

**The ecological effects of changes in surface water availability on  
larger mammals in the Ruaha National Park, Tanzania**

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## **Selbständigkeitserklärung**

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Ruppichtheroth, den 16.12.2016

Claudia Stommel



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## Zusammenfassung

Der Great Ruaha River (GRR) stellt die Hauptwasserressource für Wildtiere im Ruaha Nationalpark (NP) dar. Durch die Entnahme von Wasser oberhalb des NP für eine großflächige landwirtschaftliche Bewässerung wird seine Wassermenge jedoch deutlich reduziert. In den frühen 1990er-Jahren führte der GRR noch ganzjährig Wasser, während in den folgenden Jahren die Reduktion der Wassermenge zur großflächigen Austrocknung des Flusses während der Trockenzeiten führte. Ziel meiner Arbeit ist es, diese Reduktion im Hinblick auf die Verfügbarkeit und Qualität von Wasser des GRR und anderen Wasserstellen innerhalb des Ruaha NP im Rahmen von drei Trockenzeiten aufzunehmen und deren Einfluss auf größere Säugetiere zu untersuchen.

Die Ergebnisse belegen eine Verschlechterung der Wasserqualität bei stagnierendem Durchfluss durch ansteigende Salinität und Gesamtkeimzahl. Ich dokumentierte, dass mit fortschreitender Trockenzeit verschiedene Säugetierarten aktiv nach Wasser gruben und auch andere Arten diese Wasserlöcher nutzten, selbst wenn in unmittelbarer Nähe Oberflächenwasser vorhanden war. Die statistischen Analysen zeigten, dass das Grabeverhalten mit höherer Gesamtkeimzahl in den benachbarten Wasserstellen wahrscheinlicher wurde, hingegen die Salinität hierauf keine Auswirkungen hatte. Die Ergebnisse weisen somit darauf hin, dass dieses Verhalten dazu dient, Wasser mit einer geringeren Keimbelastung und somit auch weniger potentiell gefährlichen Pathogenen nutzen zu können (Kapitel 2).

Auf einem 104 km langen Flussabschnitt des GRR wurden die Konsequenzen der verringerten Wasserverfügbarkeit für das Flusspferd (*Hippopotamus amphibius*) untersucht. Der GRR stellt die wichtigste Wasserquelle für diese Art im Untersuchungsgebiet dar. Flusspferde benötigen Tagesruheplätze im Wasser, um Hautschäden durch Sonneinstrahlung und Überhitzung vorzubeugen. Die Ergebnisse zeigten einen wesentlichen Wandel in der Verteilung der Flusspferde während der Trockenzeiten. Die Anzahl der Individuen stieg an den Beobachtungspunkten mit der Menge, jedoch unabhängig von der Qualität, des vorhandenen Wassers an. Die Austrocknung von flussabwärts gelegenen Tagesruheplätzen führte zu einer Akkumulation der Tiere in den wenigen verbleibenden Tümpel flussaufwärts. Dies stellt einen massiven Habitatverlust, auch in Bezug auf nächtliche Nahrungshabitate, während Trockenzeiten dar (Kapitel 3).

## Zusammenfassung

Mithilfe eines 200 km langen Netzwerkes von Transekten wurden die Effekte der veränderten Wasserverfügbarkeit auf die räumlich-zeitlichen Verteilungsmuster von neun Arten größerer Säugetiere erfasst und die durchschnittliche Distanz jeder Art zur nächstgelegenen Wasserquelle modelliert. Die Ergebnisse zeigen, dass (i) Grasfresser (Afrikanischer Büffel [*Syncerus caffer*], Wasserbock [*Kobus ellipsiprymnus*] und Zebra [*Equus quagga*]) die geringsten Distanzen, (ii) Gemischtfresser (Impala [*Aepyceros melampus*], afrikanischer Savannenelefant [*Loxodonta africana*]) und Blattfresser (Massai-Giraffe [*Giraffa tippelskirchi*], Großer Kudu [*Strepsiceros zambesiensis*]) mittlere Distanzen und omnivore Arten (Warzenschwein [*Phacochoerus africanus*], Kronenducker [*Sylvicapra grimmia*]) die größten Distanzen zum Wasser tolerierten. Die Verteilungsmuster von Büffel und Elefant zeigten darüber hinaus eine flussaufwärts gerichtete Bewegung am Ende der Trockenzeit (Kapitel 4).

Die vorliegende Arbeit belegt die besondere Bedeutung des GRR für das Überleben der Populationen größerer Säugetiere im Ruaha NP sowie die Dringlichkeit, einen ganzjährigen Durchfluss während der Trockenzeit zu gewährleisten.

## Summary

Large-scale crop irrigation is thought to be responsible for a substantial reduction in the dry season flow of the Great Ruaha River (GRR), the main dry season water source for wildlife in Ruaha National Park (NP), Tanzania. In the early 1990s the GRR was perennial, whereas currently a substantial reduction in dry-season flow has resulted in large sections of the GRR drying out. This thesis aimed to investigate the impact of reduced flow in the GRR on the quantity and quality of water available in the GRR and alternative water sources to assess the effect of these parameters on the distribution of mammal species inside Ruaha NP during three dry seasons. The results revealed a deterioration of water quality (increased salinity and total aerobic bacterial load) when water flow stopped. I document that several mammal species actively dug for water or drank from animal dug waterholes, and did so even when surface water was present. Statistical analyses revealed that digging was more likely when the total aerobic bacterial load in surface water was high but independent of salinity. These findings indicate that digging accesses less contaminated sub-surface water, thereby providing better quality water with fewer harmful pathogens (Chapter 2).

I examined the consequence to the common hippopotamus (*Hippopotamus amphibius*) of reduced water availability along a 104 km stretch of the GRR during two dry seasons. Hippos are highly dependent on aquatic day resting sites to prevent skin damage by solar radiation and overheating. My findings revealed substantial changes in hippo distribution as the dry season progresses. Hippo numbers at monitored locations increased with the expanse of surface water present and was independent of water quality. As downstream resting sites dried out, hippos accumulated in large numbers at a few upstream locations – an extensive loss of dry season habitat in terms of resting sites and night foraging areas. The GRR provided the most important day resting sites for hippos within the study area (Chapter 3).

I also examined the effect of water availability on the spatio-temporal distribution of nine species along a total network of 200 km ground transects and modelled the distance each species maintained to the nearest surface. This showed (i) grazers (African buffalo [*Syncerus caffer*], waterbuck [*Kobus ellipsiprymnus*] and plains zebra [*Equus quagga*]) maintained the shortest distance throughout the dry season to surface water, (ii) species that both grazed and browsed (impala [*Aepyceros melampus*], African savanna elephant [*Loxodonta africana*]) and those that were predominantly browsers (Masai giraffe [*Giraffa tippelskirchi*], greater

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kudu [*Strepsiceros zambesiensis*]) maintained intermediate distances to water, and, (iii) omnivores (warthog [*Phacochoerus africanus*], common duiker [*Sylvicapra grimmia*]) tolerated the largest distances to surface water. Species distribution data revealed upstream movements of buffalo and elephant at the end of the dry season (Chapter 4).

My thesis demonstrates the profound importance of the GRR for the viability of populations of larger mammals within Ruaha NP and the urgent need to restore dry season flow.

# Chapter 1

## General Introduction

The growth of the human population worldwide and the human activities connected to it have caused the degradation and disruption of habitats, particularly those associated with freshwater (Malmqvist and Rundle 2002, Saunders et al. 2002, Abell et al. 2008, Islam and Gnauck 2009). In arid and semi-arid regions the availability of surface water is vital for the existence of a variety of different terrestrial species, including mammals, and changes in the abundance and distribution of surface water can severely affect mammal species in various ways.

### Water availability

Only 3 % of the worldwide water is freshwater and more than two-thirds of this is locked-up in the form of ice, in glaciers and the Polar ice caps. The freshwater in lakes and rivers globally hold less than 0.01 % of all water on earth (Schwarz et al. 1990, Jackson et al. 2001) and this renewable freshwater is the basis for life in terrestrial and freshwater ecosystems (Jackson et al. 2001).

Worldwide, the presence of surface water is temporally variable in most regions; its availability and distribution depend on rainfall, evaporation rates and geology (e.g. Gaylard et al. 2003). In East Africa, precipitation is dominated by the monsoon which is responsible for major seasonal differences in rainfall. Typically, most areas of East Africa experience annually one wet season (or two wet seasons in some areas, termed the short and long rains), during which most precipitation occurs, and also one dry season (or two dry seasons in some areas) when little or no precipitation occurs (Nicholson 1996). Rainfall delivers surface water; the persistence of surface water depends on factors such as the rate of evaporation. During the dry season, high radiation and hence high temperatures in African savannah ecosystems result in high rates of evaporation (Scholes and Walker 1993). The persistence of surface water is also influenced by the geology of an area, with surface water persisting for longer on clay soils than more permeable soils such as those containing a high proportion of sand (e.g. Gaylard et al. 2003). The underlying geology of an area can determine the location of freshwater springs. East Africa has several large bodies of

freshwater, such as Lake Victoria and Lake Nyasa, plus several large soda lakes in the Great Rift Valley. Rivers represent linear water sources and are categorised as: (1) seasonal rivers, where flow is limited to the wet season and surface water typically dries out as the dry season progresses, sometimes leaving a small number of persisting pools (Gaylard et al. 2003, Steward et al. 2003), and (2) perennial rivers where surface water flow is maintained throughout the year.

In addition to the natural variability in the availability of surface water, human activities (including the effects of climate change) can increase this variability, leading to greater extremes. Owing to the increase of human populations (Roberts 2011) and their growing demand for water for household use, agriculture and industries, freshwater resources are increasingly under pressure (Bobbink et al. 2006, Vörösmarty et al. 2010). Human threats to surface water resources include the construction of dams, the withdrawal of water for a wide range of human activities and the discharge of sewage and pollutants from industry and agriculture (Revenge et al. 2005).

The impact of human activities on river and riparian ecosystems are particularly severe in the arid and semi-arid regions of the world. Because groundwater resources in East Africa are limited, most local communities depend on rivers to cover their demands for freshwater (Sinibaldi et al. 2004). As a consequence, this creates potential conflicts between the needs of people and those of ecosystems (Christensen et al. 2007) and this conflict appears set to increase given that future climate change is expected to negatively affect the distribution, abundance and life cycles of most freshwater species and ecosystems (Araújo et al. 2005, Schröter et al. 2005). Under the predictions of future climate change, most parts of the African continent are expected to face a reduction in rainfall and rising temperatures, and the observed trend for decades has been a decrease in rainfall (Lyon and DeWitt 2012, Chen and Georgakakos 2015, Rowell et al. 2015). Even so, some climate models predict an increase in rainfall for East Africa (e.g. Christensen et al. 2007), and even if climate change proves to be less severe than expected, human population growth will still result in increased pressure on river systems, protected areas and ecosystems that depend on perennial sources of water.

### **Human impact on freshwater sources**

The current human impact on freshwater sources is enormous and has been documented worldwide. Human water consumption can have extreme effects on local and regional ecosystems. A famous example is the Aral Sea basin, where large-scale river diversion caused this inland water body to shrink by 75 % within only four decades (Kindler 1998). As a consequence, water quality declined; between 1960 and 1990 water salinity increased to a level comparable to the salinity of oceans (Stone 1999). As a result of human activities, many of the world's largest rivers such as the Ganges, Brahmaputra, Yangtze, Nile and Colorado temporarily stopped flowing during dry periods (Postel 2000). Together, these represent 65% of the global river discharge and the aquatic habitat that depends on this water is categorised as being under moderate to high threat (Vörösmarty et al. 2010). The basins of large rivers, such as the Ganges or Yangtze, are often highly populated, resulting in a high pollution and large modifications such as dams. The Yangtze River dolphin (*Lipotes vexillifer*) is most likely extinct in the wild (Turvey et al. 2007) and illustrates the dramatic decline of many aquatic species (Dudgeon 2010). The ecological effects are not restricted to aquatic or amphibian species and include floodplain mammals such as the Chinese water deer (*Hydropotes inermis*) and Pere David's deer (*Elaphurus davidianus*), the latter extinct in the wild until it was reintroduced in the Yangtze Tianezhou Reserve (Dudgeon 2010, Jiang and Harris 2016).

### **The role of water availability in protected areas**

Owing to the negative impact of human activities, wildlife habitats are continuously shrinking. For species unable to live in human dominated landscapes, protected areas where human activities are limited are necessary for the survival of some species or populations. The importance of areas surrounding protected areas are rarely considered, even though their use can have profound effects on protected areas (Beale et al. 2013). Effects of human activities in areas adjacent to protected areas, and conflicts between people and wildlife can be reduced by designating areas in the neighbourhood of protected areas as 'buffer zones', where some but not all human activities are permitted. In countries such as Tanzania, buffer zones are normally areas where hunting by licence is permitted. In some circumstances, protected areas may be impacted by human activities well removed from the geographical location of the protected area, for instance if they affect important wildlife corridors, as

these facilitate dispersal and genetic flow between populations, thereby preventing genetic isolation. Such corridors are particularly important for species with extensive ranges (Beale et al. 2013), and rivers often serve as important wildlife corridors. River catchments are also often geographically remote yet important for the well-being of specific protected areas, as they can be important for supplying water to rivers that flow through protected areas (Beale et al. 2013). In many cases, increasing urbanisation, industrialisation and intensive agriculture combined with the construction of dams and the withdrawal of water in regions near protected areas has caused the reduction of various species inside the areas established to protect them (Ashton 2010).

The pollution from mining and agricultural activities upstream of the Oliphant's river of Kruger NP is considered to be a major contributing factor to the mass die off of Nile crocodiles (*Crocodylus niloticus*) inside the park (Ashton 2010). Owing to upstream damming of the Kihansi river in the Udzungwa Mountains of Tanzania and the resulting changes in river flow, the Kihansi spray toad (*Nectophrynoides asperginis*) became extinct in the wild (Channing et al. 2006). Apart from direct lethal consequences that threaten the survival of species, long-term consequences of modifications of river flow that are more difficult to detect can also threaten the existence of species. The reduced flow of the South African Black Umfolozi River produced a higher accumulation of sediment in the riverbed during the 1960s, whereupon the river became shallower and therefore lost most of its riparian woodland during a flood in 1984 (Vincent 1970). Modifications in the hydrological regime are also known to provide the stimulus for the establishment of opportunistic plants, particularly alien invasive species (Røslett 1988). Mumba and Thompson (2005) described how the Kafue National Park in Zambia experienced rapid vegetation changes as a consequence of human-induced changes to the flow regime of the Kafue River. One species of mimosa (*Mimosa pigra*) which only covered 2 ha in one upstream area before 1980 had spread to cover approximately 2500 ha over large parts of the river's basin by 2003. The mimosa benefitted from the rising water levels and longer flooding periods that were a consequence of the construction of dams. Species which cannot withstand longer periods of flooding, such as *Nymphaea* waterlilies, are now completely absent and the mimosa is quickly replacing grassland vegetation previously dominant on the river flats. These dramatic vegetation changes will impact the habitat and biodiversity in the long term and the extent

of the decline in available grassland is expected to have detrimental implications for grazers such as the endemic lechwe antelope (*Kobus lechwe* ssp. *kafuensis*).

Anthropogenic disturbances of habitats are increasing both in number and magnitude. The impact of these disturbances on wildlife needs to be better known, so that potential changes to habitats and biodiversity can be better detected and managed or averted to limit their negative consequences. An evidence-based approach which includes some component of wildlife monitoring to assess potential changes is therefore essential (Mumba and Thompson 2005).

### **Water availability and mammal distribution**

The earth's greatest diversity and density of large mammal species is found in African savannahs (e.g. Du Toit and Cumming 1999), where access to surface water is essential for many but not all species. Despite the relevance of surface water availability for mammal communities and their conservation in savannah ecosystems, relatively few studies are available on this topic. In the semi-arid savannah of the Kenyan Amboseli ecosystem, the large mammal community showed a strong response to seasonal changes in the distribution of surface water (Western 1975). Water dependent species (obligate drinkers) spread during the wet season and concentrated near water sources during the dry season. The availability of surface water was identified as the crucial parameter to determine the carrying capacity of the area. During the dry season, 99 % of the of the herbivore biomass occurred within 15 km of surface water, a region representing only 52 % of the total area of the ecosystem. Furthermore, water independent species were almost exclusively browsers whereas the majority of water dependent species were grazers (Western 1975). These differences in species with different foraging strategies were explained by the assumption that browser had access to plant material with a higher moisture content and therefore were less dependent on surface water than grazers that consumed drier grasses.

The distribution of herbivores was therefore dominated by the trade-off between water requirements and nutritional needs (Western 1975, Owen-Smith 1996). During the dry season, when water resources become scarce and patchily distributed, high numbers of animals accumulated around the remaining water resources. These accumulations result in overgrazing and degradation around water holes, an effect termed the piosphere effect (e.g. Thrash and Derry 1999). The presence of surface water also affects the distribution of some

carnivores. For example, the location of territories occupied by lion prides tended to be related to the presence of perennial sources of water that represent an obvious herbivore attraction (Smuts 1978, Valeix et al. 2009).

In the early 1960s, several National Parks predominantly in southern Africa established artificial water holes to expand the dry season distribution of water dependent species and reduce animal mortality during severe droughts (Owen-Smith 1996). This resulted in a number of unforeseen and highly negative consequences particularly well documented for Kruger NP (Harrington et al. 1999, Parker and Witkowski 1999). These included a dramatic decline in the roan antelope (*Hippotragus equinus*) population of about 90 % within 7 years caused by changes in the distribution of other herbivores that moved to artificial water holes where roan antelopes lived, thereby modifying the habitat to the detriment of roan antelopes and increasing competition, disease transmission and predation.

Redfern et al. (2003) suggested the trade-off between nutritional requirements and constraints imposed by the distribution and access to surface water varied with species differences in water dependence, size, and gut morphology. Whereas browsers were less dependent on surface water, ruminant grazers such as African buffalo (*Syncerus caffer*) and blue wildebeest (*Connochaetes taurinus*) were more strongly dependent on surface water. Among grazers, larger species were further away from water when forage quantity was reduced, whereas smaller species were further away from water when the forage quality was reduced.

Smit et al. (2007) discovered differences in preferences of drinking sites. Whereas artificial water holes were used by mostly grazer species, browsers and mixed feeders preferred to drink from the main rivers.

### **Species adaptations and response to changing water availability**

Most terrestrial mammals need to drink water regularly (Caughley and Sinclair 1994) to compensate for water loss by cutaneous and pulmonary evaporation, and in urine and faeces (Cain et al. 2006). There are various adaptations of mammals to avoid and cope with heat, and to cope with water scarcity that occurs in arid and semi-arid regions. A few specialised ungulates are able to survive longer periods without drinking and some are tolerant to the loss of water. Camels are known to survive a water loss of 30-40 % of their body weight, whereas a water loss of 15 % can be fatal for species such as waterbuck (*Kobus*

*ellipsiprymnus*, Taylor et al. 1969, Louw 1984). Oryx (*Oryx beisa*) and Grant's gazelle (*Nanger granti*) survive drought periods in hot deserts without surface water because they are able to use hygroscopic forage at night (Taylor 1968).

In addition to the need for organisms to maintain their water balance, water is also of physiological importance for lactation, temperature maintenance by perspiration and for voiding excretory products. In Africa, several mid to large mammals such as the African elephant (*Loxodonta africana*), warthog (*Phacochoerus africanus*) and African buffalo depend on frequent access to sources of surface water and mud wallows to help reduce their core body temperature and external parasite burden, and in the case of the hippopotamus (*Hippopotamus amphibius*) (hereafter termed hippo), to prevent serious skin damage by solar radiation (e.g. Owen-Smith 1992, Vanschoenwinkel et al. 2011).

### **Physiological adaptations**

Most mammal species exposed to high temperatures perspire to use the evaporation of water to reduce their body temperature, i.e., the ability to lose excess heat is one key component of homeostasis. Failure to maintain body temperature below species specific upper limits can be fatal. Furthermore, elevated body temperatures can have direct negative effects on mammalian reproduction (Hansen 2009). During lactation the water requirements of females are increased (Nicholson 1985). In most mammals, considerable water loss occurs when faeces and urine is voided (Cain et al. 2006). Species substantially differ in the moisture content of faeces and the volume and osmolarity of urine produced (Cain et al. 2006). For example, the common duiker (*Sylvicapra grimmia*) can survive without drinking water for months at a time and is independent of water, and even when surface water is available the animal rarely drinks. This is possible because it produces highly concentrated urine and reabsorbs water from faeces (Kingdon et al. 2013).

Equids such as the plain zebra (*Equus quagga*) have a higher content of moisture in their faeces and a more watery urine than most ruminants which have a lower water loss through faeces (e.g. Maloiy et al. 1979, Woodall and Skinner 1993). In contrast to ruminants, all equids are hindgut fermenters and thus can extract nutrients from a low quality, fibre rich diet. As a consequence they have a higher digestive throughput than ruminants which require a higher quality, lower fibre diet (Duncan et al. 1990).

The above mentioned examples illustrate some adaptations of species to cope with challenges that occur in arid and semi-arid environments. As the influence of people on natural systems is increasing (Wikelski and Cooke 2006), this may reduce the resilience of some species to survive or reproduce in such environments. Whilst direct effects such as severe water pollution can prove lethal for species in the short term (Ashton 2010), in the longer term anthropogenic changes to these environments may act as 'stressors', defined as a harmful stimulus by Hofer and East (1998) and Romero (2004), elevating cortisol concentrations and depressing immune responses, which could have negative fitness consequences for individuals, leading to either the decline or extirpation of wildlife populations (Hofer and East 2012). Whereas an acute stress response, such as one resulting from a (failed) predator attack, is beneficial in priming 'the flight response' which normally lasts for a short period, chronic stress, resulting from a prolonged rise in body temperature or starvation, results in the secretion of elevated concentrations of cortisol for an extended period and can cause various pathologies (Wingfield 2005, Wikelski and Cooke 2006). Cizauskas et al. (2015) found high concentrations of cortisol in zebras correlated with decreased rainfall and suggested this seasonality was likely to be driven by environmental factors such as decreased nutrition and water availability in the dry season. The reduction of forage quality and quantity is also expected to cause nutritional stress in herbivores that are forced to extend their range to cover nutritional needs, which results in additional energetic costs (Owen-Smith 1992, Redfern et al. 2003). Hence, a potential stressor such as limited water availability can have various and complex effects at the individual and population level by increasing morbidity and reducing reproductive output and survival (Hofer and East 2012).

### **Aims and scope of the thesis**

Given that surface water availability is thought to be one of the key factors that determine the distribution, density and dry season survival of mammal species in many ecological communities, it is surprising that relatively little research has been focused on the effects of changing water availability on mammals, particularly in relation to anthropogenic over-utilization of surface water resources and projected climate change scenarios.

Most studies focus on national parks and other kinds of protected areas in which natural dynamics are modified by the provision of artificial water holes. The data collection for this

thesis took place in the Ruaha NP that is part of one of the largest protected ecosystems in Africa and one that is unaffected by fencing or artificial water supply. The Great Ruaha River (GRR) is the major source of water inside the park and one of the largest tributaries of the Rufiji river in Tanzania (Mtahiko et al. 2006). Both the Ruaha NP and the Great Ruaha River occur within a landscape known as miombo woodland. Its vegetation development is driven by seasonal monsoon rains and subsequently a strong difference of water availability between the dry and wet season.

Owing to human activities outside the park, the formally perennial river dries up along a substantial part of the course of the river within the park during the dry season. This has been identified by the Tanzanian National Parks Authority as a key threat to the long-term viability of populations of several mammal species. Despite this, there has been little detailed research on the potential threat the drying out of the river presents to mammals. The aim of this research was to plug this gap in knowledge. Hence this thesis is focused on how changes in surface water availability during the dry season affects the large mammal community in terms of their behaviour and spatial distribution. The human induced withdrawal of water from the GRR and its consequences inside the Ruaha NP are likely to be representative for other comparable ecosystems facing similar conditions currently and in the future.

The field period of my study covered the maximum of surface water variation from the beginning of the dry season in June (with high water availability) until its end in November (with lowest water availability). The study focused on different herbivore species, representing a multi-species approach that allows the coverage of variation in species specific physiological and behavioural responses to changing water availability. I also included a few large mammals of economic value for eco-tourism in Tanzania.

I first (Chapter 2) focused on three major aspects of the surface water in the GRR and elsewhere in my study area in the Ruaha NP on the location of permanent surface water, the occurrence of flowing water along the course of the GRR and the quality of water in terms of salinity and bacterial load in the GRR and at other locations. I then examine how these parameters determine the drinking behavioural response of large mammals and the construction and use of water holes dug by wildlife during the dry season.

In Chapter 3 I focus on a species with a low resilience to the absence of surface water: the hippopotamus. I examine the effects of the loss of daytime resting sites used by this semi-

aquatic species during the dry season on the distribution and health of a substantial proportion of the hippopotamus population in Ruaha NP.

In Chapter 4 I use a statistical approach to compare the distance of different herbivore species to the nearest source of surface water, and changes in the distribution patterns on a landscape level between the early and late dry season.

The overall aim of this study is to provide the first detailed investigation on the consequences of the anthropogenically induced decline in the dry season water flow of the GRR on a range of herbivore species within the park and the greater ecosystem. It also aims to deliver essential baseline data necessary for the long-term assessment of the on-going degradation of the GRR from a perennial to a seasonal river, and the likely impact of this for the populations of the larger herbivorous mammals in the Ruaha ecosystem.

### **Study site**

#### **Ruaha National Park**

The Ruaha National Park (RNP) is located in south-central Tanzania (Chapter 2: Fig 1) and bounded by the seasonal Mzombe River in the north and the GRR in the south.

The area along the GRR (Picture 1), which represents approximately 20 % of the park is part of the Rift valley stratum (Barnes 1985).



*Picture 1: The Ruaha NP with the course of the Great Ruaha River near Msembe. Photo: Claudia Stommel*

The climate is semi-arid to arid with an average annual rainfall of 580 mm of which 94 % occur between December and April (Norton-Griffiths 1975). The dry season extends from June, when daytime temperatures are approximately 25°C, to November, when peak temperatures reach 40°C (Mtahiko et al. 2006).

After the annexation of the Usangu Game Reserve and parts of Usangu basin in 2008, the area contained within the Park boundaries was extended to cover an area of 20,226 km<sup>2</sup>, thus making the Park not only the largest National Park in Tanzania but also in East Africa (Tanzanian National Parks 2016). Including the surrounding buffer zones that border the park, which include the Game Management Areas of Rungwa, Kizigo and Muhesi and the Wildlife Management Area of Pawaga Idodi, the Park is in the centre of the Rungwa-Ruaha ecosystem which encompasses more than 45,000 km<sup>2</sup>.

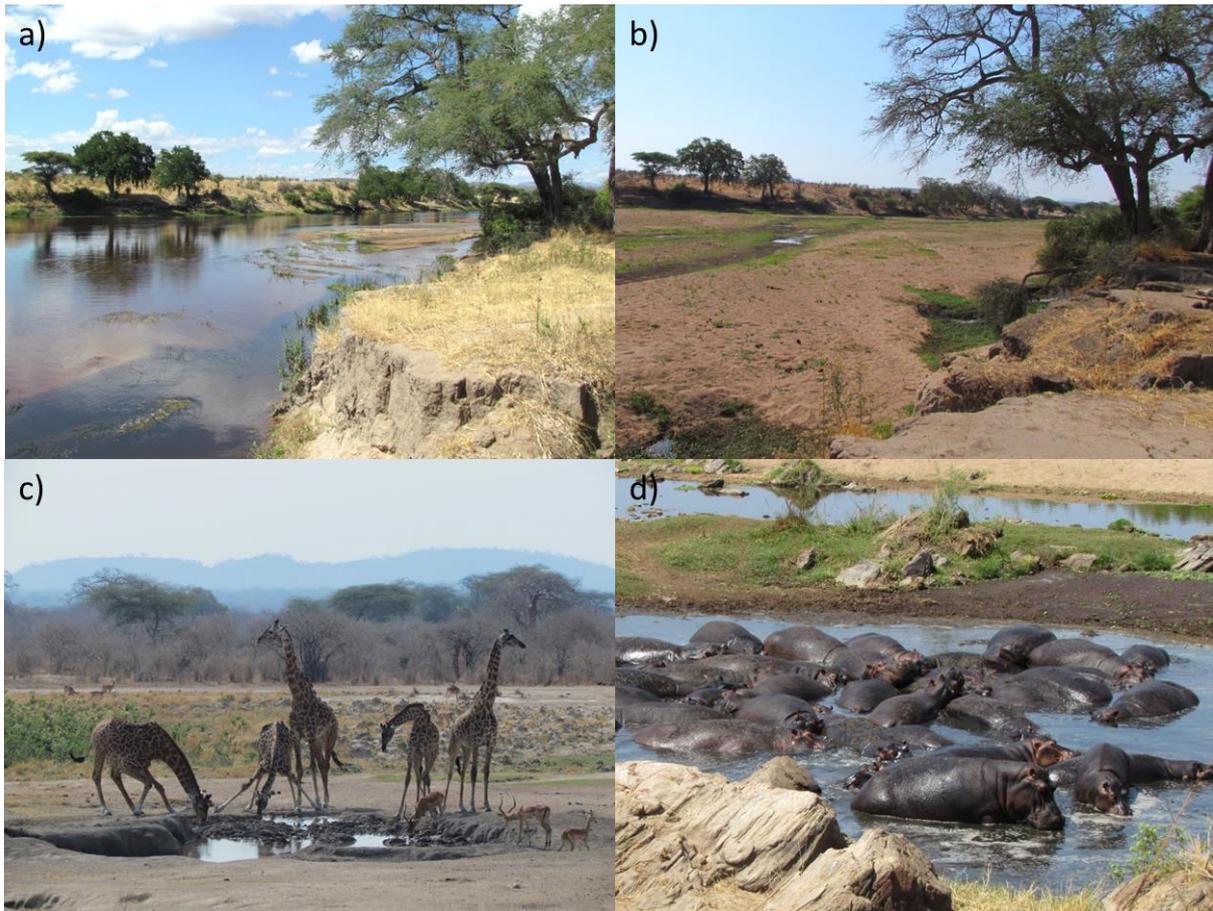
The Ruaha NP represents the transitional zone between the East African miombo woodland belt and the southern African *Brachystegia* acacia zone and harbours a high diversity of plant and animal species. Apart from more than 1,600 different plant species (Bjørnstad 1976), 571 bird species (Glen 2011) were documented within the park, and mammal species included the lesser kudu (*Ammelaphus imberbis*) and greater kudu (*Strepsiceros zambesiensis*), sable (*Hippotragus niger*) and roan antelope. The Ruaha NP is the most southerly extent of the range of several species, including Grant's gazelle, lesser kudu and striped hyaena (*Hyaena hyaena*).

### **The Great Ruaha River (GRR)**

The GRR has its source in the Kipengere Mountains, east of Mbeya, in the southern highlands of Tanzania. After flowing to the southeast, the waters reach the Usangu basin of 21,500 km<sup>2</sup>, forming the headwater of the GRR and the sub-basin of the Rufiji River (Lankford et al. 2004), with 177,000 km<sup>2</sup> the largest basin in Tanzania (Mtahiko et al. 2006). From the Usangu basin, the GRR enters the National Park flowing northeast, and once the river has passed out of the Ruaha NP it flows into Mtera Reservoir. Further downstream the GRR joins the Rufiji River which flows into the Indian Ocean (Mtahiko et al. 2006). During the dry season the GRR is the major source of water for wildlife in Ruaha National Park (Epaphras et al. 2008), as none of the other rivers (Mdonya River, Mwangusi River and Mzombe River) are perennial, and hence only hold water for a short time during the wet season before turning into 'sand rivers' with a few scattered water pools. Apart from these

rivers, there are a few springs in the hinterland (Chapter 2: Fig. 1) such as Makindi, Mkwawa, and Mwayembe (Picture 2 c).

The GRR is the major perennial water source of Ruaha NP. In the early 1990s, water flow declined, resulting in sections of the river drying out during each dry season (Picture 2 a, b, d), and evidence that this trend has increased over time. Before the 1990s, there is no documentation of any extensive drying out of GRR inside the Park, apart from the 1954 dry season (Mtahiko et al. 2006). In 1993, the river stopped flowing at the end of the dry season, and there is a suggestion that water has ceased to flow at an earlier date in the dry season in successive years. As there were no changes in the intensity, distribution and timing of rainfall that may explain the decrease in dry season flow, it is most likely that the agricultural activities upstream and outside the Ruaha NP have caused the noted decrease in flow (Mtahiko et al. 2006).



*Picture 2: Characteristic changes during the dry season in the Great Ruaha River in June (a) and October (b) in 2011 (near Msembe). Giraffe and Impala drinking at Mwayembe Spring (c), one of the few permanent water sources in the hinterland. Aggregation of hippos in the last remaining pools of the GRR during the end of dry season (d). Photos: Claudia Stommel*



## **Outline of the study**

The main focus of this study was to gather information on the seasonal variability of water availability and its consequences for larger mammals in Ruaha NP, as part of the most important catchment area in Tanzania. The results of this study are presented in three chapters.

## **Chapter 2**

### **Large mammals in Ruaha National Park, Tanzania, dig for water when water stops flowing and water bacterial load increases**

In arid and semi-arid ecosystems water becomes scarce during the dry season and animals have adaptations to survive these periods of water shortages. Digging for water is a strategy allowing some African mammals to reach water below the surface and might also provide water with a higher quality when surface water quality is poor. In this study I investigated the digging of waterholes by wildlife during the dry seasons 2011 to 2013 from June to November in Ruaha NP. I monitored surface water availability and water quality at 10 sites along the GRR and eight non-GRR sites. Camera-traps and direct observations were used to observe when and where digging to access water occurred. I could observe four species that actively dug waterholes (elephant, plains zebra, warthog and yellow baboon (*Papio cynocephalus*)) and another four species that drank from these holes. I documented that waterholes were dug later in the dry season along the GRR (October) than at other sites (July). The digging and drinking from dug waterholes appeared more often at non-GRR sites than along the GRR and did not depend on the absence of surface water, but increased when surface water stopped flowing. I found that digging was more likely when the bacteria load in available surface water increased and that it was independent of salinity levels. The measured total aerobic bacteria load increased with the *Escherichia coli* load which was used as an indicator of faecal contamination. The results suggest that digging is an adaptation to avoid the ingestion of poor quality surface water highly contaminated with faeces, and thereby possibly also potentially pathogenic microbes, in addition to providing access to water when surface water is absent. My findings highlight the vital role of the GRR as a key water source for wildlife during the dry season and the importance of water flow throughout the dry season to prevent the deterioration of water quality within the GRR.

### **Chapter 3**

#### **The effect of reduced water availability in the Great Ruaha River on the vulnerable common hippopotamus in the Ruaha National Park, Tanzania**

In this chapter I focused on a single species which is expected to have the lowest resilience to water scarcity because of its semi-aquatic life. The hippo depends on water resources as daytime resting sites for thermoregulation and to prevent skin damage by solar radiation. The flow of the GRR is reduced during dry season, leaving large sections without water. I investigated the impact of the decreased water flow on daytime hippo distribution along a 104 km section of the GRR within the Ruaha NP during two dry seasons (2012, 2013). The regular censuses at monitoring locations, transects and camera trap records were used to estimate any changes in the distribution of hippos. I found that the minimum number per monitoring location increased with the expanse of surface water as the dry seasons progressed, and was not affected by water quality. The hippo distribution significantly changed with the progress of the dry season; hippos accumulated in large numbers within the last few locations with a sufficient amount of water. I emphasise in this chapter that if the water loss from GRR continues in future years, the hippo population and other water dependent species will face serious consequences within the Ruaha NP.

### **Chapter 4**

#### **Spatio-temporal changes in the dry season distribution of herbivores in Ruaha National Park, Tanzania**

Chapter 4 presents a multi-species approach to investigate how water availability affects the distribution patterns of different species and the distance each species maintained to the nearest source of surface water during the dry season. This analysis was based on the nine most numerous large herbivores within the RNP. During the dry seasons (June – November, from 2011 to 2013) the distribution of these focus species was assessed twice a month along 10 ground transects that covered a total of 200 km. The location of surface water resources was also regularly monitored. Results of the generalised linear mixed effect model revealed significant differences in the species-specific distance maintained to the nearest surface water throughout the dry season. The results revealed that grazers (i.e., buffalo and waterbuck) maintained the closest vicinity to surface water throughout the dry season. Mixed feeders (i.e., impala and elephant) maintained an intermediate distance. Browsers

(i.e., greater kudu and giraffe) also maintained an intermediate distance to the nearest surface water, but a larger distance than the mixed feeders. Omnivores (i.e., warthog and common duiker) maintained the largest distance to surface water. During the late dry season when the GRR starts to dry out in the downstream stretches, some highly mobile species such as African buffalo shift their distribution upstream of the GRR, whereas territorial species such as common duiker maintain their territories in the same location throughout the dry season. These results underline the importance of a perennial flow of the GRR as otherwise several terrestrial species such as buffalo which are less obviously water dependent than the hippo might also suffer from a comparable loss of dry season habitat.

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## Chapter 2

### Manuscript 1

#### **Large mammals in Ruaha National Park, Tanzania, dig for water when water stops flowing and water bacterial load increases**

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**Abstract**

As water is essential for life, animals have adaptations that increase their ability to survive during periods of water shortage. Accessing water by digging is one behavioural adaptation to water shortage used by some African mammals. Digging might also provide access to higher quality water below ground when surface water quality is poor. We investigated the digging of waterholes by wildlife in the Ruaha National Park (NP), in central Tanzania, during three dry seasons (June to November from 2011 to 2013). We monitored surface water availability and water quality at 10 sites along the Great Ruaha River (GRR) and eight non-GRR sites. We used camera-traps and direct observations to determine when and where digging to access water occurred. Elephant (*Loxodonta africana*), plains zebra (*Equus quagga*), warthog (*Phacochoerus africanus*) and yellow baboon (*Papio cynocephalus*) dug waterholes and a further four species drunk from these holes. Waterholes were dug later in the dry season along the GRR (October) than at other sites (July). The likelihood of digging and drinking from waterholes was lower along the GRR than at non-GRR sites and did not depend on the absence of surface water but increased when surface water stopped flowing. Digging of waterholes was also significantly more likely when the bacterial load in available surface water increased but was independent of salinity levels. *Escherichia coli* load, indicative of faecal contamination, significantly increased with total aerobic bacterial load. Our results suggest that digging is an adaptation to avoid the ingestion of poor quality surface water highly contaminated with faeces, and thereby possibly also potentially pathogenic microbes, in addition to providing access to water when surface water is absent. Our findings also highlight (1) the essential role of the GRR as the key water source for wildlife in the Ruaha NP during the dry season, and (2) that maintenance of water flow throughout the dry season is essential to prevent deterioration of water quality in the GRR.

## Introduction

Water is essential for life. Where water availability is seasonally limited, animals have evolved physiological and behavioural adaptations to survive periods of water shortage (e.g. Tieleman et al., 2003; Willmer et al., 2005; Withers and Cooper, 2014). In semi-arid areas of Africa, rainfall during the wet season provides wildlife with numerous water sources in terms of ephemeral rivers and water pools. As a result of low rainfall during the dry season, ephemeral water sources dry out and water flow in permanent rivers declines. These changes in the distribution and abundance of water can have a profound impact on mammalian species that need to regularly drink water to survive (Redfern et al., 2003; Western, 1975).

As the availability of surface water declines, wildlife usage of the remaining sources of surface water increases, as does faecal contamination, bacterial load and eutrophication of water sources (Ramey et al., 2013; Wanke and Wanke, 2007), particularly where there is little or no water flow. The coliform bacterium *Escherichia coli* is an indicator of faecal contamination of water (Hellberg and Chu, 2015) and *E. coli* is transmitted when water contaminated with infected faeces is ingested (Johnson et al., 2004). The aggregation of animals at water sources can result in increased transmission of infectious and water borne diseases (Bengis et al., 2002; Keet et al., 1996; Lindeque and Turnbull, 1994) and, in the case of virulent diseases, can lead to significant declines in wildlife populations (East et al., 2010; Lindeque and Turnbull, 1994). Furthermore, water evaporation during periods of dry weather would result in rising water salinity which could reduce the value of water for drinking.

It is well documented that the African savannah elephant (*Loxodonta africana*) can access water below the surface of the ground by digging holes, sometimes to a depth of more than one meter (Dudley et al., 2001; Poché, 1974; Ramey et al., 2013). Other African mammals that dig to access water include chimpanzee (*Pan troglodytes*) (McGrew et al., 2007), chacma baboon (*Papio ursinus*), gemsbok (*Oryx gazella*) and plains zebra (*Equus quagga*) (Epaphras et al., 2008; Hamilton, 1985). Surprisingly there has been little research on this behaviour. Currently it is unclear which factors determine where, when and why African mammals dig to access water. We investigated this behaviour in an African habitat during the dry season, the annual six month period when little or no precipitation occurred. We reasoned that animals should not spend energy and time digging for water when surface water of a reasonable

quality was available. We predicted that digging should occur not only when the availability of surface water was absent or limited but also when the quality of surface water was poor in terms of increased salinity and bacterial contamination. We tested these predictions by studying digging behaviour and water quality in the Ruaha National Park (NP) in central Tanzania, at sites along the Great Ruaha River (GRR), which is the main source of surface water in the park, and at sites with surface water in other locations in the park (Fig. 1).

### **Methods**

#### *Study site*

The study was conducted in Ruaha National Park (Ruaha NP) in central Tanzania which forms the core of the Greater Ruaha ecosystem, one of the largest wilderness areas (encompassing approximately 110,000 km<sup>2</sup>) in Africa. The study area was a 130 km stretch of the Great Ruaha River (GRR) and an area 25 km north-west of GRR (Fig. 1). Ruaha NP encompasses a transitional vegetation zone between the East African *Acacia-Commiphora* zone and the Southern African *Brachystegia* and *Miombo* zone (Barnes, 1983; Bjornstad, 1976) and harbours a high biodiversity of larger mammals (Barnes, 1983). Mean annual rainfall is approximately 580mm, mostly falling during the wet season from November to May (Barnes, 1983). The dry season typically spans June to November, when the study was conducted during 2011, 2012 and 2013.

#### *Sources of surface water*

The GRR (Fig. 1) is the main permanent water source for wildlife in the Ruaha NP. Large-scale human utilization of water upstream of the Ruaha NP, particularly for agricultural irrigation since 1993, has significantly reduced its flow during the dry season (Mtahiko et al., 2006). During the dry seasons of our study, large sections of the GRR dried up, leaving discrete water pools separated by expanses of dry river bed. Tributaries of the GRR that contained flowing water during the wet season dried up at the beginning of the dry season and turned into dry sand-rivers containing occasional discrete water pools. There were other isolated sources of surface water, some of which (as detailed in the results) persisted throughout the dry season. In addition, numerous transient rain-fed water pools formed away from rivers during wet seasons and dried up during dry seasons. We assessed the persistence of water in the larger (minimum diameter of 5m) rain fed pools, but did not monitor water quality in these pools. Finally, sources of water below the surface of the ground also became available

for short periods when wildlife excavated holes to access water.

We thoroughly searched for water sources at the beginning of the dry season and monitored these locations for the presence or absence of water throughout the dry season. We consider that we monitored most of the known permanent and semi-permanent sources of surface water in the study area away from the GRR. Our monitoring covered 13 sites along the GRR (sites 1-10 and B, D, F, Fig. 1), and 8 “non-GRR” sites: three springs away from the river (sites 11, 12, 14, Fig. 1) and five sampling sites in the beds of sand rivers (sites 13, 15-18, Fig. 1). We also assessed the persistence of water at 17 transient rain fed pools.

### *Sampling Water Quality*

Water quality was assessed at sites 1 to 18 (Fig. 1, Table 1) in terms of salinity and total aerobic bacterial load. Water was collected from sampling sites at existing water bodies, some of which were located in the vicinity of waterholes observed by us as dug by wildlife (see below). Water quality in waterholes dug by wildlife was not assessed.

*Escherichia coli* load was also measured in a subset of water samples from several sites in 2012 and 2013 as an indicator of the level of faecal contamination (Hellberg and Chu, 2015) and to determine the relationship between *E. coli* load and total aerobic bacterial load.

Water samples used to measure salinity and total aerobic bacterial load were collected mostly at intervals of two weeks successively from June to November at a total of 18 sampling sites, including sampling sites 1-10 on the GRR and sampling sites 11-18 at non-GRR sites (Fig. 1). Not all non-GRR sites away from the GRR were sampled in all years: water samples were collected from sites 11, 12, 14, 15, 16 in 2011; sites 11, 13, 14, 15, 16, 17, 18 in 2012; and sites 11, 13, 14, 15, 16, 17 in 2013 (Table 1).

To measure salinity, water was collected in a clean 50 ml container at a depth of approximately 0.1m below the water surface at a location where animals were known to drink. Water salinity was measured with a Multi 340i Multimeter (Wissenschaftlich Technische Werkstätten GmbH, Weilheim, Germany) and expressed in units of micro Siemens per cm ( $\mu\text{S}/\text{cm}$ ). To record the current status of each sampling site for every visit the status was categorised as flowing, stagnant or dry. Salinity was measured at 10 sampling sites along the GRR from 2011 to 2013. Non-GRR sampling sites included 5 sampling sites in 2011, 7 sampling sites in 2012 and 6 sampling sites in 2013 (Table 1).

Total aerobic bacterial load was measured as the number of colony forming units per ml

(cfu/ml) using 3M Petrifilm Aerobic Count Plate and a tetrazolium indicator (*3M™ Petrifilm™ Aerobic Count Plates* (U.S. AOAC®)), following the manufacturer's instructions. Each petrifilm was inoculated with 1 ml of water sample using 3ml sterile one-way pipettes. Petrifilms were then incubated for  $51.7 \text{ h} \pm 0.3$  (SEM) at  $30^\circ\text{C} \pm 3^\circ\text{C}$  in a styrofoam box. The styrofoam box was stored in a room with dry season temperatures of approximately  $30^\circ\text{C}$ . The temperature within the box was regularly monitored with a thermometer. When the temperature moderately deviated from the recommended incubation temperature the box was either placed on the ground to reduce the temperature or located in a higher position within the room to elevate the temperature. When the temperature deviated more substantially, bottles of hot water were used to increase the temperature and bottles of cooled water to decrease the temperature inside the box to the required level.

Following incubation, each petrifilm was labelled with information about the sampling date and site and photographed. Bacterial colonies were clearly visible on photographed petrifilms and later counted using the petrifilm standard grid.

The manufacturer's recommendations are that bacterial colonies should be counted after a  $48 \text{ h} \pm 3 \text{ h}$  incubation period. Because of constraints during field work it was not possible to photograph all petrifilms within  $48 \text{ h} \pm 3 \text{ h}$ . Photos were taken at  $48 \pm 3 \text{ h}$  (i.e. within 45 to 51 hours of incubation period,  $n = 187$ ),  $48 \pm 6 \text{ h}$  ( $n = 118$ ),  $48 \pm 12 \text{ h}$  ( $n = 57$ ),  $+24 \text{ h}$  ( $n = 28$ ) and  $48 +36 \text{ h}$  ( $n = 15$ ). Samples with incubation times below 36h (2011  $n = 14$ ) or above 84h (2011  $n = 4$ ) were not used for analysis. To assess whether the variation in incubation time influenced results, we compared the number of bacterial colonies counted on one petrifilm in each of the different incubation periods (36 h, 40 h, 43 h, 46 h, 48 h, 50 h, 53 h, 56 h, 59 h, 72 h, 85h) using water from one GRR sample. The results of this test showed that the number of bacterial colonies did not increase after 36h of incubation, although an increase in colony size on petrifilms incubated for 85h made distinguishing separate colonies problematic. Hence the variation in incubation period of the samples used for the analysis did not influence the results.

If the number of bacterial colonies on a petrifilm was too dense to permit counts of individual colonies, the maximum possible count of 2500 cfu/ml was set as the minimum conservative estimate and described as  $\geq 2500 \text{ cfu/ml}$  ( $n = 31$  water samples).

The *E. coli* load was measured at sampling sites 1-10 (Fig. 1) along the GRR and seven non-GRR sampling sites (11,13-18, Fig. 1) in 2012, once in October and once in November, and at

sampling sites 1-10 along the GRR and at six non-GRR sampling sites (sites 11, 13-17, Fig. 1) in 2013 once in June and once in July at the start of the dry season, and once in September, October and November in the final three months of the dry season (Table 1). The *E. coli* load was measured using 3M Petrifilm 'E.coli and Coliformes (EC), BCIG and tetrazolium indicator' (3M Microbiology Products, St. Paul, Minnesota, USA), following the manufacturer's instructions. These petrifilms permit the differentiation between *E.coli* and other coliform colonies, which both grew on the plates, by colour differences of colonies and differences in gas production. We only counted *E.coli* colonies on these petrifilms and did so by following the manufacturer's instructions.

Each petrifilm was also inoculated with 1 ml of water sample using 3ml sterile one-way pipettes, then incubated for  $48.9 \text{ h} \pm 0.4$  (SEM) at  $32^\circ\text{C} \pm 3^\circ\text{C}$  in a styrofoam box, and labelled and photographed as for total aerobic bacterial load. All blue to red-blue colonies were counted as *E. coli*. If the number of bacterial colonies on a petrifilm was too dense to permit counts of individual colonies, the maximum possible count of 500 cfu/ml was set as the minimum conservative estimate and described as  $\geq 500$  cfu/ml ( $n = 1$ ).

### *Observations and camera trapping*

Records of species digging for water and those using water in waterholes dug by wildlife were collected: (i) when water quality was assessed from sampling sites along the GRR and at non-GRR sites; (ii) incidentally; and (iii) from photographs from camera-traps (Reconyx PC800) at seven monitoring positions along the GRR (camera trap position A-G, Fig. 1), at five pools in dry sand-rivers (camera trap position I, K-N, Fig. 1) and at two springs (camera trap position H and J, Fig. 1) from August to November in 2012 and from June to November in 2013.

Each position was monitored for a mean of  $960.2 \pm 36.3$  h (SEM) in 2012, and a mean of  $1473.0 \pm 86.3$  h (SEM) in 2013. Positions were monitored for a total of 13,443.06 h in 2012 and 20,622.14 h in 2013, and a total of 205,959 camera pictures were analysed. All camera-trap pictures were examined for clear images of animals digging for water (obvious digging movements of legs and trunk and the visible excavation of sand) or animals using waterholes known to have been dug by wildlife – confirmed when an animal lowered its head or trunk into a waterhole known to have been dug by wildlife. To define an independent "camera trapping event" of a species drinking from a dug waterhole we set a minimum period of 15

minutes between the last picture of the previous trapping event and the first picture of the next trapping event for each specific species. Such trapping events usually involved groups rather than individual animals of a given species.

### *Statistical Analysis*

Means are reported  $\pm$  standard error of the mean. Statistical tests were performed using SPSS Statistics for Windows version 21.0 (IBM Corp, Armonk, NY; USA) and Systat version 13 (Systat Software Inc., Richmond, VA, USA).

To compare measures of water quality within years between the GRR and other water sampling sites we applied Mann-Whitney U-tests. To examine whether *E. coli* load increased with total aerobic bacterial load we applied a Spearman rank correlation. We also examined whether salinity and total aerobic bacterial load increased with the length of the dry season using Spearman rank correlations. To examine the effect of water flow on water quality we compared mean salinity and total aerobic bacterial load at each of the 10 sampling sites along the GRR when water flowed and when water had ceased to flow using the Wilcoxon signed-ranks test.

To investigate factors affecting the likelihood of wildlife digging to access below ground water we proceeded in two steps. First, we tested – using the log likelihood ratio test – whether the presence or absence of surface water influenced the likelihood of digging. Secondly, for those conditions when water was actually present, we used a logistic regression model which included measures of water quality (salinity and bacterial load), as well as location (in two categories: GRR and non-GRR) and a categorical variable which described whether water flowed or was stagnant. This was available for 382 sampling incidents. We used information criteria (the Bayesian Information Criterion according to Schwartz [BIC<sub>S</sub>] and the Akaike Information Criterion [AIC]) to check whether the final model was superior to an intercept-only model. In a preliminary run we included year as a categorical factor, with an additional 2 degrees of freedom. In this model, year was not significant but produced the same significant effects as the one we report in the results. It had a BIC<sub>S</sub> of 134.5 and an AIC of 106.9. The model we report in the results had BIC<sub>S</sub> and AIC values of 126.4 and 106.7, respectively. Based on recent simulation studies, models can be considered similar if differences in the Bayesian Information Criterion according to Raftery (BIC<sub>R</sub>) were less than 2.0, a positive degree of preference if values of BIC<sub>R</sub> varied between 2.01 and 6.0 and a

strong degree of preference if values of  $BIC_R$  differed by more than 6 (A. Raftery in Hilbe 2011, p73), and similar if differences in AIC were less than 2.5 and preferable if the difference exceeded 6.0 (Hilbe 2009). As the  $\Delta BIC_S$  value of 8.1 was much larger than the recommended minimum differences for any of the information criteria investigated in these studies, and as year was not part of our hypothesis testing, we decided to go with the simpler model we report in the results. The intercept-only models had a  $BIC_S$  of 138.8 and an AIC of 134.9, thus being clearly inferior to the model we report in the results.

## Results

### *Water availability*

#### *Transient Pools*

The proportion of 17 transient rain fed pools containing water rapidly declined during the dry season (100% May, 59% June, 24% July, 6% August, 4% September, 2% October 0% November).

#### *Great Ruaha River*

In all three years of the study, by September the GRR contained no surface water downstream of sampling site 10 (Fig. 1) and this section of the river remained dry until the end of the dry season in November. However, in early November 2012 a local rain storm resulted in the formation of water pools in this area that persisted for a few days. In all three study years camera trap position F and sampling sites 9, 8 and 5 dried out in October with the loss of surface water most extensive in the 2013 dry season. In November in all three study years most upstream sampling sites (site 4, 3, 2 and 1, Fig. 1) were also mostly dry with a few scattered pools remaining.

#### *Non-GRR water sampling sites*

Sampling site 12 was dry throughout the entire dry season in 2012 and 2013. In 2013 sampling site 18 dried out in August and sampling site 13 was dry in November.

#### *Waterholes dug by wildlife*

In 11 out of 26 waterholes dug by wildlife we observed the species that dug the waterhole (Table 2). These were elephant (7 waterholes), plains zebra (2 waterholes), yellow baboon (*Papio cynocephalus*) (1 waterhole) and warthog (*Phacochoerus africanus*) (1 waterhole). Elephants dug close to sampling site 7 on the GRR and close to non-GRR sampling sites 16, 17 and 18, zebras close to sampling site 9 on the GRR and close to non-GRR sampling site 13,

and one warthog dug close to sampling site 12 (Fig. 1). Four additional species were observed drinking from wildlife dug water holes, greater kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*), vervet monkey (*Cercopithecus aethiops pygerythrus*) and helmeted guineafowl (*Numida meleagris*). Animals were observed digging and drinking from waterholes dug by wildlife in all three study years. Waterholes dug by wildlife were observed in July away from the GRR and at the earliest along the GRR in October.

While they persisted, animals visited dug waterholes on a daily basis to drink and on average most camera trapping events which recorded drinking involved elephants, followed by impala, zebra, warthog, baboon, guineafowl, greater kudu and vervet monkey (Table 3). The highest daily drinking visitation rate for elephants was reached in August when surface water was still present in the vicinity (camera trap position L, Fig. 1). For impala, zebra and warthog the highest daily drinking visitation rate was reached in November (camera trap position I, Fig. 1) when no water was present in the vicinity (Table 3).

Five of 26 waterholes dug by wildlife were created when no surface water was available within a distance of approximately five kilometres of the waterhole (Table 2). Two of these waterholes persisted for at least 8 days because further digging activity by animals removed sand that collapsed into the waterholes. The other 21 waterholes dug by wildlife were within a maximum of 200m of the nearest surface water. Five of these waterholes persisted for at least 6 days and up to 14 days (Table 2).

#### *Water quality and river flow*

Dry season measures of salinity ( $\mu\text{S}/\text{cm}$ ) were significantly lower at sampling sites in the GRR than at non-GRR sampling sites ( $U = 4193.50$ ,  $n_{\text{GRR}} = 296$ ,  $n_{\text{non-GRR}} = 143$ ,  $p < 0.000001$  Fig. 2). Measures of total aerobic bacterial load (cfu/ml) were also significantly lower from sampling sites along the GRR than non-GRR sampling sites ( $U = 3372.50$ ,  $n_{\text{GRR}} = 265$ ,  $n_{\text{non-GRR}} = 122$ ,  $p < 0.000001$ , Fig. 3). The *E. coli* load in water samples significantly increased with total aerobic bacterial load (Spearman's rank correlation  $r_s = 0.50$ ,  $n = 90$ ,  $p < 0.0001$ ).

The water salinity at sampling sites along the GRR was considerably lower than at non-GRR sampling sites at the beginning of the dry season (Fig. 4a, b). Water salinity in the GRR significantly increased as the dry season progressed in all three years of the study (Fig. 4a) (2011:  $r_s = 0.87$ ,  $n = 100$ ,  $p < 0.0001$ ; 2012:  $r_s = 0.85$ ,  $n = 101$ ,  $p < 0.0001$ ; 2013:  $r_s = 0.86$ ,  $n = 95$ ,  $p < 0.0001$ ).

Total aerobic bacterial load in the GRR also significantly increased during the course of the dry season (Fig. 5) (2011:  $r_s = 0.25$ ,  $n = 74$ ,  $p = 0.032$ ; 2012:  $r_s = 0.57$ ,  $n = 99$ ,  $p < 0.0001$ ; 2013:  $r_s = 0.61$ ,  $n = 92$ ,  $p < 0.0001$ ).

Comparison of the mean water salinity in the GRR when water flowed at a sampling site and when flow had stopped at the sampling site revealed that across all three study years salinity in the GRR significantly increased after water flow had stopped (Wilcoxon signed-rank test,  $T = 350$ ,  $p < 0.0001$ ,  $n = 26$ ). Similarly, the mean total aerobic bacterial load significantly increased after water had stopped flowing at a sampling site ( $T = 241$ ,  $p < 0.0001$ ,  $n = 22$ ).

### *Digging and water quality*

Waterholes dug by wildlife along the GRR occurred close to three widely separated sampling sites (1, 7 and 9, Fig. 1) and occurred in all three years close to sampling site 9. Wildlife also dug waterholes in the GRR close to sampling site 7 in 2012 and close to sampling site 1 in 2013. Away from the GRR, waterholes dug by wildlife occurred close to six sampling sites (sites 12, 13, 15, 16, 17, 18, Fig. 1).

Waterholes were equally likely to be dug when water was present (and stagnant) and when there was no water ( $G = 0.0034$ ,  $df = 1$ ,  $p = 0.95$ ). A logistic regression model ( $G = 36.15$ ,  $df = 4$ ,  $p < 0.00001$ , Table 4) revealed that the likelihood of wildlife digging to access below ground water was significantly less likely to occur along the GRR than at non-GRR locations, significantly more likely when surface water was stagnant rather than flowing and increased as total aerobic bacterial load increased. Salinity had no significant effect on the likelihood of digging.

### **Discussion**

Our results demonstrate that wildlife digging to access water was less likely to occur and was observed later in the dry season along the GRR than at non-GRR sites. In most cases when waterholes were dug by wildlife, surface water was present in the vicinity (Table 2). This is consistent with the idea that when the quality of surface water is poor, animals dig to access water of better quality in locations where water is available below the surface of the ground (Galat et al., 2009; Ramey et al., 2013). The results of our model is consistent with this idea as they indicate that digging was more likely when the quality of available surface water was low in terms of containing a high total aerobic bacterial load (Table 4). However, we found no evidence that water quality, in terms of the salinity levels reported in this study, prompted

digging.

Our results highlight the importance of the GRR as the key source of high quality water for wildlife in the Ruaha NP, in terms of significantly lower total aerobic bacterial loads and salinity than at non-GRR water sites such as in springs and pools in the beds of sand rivers. Reduced water flow can contribute to poor water quality (Wanke and Wanke, 2007; Wolanski and Gereta, 1999). In line with this idea, our matched comparison of water quality at sampling sites when water flowed and after flow had ceased revealed a significant deterioration in water quality after water stopped flowing, in terms of increased total aerobic bacterial load and increased water salinity. The deterioration in water quality in the GRR as the dry season progressed is most likely explained by the profound decline in water flow during the dry season. Hence our results highlight the great importance of maintaining water flow in the GRR to prevent a significant deterioration of water quality in this key wildlife water source.

Waterholes dug by wildlife were sometimes the only known source of water within a radius of approximately five kilometres of the dug waterhole. It is possible that the presence of waterholes dug by wildlife may permit some species to utilize habitats during the dry season that they otherwise would be absent from. Once created, waterholes dug by wildlife were utilised for periods ranging from a few days to approximately two weeks. In some waterholes, access to water was maintained by animals digging to remove sand that accumulated at the bottom of the waterhole. Elephants were the species most often observed digging waterholes and as elephants are thought to be the only species able to access water more than one metre below the surface of the ground (Dudley et al., 2001), they probably play an important role in providing water to other species when the water table is low (Poché, 1974). In addition to the larger species (both mammals and birds) we observed using waterholes dug by wildlife, smaller species not recorded by camera-traps may no doubt also used such waterholes.

Many pathogens use water as a means of transmission between hosts, including bacteria. We did not characterize all bacteria present in water collected from sampling sites and instead used *E. coli* as an indicator of faecal contamination. There was a significant positive relationship between *E. coli* load and total aerobic bacterial load. This suggests that as total aerobic bacterial load increased so did faecal contamination, and with it possibly harmful bacteria, including *E. coli* strains which may be pathogenic to some of the wildlife species

(Hellberg and Chu, 2015). Furthermore, within certain limits, *E. coli* could also serve as an indicator of viral contamination in water (Gersberg et al., 2006). Interestingly, Ramey et al. (2013) found that coliform counts were significantly lower in waterholes dug by elephants than in the nearest available water source. Currently, little is known about the cues prompting animals to invest energy accessing water below ground when surface water is available but of low quality. Perhaps either the taste or smell of certain metabolites of microorganisms may be involved (Safferman et al., 1967; Young et al., 1996).

In conclusion, our study provides evidence that water quality in terms of total aerobic bacterial load can cause wildlife to dig waterholes. Our results predict that if the current trend of low dry season flow in the GRR continues, contamination of river water with high total aerobic bacterial loads will prevail during dry seasons. Any further declines in water flow in the GRR during the dry season, as a result of water off-take or future climate change, may cause a more extensive drying-up of the river, high total aerobic bacterial loads in river water at an earlier stage in the dry season, plus increased salinity levels. These effects are likely to have potentially negative health consequences for wildlife.

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### Table Legends

**Table 1** The number of measurements at water sampling sites and camera trap positions used for analysis per sampling site and year in Ruaha National Park along the Great Ruaha River (GRR) or at non-GRR sites during the dry season.

**Table 2** Characteristics of ephemeral waterholes dug by wildlife in Ruaha National Park along the Great Ruaha River (GRR) or at non-GRR sites during the dry season. Inc.obs – incidental observations; CT – camera trapping; GRR – Great Ruaha River; BA – baboon; EL – elephant; GU – guinea fowl; IM – impala; KU – greater kudu; VE – vervet monkey; WA – warthog; ZE – zebra.

**Table 3** Usage of ephemeral waterholes dug by wildlife in Ruaha National Park monitored at camera trapping positions on the Great Ruaha River (GRR) or at non-GRR positions during the dry season. Species specific usage: the number of independent camera trapping events per species drinking day<sup>-1</sup>.

**Table 4** Logistic regression of factors affecting the occurrence of digging of waterholes by wildlife if water was still present in the vicinity. Shown are the logistic regression coefficient estimates with their standard errors (SE) and 95% confidence limits, their conversion into odds ratios with their respective 95% confidence limits, and the z-value with associated p-values for each parameter. Positive (negative) estimates indicate that an increase in the value of the parameter increased (reduced) the incidence of digging.

## Chapter 2

**Table 1**

Year		2011					2012					2013			
Site		Measurement sample sizes					Measurement sample sizes					Measurement sample sizes			
Water sampling site	Camera trap position	Site type	Salinity	Total aerobic bacterial load	<i>E.coli</i> load	Camera trapping (h)	Salinity	Total aerobic bacterial load	<i>E.coli</i> load	Camera trapping (h)	Salinity	Total aerobic bacterial load	<i>E.coli</i> load	Camera trapping (h)	
1		GRR	11	9	-	-	11	11	2	-	9	9	5	-	
2		GRR	11	9	-	-	11	11	2	-	10	10	5	-	
3		GRR	11	8	-	-	11	11	2	-	10	10	4	-	
4		GRR	11	8	-	-	11	10	2	-	9	8	5	-	
5		GRR	9	6	-	-	10	9	1	-	10	10	5	-	
6	A	GRR	9	8	-	-	10	10	1	1065.31	9	8	5	1861.62	
	B	GRR	-	-	-	-	-	-	-	1071.62	-	-	-	1747.88	
7	C	GRR	11	6	-	-	10	10	1	764.00	11	10	4	1748.54	
8		GRR	11	7	-	-	9	9		-	10	10	5	-	
	D	GRR	-	-	-	-	-	-	-	1052.91	-	-	-	1750.46	
9	E	GRR	10	7	-	-	11	11	2	1056.50	10	10	5	1752.82	
	F	GRR	-	-	-	-	-	-	-	1054.67	-	-	-	1750.44	
10	G	GRR	6	6	-	-	7	7	-	1055.27	7	7	4	1750.08	
11	H	Spring	11	6	-	-	11	10	2	917.42	10	8	4	1317.01	
12		Spring	11	5	-	-	-	-	-	-	-	1*	-	-	
13	I	Water in sand river	-	-	-	-	8	8	2	985.00	8	7	4	1250.92	
14	J	Spring	5	4	-	-	10	9	2	985.12	10	9	5	1084.79	
15	K	Water in sand river	5	5	-	-	11	11	1	985.34	10	9	5	1246.23	
16	L	Water in sand river	4	3	-	-	9	8	1	984.83	9	8	5	868.87	
17	M	Water in sand river	-	-	-	-	2	2	1	600.92	2	2	0	1249.53	
18	N	Water in sand river	-	-	-	-	6	6	2	864.15	1	1	1	1242.95	
Total			136	97			158	153	24	13443.06	145	137	71	20622.14	

\* Site 12 was categorised as dry in 2013 as it contained negligible water (<5ml) but this was sufficient to determine total aerobic bacterial load.

## Chapter 2

**Table 2**

Animal dug hole	Method	Position name	Location	Water present?	Digger	Users	Distance to nearest surface water	Persistence (days)	Date dug	First obs. use	Last obs. use
1	inc.obs.	15 K	non-GRR	yes	?	EL, WA	≤ 50 m	≥ 1	?	20110613	20110613
2	inc.obs.	15 K	non-GRR	yes	?	EL	≤ 50 m	≥ 1	?	20111007	20111007
3	inc.obs.	9 E	GRR	yes	?	EL	≤ 50 m	≥ 1	?	20111030	20111030
4	CT	13 I	non-GRR	yes	?	EL, IM, VE, WA, ZE	≤ 50 m	≥ 12	?	20120811	20120822
5	CT	16 L	non-GRR	yes	EL	EL	≤ 50 m	3	20120814	20120814	20120816
6	CT	16 L	non-GRR	yes	?	EL	≤ 50 m	2	?	20120815	20120816
7	inc.obs.	12	non-GRR	no	WA	WA	> 5 km	≥ 1	20120829	20120829	20120829
8	CT	17 M	non-GRR	yes	EL	EL	≤ 50 m	1	20120923	20120923	20120923
9	CT	16 L	non-GRR	yes	?	EL	≤ 50 m	≥ 1	20120928	20120928	20120928
10	inc.obs.	18 N	non-GRR	yes	EL	EL	≤ 50 m	≥ 1	20121015	20121015	20121015
11	CT	16 L (hole1)	non-GRR	yes	EL	EL	≤ 200 m	≥ 2	20121015	20121015	20121016
12	CT	17 M (hole1)	non-GRR	yes	?	BA, EL, GU, IM, KU	≤ 200 m	≥ 15	?	20121015	20121029
13	CT	16 L (hole2)	non-GRR	yes	EL	EL	≤ 200 m	2	20121016	20121016	20121017
14	CT	17 M (hole2)	non-GRR	yes	?	EL, GU	≤ 200 m	3	20121016	20121016	20121018
15	CT	13 I	non-GRR	yes	?	EL, IM, WA, ZE	≤ 200 m	≥ 13	?	20121016	20121028
16	CT	18 N	non-GRR	yes	EL	EL	≤ 50 m	≥ 1	20121029	20121029	20121029
17	inc.obs.	9 E	GRR	yes	?	EL, ZE	≤ 50 m	≥ 1	?	20121031	20121031
18	CT	F	GRR	no	?	BA, GU, IM, ZE	> 5 km	≥ 9	?	20121109	20121117
19	inc.obs.	7 C	GRR	yes	EL	EL	≤ 50 m	≥ 1	20121110	20121110	20121110
20	CT	13 I	non-GRR	yes	?	EL	≤ 50 m	≥ 7	?	20130701	20130707
21	inc.obs.	13 I	non-GRR	yes	ZE	ZE	≤ 50 m	≥ 1	20130930	20130930	20130930
22	CT	13 I	non-GRR	yes	?	IM, WA, ZE	> 5 km	≥ 12	?	20131001	20131012
23	inc.obs.	1	GRR	yes	BA	BA	≤ 50 m	≥ 1	20131028	20131028	20131028
24	inc.obs.	13 I	non-GRR	no	?	IM, WA	> 5 km	≥ 1	?	20131101	20131101
25	CT	13 I	non-GRR	no	?	BA, EL, KU, WA, ZE, IM	> 5 km	≥ 14	?	20131101	20131114
26	inc.obs.	9 E	GRR	no	ZE	ZE	> 5 km	≥ 1	20131117	20131117	20131117

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**Table 3**

Site ID	Camera trap position	Location	Month	Number of species	Water present	Species specific usage								Persistence of animal dug waterholes (day)
						Elephant	Impala	Zebra	Warthog	Greater kudu	Baboon	Vervet monkey	Guineafowl	
13	I	non-GRR	Jul	1	Yes	0,43	0,00	0,00	0,00	0,00	0,00	0,00	0,00	7
16	L	non-GRR	Aug	1	Yes	2,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	2
16	L	non-GRR	Aug	1	Yes	1,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	3
13	I	non-GRR	Aug	5	Yes	0,50	1,00	0,14	0,29	0,00	0,00	0,14	0,00	12
16	L	non-GRR	Sep	1	Yes	1,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1
17	M	non-GRR	Sep	1	Yes	1,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1
18	N	non-GRR	Oct	1	Yes	1,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1
17 (hole1)	M	non-GRR	Oct	5	Yes	0,33	0,86	0,00	0,00	0,29	0,14	0,00	0,29	15
17 (hole2)	M	non-GRR	Oct	2	Yes	1,00	0,00	0,00	0,00	0,00	0,00	0,00	0,14	3
16 (hole1)	L	non-GRR	Oct	1	Yes	1,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	2
16 (hole2)	L	non-GRR	Oct	1	Yes	1,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	2
13	I	non-GRR	Oct	4	Yes	0,08	1,00	1,43	1,00	0,00	0,00	0,00	0,00	13
13	I	non-GRR	Oct	3	Yes	0,00	0,29	1,43	0,57	0,00	0,00	0,00	0,00	12
F	F	GRR	Nov	4	No	0,00	0,29	0,43	0,00	0,00	0,43	0,00	0,14	9
13	I	non-GRR	Nov	6	No	0,43	1,86	2,00	1,71	0,14	0,14	0,00	0,00	14
Mean				2,5		0,72	0,35	0,36	0,24	0,03	0,05	0,01	0,04	6,5

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**Table 4**

Parameter	Regression coefficients					Odds ratios			
	Estimate	SE	z	P	95% Confidence Interval		Estimate	95% Confidence Interval	
					Lower	Upper		Lower	Upper
Constant	-3.681	0.848	-4.343	0.000014	-5.34	-2.02			
Salinity	-0.0011	0.00081	-1.365	0.17	-0.0027	0.00048	0.999	0.997	100.048
Location: elsewhere > Great Ruaha River	1.952	0.80	2.428	0.015	0.376	3.528	7.044	1.457	34.062
Total bacterial load	0.00091	0.00042	2.180	0.029	0.000092	0.0017	100.091	1.000.092	10.017
Did the water flow? yes < no	-2.016	0.64	-3.151	0.0016	-3.270	-0.76	0.133	0.038	0.467

### Figure legends

**Figure 1** Ruaha National Park (RNP) in central Tanzania. Sites monitored for the presence or absence of water were located along the Great Ruaha River (GRR, sites 1-10, B, D, F) and non-GRR sites which included pools in dry sand rivers (sites 13,15-18) and isolated springs (sites 11,12,14). Open circles: sites where water samples were taken along the Great Ruaha River (sampling sites 1-10) and at non-GRR sites (sampling sites 11-18). Square boxes: Positions where camera traps were set up along the Great Ruaha River (sites A to G) and non-GRR sites (sites H to N).

**Figure 2** Water salinity ( $\mu\text{S}/\text{cm}$ ) concentrations at sampling sites along the Great Ruaha River (sites 1-10) and at non-GRR water sampling sites (sites 11-18). Boxplots summarise all measurements per site obtained throughout the dry seasons from June to November between 2011 and 2013. Boxes include data points with values between the first and the third quartile, with the central horizontal line marking the median. The whiskers incorporate data points with values up to 1.5 times larger or smaller than the box length (the difference between the third and first quartile). Asterisks mark data points with values between 1.5 and up to 3 times larger or smaller than the box length, open circles represent data points with values beyond this range.

**Figure 3** Total aerobic bacterial load quantified as colony forming units per ml (cfu/ml) at sampling sites along the Great Ruaha River (sites 1-10), and at non-GRR sites (sites 11-18). Boxplots summarise all measurements per site obtained throughout the dry seasons from June to November between 2011 and 2013. Boxes include data points with values between the first and the third quartile, with the central horizontal line marking the median. The whiskers incorporate data points with values up to 1.5 times larger or smaller than the box length (the difference between the third and first quartile). Asterisks mark data points with values between 1.5 and up to 3 times larger or smaller than the box length, open circles represent data points with values beyond this range.

**Figure 4** The increase in water salinity concentrations at sampling sites along the Great Ruaha River and at non-GRR sampling sites during the dry season (June to November). The scatterplots summarise all measurements at sampling sites (1-10) along the Great Ruaha

River (a) and at non-GRR sampling sites (11-18) (b), obtained throughout the dry seasons from June to November between 2011 and 2013.

**Figure 5** The increase in total aerobic bacterial load at sampling sites along the Great Ruaha River and at non-GRR sampling sites during the dry season (June to November). The scatterplots summarise all measurements at sampling sites (1-10) along the Great Ruaha River (a) and all non-GRR sampling sites (11-18) (b), obtained throughout the dry seasons from June to November between 2011 and 2013.

Figure 1

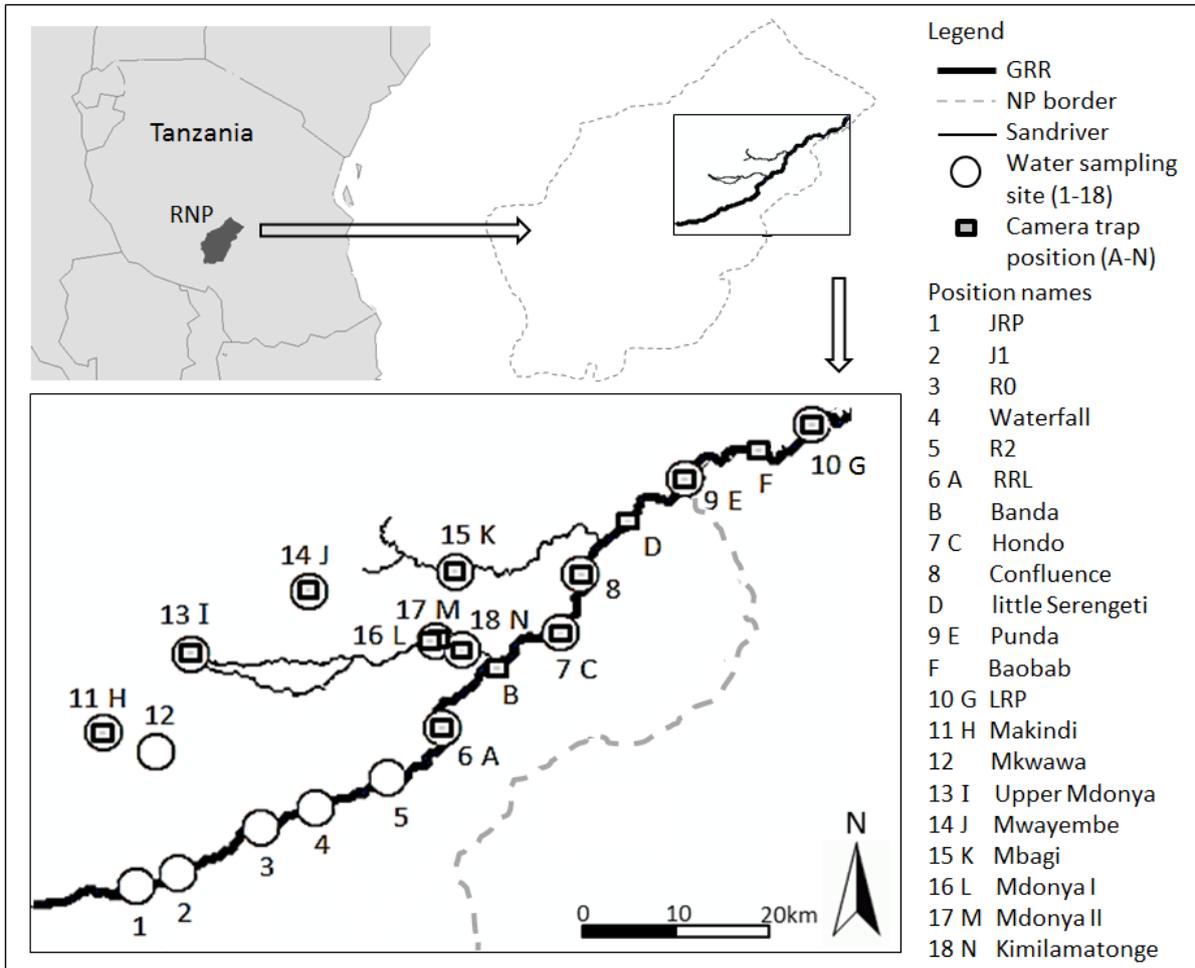


Figure 2

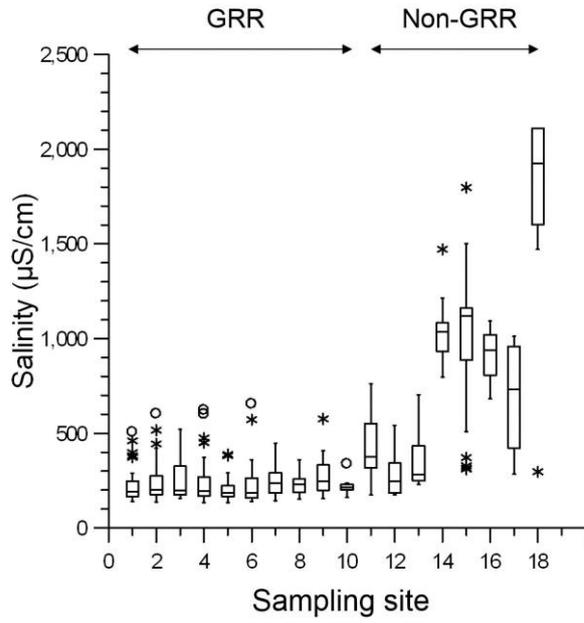


Figure 3

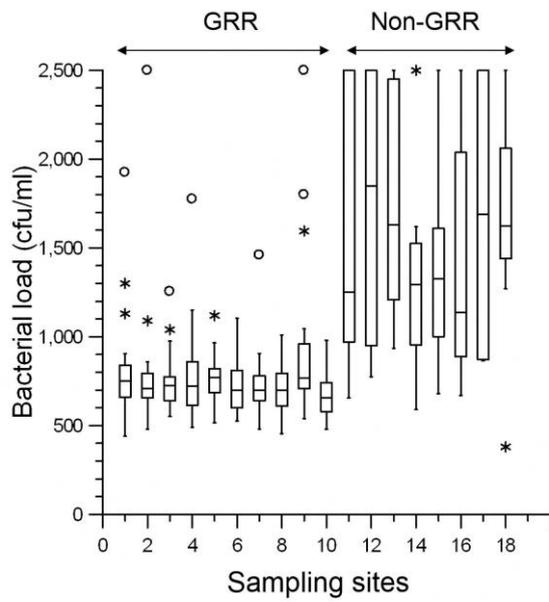


Figure 4

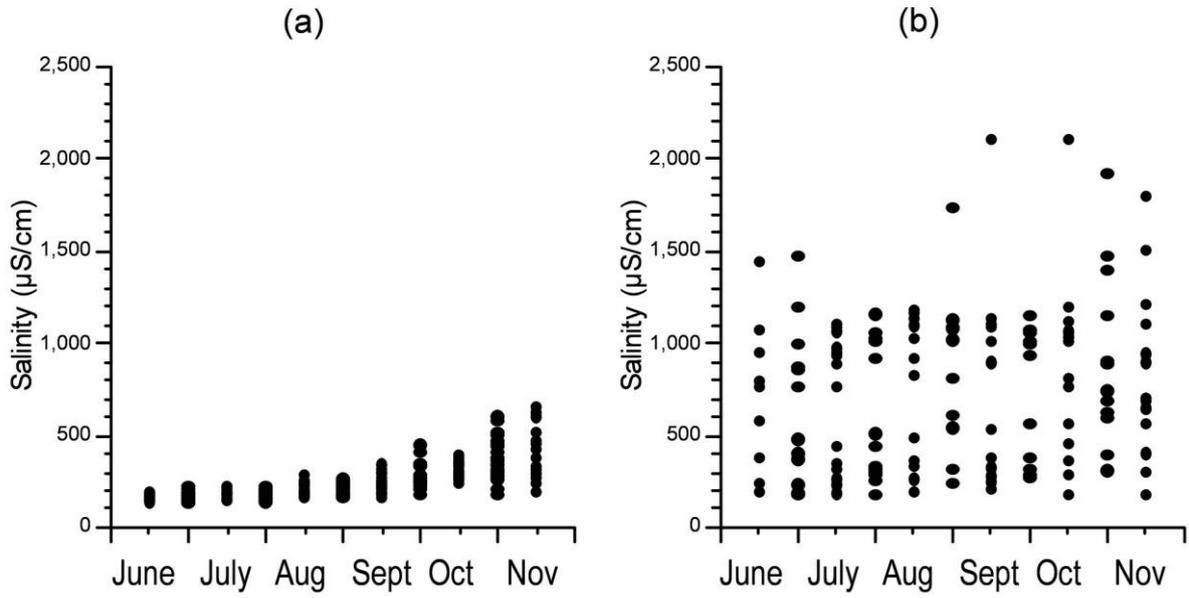
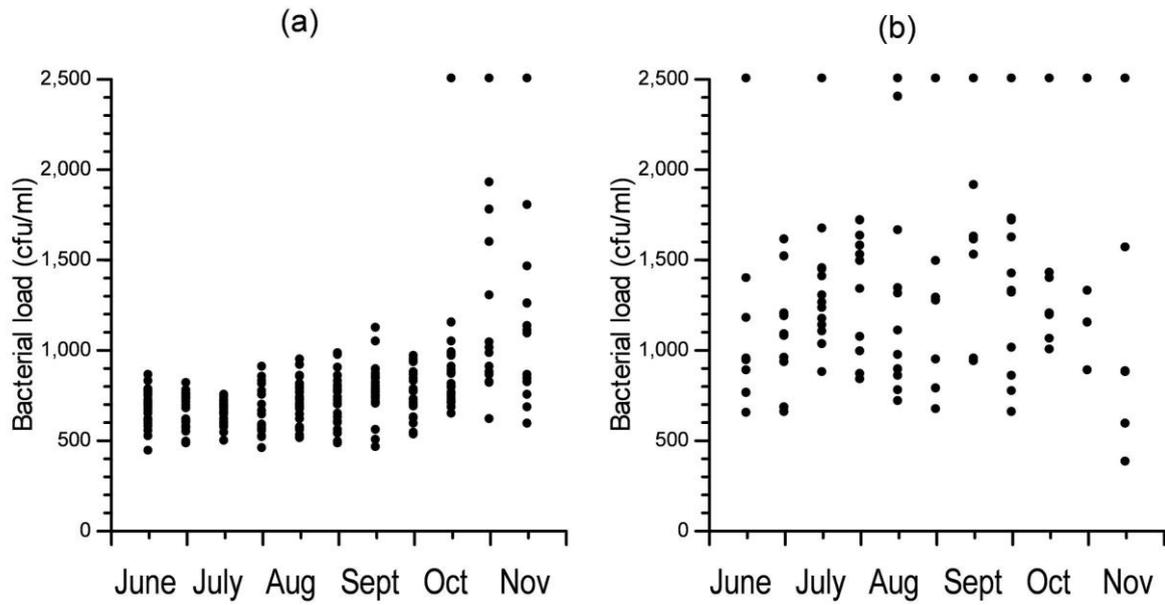


Figure 5



## CHAPTER 3

### Manuscript 2

#### **The effect of reduced water availability in the Great Ruaha River on the vulnerable common hippopotamus in the Ruaha National Park, Tanzania**

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#### **Author contributions:**

Conceived and designed the experiments: CS ME. Performed the experiments: CS. Analysed the data: CS HH. Contributed reagents/materials/analysis tools: CS ME HH. Wrote the paper: CS ME HH.

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**Abstract**

In semi-arid environments, 'permanent' rivers are essential sources of surface water for wildlife during 'dry' seasons when rainfall is limited or absent, particularly for species whose resilience to water scarcity is low. The hippopotamus (*Hippopotamus amphibius*) requires submersion in water to aid thermoregulation and prevent skin damage by solar radiation; the largest threat to its viability are human alterations of aquatic habitats. In the Ruaha National Park (NP), Tanzania, the Great Ruaha River (GRR) is the main source of surface water for wildlife during the dry season. Recent, large-scale water extraction from the GRR by people upstream of Ruaha NP is thought to be responsible for a profound decrease in dry season water-flow and the absence of surface water along large sections of the river inside the NP. We investigated the impact of decreased water flow on daytime hippo distribution using regular censuses at monitoring locations, transects and camera trap records along a 104 km section of the GRR within the Ruaha NP during two dry seasons. The minimum number of hippos per monitoring location increased with the expanse of surface water as the dry seasons progressed, and was not affected by water quality. Hippo distribution significantly changed throughout the dry season, leading to the accumulation of large numbers in very few locations. If surface water loss from the GRR continues to increase in future years, this will have serious implications for the hippo population and other water dependent species in Ruaha NP.

## Introduction

Human utilisation of water resources is increasing worldwide and is likely to accelerate given the projected growth in the human population [1], and the increasing volume of water required for domestic, agricultural and industrial purposes [2, 3]. This growing demand on water resources is likely to have potentially negative consequences for ecosystems and the wildlife they support.

In regions of the world that experience 'dry seasons' when little or no precipitation falls for several months, seasonal rivers and other sources of surface water typically dry up soon after the onset of the dry season, hence sources of surface water are scarce. 'Permanent' rivers that persist throughout the dry season provide a vital source of water to the areas through which they flow. Human extraction of water from permanent rivers can result in a decrease in dry season flow and the absence of surface water during dry seasons. This may have negative consequences for wildlife populations that depend on water from permanent rivers during dry seasons, yet current knowledge on the resilience of many species to anthropogenic restrictions of water resources is limited.

Historically the common hippopotamus (*Hippopotamus amphibius*), hereafter termed the hippo, was once widely distributed throughout sub-Saharan Africa. Its range has declined and become fragmented and its population size has contracted chiefly as a result of human activities [4]. Since 2006, the hippo has been listed by IUCN as a threatened species, vulnerable to extinction ([www.iucn-redlist.org](http://www.iucn-redlist.org)). One of the main threats to this species is habitat loss caused by human conversion of wetlands to agricultural land and the redirection of water from rivers and lakes to agricultural areas (e.g. [5-7]). Hippo populations may crash in drought years because of reduced conception/fertility and increased mortality associated with heat stress, poor nutrition and an increased vulnerability to diseases, as large numbers of animals congregate in declining water sources [6, 8]. Although some climate models predict a future increase in rainfall for East Africa, there has been a downward trend in rainfall in the region since the 1980s [9-11]. If this trend continues it is likely to negatively affect hippo populations.

Hippos are particularly vulnerable to changes in their aquatic environment because they require regular daytime submersion in water to prevent skin damage by the sun and to help body temperature regulation [4, 12]. Their skin is to some extent protected from sun damage by a viscous fluid produced by sub-dermal glands that turns red-brown after

secretion and also has antimicrobial properties [13]. At night, hippos leave their daytime resting areas and may move several kilometres to their grazing areas [14]. A recent stable isotope study indicates that hippos consume browse [15] and hence may not be the strict grazers they were previously assumed to be [4]; they are also opportunistically carnivorous [16].

In areas containing permanent water, hippo bulls may hold a territory for many years and in some cases throughout adult life (~ 20 years or more). Territory ownership is advertised by ritualized defecation, urination and dominance behavioural displays. Contests between neighbouring bulls are normally ritualized but fights can result in serious wounds [17]. Mating occurs in water; territorial males are thought to monopolise mating access to receptive females in their territory [17]. Non-territorial males may join bachelor herds and are tolerated inside the territories of bulls provided they display submissive behaviour [4, 17]. Adult females normally establish a home range in their natal area that encompasses the territory of more than one bull. Females give birth in water to a single offspring that can suckle even under water [12].

When their day resting areas dry out, hippos may travel beyond their territory and normal range to locate alternative suitable daytime resting sites [18]. This disrupts established relationships among hippos in an area and increases the probability of interactions with less familiar hippos [19] and hence the chance of intra-specific aggression [19, 20, 21, 22]. Females may encounter sexual harassment [17] and calves may be killed by infanticidal bulls that aim to bring their mothers into oestrus [23]. Film footage of a subadult hippo committing infanticide also suggests that the disruption of normal relationships and physiological stress associated with high hippo densities in some day resting areas may also precipitate infanticide [17].

The Great Ruaha River (GRR) is an important permanent river in central Tanzania that flows through Ruaha National Park (NP) where it is the main source of surface water for wildlife, especially during the dry season [24, 25]. It is thought that during the dry season most hippos in the Ruaha ecosystem reside in Ruaha NP and probably most are confined to the GRR [25]. Large scale human utilization of water from the GRR upstream of Ruaha NP since 1993 is considered chiefly responsible for a significant reduction in the dry season flow and the loss of surface water from extensive stretches of the GRR within Ruaha NP [24]. The reduced dry season flow of water also results in a significant reduction in water quality, in

terms of increased salinity, aerobic bacterial load and faecal contamination [25]. The impact of the reduced flow and quality of surface water, and the decline in the availability of surface water in the GRR during the dry season on the distribution of hippos has not been investigated. Knowledge on the current impact of reduced water flow on hippos is important and can serve as a benchmark for future studies.

Our study focused on daytime resting sites used by hippos along a substantial section of the GRR within the Ruaha NP. We expected changes in hippo distribution during the dry season to be driven by a decline in surface water and water quality, leading to a reduction in suitable daytime resting sites. If hippos have to abandon unsuitable daytime resting locations and relocate to another suitable location, this should result in the congregation of hippos at a few key locations as the dry season progresses. We aimed to identify whether the same key daytime resting areas are used across years and expected hippo mortality associated with poor nutrition, intra-specific aggression and disease to be lower in the early than the late dry season. We discuss the implication of our findings in relation to the long-term prospects for the GRR population of hippos within Ruaha NP.

## **Methods**

### *Study area*

Our study took place in the Ruaha NP in central Tanzania, the largest (20,226 km<sup>2</sup>) National Park in East Africa (Fig. 1). Data were collected during the 2012 and 2013 dry seasons, both of which spanned a period of six months (June to November). The RNP receives a mean annual rainfall of approximately 580mm which almost exclusively falls during the wet season [26]. During the 2013 dry season negligible precipitation occurred in a few local showers (< 6mm) that evaporated within a few hours. In November 2012, one rainstorm delivered 52mm of rain which briefly increased surface water availability in the study area [25].

During the 2012 and 2013 dry season, large sections of the GRR dried out, leaving discrete water pools separated by stretches of dry river bed [25]. Tributaries of the GRR that flowed in the wet season became dry sand-rivers with occasional, localised pools of water during these dry seasons. Springs at some distance northwest of the GRR also contained relatively small amounts of surface water [25].

*Censusing the distribution and numbers of hippos*

Previous censuses of the Greater Ruaha ecosystem, encompassing 43,601 km<sup>2</sup> [27, 28] and including Ruaha NP, Rungwa, Kizigo and Muhesi Game Reserves demonstrated that the distribution of hippos is limited to the GRR and Mzombe River and that the majority occurred in the GRR inside Ruaha NP. We therefore censused the distribution of hippos inside Ruaha NP at 14 locations (from now on called monitoring locations) that were used by hippos for daytime resting (locations 1 to 14, Fig. 1). The topographical gradient of the GRR changed across the study site. The elevation of the river declined by 156 m along the 53.5 km covered between monitoring location 1 to camera trap position B (Fig. 1), whereas it changed only 43 m over a distance of 50.5 km between camera trap positions B and G (Fig. 1). Hence, we categorised the topographic gradient between locations 1 and B as “upstream” and “steep” and the gradient between locations B and G as “downstream” and “flat”.

All monitoring locations could be viewed from the game viewing roads along the northern bank of the GRR. We aimed to count hippos at these 14 monitoring locations during censuses twice per month but, this was not always feasible. Twelve out of 14 monitoring locations were censused once in November, locations 5 in 2012 and 8 in 2013 were not monitored. As it was not possible to count hippos at all 14 locations along the GRR within one day, the river was divided into three censusing sections. Hippos were counted in two sections between monitoring locations 1 and camera trap position B (Fig. 1) on two consecutive days; those in the section between camera trap position B and monitoring location 14 (Fig. 1) were counted on one day. Counts of all 14 monitoring locations were completed within a mean of  $4.41 \pm 0.23$  successive days (SEM).

Hippos were counted by scanning each monitoring location for at least seven minutes using binoculars. This minimum observation period was used because hippos can stay submerged for up to seven minutes [29]. Even so, some counts are likely to be minimum estimates of the number of hippos present, particularly in large congregations when juveniles may have been overlooked. When feasible, hippos were also sexed and allocated to three age categories: infants (estimated age < one year), juveniles (estimated age from > one year to not yet adult) and adults (fully grown animals). We defined counts from June to August as early dry season counts and those from September to November as late dry season counts. To illustrate changes in hippo distribution in greater detail we focused on two upstream

monitoring locations (1 and 4, Fig. 1) and two downstream monitoring locations (9 and 11, Fig. 1) which we have censused most frequently throughout both dry seasons. The GPS coordinates for these four monitoring locations are: 1 = 674821.00 mE, 9125948.00 mS; 4 = 693486.00 mE, 9134339.00 mS; 9 = 714169.00 mE, 9150895.00 mS; 11 = 727870.00 mE, 9166962.00 mS (UTM zone 36 M).

#### *The state of water expanse at monitoring locations*

The monitoring locations (except no. 12 in 2012 and 2013, and no. 8 in 2013) were categorised every two weeks in terms of the estimated depth and expanse of water they contained. The status categories were: (1) dry – no water present, (2) shallow – an amount of water to rest in throughout one day that is inadequate for an adult hippo (< approximately 10 cm deep), (3) moderate – an expanse of water (>0.5m deep) assessed to be sufficient to accommodate approximately 15 resting hippos, (4) large – an expanse of water (>0.5m deep) sufficient to accommodate more than 20 hippos.

#### *Water quality*

Water quality was measured in terms of salinity and total aerobic bacterial load. Water salinity was measured for water samples collected every two weeks from June to November at ten sampling points along the GRR as previously described in detail [25]. Briefly, salinity was measured in micro Siemens per centimetre ( $\mu\text{S}/\text{cm}$ ) using a Multi 340i Multimeter (Wissenschaftlich Technische Werkstätten GmbH, Weilheim, Germany). Total aerobic bacterial load was measured as the number of colony forming units per ml (cfu/ml) using the 3M Petrifilm Aerobic Count Plate including a tetrazolium indicator (*3M™ Petrifilm™ Aerobic Count Plates* (U.S. AOAC®)), following the manufacturer's instructions – for details see [25].

Water flow was categorised as “dry” (no surface water), “stagnant” (non-flowing surface water) and “flowing” (moving surface water) twice every month at these ten water sampling points – for details see [25].

#### *Camera trapping*

We used Reconyx PC800 camera traps (Reconyx Inc., Holmen, Wisconsin, USA) to record the presence of hippos at seven sites along the GRR (camera trap positions A-G, Fig. 1), at five locations with surface water in dry sand rivers (camera trap positions I, K-N, Fig. 1) and at two springs (camera trap positions H and J, Fig. 1) from August to November in 2012 and

from June to November in 2013. One camera monitored each location for a mean of  $960.2 \pm 36.3$  h in 2012 and a mean of  $1473.0 \pm 86.3$  h in 2013. Total monitoring time was 13,443.1 h in 2012 and 20,622.1 h in 2013. A total of 205,959 camera pictures were analysed. To define an independent “hippo camera trapping event” we set a minimum period of 15 minutes between the last picture of the previous hippo trapping event and the first picture of the next hippo trapping event.

#### *Transect observations*

The distribution of larger mammals, including hippos, was recorded along ten ground transects, each 20 km in length, from June to November in 2012 and 2013. Transects were driven every two weeks between 7:00 and 11:00hrs. Five transects followed the game viewing road along the northern bank of the GRR. Five transects followed game viewing roads leading away from the GRR in northerly directions.

#### *Mortality*

Hippo carcasses were encountered and recorded during transects, censuses at monitoring locations and during incidental encounters, or were reported by National Park personnel and tourist guides and then verified.

#### *Statistical Analysis*

The chi-square test of independence or association with the log likelihood ratio as test statistic was used to check whether the state of water at the monitoring locations was related to the topographic gradient [30].

We used generalised linear models (GLMs – here, binary and multinomial logistic, poisson and negative binomial regression models, see below) to assess the impact of predictor variables on the (1) change in the expanse of water (status) at monitoring locations, (2) minimum number of hippos at the 14 monitoring locations, (3) total number of hippos counted within the study area, and (4) chance of encountering females and calves in a group of hippos.

Potential predictors of the change in the expanse of water (status) at monitoring locations included the topographic gradient (steep versus flat), month as an index of the progression of dry season and year. We ran a multinomial logistic regression in Systat 13 to assess

whether these predictors significantly affected the status and report the global summary of the effect of each predictor on the probability of occurrence of each status.

Potential predictors of the minimum number of hippos at 14 monitoring locations included the fixed effects of water quality (salinity and aerobic bacterial load), the state of the water at monitoring locations (scored in the four categories defined above), water flow (scored in the three categories defined above), the month, the year and the identity of the location. For monitoring locations which were not directly water-sampled, values of salinity, total aerobic bacteria load and water flow were assigned from the nearest water sampling point to them.

We selected a negative binomial regression model, after an initial fit with a fixed-effects Poisson regression model demonstrated substantial over-dispersion, since the residual scaled deviance was an order of magnitude larger than the residual degrees of freedom (e.g. [31]). The negative binomial regression model substantially reduced dispersion in this respect (dispersion parameter  $\sigma = 0.27$ ). We fitted a mixed-effects zero-inflated negative binomial regression in order to account for the fact that counts were repeated at the same location and because a substantial number of counts observed an absence of hippos. The mixed-effects zero-inflated negative binomial regression was fitted by applying the function `gamlssNP` from package `gamlss` version 4.3-2 plus complement package `gamlss.mx` [32] in R [33]. We chose a nonparametric maximum likelihood approach in `gamlssNP` specifically designed to fit overdispersed generalized linear models and extended to generalized linear models with shared random effects which may originate from, for instance, a repeated measures structure [34, 35]. The census number for each dry season was entered as a random factor on the intercept, assuming a nonparametric discrete distribution of  $K$  intercept match points and thereby converting it essentially to a nonparametric model [31]. As recommended by [31], we varied the number of  $K$  intercept match points between  $K = 1$  and  $K = 5$  and chose the model with the lowest AIC (see below), which was the model with  $K = 1$ . We also calculated  $\rho$ , the proportion of the total variance explained by the random effect, as  $\rho = \sigma^2 / (1 + \sigma^2)$  where  $\sigma$  is the dispersion parameter [31]. Total sample size was  $n = 182$  counts.

The total number of hippos counted within the study area during a census was analysed with a standard negative binomial regression model. Predictor variables included the number of monitoring locations censused and the year of observations. We checked for autocorrelation

of residuals  $\lambda$  using function `acf` in R [32] to check for independence of data points. Lag 1 (immediate neighbour) data points showed a marginally significant level of  $\lambda$  of 0.433. In order to assess the consequences for testing the significance of predictor variables, we followed Cerioli's approach [36], divided the difference between the log-likelihoods of the full and the reduced models (see below) by  $(1+\lambda)$  and then re-calculated the p-values. This correction had no effect on the significance of the p values for the predictor variables, so we are reasonably confident that the outcome of this model is sufficiently robust. The negative binomial regression was fitted by applying function `glm.nb` from package MASS version 7.3-43 [37] in R [33].

Potential predictors of the chance of encountering females, infants or juveniles in a group of hippos included the year (2012 or 2013), the stage of the dry season and the state of the water at monitoring locations. We ran a mixed-model binary logistic regression, with the census number for each monitoring location entered as a random factor on the intercept, for those data points when there was at least one hippo observed at a monitoring location ( $n = 86$ ). This was therefore a subset of the data used to predict the minimum number of hippos at each monitoring location. Given the reduced sample size, we focused on predictors relating to the expanse of water at monitoring locations, the progression of the dry season (early, i.e. June to August, versus late, i.e. September to November) and the year of census (2012 versus 2013). The mixed-effects binary logistic regression was fitted by applying function `glmer` from package lme4 version 1.1-8 [38] in R [33].

We used log-likelihood ratio tests (G-tests) and information criteria (the Akaike Information Criterion [AIC], the quasi-likelihood Information Criterion [AIC<sub>qh</sub>] introduced by Hannan and Quinn [39] and Raftery's Bayesian Information Criterion [BIC<sub>R</sub>]) to check whether the final model was superior to an intercept-only or a reduced model. Models were considered similar if differences in AIC were less than 2.5 and preferable if the difference exceeded 6.0 [40], similar if differences in BIC<sub>R</sub> were less than 2.0, preferable if values of BIC<sub>R</sub> varied between 2.01 and 6.0, and strongly preferable if values of BIC<sub>R</sub> differed by more than 6 (A. Raftery in [31], p73). As the evaluation of our models with both Akaike and Bayesian information criteria produced similar conclusions, we report only AIC values. We also report the AIC<sub>qh</sub> values, since they can be of interest in the case of substantial dispersion and were developed in the context of correlated data. The significance threshold of these tests was fixed at 5%. All tests were two-tailed, except for the test on the direction of movements of

hippos encountered in transects, where because of the results on changes in the expanse of water at monitoring locations (Table 1) we expected hippos to be more likely to move upstream.

The significance of each fixed-effects predictor variable was assessed as the marginal contribution of each parameter to the full model by subtracting from the full model the log-likelihood of a second model with each specific fixed effects predictor removed and testing the difference against a chi-square distribution with the appropriate degrees of freedoms (see discussions in [31, 41]).

Means are reported  $\pm$  standard error of the mean. Statistical tests were performed using SPSS Statistics for Windows version 21.0 (IBM Corp, Armonk, NY; USA), Systat version 13 (Systat Software Inc., Richmond, VA, USA) and R version 3.2.2 [33].

The map in Fig. 1 was created using Esri ArcGIS Desktop, ArcGIS release 10.3.1. (Environmental Systems Research Institute, Redlands, California, USA) and included a modified outline of the rivers derived from "Diva-GIS" [42] and a modified outline of the border of the National Park derived from "The World Database on Protected Areas" (WDPA) [43].

#### *Ethics Statement*

The Tanzanian Commission of Science and Technology, the Tanzania Wildlife Research Institute approved the research and the Tanzania National Parks granted permission to conduct research in Ruaha National Park. The work was also approved by the Internal Ethics Committee of the Leibniz Institute for Zoo and Wildlife Research (IZW), Approval No. 2011-04-02.

#### **Results**

The expanse of water (state) of monitoring locations was significantly associated with the topographic gradient, the progression of the dry season and significantly varied between years (multinomial logistic regression, log-likelihood ratio test, test statistic = 242.25,  $n = 289$ ,  $p < 0.00001$ ): locations along the upstream (south-westerly) section of the GRR with the steep topographic gradient were significantly more likely to be categorised as "large" in terms of the expanse of water than those along the downstream (north-easterly) section of the river with the flat gradient. As the dry season progressed, the chance of a monitoring

location being in the states of “large” or “moderate” significantly decreased and being in the states of “shallow” or “dry” significantly increased. In 2013, monitoring locations were significantly less likely to be “large” and “shallow” and significantly more likely to be “moderate” and “dry”, suggesting that larger and smaller expanses of water shrank in a consistent manner from 2012 to 2013.

The mean minimum number of hippos counted (termed hereafter mean hippo counts) per monitoring location across both seasons was  $10.5 \pm 1.3$  hippos (range 0 to 95,  $n = 207$  counts),  $13.3 \pm 2.1$  (range 0 to 95,  $n = 97$  counts) in 2012 and  $8.1 \pm 1.6$  hippos (range 0 to 80,  $n = 110$  counts) in 2013.

#### *Changes in hippo distribution between the early and late dry season*

Hippos occurred at more monitoring locations during the early than late dry season in both study years and the general overall trend was for hippos to move from downstream locations on the GRR to those upstream (Fig. 2). The highest mean hippo counts were at locations 1 and 4 in the upstream section of the river in the late dry season period of 2012 and at location 1 in the late dry season of 2013. In 2013, both the early and late dry season mean hippo counts at location 4 were well below those at this location in 2012. In 2013, the early and late mean hippo counts at the downstream location 9 were similar, and both these counts were higher than those in 2012 (Fig. 2). In 2013, the mean hippo count during the early dry season at downstream location 12 was relatively high but the mean late dry season count was only 0.25 animals, even though it was 24 animals in the late dry season of 2012.

A more detailed monthly examination (Fig. 3) of changes in mean hippo counts at the two upstream locations 1 and 4 (Fig. 1) and the two downstream locations 9 and 11 (Fig. 1) revealed considerable changes in the mean hippo counts observed at these locations throughout the 2012 and 2013 dry seasons. At location 1, the mean hippo count was at its lowest (17 animals) in June 2012; counts increased throughout the dry season reaching the highest mean count (95 animals) in November. In contrast, at this location in 2013, the highest hippo count occurred in September (74 animals) and then declined. At location 4 in 2012, the mean hippo count increased in August and remained at roughly the same level until November. Between August and October mean hippo counts were generally lower in 2013 than in 2012. Apart from a single individual, all hippos had vacated location 9 by September 2012, whereas in 2013 mean hippo counts at this location in August and

September were 40 animals and 54 animals respectively. No hippos were observed at location 9 in November in either dry season. Location 11 was typical of several downstream sites where a limited and changing number of hippos were counted in the early months of the dry season, but only single (presumably territorial bulls) remained there during the last months of the dry season.

#### *Factors influencing the number of hippos and the composition of hippo groups at monitoring locations*

The minimum number of hippos per monitoring location significantly changed with its expanse of water (status), significantly differed between the 14 monitoring locations and significantly increased with the progression of the dry season (mixed-model zero-inflated negative binomial regression, log-likelihood ratio test = 201.6, df = 20,  $p < 0.00001$ ,  $n = 182$ , Table 2). Salinity, total aerobic bacterial load, water flow and year had no influence on the minimum number of hippos counted at monitoring locations (Table 2). The proportion  $\rho$  of 0.068, the contribution of the random effect (census number), explained a modest amount of the total variance.

The likelihood of groups of hippos containing infants, juveniles and/or females significantly increased with the state of the water expanse per monitoring location, improving from “shallow” via “medium” to “large” (mixed-model binary logistic regression, log-likelihood ratio test = 16.691, df = 4,  $n = 86$ ,  $p = 0.0022$ , Table 3), and was independent of the year and the stage of the dry season (Table 3).

#### *Camera trap records*

We obtained 78 and 83 independent hippo camera trapping events in 2012 and 2013, respectively. Hippos were captured at most (6 of 7) camera trap positions along the GRR and only few (2 of 7) camera traps positioned at water sources away from the GRR (non-GRR positions, Table 4). No hippo cows or immature hippos were detected by camera traps at the furthest downstream camera traps (G and F) on the GRR from September to November in both study years (Table 4). Hippo cows with infants and/or juveniles were recorded by camera trap positions A, B, D and E throughout both dry seasons. At position C a single hippo bull was detected in September 2012. Camera traps at non-GRR positions only captured solitary males. The two non-GRR positions furthest away from the GRR (L and N, Fig. 1) were located at a distance of 3 km and 5.7 km from the GRR.

### *Transects*

Twenty five hippos were recorded on land during daytime transects (Table 5). All were sighted along the GRR either as solitary animals or in small groups, with a mean group size of  $4.4 \pm 1.9$ . All groups for which a direction of movements could be clearly identified were walking upstream in the dry river bed, a result unlikely to be a consequence of chance alone (Wilcoxon signed-ranks test,  $W = 15.0$ , exact  $p = 0.031$ , one-tailed). Such daytime movements of hippos were not observed in the early dry season in June. One larger group of 12 animals was observed moving upstream in October 2012. Hippos were not seen on any transects leading away from the GRR.

### *Mortality*

Of nine cases of observed mortality, six occurred in 2012 and three in 2013. Mortality in three adult hippo bulls on 15th September 2012, 7th October 2012 and 8th August 2013 were attributed to intraspecific aggression based on the nature of the severe wounds on the carcasses or observed intense intraspecific aggression. Three juveniles died without signs of external wounds on 27th August 2012, 1st November 2012 and 21st August 2013, respectively. Lion predation of one calf was recorded on 28th August 2012, one adult most likely died from malnutrition on 25th September 2012, and one adult died of unknown causes on 23rd July 2013.

### *Minimum population size of hippos*

If we assume that the distribution of hippos in the 14 monitoring locations did not change substantially between counts on different days along the three censusing sections of the GRR during each census, then the sum of the minimum numbers counted per location across these sections provides an approximate estimate of the hippo population along the monitored section of the GRR (Fig. 1). The highest number of hippos observed during a census was 216 in 2012 and 152 in 2013. The total minimum number of hippos per census significantly increased (negative binomial regression, overall model, log-likelihood ratio test, test statistic = 22.167,  $df = 2$ ,  $p = 0.000015$ ,  $p$  adjusted for autocorrelation = 0.00044, Fig. 4) with the number of monitoring locations at which hippos were counted during any one census (log-likelihood ratio test, test statistic = 20.115,  $df = 1$ ,  $p = 0.0000073$ ,  $p$  adjusted for autocorrelation = 0.00018) and was significantly higher during 2012 than 2013 (log-

likelihood ratio test, test statistic = 8.170, df = 1 p = 0.0043, p adjusted for autocorrelation = 0.017).

## Discussion

Our results revealed that, in both study years, an estimated population of between 152 and 216 hippos were more dispersed during the early than the late dry season (Fig. 2) along the GRR in the Ruaha NP (Fig. 1). As the dry season progressed, the incidence of water flow and the availability of surface water in the GRR declined (Table 1), hippos abandoned unsuitable daytime resting locations and moved to other, more suitable ones (Table 2, Fig. 3). This resulted in the congregation of hippos in relatively large numbers in a few locations (Fig. 2), with the highest mean counts recorded at location 1 at the end of the dry season in November 2012 (Fig. 3), at the upstream end of the study area (Fig. 1). The results of our model (Table 2) revealed that minimum hippo numbers per monitoring location on the GRR increased with the progression of the dry season and were significantly higher as the expanse of available surface water per monitoring location increased. Groups of hippos were more likely to contain infants, juveniles and/or females, regardless of the year or stage of the dry season, as the expanse of water per monitoring location increased (Table 3). Consistent with the finding of studies on other hippo populations in Africa [8, 17, 44, 45] our results indicate that when water dries up at a resting location, hippos move to a more suitable one. The availability of suitable daytime resting locations along the GRR declined during the dry season, particularly in the downstream section, causing hippos to congregate in a relatively limited number of locations, the majority of which were located in the upstream section of the river (Fig. 2). During both dry seasons, the downstream section of the GRR contained extensive sections of dry riverbed or relatively small isolated pools of water [25] which, if not empty, were mostly occupied by solitary male hippos (Table 4). We expected hippos to prefer locations with better water quality, in terms of water flow, lower salinity and total aerobic bacterial load, but found no evidence for this (Table 2).

There were significant differences between minimum hippo numbers per monitoring location in 2012 and 2013 (Table 2). We speculate that this difference between years may be explained by more hippos in 2013 moving to locations further upstream of location 1 (Fig. 1) and hence outside our study area than in 2012. In 2012, the largest aggregation of hippos was recorded at location 1 at the end of the dry season in October and November (Fig. 3),

whereas in 2013, the peak count at this location occurred in September, and then counts declined in both October and November, suggesting movement of hippos further upstream. This idea is consistent with more monitoring locations in 2013 having few or no hippos than in 2012 (Fig. 2), which suggests that during the 2013 dry season more daytime resting locations were unsuitable for moderate to large herds of hippos than in 2012, and hence were responsible for the smaller estimated total number of hippos in the study area in 2013 than 2012 (Fig. 4). Our sightings of hippo groups only walking upstream (Table 5) during daylight hours is also consistent with our suggestion that hippos searching for daytime resting sites predominantly move upstream.

We present several lines of evidence (hippo censuses, transect data, camera trap data) that the vast majority of hippos in our large study area depended on the GRR for their day resting locations, and that location 1 was important for a large number of animals during the late dry season. Our camera trapping data revealed that only a few solitary males occurred at water sources away from the GRR during the dry season.

Our limited results on hippo mortality are consistent with our expectation that intra-specific aggression is a mortality factor during the dry season. Although 2013 was apparently a less favourable year for hippos than 2012, we detected fewer cases of mortality in 2013 than 2012. We suggest that this may be due to fewer hippos remaining in our study area throughout the late dry season of 2013 because many probably moved upstream and beyond our study area, hence reducing our chance of observing mortality. Hippos in large aggregations and those forced to move during daylight hours to find daytime resting sites are likely to experience elevated levels of physiological stress [17, 19, 46] and the possible negative consequences this might have on immune processes may be compounded by increased feeding competition at night, particularly in females that have to increase nutrient intake to fulfil the high nutritional demands of pregnancy and lactation [47-49]. Although disease transmission can be facilitated by high host densities we found no evidence of this during our relatively short-term study. We observed three incidences of hippos mating in the GRR in June and July (personal obs), which is also consistent with the idea that oestrus can occur during the dry season and hence oestrus females forced to use daytime resting locations outside their normal range may be particularly vulnerable to sexual harassment.

We speculate that the scale of changes in hippo daytime resting locations revealed by our study is likely to be more extreme, in terms of the numbers of relocations undertaken by

hippos and the distances travelled to alternative locations, than those before the significant reduction in the GRR dry season flow since 1993, attributed to large-scale water extraction for agriculture, upstream of the Ruaha NP [24]. Females with wet season ranges in the furthest downstream section of our study area are likely to have relocated by at least 80 km by the end of the dry season. Females and their offspring probably move upstream from one localised source of water to another, until they eventually reach a more permanent site such as location 1. Even so, in some years, may have to move even further upstream, as indicated by our results from 2013.

Are these changes likely to have negative consequences for the hippo population? To what extent is the resilience and long-term prospect of the hippo population compromised if human water extraction continues at current levels, or increases with human population growth? As in so many conservation issues, data prior to the start of this anthropogenic change are, to our knowledge, not available, hence assessing the scale of its impact is problematic. We approach this issue by considering some evidence that allows us to estimate what proportion of the entire hippo population of the Ruaha ecosystem (approximately 45,000 km<sup>2</sup>) resides in Ruaha NP, and in our study area, and look at the results of previous aerial transect surveys of the wildlife populations of the Greater Ruaha ecosystem. Previous 'counts' of hippos in the Greater Ruaha ecosystem were a by-product of dry season aerial transect surveys of large mammals conducted in 1993, 1999, 2002, 2006 and 2009 [27, 28]. Although these surveys were not at all suited to provide reliable quantitative estimates of population size (and thus are not really suitable to indicate population trends), they provide at least an index of the distribution of the hippo population. They indicate that during the dry season more than 90 % of the entire hippo population of the Greater Ruaha ecosystem appeared to be restricted to the GRR inside the National Park (e.g. the dry season survey in October 2009, [28]).

One of the main threats to hippos is habitat loss caused by humans (e.g. [5-7]). The results of our study indicate that human extraction of water from the GRR is changing the distribution of the hippo population within Ruaha NP. As a considerable part of the GRR within our study area dried out towards the end of dry season [25], this represented an extensive loss of dry season habitat for the hippo population in Ruaha NP. The resilience of the hippo population to these changes is currently unknown, but requires investigation.

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**Table 1.** Multinomial logistic regression of predictors affecting the chance of a change in the expanse of water at monitoring locations.

Predictor	Direction of effect on chance of expanse of water being in a given state*				df	G	p	AIC	$\Delta$ AIC	AIC <sub>qh</sub>	$\Delta$ AIC <sub>qh</sub>
	dry	shallow	moderate	large							
Year	-0.032	0.030	-0.118	0.120	3	11.593	0.0089	433.70	5.59	1.575	-0.029
	2012 < 2013	2012 > 2013	2012 < 2013	2012 > 2013							
Topographic gradient	-0.024	-0.120	-0.348	0.492	3	130.348	< 0.00001	552.45	124.35	1.986	0.382
	steep < flat	steep < flat	steep < flat	steep > flat							
Month of dry season	0.022	0.049	-0.035	-0.037	3	117.211	< 0.00001	539.31	111.21	1.941	0.336
	↑ as dry season progresses	↑ as dry season progresses	↓ as dry season progresses	↓ as dry season progresses							

Tests for significance of each parameter used log-likelihood ratio tests (G) with associated degrees of freedom (df) and p-values (p). Values for the Akaike Information Criterion (AIC) and the quasi-likelihood information criterion (AIC<sub>qh</sub>) and the respective differences to the full model ( $\Delta$ AIC,  $\Delta$ AIC<sub>qh</sub>) are shown for each alternative model when the specific predictor was removed. For the full model, AIC was 428.10 and AIC<sub>qh</sub> was 1.605.

\* Global change of the probability of each of the four states of the expanse of water in response to a change in the value of each predictor variable. The sum of the values for each predictor is 0, as an increase in the probability in one state must be compensated for by a decrease in other states.

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**Table 2** Mixed-model zero-inflated negative binomial regression of predictors affecting the minimum number of hippos per location.

Predictor	Estimate	SE	df	G	P	AIC	ΔAIC	AIC <sub>qh</sub>	ΔAIC <sub>qh</sub>
Intercept	700	396.3		1.766 <sup>a</sup>	0.079	916.59 <sup>b</sup>	158.82	5.039 <sup>b</sup>	0.301
Census number (random effect, intercept)	0.144	0.195		0.736 <sup>a,b</sup>	0.46				
State of water at location: shallow < moderate ≈ large									
shallow	-4.002	-4.002	2	29.959	<0.00001	783.73	25.96	4.812	0.074
moderate	-0.459	-0.459							
Water flow: (flowing ≥ stagnant)	0.320	0.400	1	0.741	0.39	756.51	-1.26	4.696	-0.042
Salinity	0.003	0.002	1	3.016	0.082	758.78	1.02	4.709	-0.029
Total aerobic bacterial load	-0.00008	0.0005	1	0.054	0.82	755.82	-1.95	4.693	-0.045
Month of dry season (linear trend)	0.270	0.150	1	4.134	0.042	759.90	2.13	4.715	-0.023
Square of the month of dry season (quadratic trend)	-0.024	0.013	1	4.076	0.043	759.84	2.07	4.715	-0.023
Year: (2013 ≤ 2012)	-0.347	0.197	1	2.406	0.12	758.17	0.40	4.706	-0.032
Monitoring location along the river (see Fig. 1)									
1* (steep)	1.130	0.520	13	134.1	<0.00001	865.88	108.11	4.927	0.189
2* (steep)	-5.225	1.119							
3* (steep)	-1.723	0.488							
4	0.264	0.508							
5* (steep)	-2.6 * 10 <sup>16</sup>	2.1 * 10 <sup>15</sup>							
6	-0.088	1.128							
7	0.159	0.496							
9	0.604	0.321							
10* (flat)	-3.523	0.856							
11	0.562	0.684							
12	0.827	0.596							
13	-0.536	0.664							
14* (flat)	-3.678	1.091							

Shown are regression coefficients (estimates) and standard errors (SE) of predictors in natural log-units (logits). Positive (negative)

### Chapter 3

estimates indicate that an increase in the value of the predictor increased (reduced) the minimum number of hippos. Tests for significance of each parameter used log-likelihood ratio tests (G) with associated degrees of freedom (df) and p-values (p). Values for the Akaike Information Criterion (AIC) and the quasi-likelihood information criterion ( $AIC_{qh}$ ) and the respective differences to the full model ( $\Delta AIC$ ,  $\Delta AIC_{qh}$ ) for each reduced model are shown when the specific predictor was removed. For the full model, AIC was 757.77 and  $AIC_{qh}$  was 4.738.

<sup>a</sup> based on Wald tests (z-values = estimate/SE and their associated p-values); <sup>b</sup> intercept-only model \* significantly different from the reference monitoring location ("8", Fig. 1)

**Table 3** Mixed-model binary logistic regression of predictors affecting the likelihood of encountering females and calves per monitoring location.

Predictor	Estimate	SE	df	G	P	AIC	$\Delta$ AIC	AIC <sub>qh</sub>	$\Delta$ AIC <sub>qh</sub>
Intercept	-1.230	1.346		-0.914 <sup>a</sup>	0.36	73.51 <sup>b</sup>	8.69	0.840	-0.024
Census number (random effect, intercept)	1.819	0.311		5.846 <sup>a,b</sup>	<0.00001				
State of water at location: large > moderate $\geq$ shallow									
Moderate	2.706	1.521	2	14.144	0.00085	74.96	10.14	0.908	0.043
Large	4.916	1.699							
Year: (2013 > 2012)	1.421	0.895	1	3.048	0.081	65.87	1.05	0.836	-0.027
Season: (early [Jun to August] $\leq$ late [September to November])	-1.056	0.882	1	1.623	0.20	64.44	-0.38	0.820	-0.044

Shown are the regression coefficients (estimates) and their standard errors (SE) of predictors in natural log-units (logits). Positive (negative) estimates indicate that an increase in the value of the predictor increased (reduced) the likelihood of encountering females and calves per monitoring location. Tests for significance of each parameter used log-likelihood ratio tests (G) with associated degrees of freedom (df) and p-values (p). Values for the Akaike Information Criterion (AIC) and the quasi-likelihood information criterion (AIC<sub>qh</sub>) and the respective differences to the full model ( $\Delta$ AIC,  $\Delta$ AIC<sub>qh</sub>) are shown for each alternative model when the specific predictor was removed. For the full model, AIC was 64.82, AIC<sub>qh</sub> was 0.864.

<sup>a</sup> based on Wald tests (z-values = estimate/SE and their associated p-values); <sup>b</sup> intercept-only model

**Table 4** Independent camera trapping events of hippos at monitoring locations during the dry season in 2012 and 2013.

Year Month Cameratrap position (site)	2012						2013					
	JUN	JUL	AUG	SEP	OCT	NOV	JUN	JUL	AUG	SEP	OCT	NOV
A (GRR)	-	-	-	2,3,1,4	1	2,3,1,4	0	2,3	0	2,1,3	2,3	-
B (GRR)	-	-	-	2,4	0	2,3,	0	2,1,3,4	0	0	0	-
C (GRR)	-	-	-	1	0	2,	0	0	0	0	0	-
D (GRR)	-	-	-	0	0	2,1,	4	0	0	0	2,3	-
E (GRR)	-	-	-	1	2,1	2,3,4	2,1,4,	2,3	2,1,3	2,1,4,	2,1	-
F (GRR)	-	-	-	0	0	0	1,	0	0	0	0	-
G (GRR)	-	-	-	0	1	2,1	2,4	0	0	0	0	-
H (Non-GRR)	-	-	0	0	0	-	-	0	0	-	0	0
I (Non-GRR)	-	-	0	0	0	-	-	0	0	-	0	0
J (Non-GRR)	-	-	0	0	0	-	-	0	0	-	0	0
K (Non-GRR)	-	-	0	0	0	-	-	0	0	-	0	0
L (Non-GRR)	-	-	0	0	0	-	-	1	1	-	0	1
M (Non-GRR)	-	-	0	0	0	-	-	0	0	-	0	0
N (Non-GRR)	-	-	1	0	0	-	-	1	0	-	0	0

Numbers indicate the sex and number of animals captured if a camera trap was activated (dash: no camera trap activated): 0 = 0 hippos; 1 = single adult male; 2 = single adult female or single adult unknown; 3 = at least one immature with one or more adults; 4 = more than one adult.

GRR: location at Great Ruaha River; Non-GRR: location at water sources away from the river

**Table 5** Observations of hippos on land during transects along the Great Ruaha River.

<b>Site (closest monitoring location)</b>	<b>Date</b>	<b>Time</b>	<b>Number of individuals</b>	<b>Adults</b>	<b>Juveniles</b>	<b>Special observation</b>
3	06 Jun 2012	8:35	2	2	0	-
11	12 Sep 2012	8:28	1	1	0	walk upstream
13	12 Oct 2012	8:55	12	9	3	walk upstream
12	12 Oct 2012	9:06	3	2	1	walk upstream
11	15 Jul 2013	8:20	2	2	0	walk upstream
8	05 Aug 2013	7:02	1	1	0	-
2	12 Aug 2013	8:36	1	1	0	-
13	30 Oct 2013	8:29	3	2	1	walk upstream

### Figure legends

**Figure 1** The Ruaha National Park in central Tanzania with the study area in the east (grey square frame). Monitoring locations (circles) were located along the Great Ruaha River (GRR, sites 1-14). The camera traps (black square boxes) were located along the GRR (A-G) and at non-GRR water sources, sites (H-N). The map was created using ArcGIS and includes a modified outline of rivers derived from “Diva-GIS” [42] and a modified outline of the border of the National Park derived from “The World Database on Protected Areas” [43].

**Figure 2** The mean minimum number of hippos at 14 monitoring locations along the Great Ruaha River, during the early dry season (June to August in light grey) and late dry season (September to November in dark grey) in (a) 2012 and (b) 2013. Locations 1-7 were defined as upstream and location 8 -14 as downstream sections of the river. Thin black lines at zero on the x-axis indicate a mean minimum count of zero hippos at the location, an absence of a line or bar indicates that the location was not monitored.

**Figure 3** Mean minimum number (per month) of hippos during the (a) 2012 and (b) 2013 dry season (June to November) at monitoring locations 1 and 4 (upstream) and 9 and 11 (downstream) along the Great Ruaha River. A thin black line at zero on the x-axis indicates a count of zero hippos at the monitoring location, an absence of a line or bar indicates that no records were available from the monitoring location in that month.

**Figure 4** Minimum total numbers of hippos along the Great Ruaha River as a function of the number of hippo pools counted during the dry season 2012 and the dry season of 2013. Dashed (for 2012 crosses) and dotted (for 2013 squares) are the regression lines from the negative binomial model.

Figure 1

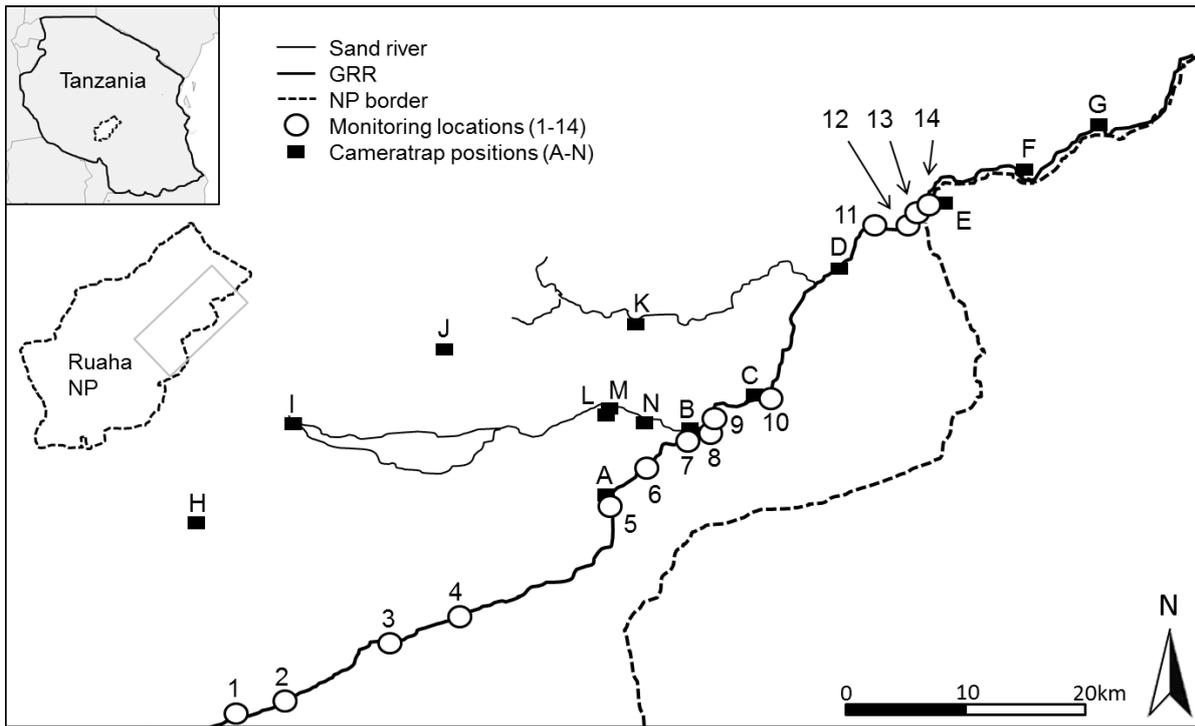


Figure 2

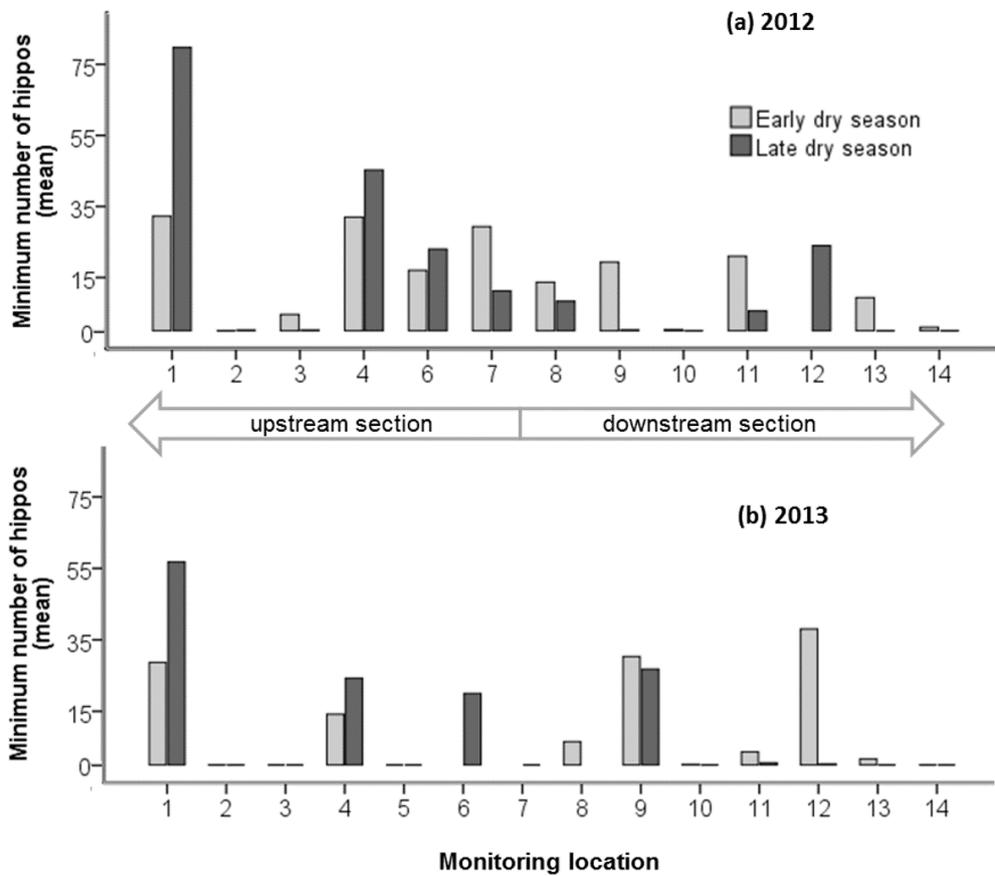


Figure 3

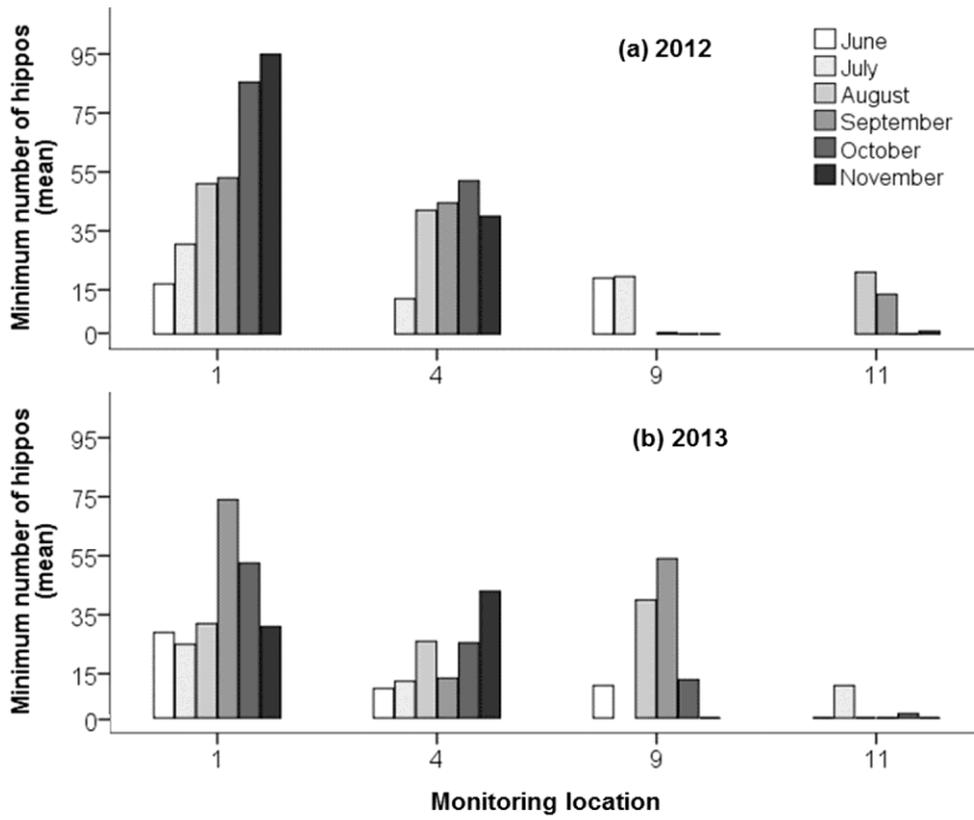
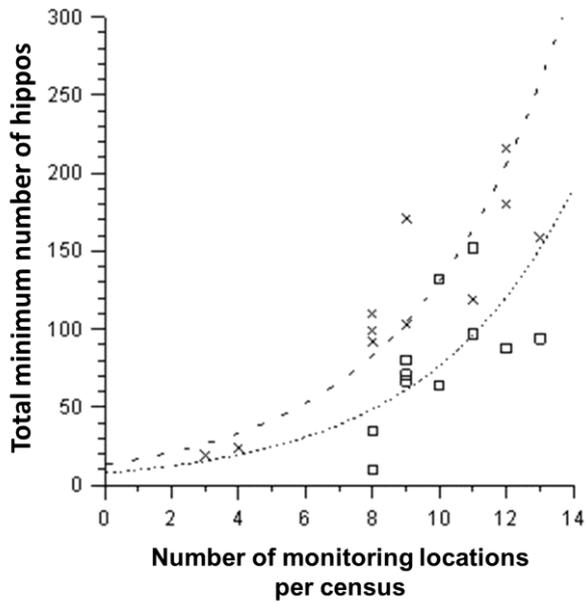


Figure 4



## Chapter 4

### Manuscript 3

#### **Spatio-temporal changes in the dry season distribution of herbivores in a semi-arid habitat**

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#### **Author Contributions:**

CS and ME developed the original idea. CS established Logistics and conducted fieldwork. CS and SKS analysed the data. CS, HH, ME and SKS wrote the manuscript.

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## **Abstract**

The distribution of wildlife species in relation to sources of surface water is expected to be determined by their daily water requirements, which in turn is influenced by physiological and dietary needs, their digestive system plus the water content of ingested food. In the Ruaha National Park (NP), surface water in large sections of the formally perennial Great Ruaha River (GRR) is substantially reduced or absent during the dry season. I investigated how this change in the distribution of surface water affected the spatio-temporal distribution of the nine most important larger mammalian herbivores. During three dry seasons (2011-2013), herbivores were monitored twice a month along 10 ground transects. The presence of surface water was also monitored along a 104 km section of the GRR and at other locations. The distance to the nearest surface water was analysed using a generalised linear mixed-effects model, and changes in the distribution of species were visualised. My results showed that (i) grazers (buffalo, waterbuck and zebra) maintained the shortest distance to surface water; (ii) mixed feeders, which both graze and browse (impala, elephant), and browsers (giraffe, kudu) maintained intermediate distances to water; (iii) omnivores (warthog, common duiker) were found at the largest distances to surface water. Buffalo remained a short distance to surface water by vacating areas without surface water and those with small pools and moving upstream to areas of the GRR with larger stretches of surface water. The movement of zebras and waterbuck upstream was less pronounced as they continued to utilise small, shrinking sources of water in the downstream stretch. As the GRR is the main source of surface water in the park, our results highlight the importance of this river for the majority of the larger mammalian herbivores. Habitats too distant from surface water were vacated, particularly those in the drier downstream section of the GRR. Restoration of the GRR dry season flow would reduce the substantial loss of habitat for several herbivores during the dry season.

## Introduction

Although the presence of surface water is a key resource determining the distribution and abundance of species (e.g. Western 1975, Thrash et al. 1995, Owen-Smith 1996, Redfern et al. 2003), the effects of human induced water scarcity on the distribution of mammals have rarely been studied. Seasonal changes in water availability are known to severely affect the spatio-temporal distribution of many mammal species (e.g. Western, 1975), particularly those with physiological and dietary needs that require the regular intake of water. In climatic zones experiencing dry seasons in which little or no precipitation occurs for several months, ephemeral pools and rivers dry out and the water flow in permanent rivers declines (e.g. Stommel et al. 2016a). When these conditions prevail, water dependent herbivores typically remain close to sources of surface water (Redfern et al. 2003), which can prevent the use of foraging areas that are too far away from water sources. This in turn can lead to an aggregation of animals in a few places followed by overexploitation and degradation of foraging areas near water sources. For instance, in the Amboseli ecosystem (Kenya) during the dry season 99 % of the herbivore biomass occurs within 15 km of surface water, an area representing only 52 % of the ecosystem (Western 1975). The 'piosphere' is the area negatively influenced by an increasing gradient of grazing, browsing and trampling towards a water point used by animals to drink (Andrew 1988) and this influence can be sufficiently severe to cause herbivores to extend their range in order to obtain sufficient forage (Redfern et al. 2003).

The water requirements of mammal species are strongly influenced by basal metabolic rates, diet, digestive system, body size and activity patterns (Robbins 1993) and therefore species vary considerably in the distance they need to maintain to accessible surface water source (Western 1975, Redfern et al. 2003, Redfern et al. 2005). In terms of digestion, all hindgut fermenters such as the plains zebra (*Equus quagga*) with a high throughput of food generally lose more water via faeces than most ruminants (Cain et al. 2012). In terms of diet, grazers are generally considered more water dependent than browsers because in the dry season the moisture content of grasses is less than that of browse (Western 1975). The greater kudu (*Strepsiceros zambesiensis*), which is a browser, can survive without water if the food they consume contains sufficient moisture (Owen-Smith 2013). As a consequence of their behavioural adaptations, warthogs (*Phacochoerus africanus*) have the ability to remain in dry areas without surface water because they can reduce water loss by sheltering

in burrows when daytime temperatures are extreme and dig waterholes in dry riverbeds to obtain access to water close to the surface (Stommel et al. 2016a). Relatively few species are independent of surface water sources. The common duiker (*Sylvicapra grimmia*) is one African species with both physiological and behavioural adaptations to dry environments such as the production of highly concentrated urine and the re-absorption of water from faecal material in the colon before it is voided. Additionally, it has an opportunistic diet that includes eggs and fruits (Wilson 2013) which is also thought to aid survival without surface water.

Human population growth and its associated increased demand for water (Roberts 2011) plus projected climate change (Chen and Georgakakos 2015, Rowell et al. 2015) is expected to have a detrimental impact on permanent water resources in East Africa and hence the wildlife populations that depend on them. In the Ruaha National Park (NP), in central Tanzania, current levels of water extraction from the Great Ruaha River (GRR) upstream of the park are thought to be responsible for a substantial decline in flow and the drying out of the formerly perennial GRR during the dry season (Mtahiko et al. 2006).

This study aims to determine the vulnerability of the most important larger mammalian herbivores to the projected decline in the dry season availability of surface water in the Ruaha NP during the coming decades. Here we determine the distance grazers, browsers, mixed feeders and omnivores maintained to the nearest source of surface water and compare the spatial distribution of nine species during the early and late dry season. We hypothesise that if diet is a key determinant of water requirements then: (i) grazers should maintain a closer distance to surface water during the dry season than browsers; (ii) both grazers and browsers should remain closer distances to surface water than omnivores. As a result of variation in dependence on surface water we also expect greater changes in the spatial distribution of grazers and browsers than in omnivores during the dry season.

### **Methods**

#### *Study site*

The study was conducted in Ruaha NP in central Tanzania (Fig. 1) (for details see Stommel et al. (2016a)). The spatial and temporal dry season distribution of surface water during the years of this study (2011-2013) was generally similar, although there were some differences between years (Stommel et al. 2016a, 2016b). At the beginning of dry season (June) water

was present in depressions filled by rain, at discrete locations in dry seasonal riverbeds, at a few springs and in the Great Ruaha River (GRR), where it covered the entire river bed and flowed along the entire stretch contained within the National Park. During the dry season, a few non-GRR water sources persisted throughout but all water-filled depressions dried out quickly, the smaller ones faster than the larger ones (see Fig. 1). In the GRR, water level decreased throughout the dry season, the river water stopped flowing by the end of August, and by September the first stretches of the riverbed were dry along the furthest downstream section in the northeast of the National Park (Fig. 1), except for a few drying scattered pools. The riverbed continued to dry out and surface water continued to decline so that by October most of the downstream section of the GRR was dry, apart from a few pools.

#### *Data collection*

Mammalian herbivore distributions were regularly monitored during the dry season (twice a month in June-October and once in November) during the three years of 2011 to 2013 using ground transects (hereafter called transects) along existing game viewing roads (Fig. 1), each approximately 20 km ( $19880 \text{ m} \pm 115.3 \text{ m}$  [SEM]) in length, including five transects along the GRR, the “GRR transects”, and five leading away from the GRR, the “non-GRR transects” (Fig. 1). Most data were collected between 07:00 and 11:00 hours in the morning. For each sighting of an individual animal or a group, the GPS coordinates, the perpendicular distance of the animal or the group to the transect and the number of individuals seen was recorded. To avoid any bias linked to the possibly varying probability of detecting an animal in different habitat types, we used only the observations located within 100 m of each transect. The distribution of available surface water was monitored from the beginning to the end of the dry season as detailed by Stommel et al. (2016a). We measured the Euclidean distances from all sightings to the next available water source (hereafter distance to water), using the statistical software package R version 3.3.1 (R Core Team 2016) and ArcGIS version 10.3.1 (ESRI Inc., Redlands, CA, USA). The global position system (GPS) coordinates of an animal sighting was collected at the car position on the transect, resulting in a maximum bias of  $\pm 100 \text{ m}$ , as this was the maximum distance of animal sightings right and left from the transect. We focused on the following nine most numerous large mammalian herbivores observed within the study area, including the grazers African buffalo (*Syncerus caffer*),

waterbuck (*Kobus ellipsiprymnus*), plains zebra, the browsers Masai giraffe (*Giraffa tippelskirchi*) and greater kudu (hereafter kudu), the mixed feeders impala (*Aepyceros melampus*) and elephant (*Loxodonta africana*), and the omnivores warthog and common duiker (hereafter duiker). Results for hippopotamus (*Hippopotamus amphibious*) were published in a separate study (Stommel et al. 2016b).

The changes in spatial distribution during the dry season were visualised using maps of the study area, by showing the distribution for each species during the early dry season between June and August and the late dry season during September to November (Fig. 2).

### *Statistical analysis*

The following analyses were done in R version 3.3.1 (R Core Team 2016). We used a generalised linear mixed-effects model framework (GLMM) to ask how the minimum distance to the nearest available water source was related to species identity and affected by time, i.e. the progression of the dry season expressed as dry season date with day 1 set to 1<sup>st</sup> of June. Before fitting the final model, we checked for linearity by exploring the shape of the response in relation to time (dry season date) with a generalised additive model (GAM, package 'mgcv', Wood 2006). Visual inspection of the smoothed variable did not show any deviation from linearity (Fig. 3). We then fitted the GLMM with a Gamma error distribution and a log link function. As random intercept effect, we entered a unique identifier for the repetitions per transect and year. We used the function HLfit (package spaMM, Rousset and Ferdy 2014) to fit the data to the model with the fixed effects as interaction terms. Before, we had tested the significance of the fixed effects interaction term with a likelihood ratio test (LRT) by using restricted maximum likelihood estimates to compare GLMMs with the same random error structure but different fixed effect structures (additive effect of species versus interaction of species with time, i.e. dry season date, function glmer in package lme4). We also used LRT to assess the significance of the random effect and the optimal model structure for random effects. For the latter purpose we compared the fit of the model with a simple random intercept with a model where the random variables are entered both on the random intercept and the slope. Here, we compared two GLMMs with the same fixed effect structure but different random structures to a fixed effects model only using generalised least squares (GLS) following the protocol by Zuur et al. (2009). The mean for

transect length is reported  $\pm$  standard error of the mean and was obtained by using SPSS Statistics for Windows version 21.0 (IBM Corp, Armonk, NY; USA).

## Results

### *Species distribution along GRR transects and non-GRR transects*

The total counts for each dry season per species along GRR and non-GRR transects are presented in Table 1. These counts reveal that 6 of the 9 monitored species (buffalo, waterbuck, zebra, kudu, impala and elephant) occurred in higher numbers along the GRR transects than in areas away from the river. The numbers of giraffe and warthog observed were roughly similar along both GRR and non-GRR transects. Only duiker occurred predominantly along non-GRR transects.

### *Temporal changes in the spatial distribution of herbivores*

Amongst grazers, buffalos (Fig. 2: 1a) were distributed along both the downstream and upstream section of the GRR in the early dry season and often occurred in large herds of more than 300 animals. By the late dry season (Fig. 2: 1b), most buffalo had vacated the downstream section of the GRR and were mostly observed in the upstream section of the GRR along stretches of the river where surface water occurred (Fig. 2: 1a). Waterbuck were predominantly distributed along both the downstream and upstream sections of the GRR, and there was little change in the distribution of this species between the early (Fig. 2: 2a) and late (Fig. 2: 2b) dry season. Zebras were distributed along the GRR and in areas away from the river in both the early and late dry season periods (Fig. 2: 3a-b). The most important area for zebras in both the early and late dry season was the downstream section of the GRR.

Amongst browsers, giraffes (Fig. 2: 4a-b) were distributed along the GRR and in areas away from the river. There was no marked change in their distribution between early and late dry season. Kudu were distributed along the GRR and in areas away from the river during both the early and late dry season period (Fig. 2: 5a-b), with an increase in kudu along the GRR during late dry season, particularly along the downstream section of the river.

Amongst mixed feeders, impala was the most numerous species in the study area (Table 1). This species was distributed along the GRR and in areas away from the GRR during both the early and late dry season and there was little change in the overall distribution between

these two periods (Fig. 2: 6a-b). Although elephants were distributed along both the downstream and upstream section of the GRR during both the early and late dry season periods, their distribution shifted upstream during the late dry season (Fig. 2: 7b). Elephants also occurred in areas away from the GRR, in both the early and late dry season.

Amongst omnivores, warthogs (Fig. 2: 8a-b) were distributed both along the GRR and in areas away from the river, and there were no obvious changes in the distribution of this species between the early and late dry season period. Duikers (Fig. 2: 9a-b) were almost exclusively distributed in areas away from the course of the GRR, and this distribution did not alter between the early and late dry season periods.

#### *Species sightings in relation to their distance to the nearest water source*

The likelihood ratio test (LRT) to test for the optimal random structure of the model revealed a significant effect of the random intercept on model fit (Table 2, a), indicating substantial variance in response strength per repetition and year. Including a random slope did not further improve model fit (Table 2, a), indicating that response strength per repetition across transects was similar over time in that in principle the distance to the nearest water source increased over time for all species. The significant interaction term in the fixed effects structure (Table 2, b) indicated important differences between species responses.

Results of the final model (Table 3) revealed that the differences between species in the distance to the nearest water source varied substantially with the progress of the dry season (Fig. 3).

Amongst grazers, buffalo showed the weakest response and remained close to surface water, with animals sighted within a distance of 1000 m to the nearest surface water throughout the entire dry season (Fig. 4). Waterbuck maintained a similar distance to the nearest surface water, with a slight increase in distance towards the end of the dry season. Zebras remained at a slightly larger distance (1800 m) to surface water throughout the dry season which changed little (Fig. 4).

Amongst browsers, giraffes were also at a similar mean distance as zebras at the start of the dry season (1800 m) but this distance nearly doubled during the dry season to a mean of 3000 m (Fig. 4). The mean distance of kudu to the nearest surface water (2400 m) at the start of the dry season was greater than buffalo, zebra or giraffe, and this distance increased to a mean of 3200 m at the end of the dry season.

Amongst mixed or intermediate feeders, the mean distance of impala to the nearest source of surface water was 1000 m at the start of the dry season, but by the end of the dry season this had increased to a mean of 3000 m. Similarly, the mean distance of elephants from the nearest surface water source was 1000 m, and this only increased to 1500 m at the end of the dry season.

Amongst omnivores, warthogs were less dependent on the presence of surface water than the species previously mentioned. The mean distance of this species from the nearest surface water at the start of dry season was 3600 m and remained at this distance throughout the dry season. The mean distance of duikers to surface water at the start of the dry season was about 3500 m, and this distance increased substantially, reaching 10,000 m at the end of dry season.

## **Discussion**

This study revealed substantial differences between the early and late dry season distribution for three mammal species (buffalo, zebra and kudu) amongst the nine monitored species. These distribution changes were most probably caused chiefly by the response of animals to declining surface water availability and their need to maintain the required species-specific distance to the nearest available source of surface water. Consequently, two of these three species (buffalo and zebra) showed no or very limited changes in the minimum distance to the nearest water source throughout the dry season (Fig. 4).

Most individuals of most monitored species (Table 1) were observed in areas close to the GRR throughout the dry season, highlighting the importance of this river as a source of water and other essential resources such as forage. At the start of the dry season water flowed along the entire section of the GRR in the study area but by the late dry season large downstream sections of the river were dry, with isolated water pools within the bed of the river (Stommel et al. 2016a). These changes most notably affected the distribution of one grazing species, the buffalo, which moved upstream to areas containing larger expanses of water. In contrast, the distribution of two other grazers, the waterbuck and the zebra, revealed that these two species occurred in the downstream section of the GRR during the late dry season and were observed to drink from the few small scattered pools which apparently provided sufficient water. Both species may be highly dependent on these water

pools present in the downstream GRR river bed as there are no alternative water sources to the northwest. The presence of green forage growing within the dry downstream GRR riverbed is probably an important food source for these species.

As browsers, kudu are considered to be well adapted to dry environments (Cain et al. 2006). Even so, the distribution of this species shifted in the late dry season to the GRR (Fig. 2, 5b), including the most downstream transects. This shift may be explained by two factors. Firstly, bushes and trees along the GRR would retain green foliage for longer than those at a distance from the river and secondly, increased consumption of dry forage increases need for water intake in this species (Owen-Smith 1990), which could be supplied by the water upstream of the GRR and isolated pools in the riverbed downstream.

Elephants can access water beneath dry rivers by digging holes (Santiapillai et al. 1984, Stommel et al. 2016a). This behaviour permits them to continue to access water along the downstream section of the GRR, even when it was dry at the surface. However, larger elephant herds vacated the downstream section of the GRR in the late dry season (personal observation). This is in line with the suggestion that the high water requirement of a herd with a large biomass requires larger expanses of water (Owen-Smith 1996) which only occurred along the upstream section of the GRR during the late dry season period.

The species whose distribution changed least between the early and late dry season were impala, giraffe, warthog and duiker. Giraffe are a browser and impala are an intermediate, mixed browser and grazer which utilise both water and forage associated with the GRR during the dry season, but their distribution is not restricted to the river. Amongst the omnivores warthog and duiker, the distribution of warthog was not restricted to the GRR, but there were some shift of its distribution towards the GRR during the late dry season (Fig. 2: 8b). This is not the case for the distribution of the duiker, which is predominantly away from the GRR throughout the dry season (Fig. 2: 9a-b).

The model results confirmed substantial species-specific differences in the minimum distance maintained to the nearest water source during the dry season (Table 3, Fig. 4). Grazing species are considered to have a high water demand, and the model results generally confirmed this: The three grazers (buffalo, waterbuck and zebra) maintained a closer spatial proximity to surface water throughout the dry season than browsers, mixed feeders or omnivores (Fig. 4a-c). Hence, the spatial distribution of these grazers would alter as the distribution of water sources both in the GRR and elsewhere dried up.

As expected, browsers (giraffe and kudu, Fig. 4d-e) and mixed feeders that both browse and graze (impala, elephant, Fig. 4f-g) were less restricted by the presence of water, particularly at the end of the dry season. The distance to the nearest water in all four species had increased moderately by the end of the dry season, indicating a lower need to access water than grazers.

The warthog maintained a similar minimum distance to the nearest water source throughout the dry season, a distance comparable to the minimum distance to water maintained by browsers at the end of the dry season. Warthog require night refuges in underground burrows, and it is likely that access to burrows is also an important factor determining their distribution and relationship to water sources. Western (1975) described the warthog as a water-bound species. The results of this study do not support this, as this species maintained a relatively constant minimum distance of approximately 3000 m to water.

The steepest dry season increase in the distance to the nearest surface water source was apparent in the duiker. I interpret this result to indicate that duikers can live for extended periods without water and probably remain within their territories throughout the year. Hence, as the Ruaha NP dries out, the distance from their territory to the nearest source of water sharply increases as the animals apparently do not move. Therefore, within the spectrum of large mammalian herbivores included in this study, the duiker is the species least dependent on surface water and the most resilient to the drying out of the GRR during the dry season.

In conclusion, of the nine species examined, the distribution of buffalo in the Ruaha NP during the dry season was constrained by the need to remain close (approximately 1000 m) to surface water, whereas the distribution of duiker displayed little change and the most extreme minimum distance to water (approximately 10,000 m) at the end of the dry season. All the other investigated species were between these two extremes and kept at a minimum distance to water of less than 4000 m, suggesting that access to water during the dry season for these species was essential but not frequent. Buffalo suffered the largest relative habitat loss of all species considered, comparable to the habitat loss already documented in hippo (Stommel et al. 2016b) and hence is the species most vulnerable to the current drying out of the GRR as the dry season progresses. Overall, the results underline the importance of water resources in Ruaha NP for mammals and the importance of water flow during the dry season in the GRR to avoid further dry season habitat loss for various species.

## Acknowledgements

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**Table 1** The total number of animals per species counted in five transects (a) along the GRR and (b) five transects away from the GRR, the non-GRR transects, during the dry season (June –November) in 2011-2013.

Species Transect location	Buffalo		Waterbuck		Zebra		Giraffe		Kudu		Impala		Elephant		Warthog		Duiker	
	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b
Number 2011	1339	2	61	2	130	188	195	145	148	88	5636	1235	287	58	62	56	0	22
Number 2012	1280	2	37	0	362	124	154	148	172	117	6491	1561	246	199	37	55	0	13
Number 2013	277	90	48	14	206	109	148	114	170	147	6803	1286	430	139	26	45	1	24

**Table 2** The model fit statistics using the likelihood ratio test designed to obtain (a) the most suitable structure of random variables for the generalised linear mixed-effects model, by comparing a simple model where the random variables operated on the random intercept versus a model where random variables operated on both random intercept and slope and (b) to obtain the appropriate fixed effects structure comparing additive versus interacting effects.

	Model	df	AIC	BIC	logLik	Test	L.Ratio	p-value	Corrected p-value
a)	1 gls	19	67526.97	67644.91	-33744.49				
	2 lme (intercept)	20	67518.88	67643.03	-33739.44	1a vs 2a	10.09	0.0015	0.0007
	3 lme (intercept and slope)	22	67518.71	67655.27	-33737.36	2a vs 3a	4.17	0.1243	0.083
							Chi-square		
b)	1 additive (species + dry season date)	12	61808	61882	-30892				
	2 interaction (species * dry season date)	20	61797	61921	-30879	1b vs 2b	26.801	0.00077	NA

**Table 3** The minimum distance to the nearest accessible water source as a function of species identity, time (progression of the dry season expressed as dry season date with 1 set to 1<sup>st</sup> of June) and the possible interaction of particular species with time. Estimates of regression coefficients are displayed on a logarithmic basis and take the effect of impala as a reference value. This means, for instance, that giraffe have a significantly larger distance to the nearest water than impala because the estimate is positive. Species identities were sorted by diet. Results from the final generalised linear mixed-effects model with a logarithmic link function and a gamma error structure.

	{Diet}	Estimate	SE	t-value	p-value
Intercept (Impala)		6.708	0.077	86.790	< 0.00001
Dry season date		0.006	0.001	7.755	< 0.00001
Buffalo (vs Impala)	{grazer}	-0.695	0.334	-2.078	0.038
Waterbuck (vs Impala)	{grazer}	-0.476	0.311	-1.527	0.13
Zebra (vs Impala)	{grazer}	0.759	0.204	3.718	0.0002
Giraffe (vs Impala)	{browser}	0.659	0.128	5.171	< 0.00001
Kudu (vs Impala)	{browser}	1.058	0.190	5.582	< 0.00001
Elephant (vs Impala)	{mixed}	0.170	0.170	1.001	0.32
Warthog (vs Impala)	{omnivore}	1.456	0.225	6.474	< 0.00001
Duiker (vs Impala)	{omnivore}	1.433	0.346	4.137	0.00004
Interaction buffalo*dry season date	{grazer}	-0.005	0.004	-1.418	0.16
Interaction waterbuck*dry season date	{grazer}	-0.160	0.003	-0.528	0.60
Interaction zebra*dry season date	{grazer}	-0.006	0.002	-2.915	0.0036
Interaction giraffe*dry season date	{browser}	-0.002	0.001	-1.917	0.055
Interaction kudu*dry season date	{browser}	-0.003	0.002	-2.176	0.03
Interaction elephant*dry season date	{mixed}	-0.290	0.002	-1.799	0.072
Interaction warthog*dry season date	{omnivore}	-0.006	0.002	-3.034	0.0024
Interaction duiker*dry season date	{omnivore}	0.000	0.003	0.010	0.99

Number of observations: 3686. Number of groups (repetition of transect counts per year): 33. Effective df: 3661.62, conditional AIC= 61685.924. The random intercept was normally distributed (mean 0, SD 0.18), and so was its residual term (mean 0, SD 1.09).

## Figure legends

**Figure 1** Map of the study area covering the east of Ruaha National Park in central Tanzania. Ground transects were located in northwesterly direction either leading away from the GRR, the “non-GRR transects” 1-5, or along the GRR, the “GRR transects” 6-10. Stars: Permanent non-GRR locations with surface water during all years of the study period and during the whole time of dry season. (Modified after Stommel et al. 2016a).

**Figure 2** The distribution of nine large mammalian herbivores during the (a) early (June-August) and (b) late dry season (September-November), summarised across all three dry seasons from 2011 to 2013. (1a,b) African buffalo, (2a,b) waterbuck, (3a,b) plains zebra, (4a,b) Masai giraffe, (5a,b) greater kudu, (6a,b) impala, (7a,b) elephant, (8a,b) warthog, (9a,b) common duiker. The yellow circles represent the location of transect sightings and the number of observed animals, the size classes are species-specific. The red lines represent the location of ground transects, the blue line the course of the Great Ruaha River and the grey line the course of sand rivers.

**Figure 3** The best estimate of the smoothing curve of the generalised additive model (GAM) as a function of time, i.e. the progress of dry season expressed as dry season date with 1 set to 1<sup>st</sup> of June. The smoothing curve was estimated to assess to what extent linearity applies. The y axis shows the dry season date predicted by the smoothing function fitted by the GAM on the actual dry season date on the x axis. The solid line shows the smoothing function, the dotted lines indicate the 95 % confidence limits. The little vertical lines along the x axis indicate the position of the actual data. The shape of the smoothing function confirmed linearity.

**Figure 4** The effect plots for each species, showing the distance to the nearest surface water as a function of time, i.e. the progress of dry season expressed as dry season date with 1 set to 1<sup>st</sup> of June. Grey area: the 95% confidence interval around the estimated regression line. (a) African buffalo, (b) waterbuck, (c) plains zebra, (d) Masai giraffe, (e) greater kudu, (f) impala, (g) elephant, (h) warthog, (i) common duiker. As a reference, the distance of 5000 m is marked with a dotted line. Note that the y axis for common duikers encompasses 15 km rather than 7 km as for all other species.

Figure 1

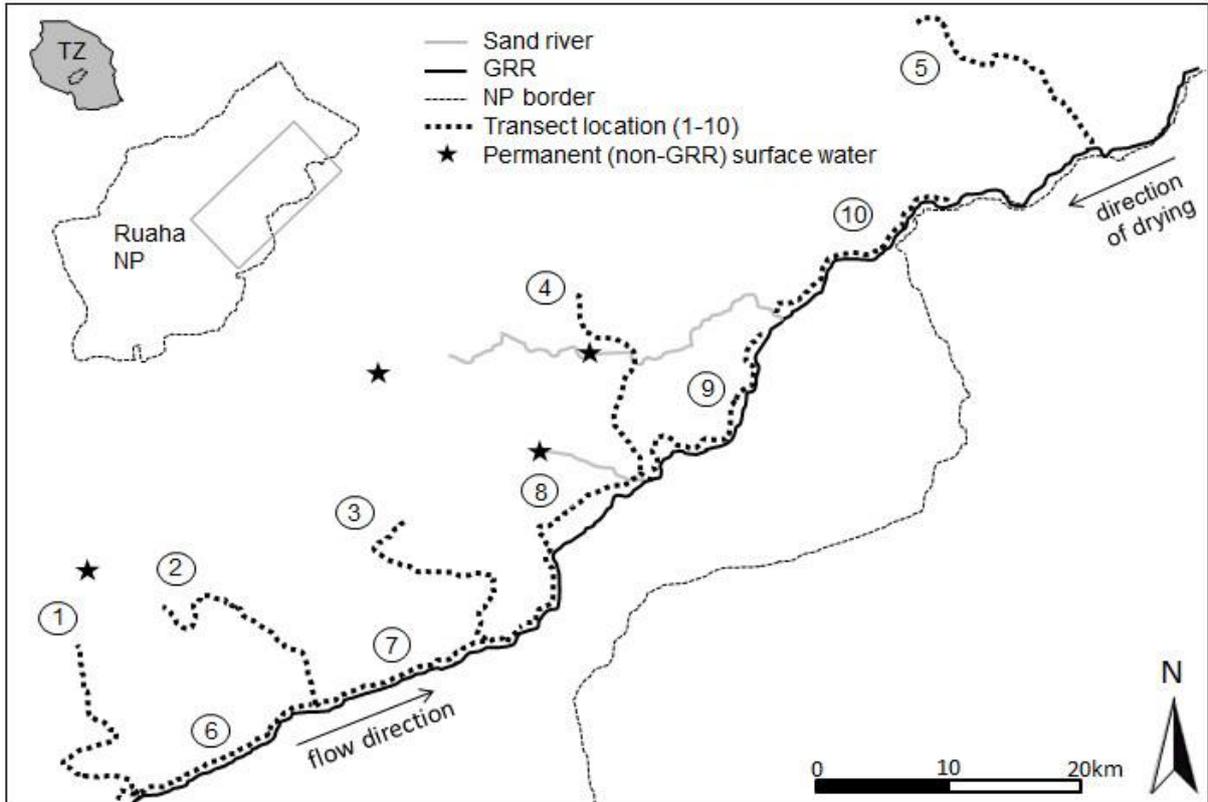
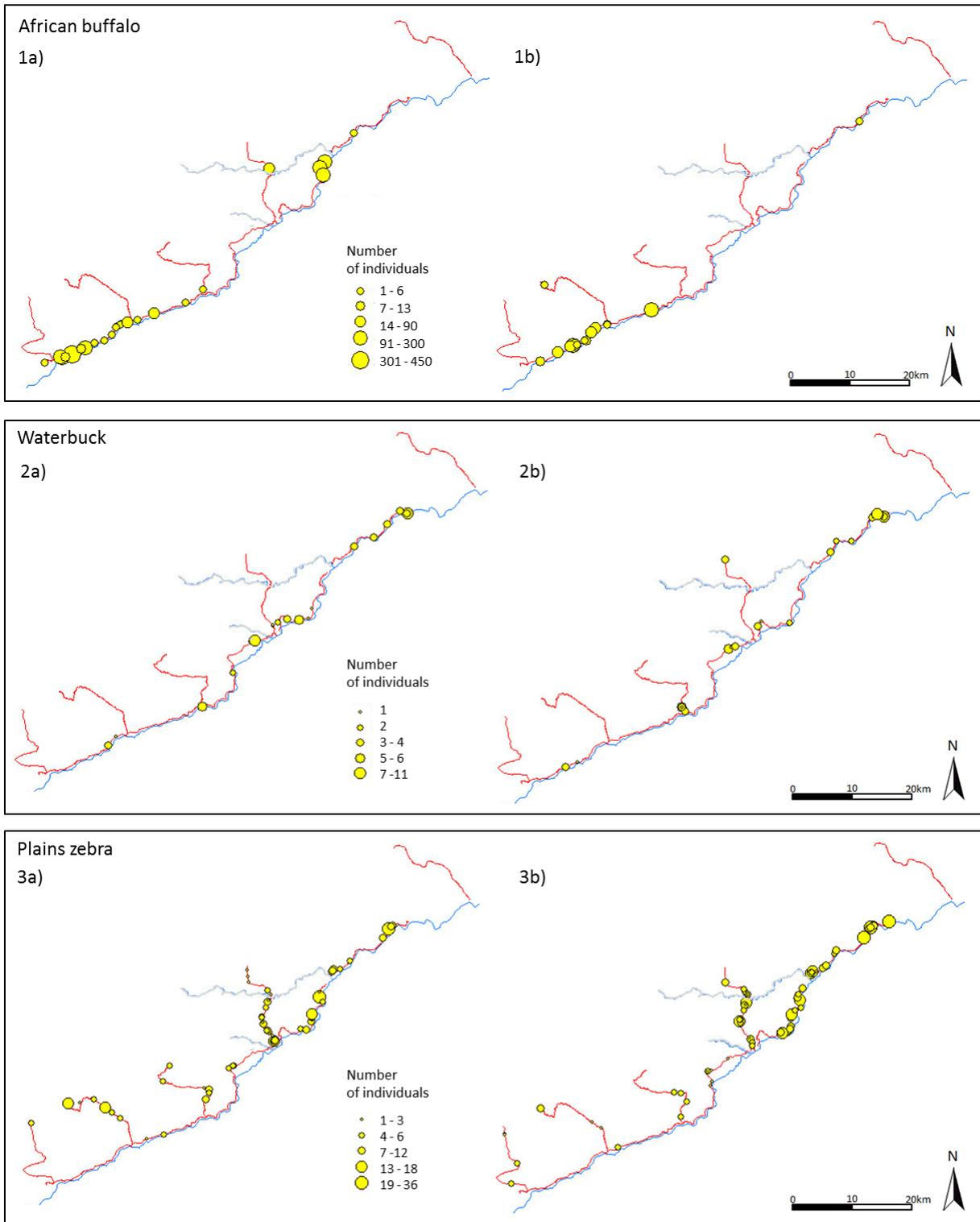
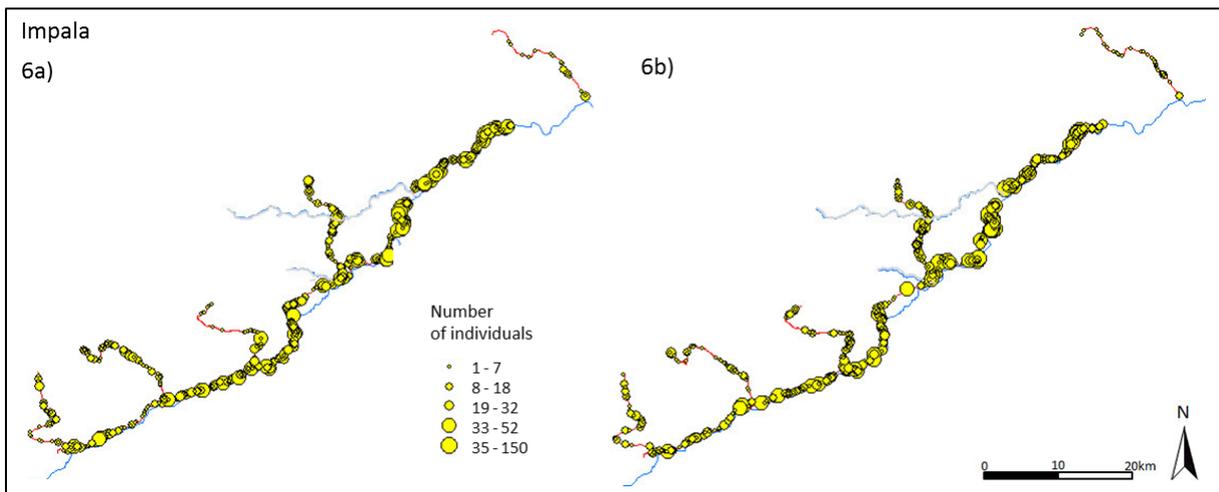
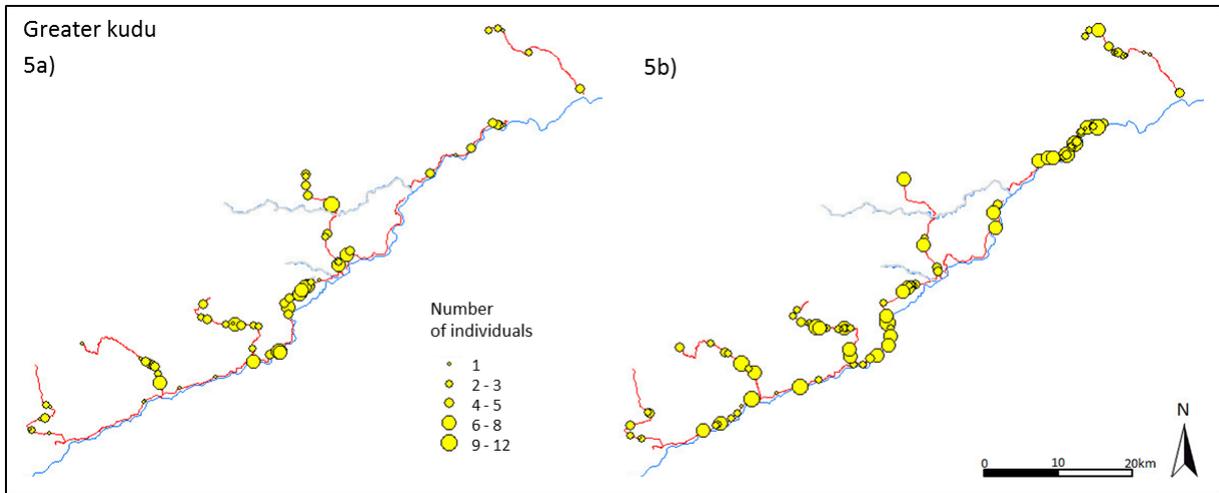
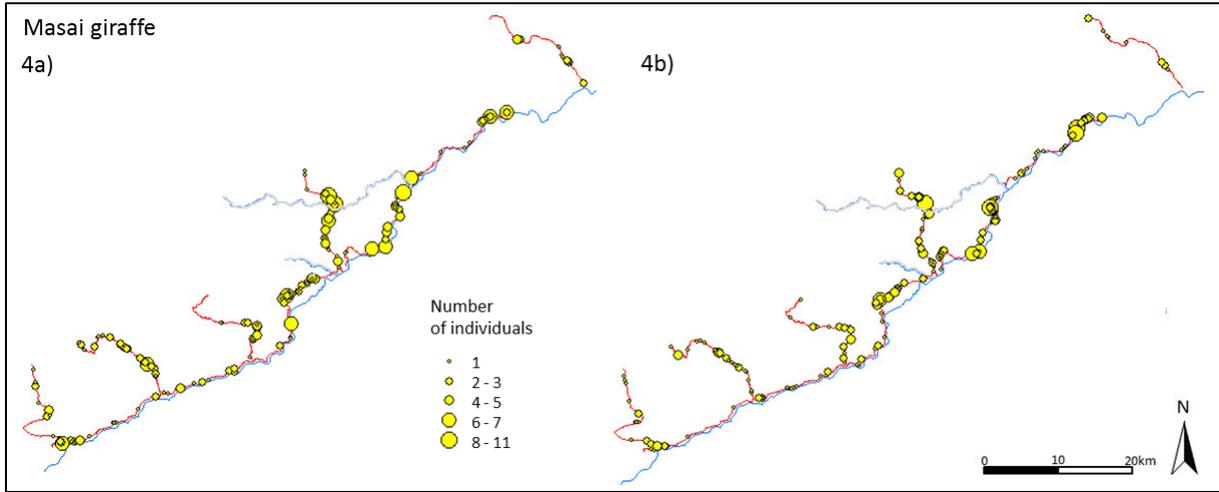


Figure 2





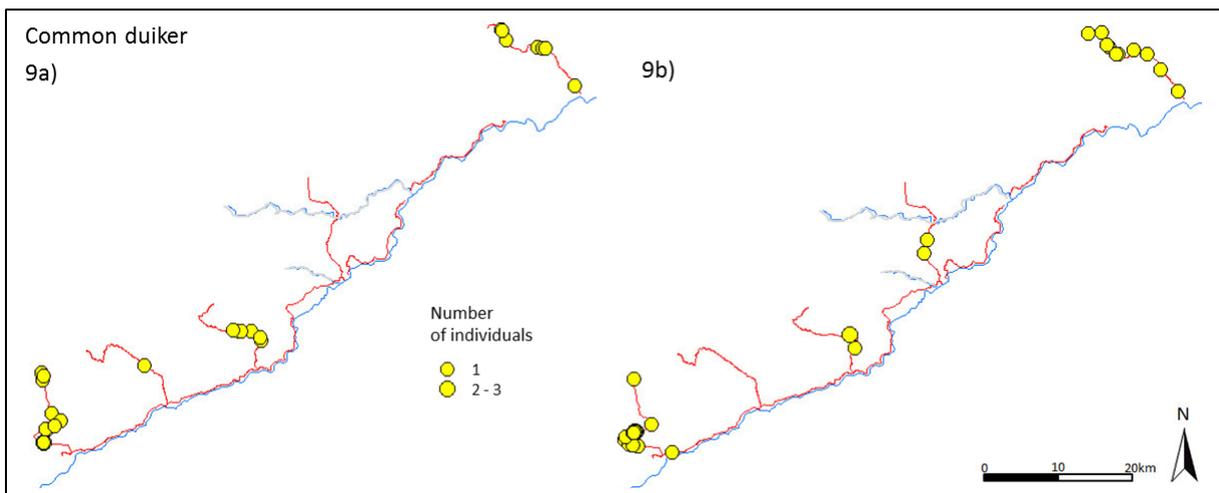
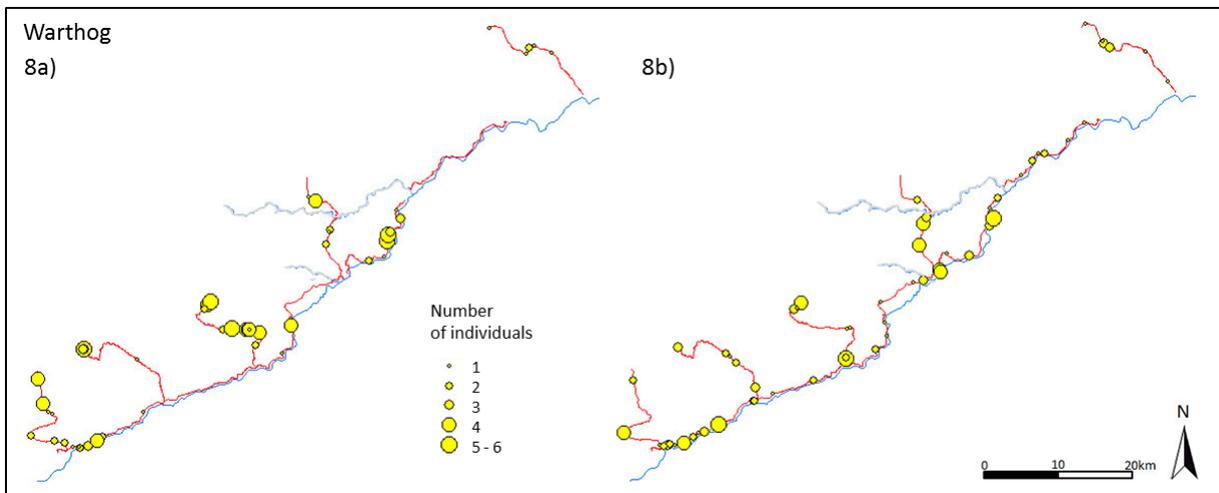
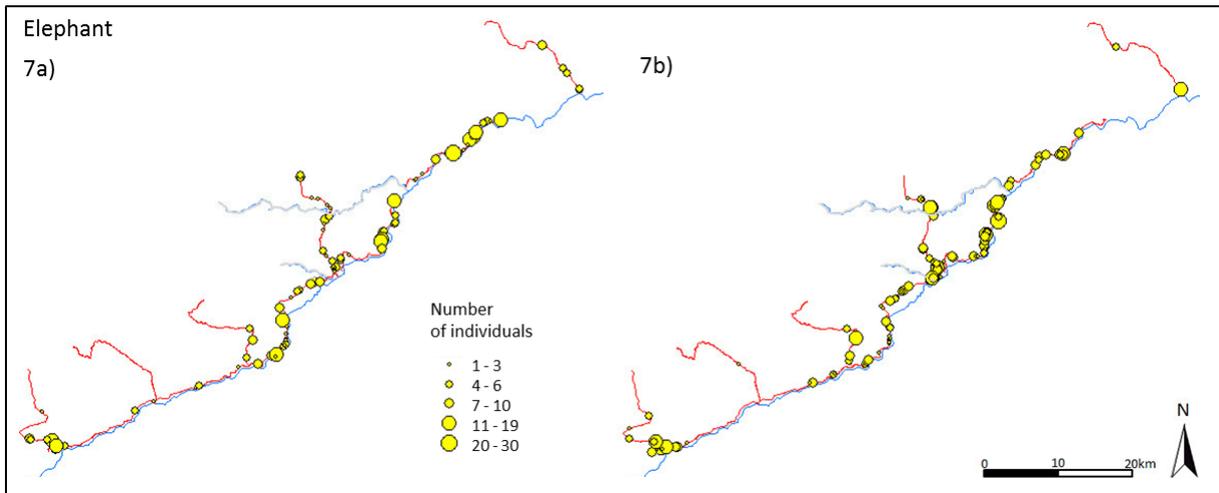


Figure 3

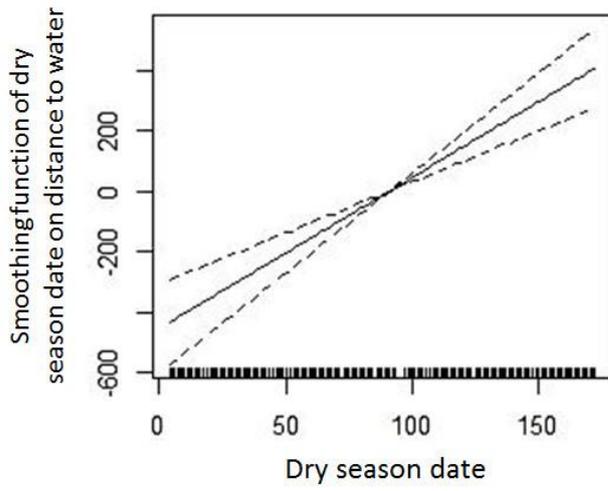
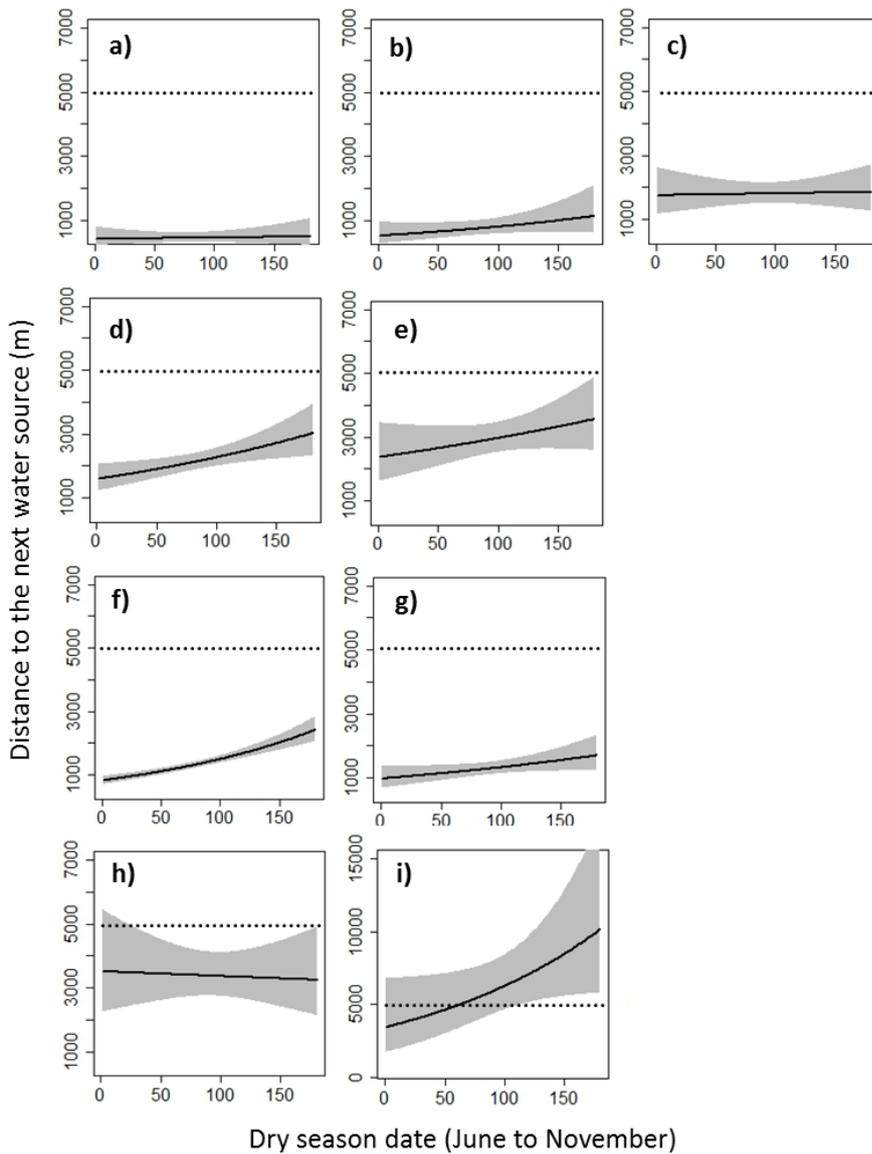


Figure 4





## Chapter 5

### General Discussion

The presence of surface water is essential for the survival of most mammalian species. Human activities and the increasing demand for water by people has caused severe changes in surface water availability in the Ruaha ecosystem and has resulted in a reduction in the surface water availability that exceeds the decline typically expected during dry seasons. This thesis sheds light on the ecological consequences for larger mammals of human induced water extraction, outside the Ruaha NP, in terms of a substantial reduction in water flow and an absence of surface water from large downstream sections of the formally perennial Great Ruaha River (GRR) during the dry season. In this thesis, I focused on the decline in surface water availability and its impact on both the quality and quantity of water during the progress of dry season and the influence this has on the behaviour and dispersion of larger mammals.

Worldwide, freshwater resources are under increasing human pressure (Vörösmarty et al. 2000), resulting in a rising concern about the current and future ecological consequences of human water utilization on freshwater ecosystems. Most environmental impact studies focus on large dam projects or industrial scale irrigation projects. More complex situations that result in a gradual loss of water volume from rivers caused by smaller scale arable farming or livestock production receive little attention (Elisa et al. 2010). Ecological impact studies of human changes to freshwater systems usually focus on aquatic species (e.g. Dudgeon et al. 2006), rather than terrestrial species, especially terrestrial mammals, reflecting the well known traditional boundaries between terrestrial and aquatic ecology (Rillig et al. 2015). The decline of water flow in the GRR during the dry season has been identified by Tanzanian National Parks as a key threat to the long-term resilience of wildlife populations in the Ruaha NP and the greater ecosystem of which it is a part (e.g. Mtahiko et al. 2006, Epaphras et al. 2007). Before this thesis there was little evidence available on the scale of this threat and therefore insufficient information on which to base any predictions of its long-term consequences.

This thesis represents the first approach at the species community level to examine the effects of human induced changes in water availability on the ecology of larger mammals

within the Ruaha NP (Chapters 2, 3 and 4). The investigation of changes in the quantity and quality of surface water during the three dry seasons 2011 to 2013 revealed interesting effects on the behavioural response of larger mammals to changing water quality as the dry season progresses (Chapter 2). In previous studies, the quality of surface water available to wild mammals was overlooked (Western 1975, Redfern et al. 2003) or was thought to play a minor role (Elisa et al. 2010). In contrast to these studies, my results confirm that several species invest time and energy to dig for access to water rather than drinking at available surface water sources. My results indicate that digging is an adaptation to avoid the ingestion of poor quality surface water containing potentially pathogenic microbes (Chapter 2).

The choice of day resting sites by hippos during the dry season (Chapter 3) demonstrated that the expanse of water present at sites monitored throughout the dry season was the driving factor which determined the distribution pattern of hippos, not water quality. Further results showed that hippos leave the downstream stretch of the river as surface water dried out and moved to a restricted number of locations mostly in the upstream section of the river. This large movement of hippos implies an extensive dry season habitat loss for this species both in terms of crucial day resting sites and night time grazing areas.

A generalised linear mixed-effects model was used to determine possible differences among the nine most numerous large mammalian herbivores in the minimum distance they maintained to the nearest source of surface water throughout the dry season (Chapter 4). The results revealed that the nine studied species maintained a minimum distance which varied by an order of magnitude, between 1000 m and 10,000 m. These differences were most likely linked to differences in diet, with grazers maintaining the closest association to surface water, browsers an intermediate distance and omnivorous species the largest distance.

Results on the spatio-temporal distribution patterns of these nine species at a landscape scale also revealed that highly water dependent species such as the African buffalo move upstream during the dry season, probably indicating an effective habitat loss along downstream stretch of the GRR comparable to that found for hippo. In contrast, less water dependent species such as waterbuck can continue to use smaller pools of surface water that remain in the dry river bed and hence do not show such a marked upstream movement during the dry season.

The results of my thesis link behavioural adaptations (Chapter 2) and profound spatio-temporal distribution changes at a landscape scale (Chapter 3 and 4) driven by the decline in surface water availability and its quality in the GRR during the dry season.

### **Behavioural response to changing water availability and water quality**

Headwater streams in temperate, subtropical and tropical zones can cease to flow on a seasonal basis, leaving behind perennial pools amongst dry sections of the riverbed of rivers that only flow at certain times of the year (Steward et al. 2012). In some seasonal rivers, water continues to flow beneath the dry riverbeds along subsurface routes (Steward et al. 2012).

Among mammals, elephants are well known to detect such subsurface flows and dig holes into dry riverbeds to reach subsurface sources of water (e.g. Douglas-Hamilton and Douglas-Hamilton 1975, Dudley et al. 2001). The behaviour is common in elephants and in arid regions it may provide the only access to water during the dry season (Weir 1972). During the course of my doctoral thesis I have observed this behaviour in several other species and was particularly interested in the observation that in most cases, holes to access subsurface water were dug next to available surface water (Chapter 2). This observation did not tally with the assumption that digging for water was primarily a behavioural adaptation to reach drinking water (Dudley et al. 2001). Clearly, prior to my study (chapter 2), little was known about the factors that determined where, when and why animals dug holes to access subsurface water. The results (Chapter 2) first verified the deteriorating quality of available surface water sources within the study area during the progress of the dry season. In contrast to my expectation, the GRR had a higher water quality (in terms of total aerobic bacterial load and salinity) than water in springs and other non-GRR water sources in my study area. The findings of my study support the idea that digging occurred to access water of a better quality, and hence are consistent with the findings of one study on baboon dug water holes (Galat et al. 2008) and another on waterholes dug by elephants (Ramey et al. 2013). Interestingly, water quality within the GRR was not a significant factor influencing the choice of aquatic resting sites by hippos (Chapter 3).

Even so, the quality of water in the GRR decreased swiftly when the river stopped flowing (Chapter 2) and digging events were significantly linked to poor water quality. These findings are pertinent because the human off-take of water from the GRR has caused a dramatic

decline in dry season flow. I found a significant positive relationship between the concentration of *Escherichia coli*, as an indicator of faecal contamination, and total aerobic bacteria load. This result suggests that water sources with a high total aerobic bacteria load could contain potentially harmful bacteria, including *E. coli* strains which may be pathogenic to wildlife species (Hellberg and Chu 2015). Furthermore, within certain limits, *E. coli* could also serve as an indicator of viral contamination in water (Gersberg et al. 2006). My assessment of bacterial load can only be the beginning - more detailed data on changes in the load of pathogenic bacteria in water sources is needed.

Currently it is not clear by which sensory mechanism, e.g. smell or taste, animals recognize deteriorating water quality; this deserves further investigation.

The thesis results underline the need to restore the perennial flow of the GRR to prevent further deterioration of water quality, reduce faecal contamination and hence the risk of disease transmission through water in remaining pools that attract large numbers of animals. If water extraction from GRR continues, larger stretches of the river are likely to fall dry and it is possible that the water table may fall beyond the depth to which most animals can dig. If this were the case, then species that currently depend on accessing water from freshly dug water holes may seek water elsewhere, perhaps outside the Ruaha NP, and for less mobile species it is likely their range would contract, resulting in an effective dry season habitat loss, and their populations decline. The mortality caused by the drying of elephant wells is already documented in several species such as anubis baboons (*Papio anubis*), patas monkeys (*Erythrocebus patas*), genets (*Genetta genetta*), civet cats (*Viverra civetta*) and slender mongoose (*Herpestes sanguineus*) (Poché 1974).

### **Distribution changes at a landscape scale**

Mammals have evolved different strategies to survive in semi-arid environments, including several behavioural and physiological adaptations to water scarcity (e.g. Cain et al. 2006). Whereas most larger mammal species depend on drinking surface water to cover their water requirements (Chapter 3), the semi-aquatic hippo also requires surface water as a daytime resting site. By submerging their bodies in water, hippos prevent overheating and skin damage from solar radiation (Eltringham 1999). The hippo is expected to be most sensitive to changes in the presence of water and was therefore used in my study as a highly sensitive indicator to detect the effects of changing water availability (Chapter 3).

I focused on the presence of hippos at their aquatic day resting sites to detect possible spatio-temporal changes in their distribution. My results confirmed significant changes of hippo distribution during the dry season and the accumulation of high numbers of hippos at a few locations with sufficient amounts of water during the end of dry season, as observed in other studies (e.g. Eltringham 1999, Timbuka 2012). Smaller pools, predominantly along the downstream stretch of the river, were vacated during the progress of dry season. In comparison with other water sources within the study area (Chapter 3: Fig. 1), the GRR was identified to be the most important water body for the hippo population. My results therefore indicate an extensive dry season habitat loss for this vulnerable species within Ruaha NP. Habitat loss is identified to be one of the major threats for this species (Lewison and Oliver 2008). These results illustrate that the expanse of surface water present in a specific location is the most relevant factor for this species rather than the “simple” presence of water. Other semi-aquatic species such as the Nile crocodile (*Crocodylus niloticus*) are also likely to be forced to move upstream in search for pools with sufficient amounts of water where they congregate during the dry season, as observed in seasonal rivers (Kofron 1993).

Insights into the relationship of the most numerous nine larger mammalian herbivores to the minimum distance from surface water were gathered from the establishment of a network of regularly monitored ground transects spanning a total length of 200 km (Chapter 4). As expected, the results demonstrated a species-specific minimum distance to the nearest available source of surface water and a relationship between the distance to water (water requirements) and diet.

The pattern of the observed minimum distances of herbivore sightings to the nearest water source showed that: (i) grazers (buffalo, waterbuck and zebra) maintained the shortest distance to surface water, (ii) species that both graze and browse (impala, elephant) and those that are predominantly browsers (giraffe, kudu) maintained intermediate distances to water and (iii) omnivores (warthog, duiker) had the largest distances to surface water. This is consistent with the findings of Western (1975) who found the water dependent species to be mostly grazers and the water independent species to be mostly browsers.

The analysis of changes in the spatio-temporal distribution delivered several interesting findings. The African buffalo left the drying downstream stretches of the GRR first, despite the presence of smaller sources of water. In contrast, other water dependent species such as

zebra or waterbuck were observed to use the small remaining (and shrinking) pools within the downstream stretch until they dried up. Other species such as the common duiker were far less dependent on the presence of surface water. My results suggest that the amount of surface water present is not only important in terms of resting sites for hippos (Chapter 3) but regular access to local surface water nearby is essential for at least the African buffalo (Chapter 4).

The results of my thesis emphasise the importance of water quality (Chapter 2), and water quantity, distribution and proximity (Chapter 3, 4) with regard to species requirements. They demonstrate that it is not sufficient to confine yourself to simple records of the presence or absence of surface water.

### **Limitations and further research**

The questions about the scale of the impact of human induced modifications of the flow of the Great Ruaha River is hard to answer, since detailed data on the flow regime before large-scale water extraction began are missing. The flow of the Great Ruaha was reduced from 1993 onwards, with periods of several weeks with zero flow resulting in the drying of extended stretches of formally perennial GRR (Mtahiko et al. 2006). During this time no changes of intensity, distribution or timing of rainfall are likely to explain the decrease in dry season flow (Mtahiko et al. 2006). Hence it is reasonable to assume that without human water extraction upstream of the National Park, the GRR would have a perennial flow today as documented before 1993. Therefore, all effects on larger mammals caused by the reduced flow and drying of the GRR can be traced back to human activities and can be considered to be a result of human impact.

My research was focused within a study area along the GRR and the adjacent habitat northwest of it (Chapter 2: Fig. 1), representing only a small part of the total area of 20,226 km<sup>2</sup> of the Ruaha NP. Nevertheless, this area included most of the course of the GRR inside the Park and all perennial non-GRR water sources within this study area (Chapter 2: Fig. 1). The Mzombe river at the northwestern border is seasonal and not expected to be as relevant as the GRR for wildlife within the Park during the dry season. The escarpment plateau further northwest of the study area has no main source of surface water during the dry season; therefore the study area covered the most important water sources for wildlife

within the Ruaha NP. The southwestern area upstream of the GRR, annexed in 2008, needs further investigation to assess the presence of wildlife and water sources there.

In my thesis I concentrated on abundant species that were present in higher numbers within the most accessible regions of the Ruaha NP. Besides these species, rare mammal species that occur at low densities, such as the roan antelope (*Hippotragus equinus*), the sable antelope (*Hippotragus niger*) or the African wild dog (*Lycaon pictus*), might also be affected by human induced changes of water availability in the GRR.

The GRR passes an intensively used agricultural area before entering the Ruaha NP. Therefore, in addition to the water parameters measured in this thesis, water pollution by pesticides, fertilisers, heavy metals or human pathogens and their possible contaminants may be released into the National Park and deposited along the downstream section of the GRR during the dry season. The potential build-up of such contaminants, many of which will have long-term persistence, is a concern and therefore warrants a detailed investigation as a measure of the long-term health of Ruaha NP.

It would also be helpful to have more detailed, quantitative measures of the increased grazing pressure of herbivores such as hippos near occupied pools as the dry season progresses to evaluate whether increased grazing around permanent pools is a source of habitat degradation. Likewise, does the decrease in grazing in the downstream areas of the GRR contribute to habitat changes there? A decrease in grazing may result in a decrease in the growth of grass species, lead to a change in the community composition of grasses with a concomitant decline in species richness (e.g. McNaughton 1985, Milchunas et al. 1988, Huntly 1991, Frank 2005) and acceleration in the regeneration of woody, i.e. bush and tree, species (Sinclair and Arcese 1995).

### **The future of ecosystem health of the Ruaha ecosystem**

Human modification of the flow regime might have additional consequences, besides the investigated effects on larger mammalian herbivores. The sediment transported by the river will be deposited more rapidly along the river stretches inside the National Park and thus accumulate because of the reduction in and lack of flow, thereby contributing to the river bed becoming more shallow. This might lead to a widening of the riverbed, resulting in the loss of riparian vegetation during flooding periods, as reported from the South African Black Umfolozi River (Vincent 1970).

Modifications in the flow regime of rivers have an impact on various taxonomic groups including riverine plants, invertebrates and fish. Bunn and Arthington (2002) identified four key points linking impacts of flow regimes to aquatic biodiversity: (i) Flow is a major factor to set the parameters of the physical properties of the aquatic and transitional habitats, and therefore its biotic composition; (ii) life histories of species dependent on river habitat are adapted to flow regimes unaffected by human intervention, (iii) the longitudinal and lateral connectivity is essential for the survival of many species, and (iv) alterations in the flow regime aids the invasion of exotic species. Whereas changes caused by the variation in flow might be hard to detect, the complete drying out of a riverbed, with its resultant complete loss of longitudinal connectivity for aquatic biota (Steward et al. 2012), has more obvious impacts.

In 2006, the massive die off in river fishes drew attention to the impact on aquatic biota in the GRR (Epaphras et al. 2007). The fishes died in pools in the drying river and hence were exposed to high water temperatures, and hypoxia resulted in the death of aquatic life (Epaphras et al. 2007). Flocks of great white pelicans (*Pelecanus onocrotalus*) and yellow-billed storks (*Mycteria ibis*) are attracted to pools containing stranded fish and seemingly forage until no fishes remain (pers. obs.). Despite this short-term foraging benefit to individual species, the overall avifauna is likely to also suffer from water scarcity during the dry season. Other bird species might suffer from changing conditions concerning possible breeding sites, as several species such as the white-headed lapwing (*Vanellus albiceps*) breed on sand benches inside the riverbed (pers. obs.). Predators such as the banded mongoose (*Mungos mungo*), the African civet (*Civettictis civetta*) or the yellow baboon (*Papio cynocephalus*) are prevented from accessing the nests as long as the water is deep and flowing, and inhabited by Nile crocodiles, but this situation changes fast as the water start disappearing (pers. obs.).

Apart from shorebirds and other water associated birds, even non-water associated birds such as several species of sandgrouse (Pteroclididae) might be affected. Their nests are located far from water, forcing adults to fly long distances to soak their belly feathers in water which is then transferred to their young so that they can drink (Cade and Maclean 1967). If water disappears completely from the river, their breeding success might also be reduced.

The GRR is also likely to play an important role for numerous migrating birds, both intra-African migrants such as Abdim's stork (*Ciconia abdimii*) and European migrants. Riparian areas in semi-arid zones are critical in providing stopover areas for en route migrants (acting as 'dispersal filters'), and therefore affect the breeding success of northern bird populations (Skagen et al. 1998) too. Even the endangered Madagascar pond heron (*Ardeola idea*) with a population of only 2,000-6,000 individuals worldwide (Delany and Scott 2002) depends on the availability of water in Ruaha NP and the GRR. Two records during the study period (pers. obs.) suggest that the GRR constitutes an important part of the non-breeding range of this rare species which has been massively reduced by habitat loss through water modifications elsewhere (Kushlan and Hancock 2005). These examples underline the local and global relevance of the GRR as a critical dry season habitat for various species.

In a bid to improve conditions, in 2008 the Tanzanian Government annexed the Usangu Wetlands to the Ruaha NP. Although this measure was designed to safeguard wetland areas upstream of the National Park, this measure will lose any effectiveness, if the current rate of water extraction outside the National Park continues and the annual drying out of the GRR is repeated.

### **Further implications**

The results presented in my thesis document that several species such as the hippo and the African buffalo leave formerly suitable habitats as dry season progresses when water availability decreases (Chapter 3, 4). This can result in an increase in human wildlife conflict, as wildlife might also move outside Ruaha NP in search of water and interact with villages or herders (e.g. Kendall 2011). These movements will also increase the likelihood of pathogen encounters, as contact between domestic and wild animals increases the risk of disease transmission (e.g. Clifford et al. 2013).

In addition to these ecological and epidemiological consequences, the drying of the GRR might also have negative economic consequences for the tourism industry if wildlife populations in Ruaha NP decline. My results confirm that the sightings of hippos is significantly reduced along the downstream stretch of the GRR during the dry season (Chapter 3) and African buffalo are rarely sighted along this stretch of GRR during the late dry season (Chapter 4).

The reduced dry season flow and drying out of the GRR already has severe implications for the Tanzanian economy. The hydroelectric dams at Mtera and Kidatu downstream of the Ruaha NP depend on the water from the GRR. During the dry season 2004, the lack of water caused a financial loss of US\$120 million and led to the closure of the power plants (Mtahiko et al. 2006). This had a detrimental impact on Tanzania's industrial development (Confederation of Tanzanian Industries 2004) as the GRR provides half of the electric power capacity of Tanzania (Mtahiko et al. 2006). Despite the efforts by the Tanzanian Government and the annexation of the Usangu wetland, the perennial flow of the GRR has not yet been restored. The restoration of a minimum flow during the entire dry season could prevent further degradation of the Ruaha ecosystem.

### **Conclusions**

In this thesis, I have explored the behavioural response of larger mammals to human induced water scarcity in Ruaha NP as the dry season progresses. I investigated the processes underlying special behavioural adaptations to cope with absent water and poor water quality and the habitat choices in a landscape with decreasing availability of water sources.

I regularly monitored water quantity and quality within my study area, used camera traps and observations as well as a network of ground transects to assess behaviour and determine spatio-temporal changes in larger mammals. The results obtained by these methods were analysed using appropriate statistical analyses. Consistent with previous studies, I found that digging behaviour was a behavioural adaptation to access drinking water from below ground level. In addition, I identified poor water quality as the trigger for digging behaviour, rather than the absence of water as such. The GRR was identified to deliver better quality of water (in terms of total aerobic bacterial load and salinity) in comparison to non-GRR water sources. Water quality in all sources deteriorated with decreased flow, including water in the GRR. The progressive decline in water availability during the dry season caused severe changes in the spatio-temporal distribution of the vulnerable hippo and the most numerous nine larger mammalian herbivores within the Ruaha NP, leading to an extensive loss of dry season habitat especially for the most water dependent species such as the hippo and the African buffalo. Thus, my thesis provides important insights into the complexity of species-specific water requirements and their

consequences for spatio-temporal distribution patterns within a semi-arid landscape. The results of this thesis emphasize the importance of the GRR and the restoration of its dry season flow to prevent further dry season habitat loss for numerous species within the Ruaha NP. Moreover this thesis delivers important results to evaluate the impact of future climate change and water abstraction at a local and global scale.

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