution of permanent water sources seems to impose landscape-scale constraint on seasonal movement patterns of grazers. If surface water is evenly distributed across the ecosystem will result into homogenization of habitats that will subsequent reduce habitat diversity and ecosystem resilience. In order to ensure maintenance of heterogeneities, conservation of water catchments must be given a high priority so as to ensure sustainable surface water supply in rivers for ecosystem processes. This study suggest that water requirement is an additional dimension for niche partitioning for grazers in African savannah ecosystems. Thus the findings of this study can be used as a snap-shot to other ecosystem however, caution has to be considered because of different distribution of water sources and vegetation community. Importantly, continuing with this study to include more years and incorporate the assessment of drinking frequency will further allow prediction for climatic extreme years.

Supplementary information

Table S1: Number of observation for the different species for the dung count dataset and visual count dataset.

Species	Dung counts			Visual counts		
	Total	Dry season	Wet season	Total	Dry season	Wet season
Buffalo	409	175	234	69	22	47
Dik.dik	17	11	6	31	11	20
Eland	210	110	100	25	9	16
Elephant	231	88	143	30	16	14
Giraffe	206	90	116	68	28	40
Grant.gazelle	436	246	190	250	107	143
Hartebeest	NA	NA	NA	122	36	86
Hartebeest/Topi	1591	569	1022	NA	NA	NA
Hippopotamus	50	26	24	25	10	15
Impala	751	411	340	211	93	118
Oribi	69	31	38	NA	NA	NA
Tomson.gazelle	1693	1088	605	462	299	163
Topi	NA	NA	NA	133	54	79
Warthog	0	0	0	146	72	74
Waterbuck	10	10	0	8	3	5
Wildebeest	3163	1591	1572	183	39	144
Zebra	1575	673	902	224	96	128

Table S2: Results of logistic regression models for each species and season.

Species	Parameter	Dry season				Wet season			
		Estimate	SE	F	P	Estimate	SE	F	P
Buffalo	Intercept	-2.55	0.13	-20.32	0.00	-2.83	0.13	-21.38	0.00
Buffalo	Distance to water	-0.01	0.05	-0.22	0.83	0.18	0.04	4.10	0.00
Buffalo	Distance to water ²	-0.01	0.00	-2.43	0.02	-0.02	0.00	-5.19	0.00
Dik-dik	Intercept	-5.46	0.53	-10.40	0.00	-6.39	0.80	-7.97	0.00
Dik-dik	Distance to water	0.12	0.29	0.42	0.68	0.31	0.41	0.76	0.45
Dik-dik	Distance to water ²	-0.02	0.03	-0.86	0.39	-0.04	0.04	-0.97	0.33
Eland	Intercept	-3.68	0.19	-19.47	0.00	-3.58	0.18	-19.45	0.00
Eland	Distance to water	0.13	0.05	2.62	0.01	-0.01	0.04	-0.32	0.75
Eland	Distance to water ²	-0.01	0.00	-3.67	0.00	0.00	0.00	-0.34	0.74
Elephant	Intercept	-2.72	0.14	-18.76	0.00	-2.50	0.13	-19.67	0.00
Elephant	Distance to water	-0.31	0.06	-4.94	0.00	-0.12	0.05	-2.32	0.02
Elephant	Distance to water ²	0.01	0.00	1.76	0.08	0.00	0.00	-0.99	0.32
Giraffe	Intercept	-3.24	0.17	-19.41	0.00	-2.92	0.15	-19.66	0.00
Giraffe	Distance to water	-0.10	0.05	-2.13	0.03	-0.04	0.06	-0.74	0.46
Giraffe	Distance to water ²	0.00	0.00	0.28	0.78	-0.01	0.00	-1.66	0.10
Grant's gazelle	Intercept	-4.84	0.25	-19.15	0.00	-4.72	0.26	-17.84	0.00
Grant's gazelle	Distance to water	0.26	0.04	6.69	0.00	0.10	0.04	2.55	0.01
Grant's gazelle	Distance to water ²	-0.01	0.00	-4.35	0.00	0.00	0.00	0.66	0.51
Hippopotamus	Intercept	-3.68	0.25	-14.84	0.00	-3.15	0.29	-10.78	0.00
Hippopotamus	Distance to water	-0.52	0.16	-3.23	0.00	-1.54	0.52	-2.97	0.00
Hippopotamus	Distance to water ²	0.01	0.01	1.25	0.21	0.05	0.02	2.12	0.03
Impala	Intercept	-1.70	0.09	-19.11	0.00	-1.82	0.09	-19.26	0.00
Impala	Distance to water	0.03	0.03	0.75	0.45	0.00	0.04	0.03	0.98
Impala	Distance to water ²	-0.01	0.00	-4.32	0.00	-0.01	0.00	-3.47	0.00
Oribi	Intercept	-6.61	0.67	-9.84	0.00	-6.97	0.74	-9.42	0.00
Oribi	Distance to water	0.65	0.19	3.32	0.00	1.39	0.28	4.89	0.00
Oribi	Distance to water ²	-0.04	0.01	-2.96	0.00	-0.13	0.03	-4.98	0.00
Thomson's gazelle	Intercept	-3.80	0.15	-24.51	0.00	-4.20	0.18	-23.31	0.00
Thomson's gazelle	Distance to water	0.27	0.02	11.02	0.00	0.28	0.03	10.21	0.00
Thomson's gazelle	Distance to water ²	0.00	0.00	-3.37	0.00	-0.01	0.00	-5.72	0.00
Topi/Hartebeest	Intercept	-1.54	0.08	-18.82	0.00	-1.06	0.07	-15.64	0.00
Topi/Hartebeest	Distance to water	0.09	0.03	3.15	0.00	0.01	0.02	0.35	0.73
Topi/Hartebeest	Distance to water ²	-0.01	0.00	-6.50	0.00	0.00	0.00	-2.38	0.02
Waterbuck	Intercept	-5.59	0.58	-9.66	0.00	NA	NA	NA	NA
Waterbuck	Distance to water	0.59	0.51	1.16	0.25	NA	NA	NA	NA
Waterbuck	Distance to water ²	-0.12	0.09	-1.40	0.16	NA	NA	NA	NA
Wildebeest	Intercept	-0.32	0.07	-4.66	0.00	-1.65	0.08	-21.89	0.00
Wildebeest	Distance to water	0.40	0.03	11.85	0.00	0.12	0.01	8.11	0.00
Wildebeest	Distance to water ²	-0.04	0.00	-14.37	0.00	0.00	0.00	-1.67	0.09
Zebra	Intercept	-1.59	0.09	-18.66	0.00	-1.86	0.08	-22.48	0.00
Zebra	Distance to water	0.26	0.04	7.07	0.00	0.04	0.02	2.15	0.03
Zebra	Distance to water ²	-0.03	0.00	-8.65	0.00	0.00	0.00	1.21	0.23

Figure S1: Dry season dung moisture is positively related to body mass for both grazers (red triangles) and browsers (black dots). Lines indicate linear regressions for grazers (red dashed) and browsers (black solid).

Figure S3: Dry season dung moisture (A,C) and body mass (B,D) explain variation in mean distance to water for grazers in the dung count dataset (A,B) and visual count dataset (C,D) during the wet season. Grazer (red triangles) and browser (black dots) species are identified by the first two letters of their genus and species name. Lines represent linear regressions for grazers (red dashed) and browsers (black solid).

Figure S2: Comparative spatial responses of herbivore species distribution relative to distance to water between dry and wet seasons. General trends identified from slope estimates using logistic regressions (see Table S2) indicate positive association (+), a negative association (-) or an optimum (0). P-values > 0.05 are indicated by NS, P-values < 0.05 are indicated by *, P-values < 0.01 are indicated by ** and P-values of < 0.001 are indicated by ***.

Chapter 6

Synthesis: Water and wildlife in Serengeti-Mara ecosystem

Emilian S. Kihwele

Introduction

In this thesis, I contribute to the knowledge base on understanding the drivers of changes in surface water availability and how the changes affect African herbivore communities in savannah ecosystems. Here, I explain how different herbivores with different water requirements can coexist in landscapes which are water constrained especially in the dry season. The central focus of this chapter is to provide an overview of how distance to water, dung moisture content and body mass affect surface water dependence of Africa large herbivores. Understanding the dynamics of river flow (an index of surface water availability for herbivores) given the changes in land use and climate change and the drivers of large herbivore distributions across the landscape and seasonal dispersion is now intriguing ecological researchers. In this thesis therefore, I have (i) investigated the effect of upstream land use changes on the river flow dynamics in Serengeti ecosystem (Chapter 3); (ii) developed a method to quantify surface water requirements for African savannah herbivore using functional traits (Chapter 4). Subsequently, I (iii) tested how surface water affects herbivore' landscape use through quantifying mean distance distribution along water gradients and integrating it with dung moisture content (an index for water dependence) and body size (Chapter 5). Here, I will provide an overview of my main findings, recommendations for future research and a conclusion.

Surface water constraints in savannah large herbivores

Savannah herbivores are constrained with available water for drinking mostly during dry season as a result, they have developed physiological, ecological and behavioural adaptations for reducing surface water dependence in-order to allow them inhabit these habitats. Insufficient surface water availability in space affect herbivore landscape use thereby allowing large herbivores to exhibit seasonal movements so as to meet their water requirements. In this study, we have shown that minimum dung moisture content (a proxy for water dependence) and body mass are strong determinants of ungulates' water requirement. Such that savannah ungulates reduce water loss through multiple pathways simultaneously (Chapter three). Implicitly suggesting that each functional trait can independent be a reliable index explaining the species differences in water requirement among ungulates.

Various studies (Western 1975; Redfern et al. 2003; Redfern et al. 2005; Kihwele et al. 2020) have provided evidence on the differences in water requirements between grazers and browsers based on feeding types, with browsers categorised as less water dependent than grazers. Given the species specific water requirement, we predict that climate change constraints will relatively be more critical to grazers than browsers. Such that grazers are expected to switch to foraging on plant species with higher moisture content so as to increase water intake especially during droughts to compensate

for body water. Therefore, a conceptual integrative framework that develop a two dimensional trait space of body size and minimum dung moisture content that captures the combined effects of both food and water requirements of large herbivores is proposed. This novel mechanism improves our understanding on how interspecific differences in adaptation to droughts of African ungulates can be explained by the variation in body size and dung moisture content. It has been suggested that ungulates' position relatively to water source (distance to water) indicates water dependence (Owen-Smith 1997; Gaylard et al. 2003; Ogotu et al. 2010; Smit 2011; Cain et al. 2012; Ogotu et al. 2014). But the distribution of ungulates in the landscape is confounded by other factors such as food requirement and sensitivity to predation risk.

Sustainable water availability for herbivore is depended on land uses

Land use change and human population growth are accelerating watershed degradation through increased deforestation, irrigated agriculture, and livestock production (Mati et al. 2008; Gereta et al. 2009; Mwangi et al. 2017; Veldhuis et al. 2019). Importantly, degradation of water catchments has a negative effect on the water supply for savannah ecosystems thereby livelihoods of people and wildlife in these areas entirely depend on it. Savannah ecosystems are necessary for sustaining ecosystem services, but still they are threatened by progressive decline in water especially river flows that might ultimately result into effects of large herbivore community assemblages (McClain et al. 2013; Mnaya et al. 2017; Kihwele et al. 2017). Recent studies have shown that continuous decline in water flow of the Mara River is a major conservation challenge to Serengeti-Mara ecosystem whose integrity is centered on the existence of two dominant migratory species, the wildebeest and zebra (Thirgood et al. 2004; Gereta et al. 2009; Hopcraft et al. 2013). In this thesis, we have shown that livestock grazing and wildfire has strong effect on water yields through their effects on the quality of catchments through their effects on water pathways. More importantly, we have shown that the recession time scale of Mara River has reduced from 100 days in 1972 to 16 days in 2018 while that of the Mbalageti River remained constant at 70 days indicating that unprotected catchment are highly affected by land use changes. By contrast the hydrology of protected areas in Serengeti National Park has not changed, demonstrating the maintenance of the quality of the watershed (Chapter 2).

The most apparent effect of the land use change on the river hydrology are catchment deforestation and increase in irrigation (Wolanski et al. 2002). These effects have affected the Mara River flow through reduced recession time scale. In contrast, the Mbalageti River maintained its recession time scale indicating the persistence of the quality of the watershed. That means, Mara river with a catchment and head water at unprotected areas has been degraded due to land use changes while the head water of Mbalageti River which is entirely within Serengeti National Park has maintained its hydrology processes as it has maintained its watershed condition. This indicates that

protected areas are not only important for biodiversity conservation but also potential and critical for maintaining river flows and watershed condition. Similarly, livestock grazing and fire have effects on the catchment quality, and thus stream flow suggesting that intensive livestock grazing as well as the use of wildfires outside the National Park result in degradation of land cover and increased erosion, that in turn degrades catchments and affecting water supply for people and wildlife. This means that integrated catchment basin wide approach is necessary for sustainable water management.

The failure to address water management issues at basin scale and given the rate of climate change, will result into seasonality of rivers with consequent effects on wildlife. This will not only affect large herbivore through lack of drinking water but will also affect other ecosystem processes such as spatial niche differentiation of grazing herbivores.

Differences in water requirements allow coexistence of different herbivores

Savannah ecosystems are characterised by the co-existence of different species of large herbivore (Cromsigt et al. 2009; Owen-Smith 2015; Kihwele et al. 2020) and vegetation types, mainly a mixture of grasslands and woodlands (Scholes and Archer 1997) in a water limited environment. The high diversity of species is a result of gradients in resources such as surface water (Redfern et al. 2003; Cain et al 2006; Smit 2011; Cain et al. 2012; Owen-Smith and Traill 2017), nutrients (Anderson et al. 2007; Anderson et al. 2010; Anderson et al. 2016), and disturbances like fire (Eby et al. 2014). Various theories have been developed to explain coexistence of savannah ungulates and resource partitioning relatively to interspecific differences in body size and feeding types (Owen-Smith 1997; Olff et al. 2002; Gordon and Prins 2008; Anderson et al. 2010; Hopcraft et al. 2010; Hopcraft et al. 2012; Owen-Smith 2015). Body size variation has been used successful to predict food requirements and predation risk of large herbivores (Olff et al. 2002; Sinclair et al. 2003; Cromsigt and Olff 2006; Hopcraft et al. 2012). However, recent study (Kihwele et al. 2020) has suggested that differences in water requirement of various herbivore species is also important as it enables for coexistence of diverse herbivore species.

Heterogeneity in surface water might be of critical ecological importance for promoting herbivore diversity through ensuring the existence of both water dependent and independent species. It is now a concern for most protected area management on declining surface water availability. Much attention is focused on provision of artificial water sources for wildlife especially during dry season and drought years. This homogenization in surface water across the landscape will likely prevent herbivore movements to historical ranges, thereby causing adverse effects to ecosystem processes. Furthermore, it is known that water sources facilitate predation risk such that provision of surface water to drier areas which are generally inhabited with less water dependent ungulates will impose a higher risk of e predation while also increasing environmental

degradation from overgrazing as a result of confinement and concentration of abundant grazing herbivores in localized areas (Western 1975; Weeber et al. 2020).

Our result suggests that heterogeneity in water is important for improving wildlife conservation because it enables the coexistence of diverse community assemblages of herbivores. Importantly, unevenly distribution and access of water allow for seasonal movements of ungulates that in-turn facilitate maintenance of ecological processes that are critical for ecosystem health. For instance, the annual migration of wildebeest in the Serengeti National Park that is driven by surface water and forage has been shown to contribute to fire suppression and nutrient transfer across the landscape. The homogenization of surface water may result into preventing the annual ungulate migration that will subsequently have devastating impact on ecosystem processes and tourism revenue and experience.

Water requirements can better explain spatial niche partitioning than body size

Much work has been devoted to understand the mechanisms that explain the coexistence of diverse ungulates assemblages in African savannah ecosystems. Various studies have shown that the variations in dietary resources allows for co-existence of different herbivores along body size dimensions such that small sized mammalian herbivores preferring to occupy areas of high quality grasses and large sized ungulates occupying areas of low quality but abundant grass biomass. Furthermore, body mass has been well established as a dimension that is used predict species sensitivity to predation. In addition, distinctions in feeding guilds (grazers vs. browsers) and digestive physiology (ruminants vs. non-ruminants) have also been identified as dietary niche differentiations that allow different species to occupy the same habitat because of being capable to separate their diets. More important, recently it has been established that dung moisture, a proxy of water requirement for African savannah herbivore is strongly correlated with body size.

Savannah are water constrained ecosystems such that ungulates inhabiting these areas require physiological, behavioural and anatomical adaptations for water conservation in-order to survive in these areas especially during dry season. A recent study has established a wide range of water requirements among the savannah herbivores with browsers being comparatively less water dependent than grazers (Kihwele et al. 2020). The observed clear spatial habitat separation in relation to surface water especially during dry season for grazers and browsers showed congregated pattern closer to surface water is of ecological and conservation importance. This implies that water and forage requirements facilitate habitat separation among herbivores thereby reducing resource competition and environmental degradation. In contrast, a relatively stronger association of mean distance to water with minimum dry season dung moisture content instead of body mass provides a new contribution to the role of different functional traits on niche differentiation among different herbivores. Therefore, we propose that

water requirement better explains niche partitioning than body mass. Protected area managers need to take it into consideration when there is a need of artificial water provision, and at all cost homogenisation of surface water availability must be avoided.

Maintaining access to natural water sources

Diverse community assemblages of ungulates in savannah ecosystems are strongly associated with gradients and diversity in surface water and forage (Anderson et al. 2016; Veldhuis et al 2019; Kihwele et al. 2020). Increasing decline in surface water availability is threatening large herbivores in savannah and arid ecosystems and subsequently affecting ecosystem processes. Considering the threats posed by land use land cover changes, compounded by climate change impacts, it is expected that surface water in savannah ecosystems will be unavailable especially in dry season and resulting into effects on ungulate landscape use. Given these threats, conservation managers may increase efforts towards artificial water provision through water points of which their effects on wildlife health is unclear. For instance, it has been established that water from bore holes supplied to wildlife in Central Kalahari Game Reserve has poor quality that has health implications to wildlife (Selebatso et al. 2018).

It is now clear that Mara river flow is guaranteed to dry in the near future as the current study has shown that the recession time scale for Mara river, the only permanent water source for wildlife in Serengeti National Park, has decreased by 6 folds

Figure 6.1: Map of Serengeti National park with areas potential for providing water to wildlife in Speke and Loliondo Game Controlled Areas in red circles.

between 1972 – 2018. If this trend is not intervened and appropriate measures instituted, there is huge likelihood for the river to stop flowing in the dry season and therefore causing devastative impacts to large herbivores especially migrants. Moreover, increasingly human population growth in areas around the park with associated growth in livestock numbers particularly in Loliondo Game Controlled area, a headwater for Grumeti River will further have compounding effects on future surface water availability for the ecosystem. In-order to sustain wildlife and ecosystem health, it is critically important for immediate actions that will ensure the continuous accessibility of surface water from natural sources.

Enhancing integrated watershed management through ecohydrology based solutions in the Grumeti River headwaters may enable availability of water in pools along the entire river course (Figure 6.1). This entail total protection of areas that form head waters for Grumeti River in Loliondo Game Controlled area. Furthermore, upgrading the Speke Bay Game Controlled Area and annex it to Serengeti National Park to allow wildlife movements to access water from Lake Victoria will enhance ecosystem functions and processes (Figure 6.1). The proposed interventions involve restrictions from people using the areas, meaning that human settlements have to be removed from those areas so that to allow recovery of ecosystem components.

Future avenues for research work

In this thesis, I have contributed to the understanding of ecological implications of surface water on ungulates landscape use and how different large herbivore species dependence respond to surface water constrains especially during dry season. I have also developed a mechanism to quantify water requirements of African savannah herbivores using functional traits related to physiological, behavioural and ecological adaptation towards water conservation. I believed this increases our understanding on the role of surface water in maintaining savannah ecosystems. It also shows how water requirements allow for spatial niche differentiation between various herbivores species. But still, there are several questions that remain unanswered. Here therefore, I suggest and provide areas of future researches.

Although land use changes are recognised as important driver of reduce flow levels in rivers in the dry season through altering the condition of watersheds, but the proportional impacts of each specific land use and how does the interaction of different land uses affect water yields and flow levels remain understudied. Within the concept of ecohydrology we may expect large differences in proportional contribution to catchment degradation and each driver may require different intervention. Therefore, I recommend investigations of effects of different land uses on the condition of the watershed and consequently river flow dynamics. More important is the quantification of intensity and severity of livestock grazing and fire that are destructive to the quality of watershed.

Enormous attention has been given to forage resource differentiation of African savannah ungulates contributing to the understanding of mechanisms of coexistence. In addition, a new axis (water requirement) of niche dimension that is independent of body size explaining spatial partition of grazing herbivores along surface water gradients has provided insights of how ungulate position themselves and use the landscape. Because the water requirement niche axis is also confounded by forage availability, how different plant species account for water requirement is largely unknown. Thus I recommend a study on the interplay between preformed water (water obtained from food) and species water requirement under different treatments (condition) of water availability across the landscape. Furthermore, an understanding of the effects of distance to water distribution of large herbivores on the composition and structure of vegetation and its implication on the environment along a grazer-browser continuum is required.

Extensive research work has been executed to understand differences in water dependence between browsers and grazers such that browsers are considered less water dependent as they rely on water from the food rather than drinking. We might expect that there are plant species specific differences in the water content and these may be linked to the nutritional quality of the forage and its physiological and ecological adaptation related to reducing transpiration. This means that, to compensate for water requirements, herbivores, especially during dry season and drought years might switch to foraging from plants with high water content, thereby reducing their dependence from drinking. Therefore, it is still unclear what is the proportional contribution of water from different plant species eaten by grazers and browsers. Nevertheless, establishing inter-species specific variation of water requirements and species specific tolerance threshold between drinking intervals for herbivores is required.

Finally, applying the mechanism of large herbivores surface water dependence described in this thesis to other ecosystems is critically important to test the generalised applicability. Finding similarities and differences will further facilitate the its application.

Conclusion

It is evident that surface water availability for large herbivores in Serengeti ecosystem is at stake due to ever increasing land use changes with consequences for herbivore landscape use. These effects are expected to worsen with climate change thereby imposing constraints to large herbivores diversity, abundance and distribution across the landscape. Because grazers are more water dependent than browsers, and thus the water content of browse is higher than that of a grass, given climate change impacts, grazers will most suffer than browsers. Implying that protected area management should

take into consideration heterogeneity in surface water as a facilitative entity for maintaining herbivore diversity while homogenization will result into squeezing of historical ranges thereby resulting into environment degradation due to congregation. In addition, the homogenization of surface water will attract water dependent species to access areas that are occupied by less water dependent species and therefore subjecting them into increased predation risk. Importantly, we have now developed a mechanisms of quantifying surface water dependence using functional traits and also we have shown that water requirements allow for spatial niche partitioning for large herbivore suggesting that heterogeneity in water have ecological importance on ecosystem processes and functioning such that failure to maintain it will likely result into ecosystem degradation of not collapse in the worst case situations.

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Summary

Samenvatting

Water and wildlife in the Serengeti-Mara ecosystem

African savanna ecosystems are often characterised by the coexistence of diverse herbivore assemblages along landscape gradients of surface water and forage. Increasingly reduction in the surface water availability in these ecosystems especially in the dry season caused by escalating changes in land uses compounded by climate change will continue posing major constraints to the coexistence of large herbivore with consequences for wildlife conservation and ecosystem services. Variation of surface water and forage in space and time in the Serengeti Mara ecosystem are often explained by the existence of two opposing pronounced gradients of rainfall and soil quality. Distinctions in rainfall and soil quality is further translated into available quantity and quality of plant biomass that is the key driver of abundance and distribution of large herbivores. For instance, body size variation is commonly used to explain niche differentiation and coexistence along major landscape gradients of plant available moisture and nutrients that together determine the availability and digestive quality of plant biomass. However, we are insufficiently understand what traits can be used as proxy for species water dependence. Furthermore, it is unknown how the distance to water distribution of large herbivore allows for spatial niche partitioning of grazing herbivore and therefore their coexistence in landscapes that are increasingly threatened by progressively declining surface water availability due land uses and climate change. Here, we experimentally investigate how livestock grazing and fire affect watershed condition and ultimately streamflow and river flow dynamics. We also quantified surface water requirement of African savanna ungulates using six different functional traits related to three water loss pathways, which are through dung, urine and evapoaration. We further investigated how distance to water distribution of large herbivore can add-up another new dimension of niche partitioning that is independent to body size.

In **Chapter 2**, We conceptually reviewed and developed a two dimensional trait space of body size and minimum dung moisture content that characterises the combined food and water requirements of large herbivores. In this, we developed five testable hypotheses (H1-H5) that aimed at capturing the main axes of variation related to physiology, ecology and evolutionary history to an integrative frameworks. We hypothesize that large herbivores need to balance between food, water and thermoregulatory requirements and related them with body size. Body size variation is used as a key dimension for predicting niche partitioning relatively to quantity and quality of plant materials. Additionally, as explained, body size is a key trait that governing species sensitivity to water and thermoregulation. In this we propose that large herbivores are likely to suffer more from climate change impacts than small sized herbivores. In order to sustaining large herbivore assemblages in savanna ecosystems, we suggest an integration of food and water requirements, predation risk and thermoregulatory constraints

into a generalisable framework. This implies that given climate change impacts, savanna large herbivores will need to negotiate simultaneously between a landscape of fear, a landscape of food, a landscape of heat and a landscape of water whereby body mass and minimum dung moisture content capture important axes that demonstrate niche differentiation and coexistence opportunities in a landscape.

In **Chapter 3**, I experimentally quantified how different land management regimes (Fire and livestock grazing) affect water pathways and subsequently stream flows. In this I continuously monitored river flow dynamics in major rivers and small streams in experimental small watersheds. In addition, I quantified grass biomass and infiltration rates as proxies for the quality of watershed. I also collected historical data on river discharges for Mara and Mbalageti Rivers that was used as a baseline to explore what changes have occurred since. I found that the baseflow recession time scale for Mbalageti river with catchment inside Serengeti National Park, natural system, has remained unchanged at 70 days. By contrast the baseflow recession time scale for Mara River with watershed in community land has changed from 100 days in 1970s to 16 days at present due to land use changes upstream. Moreover, I showed that small watersheds in livestock grazing watersheds have spiky, high peak but short-lived flows compared to fire and control watersheds. Given the development of proposed water development in Kenya and threats of climate change, I plea for an ecohydrological solution to rescue Mara river from ceasing to flow in the dry season to avoid devastating consequences to wildlife conservation in Serengeti National Park and Maasai Mara National Reserve.

In **Chapter 4**, I quantified water requirements for 48 African large mammalian herbivore species using six functional traits. I combined data on dung properties collected in Serengeti National Park and Gorongosa National Park with physiological and ecological traits from published studies. I then explore the relationships between minimum dung moisture, dung pellet size, distal colon area, urine osmolality, medullary thickness, and evaporation rate to find the best indicator(s) for water requirements of mammalian herbivores. Subsequently, I investigate the relationships between our predicted water requirements with herbivore feeding types, phylogeny, and classifications of surface water dependence based on literature assessment. Here I find a wide variation in water requirements among African large herbivores, resulting in two broader groups of water dependent and water independent species. In this, I showed that less dependence on drinking water is enhanced through developed physiological and ecological traits related to water loss such that ungulates adapted to arid environments are capable of preventing water loss through multiple pathways simultaneously. I therefore suggest that minimum dung moisture content is an index of the hydration state of African ungulate species, while relative dung size is an index of the species' capacity to conserve water. However, my result proposes that heterogeneity in surface water distribution

has a positive effects on increased diversity and coexistence of large herbivore. Importantly, thus given climate change, such as drought, it is likely to most affect water dependent species than water independent species. I argue to protected area managers that they need to consider water requirements when instituting water provision policy through artificial water points.

In **Chapter 5**, I investigate effects of surface water on the distributions of large mammalian herbivores across the Serengeti National Park in time and space. I further relate the mean distance to water distributions through variation in water requirements, body size and feeding type to unravel whether variation in water requirements allows for spatial niche partitioning between herbivores. Results show strong spatial variation in the distribution of grazers in relation to distance to water but not between browsers. Interestingly, I found that dry season dung moisture consistently better predicted the variation in mean distance to water than body mass for grazers and these relationships were stronger during the dry season suggesting that water requirements is a strongest predictor of spatial niche partitioning of grazing herbivores.

All-together, I presented a novel contributions to the understanding of water requirements for African savanna ungulates. The evidences suggested on the use of functional traits to predict water requirement and in particular the proposed minimum dung moisture content as an index of water requirement is imperative to the management of wildlife given climate change threats. Furthermore, the explained evidence of water requirement in influencing niche differentiation is now critical and need a serious consideration when implementing a water provision policy.

Water en wilde dieren in de Serengeti

De beschikbaarheid van oppervlaktewater voor grote grazers in savanne ecosystemen wordt steeds meer bedreigd door veranderingen in landgebruik, ontbossing, toegenomen irrigatie en klimaatverandering. Daarnaast is er sprake van een sterke achteruitgang van de beschikbaarheid van oppervlaktewater in de droge tijd, met mogelijk grote gevolgen voor de aantallen planteneters en het functioneren van ecosystemen. Veranderingen in de beschikbaarheid van oppervlaktewater hebben invloed op de interacties tussen soorten onder meer door veranderingen in de seizoensgebonden migraties van deze soorten. Eerder onderzoek heeft de ruimtelijke verspreiding van herbivoren al in verband gebracht met hun waterafhankelijkheid. Maar de ruimtelijke verspreiding van grote herbivoren over het landschap wordt ook bepaald door andere factoren, zoals roofdieren en hun voedselbehoefte. In dit proefschrift onderzoek ik de oorzaken en gevolgen van hydrologische veranderingen op herbivoren in de Afrikaanse savanne en invloed van de beschikbaarheid van oppervlaktewater op hoefdieren in het Serengeti-Mara-ecosysteem, een wereldwijd bekend ecosysteem op de grens van Tanzania en Kenia.

In **Hoofdstuk 2** ontwikkelen we een nieuw theoretisch kader over hoe de combinatie van lichaamsgrootte en het minimale vochtgehalte van de mest een voorspelling opleveren voor de gecombineerde voedsel- en waterbehoefte van grote herbivoren. Hiermee voorspellen we dat een grotere ruimtelijke homogeniteit in de beschikbaarheid van water in droge gebieden de diversiteit van hoefdieren dat kan samenleven, vermindert. Onze nieuwe theorie integreert meerdere gelijktijdige stressoren voor herbivoren en levert verschillende testbare hypothesen op over de verwachte veranderingen in de samenstelling van grote herbivorengemeenschappen onder invloed van klimaatverandering.

In **Hoofdstuk 3** kwantificeren we de effecten van landgebruik door continue monitoring van de waterafvoer van zeven grote rivieren in 4 grote stroomgebieden gedurende 2 jaar, en combineren deze gegevens met historische gegevens van de waterafvoer. We vinden voor de belangrijke Mara rivier dat de recessieperiode van de afvoer (hoe lang het duurt tot de rivier na een sterke regenvalperiode weer terugkeert naar z'n basis niveau) is afgenomen van 100 dagen in de jaren 70 van de vorige eeuw tot tot 16 dagen tegenwoordig, samenvallend met de toename van grootschalige commerciële irrigatie in Kenia. Daarentegen is voor diezelfde 2 perioden de recessieperiode van de basisstroom voor de Mbalageti-rivier (die geheel binnen beschermd gebied ligt) ongewijzigd gebleven op 70 dagen. We hebben ook hogere plotselinge overstromingen en langdurige perioden van droogval waargenomen in kleine stroompjes die gebieden afwateren die intensief worden begraaasd door vee, in combinatie met sterke erosie en geulvor-

ming. Dit laat zien dat te sterke begrazing met vee de waterhuishouding negatief beïnvloedt; in de droge tijd zal er minder lang water blijven staan.

In **Hoofdstuk 4** ontwikkelen we een nieuwe gecombineerde maat voor de waterbehoefte van 48 Afrikaanse hoefdieren af door zes verschillende functionele eigenschappen te combineren die verband houden met fysiologische aanpassingen om waterverlies te verminderen, namelijk minimaal vochtgehalte van de mest, relatieve keutelgrootte van de mest, diameter van de endeldarm, osmolariteit van de urine, relatieve dikte van het niermerg (*medulla renalis*) en vochtverlies via de ademhaling (verdamping). Daarnaast hebben we onderzocht hoe de resulterende verschillen in waterbehoefte verband houden met verschillen in wateropname via het voedsel. We vinden sterke verbanden tussen eigenschappen die verband houden met waterverlies door mest, urine en verdamping, wat suggereert dat hoefdieren waterverlies via meerdere paden tegelijkertijd minimaliseren.

In **Hoofdstuk 5** onderzochten we de ruimtelijke niche-verdeling van 16 herbivoren soorten in relatie tot oppervlaktewater door middel van tellingen van mest en directe observaties van dieren langs transecten van veraf tot dichtbij permanente waterpunten in het Serengeti National Park. De resultaten laten een sterke variatie zien tussen grazers, waarbij sommige soorten vooral dichtbij water voorkomen en anderen meer veraf. Maar voor snoeiers (browsers) waren dergelijke verschillen er veel minder. Het vochtgehalte van de mest in het droge seizoen, een index van de waterbehoefte, verklaarde het beste de variatie in gemiddelde afstand tot oppervlaktewater tussen de grazers, wat ondersteunt dat verschillen in waterbehoefte leiden tot ruimtelijke nichescheiding tussen grazers.

In het onderzoek hebben we dus nieuwe methoden ontwikkeld om de afhankelijkheid van oppervlaktewater van hoefdieren te kwantificeren met behulp van functionele eigenschappen en we hebben ook aangetoond dat de verschillen in waterbehoefte zijn voor de co-existentie van verschillende soorten in het landschap doordat het verschillende niches oplevert. Sommige soorten moeten altijd dicht bij water leven, andere soorten kunnen daar lange tijd zonder en kun dus gebieden ver van water gebruiken. Dit suggereert weer dat ruimtelijke heterogeniteit in de beschikbaarheid van oppervlaktewater erg belangrijk is voor de structuur en functioneren van savanne ecosystemen.

Acknowledgements

Now the thesis is done and three papers published. Tracking back and moving along the four years, I realized that there were way more ups than downs. This perhaps, makes this section one of the most difficult to write in this PhD thesis, not because I do not have people to thank and appreciate but rather how can I express the enormous amount of facilitation and support I had received from preparation of concept note, PhD enrolment, proposal development, field work to thesis production. To be honest with myself, the four years of a PhD project has been one of the most adventurous journey that I had a privileged opportunity and pleasure to participate. As the journey always involve a number of key people (Crew), I am now ready to write words of thanks to some if not all of them whom immensely contributed to the achievements and milestone that I reached over the past couple of years.

Firstly; Han Olff, Eric Wolanski and Michiel Veldhuis, my supervisors, thanks you for all of your mentorship, advice and guidance. Han and Michiel, we met for the first time during the AfricanBioServices (ABS) consortium meeting of 6-10 December 2015 in Mugumu when I participated as member of the consortium and head of ecology department from Serengeti National Park. By that time, I was somehow frustrated because the ABS project couldn't manage to pay fees for me to start a PhD programme at the University of Dar es Salaam. Michiel, you were the first person I approached and shared my concept note on the ecohydrology of Serengeti river systems. Your interest in Science and the fact that none among the ABS researchers had an interest on water which is necessarily important for the ecosystem imposed you to positively consider and recommend on my concept note. You took the concept note and further shared with Han who truly has confidence in you and eventually accepted me as his PhD student. From this meeting, it is where my PhD study journey to Groningen University started. Eric, we first met way back in 2008 when you visited Tanzania to train TANAPA ecohydrologists (Ecologist that form TANAPA water management Team) on ecohydrology as a tool in addressing growing freshwater crisis in Tanzania. This trip made us visit Lake Manyara, Mikumi, Ruaha and Katavi National Parks and incredibly uplifted my interest on ecohydrology. Eric, surprisingly I happened to be one of your best trainee and this impressed you such that you acquired a JAPAN scholarship in 2011 for me to pursue a PhD study in Japan. It was very unfortunate and unknowingly that I was one month older than the required age limit, thus prevented me from going to Japan for a PhD study.

Secondly, Grant Hopcraft, not only supported my PhD through funding but also acted as an invisible supervisor. This was necessary as he has enormous experience with Serengeti as he has more than 20 years working as a landscape ecologist under Frankfurt Zoological Society (FZS) and later under the Serengeti Biodiversity Research Program. His enthusiasm with monitoring surface water, combined by his capacity to

solicit fund, helped me to acquire funds to purchase automatic water monitoring loggers for field work. Grant thank you very much for facilitating the acquisition of research equipments and stipends to allow me travel to Groningen for data analysis and courses.

Thirdly, Dr. Roberty Fyumagwa, the Center Director for Serengeti Wildlife Research Institute, not only Dr. Fyumagwa included my name in the ABS project but also made sure that the opportunity for me to go for a PhD study is not taken by another person. It is because of Dr. Fyumagwa, the one PhD position ended supporting three PhDs. Honestly without you Dr. Roberty my position that was taken by the other candidate could have disappeared and this thesis could have not been written. I thank you very much for fighting on my behalf.

I would also like to thank Corrine Eising, Ingeborg Jansen, Jacob Hogendorf and Joke Bakker; without these important people, life at Linneausbodg would not have been conducive. Ingeborg, you were very instrumental throughout the four years journey of PhD project, I am confident to say that our research group would be incomplete and functionless without you. Thanks you for arranging and facilitating my enrolment to Groningen University and indeed your logistical and timely responses to financial management. Furthermore, all the CONSECO staff, colleagues and office mates, I know that I was only available in Groningen on part-time basis but my presence was definitely made enjoyable and more fun. Importantly, my interaction with you people especially during lunch meeting and other social gathering was real productive.

On the TANAPA perspectives, thanks to the Conservation Commissioner, Dr. Allan Kijazi and Deputy Conservation Commissioner for Conservation and Business Development Mr. William Mwakilema; thank you for your facilitation from the start to the accomplishment of this PhD research project. Dr. Kijazi you provided me not only with the permission for a study leave but also with financial and moral support at the time when I needed them the most. To you Mwakilema, as a Chief Park Warden for Serengeti National Park, you provided and made a timely availability of the vehicle during field works. You did not only facilitated my field work but also your moral support as my leader and a brother was of much importance and immense contribution to the project. My colleagues from the Department of ecological monitoring in particular Damari Samwel, Asheeli Loishooki, Gerald Mafuru, Kelvin Mollel, Ally Shaha, Haji Mdugi, Grayson Mtera, Gervas Swalo, and John Reuben, all were real helpful and supportive. Their participation in field work especially during installation of water level monitoring loggers and sampling large mammals through dung count made this PhD project a success. Senior rangers, Marando Maratu and Kerenge Magige, their long service and experiences allowed us to have precise identification of dung pellet to species. Last but not

on importance, Maheli Machota, a head for our garage made sure that the vehicle was in a good condition when going for field work. Maheli was a flexible man and made sure that at any given time the field vehicle was available. Thanks you all for the support you provided to me during the whole time of field work in the landscape of Serengeti National Park.

My young energetic field assistants, Victor Mbasha, Emmanuel Shemweta, Lushinge Ndonje, Emmanuel Kitula, Emmanuel Christian, Selemani Junior, Emmanuel Charles, Magharincha Magharibi and Amos Mayunga, you made the toughest time of field work on dung count a success. We spent the whole day in the field when rain and not rain, and in sun to make sure that we accurately and consistently collect data. My colleagues from TAWIRI, Onesmo Mwakalebe, Emilian Mayemba, Itaeli Nassary and Noel Alfred, we worked together on the early stage of field work in particular during installation of automatic loggers and Sediment socks in rivers and streams. I thanks you very much for the support you all provided.

My lovely family! My wife Irene James Muggo, Our Sons, Eron, Elvin and Elian. Thank you very much for supporting and encouraging. My absence for either going in the Netherlands or Field work had tremendously affected our family affairs especially parenting. Irene thank you for patience and enthusiasm. Thanks you for listening avidly to my explanation and proposal to go for a PhD study.

Curriculum vitae

Basic personal information and contacts

Surname	Kihwele	Mr.
First Name	Emilian	
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Date of Birth	19 th June 1975	
Marital Status	Married with three children	
Religion	Christian, Roman Catholic	
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Current Job	Principal Conservation Officer for Nyerere National Park	
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Education background

Institution	University of Groningen
Date	April 2021
Degree	Doctor of Philosophy (PhD) in Ecohydrology and Ecosystem Functions
Institution	University of Dar es salaam
Date	November 2015
Degree	Master of science (MSc) in Wildlife Ecology
Institution	Sokoine University of Agriculture
Date	November 2001
Degree	Bachelor of Science (BSc) in Wildlife Management

Professional / working experience record

Date:	February 2002 to March 2010
Institution	Tanzania National Park, Lake Manyara National Park
Position	Park Ecologist and Head of Ecology and Wildlife Veterinary Department
Date:	March 2010 to September 2011
Institution	Tanzania National Park, Ruaha National Park
Position	Park Ecologist and Head of Ecology and Wildlife Veterinary Department
Date:	September 2011 to March 2020
Institution	Tanzania National Park, Serengeti National Park
Position	Principal Conservation Officer and Head of Conservation Science Department
Date:	April 2020 to-date
Institution	Tanzania National Park, Nyerere National Park
Position	Principal Conservation Officer and Head of Conservation Science Department

Consultancy experiences and tasks

- June 2018 to May 2019: Commissioned by Saadani Bush Beach Hotel to undertake Environmental Impact study of the Development of Tourist Hotel along Saadani Beach in Buyuni Village, Mkwaja Ward, Pangani District in Tanga Region.
- June to October 2018: Nominated by Permanent Secretary in the Ministry of Natural Resources and Tourism to finalize the Government decision to annex Speke Gulf Game controlled area and section of Lake Victoria into Serengeti National Park.
- May to September 2018: Involved in the development of General Management Plan for Mahale Mountains National Park, in Kigoma Region.
- October 2013 to August 2014: Nominated by Regional Commissioner for Mara Region as a member of the task force to implement the process of annexing the Speke Gulf Game Controlled Area to Serengeti National Park.
- February to November 2013: Sub-contracted by City Engineering Company Limited of Dar es Salaam to participate on Environmental Impact Assessment study for MORU HOLDINGS LTD to construct Extra Sopa Lodge at Warangi area in Serengeti National Park at the capacity of biodiversity specialist.
- November 2012 to March 2014: Involved in the development of General Management Plan for Serengeti National Park.
- July 2013 to May 2014: Contracted by the African Wildlife Foundation to develop Resource Zone Management plan for Lake Natron Wildlife Management Area.
- November 2012 to March 2013: Contracted by the Howard Humphreys Consultant Company to participate in the development of integrated water resource management and development plan for the Ruvuma River and Southern Coasts Basin.
- July 2012 to January 2013: Contracted by RE-TOUCH AFRICA to participate in the development of Joint Trans-boundary protection and monitoring Plan for Serengeti Maasai Mara ecosystem.
- January 2012 to July 2012: A member of the Inter-ministerial task force on Biodiversity Conservation and Development in World Heritage Sites in Tanzania.
- January 2012 to August 2012: Participating on the ongoing Environmental Flow Assessment for the Mara river Basin.
- May 2011: Contracted by Bede Lyimo to undertake Environmental and Socio- Economic Impact Assessment for the establishment of Botanical Garden in Bagamoyo.
- March 2008: Contracted by the Makumbusho Village Museum to undertake Environmental Impact Assessment for the establishment of Zoo at Kijitonyama area in dar es salaam.
- July 2007 to August 2010: Carried out research on the seasonal variations of some Limnological parameters in relation to flamingos Population abundance in Lake Manyara National Park, Arusha, Tanzania (MSc. Thesis).
- March 2010: Involved in the Environmental Flow Assessment of the Usangu wetlands and the Great Ruaha River.
- June 2006 to September 2006: Participated on a vegetation study in Marang Forest Reserve, a part of Lake Manyara National Park.
- April 2004 to October 2004: Carried out assessment of the status of water resources within Lake Manyara Sub-catchment basin.
- February 2002 to July 2005: Participated as a member of task team to develop Cabinet papers for the extension of Lake Manyara, Arusha and Kilimanjaro National Parks and establishment of Kitulo and Saadani National Park.
- February 2002 to November 2002: Involved in the development of General Management Plan for Lake Manyara National Park.

Other generic skills

Computer Skills	Highly computer literate (Microsoft office, statistical packages – SPSS, Internet, etc)
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Research publications

- M. Elisa, E. Kihwele, E. Wolanski et al., Managing wetlands to solve the water crisis in the Katuma River ecosystem, Tanzania, *ecohydrology and hydrobiology*, <https://doi.org/10.1016/j.ecohyd.2021.001>
- E.S. Kihwele; M.P. Veldhuis; A. Loishooki; J.R. Hongoa; J.G.C. Hopcraft; H. Olff and E. Wolanski (2021). Upstream land-use negatively affects river flow dynamics in Serengeti National Park. *Ecohydrology and hydrobiology*, <https://doi.org/10.1016/j.ecohyd.2020.12.004>
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- Muse, E.A., Lejora, I., Wakibara, J., Kilewo, M., Chuma, S.I., Kihwele, E., Samwel, D., Mtui, A., Sindato, C., and Malele, I. (2015). The Contribution of Tanzania National Parks in Controlling Vectors of Sleeping Sickness. *Open Journal of Ecology*. 5. 306–314.
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- Kaswamila, A.L., Gereta, E, Othman O.C, Bevanger, K, Mwakipesile A, Haule K, Kihwele, E, and Summay, G. (2014). Assessment of Water Quality along the Proposed Highway through Serengeti National Park, Tanzania. *International Journal of Environment and Bioenergy*. 9(2): 95–104.
- Fyumagwa RD, Z Bugwesa, M Mwita, ES Kihwele, A Nyaki, RH Mdegela and DG Mpanduji, (2013). Cyanobacterial toxins and bacterial infections are the possible cause of mass mortality of lesser flamingos in soda lakes in northern Tanzania. *Res. Opin. Anim. Vet. Sci.*, 3(x), xxx.
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- Kihwele, E.S; Lugomela, C. and Howell, K.M (2011). Physico-chemical factors as drivers to the variation in the abundance of phytoplankton in Lake Manyara, proceedings of TAWIRI annual Scientific Conference, 2011.
- Fyumagwa, R. D; Wiik, H; Lukasik, M; Kilewo, M; Semuguruka, W.D; Kihwele, E.S; Wambura, P.N and Sudi, F.F (2003). Genital infection in Baboons in Manyara and Gombe National Parks, Tanzania, Proceeding of the fourth Annual Scientific Conference, 4-6 December, 2003, Arusha tanzania.

Language Skills

Language	Reading	Spoken	Written
Swahili and English	Excellent	Excellent	Excellent

Professional Referees

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