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The importance of water sources for space-use of mammals in African savannah

Význam vodních zdrojů pro využívání prostoru savci v africké savaně

Bachelor's thesis

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Prohlášení:

Tímto prohlašuji, že jsem tuto závěrečnou práci vypracoval samostatně a že jsem uvedl všechny použité informační zdroje a literaturu. Tato práce ani její podstatná část nebyla použita k získání jiného nebo stejného akademického titulu.

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Podpis:

Abstrakt:

Africká savana je sezónním ekosystémem charakterizovaným významným obdobím sucha. Nedostatek vodních zdrojů během tohoto období výrazně ovlivňuje pohyby velkých savců jak v prostoru, tak v čase. Některé druhy savců se s těmito omezeními dokážou vypořádat lépe než jiné. Jedná se o savce nezávislé na vodě, kterými jsou převážně okusovači (žirafa, kudu, antilopa losí), a tato zvířata lze tedy nalézt dále od vody. Někteří z nich však využívají biotopy kolem řek k získávání potravy. Druhy závislými na vodě jsou spásači a nepřežvykující druhy (zebra, pakůň, slon). Nedostatek vody v suchém období roku nutí tyto savce pohybovat se v blízkosti vodních zdrojů. Šelmy (lvi) využívají této prostorové restrikce v pohybu kopytníků pro lov a loví převážně v blízkosti vodních těles. Predovaná zvířata (jak šelmy, např. pes hyenový, tak kopytníci) vyvinula anti-predační strategie ve využívání prostoru v podobě vyhýbání se lvům v prostoru nebo čase. Kopytníci omezují aktivitu pití na denní čas, kdy lvi nejsou aktivní, a psi hyenoví využívají nory dále od vodních zdrojů. Tato časoprostorová segregace je užitečná i pro řešení kompetičních interakcí. Denní aktivita u vodních zdrojů je variabilní, což naznačuje, že další faktory (např. termoregulace) tuto aktivitu ovlivňují.

Klíčová slova: využívání vody, prostorové rozšíření, ekologický prostor, savci, Afrika, sezónnost, kompetice, predace

Abstract:

African savannas are seasonal ecosystems experiencing a significant dry period each year. During the dry season, water scarcity has both, spatial and temporal consequences on the movements of large mammals. Some mammals can cope with these resource restrictions better than others. These water independent mammals predominantly feed on browse (giraffe, kudu, eland) and can be found further from water sources. However, these mammals can utilize areas near rivers as these areas provide food resources. Water dependent species are predominantly grazers and non-ruminants (zebra, wildebeest, elephant). Water shortage during a dry season restricts the movements of these species, which can be generally found in the vicinity of water bodies. Carnivore species (lions) react on the spatial restrictions of ungulates by adjusting their hunting areas to the vicinity of water sources. Both intra-guild (African wild dog) and inter-gild prey species (ungulates) develop anti-predatory strategies such as temporal and spatial segregation. African wild dogs use dens far from water points and ungulate species use to drink during daytime when lions are not active. Spatial and temporal segregation are also strategies to cope with competitors. Daily patterns of water point visitations can vary suggesting other factors (e.g., thermoregulation) also affect these patterns.

Contents

Introduction

African savannah is a tropical ecosystem well known thanks to its animal icons such as the tallest animal in the world - giraffe (*Giraffa* spp.), one the last remnant of megafauna - African bush elephant (*Loxodonta africana*), large herds of zebras (*Equus* spp.) and wildebeests (*Connochaetes* spp.), or prides of lions (*Panthera leo*). These and other African iconic animals promoting tourism and sport hunting in Africa economically contribute to local people. On the other hand, these animals, particularly carnivores and elephants, come together with people into a human-wildlife conflict (HWC). As both elephants and large carnivore species such as lions are found near water sources (Harris et al., 2008; Mills et al., 2020), manipulation of these resources (access restriction or spatial manipulation) could possibly mitigate the human-wildlife conflict.

In regard to climate, the African savannah is mostly dependent on precipitation and the availability of water (Archibold, 1995). Ultimately, we can distinguish two seasons in savannas regarding the amount of rain, a dry season with minimal precipitation, and a wet season, in which most of the rain falls. Thus, water is a key resource which animals (and people) need to operate with. In the wet season, animals usually have plenty of opportunities to obtain this resource (ephemeral waters, e.g., mapped by Naidoo et al., 2020). During the dry season when water is scarce, some animals need to seek long-term sources of water (e.g., swamps, rivers, boreholes or dams) (Western, 1975). As herbivores spend a long time near the water source, they feed on ambient vegetation. This behaviour results in the piosphere effect, which is the degrading of the vegetational structure of habitat in the vicinity of the water source (Lange, 1969; for African savanna see Egeru et al., 2015). After the exploitation of this source of food, animals need to depart from water to forage for resources (e.g., Venter & Watson, 2008). Therefore, water sources are the key determinants of the animal distribution across African savannas. Artificial water sources promote tourism by creating 'hotspots' of game abundance (Owen-Smith, 1996) and managers of protected areas can change the spatial distribution of mammals by manipulating the distribution of this resource [modelled e.g., by Shannon et al. (2009)].

In this thesis, I present a summarisation of the effect of water sources modulating the space usage mammals in African savannas on the scale of habitats (thus not concentrating on migration). The thesis focuses on space-use of iconic African mammals – ungulates, large and intermediate carnivores (larger than 20 kg), and African bush elephant (Afrotheria). Special

1

attention is given to the latter mentioned elephants in the scientific literature because of their role as ecosystem engineers (Beuchner & Dawkins, 1961) and because of the reasons mentioned above (HWC, piosphere effect). The thesis also looks at ecological interactions (competition and predation) of these mammals near water sources and how these contribute to the change in the distribution of animals. Lastly, the thesis summarizes a diurnal and seasonal utilization of water sources by animals and the effect of water dependency on habitat use.

1.   How is space-use modulated by water sources?

1.1 Elephants

Importance of water. In general, elephants can more frequently be found in the vicinity of water sources or habitats specific for their occurrence near water bodies than in areas farther from water (Harris et al., 2008; Shannon et al., 2009). De Beer & van Aarde (2008) illustrated a water resource as a strong predictor (stronger than environmental heterogeneity) of elephant occurrence in their home ranges. The home ranges tended to decrease with water sources being denser. Smit et al. (2020) found out that during droughts (dry years, for dry season see below), elephant densities increase in private reserves where water is provisioned more than in the Kruger National Park (NP; South Africa). Similar relation was found in Hwange NP (Zimbabwe), where elephants aggregate in those parts of the park, where water points are abundant. During droughts, elephant densities increase in those parts (Chamaillé-Jammes et al., 2007c; see also Western, 1975; Roux & Bernard, 2009 or Gaugris & van Rooyen, 2010). In the Mara region, elephants also do not concentrate in areas where human presence poses a high pressure on the animals (Bhola et al., 2012).

Water vs food. Redfern et al. (2003) compared dry season distributions of elephants and other herbivores in Kruger NP during dry and wet years and on landscapes either rich or poor in nutrients. Herd densities of elephants decrease with the distance to a water source, but in wet years and in nutrient-rich areas, this decrease is not as steep as under other predictor combinations. Among several herbivore species considered, the distribution of elephants is the second or the third nearest to a water sources (after waterbuck and buffalo) during dry years and also during wet years in the nutrient-rich areas. During wet years and in areas poor in nutrients elephants tend to roam further away from the water source. These findings show that water is an important factor for the distribution of elephants, although this study was held during high-water supply time period (a time period until ~ 1998). During this period, water holes were more abundant in Kruger NP and not many areas of the park occurred farther than 6 km away

from water (Gaylard et al., 2003 cited in Smit & Ferreira, 2010; see also maps in Redfern et al., 2005). The results of the Redfern's study might also show elephants to save energy by feeding near water sources rather than obtaining food somewhere else during wet years in nutrient rich areas. However, authors warn against the over-interpretation of those findings as elephants were more abundant in areas poor on nutrients. Elephants could therefore, as authors suggested, mitigate intraspecific competition in nutrient-poor areas by roaming to areas farther away from water to seek food. Smit et al. (2007b) reported a stronger positive relationship of elephants and water sources (rivers) in areas on basalts, which are rich in nutrients. This also supports the hypothesis that elephants can obtain food in the vicinity of water sources on nutrient-rich landscapes.

Rivers. We can divide water sources into two groups – artificial water sources (i.e., boreholes, dams, etc.) and natural water sources (i.e., rivers, pools, etc.). Speaking of rivers, elephants in Kruger NP are drawn more to large perennial rivers with riparian vegetation zone than to small seasonal rivers. This attraction to large rivers increases when artificial water sources are closed, which indicates the ability of park managers to change the spatial utilization of landscape in elephants (Smit & Ferreira, 2010). Same attraction to rivers and riparian zones was observed by Orrick (2018) in a South African private game reserve and this attraction occurred regardless of herd composition (sex) or seasons. In Kruger NP, the closing of water points is based on its occurrence near or away from rivers. Water holes that were built in naturally dry areas are being closed, but those close to rivers can be used as 'hotspots' of animals for tourism. Nevertheless, areas with closed water holes are expected to become refugia for plants affected by piosphere effect (Smit, 2013). Both, the river-bound spatial distribution of elephants and the increase of this river-dependence after artificial water closure under dry years, was also modelled by Hilbers et al. (2018).

Water holes. Together with season, water holes were also found to be a significant contribution while modelling the elephant occurrence in Kenya (Williams et al., 2018). Williams et al. (2018) used several environmental predictors including the NDVI – normalized difference vegetation index – which is often used as a proxy for vegetation productivity. The authors think that water holes are a stronger predictor for elephant occurrence than food resources because of their sparsity. Despite this, food still plays a significant role in the survival of elephants which is still dependent on rainfall in areas well provisioned with water (Shrader et al., 2010). Since culling - one of the techniques used to control elephant numbers - was stopped in Hwange NP, the elephant population has grown. The more elephants per water hole

there is the more evenly distributed they are across the water holes. Elephants also tend to start occupying those water holes that are not yet occupied by a high number of elephants (Chamaillé-Jammes et al., 2007c; Chamaillé-Jammes et al., 2008). In Etosha NP (Namibia), water holes were also found to play a significant role in elephant spatio-temporal distribution. Although water sources were the most important predictors, roads and fences were also found to be a strong influence. As water points are situated near roads, these roads could be used by elephants for a fast travel between two water holes (Tsalyuk et al., 2019). Quality of water has also a large impact on spatial distribution of elephants. Elephants prefer cleaner water which is less polluted with faeces (Ndlovu et al., 2018), but the concentration of minerals nowadays has no important effect on which water holes elephants aggregate at (Chamaillé-Jammes et al., 2007a).

Rivers vs water holes. In Kruger NP, elephants use ~ 30% more area of the national park while visiting rivers and artificial water holes than they would when only visiting the rivers [see also a Namibian example in Loarie et al. (2009)]. Elephants also tend to stay at rivers longer than at water holes, probably due to foraging opportunities near rivers (Purdon & van Aarde, 2017). Results in the study of Smit et al. (2007b) also show that elephants significantly prefer areas near rivers in Kruger NP during a high-water supply time period. The spatial relation to water holes was negative (elephants occurred farther than if they were randomly distributed). Smit et al. (2007c) investigated the differences in water source utilization between sexes during high-water supply time period in Kruger NP. Mixed herds (females and offspring) were not found in the vicinity of water holes. On the other hand, bulls were found near both, water holes and rivers. Polansky et al. (2015) also reported that females in Etosha NP tend to move farther away from a water hole where they drink to a probable foraging area where they feed. In Pongola Game Reserve (South Africa), female elephants in contrast to bulls on their own are present in floodplain grasslands (Duffy et al., 2011). De Knegt et al. (2011) propose that elephants were not limited by water during the time of the high-water supply in Kruger NP because they exhibited no or negative reaction to water presence in a large spatial scale.

Piosphere effect. Elephants as ecosystem engineers contribute significantly to piosphere effect and the mortality of trees. In Chobe NP (Botswana), both landscape-scale and local-scale relation of debarking of trees to the distance to water was found. Elephants debark trees closer to the river. On the other hand, feeding on branches occurs both in the vicinity and farther away from the river (~20 km, cubic relation; Fullman & Child, 2013). In Mana Pools NP (Zimbabwe), the damage to baobabs by elephants was spatially correlated to a distance to a river with more

baobabs being damaged near the water source (Ndoro et al., 2016). Similar results were found in Etosha NP, where the survival of shrubs and trees is greater in areas farther away from water sources (De Beer et al., 2006), and in other sites such as Hwange NP, Tembe Elephant Park, or northern Botswana (Mukwashi et al., 2012; Gaugris & van Rooyen, 2010; Ben-Shahar, 1993). An opposite relationship was found by Shannon et al. (2008) in Kruger NP, however, the probable reason is the mirroring of the distribution of tree species. Chamaillé-Jammes et al. (2009) found a very low impact of the distance to water on woody vegetation occurrence because of a great variability in woody cover near water holes.

Elephants react to the piosphere effect via distinguishing between drinking/watering periods and foraging periods. Even though water is a better predictor of elephant occurrence, elephants occur near water sources, and also further away from them. This second peak of occurrence in relation to the distance to water is positively associated with the higher NDVI (Ndaimani et al., 2017) or lower temperature (Fig. 1, Thaker et al., 2019). Elephants travel between the water sources and areas farther away from them to obtain food. These foraging places are characterized by a low water hole density (Valls-Fox et al., 2018b). Thaker et al. (2019) found elephants in Kruger NP to walk up to 2.6 km away from water holes and to walk away from or to water holes at higher speed (Fig. 1). They also found out that elephants spend ca. 22% of the time near a water source. Next visit of elephants to water sources usually occurs in 12 – 36 hours (Purdon & van Aarde, 2017) or 36 – 60 hours [more than 30% of "trips" found by Chamaillé-Jammes et al. (2013)] period. Chamaillé-Jammes et al. (2013), while studying elephants in Hwange NP, also found that elephants decrease their speed ca. in the middle of the foraging trip and increase it again at its end. They also found that elephants do not drink from the nearest water hole to the foraging area in ~ 40% of the trips, although the used water hole was not usually situated far away from the nearest one. This indicates the choice of a water hole to be driven, for example, by water quality (see above). When the duration of the foraging trip was greater, elephants betook to areas further away from the water source. The authors also reported almost 17% of the trips to be shorter than 12 hours and suggested, that these may be the transitions between two water holes when the first visited was either already occupied or of lower quality. Different movement speeds during the trip from one water hole to the same/another one were also reported in Etosha NP, where elephants move with a higher velocity when approaching/moving out of the water hole in 97% of reported cases. The distance from which elephants decide to move towards a water hole is usually lower than 10 km but can stretch up to almost 50 km (Polansky et al., 2015). However, in contrast with those findings, Duffy et

al. (2011) found that the speed of movement differs less across habitat types than a torsion of movement.
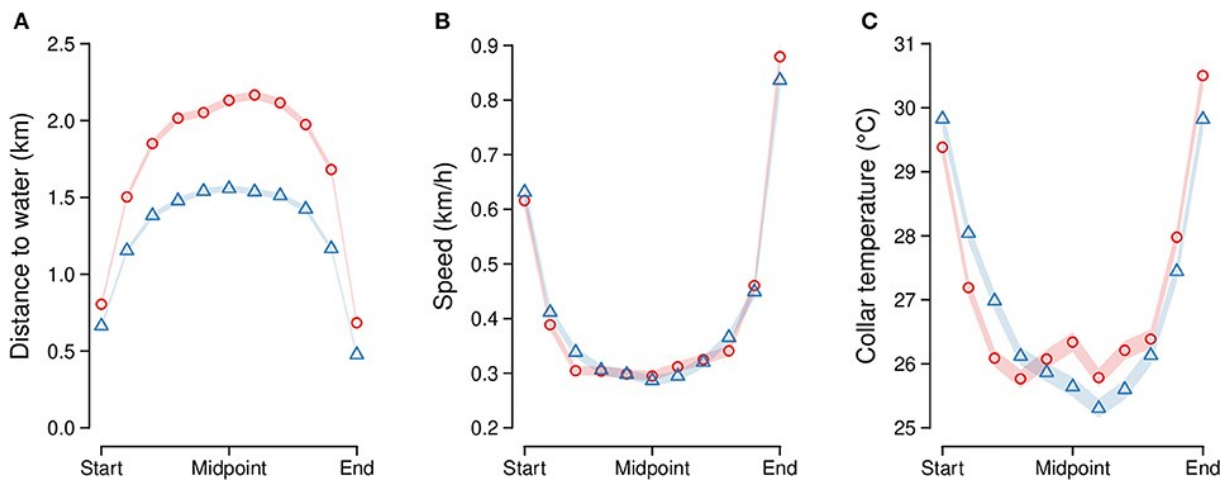
Figure 1 Changes in distance to water, velocity of movement and temperature of a GPS collar in relation to the progress of the trip between two visits at water points. Dry season shown in red, wet season in blue. From *Thaker, M., Gupte, P. R., Prins, H. H. T., Slotow, R., & Vanak, A. T. (2019). Fine-scale tracking of ambient temperature and movement reveals shuttling behavior of elephants to water. Frontiers in Ecology and Evolution, 7. https://doi.org/10.3389/fevo.2019.00004*

1.1.1 Seasonal changes in space-use of elephants in relation to water sources

African savannas are highly seasonal ecosystems (Archibold, 1995) so the seasonal changes in water availability also influence the spatial distribution of elephants. For example, elephants tend to move in less spatial scales during the wet season than during the dry season (Venter et al., 2015) probably due to the need to obtain food and to mitigate the piosphere effect during the dry season. Dry season core home ranges of the elephant more often occur in areas with less water holes than the edges of the home ranges where the amount of water holes is higher (Valls-Fox et al., 2018b). Thomas et al. (2008) think, that the spatial shifts of home ranges between the wet season and the dry season are based on the abundance of water. Sadly, this hypothesis was not tested in Thomas et al. (2008). However, there is a need to compare elephant populations across the west-east gradient in southern Africa because Loarie et al. (2009) discovered that most of their study animals move more during a wet season (see also Western & Lindsay, 1984). Although, elephants in drier areas move more than in wetter areas regardless on the season.

Elephants travel farther from water during the dry season in Etosha National Park (NP), even though they prefer the vicinity to permanent water sources in the dry season (Tsalyuk et al., 2019) and are not limited by water availability during wet seasons, when ephemeral water

sources are filled by precipitation. The reason could be a food availability and the fact that in wet seasons elephants are able to find enough food near water sources. In this case, these results also illustrate the vegetational distribution in Etosha NP (Harris et al., 2008). In the Mara region, elephants are observed in intermediate distances to rivers in the wet season but tend to move closer to the water sources during the dry season (Bhola et al., 2012). Elephants tend to feed on vegetation nearer to a water hole during the wet seasons rather than during the dry seasons (Polansky et al., 2015). This is also pronounced with findings of Thaker et al. (2019) about the mean distance to a water source in Kruger NP, which was 1.5 km in the dry season and 0.9 km in the wet season. Authors also found that the time spent by elephants near a water source in the dry season is longer by almost one hour than in the wet season. However, the probability of walking to a water source is greater in the dry season than in the wet season in Kruger NP (Purdon & van Aarde, 2017).

Seasonal differences between distances to water depend on the study area. Buchholtz et al. (2019) found a reverse situation to the results of Thaker et al. (2019) in the Okavango region. In this region, the mean daily distances of elephants to permanent water sources were ~26 km in the wet season and ~17 km in the dry season. However, authors also found that elephants were nearer to human settlements during the dry season. As human settlements are located in the vicinity of permanent water sources, elephants could take the advantage of crops and could therefore not be forced to mitigate a piosphere effect during the dry season. Ephemeral waters and higher 'natural' productivity during the wet season then enabled the elephants not to be spatially constrained by water and food such as during the dry season. Elephants move away from the Okavango river almost immediately when the wet season starts. However, they come back in ~2 days as the rains have yet not secured the sufficiency of ephemeral pools (Loarie et al., 2009; similar results from Kenya in Western, 1975; or Western & Lindsay, 1984). The quick departure of elephants from areas near water holes was found to correspond with the mean annual rainfall in Hwange NP. The same situation was reported for the dry years. As the first rains come, elephants almost immediately move to locations further away from water holes, probably seeking a higher quality food that was not present in the depleted area near water holes (Valeix, 2011). Not only drinking, but water-related behaviours such as wetting, bathing, and wallowing in the mud occurred more during a hot, dry season in the Okavango region (Mole et al., 2016). In Kenya, elephants were seen to move from bushlands to swamps - the only habitats retaining water, when the dry season progressed (Western & Lindsay, 1984).

Occurrence of elephants not being affected by human settlements in any way during the dry season was also found by Bastille-Rousseau et al. (2020) in Kenya. They also found that the occurrence of elephants near permanent water sources decreases about 3 times (300%) and increases near seasonal water sources (16%) and far from permanent human settlements (20% decrease near the settlements) in the wet season. This probably reflects the same situation displayed by Buchholtz et al. (2019), i.e., humans and elephants aggregate near water bodies during the dry season. Elephants move more during a single day in the wet season than in the dry season. Despite these findings, elephants chose areas with high NDVI regardless on the season.

Orrick (2018) described that the association of elephants with dams – artificial water sources in the South African private reserve – differs between seasons and sexes. Bulls were attracted to these sources in the wet season, but females with offspring in both seasons. In Chobe NP bulls were not attracted to rivers during the dry season as much as cows with offspring (Stokke & Du Toit, 2002). Naidoo et al. (2020) evaluated the importance of transitory water pools in Bwabwata NP (Namibia). Elephants use these ephemeral water sources, and these water bodies indeed affect the distribution of elephants. Despite this, elephants prefer the permanent water sources (i.e., rivers) more. Also, the association with those temporal sources do not play a role during the dry season. Those findings probably show that even though there can be some temporal water sources during the dry season, elephants do not count on them during those times.

Roever et al. (2012) compared habitat selection in elephant populations across the west-east gradient of precipitation and found that the selection for water varies between seasons. Most elephants choose both the proximity and the farness from water sources during the dry season, thus reflecting the "drinking" and "foraging" periods (see above). During the wet season, a greater variability was found in the elephants' selection for proximity, farness or intermediate distance to a water hole.

Overall, water sources play a significant role in the spatial distribution of elephants. Elephants prefer perennial water bodies with greater preference for rivers. Permanent water sources constrain the movements of elephants during the dry season, but elephants roam farther from them with first rains of the wet season. Distance to water also influences the interactions of elephants and vegetation.

1.2 Other herbivores

Buffalo. Buffalos (*Syncerus caffer*) are drawn to natural water sources under dry as well as wet conditions and in areas both poor and rich in nutrients. However, during droughts, buffalos are also found farther away from water, probably not being able to forage near the water source because of the piosphere effect (Redfern et al., 2003). Before 1997, buffalos were distributed approximately 1.5 km from water in Kruger National Park (NP) (Smit & Grant, 2009). Buffalos are drawn to the vicinity of both man-made water holes and rivers (Smit, 2011; for buffalos in west Africa see Cornélis et al., 2011). In Kruger NP, buffalos were also observed to utilize areas both near and far from man-made water sources on granites, which are poor in nutrients. On basaltic landscapes, the association with artificial water holes was not observed (Smit et al., 2007b). Ephemeral water pools are also a strong predictor for the occurrence of buffalos and the importance of these resources increases with a distance to a river (Naidoo et al., 2020). Hilbers et al. (2018) modelled densities of buffalos in Kruger NP and found that buffalos occur in the vicinity of rivers and move closer to them when modelled under conditions of the artificial water holes closure. Jarman (1972) found buffalos to select a drinking site by a lake according to the adjacent habitat. Shortly before dry years in Kruger NP, buffalos moved from the park to bordering private reserves where water provisioning is greater. After depleting the herbaceous food supplies, numbers of buffalos in these reserves declined dramatically (Smit et al., 2020). Buffalos themselves have a great degradational impact on grass vegetation near permanent water points (Epaphras et al., 2008).

The changes of spatial responses of buffalos to river habitats occur also between seasons. During wet seasons buffalos utilize riverine thickets, but they move out from this habitat during the dry season, reacting on the depletion of grass vegetation (Venter & Watson, 2008). On the other hand, Fynn et al. (2014) observed buffalos to utilize swamps during both seasons in Botswana. Omphile & Powell (2002) reported buffalos utilizing floodplain grasslands in Chobe NP more during a progressed dry season. Traill (2004) reported buffalos to use areas near water during the hot-dry season in Zimbabwe. Despite these findings, Bhola et al. (2012) reported the distribution of buffalos in Kenya not to be affected by the vicinity to a river in both seasons in a reserve but by the NDVI. The vicinity to water has an impact on whether two groups of buffalos split or merge during the dry season, with merging events being probable nearer to water. However, buffalos usually spend their time in the specific distance to water where both splitting and merging events occur at the same rate (Wielgus et al., 2020).

Zebra. The relation of the occurrence of plains zebras (*Equus quagga*, hereafter also "zebra" if not stated otherwise) in Kruger NP and the distance to water is weak. Plains zebras utilize areas farther away from water sources on landscapes that are poor in nutrients more than on landscapes rich in nutrients, but the difference is not notable. During dry years, plains zebras tend to occupy areas farther from water than during wet years (Redfern et al., 2003), probably reacting to the piosphere effects near water sources. This spatial relation is pronounced towards rivers, but positive association is exhibited towards artificial water sources in Kruger NP (Smit et al., 2007b; Smit, 2011). Areas near rivers in Namibia are utilized by Hartmann's mountain zebras (*Equus zebra hartmannae*), predominantly during the dry season (Muntifering et al., 2019). Plains zebras can range to areas naturally dry following the construction of artificial water holes. They also leave areas with these water sources being closed down (Harrington et al., 1999). Using modelling methods, zebras in Kruger NP were found farther away from rivers and this occurrence did not change when modelled under moderately dry conditions (when natural water sources become sparser). Zebras moved closer to rivers under especially dry conditions (Hilbers et al., 2018).

In Mozambique, Mandlate et al. (2019) found that the probability of occurrence of plains zebras is lower with a greater distance to water during the dry season. On the other hand, Groom & Harris (2010) observed plains zebras several kilometres away from a water source during the dry season (see also Traill, 2004). Although being closer to a man-made water point, the authors did not observe plains zebras to utilize this resource. During dry season, plains zebras were also observed to dig water holes in areas of dried-up rivers (Epaphras et al., 2008). Bhola et al. (2012) reported that plains zebras use areas in moderate distances to a water source in a Kenyan reserve during the dry season. In ranches, however, densities of plains zebras peaked farther away from a water source during the dry season (see also Ogutu et al., 2010). Despite these findings, Ogutu et al. (2010) reported plains zebras to be present closer to water sources in Kenyan ranches during the wet year, probably due to foraging options. Plains zebras were also attracted to temporal pastoral settlements. Areas near and in intermediate distances to a water source are also occupied by Grévy's zebras (*Equus grevyi*) (De Leeuw et al., 2001). De Leeuw et al. (2001) also found plains zebras to occur in the vicinity of water sources despite livestock being present as well. Applying for most of their study animals, Brooks & Harris (2008) found that plains zebras depart from water holes using a direct path to a feeding ground more than 3 km away.

Wildebeest. Although water sources play a role in the probability of occurrence in the blue wildebeest (*Connochaetes taurinus*, hereafter "wildebeest"), other variables related to foraging have a greater effect on the occurrence of wildebeests (Mandlate et al., 2019). As well as zebras, wildebeests do not considerably respond to a distance to rivers in their choice of habitat, especially not in areas that are poor in nutrients (Redfern et al., 2003). However, they utilize areas near the man-made water holes (Smit et al., 2007b; Smit, 2011) and leave those areas where man-made water holes are being closed (Harrington et al., 1999). When artificial water holes were closed down in central Kalahari, wildebeests travelled longer distances in a day looking for a new source of drinking water (Selebatso et al., 2018). Artificial water points can promote the perseverance of wildebeests during dry seasons in areas that are naturally very dry (see also Harrington et al., 1999; or Knight, 1995). In those localities, wildebeest tend to drink from and occur in areas near the water holes that provide fresh water. If water holes provide water with more minerals, the probability of their utilization by wildebeest increases with higher NDVI (Weeber et al., 2020). Although, Child et al. (1971) found no significant association between the choice of a water point and minerals.

During the wet season, the occurrence of wildebeests is not limited with water as much as during the dry season (Weeber et al., 2020). During the wet season, wildebeests choose areas farther away from a river in the protected area of the Mara region. During the dry season, wildebeests occupy the reserve more evenly in relation to the water source. In pastoral areas, the occurrence of wildebeests is not affected by the distance to a river (Bhola et al., 2012). Ogutu et al. (2010) found wildebeests in Kenya to occur in areas of intermediate distances to water sources in a reserve during the dry and the wet year. In ranches, this species was seen to choose areas in the intermediate distance to water in the dry year. They came closer to water sources located farther away from pastoral settlements in the wet year, probably not being limited by a piosphere effect in the wet year. In Zimbabwe, wildebeests occur in areas far from water during the hot-dry season (Traill, 2004; see also Groom & Harris, 2010). However, the movement of wildebeests from open grassland foraging areas are usually due to a need to obtain water and are more frequent during dry seasons (Owen-Smith & Traill, 2017). Occurrence of wildebeests modelled in Kruger NP peaked in areas farther away from rivers (Hilbers et al., 2018).

Waterbuck, lechwe. Densities of waterbucks (*Kobus ellipsiprymnus*) in general peak in the vicinity of water sources. However, as well as buffalos and other herbivores, waterbucks need to cope with the piosphere effect during droughts, thus occurring also in areas farther away

from water. This is pronounced especially in nutrient-poor areas (Redfern et al., 2003). However, waterbucks are drawn to rivers and habitats related to rivers and do not show an invariable spatial relation to artificial water points (Smit et al., 2007b). Properties of habitats situated near rivers could potentially be more important for this species than water itself (Smit, 2011). Before 1997, waterbucks were found approximately 1 km away from a source of water in Kruger NP (Smit & Grant, 2009). In Zimbabwe, waterbucks were seen to choose habitats close to water during the hot-dry season (Traill, 2004). As well as waterbucks, lechwes (*Kobus leche*) were observed to utilize habitats related to a water supply in Botswana, mostly floodplains and swamps (Fynn et al., 2014).

Hippo, warthog, rhino. During droughts in Kruger NP, hippos (*Hippopotamus amphibius*) were seen to move into seasonal water sources more recurrently rather than to persevere in the perennial rivers. Probably due to searching for food resources (Smit et al., 2020). White rhinos (*Cerathoterium simum*) do not respond spatially to either man-made or natural water points, but they slightly tend to be present nearer to water holes than farther away from them (Smit et al., 2007b; see also Traill, 2004). However, Smit (2011) found that areas near to artificial water sources are significantly more preferred by white rhinos. On the other hand, water is found to be an important predictor for black rhinos (*Diceros bicornis*) as their home ranges shrink during the dry season (le Roex et al., 2019). Warthogs (*Phacochoerus* spp.) in Kenya are distributed in areas of intermediate distances to both waters and the settlements of pastoralists in pastoral areas during both the wet and the dry year. Warthogs are distributed similarly in a reserve in the wet year. Pastoral areas under wetter conditions were evenly occupied by warthogs (Ogutu et al., 2010). In Zimbabwe, warthogs were observed to utilize areas near water sources (Traill, 2004).

Roan and sable antelopes. Both roan antelopes (*Hippotragus equinus*) and sable antelopes (*Hippotragus niger*) are observed to be drawn to artificial water points. On the other hand, these species do not utilize areas near rivers in the Kruger NP (Smit et al., 2007b; Smit, 2011). During the dry season in Zimbabwe, sable antelopes were seen to choose areas farther away from water (Traill, 2004). On the other hand, Cain et al. (2012) reported sable antelopes to occupy two home ranges with the dry season home range being closer to permanent water sources. In Kruger NP, a lower number of roan antelopes persisted in areas where artificial water holes were not closed after the changes in a water supply policy. These changes were applied after reconsidering the effects of high-water supply in the 1990s. Areas far from artificial water holes are also important for the reproduction of this species (Harrington et al.,

1999). Roan antelopes are shown by the method of modelling to occur in moderate distances to rivers, but they move closer to rivers when artificial water holes are sparser (Hilbers et al., 2018).

Impala. Impalas (*Aepyceros melampus*) occur close to water bodies. During droughts, impalas were observed to go further away from the water source in areas rich in nutrients. In areas poor in nutrients, impalas utilized similar areas in relation to a distance to water in both wet and dry years (Redfern et al., 2003). Impala occurs closer to natural water sources but shows no preference for water holes or even avoids them in Kruger NP (Smit et al., 2007b). In contrast, in Ruaha NP impalas used man-made water holes more than natural water points (Epaphras et al., 2008). In the Kenyan reserve, densities of impalas were concentrated either in the vicinity of water and far from pastoral settlements, or near the settlements but farther away from water under both the dry and the wet year conditions. This probably shows impalas not being limited by water sources (Ogutu et al., 2010). In Botswana, impalas were seen to utilize areas of swamps and floodplains during both seasons (Fynn et al., 2014). In Chobe NP, they were observed to utilize the floodplain grasslands more during the dry season than during the wet season (Omphile & Powell, 2002). Impalas were also observed to use water holes dug up by elephants (Jarman, 1972). Modelled occurrence of impalas peaked further away from rivers and the closure of water holes did not impact the occurrence of these animals under the conditions of unlimited natural water sources. In contrast to the findings of Redfern et al. (2003) regarding the distribution of animals under natural dry conditions, results of the model suggest that impalas moved closer to rivers (Hilbers et al., 2018).

Thomson's and Grant's gazelle. Bhola et al. (2012) observed Thomson's gazelles (*Eudorcas thomsonii*) as well as impalas further away from rivers in the wet season in a Kenyan reserve, however, they are shown to move closer to water bodies in ranches. Ogutu et al. (2010) found Thomson's gazelle to utilize areas in moderate distances to a water source while being near the settlements of pastoralists. Thomson's gazelles were also observed close to water sources while being far from the settlements in a Kenyan reserve during a wet year. During the wet year, Grant's gazelle (*Nanger granti*) showed the distribution peaking in the vicinity of temporal human settlements and in intermediate distances to water sources in the Kenyan protected area (Ogutu et al., 2010; De Leeuw et al., 2001).

Giraffe, steenbok, nyala, bushbuck and kudu. Both giraffe and greater kudu (*Tragelaphus strepsiceros*, hereafter also "kudu" if not stated otherwise) show a small spatial relation of their densities to the distance to water sources. Giraffes also do not respond spatially

13

to the amount of nutrients. On the other hand, kudus were observed to utilize areas farther away from water in landscapes high in nutrients during droughts. However, this difference was not seen under wet conditions (Redfern et al., 2003). On the other hand, giraffes and kudus were seen to occupy areas nearer to rivers but show no or negative spatial response towards artificial water holes in Kruger NP during the high-water supply period (Smit et al., 2007b). Giraffes were observed closer to rivers and in areas without human presence in both the protected reserve and pastoral areas during both dry and wet season in Kenya (Bhola et al., 2012). Similarly, nyalas (*Tragelaphus angasii*) are situated close to water sources during the hot-wet season (Traill, 2004). In Ruaha NP, giraffes were observed to utilize artificial water holes more than natural water holes (Epaphras et al., 2008). In Chobe NP, giraffes were seen to utilize floodplain grasslands and this utilization advanced from February to June (Omphile & Powell, 2002). De Leeuw et al. (2001) found giraffes to keep away from areas less than 10 km away from water. While modelling their densities, giraffes were not observed to be spatially restricted to the vicinity of rivers in Kruger NP under any of wet-to-dry conditions. Steenbok (*Raphicerus campestris*) as well as giraffe was not shown to be spatially affected by the distance to rivers (Hilbers et al., 2018). In Chobe NP, kudus utilize 3 habitat types adjusted to the river (including floodplain grasslands) equivalently (Omphile & Powell, 2002). Modelling the occurrence of kudus, kudus were seen to occupy areas farther away from rivers and moved closer to them under dry conditions when water holes were closed. The occurrence of bushbucks (*Tragelaphus scriptus*) was modelled similarly to the occurrence of kudus in Kruger NP (Hilbers et al., 2018).

Eland, tsessebe and hartebeest, gemsbok and springbok. Elands (*Taurotragus oryx*) in Kruger NP utilize areas closer to artificial water sources but they show no spatial association with rivers (Smit et al., 2007b). Presence of artificial water sources can also promote movements of elands to dry areas (Knight, 1995). Tsessebes (*Damaliscus lunatus*) are observed to strongly utilize areas near man-made water holes, areas near rivers are utilized randomly (Smit et al., 2007b; Smit, 2011). Tsessebe was observed to utilize areas farther away from water in a Kenyan reserve during the wet season. However, as well as impalas and Thomson's gazelles, tsessebe was observed closer to rivers in ranches. During the dry season, tsessebe and hartebeest (*Alcelaphus buselaphus*) occupy areas nearer to water in the reserve, but in ranches they tend to move to areas farther away from river (Bhola et al., 2012). During the wet year, tsessebe was seen to occur in areas in the vicinity of temporal human settlements and in moderate distances to water bodies in a Kenyan reserve (Ogutu et al., 2010). The occurrence of springbok (*Antidorcas marsupialis*) at water points could be affected by adjacent habitats. Their

defecation rate is higher at distances further away from water points adjacent to the desert in Kalahari. The choice of water points by springbok and hartebeest is not affected by minerals. On the other hand, gemsbok (*Oryx gazella*) occurrence at water point is positively associated with the amount of carbonate, bicarbonate, and fluorine ions (Child et al., 1971).

Herbivores vs water provisioning and droughts. Smit & Grant (2009) modelled the possible effects of drought on a distance to water in several grazers in Kruger NP. They found out that drought would affect those distances least during the high-water supply period. Under no evaluated dry conditions, the artificial water provisioning changed the occurrence of most grazers in relation to a distance to water significantly. The present water supply policy in Kruger NP, when nearly half of the pre-1997 water holes are closed, would have a significant effect only under the conditions of drought. Authors argue that food resources rather than water resources were driving the distribution of grazers during the high-water supply period in Kruger NP. They also argue that common grazers (zebra, wildebeest) are able to adjust their distribution regarding the placement of water holes more than rarer species (roan, sable). Current water provisioning could create a natural distribution of grazers under dry conditions because water would be a more limiting resource than it was before 1997. As provisioning of water sources in naturally dry areas lure herbivores to move into these locations, it can lead to herbivore species dying from lack of food resource in these areas rather than from the lack of water (Knight, 1995).

Piosphere effect. Changes in herbaceous vegetation due to foraging pressure of herbivores does not differ between areas near artificial and natural water resources (Thrash, 1998). Densities of grazers mostly increase drastically with the decreasing distance to water sources (Thrash et al., 1995). As they feed on grasses ambient to water points, changes in distribution of grass species occur. Tall grasses are found farther away from these heavily grazed areas near water sources, but short grasses are promoted in those areas near water (Sianga et al., 2017). These changes in height classes of grasses can result into spatial and populational changes in those herbivore species, which prefer the high grass species (e.g., roan antelope, Harrington et al., 1999; see also Thrash et al., 1995). Grazing near water points also causes that grasses preferring disturbances, unlike perennial grasses, occur near those utilized water sources. However, these annual grass species provide less amount of forage than perennial ones (Thrash et al., 1993) which could lead to animals departing from water points to obtain food resources.

Thrash (2000) reported in the study site in southern Africa that the impact on herbaceous vegetation caused by herbivores occurs up to 200 metres from a water resource. He also found that congregated water points have a larger negative impact on the conditions of adjacent vegetation than a single water point. However, Van Rooyen et al. (1994) found that changes in herbaceous vegetation are not associated with the distance to water but are associated with the grazing pressure in Kalahari Gemsbok NP (South Africa). These finding may not contradict the previously mentioned relation of distance to water and compositional changes in vegetation. Results in Van Rooyen et al. (1994) may show the scarcity of grazeable vegetation in Kalahari. Parker & Witkowski (1999) found that areas farther away from permanent water sources promote perennial grasses more than areas near these water sources during the wet season. The smallest amount of perennial grasses was, however, found near seasonal water sources. This suggests that herbivores use seasonal ephemeral water sources more than permanent water sources during the wet season.

Lakes. Jarman (1972) evaluated the importance of a newly established lake as a source of drinking water for wildlife. He found that the lake was primarily used by animals during the dry season and animal-originated ephemeral pools were used by animals during the wet season. The sites where animals drink from the lake are specific. For example, for most species, these sites are characterized by a mild slope of the shore.

In general, water sources affect spatial distribution of ungulate species with some species preferring rivers (waterbuck, buffalo), some preferring artificial water holes (zebra, wildebeest, white rhino). Some species occur further away from water sources (roan and sable antelope, browsers) but can use riverine vegetation for foraging.

2. How do ecological interactions (predation and competition) influence the water-related space-use?

2.1 Predation

Looking at the previous chapter concerning the utilization of space in relation to the distance to water sources in herbivore species, it is a logical outcome that predators feeding on these species will come closer to water sources. Indeed, predators such as lions or cheetahs (Acinonyx jubatus) prefer areas near water sources such as rivers (Tagwireyi et al., 2020; Spong, 2002) or man-made water holes (Valeix et al., 2010; Epaphras et al., 2008) following the distribution of prey animals (Mills et al., 2020). It is evident that predator-prey interactions

are prevalent in areas near those water resources. This spatial distribution of predator-prey interactions near water sources strongly applies for water dependent species of herbivores (i.e., grazers, see below) and lions, as most of their kills occur in the vicinity of water points (Davidson et al., 2013; Hopcraft et al., 2005; Hutson, 2016). Kittle et al. (2016) noticed that lions are usually spatially arranged to occur between a water source and a prey animal.

Bhola et al. (2012) found that small and medium-sized herbivores avoid rivers in a reserve during the wet season. Bhola et al. explain it with the effect of predation as riverine habitat provides cover for ambush predators. The effect of the size of prey species on its occurrence at water holes under the risk of predation was also noted by Sutherland et al. (2018). They observed impalas but not elephants or rhinoceros being affected by the occurrence of carnivores at a water hole. This is one of the evidence of large herbivores being less predated upon (Owen-Smith & Mills, 2008). Lions can be lured into new locations following the construction of water points and movements of common grazers dependent on these water sources. The utilization of new areas by lions can have a negative effect on both, space utilization and population dynamics of herbivore species that are used to lower predation and competition interactions (e.g., roan) (Harrington et al., 1999). Even though lions hunt almost exclusively in the vicinity of water points, some prey species (kudus, small antelopes) are hunted down farther away from water unlike other prey (elephants, giraffes) (Davidson et al., 2013).

The body size of prey species also produces a difference in herd sizes while herbivores are present at a water hole. Zebras and wildebeests tend to form larger groups at water holes in areas where lions are the main predators (see also Valeix et al., 2009c). Contrary to this, smaller species as gemsbok, warthog, and red hartebeest form larger groups at water points in areas, where cheetahs and African wild dogs (*Lycaon pictus*) are the main predators. This and the higher vigilance of all herbivore species in the area where lions hunt suggest that lions are a bigger threat than cheetahs or African wild dogs (Makin et al., 2017). Kudus, as well as giraffes, and sable antelopes prefer drinking in larger herds (Crosmary et al., 2012a; Valeix et al., 2008). Despite this, the association of the herbivore herd size and the threat of coming across lions at water holes was found to be inconsiderable. During a regularly wet year (but not during a drought), a smaller number of groups of buffalos were observed utilizing a water source when lions posed a greater long-term threat. In contrast, there was more groups of zebras, wildebeests, sable antelopes, and roan antelopes observed when the long-term threat of coming across lions was higher. Buffalos, giraffes and kudus come to water holes to drink more often when there are no lions nearby (Valeix et al., 2009c; for wildebeests see Martin et al., 2015). The long-term

threat of meeting lions has a different effect on different guilds of herbivores in comparison with the distance to water (for grazers: long-term lion threat < distance to water; for water-dependent browsers: long-term lion threat * distance to water; for water-independent browsers: negative effect of long-term lion threat) (Valeix et al., 2009a).

As apex predators of southern and eastern African savannas [i.e., lions and spotted hyenas (Crocuta crocuta)] are mostly active at night (Crosmary et al., 2012b), prey species should constrain their visits at water source to the daytime. On the other hand, human hunters are mostly active during daytime, thus causing additional mortality risk to game species. Crosmary et al. (2012b) discovered that, indeed, herbivore species such as impala, kudu, and sable antelope were visiting water holes mainly in daytime, particularly during the midday, in Hwange National Park (NP) (for buffalos see Valeix et al., 2009c). Although, these herbivores also compensate the risk posed by hunters in adjacent hunting areas by visiting water holes also at night in 20% of cases for kudu, 24% for impala, and 50% of cases for sable antelope (for modelling see also Sirot et al., 2016) (Fig. 2). According to these shifts, sable antelopes came to water holes on average after 18:00 in hunting areas contrary to almost midday in the NP (Fig. 2). The choice of impalas to visit water points at night was also affected by the presence of offspring. The odds of the night visit were lower in herds with offspring. In the NP, the odds for kudu coming to a water hole at night is lower than for impala and sable, which probably shows the vulnerability of kudus caused by the risk of being killed by lions or hyenas. In hunting areas, visits of these herbivores at water holes are also variable in time causing hunters not knowing where they can encounter these animals (Crosmary et al., 2012b). Zebras, wildebeests,
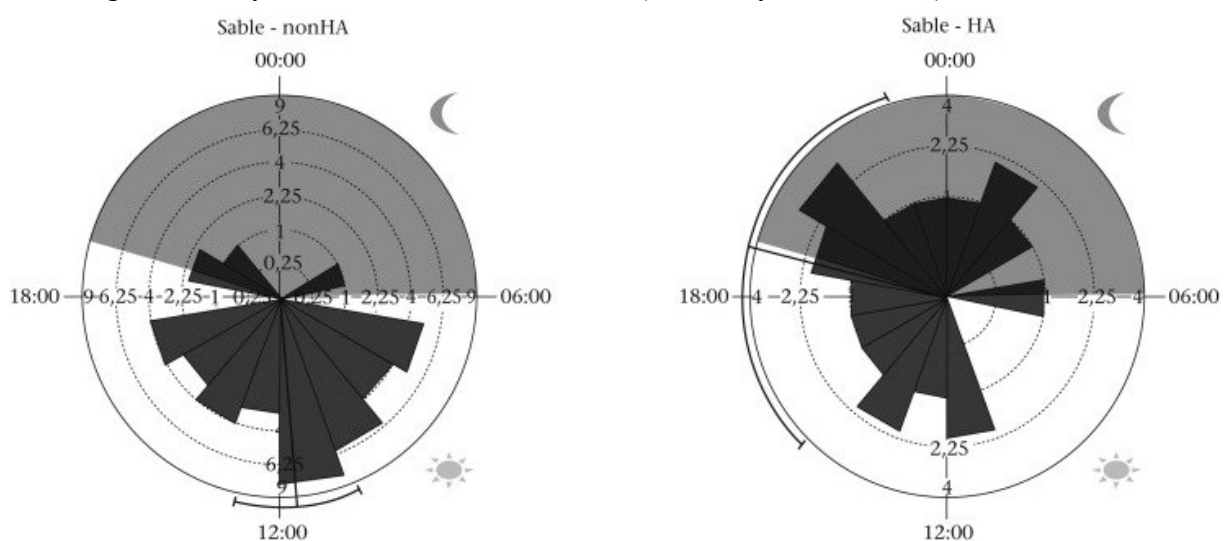
Figure 2 Activity of sable antelopes (black columns) at water bodies in a national park (nonHA) and a hunting area (HA). Night hours in grey. Adapted from *Crosmary, W. G., Valeix, M., Fritz, H., Madzikanda, H., & Côté, S. D. (2012b). African ungulates and their drinking problems: Hunting and predation risks constrain access to water. Animal Behaviour, 83(1), 145–153. https://doi.org/10.1016/j.anbehav.2011.10.019*

and gemsbok also visit water holes less during the night in areas where lions are the main predators [thus zebras having a lower encounter rate (Courbin et al., 2016)], in contrast to areas where cheetah and African wild dogs hunt (Makin et al., 2017).

Predators can also avoid the vicinity of water holes as presented in Kushata et al. (2018) who evaluated the relationship of resting localities of spotted hyenas to the distance to a water hole during the wet season. They discovered that during this part of the year, water sources do not affect the localization of the resting sites of hyenas. This was probably because of the avoidance of prey animals or because of the wider distribution of water resources during this season. Herbivore species (see below) temporally and spatially segregate at water points, and carnivore species can be forced to do so as well (Edwards et al., 2015). This segregation could impact, as reviewed above, some herbivore species so these will tend to be present at water holes mainly during daytime.

Despite utilizing areas near artificial water holes, zebras are found farther away from these resources at night more than during daytime. If zebras come across lions at water holes, they move up to 4 km away from these water bodies. If they do not meet lions, they move mostly 1.5 km away. Zebras seem to have two flight strategies. As the first option, they run away instantly after the contact with lions to areas farther away from water holes and then they proceed to follow regular spatial activities the next day. As the second option, they prolong their getaway and continue to follow the normal spatial behaviour towards the water holes the second day after the contact. This could explain why lions tend to move to another water hole after a successful hunt (Courbin et al., 2016; Courbin et al., 2019) as presented in Valeix et al. (2011). Valeix et al. (2011) showed that lions moved towards another water hole when they had killed a prey animal near a man-made water point. They also discovered that lions were shifting their hunting areas among the water holes more if there were more water holes in their home range. Zebras exhibit spatial segregation between night and day in distance to water more during the dry season than during the wet season (Courbin et al., 2019).

Van der Meer et al. (2012) found that the simulated occurrence of African wild dogs near water holes had no impact on the time kudus and impalas used for actual drinking from a water hole. It also has no impact on the number of groups coming to a water hole. However, simulations may not increase the predation risk at water holes where natural predation risk is notable. Although, authors noticed that kudus drank for a smaller amount of time in the later afternoon, suggesting that they were aware of predators actively hunting during daytime. African wild dogs themselves can be a prey species for lions (Reich, 1981 cited in Van der

Meer et al., 2013). They choose to dig/use dens farther than 2 km away from a water hole, where most of the kills by lions occur (Valeix et al., 2010). This spatial use of farther located areas is more prevalent in areas with a high-level threat of encountering lions (Van der Meer et al., 2013).

Herbivores tend to drink more in the national park than in hunting areas, where mortality risk is higher (cumulative effect of hunters and natural predators). The odds of drinking is greater at water holes, at which bush vegetation is closer (see also Valeix et al., 2008). Higher vigilance is used by kudu, impala, and sable while moving towards and departing from a water point rather than while drinking. Impalas and sable antelopes apply higher vigilance in hunting areas rather than in a NP while departing from a water point (Crosmary et al., 2012a). Most ungulate species also spend more time approaching water bodies while there is a higher chance of meeting lions in the long term (Valeix et al., 2009c; Valeix et al., 2008), when bush vegetation is further away from a water hole, or when offspring of herbivores are present. On the other hand, the time spent approaching water sources is lower when herbivores (giraffe, roan, sable, waterbuck) form bigger groups (Valeix et al., 2008). Additionally, wildebeests spend less time in the vicinity of a water hole when woodlands are closer to the water hole (Martin et al., 2015), probably because lions could use this vegetation to hide themselves. This different view at bush/woody vegetation could mean that some herbivore species use this vegetation for hiding and other see it as a potential threat.

2.2 Competition

Most herbivore species need to use water sources regularly and these sources are usually numerically and spatially rare during the dry season. It is obvious that animals would need to cope with the presence of other animals of the same or different species at water bodies. They could avoid the competitors either in space (i.e., using a different water source), or in time (i.e., coming to a water source in a different time than others).

It was shown that other herbivore species do not pose a competitional pressure to kudus and impalas in terms of time spent actually drinking (van der Meer et al., 2012). On the other hand, giraffes and roan antelopes hesitate with the decision to drink at a water hole when it is crowded by elephants. Sable antelopes are also affected by competition, in this case not by elephants but other species of herbivores (Valeix et al., 2008). Looking at a finer scale of the utilization of a water hole by herbivore species, elephants were observed to drink fresher water (i.e., from a trough) than other herbivores (zebras, kudus, …). These species were placed on the

opposite side of a water hole where water was enriched with organic materials. Even when elephants were absent, these species stayed at the same drinking spot. However, roan and sable antelopes were noticed to drink in a variety of places at a water hole, thus being possibly more exposed to competition with elephants (Ferry et al., 2020). During the dry season, zebras, kudus, and giraffes tend to be present at water holes occupied by elephants more than during the wet season. Consequently, aggressive behaviour between elephants and other herbivores increased in frequency during the dry season (Ferry et al., 2016; for a dry year see Valeix et al., 2007). This behaviour was also seen more in female elephants in contrast to male elephants (Berger & Cunningham, 1998). However, a clear spatial segregation from elephants was observed only in zebras at the start of the dry season, not at the end of it (Ferry et al., 2016). The number of elephants at a water hole also has an impact on the number of interplays with elephants for impalas, kudus, warthogs, and sable and roan antelopes. Excluding warthog and adding buffalo, these species also showed a temporal segregation from elephants at a water hole, either for decreasing the probability of interactions or for not having enough space at a water hole while elephants are present. On the other hand, giraffes, wildebeests and waterbucks showed no temporal segregation from elephants (Valeix et al., 2007).

Modelling the space utilization under different scenarios of the water provision and the level of drought, Hilbers et al. (2018) described that the movement of elephants towards rivers causes other herbivores (except buffalos) to leave those areas. Despite this, Valeix et al. (2009b) found that zebras, roan and sable antelopes, impalas, and warthogs spend significantly more time using a water hole when elephants use it as well. They delineate these findings by assuming that the herbivores either feel safe by the presence of elephants, or that they need to spend more time in vigilance.

Opening new man-made water holes can lead to movements of some herbivore species preferring this resource into new areas. The grazing pressure on herbaceous vegetations can lead to the creation of areas unfavourable by other species (e.g., roan antelope), who prefer higher grasses (Harrington et al., 1999). As water is used by animals also for other than drinking purposes, Jarman (1972) described the use of mud baths by elephants, rhinos and buffalos. He discovered that those three species do not use mud bath sites of one another.

Wild herbivores compete not only with other wild herbivore species, but also with livestock and other individuals of the same species. During a dry season, tsessebes, hartebeests, and zebras usually use areas far from the rivers in ranches where livestock does not occur. On the other hand, giraffes were situated near rivers in those areas. This shows no or little overlap

of resource usage between giraffes and livestock (Bhola et al., 2012). As home ranges of buffalos are more concentrated near water sources during the dry season, their home ranges overlay with areas used by cattle. Consequently, buffalos drink at dawn and dusk when chances of meeting cattle are low. Elephants solve the potential undesirable interactions with cattle by drinking at night (Valls-Fox et al., 2018a). Sitters et al. (2009) observed spatial segregation of cattle and water-dependent grazers in relation to persistent water points and seasonal swamps. The spatial closeness to these water sources was seen in wild water-dependent grazers but not in cattle. Despite the clear segregation, this can be also explained only with the dependency of some herbivores on water. Intraspecific competition in elephants regarding the use of water sources is shown in Wittemyer et al. (2007). The authors showed that subordinate elephant groups utilize areas in greater distance to water more than dominant groups. The hierarchy of elephant groups also played a role in using areas less than 1 km from a water point, but not in areas more distant during the wet season.

Mainly, herbivore species react on the presence of other animals (both predators and competitors) at water points by adjusting their spatio-temporal distribution to time periods when the odds of ecological interactions are lower. We can thus observe spatio-temporal segregation of mammalian species at water bodies.

3.   How much do animals need to drink and when do they drink?

3.1 Water dependency

The utilization of space in relation to water differs among herbivore species, as shown in the chapters above. Some of these species are found close to water sources, some farther away. Western (1975) divided the large herbivores into two groups according to their spatial occurrence in relation to water sources – water dependent species and water independent species. He showed that grazers (zebra, wildebeest, warthog, etc.) and elephants (mix-feeders) are primarily water dependent species. Contrary to this, browsers [giraffe, lesser kudu (*Tragelaphus imberbis*), eland, etc.] are water independent species. Water dependent species thus concentrate near water sources during the dry season. However, water independent species can utilize the same areas far from water points year-round. The inter-guild differences in water dependency arise from different water intake via food and gut physiology. Browsers feeding on leaves that contain more water than grass are water independent and non-ruminants are more water dependent (Kihwele et al., 2020).

Therefore, a distinction of water dependencies between zebras (non-ruminants) and sable antelopes (ruminants) should occur. Indeed, zebras need to drink more often than sable antelopes and visit water sources once in one to two days. Sable antelopes visit a water point once in three to four days. Sable antelopes cover larger distances than zebras while moving from a foraging site to a water source. Despite this, time used for accessing a water point is similar for both species as zebras use to forage while departing from a water body (Cain et al., 2012).

Precipitation has no impact on the spatial occurrence of giraffe and greater kudu in relation to water sources, thus showing their water independence. On the other hand, all considered grazers had to solve a trade-off between food and water resources, thus suggesting a more significant importance of water to them (Redfern et al., 2003; Smit et al., 2007b). A specific comparison between water dependent wildebeest and water independent gemsbok showed that wildebeests, unlike gemsbok, almost never occur further than 20 km away from water sources (Boyers et al., 2019).

Even though water requirements are high for some species (greater kudu, Grévy's zebra), these species can supress their need to drink often (Kihwele et al., 2020). Water dependency can also affect predation risk as water dependent species cannot escape predation at water sources (Hutson, 2016). Those species are killed by lions more in the vicinity of water sources, but lions do not choose their prey according to its water dependency (De Boer et al., 2010).

Models of Hilbers et al. (2018) propose a higher water dependency of roan antelope and buffalo, as these two species changed their occurrence towards rivers in the model under moderately dry conditions. The models also show giraffe and steenbok to be water independent, as their occurrence did not contract towards rivers in the model. Water dependence of elephant was modelled by Dunkin et al. (2013), who showed that elephants can lose more than 100 litres of water a day for cooling under the dry climate conditions of Namibia.

Overall, water dependency of certain species depends on the feeding niche (browser/grazer) and gut physiology (ruminant/non-ruminant). Consequently, mammalian species are distributed differently in relation to the distance to water sources.

3.2 Diurnal patterns of visitations at water sources

As described in the *Predation* and *Competition* chapters, animals can visit water sources in different times of the day. Temporal shifts in the visitations of herbivores at water sources as reaction to other animals are described in chapters mentioned above. Thus, in this chapter, other temporal patterns of utilization of water bodies without the effects of predation and competition are reviewed.

Elephants. In Kruger National Park (NP), elephants utilize water sources during the hottest period of a day. Elephants usually depart from the water source at 2 pm and come back to it at 11 am the next day during the dry season. During the wet season, this whole process takes place approximately one hour earlier (Thaker et al., 2019; Sutherland et al., 2018; Hayward & Hayward, 2012). However, Purdon & van Aarde (2017) described that elephants in Kruger NP use water holes in the afternoon, evening and the first half of the night. Contrary to findings of Thaker et al. (2019), elephants in Etosha NP utilize water holes during the evening and night and move farther away from them for a midday (Tsalyuk et al., 2019). In the Okavango region, the closeness of elephants to a water source peaks in the evening, in the afternoon and at night. In the morning, elephants use areas farther away from water sources (Buchholtz et al., 2019). On the other hand, Mole et al. (2016) found that elephants drink the most in the morning and their activity at water sources declines through other parts of the day. Results of Loarie et al. (2009) show that across the west-east gradient of southern Africa, elephants are most active at water sources at night, predominantly at midnight. Elephants are also shown to be least active during midday. Number of groups of elephants coming to a water hole in one day differs accordingly to precipitation. During the dry year, more groups of elephants come to a water hole in a day than during a regularly wet year (Valeix, 2011). In Hwange NP, elephants also use water holes in earlier parts of the day when yearly precipitation declines (Valeix et al., 2007). In Chobe NP, elephants utilize floodplain grasslands more than any other habitats during the afternoon (Omphile & Powell, 2002). Wittemyer et al. (2017) showed that elephants use to rest near rivers in a protected area during a day, but they rest in further distances from rivers at night. In unguarded areas, the time of the day does not affect the distance from water to a resting site. This resting site occurs further away from rivers.

Grazers. White rhinos were noticed to use areas near water holes at dusk in Kruger NP (Sutherland et al., 2018). In Waterberg NP (Namibia), white rhinos, as well as buffalos, used water points from dusk to midnight (Kasiringua et al., 2017). During the dry year, more groups

of buffalos, zebras, roan antelopes, and sable antelopes come to a water hole to drink in a day than during a regularly wet year (Valeix, 2011). In Chobe NP, buffalos are seen to use floodplain grasslands mainly during the afternoon during the dry season and the end of the wet season (Omphile & Powell, 2002). Both zebras and sable antelopes start a travel to a water source in early hours, usually at dawn, and they arrive at the water source before noon. Both species leave the areas near water bodies in an early afternoon, usually before 3 pm (Cain et al., 2012; for sable and roan see Kasiringua et al., 2017). Common reedbuck (*Redunca arundinum*) and wildebeest used a water hole mostly around 4 pm. Waterbucks were most active at water holes before noon. Similarly, warthogs were most active before noon and continued to be active at water holes till ~3 pm (Hayward & Hayward, 2012; Kasiringua et al., 2017).

Browsers and impalas. Impalas utilize water holes during the hottest period of the day in Kruger NP (Sutherland et al., 2018). On the other hand, Hayward & Hayward (2012) observed impalas to be present at water points at most before noon. Despite the peak of the activity before noon, the activity of impalas at water holes was observed throughout a day. However, impalas did not use water holes at night. The authors also observed eland as the only ungulate species to use water points also at night (for elands in Namibia see Kasiringua et al., 2017). Kudu, as well as giraffe utilized water holes mainly in the evening. Contrary to these browsers, nyalas were noticed to use a water hole before and during midday. In Waterberg NP, giraffes were observed to drink from a water hole between 11 am and 3 pm (Kasiringua et al., 2017). In Chobe NP, giraffes, impalas, and kudus were observed utilizing floodplain grasslands during the afternoon (Omphile & Powell, 2002). Kudus in Hwange NP are used to drink more in the morning and early afternoon than later in the day (van der Meer et al., 2012). Black rhinos come closer to permanent water sources at night, and they utilize areas farther away from these water bodies during daytime (le Roex et al., 2019; Kasiringua et al., 2017).

Daily patterns of visitations of water holes also vary among species and among individuals. This variation is probably due to several factors influencing these patterns such as segregation from other animals, site characteristics, thermoregulation.

Conclusion

The aspects of importance of water to spatial and temporal dynamics of elephants, ungulates, and large and intermediately sized carnivores in African savannas are reviewed in this thesis. As shown, water sources are the key drivers of how these animals use their habitats

accordingly to their water dependency and the presence of other individuals of the same or different species.

Elephants are considered a water dependent species, thus preferring to occur in the vicinity of water sources. This preference is shown predominantly towards rivers. Elephants can utilize not only a water source at rivers, but also adjacent food resources such as riverine vegetation. As elephants feed on the woody vegetation, they cause its degradation and mortality of trees in the vicinity of water sources. However, elephants usually distinguish between drinking sites and feeding sites and they move between those two in frequency of once per 12 to 60 hours. To save time, elephants approach and depart from the water sources in a higher speed than the one used during feeding. The attraction of elephants to water sources is more profound during the dry season because ephemeral water sources promote the movements of elephants further away from a permanent water body during the wet season. Elephants are involved in interactions with other animals at water sources. However, temporal segregation of elephants and other species coming to a water point is prevalent and some species are not discouraged by elephants to drink at the same water point at the same time. One of the potential tools to manage elephant populations is the reduction or the construction of artificial water sources. However, consideration on implications of these management interventions is advised as experts see several possible effects of such actions (Chamaillé-Jammes et al., 2007b; Smit et al., 2007a; Owen-Smith et al., 2006).

As well as elephants, other herbivore species use water sources accordingly to their water dependence. Generally, grazers and non-ruminants are more water dependent than browsers. Thus, grazers use water points more frequently. Some of the grazing species (white rhinos, zebras, and wildebeest) are drawn to artificial water sources. On the other hand, buffalos, waterbucks, and lechwes are found more near rivers where they also profit from the vegetational structures. Some species show variable spatial responses to water sources (impala) or occur in intermediate distance to water bodies (Thomson's and Grant's gazelles). Browsers (e.g., giraffe and kudu) are water independent, however, they can use areas near rivers due to foraging opportunities.

The utilization of the areas near water sources by lions is a hunting strategy, as odds of encountering prey species dependent on these resources are high. Thus, prey species incorporate anti-predatory types of behaviour such as spatial or temporal segregation. Competitive interactions also occur between ungulate species. These interactions can even have a very harsh

impact on one of the competing species as shown on the example of roan antelopes and common grazers. Activity at water bodies can vary in time for different species and study sites.

This review clearly shows that the results of the research of great mammals in African savannas are site-specific and it is difficult to extrapolate these on other sites. Hence, future researchers are advised to combine data from different study sites to extrapolate the results to find the general rules. On the other hand, profound knowledge of the specific protected area is important as an advisory background for management actions. Without the knowledge of spatial preferences of animals and their ecological interactions, management actions can have negative consequences. A cautionary tale could be large water provisioning in Kruger NP before ~1997 which negatively affected populations of roan antelopes. Contrary, if water provisioning is done well and all other ecological aspects are considered, it can promote both tourism and ecological gradients, thus biodiversity.

The attractiveness of a reserve or a national park to tourists probably corresponds with the occurrence of iconic animals such as zebras, elephants, or lions. As these species are promoted with water provisioning, it would appear logical to create many artificial water holes to boost a revenue from tourism industry. Although, such decisions would not be moral as wildlife become sparser in more parts of the world. Creating ecological conditions including adequate spatial distribution of water sources nurturing a wide variety of wildlife seems to be a better decision. Overall, scientific background related to water provision should be recognised and followed while deciding over management actions.

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