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Spatio-temporal activity of African ungulates at water sources in Mogalakwena River Reserve, South Africa

Časoprostorová aktivita afrických kopytníků u vodních zdrojů v Mogalakwena River Reserve, Jihoafrická republika

Diploma 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.

V Praze dne 29. 4. 2024

Podpis:

A handwritten signature in black ink, appearing to read 'Homo laus', with a long horizontal flourish extending to the right.

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## **Abstrakt:**

Velcí savci africké savany jsou společenstvo živočichů značně probádané, nicméně málo studií se věnuje časové, cirkadiánní aktivitě této skupiny. Takové studie používají buď problematické způsoby sběru dat (webkamery, přímá pozorování) anebo byly provedeny v národních parcích či velkých rezervacích, kde pohyb zvěře není limitován antropogenními strukturami. Na takových územích je společenstvo velkých savců většinou úplné, včetně gildy velkých predátorů. Z tohoto hlediska jsou malé, oplocené rezervace bez úplného společenstva těchto zvířat málo prostudované. Tato práce se tedy zaměřuje na získání poznatků o časoprostorové aktivitě kopytníků u vodních zdrojů v Mogalakwena River Reserve v Jihoafrické republice, která je příkladem právě takové rezervace bez velkých predátorů kromě levharta (*Panthera pardus*). Pro monitoring aktivity kopytníků jsem použil fotopasti, které jsem rozmístil u řeky Mogalakwena a u napajedel, a s pomocí umělé inteligence jsem fotografie klasifikoval na úroveň aktivity jednotlivých druhů. Tuto aktivitu jsem dále vztáhnul k prostoru (typ vodního zdroje) a k biotickým a abiotickým faktorům prostředí. Aktivita kopytníků u vodních zdrojů je ovlivněna maximální denní teplotou – při vyšších teplotách se aktivita posouvá k večerním hodinám, nejspíše z důvodu ochlazení. Dále je tato aktivita ovlivněna velikostí zvířete, druhy s velikostí těla 10 – 100 kg navštěvují vodní zdroje signifikantně více v denních hodinách, zatímco zvířata s velikostí těla 100 – 1000 kg se se svou aktivitou signifikantně neliší mezi denními a nočními hodinami. Přítomnost mláďat ovlivňuje časovou aktivitu, nejspíše více u větších druhů. Z literatury je zjevné, že důvodem těchto rozdílů je nejspíše aktivita predátorů. Některé druhy kopytníků vykazují prostorovou segregaci, kdy druhy rodu *Tragelaphus*, vodušky (*Kobus ellipsiprymnus*) a žirafy (*Giraffa giraffa*) navštěvují řeku více, než by bylo očekáváno. Některé druhy se jiným naopak vyhýbají v časové škále, ale relativní množství společné aktivity signifikantně nekoreluje s rozdílem ve velikosti těla. Signifikantní rozdíl je však mezi páry druhů, z nichž alespoň jeden je mix-feeder či omnivor, a páry druhů, které jsou okusovači či spásači. Prvně zmíněné páry druhů mají menší relativní množství společné aktivity u vodních zdrojů.

**Klíčová slova:** savci, kopytníci, savana, vodní zdroje, Afrika, časoprostorová variabilita, časová aktivita, fotopasti, AI

**Abstract:**

The large mammals of African savannah are a well-studied group of animals, but few studies focus on the temporal, circadian activity of this group of mammals. Such studies either use problematic methods of data collection (webcams, direct observations) or have been conducted in national parks or large reserves, where movement of the animals is not limited with anthropogenic structures. In such sites, the community of large mammals is usually complete, including the guild of large carnivores. Thus, small, fenced off reserves without a complete community of large mammals are understudied. Therefore, this work focuses on the spatio-temporal activity of ungulates at water sources in the Mokalakwena River Reserve in South Africa, which is an example of a reserve without large predators except the leopard (*Panthera pardus*). I used camera traps to assess the activity of ungulates, which I placed alongside the Mokalakwena River and at the water holes. With the help of artificial intelligence, I classified the photos to the level of activity of each species. I then tested this activity over space (type of water source) and against biotic and abiotic factors. The activity of ungulates at water sources is influenced by the maximum daily temperature, as the activity shifts to the evening hours during higher temperatures, most likely due to cooling. This activity is also influenced with the size of the animal. Species with a body size of 10 – 100 kg visit water sources significantly more during daytime hours, while animals with a body size of 100 – 1000 kg do not differ significantly in their activity between day and night. The presence of juveniles affects temporal activity, probably more in larger species. It is clear from the literature that the reason for these differences is most likely the activity of predators. Some species of ungulates show spatial segregation, with species of the genus *Tragelaphus*, waterbuck (*Kobus ellipsiprymnus*) and giraffes (*Giraffa giraffa*) visiting the river more than expected. Conversely, some species avoid others in the temporal scale, but the overlaps of activity are not significantly influenced with body mass difference between the species. However, there is a significant difference between pairs of species, where at least one species is a mix-feeder or an omnivore, and pairs of species that are browsers or grazers. The overlaps are lower in the first group.

**Key words:** mammals, ungulates, savanna, water sources, Africa, spatio-temporal variability, temporal activity, camera traps, AI

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# 1. Introduction

African savannas are tropical, seasonal ecosystems with distinctive dry and wet season. During the dry season, no precipitation occurs, thus water as a resource for animals and other organisms is limited. During the wet season, all annual precipitation occurs (Archibold, 1995), however, the total amount is variable depending on the geographical location of the ecosystem (Hijmans et al., 2005). Thus, water is an important resource that shapes not only the ecosystem structure, but also spatial and temporal processes and behaviour of its inhabitants.

Large mammals are an iconic group of organisms inhabiting the African savannas. As such, they attract not only researchers, but also vast public such as tourists or hunters. Due to their size, these animals have important impact on the environment they live in and on other organisms through the trophic cascades (Polis et al., 2000) or production of resources or desirable habitat patches (fertilized soil at middens, carcasses, effects on vegetation). Their attractiveness and size can, however, produce conflicts with humans, which often lead to the extensive reduction in the megafauna numbers that can ultimately lead to extinction and changes in the entire ecosystem. On the other hand, due to their attractiveness to humans, they can serve as umbrella and flagship species for ecosystem conservation. Despite being studied for decades, the knowledge about the ecology or behaviour of large mammals in African savannas is still incomplete. Additionally, in the ever-changing world of Anthropocene and creation of alternative ecological communities or environments in sub-Saharan Africa, the research into these topics is still needed.

Ungulates (both orders Perissodactyla and Cetartiodactyla excluding cetaceans) are important megafauna of African savannas, as their biomass (Hatton et al., 2015) and activity in terms of feeding behaviour shapes the ecosystem (Augustine & McNaughton, 2006; du Toit & Cumming, 1999; Goheen et al., 2007; Hirst, 1975; Sankaran et al., 2013). The heterogeneity of the savanna ecosystem supports wide variety of ungulate species ranging through several size classes (from single kilograms in dik-diks to several tons in hippos and rhinos) and three feeding guilds. These are grazers (zebras, wildebeests, warthogs, waterbucks, etc.) feeding mostly on grasses and ground level herbs; browsers (kudus, elands, giraffes, etc.), feeding on leaves of bushes and trees; and mix-feeders (impalas, nyalas), feeding on both in dependence of availability (Hofmann & Stewart, 1972).



Western (1975) differentiated ungulates of African savanna into two functional groups based on their relationship to water sources. Water dependent species are found near the water sources in dry season and water independent species are found farther away. These two functional groups correlate with the animals' feeding habits, as grazers and non-ruminants are more dependent on water intake through drinking than browsers or ruminants (Kihwele et al., 2020; Western, 1975). Thus, we can also expect different temporal activity of these two functional groups in terms of visiting the water sources, as showed for zebra and sable antelope and their different frequencies of visiting the water sources in Cain et al. (2012). With different frequencies of visitations, the actual temporal moment of the animal's occurrence at a water source can differ between these groups, and browsers might be in advantage in terms of temporal avoidance of competitors at water sources.

Spatially, African ungulates differentiate between natural and artificial water sources as well. For example, plains zebras and wildebeests exhibit positive spatial attraction towards artificial water holes, but waterbucks, impalas, kudus, and giraffes tend to occupy areas with natural water bodies (Redfern et al., 2003; Smit, 2011; Smit et al., 2007). Spatial attraction toward water sources is also modulated by season (e.g. Weeber et al., 2020), as precipitation during the wet season provide ephemeral water sources (Naidoo et al., 2020).

Temporal activity and activity budgets have been studied in African ungulates (see the segment 2.2 *Study species* below). However, overall activity consists of different types of behaviour of the studied species and wide spatial context. The highly mobile megafauna moves through its home ranges and, potentially, through different habitats, utilizing different resources at time. Activity at water sources and time of visitations of these sources have been studied mostly in national parks (e.g., Crosmarj et al., 2012) with the whole large mammal community intact, or with methods such as personal observations or webcams that are largely limited (Hayward & Hayward, 2012; Kasiringua et al., 2017). The limitations arise from modulation of behaviour of studied animals that can react to human observers and thus modulate their activity at water sources, or from opportunistic obtainment and thus problematic standardization of the data and comparison among different sites or species.

Activity in large animals and their spatial occurrence can be studied with different methods, each having certain amount of limitation, but also advantages. **Personal observations** are probably the easiest method. These can be done from hides, vehicles or on foot. Advantage of this method is its implication for citizen science. With over 6 million visitors each year

in South African National parks<sup>1</sup>, who are mostly interested in large mammals, the sightings these tourists obtain can create large datasets of spatio-temporal and behaviour data. However, this method is limited by low data obtainment at night and with possible alternation of behaviour of the observed animals. **Scat collection, track traps, fur traps** are other methods, that can be used for researching occurrence of animals in a certain area. Additionally, these might provide other data such as DNA (e.g. Inoue & Akomo-Okoue, 2015), food remains (e.g. Kartzinel et al., 2015) or bacterial/viral/parasite data (e.g. Hermosilla et al., 2017). These methods, however, do not tell us anything about behaviour of the animals or about number of individuals. **Telemetry** is, nowadays, quite popular method using VHF or GPS transmitters. The advantage of GPS telemetry is obtainment of fine resolution of data, both in temporal and spatial scale (Hebblewhite & Haydon, 2010). GPS telemetry can provide data on speed of movement or direction of movement (e.g. Thaker et al., 2019). It can also provide precise spatial data that can be than used for mitigation of human-wildlife conflict. Telemetry is limited mostly with its price, need of animal handling and not providing actual behavioural data (Hebblewhite & Haydon, 2010).

**Camera traps** combine the advantages of personal observations in terms of large amount of data production (temporal, spatial, and behavioural) and telemetry (good resolution of data and less behaviour alternation). Camera traps are devices that detect motion and thermal radiation in certain angle and distance in front of them. When motion or thermal radiation is detected, the camera trap is triggered. Depending on the settings, the camera trap then takes a certain number of photos or videos. The user can set the speed of the trigger, delay between consecutive photos, number of photos taken per trigger, resolution, length of the video etc. Camera traps can be used by amateurs, conservationists, hunters, and researchers. Camera traps can be used for casual/conservational monitoring, researching diversity of large species (e.g. Pettorelli et al., 2010), overall activity of species (e.g. Clauss et al., 2021), occurrence and occupancy of habitats by species (e.g. Pyšková et al., 2018; Rovero et al., 2014), or activity in certain area, as well as actual behaviour, which is visible sometimes even on photos.

In this thesis, I focus on mostly temporal activity of ungulates in a small, fenced off reserve in South Africa. These small privately owned reserves/farms occur in large numbers in South Africa, providing another modality of environment inhabited by large mammals. Activity of large mammals is seldomly researched in these reserves/farms, even though they

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<sup>1</sup> <https://www.sanparks.org/wp-content/uploads/2023/05/the-tourism-business-of-sanparks.pdf>

are environmentally different from national parks. Firstly, their small size and presence of perimeter fences creates a need for active management of large mammal populations. Secondly, owners can create such community of large mammals that serves them the best, thus creating communities incomplete (e.g., without predators) or communities that are larger than natural. Also, by providing artificial feed, owners can hold larger densities of animals than would occur in national parks. Thus, this thesis provide insight into the topic in such different environment from national parks. Also, activity at water sources is not a topic that is focused on in the literature as much as overall activity or other topics. For some species, knowledge about activity patterns is not robust, neither is the knowledge about the visitations at water sources. Activity at water sources can be also modulated by presence of predators (Crosmarj et al., 2012), thus providing insight into when are ungulates active in areas with large predator community absent is crucial to understand factors affecting this activity. In this thesis, I ask these questions:

- When do ungulate species come to water sources in the small, fenced off reserve; and how does these times differ between seasons and between river and artificial water sources?
- Do ungulate species visit the water sources together, or is there certain amount of spatio-temporal segregation among the species?
- What biotic and abiotic factors influence the overall times of visitations at water sources?

## **2. Methods**

### **2.1 Study site**

Mogalakwena River Reserve (henceforth ‘the reserve’ or ‘MRR’) is a small, ~1500ha large, fenced off reserve, situated in the northern part of Limpopo Province, South Africa, approximately 40 kilometres from the border of South Africa and Botswana (Fig. 1). It is privately owned by the Coetsee family, who have transformed it from a cattle ranch to a nature reserve.

The reserve lies in the savanna ecosystem, spanning the GPS coordinates of 22.710641°S to 22.74440°S and 28.755719°E to 28.817095°E. Mogalakwena Research Center (MRC) staff collects the temperature data using a standard outdoor thermometer and the rainfall data using a rain gauge. The average annual precipitation, calculated from the collected data over 2013 to 2022, equals 379.2 mm of rain (*min.* 207.5 mm, *max.* 727.8 mm, *standard deviation*

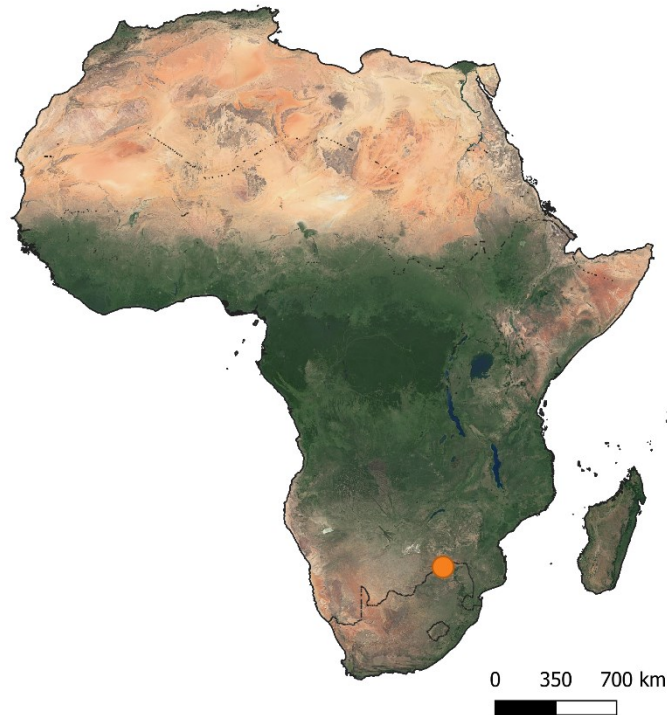


Figure 1: Location of Mogalakwena River Reserve.

155.7). The average maximum temperature in wet season 2021-22 (8<sup>th</sup> November 2021 – 20<sup>th</sup> May 2022) and in dry season 2022 (21<sup>st</sup> May 2022 – 24<sup>th</sup> October 2022) was 32.5 °C and 29.9 °C, respectively. The average minimum temperature in those two seasons, respectively, was 21.2 °C and 10.6 °C. The average maximum and minimum temperature throughout the whole period (8<sup>th</sup> November 2021 – 24<sup>th</sup> October 2022) were 31.5 °C and 17.1 °C, respectively.

The Mogalakwena River, which gave the name to the reserve, flows through the reserve dividing it into what is called the East Side and the West Side. The river is partitioned with several dam walls, which regulates the amount of water flowing through the reserve. The dam walls also serve as bridges, allowing people to cross from the East Side to the West Side. With its water, the river supports an open woodland habitat along its shores throughout the whole year. Otherwise, most of the reserve constitutes of shrubland habitat, both open and closed, and several patches of open grassland habitat (Fig. 2). Another type of water sources are man-made water holes, i.e. small concrete pans and well-like structures that are filled with water by the reserve management. There is also a natural pan that is filled with rainwater during the wet season and sometime hold water into the dry season as well. I have pooled the former two water source types into one category. Tens of lone baobab trees (*Adansonia digitata*) are scattered across the reserve. However, due to a large population of herbivores (see below), the grass is almost absent throughout the shrubland and grassland habitats (*personal observation*; David Hořák and Grietjie Stander, *personal communication*).



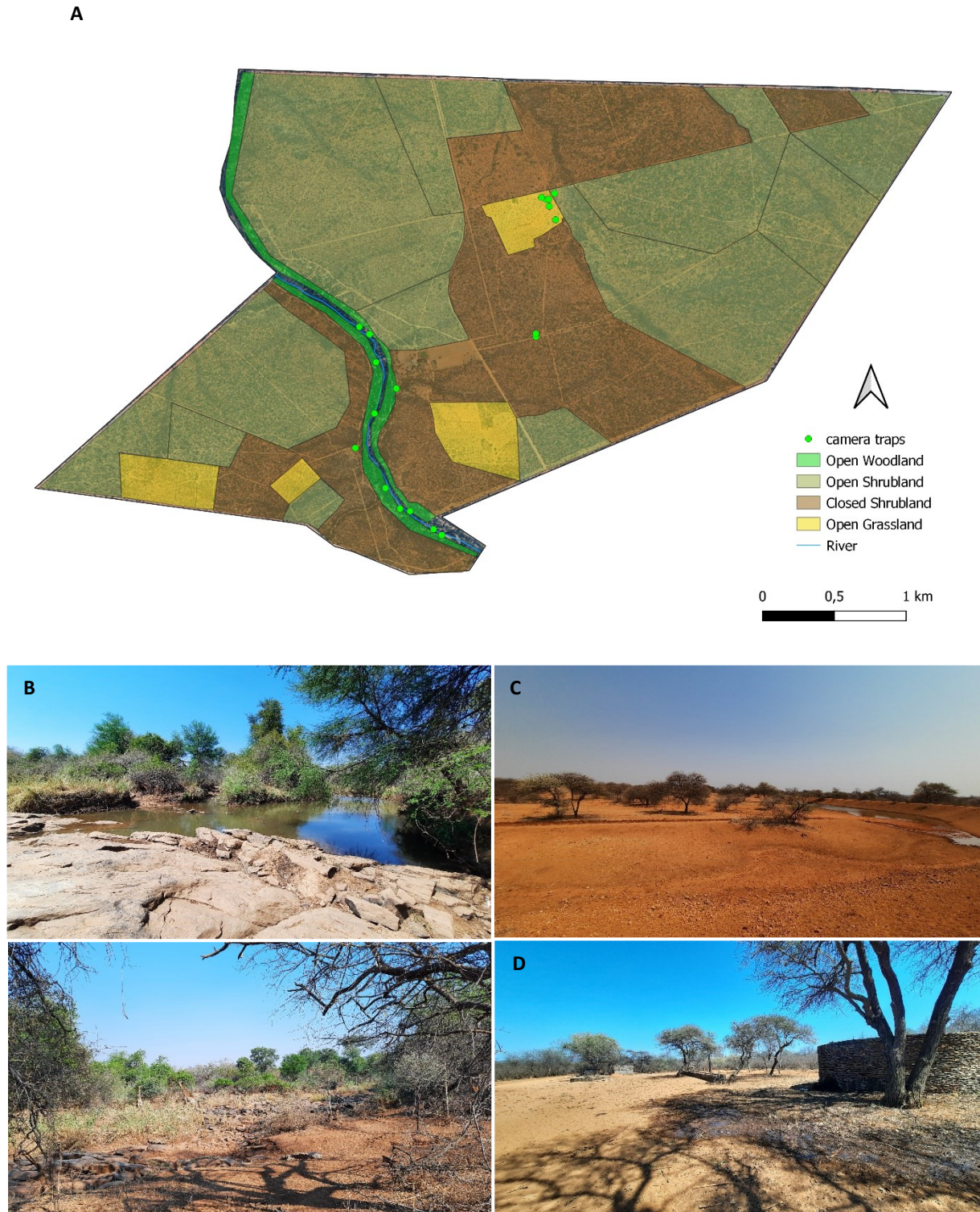


Figure 2: Habitats and placement of cameratraps in the reserve. **A** map of the reserve; **B** (left column) open woodland; **C** open grassland during dry season; **D** Bestekraal water hole surrounded with closed shrubland.

The reserve is inhabited by a wide variety of animal species and taxa. These include invertebrates (e.g., millipedes, centipedes, Solifugae, scorpions, termites, ants, baboon spiders,

etc.), fish (e.g., *Clarias* cat-fish), amphibians (e.g., Southern foam nest frog *Chiromantis xerampelina*), reptiles (e.g., rock monitor *Varanus albigularis*, water monitor *Varanus niloticus*, Southern African python *Python natalensis*, black mamba *Dendroaspis polylepis*, puff adder *Bitis arietans*, boomslang *Dispholidus typus*, leopard tortoise *Stigmochelys pardalis*, etc.), birds (e.g., ostrich *Struthio camelus*, helmeted guinefowl *Numida meleagris*, herons, sunbirds, rollers, weavers, etc.), and mammals (Table 1).

## 2.2 Study species

In this thesis, I focus on ungulate species (orders Cetartiodactyla and Perissodactyla) inhabiting the reserve (Table 1). The populations of larger ungulates are actively managed by the reserve game management staff to ensure viable population sizes that can be supported by the reserve natural food resources (Table 2). Smaller species that can move through the perimeter fence are not managed, as their migratory/dispersal routes are not disrupted by the fence. These include steenbok, common duiker, warthog, and bushpig. All other ungulate species are managed by standard game captures using bomas. Estimates of population sizes for these species from 2021 are listed in Table 2.

Table 2: Population estimates of managed ungulate species in the reserve for 2021.

| Species          | Population estimates |
|------------------|----------------------|
| Impala           | 345                  |
| Greater kudu     | 25                   |
| Waterbuck        | 160                  |
| Blue wildebeest  | 74                   |
| Common eland     | 8                    |
| Nyala            | 38                   |
| Bushbuck         | 30                   |
| Gemsbok          | 6                    |
| Blesbok          | 28                   |
| Southern giraffe | 52                   |
| Zebra            | 19                   |

Table 1: Examples of mammalian species inhabiting the reserve with fully listed resident ungulate species. \* marks species captured by camera traps (except resident ungulates which were all captured).

| <b>Taxon</b>    | <b>species</b>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
|-----------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Afrotheria      | aardvark ( <i>Oryzomys afer</i> )*                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
| Lagomorpha      | scrub hare ( <i>Lepus saxatilis</i> )*                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| Rodentia        | Bushveld gerbil ( <i>Gerbilliscus leucogaster</i> ), Southern African porcupine ( <i>Hystrix africaeaustralis</i> )*, Greater cane rat ( <i>Thryonomys swinderianus</i> )*, African tree squirrel ( <i>Paraxerus cepapi</i> )                                                                                                                                                                                                                                                                                                                                                                                    |
| Primates        | Southern lesser galago ( <i>Galago moholi</i> ), Thick-tailed larger galago ( <i>Galago crassicaudatus</i> ), chacma baboon ( <i>Papio ursinus</i> )*, Vervet monkey ( <i>Chlorocebus pygerythrus</i> )*                                                                                                                                                                                                                                                                                                                                                                                                         |
| Chiroptera      | Unidentified species                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |
| Perissodactyla  | zebra ( <i>Equus quagga</i> )                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| Cetartiodactyla | impala ( <i>Aepyceros melampus</i> ), blue wildebeest ( <i>Connochaetes taurinus</i> ), blesbok ( <i>Damaliscus pygargus</i> ), common duiker ( <i>Sylvicapra grimmia</i> ), steenbok ( <i>Raphicerus campestris</i> ), waterbuck ( <i>Kobus ellipsiprymnus</i> ), common eland ( <i>Taurotragus oryx</i> ), greater kudu ( <i>Tragelaphus streliceros</i> ), bushbuck ( <i>Tragelaphus scriptus</i> ), nyala ( <i>Tragelaphus angasii</i> ), gemsbok ( <i>Oryx gazella</i> ), southern giraffe ( <i>Giraffa giraffa</i> ), warthog ( <i>Phacochoerus africanus</i> ), bushpig ( <i>Potamochoerus larvatus</i> ) |
| Carnivora       | Leopard ( <i>Panthera pardus</i> )*, African civet ( <i>Civettictis civetta</i> )*, small-spotted genet ( <i>Genetta genetta</i> )*, large-spotted genet ( <i>Genetta tigrina</i> )*, african wild cat ( <i>Felis lybica</i> ), brown hyena ( <i>Parahyaena brunnea</i> )*                                                                                                                                                                                                                                                                                                                                       |

### 2.2.1 Impala (*Aepyceros melampus*)

Impala is a medium sized antelope with reddish colouration on the upper part of the body, with fawn flanks, and white underbelly. Black ornamentation appears on various parts of the body. Males carry lyrate horns (Skinner & Smithers, 1990). Impalas are mixed feeders, feeding on both grass and browse (Skinner & Smithers, 1990). Impalas occur in wider eastern to southern Africa<sup>2</sup>, preferring woodland habitat (Bommel et al., 2006; Chabwela et al., 2017; Evans, 1979). Adult impala males hold territory throughout a wet season, females form herds that move across territories of several different adult males. Bachelor groups are formed by subadult males. During a dry season, all sexes roam freely of any hierarchical social structure (Jarman & Jarman, 1973). Feeding activity in impala occurs mostly during the day hours. Certain feeding activity may occur during night; however, night is usually spent by laying (Jarman & Jarman, 1973). More than 30 % of the day is used for feeding. Other types of behaviour (vigilance, resting, moving, etc.) occur in ~0 – 10 % of the day each (Muposhi et al.,

<sup>2</sup> <https://www.iucnredlist.org/species/550/50180828>

2013). Hayward & Hayward (2012) and Sutherland et al. (2018) found impalas to be active at waterholes around midday.

### 2.2.2 Greater kudu (*Tragelaphus strepsiceros*)

Greater kudus are large antelopes fawn grey in colour with 5 – 14 vertical white stripes on the flanks. Males carry large spiral horns (Skinner & Smithers, 1990). Greater kudus are browsers, with more than 80 % of their food being woody plants. Grasses are being fed on during early mornings and late afternoons (which corresponds to the time when kudus drink, Annighöfer & Schütz, 2011). Greater kudu occurs throughout eastern and southern Africa<sup>3</sup> in several habitats, from forest through shrubland to cultural landscape (<sup>2</sup>, Evans, 1979). Greater kudus form herds of varying sizes over the year and with varying sex and age composition (Annighöfer & Schütz, 2011). Greater kudus are active mostly during early mornings and late afternoons. Resting then occurs during the middle of the day. Drinking occurs in single percentages of the overall time throughout the 24-hour cycle. In Namibia, kudus visited the water sources preferentially without other species being present at them (Annighöfer & Schütz, 2011). Kudus were found to be active at water sources in early mornings and late evenings (Kasiringua et al., 2017), Hayward & Hayward (2012) found out also progressively increased activity at waterholes in the evening. However, van der Meer et al. (2012) recorded more kudu herds coming to water sources in late mornings/early afternoons.

### 2.2.3 Waterbuck (*Kobus ellipsiprymnus*)

Waterbucks are large antelopes greyish in colour with a distinct white circle patch on the rump. Only males carry horns (Skinner & Smithers, 1990). Waterbucks are mainly grazers but can add some browse into their diet (Skinner & Smithers, 1990). They occur in the Sahel belt, and from eastern to southern Africa<sup>4</sup>, preferring woodland areas, but utilizing other habitats such as grasslands as well (Tomlinson, 1981; Tsegaye et al., 2015; van Lavieren & Esser, 1980). Some waterbuck males might hold a territory (Hanks et al., 1969), females share home ranges with other females, young males form bachelor groups (Spinage, 2012). During the day hours, waterbucks spend more than 30 % of their time feeding with peaks in the morning and in the evening, however feeding might occur during night as well (Spinage, 1968). Resting occurs mostly during midday (Wirtz & Oldekop, 1991). Hayward & Hayward (2012) recorded

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<sup>3</sup> <https://www.iucnredlist.org/species/22054/166487759>

<sup>4</sup> <https://www.iucnredlist.org/species/11035/50189324>



waterbucks to be active at water holes generally during mornings, with the activity decreasing throughout afternoon.

#### 2.2.4 Blue wildebeest (*Connochaetes taurinus*)

Wildebeests are large antelopes, in colours of dark grey to black. Both sexes carry horns (Skinner & Smithers, 1990). They are grazers who favour short grasslands (Skinner & Smithers, 1990). Blue wildebeest, as a subspecies of common wildebeest, occurs in southern Africa, north from the Orange river and south of the Zambezi river<sup>5</sup>. Blue wildebeests prefer open habitats but occur in woodland and shrubland as well (<sup>4</sup>, Mandlate et al., 2019; Selebatso et al., 2018). Male wildebeests hold territories, females form herds and young males form bachelor groups (Wilson & Mittermeier, 2011). Wildebeests spend around 25 % of their daytime foraging, and ~40 – 50 % of the daytime resting. Grazing occurs more in the morning and in the evening (Ben-Shahar & Fairall, 1987). In findings of Hayward & Hayward (2012), wildebeest are progressively more active at water holes in the evening.

#### 2.2.5 Common eland (*Taurotragus oryx*)

Common elands are the largest antelope in southern Africa, fawn in colour (Skinner & Smithers, 1990). Common elands are primarily browsers (Watson & Owen-Smith, 2000), distributed in eastern and southern Africa, avoiding tropical forests of Congo basin, and Namib desert<sup>6</sup>. Elands inhabit a vast number of habitats<sup>5</sup>, such as grasslands (Mtega et al., 2023) or wooded areas (Watson & Owen-Smith, 2000). Elands form herds with varying sex composition throughout the year, youngs are usually born before rainy season (Underwood, 1975). Feeding behaviour usually occurs during day hours (Underwood, 1975), but might also occur during night hours (*secondarily cited in* Underwood, 1975). At water holes, elands are usually active during sunrise and sunset hours (Kasiringua et al., 2017) and during night (Hayward & Hayward, 2012).

#### 2.2.6 Nyala (*Tragelaphus angasii*)

Nyalas are antelopes of medium size, being reddish in colour with white stripes on the flanks, adult males are dark brown in colour and carry twisted horns (Skinner & Smithers, 1990). Like impalas, nyalas shift their preferred diet from graze in rainy season to browse in the dry season (Van Rooyen, 1990; *secondarily cited in* Botha & Stock, 2005). They

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<sup>5</sup> <https://www.iucnredlist.org/species/5229/163322525>

<sup>6</sup> <https://www.iucnredlist.org/species/22055/115166135>

are distributed along Zambezi and Limpopo rivers in southern Africa, and more extensively in southern Mozambique<sup>7</sup>. Nyalas form herds, however, males tend to roam alone (Wilson & Mittermeier, 2011). Nyala calves are usually born before rainy season (Anderson, 1979). In protected areas, nyalas tend to be active mostly during the day hours, however, their night activity might be increased due to hot weather (Wilson & Mittermeier, 2011). At water holes, Hayward & Hayward (2012) observed nyalas being active around midday, with a small peak around midnight.

### 2.2.7 Bushbuck (*Tragelaphus scriptus*)

Bushbucks are medium sized antelopes, dark brown in colour with white stripes and dots on their flanks that can be absent in certain subpopulations. Only males carry triangular horns (Skinner & Smithers, 1990). Bushbucks are predominantly browsers feeding on trees, shrubs, or woody herbs (Apio & Wronski, 2005; MacLeod et al., 1996). They occur in almost whole sub-Saharan Africa, avoiding only forests of Congo basin and drier south-west of the continent<sup>8</sup>. Bushbucks occur more in wooded habitats (MacLeod et al., 1996). Bushbucks are predominantly solitary animals (Allsopp, 1978; Wronski et al., 2009), forming pairs during breeding season (Allsopp, 1978). Bushbucks are generally active during sunrise and sunset hours with the activity of adult males, but not sub-adult males, being correlated with the activity of females (Wronski et al., 2006).

### 2.2.8 Gemsbok (*Oryx gazella*)

Gemsboks are large, pale fawn-grey antelopes with dark markings covering various parts of the body, and long, straight horns in both sexes (Skinner & Smithers, 1990). Diet of gemsboks consists of graze; however, they do utilize bushes when ground vegetation is not available (<sup>9</sup>; Diekmann, 1980). Gemsboks occur in the drier west of southern Africa<sup>8</sup>. They inhabit semi-arid to arid savannas, grasslands, dunes, or shrublands (Wilson & Mittermeier, 2011), as well as deserts and salt pans<sup>8</sup>. Some gemsbok males defend a territory, in which they allow female herds or mixed herds to roam (Diekmann, 1980). At water sources, gemsboks have been seen active mostly in the morning (Kasiringua et al., 2017).

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<sup>7</sup> <https://www.iucnredlist.org/species/22052/115165681>

<sup>8</sup> <https://www.iucnredlist.org/species/22051/115165242>

<sup>9</sup> <https://www.iucnredlist.org/species/15573/166485425>

### 2.2.9 Blesbok (*Damaliscus pygargus*)

Blesboks are medium-sized antelopes, reddish-brown in colour with a distinctive white blaze on the forehead. White patches also cover a rump and legs, and horns are present in both sexes (Skinner & Smithers, 1990). Blesboks are grazers and so-called bulk feeders, i.e. not specialised grazers (Klein & Fairall, 1986), occurring primarily in South Africa, but their current range is expanding neighbouring countries via introductions<sup>10</sup>. Blesboks prefer open short grasslands, especially after fires (<sup>9</sup>; du Plessis, 1972). They form harems during rut, after calves are born, females form nursery herds. During that time, males may form all-male herds. Outside rut and calving (i.e. during dry season), blesboks form mixed herds (du Plessis, 1972). Du Plessis (1972) described the activity of blesboks to peak during afternoon and evening and then again in the early morning, with night and most of the morning spent resting.

### 2.2.10 Southern giraffe (*Giraffa giraffa*)

Giraffes are the tallest animals in the world, being usually 4 – 5 metres tall. Darker patches of fur are divided by matrix of lighter fawnish colour. Colours tend to darken with age. Two bone horns arise from the skull, which is enlarged in males (Skinner & Smithers, 1990). Giraffes are typical browsers. The range of distribution of southern giraffe is fragmented throughout southern Africa (Coimbra et al., 2021), from dry savannas in the west to more productive savannas in the east, preferring woodland habitat types (Deacon & Smit, 2017). Giraffes form loose groups with mixed sex composition, often being found solitarily, calves might form only-calves-groups (Leuthold, 1979). Giraffes spend around 60 % of the time feeding and around 20 % of the time moving. Resting constitutes less than 10 % of the time (du Toit & Yetman, 2005). Feeding occurs during the night as well (Burger et al., 2021). At water sources, giraffes were found active mostly during the day (Hayward & Hayward, 2012; Kasiringua et al., 2017).

### 2.2.11 Plains zebra (*Equus quagga*)

Zebras are horse-like animals with black and white stripes, plains zebras in southern Africa (*Equus quagga burchelli*) also possess greyish stripes between two consecutive black stripes (Skinner & Smithers, 1990). Zebras are non-specialised grazers (Owaga, 1975) feeding on both short and long grasses (Havarua et al., 2014). As a subspecies, *E. q. burchelli* occurs around Etosha National Park in Namibia and in the north-east of South Africa<sup>11</sup>, preferring more

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<sup>10</sup> <https://www.iucnredlist.org/species/30208/50197331>

<sup>11</sup> <https://www.iucnredlist.org/species/41013/45172424>

open habitats, usually grasslands (Mandinyenya et al., 2020). Plains zebras form harem groups with one male, several females and offsprings; males can also form bachelor groups and roam solitarily. Foals are born usually before the peak of a rainy season (Klingel, 1969). Movement-wise, plains zebras are mostly active in the morning and afternoon, with lower activity during the night and midday (Owen-Smith & Goodall, 2014). Feeding takes place for most of the time during daylight (Owen-Smith & Goodall, 2014). Hayward & Hayward (2012) observed plains zebras being active at water sources mainly during a day, with peaks of activity in the morning and in the afternoon.

#### 2.2.12 Steenbok (*Raphicerus campestris*)

Steenboks are small, reddish antelopes with white underbelly and rump (Skinner & Smithers, 1990). They are browsers with most of their diet consisting of forbs and woody vegetation (du Toit, 1993). Steenboks occur disjunctly in eastern Africa (Kenya and Tanzania) and then in the whole southern Africa<sup>12</sup>, occurring in variety of habitats, from dry grasslands to moist woodlands and open forests (<sup>11</sup>; Pienaar, 1974). Steenboks form pairs with common territory, which is marked by both sexes (Wilson & Mittermeier, 2011). Steenboks are active throughout the whole 24 hours, however, with a peak of inactivity during midday in a dry season (du Toit, 1993).

#### 2.2.13 Common duiker (*Sylvicapra grimmia*)

Common duikers are small antelopes with colour ranging from greyish to yellowish with white underbelly and a dark band on the forehead and on the upper part of the tail. Preorbital glands are easily visible (Skinner & Smithers, 1990) and only males carry horns (Wilson & Clarke, 1962). Common duikers are omnivores and browsers, feeding on leaves, fruits, flowers and occasionally insect or birds (Wilson & Clarke, 1962). They occur throughout the savannas of sub-Saharan Africa<sup>13</sup>, inhabiting variety of habitats, including human-altered ones (<sup>12</sup>; Pienaar, 1974). Common duikers are solitary animals (Abu Baker & Brown, 2013), males mark their territories with preorbital glands (Wilson & Mittermeier, 2011). Common duikers are mostly diurnal, with some activity during twilight. Common duikers rest usually during hot hours and then during night (Wilson & Mittermeier, 2011). Abu Baker & Brown (2013) observed duikers being active mostly during afternoon.

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<sup>12</sup> <https://www.iucnredlist.org/species/19308/50193533>

<sup>13</sup> <https://www.iucnredlist.org/species/21203/50194717>

#### 2.2.14 Common warthog (*Phacochoerus africanus*)

Warthogs are small ungulates grey in colour, with conspicuous warts on head (Skinner & Smithers, 1990). They are omnivores and grazers requiring short grass habitats, additionally feeding on fruits, tubers, occasionally small vertebrates, eggs, and carcasses (*primarily and secondarily cited in* Mason, 1982; *personal observations*). Common warthogs occur in wide sub-Saharan Africa<sup>14</sup>, following the variety of savanna ecosystem (Mason, 1982). Young warthogs form larger groups, which size decreases for adult animals, with males occurring also solitarily (White, 2010). Females give birth to ~ 3 piglets at the beginning of wet season in a burrow (Mason, 1982). Warthogs spend most of their time feeding, resting, and walking (Edossa et al., 2020). However, feeding occurs mostly during morning and late afternoon (Deribe et al., 2008). Regarding water sources, warthogs are active during the day, either in the morning (Kasiringua et al., 2017), or through-out the entire day (Hayward & Hayward, 2012).

#### 2.2.15 Bushpig (*Potamochoerus larvatus*)

Bushpigs are small, reddish ungulates with yellowish mane (Skinner & Smithers, 1990) that feed on insects, small vertebrates, eggs, carcasses, roots, leaves, bulbs, fruit, flowers, plants (*primarily and secondarily cited in* Skinner et al., 1976). They can be found in woodlands and forests (Wilson & Mittermeier, 2011) of eastern, south-central, and south-eastern Africa<sup>15</sup>. Bushpigs form herds of 4 – 6 individuals, with dominant male defending a territory and reproducing with one female in the herd. Females give birth to ~ 4 calves in a burrow nest during a wet season (Skinner et al., 1976). Bushpigs are active mostly during the night, however, temperature might influence their activity patterns, as they are active more during the day in the southern Cape in South Africa (Wilson & Mittermeier, 2011).

### 2.3 Data collection

Data were collected using camera traps Evolveo StrongVision A (Naxya Limited, Sheung Wan, Hong Kong), which take colourful pictures during a day and black-and-white pictures during the night. During low light conditions, camera traps use an infra-red flash with wavelength of 940nm, which ensures the animals are not disturbed (Henrich et al., 2020). I deployed 20 camera traps, 10 at semiartificial water holes (data from 1 camera not counted due to poor placement) and 10 alongside the Mogalakwena river (Fig. 2; see below). The camera traps were mounted on a tree (Fig. 3), most of them in breast height, and positioned to have an optimal

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<sup>14</sup> <https://www.iucnredlist.org/species/41768/109669842>

<sup>15</sup> <https://www.iucnredlist.org/species/41770/44140926>

field of view over a water hole or a river spot. One camera trap at the river was stolen during my first stay in MRC (data not counted) and consequently replaced at another site at the river. I found two camera traps missing during my second stay in MRC, thus having only 18 camera traps in total surviving the whole study period (see below). These camera traps covered 15 sites in total.

The camera traps were set to record one picture of 20Mpix resolution every time something was moving in front of them. Consecutive photos of one individual were taken ~10 seconds apart. The camera traps were deployed from 27<sup>th</sup> September 2021 to 2<sup>nd</sup> December 2022 (at least one camera trap active).

The camera traps saved the photos on a 32GB SD card, from where the photos were uploaded on a laptop and on an external hard drive. Photos from the camera traps were collected approximately once a week by me during my two stays in the reserve. Between those two stays, photos were collected by the MRC staff randomly, once per several months, as MRC staff was not paid to do it and was doing it during their usual work. Some data were lost due to SD cards being full, moisture (wrong date/time data), or due to baboons mispositioning the camera traps.



Figure 3: Camera traps mounted on trees at water sources in the reserve.

## 2.4 Data standardization and analyses

### 2.4.1 TrapTagger

For analysing photos from camera traps and obtaining the metadata contained in those, I used TrapTagger surveying software<sup>16</sup>. This software uses up to three AI algorithms

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<sup>16</sup> <https://wildeyeconservation.org/traptagger/>

for classification of species present on the photos. Firstly, MegaDetector AI developed by Microsoft detect animals' presence on the photos and filter out the photos containing no animals (i.e., triggers caused by moving branches or grass). Secondly, the species classifier (I have used specialized southern-African classifier) classify the animals into species it was trained on<sup>17</sup>. Third AI helps with recognition of individual animals (not used in this work).

The TrapTagger group the photos together into clusters, in which the photos are taken within a small bound of times at one camera trap station. Firstly, I set the AI to classify the animals into the species and I performed manual classification in cases of AI not being confident and reclassification of wrongly classified photos. Secondly, I distinguished multiple species on singular photos in the clusters, as species information was given to the whole cluster. Thirdly, I labelled the clusters of photos with information about sex (*male/female*) and age category (*adult/juvenile/subadult male*). Labels were added to sightings of those species, in which the differentiation can be seen via size difference, presence and size of horns or morphological structures typical for one sex. I performed all manual work with the camera trap photos using TrapTagger on photos containing only the study species, which was allowed by the software.

#### 2.4.2 Data standardization

I downloaded .csv files from TrapTagger containing sightings of individual species. The table contained information about ID of the photo, site, camera trap ID, date and time, species, and the sex and age labels. I pooled the tables together and standardized the data. I standardized the data for temporal activity analyses, so that independent data points were sightings of the same species at the same site more than 10 minutes apart. For the spatial analyses, I used 60-minute difference. I had to omit data from 2 water holes during dry season due to artificial feeding at these sites during the dry season. I also had to delete duplicate images that created more than one event for analyses involving predictor *presence of juveniles* to avoid pseudo replicates, as presence of juveniles was marked in TrapTagger for clusters of photos, not individual species.

#### 2.4.3 Analyses

I performed all analyses in R Statistical System v4.3.2 (R Core Team, 2023). I used 'activity' package (Rowcliffe, 2023) for analysing activity of the ungulates at water sources,

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<sup>17</sup> <https://wildeyeconservation.org/traptagger-performance-report/>

'overlap' package (Meredith et al., 2024) for analysing overlap of activities between species pairs, packages 'circular' (Agostinelli & Lund, 2023) and 'circglmbayes' (Mulder & Klugkist, 2017) for circular statistics, and package 'dplyr' (Wickham et al., 2023) for data frame manipulation.

For activity patterns, I used 'fitact' function from 'activity' package with 500 bootstrap iterations for 95% confidence intervals. For overlap of activities, I used 'overlapEst' function from 'overlap' package with 1024 points to estimate the overlap and I used *dhat4* as the overlap estimate type. To provide 95% confidence intervals of overlap, I used 'bootEst' and 'bootCI' functions. I used these functions to analyse the activity of different species, body mass classes, and activity at different type of water sources. For testing difference of visitation times between seasons, river and water holes, and through different maximum daily temperatures, I used Bayesian circular General Linear Model utilizing function 'circGLM' from package 'circglmbayes'. The model was set to count 50 000 iterations, with firstly burning 25 000 iterations. For testing the preference for daylight or night hours, I used the proportion test with function 'prop.test'. For testing the effect of competition, I used the poisson GLM of the relationship of calculated overlaps and body mass difference between the species the overlap was calculated for, and feeding guild of those species. For spatial analyses, I used  $c^2$  test using function 'chisq.test' and canonical correlation analysis CCA using package 'vegan' (Oksanen et al., 2022). The level of significance in all tests was set to  $\alpha = 0.05$ .

## **3. Results**

### **3.1 Sampling effort**

Throughout the study period, the camera traps recorded 379,634 photos totalling 1.6 TB, with 176,838 photos with animals present. In total, the study period consisted of 6,068 camera trap-days (sum of days when camera traps were active, well positioned, and recorded date/time data correctly, Table S1). Number of camera traps active during each month starting with September 2021 and ending with December 2022 is listed in Table S2. Trapping success in terms of actual camera trap-days vs all possible camera trap-days was 70 % (total possible days was set from deployment of the first camera trap to removing the last camera trap), trapping success in terms of independent events (activity of ungulates) over 100 trapping days was 4,600.2 events/100 TD. Activity of camera trap sites is plotted as a heat map generated in TrapTagger in Fig. 4. Summary of sampling effort per species is depicted in Table 5. Relative



abundance index RAI generated in TrapTagger and relative abundance index calculated according to Lim et al. (2023) correlated strongly ( $r = 0.99$ ).

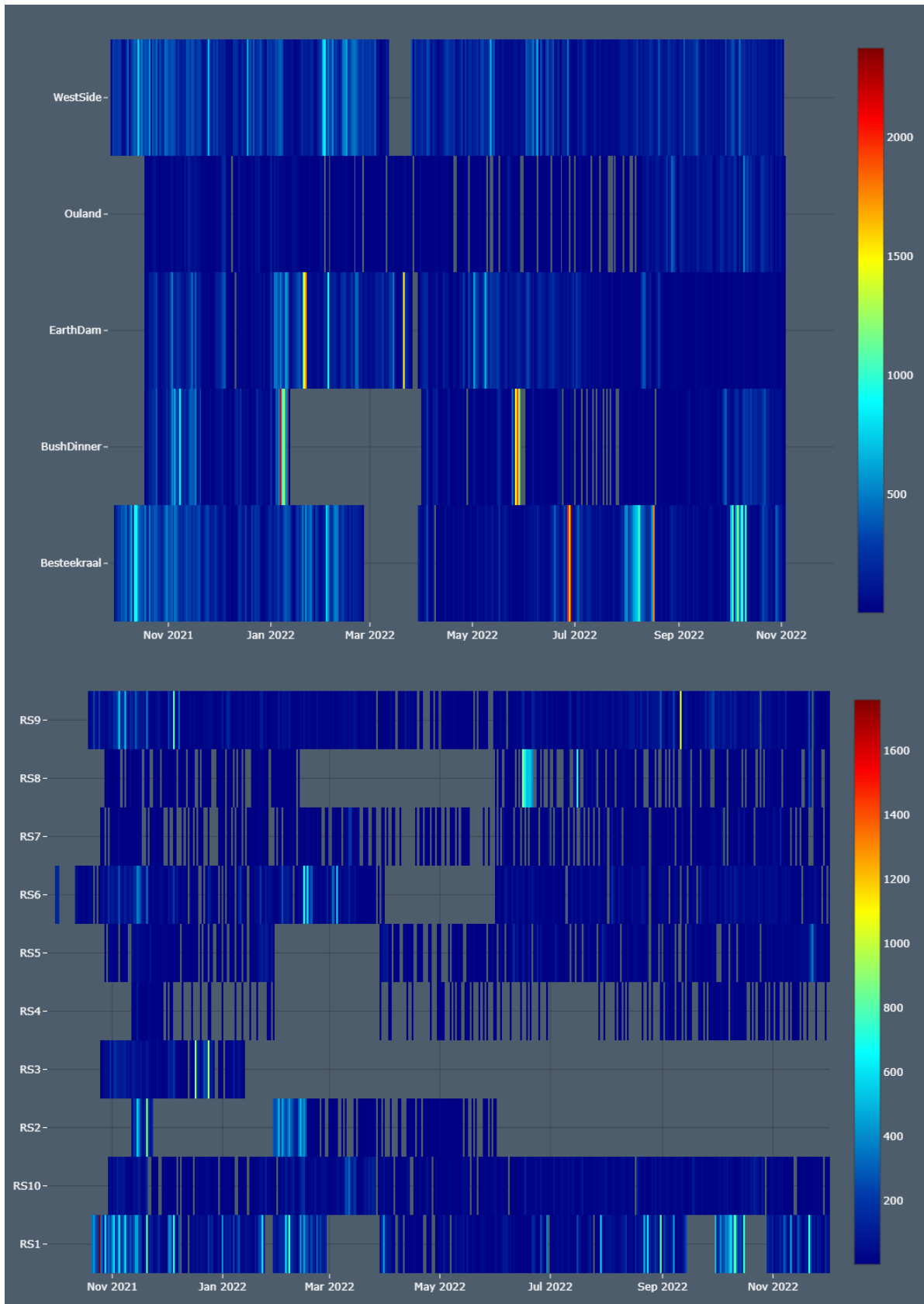


Figure 4: Heatmap of the activity of camera trap sites over the study period. The colour palette indicates number of photos taken on each day from 27<sup>th</sup> September 2021 to 2<sup>nd</sup> December 2022 at each site (upper part equals to water holes, lower part to the individual spots on the riverbanks).

Table 5: Summary of sampling effort for individual species of resident ungulates. Number of independent events corresponds to events standardized for temporal analyses (10-minute difference). Relative abundance index (RAI) is provided in two formats. Naïve occupancy corresponds to proportion of camera traps detecting the species. Values rounded up to two decimals.

| Species          | Independent events | % of all ungulate events | Number of images | RAI (TrapTagger) | RAI    | Naive occupancy |
|------------------|--------------------|--------------------------|------------------|------------------|--------|-----------------|
| Impala           | 4 159              | 20.98                    | 35 938           | 90.98            | 964.97 | 1.00            |
| Greater kudu     | 990                | 4.99                     | 7 634            | 21.13            | 229.70 | 1.00            |
| Waterbuck        | 3 559              | 17.95                    | 25 905           | 73.54            | 825.75 | 1.00            |
| Blue wildebeest  | 863                | 4.35                     | 10 742           | 15.49            | 200.23 | 0.53            |
| Common eland     | 412                | 2.08                     | 2 104            | 7.51             | 95.59  | 0.53            |
| Nyala            | 1 303              | 6.57                     | 6 529            | 25.71            | 302.32 | 1.00            |
| Bushbuck         | 626                | 3.16                     | 2 496            | 13.64            | 145.24 | 0.67            |
| Gemsbok          | 142                | 0.72                     | 595              | 2.47             | 32.95  | 0.20            |
| Blesbok          | 606                | 3.06                     | 3 560            | 11.14            | 140.60 | 0.46            |
| Southern giraffe | 4 193              | 21.15                    | 41 570           | 82.68            | 972.85 | 1.00            |
| Plains zebra     | 1 082              | 5.46                     | 7 887            | 19.67            | 251.04 | 0.53            |
| Steenbok         | 111                | 0.56                     | 354              | 2.39             | 25.75  | 0.53            |
| Common duiker    | 613                | 3.09                     | 1 365            | 11.25            | 142.23 | 0.73            |
| Common warthog   | 1 131              | 5.7                      | 6 221            | 20.35            | 262.41 | 0.80            |
| Bushpig          | 37                 | 0.19                     | 93               | 0.71             | 8.58   | 0.53            |

### 3.2 Spatial occupancy

I tested the spatial preferences of ungulate species for a type of water source [(semi)artificial water holes or river] with a  $\chi^2$  test with two categorical variables (*species* and *type of water source*). I had to drop one species – gemsbok – from this analysis as there were no records of gemsboks at the river. Results of the  $\chi^2$  test:  $\chi^2(13, N = 13,849) = 2,165.7, p \ll 0.001$ .

The correlation indicates that waterbucks, giraffes, kudus, bushbucks, and nyalas prefer river more than expected over (semi)artificial water holes. Kudus and bushbucks seem to prefer river absolutely more. No preference was found for bushpigs, but they occur at (semi)artificial water holes absolutely more. Other species seem to prefer (semi)artificial water holes more than expected and also absolutely more.

The canonical correlation analysis showed that 12.96 % of variability in the occupancy data (presence absence data of species at different water sources in individual days) can be explained with the first canonical axis, second canonical axis explains 10.9 % of the variability in the data. Direct analysis with formula  $\sim Site + Condition(Date)$  shows that

the predictor *Site* randomized over the individual dates explains 7.02 % of overall variability, which is 54 % of variability explained with the first canonical axis. The plot of the analysis is shown in Fig. 5. The results of a permutation test with 999 permutations are provided in Table 6.

Table 6: Results of a permutation test with 999 permutations of direct canonical analysis with formula  $\sim Site + Condition(Date)$ . Values rounded up to three decimals.

|                  | df    | c <sup>2</sup> | F      | P     |
|------------------|-------|----------------|--------|-------|
| <b>Model</b>     | 13    | 0.467          | 31.491 | 0.001 |
| <b>Residuals</b> | 2,562 | 2.920          |        |       |

As shown with the c<sup>2</sup> test, the canonical correlation analysis also showed that kudus, nyalas, bushbucks and waterbucks are more drawn to sites at the river.

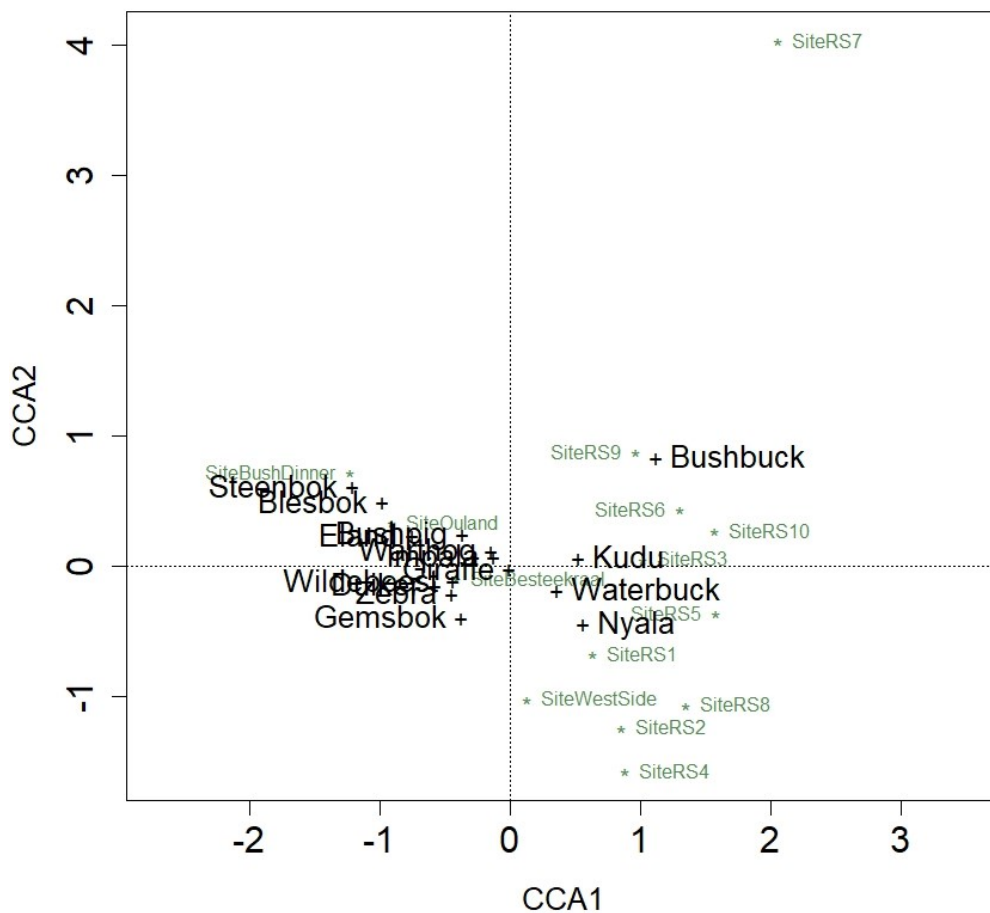


Figure 5: Plot of results of the direct canonical correlation analysis of the effect of *Site* on occupancy of ungulates in MRR during the study period.

### 3.3 Temporal activity

The overall activity of ungulates at water sources with 95% confidence intervals is provided in Fig. 6. As shown, ungulates tend to come to water sources mostly during day hours with peaks of activity at midday and around sunset. I tested the effect of maximum day temperature ( $maxT$ ), rain ( $rain.mm$ ), season (levels *dry* and *wet*), water source type (levels *water hole WH* and *river R*), presence of juveniles of at least one species (levels *Yes* and *No*) and body mass class of the species [taken from Faurby et al. (2018), levels  $10 - 100\text{ kg}$ ,  $100 - 1000\text{ kg}$ ,  $>1000\text{ kg}$ <sup>18</sup>] on this activity pattern with Bayesian circular GLM. I provide the results in Table 7.

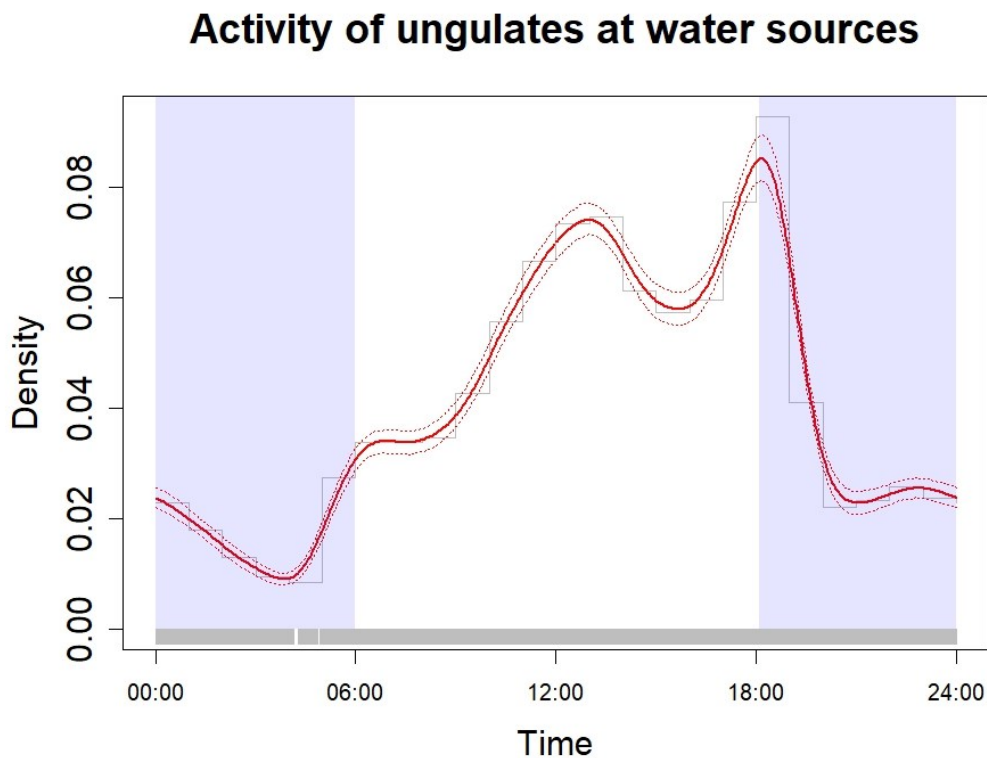


Figure 6: Activity of all studied species of ungulates at water sources (both river and water holes) through the whole study period (27<sup>th</sup> September 2021 – 2<sup>nd</sup> December 2022).

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<sup>18</sup> I have made the distinction of the categories of body mass based on logarithmic scale (1-10,10-100,100-1000,1000-10000). However, no studied species is less than 10 kg in size. When I tried to evaluate the difference between the body mass categories with the two smallest ungulates (duiker and steenbok) as one category, the model did not converge. That is why I have used three categories with the largest one being represented by one species – giraffe.

Table 7: Results of the Bayesian circular General Linear Model  $time \sim maxT + rain.mm + season + Juvenile + bodymass\_class + Water.source.type$ . Predictors, for which the interval between lower bound (LB) and upper bound (UB) doesn't exceed zero, are important and time of visitation differs with values of those predictors. Values rounded up to two/three decimals.

|                            | <b>Estimate</b> | <b>SD</b> | <b>LB</b>    | <b>UB</b>    |
|----------------------------|-----------------|-----------|--------------|--------------|
| <b>Intercept</b>           | -2.79           | 0.04      | -2.87        | -2.71        |
| <b>Kappa</b>               | 0.86            | 0.02      | 0.83         | 0.89         |
| <b>maxT</b>                | -0.03           | 0.008     | <b>-0.05</b> | <b>-0.02</b> |
| <b>rain.mm</b>             | -0.01           | 0.008     | -0.03        | 0.00         |
| <b>seasonwet</b>           | 0.003           | 0.04      | -0.07        | 0.08         |
| <b>JuvenileYes</b>         | -0.31           | 0.04      | <b>-0.39</b> | <b>-0.22</b> |
| <b>bodymass_class3</b>     | 1.07            | 0.04      | <b>1.00</b>  | <b>1.15</b>  |
| <b>bodymass_class4</b>     | 0.17            | 0.04      | <b>0.09</b>  | <b>0.26</b>  |
| <b>Water.source.typeWH</b> | -0.04           | 0.04      | -0.12        | 0.03         |

Predictors with upper and lower bounds not exceeding zero are those of interest, as either their levels (season, water source type, presence of juveniles, body mass category) or values (maximum daily temperature, rain) importantly differ in the mean time of visitation of ungulates at water sources. As seen in Table 7, these means differ with predictors maximum daily temperature, presence of juvenile, body mass category (Fig. 7). As shown, during lower (<30 °C) maximum daily temperatures, the second peak of activity starts earlier before sunset; juveniles tend to come to water sources more during day, less during night, and the midday peak of activity is larger than the sunset one; and medium sized species tend to visit water sources more during day hours (see also Table 13).

As I was unable to test interactions and predictor *Species* because of the model not converging, I provide at least exploratory graphs of overlap of activity depending on interacting predictors (Fig. 8) and those of activity of individual species at water sources (Fig. S1). It seems that predictor *Juvenile* might interact with *Body mass class* and also with *maximum temperature* in their effect on overall activity of ungulates at water sources. Large species tend to come to water sources more during day hours with juveniles than they do without them. On the other hand, the medium species seem to have similar activity trend when juveniles are present, just with larger peaks for juveniles. Juveniles during lower maximum daily temperatures (<30 °C) seem to have flat peak of activity at water sources from mid-morning to early evening. During higher maximum daily temperatures (>30 °C) juveniles seem to have higher amounts of activity at water sources during midday and sunset hours.

Only one species was completely nocturnal in its activity at water sources (bushpig), one was crepuscular (duiker, active around dawn and dusk), five species were mostly vespertine (wildebeest, zebra, eland, kudu, waterbuck, active at dusk), and the remaining eight species were active at water sources during the day hours. The activity level (proportion of time the animal was active at the water sources) with standard error is depicted in Table 8. The highest activity level was recorded for bushbuck ( $0.55\pm 0.03$ ), the lowest for eland ( $0.23\pm 0.03$ ). The mean activity level was  $0.40\pm 0.07$ .

Table 8: Activity level (proportion of time the animal spent being active at water sources) for individual species and standard error of these activity levels. Largest activity level is marked baldly, lowest boldly in red. Values rounded up to two decimals.

| Species    | Activity level | SE   |
|------------|----------------|------|
| Impala     | 0.41           | 0.02 |
| wildebeest | 0.30           | 0.03 |
| blesbok    | 0.47           | 0.03 |
| zebra      | 0.40           | 0.03 |
| giraffe    | 0.49           | 0.01 |
| waterbuck  | 0.38           | 0.02 |
| gemsbok    | 0.36           | 0.07 |
| warthog    | 0.30           | 0.01 |
| steenbok   | 0.48           | 0.06 |
| duiker     | 0.40           | 0.04 |
| eland      | <b>0.23</b>    | 0.03 |
| nyala      | 0.48           | 0.02 |
| bushbuck   | <b>0.55</b>    | 0.03 |
| kudu       | 0.47           | 0.04 |
| bushpig    | 0.28           | 0.05 |

Impalas, zebras, giraffes, warthogs, nyala, bushbucks and kudus seem to have similar temporal activity at water holes as at the river (overlap 0.75 or higher), only blesbok has much different activity at the water holes compared to river (overlap 0.25 and lower, Fig. S2). At river, it is active more during morning and midnight and in afternoon at water holes. The overlap of activity at different water source types is higher than 0.5 for other species, with quite large confidence intervals for steenbok, duiker, eland and bushpig. Confidence intervals for steenbok exceed both 0.25 and 0.75 values, confidence intervals for duiker, eland and bushpig exceed the upper 0.75 value. The overlaps between activity at different water source types is shown in Table S3.

The activity at water sources of individual species is quite similar over seasons. The overlaps of activity of individual species at water sources during the two seasons is usually higher than 0.75, or it is close to 0.75. The exception is gemsbok, in which the activity at water sources during dry season is observed during night hours (Fig. S3). The results are depicted in Table S4. Only wildebeest has lower than 0.75 overlap of activity at water sources with and without juveniles being present (Fig. S4, Table S5). However, the upper confidence interval exceeds 0.75. However, for waterbuck, bushbuck, and kudu the activity trend at water sources looks different with and without juveniles.

Overlaps of activity of individual species at water sources during maximum daily temperatures  $>30^{\circ}\text{C}$  and  $<30^{\circ}\text{C}$  are depicted in Table S6. For all species except for gemsbok (Fig. S5), this overlap exceeds 0.75, however, in steenbok, wildebeest, and bushpig only with the upper 95% confidence interval. Overlap in bushpig exceeds 0.25 with its lower 95% confidence interval as well.

I used proportion tests to test if medium sized or large sized ungulates visit water sources more during day or night. I tested amount of activity during the day against overall activity with  $H_0$  being the proportion of 0.5. I provide the results in Table 13. As seen from Table 13, the medium sized species significantly more prefer visiting water sources during the day. On the other hand, large sized species seem to have no such significant preference.

Table 13: Results of two proportion tests of amount of activity at water sources of medium sized and large sized ungulates and whether this activity during day hours (6:00 – 18:00) corresponds to 50% of overall activity of ungulates of respective body sizes at water sources. Values rounded up to three decimals.

| Body mass category | $c^2$  | df | P      | Estimate | Upper 95% CI | Lower 95% CI |
|--------------------|--------|----|--------|----------|--------------|--------------|
| Medium size        | 13.214 | 1  | <0.001 | 0.797    | 0.637        | 0.901        |
| Large size         | 0.066  | 1  | 0.796  | 0.532    | 0.371        | 0.687        |

I calculated overlaps of activities of all pairs of species (Table S7). The lowest temporal overlaps (0.25 and lower) were found for 8 pairs of species, 7 of which contain bushpig as it was the only species with nocturnal activity at water sources. Highest overlaps (0.75 and more) were found for 36 out of 104 pairs of species. I tested the effect of body mass difference and feeding guild of the pair (*grazer-grazer*, *grazer-browser*, *other-grazer*, *other-browser*, *other-other*) on these overlaps with Poisson GLM. As the overlap of activities of giraffes and other species was too great and giraffes do not really compete for food with other ungulates (DuToit,



1990), I omitted giraffes from this analysis. The  $H_0$  was that the overlap does not change with body mass difference between the species in the pair or with the feeding guild. The results of the model are provided in Table 15.

### Difference in overlaps of activity among feeding guilds

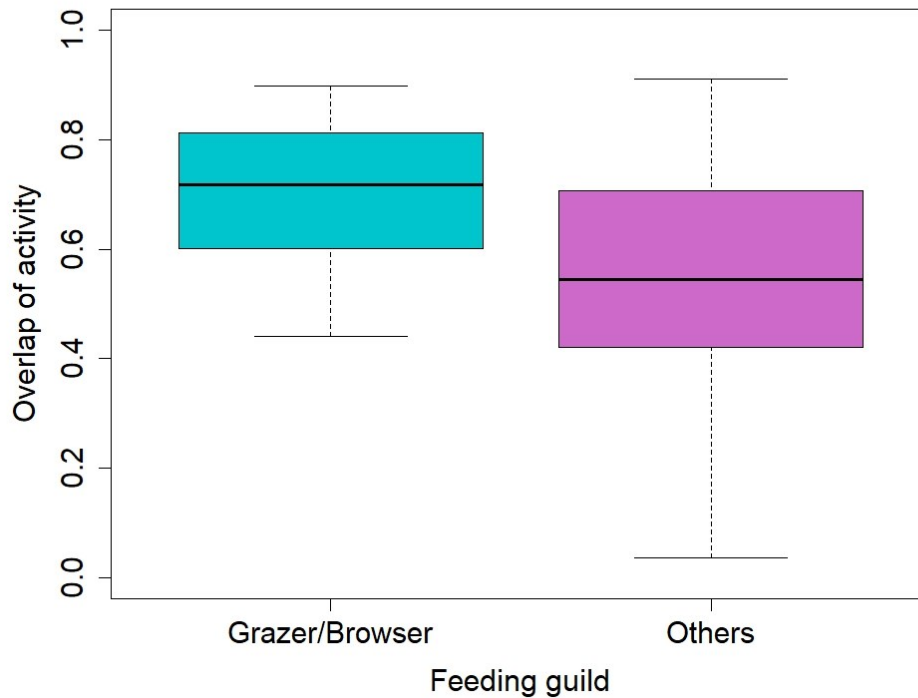


Figure 9: Plot of difference in overlaps of activity at water sources among feeding guilds with levels being pairs of strict grazers and browsers and pairs with at least one of the species being a mix feeder (impala, nyala) or an omnivore (bushpig, warthog,

Table 15: Results of poisson generalized linear model testing effect of body mass difference and feeding guild on overlap of temporal activity at water sources of all pairs of species. Values rounded up to three decimals.

| Predictor            | df | F     | P            |
|----------------------|----|-------|--------------|
| Body mass difference | 1  | 1.346 | 0.249        |
| Feeding guild        | 5  | 4.212 | <b>0.002</b> |
| interaction          | 5  | 0.418 | 0.835        |

Only the feeding guild had a significant effect on the level of overlap between individual pairs of species. As it seemed that the main difference is between pairs containing mix feeders and omnivores and pairs without those, I pooled the levels of *feeding guild* into two categories – one containing all pairs where at least one species was not a strict grazer or browser (i.e. mix feeders or omnivores) and second with just strict grazers and browsers. The results were quite similar with slight positive trend with the predictor *body mass difference* and significant

difference between pairs of strict browsers/grazers and pairs with mix feeders or omnivores (Table 16, Fig. 9).

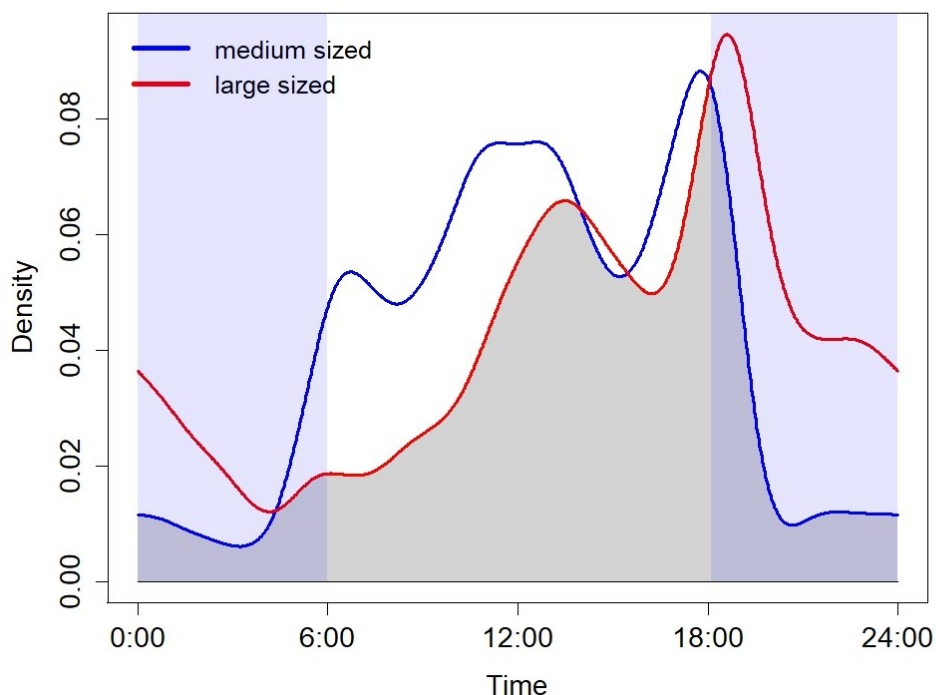
Table 16: Results of poisson generalized linear model testing effect of body mass difference and feeding guild (two levels – *pairs containing only browsers or grazers* and others, i.e. *pairs containing at least one mix feeder or omnivore* on overlap of temporal activity at water sources of all pairs of species. Values rounded up to three decimals.

| Predictor                             | df | F      | P      |
|---------------------------------------|----|--------|--------|
| Body mass difference                  | 1  | 2.986  | 0.087  |
| Feeding guild alternative interaction | 1  | 13.394 | <0.001 |
|                                       | 1  | 0.481  | 0.489  |

As shown in Fig. 9, pairs where at least one of the two species was either a mix feeder, or an omnivore, have significantly lower overlaps of temporal activity at water sources than pairs of two browsers/two grazers/browser and grazer. The trend for body mass difference was positive – the overlaps increased with larger body mass difference, but their dispersion decreased. Low temporal overlaps were found for similarly sized species. However, as mentioned, the trend was not significant. Another exceptional species (such as previously omitted giraffe) might be eland, as mass differences with elands reach around 400 – 500 kg. However, the results did not differ with omitting elands.

a

Overlap of activity at water sources for different sizes of ungulates



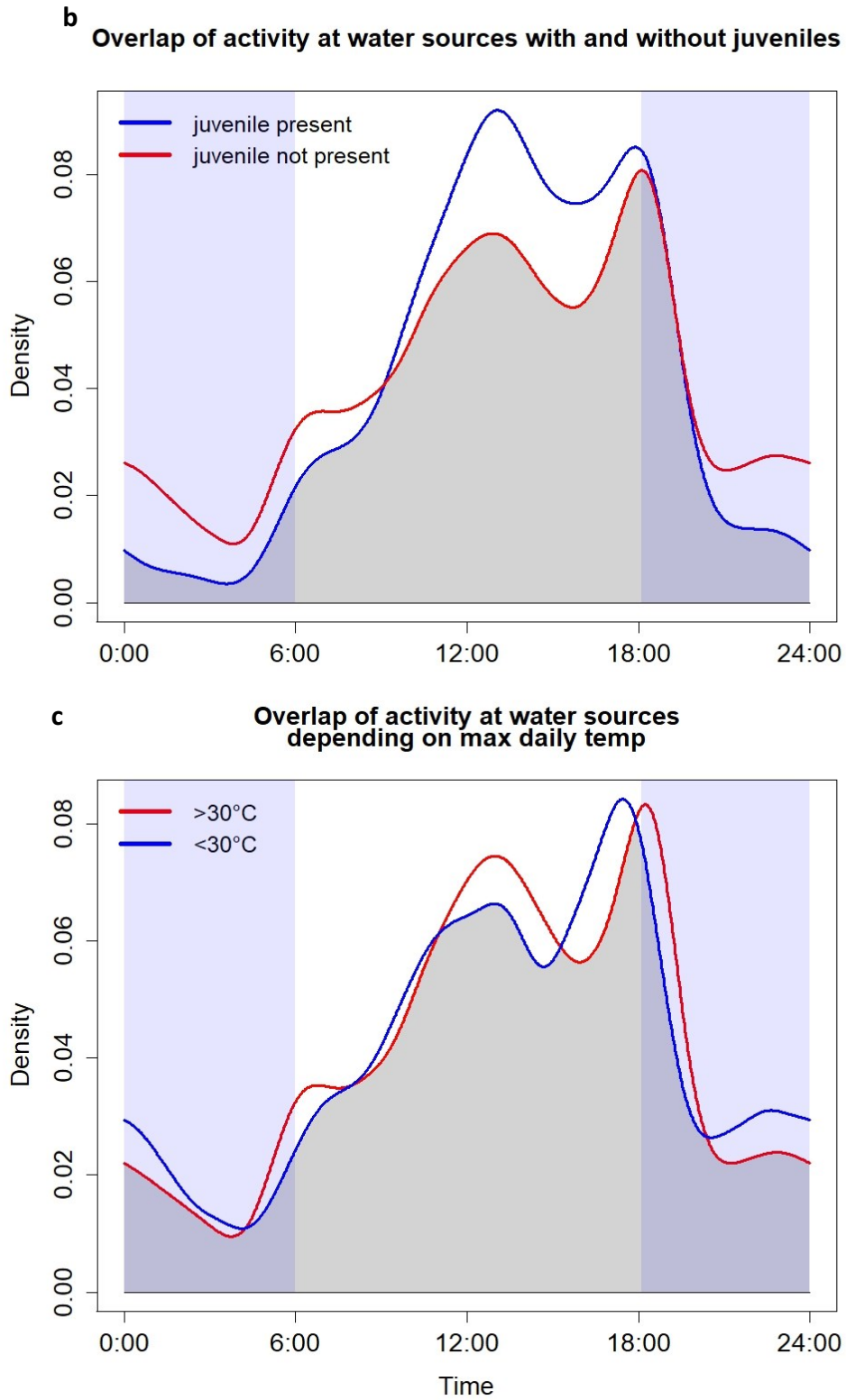


Figure 7: Plots of overlap of activity of ungulates at water sources based on **a** body mass, **b** presence of juveniles, and **c** maximum daily temperature.

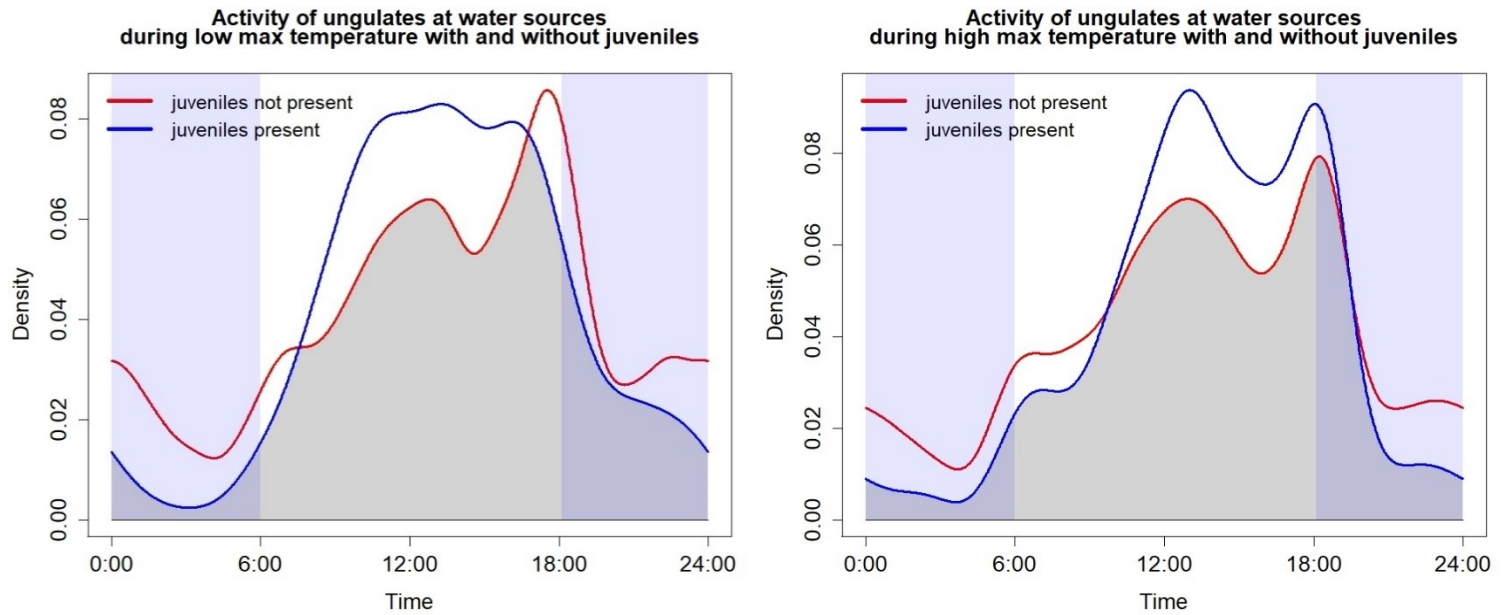


Figure 8a: Plots of overlaps of activity of ungulates at water sources based on possibly interacting significant predictors - presence of juveniles:maximum daily temperature.

As precipitation is an important factor in the ecosystem of African savannas, I have looked at the effect of rain on the activity of omnivores and herbivores at water sources and its possible change during days with precipitation  $>1$  mm and days with precipitation  $<1$  mm. As with the activity of all ungulates not changing with rain amount, there seems to be also not a strong difference between activity at water sources of omnivores or herbivores during days with rain  $>1$  mm and days with rain  $<1$  mm. The overlap of activity of omnivores and herbivores at

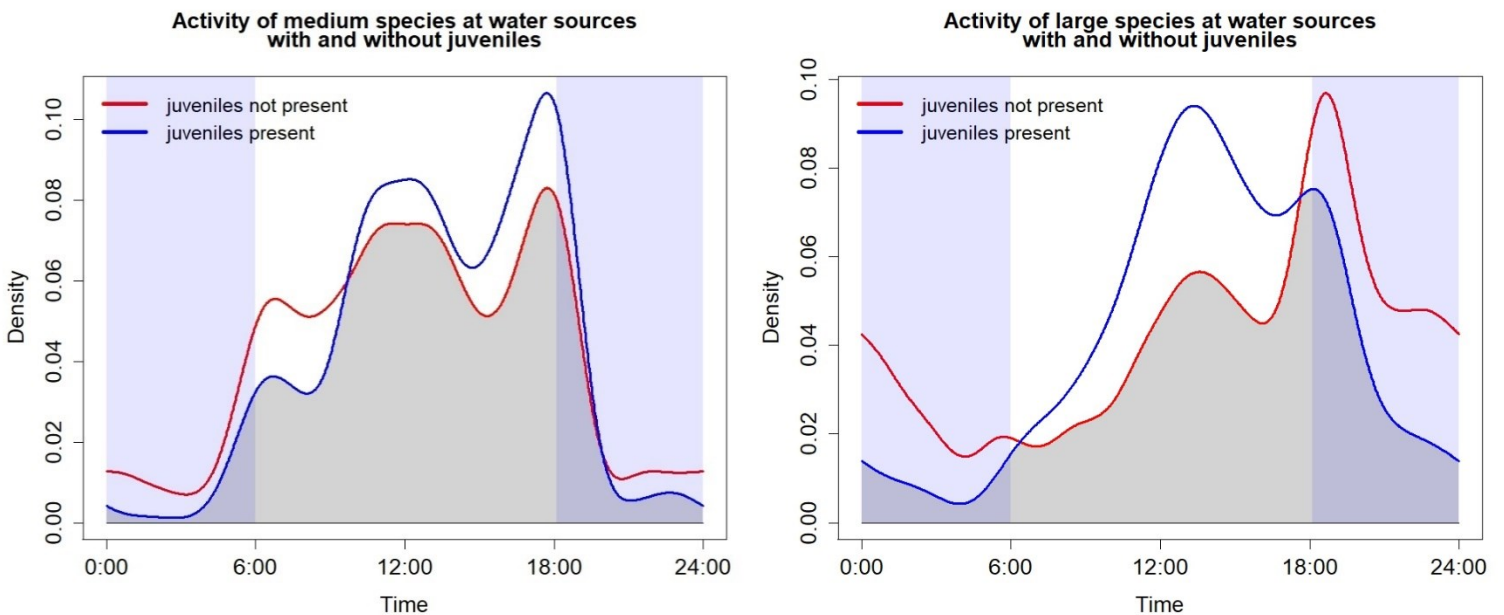


Figure 8b: Plots of overlaps of activity of ungulates at water sources based on possibly interacting significant predictors - presence of juveniles:body mass category.

the water sources during days with <1 mm and >1 mm of rain is 0.91 (corrected 95% CI 0.84 and 0.96), 0.95 (corrected 95% CI 0.93 and 0.97), respectively.

## **4. Discussion**

I used camera traps to assess the temporal and spatial activity of wild ungulates at the water sources in a small fenced off reserve in South Africa, and how the temporal activity differs throughout the changing seasons and how is this activity affected by both, biotic and abiotic, factors. Testing these factors, I found out that the temporal activity of ungulates is different with different maximum daily temperatures, whether juveniles are present or not, and for different body size classes. Effect of interaction of the factors including species identity is probable, but I haven't tested it due to high complexity. Interspecific competition in the temporal scale (overlap of activity) is also correlated with feeding guild of one or both competitors, and there is certain spatial segregation of species, as some prefer the river more than the (semi)artificial water sources.

### **4.1 Temporal activity of ungulates**

I assessed the activity of all ungulate species at the water sources. It seems that, mostly, ungulates are active during midday and then again during dusk. Overall activity of ungulates seems to appear mostly during the day hours. However, this is mostly due to the medium sized species (10 – 100 kg) and giraffes being active during the day hours, as species from 100 to 1000 kg do not significantly choose for day hours to visit the water sources. As leopards seem to avoid larger prey animals (zebras, wildebeests, elands, kudus, gemsboks, Hayward et al., 2006), these large species might not be affected with the landscape of fear as much as the medium sized species. Those might prefer the day hours as a temporal avoidance of leopards that are mostly active during the night hours (Balme et al., 2007).

This pattern, however, might be different when presence of juveniles is considered. As I show, large species seem to tend to come to the water sources more during day hours when juveniles are present. As juveniles are often preyed upon by predators (Linnell et al., 1995) and this predation is also explained with body size (Barber-Meyer & Mech, 2008; Gervasi et al., 2015; Sibly & Brown, 2009), the large species probably try to avoid predators in the temporal scale when they have juveniles. For the MRR, the avoidance might be also spatial, but that needs further testing. Overall, predators affect activity of ungulates strongly, both in spatial and temporal way. Crosmary et al. (2012) found change of ungulate activity at the water sources in

a hunting concession compared to national park, which correlated with more external mortality during the day caused by human hunters. Makin et al. (2017) found temporal change of visitation of water sources by zebras between areas with lions (*Panthera leo*) and areas with cheetahs (*Acinonyx jubatus*) and African wild dogs (*Lycaon pictus*). Courbin et al. (2019) described movements of zebras further away from water sources when encountering lions. I show that even low absolute number of large predators might contribute to changes in activity of African ungulates that can be probably more preyed upon. However, actual movement patterns of the leopards and ungulates would be needed to confirm this probable explanation of difference of activity of the ungulates in the MRR.

Medium sized species increase their activity at midday and around dusk when juveniles are present, and they further decrease the activity level at night. The increase of activity during the two peaks might be to maintain the same activity level as activity during night decreases, or because of juveniles having higher water intake requirements or higher water requirements of mothers suckling the juveniles.

These results are consistent with results of Vallejo-Vargas et al. (2022), who tested diel activity in tropical forests using large camera trap survey, and found that increased body mass in herbivores is connected to higher nocturnality. However, the activity at water sources might not precisely reflect the overall activity level and pattern. Thus, comparing data from tropical forests and from tropical savannas calls for grid design of camera trap survey to assess differences in overall activity of animals, or comparing data from water sources only. However, findings of Jůnek & Lhota (*personal communication*) of diel activity of mammals visiting mineral sources at bais in rainforest of Congo confirms the nocturnal trend in larger species.

During maximum daily temperatures not exceeding 30 °C, the second peak of activity of the ungulates is shifted to earlier hours. This might be simply because the sunset starts earlier during the dry season, during which maximum daily temperatures are low. Despite maximum daily temperatures correlating with season, the correlation wasn't great. Thus, there might be an ecological explanation for this shift of activity. One might be that the midday peak of activity is necessary due to physiological requirements, but timing of the second one might depend on ambient temperatures around the water sources. As the water holes are positioned in open areas, the ambient temperature there is higher compared to closed vegetation. Thus, during high temperatures, ungulates might wait till dusk so that they do not display themselves towards sun. The effect of ambient temperatures on the time of visitation of water sources was studied in

Kruger National Park by Trent (2016). They found a shift in activity of mammals visiting water holes into earlier morning hours with increasing average temperature. It thus seems that animals might shift their activity at water sources to colder parts of the day (early morning, dusk) when temperature during the day is high. To my knowledge, no other study was conducted on the effect of temperature on the time of visitation. However, several studies (e.g., Eliades et al., 2022; Harris et al., 2015; O'Brien et al., 2006) have investigated the effect of temperature on visitation rate at water sources, which is generally higher.

The difference in the pattern of visitation also holds for juveniles. They seem to be active at the water sources during low maximum daily temperatures from mid-morning to early afternoon, but their activity during high maximum daily temperatures exhibits the two traditional peaks. Juveniles might be active continuously through midday during the low temperatures, as they do not risk overheating. This might be important due to their smaller size, which could cause relatively higher water loss via sweating during the high temperatures. To my knowledge, no study has investigated the change in time of visitations at water sources for juveniles and adults separately and effects of interaction with climatic variable. In these terms, my descriptive investigation at least shines a light onto the need for testing such effects.

Interestingly, there is no important difference of visitation times of ungulates between seasons or between days with and without rain. As the savanna ecosystem displays not only seasonal change in precipitation, but also a slight change in temperature (Archibold, 1995), it might be that the ungulates much more react to temperature than seasonal change in vegetation greenness in their temporal activity. Temperature might affect water loss from body directly and thus affect the visitations at the water sources. This is more pronounced with the results of no effect of rain within day on the temporal activity. However, no response to rain or seasonality might be caused by the MRR management staff providing water to the wildlife all year round, thus the animals don't need to look for it elsewhere during dry seasons.

However, more robust study should be conducted within the west-east rainfall gradient of southern Africa to detangle the actual effects of rain and temperature. The probable causes for me not finding any effect of rain might be due to high number of days with no rain at all.

## **4.2 Spatial activity**

To assess the level of spatial segregation as a mean of avoiding competitors, I have tested the occupancy of ungulates at different types of water sources. As one could anticipate, the

*Tragelaphus* species (kudu, nyala, bushbuck) seem to occupy the river more than expected, and kudus and bushbucks even more in absolute numbers of occurrences. However, this preference might not be for the river itself, but for the woodland habitat, as it does not occur anywhere else in the reserve. Indeed, bushbucks in South Africa were found to prefer closed, dense habitats more than the open ones, where it finds enough food in terms of browse (MacLeod et al., 1996). The same preference was found for bushbucks in Botswana (Simpson, 1974), Mali (Smits, 1986), Senegal (Tomáš Jůnek, *personal communication*) or Ethiopia (Yazew et al., 2011). In these terms, bushbucks in MRR don't differ in their apparent preferences, even though this study was not focused on habitat utilization, but use of water resources and occupancy at those. On the other hand, Dankwa-Wiredu & Euler (2002) found bushbucks in Ghana preferring marshes over both open habitats and a riverine forest. As the distribution range of bushbucks is large, we might expect some local variation in habitat choice, but my study adds evidence that riverine woodland is probably the preferred habitat of bushbucks.

In kudus, the river might also be preferred due to food availability. As shown in studies from South Africa (Dekker et al., 1996; Dörgeloh, 2001), Zimbabwe (Fritz et al., 1996), Malawi (Evans, 1979), and with modelling (Fabricius & Mentis, 1992), greater kudus are drawn to trees. However, Hirst (1975) found no clear habitat preference and Evans (1979) found temporal difference in habitat selection in greater kudus. More so, Roque et al. (2024) found preferences for habitats containing trees, but avoidance of proximity to rivers. Same was found by Redfern et al. (2003) in South Africa. This study adds more evidence for the overall preference of woodland habitats by greater kudus and corresponds to finding from Kruger National Park, South Africa (Smit et al., 2007). It is probable that kudus do not choose the river as a preferred source of water, but more for the habitat providing enough food resources. For nyalas, preference for high productivity or woodland habitat was found in Malawi (Reece et al., 2023), Mozambique (Roque et al., 2024), Zimbabwe (Traill, 2004), and South Africa (Marshall et al., 2021). As with former two *Tragelaphus* species, nyala probably prefers the habitat along the Motalakwena River more than it would prefer the river itself.

The possible explanation for the apparent spatial preference of studied species of *Tragelaphus* is probably due to phylogenetically conservative niche and habitat preferences. All three species feed, at least partially, on browse (Apio & Wronski, 2005; Owen-Smith et al., 1983; Owen-Smith & Cooper, 1989; Smits, 1986; Van Rooyen, 1990), and the temporal activity of the bushbuck and nyala shows also high overlap. Maybe surprisingly, Ehlers Smith et al. (2020) propose spatial exclusion of bushbucks at sites of higher nyala density, when leopard



density is low. But in areas of high nyala and leopard density, bushbucks can coexist with nyalas. The authors explain it with bushbucks tolerating nyalas to certain number that might be maintained with culling/predation from leopards. As the MRR is inhabited probably by two leopard individuals (MRC staff, *personal communication*) that were seen mostly near river (David Homoláč, *unpublished data*), the coexistence of bushbucks with nyalas in the riverine woodland habitat might be due to leopard choosing nyalas over bushbucks as a prey animal and thus decreasing the amount of interspecific competition between the two antelope species. Also, as seen in Fig. 5, bushbucks and nyalas might spatially segregate on lower spatial scale and utilize different parts of the river and riverine woodland. For its size, kudu might escape any adverse effects of competition, as the last studied Tragelaphini species, the eland, being bigger in size than kudu, seems to prefer water holes more.

Waterbucks also seem to occupy the river more than expected, however, not in the absolute number of occurrences. This is in accordance with studies from South Africa (Redfern et al., 2003; Smit, 2011; Smit et al., 2007; Smit & Grant, 2009), or Zimbabwe (Traill, 2004). As a similarly sized zebra, or smaller wildebeests or blesboks (all grazers) are drawn more to water holes, waterbucks might benefit from this spatial segregation from other grazers. However, similarly to *Tragelaphus* species, the preference for river might be phylogenetically conservative, as other Reduncinae species also prefer habitats near standing/running water (Wilson & Mittermeier, 2011). As Smit (2011) reports from Kruger National Park, South Africa, the waterbuck's preference for river might be, again, preference for the habitat itself and not type of water source. My results indicate the same.

The last species that seems to occupy the river more than expected is giraffe. This is unsurprising, as the woodland habitat alongside the river provide enough palatable food in terms of leaves. This might be pronounced more during a dry season, as the woodland habitat alongside the river is probably the only source of browse in the reserve. As I could personally observe, giraffes could be found more easily during the dry season, as they seem to concentrate alongside the river. After the first rains, giraffes seemed to disperse over the reserve.

No occurrence of gemsbok at river is unsurprising, as gemsbok is an antelope of dry environments, which occurs mostly in the western part of southern Africa and get less amount of rain than the MRR (Hijmans et al., 2005). Bushpigs seem to occupy the water holes absolutely more, but not more than expected. As being omnivorous, bushpigs might prefer drinking from more approachable water holes, but they could look for food resources such as

roots, fruit, or fungi (Seydack, 1990) alongside the river, where the successful finding is more probable.

For other species, such as zebra, wildebeest, and eland, the apparent preference for artificial water holes is not in discrepancy with findings from other areas (Harrington et al., 1999; Knight, 1995; Smit, 2011; Smit et al., 2007; Weeber et al., 2020). Eland might prefer water holes more due to physical properties of open habitats around the water holes in the reserve. Due to its sheer size, the eland might have problems with movement in forested habitat, thus not occurring frequently in the woodland alongside the river. As zebras and wildebeests are grazers (e.g. Owaga, 1975), the found apparent preference for waterholes in the reserve might be due to open habitat around all waterholes. For example, Mandinyenya et al. (2020) showed the preference of plains zebras in Zambezi National Park, Zimbabwe, for open habitats and avoidance of tree cover. Similarly, according to Hirst (1975), wildebeest choose open habitats more. Thus, presence of the artificial waterholes in the reserve allows these two species to persist in the preferred habitats without a need to look for a source of water in unpreferred habitat of woodland alongside the river. Similar might apply for blesbok, as it also prefers open habitats (du Plessis, 1972). As tsessebes (*Damaliscus lunatus*) and hartebeests (*Alcelaphus buselaphus*) also show preference for man-made water sources or being farther from rivers (Bhola et al., 2012; Smit, 2011; Smit et al., 2007), this overall preference might be phylogenetically based in the whole Alcelaphini tribe.

Impalas' preference for a type of water source is reported in literature without clear conclusion. A preference for river was found in the Kruger National Park (Smit et al., 2007), but preference for artificial water sources in Ruaha National Park in Tanzania (Epaphras et al., 2008). There might not be a clear effect of large spatial scale (distribution range) as my results seem to be similar to the study from Tanzania. Other ecological explanation might be a spatial segregation with nyala, as their diets overlap (mix-feeding, Sponheimer et al., 2003; Van Rooyen, 1990), and so does the temporal activity of these two species. In the small, fenced off reserve, these two species might need to spatially segregate from each other as they cannot avoid each other within the same habitat as they might do in a large national park.

For warthog, steenbok, and duiker, the accessibility to actual water as a resource might be higher at artificial waterholes, as these relatively small animals at the shoulder might have a problem of accessing water in the river. As the only large predator in the reserve is a leopard, its preferred prey species – impala, duiker (Hayward et al., 2006), steenbok (Searle et al., 2020)

– might avoid habitats with woody cover, which might correlate with leopard hunting areas (Balme et al., 2007).

### **4.3 Temporal activity of individual species**

As the ungulates can avoid each other not only in space, but also in the temporal scale, I have described activity levels and temporal activity patterns at the water sources of resident ungulates of the MRR and tested the level of overlap against body size and foraging niche. The highest activity level was recorded for bushbuck and relatively high activity level was also recorded for kudu, nyala, and giraffe. This might reflect the activity of these species being high due to obtaining browse alongside the river, thus spending more time at the water source. This might be also indicated by waterbuck – a grazer preferring the river more – having relatively low activity level. However, high level of activity is also recorded for blesbok and steenbok. Steenboks, being territorial, might increase their activity at the water sources during regular defence of a territory and deposition of scent markings. For blesbok, as I could observe, an area around several water holes was quite preferred in the MRR, thus the high activity level being probably recorded.

On the other hand, the lowest activity level was recorded for eland. Elands are water independent species (Western, 1975) and as browsers, they might differ from other water independent browsers (giraffes) in their activity level at the water sources due to not looking for food resources at the river. For gemsbok, steenbok, and bushpig, the standard error of the activity level is higher due to lower number of sightings (< 100). As seen in Fig. S1, the confidence intervals of the activity patterns of these species are large. This might not be associated only with lower visitation rate, but also with the (probable) smaller population of these species (Table 2), thus with lower detectability. However, as elands have a comparable population size as gemsboks in the reserve, the difference in number of sightings can show higher visitation rate in elands.

As the activity level is a proportion of the day the population, not individual in this study, is active, and the kernel density is being fitted in such analyses (Rowcliffe et al., 2014), the low number of gemsboks and elands doesn't influence the shape of activity. However, the real activity pattern might be different in the species with lower number of sightings, which might be due to both lower visitation rate and smaller population sizes.

Impalas, blesboks, gemsboks, and to certain extent kudus exhibit the pattern of temporal activity similar to the overall activity pattern of all ungulates. Nyalas and bushbucks also exhibit an additional morning peak of activity. Kudus, zebras, wildebeest, elands, and waterbucks exhibit increased activity during dusk hours. The smallest species (steenbok and duiker) exhibit low or no activity during midday and increased activity in the morning and evening. Bushpig exhibits nocturnal activity. Giraffes and warthogs exhibit peak of activity during midday or mid-afternoon, but low activity during dusk.

In terms of impalas' activity during day hours, my results agree with those of Hayward & Hayward (2012) and Sutherland et al. (2018). However, both studies found impalas to be active earlier and with decreasing activity toward sunset. This might be due to impalas having larger number of predators in their study areas including nocturnal lions and hyenas (*Crocuta crocuta*), which are absent from the MRR. Regarding gemsbok, my results are in discrepancy of those of Kasiringua et al. (2017), probably due to the geographical variation, as gemsboks in drier environment of Namibia could be more restricted in terms of finding food. Thus, they might visit the water sources just for drinking itself and then move away to areas of food resources, but gemsboks in the MRR might be more flexible in the time of visitations, as they might find more food closer to the water sources. Regarding blesboks, this study adds to overall low amount of information published regarding activity of this species. Klein & Fairall (1986) reported blesboks feeding from morning to afternoon and resting starting to occur during sunset. Regarding what I have found, blesboks might drink during feeding and before resting.

Activity of kudus in the MRR is similar to those studied by Hayward & Hayward (2012) at other sites of South Africa. van der Meer et al. (2012) found more herds of kudus coming to water in late morning, which might not be in discrepancy with this study. To test this discrepancy, actual number of individual animals should be considered. However, my results are in discrepancy with those of Kasiringua et al. (2017) from Namibia, where they found kudus being active more in the morning, late afternoon, and early night. Again, we might expect certain level of geographical variation or effect of different climate. Hayward & Hayward (2012) found nyalas active at the water holes at midday the most, which agrees with my results, however, they didn't find the morning and sunset peak of activity. Similarly to impalas, nyalas might be active during crepuscular hours in the MRR more than in areas with more species of predators. Wronski et al. (2006) found bushbucks performing behaviours such as moving, feeding, and social interactions during evening and night mostly. This might be both in agreement and in discrepancy with what I have found, as activity at water sources consists of

different behaviours. Thus, bushbucks might be both active at the water sources, but not performing “active” behaviours.

For wildebeests and zebras, Hayward & Hayward (2012) also found increased activity at water holes during late afternoon/early evening. However, they didn’t find any activity at night, which is different from my results. Again, absence of large predators might be the reason for wildebeests and zebras being active at the water sources also at night in the MRR. Decreased activity of zebras at midday found by Owen-Smith & Goodall (2014) corresponds to my result as activity of zebras at the water sources is not great during midday. Activity of elands in the MRR are at least partially similar with those studied by Hayward & Hayward (2012), Kasiringua et al. (2017), and Underwood (1975). This might show that eland might avoid being predated upon in areas with larger predators than leopard due its size, and thus can afford being active during less warm evening/night hours.

I show that the activity of waterbucks in my study might agree with Spinage (1968) and Wirtz & Oldekop (1991), who reported activity of waterbucks also during evening and resting during midday. However, Hayward & Hayward (2012) reported waterbucks being mostly active during morning. The explanation can be again of predation essence. Common duikers are reported in Wilson & Mittermeier (2011) as being diurnal with some twilight activity and resting during midday. My results show that this activity spatially takes place at the water sources during early morning and late evening and, to certain level, also at night. My results quite well fit in results of du Toit (1993), as steenboks should be active throughout the day with less activity at midday. I have also found the drop of activity level at midday.

Regarding the activity of warthogs and giraffes, I have found correspondence with findings from Namibia in dry season (Kasiringua et al., 2017) and with findings from other parts of South Africa for warthog (Hayward & Hayward, 2012). However, Hayward & Hayward (2012) reported giraffes being more active at the water holes in the mid-to-late afternoon, even though my results show peak of activity at midday and then continuous decreased of activity towards sunset. Together with results of Deribe et al. (2008) we could say that warthogs graze in the morning, then spend certain amount of time at water sources resting, wallowing (David Homoláč, *unpublished data*) and then continue grazing in late afternoon and evening (David Homoláč, *personal observations*). As Vallejo-Vargas et al. (2022) reported an increase of nocturnality for African herbivores with increasing body mass, giraffe might be an exception

as it has other methods how to avoid heat stress. For example, giraffes tend to face the sun during hottest hours of a day to minimize the surface exposed to it (e.g., Mitchell et al., 2017).

To assess the actual competition, I have calculated overlaps of activity for all pairs of studied species. I have found that body mass difference between the two species has no significant effect on the level of temporal overlap. One would expect the species with low body mass difference (same in size) would competitively exclude each other in the temporal scale as found for other communities regarding overall activity (Rasphone et al., 2020) or that larger species would temporarily exclude smaller species (Hayward & Slotow, 2009; Tsunoda et al., 2020). However, this was found for carnivores, and no temporal partitioning was found for African grazers visiting grazing sites (Cromsigt, 2006). I found no significant result suggesting that the ungulates would temporarily partition in their visitations to water sources based on their body size difference. However, the distribution of overlaps was greater for species with low body mass difference and lower for species with high body mass difference. This might show, that for certain species, the temporal competitive exclusion might take place. Overlaps of activity for species less similar in size seem to have lower distribution of values and only relatively high overlaps. This might be due to these species not competing with one another, or due to smaller species being active at the same time as larger species to avoid being attacked by predators.

However, there was a significant difference in the overlaps of activity at the water sources between pairs containing at least one mix-feeder (impala, nyala) or omnivore (bushpig, warthog, duiker) and pairs containing only browsers or grazers. The overlap for the former one is significantly lower. This might be due to the mix-feeders and omnivores being able to evade other species at the water sources in pursuit of food as their foraging niche is wider than those of strict browsers and grazers. Also, omnivores might have lower water requirements, but this is probably only true for common duikers (Kihwele et al., 2020). As the overlaps are proportional, quantifying level of common activity for the pairs of species might shine light onto the amount of time these species spend together. Comparing these common activity levels to body mass and foraging niche overlap might show different results than this study. As proportional overlap could be high, but actual amount of activity low, species might tolerate each other, but just to certain amount of time.

#### **4.4 Camera traps and AI**

To perform these findings, I have used camera traps that allowed me to collect large amount of data on animal presence at the water sources in the MRR. Other students have collected the data at the water sources through direct observations. However, as the policy of the MRC is “no field after sunset”, this design of data collection clearly misses a large time frame, which might bias the results. In this term, camera trapping allowed me to detect data on activity at the water sources closer to the actual reality.

Camera traps have undergone certain evolution in terms of technical properties and their aims in the research and conservation (Trolliet et al., 2014). However, as with all methods, studies with camera traps need certain unifying study design. As providing photos and videos and being financially available, camera traps can be used for all sorts of studies (Burton et al., 2015). However, each research team decides how to place the camera traps in the field, so that the placement is best for their specific research. Thus, comparing data from different sites might be difficult not only due to site specific factors, but also because of different study design.

It might be beneficial to use the grid cell design, as with such design you can use the data for assessing the overall activity levels and patterns, habitat utilization, biodiversity, population densities etc. And if the grid was placed, so that water sources or other landscape features are covered with the camera traps, such design could yield data about utilization of these features as well. However, such design would be financially costly (requiring large amount of camera traps) and timely costly (analyses of all the data). Nevertheless, such collaborative monitoring with camera traps exists (Rovero & Ahumada, 2017) and yields data allowing researchers to compare results from all three global tropical forest areas.

Another problem with camera traps might be detectability of the animals. I have placed the camera traps to optimize and maximize the data collection. However, in certain situations, the focal animal might evade the field of view of a camera trap, thus not being detected. Duikers and steenboks usually occurred on just few (or single) consecutive photos, so the results with these small species should be interpreted cautiously, as it is probable I haven't captured all occurrences of these species at the water sources.

As analyses of the large number of images from the camera traps (as some projects might deal with millions of photos) are timely or personally costly, the recent development of artificial intelligence has great impact on these. Generally, in science, AI allows scientists to

use large computing power to conduct more robust research. Using AI to detect photos without animals and to classify animal photos into species certainly speeds up the process of creating analyses-ready data file. However, even though the developers of such systems report high precision of such systems, implementation on specific datasets of camera trap photos might show differences in performance. Holding that in mind, I have trusted the MegaDetector to filter out photos without animals, but I have then gone through pictures of ungulates manually and checked the AI classification into species. I believe that with further development of artificial intelligence systems, more data could be analysed and more robust studies using camera traps could be designed.

#### **4.5 Limitations of the study, further research**

This study has several limitations on different scales. Firstly, the duration of data collection should be longer for assessing differences between activity at water sources during the two seasons. Also, camera traps should have been visited more frequently to avoid loss of data to baboons, weather, or robbers, as baboons were manipulating with the camera traps and weather probably caused loss of metadata due to moisture inside the camera traps. Data of activity at water sources should be collected over several such small reserves and comparative studies should be done to fully understand, whether there is a change in behaviour of ungulates toward water sources between these anthropogenically managed reserves and national parks.

Artificial feeding and mineral licks are provided to herbivores in the reserve during dry seasons and all year round, respectively, probably due to their high densities. Conditioning of the animals to spatio-temporally respond to this feeding is high and might affect the spatio-temporal behaviour even during wet seasons. Also, human activity in the reserve should be assessed as the reserve hosts high number of international students conducting different kinds of ecological and behavioural research, which could influence the behaviour of studied animals. Especially so, when the research involves experiments with ungulates reacting to predator occurrence traits at the water sources. My analyses are then limited with the methods and, thus, being unable to test interactions of the tested predictors, and effects of other factors. The TrapTagger is also limited with its structure and performance. As the AI has, like the human operators, certain level of error rate, some data might have been loss due to some photos being assessed as not containing animals or being wrongly classified. Also, the information about presence of juveniles was not always precise, as the TrapTagger allowed to assign this information to clusters of photos, not species sightings on individual photos. In future research



using the TrapTagger, this information should be assigned as presence of juveniles of specific species.

Future research should further investigate the overall temporal activity of ungulates and the activity at water sources in more small, fenced off reserves and compare those findings to data collected in national parks or larger reserves with full community of large fauna. Also, other groups or species of mammals are understudied in these terms, thus future research should look into that. Furthermore, assessing spatio-temporal behaviour of individual animals in these small reserves would shine a light onto the question of how exactly water sources are accessed by the large ungulates.

#### **4.6 Implications and relevance of this study**

Despite all the limitations, the results of my study add to overall low number of studies focusing on activity of African ungulates, especially on activity at the water sources. With changing environment including climate change, and thus change in maximum temperatures, I show this change might be reflected in the activity of ungulates. Despite artificial water holes being closed in certain areas (Smit, 2013) to promote biodiversity, with increasing maximum daily temperatures the building of new water sources might become necessary. Also, the Mokalakwena River Reserve provides different community of large mammals than, for example, the Kruger National Park. Thus, providing information on activity of these animals is crucial to fully understand the actual activity of the species in different environmental settings.

Finally, this study is important to the management of the MRR to understand the importance of the artificial water holes and to provide information for the tourism and research branch of the reserve. If tourists would like to see a certain species, the information about the species spatio-temporal activity can provide valuable help. Also, further research can use these data, not only for studies regarding water utilization by the animals, but also for finding the certain species of interest. Moreover, similar studies to mine would help with management of semi-captive animals in such reserves as the MRR, which number might rise due to continuing pressure of human civilization on natural environment, especially in Africa.

## 5. Conclusion

The ungulates in the Mogalakwena River reserve are active at the water sources mainly during the day with two notable peaks of activity – one at midday and one around sunset. This pattern, however, changes with body mass of the studied species, as large species are active at the water sources at night more than the medium sized species. As presence of juveniles of the large species affect the activity pattern and shift the activity more towards the day hours, the possibility of predation from resident leopards might be a reason for these patterns of activity.

The activity is also different with maximum daily temperatures, but not with rain, which might show thermoregulatory processes affecting the visitation of water sources by the ungulate species. We might expect changing patterns in activity regarding the effect of temperature with progressing climate change. The temporal activity of the specific species at the water sources differs, with some species being fully nocturnal while visiting water sources (bushpig), some being crepuscular (duiker), some visiting the water sources only during day hours (warthog, impala, giraffe, etc.) and some vising the water sources the most during sunset hours (zebra, wildebeest, kudu, etc.). Usually, for most species, the activity doesn't differ much with predictors such as season, water source type, presence of juveniles, and with different maximum daily temperatures.

The spatio-temporal segregation at the water sources is pronounced in typically forest antelopes (bushbuck, kudu, nyala) and water-bound antelopes (waterbuck), but also giraffe occupying river more than expected. These results are probably not caused only due to competition, but more probably due to habitat and diet preferences of mentioned species. Temporal overlaps of activity at the water sources between all pairs of species are significantly lower for pairs with at least one omnivore or mix-feeder. Probably, the activity at the water sources includes foraging and the species with wider foraging niche could evade unpleasant interactions at the water sources.

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## Supplement material

Table S1: Number of days each camera was active in the field, well positioned, and recorded date/time data correctly; upper part representing camera traps deployed at the river and bottom part representing camera traps deployed at (semi)artificial waterholes.

| Site                         | RS1          | RS2    | RS3         | RS4         | RS5       | RS6       | RS7       | RS8       | RS9       | RS10  |
|------------------------------|--------------|--------|-------------|-------------|-----------|-----------|-----------|-----------|-----------|-------|
| <b>Camera number</b>         | 16           | 19     | 15          | 11          | 10        | 9         | 14        | 17        | 18        | 20    |
| <b>Number of days active</b> | 349          | 32     | 80          | 296         | 342       | 344       | 404       | 402       | 411       | 400   |
| Site                         | Bush Dinneer | Ouland | Besteekraal | Besteekraal | Earth Dam | Earth Dam | Earth Dam | West Side | West Side | Total |
| <b>Camera number</b>         | 1            | 3      | 8           | 12          | 4         | 7         | 13        | 5         | 6         | -     |
| <b>Number of days active</b> | 301          | 382    | 216         | 356         | 315       | 372       | 367       | 374       | 325       | 6068  |

Table S2: Number of camera traps that were fully or partially active during each month of the study period.

| <b>Month</b> | <b>Placement of the camera traps</b> | <b>Number of camera traps active for the full month</b> | <b>Number of camera traps active for a part of the month</b> |
|--------------|--------------------------------------|---------------------------------------------------------|--------------------------------------------------------------|
| 9/2021       | Waterholes                           | 0                                                       | 3                                                            |
|              | River                                | 0                                                       | 0                                                            |
| 10/2021      | Waterholes                           | 3                                                       | 6                                                            |
|              | River                                | 0                                                       | 8                                                            |
| 11/2021      | Waterholes                           | 9                                                       | 0                                                            |
|              | River                                | 8                                                       | 2                                                            |
| 12/2021      | Waterholes                           | 9                                                       | 0                                                            |
|              | River                                | 8                                                       | 1                                                            |
| 1/2022       | Waterholes                           | 6                                                       | 3                                                            |
|              | River                                | 5                                                       | 5                                                            |
| 2/2022       | Waterholes                           | 5                                                       | 2                                                            |
|              | River                                | 6                                                       | 2                                                            |
| 3/2022       | Waterholes                           | 1                                                       | 7                                                            |
|              | River                                | 5                                                       | 4                                                            |
| 4/2022       | Waterholes                           | 8                                                       | 0                                                            |
|              | River                                | 7                                                       | 0                                                            |
| 5/2022       | Waterholes                           | 6                                                       | 3                                                            |
|              | River                                | 7                                                       | 1                                                            |
| 6/2022       | Waterholes                           | 8                                                       | 1                                                            |
|              | River                                | 7                                                       | 1                                                            |
| 7/2022       | Waterholes                           | 7                                                       | 2                                                            |
|              | River                                | 7                                                       | 1                                                            |
| 8/2022       | Waterholes                           | 8                                                       | 1                                                            |
|              | River                                | 8                                                       | 0                                                            |
| 9/2022       | Waterholes                           | 8                                                       | 1                                                            |
|              | River                                | 7                                                       | 1                                                            |
| 10/2022      | Waterholes                           | 8                                                       | 1                                                            |
|              | River                                | 7                                                       | 1                                                            |
| 11/2022      | Waterholes                           | 0                                                       | 9                                                            |
|              | River                                | 8                                                       | 0                                                            |
| 12/2022      | Waterholes                           | 0                                                       | 0                                                            |
|              | River                                | 0                                                       | 8                                                            |



Table S3: Overlap estimates of activity of individual species at different water source types (water hole, river) with corrected 95% confidence intervals. Overlap larger than 0.75 marked boldly, overlap lower than 0.25 marked boldly and in red. Confidence intervals exceeding these values for estimates >0.25 and <0.75 marked similarly. Values rounded up to two decimals.

| Species    | Overlap estimate | Upper 95% CI (basic0) | Lower 95% CI (basic0) |
|------------|------------------|-----------------------|-----------------------|
| impala     | <b>0.80</b>      | 0.76                  | 0.83                  |
| wildebeest | 0.51             | 0.31                  | 0.72                  |
| blesbok    | <b>0.15</b>      | 0.05                  | 0.29                  |
| zebra      | <b>0.78</b>      | 0.64                  | 0.90                  |
| giraffe    | <b>0.80</b>      | 0.76                  | 0.83                  |
| waterbuck  | 0.62             | 0.58                  | 0.66                  |
| warthog    | <b>0.88</b>      | 0.82                  | 0.95                  |
| steenbok   | 0.55             | <b>0.23</b>           | <b>0.84</b>           |
| duiker     | 0.60             | 0.38                  | <b>0.83</b>           |
| eland      | 0.64             | 0.43                  | <b>0.81</b>           |
| nyala      | <b>0.79</b>      | 0.72                  | 0.83                  |
| bushbuck   | <b>0.80</b>      | 0.71                  | 0.89                  |
| kudu       | <b>0.84</b>      | 0.77                  | 0.91                  |
| bushpig    | 0.71             | 0.41                  | <b>0.92</b>           |

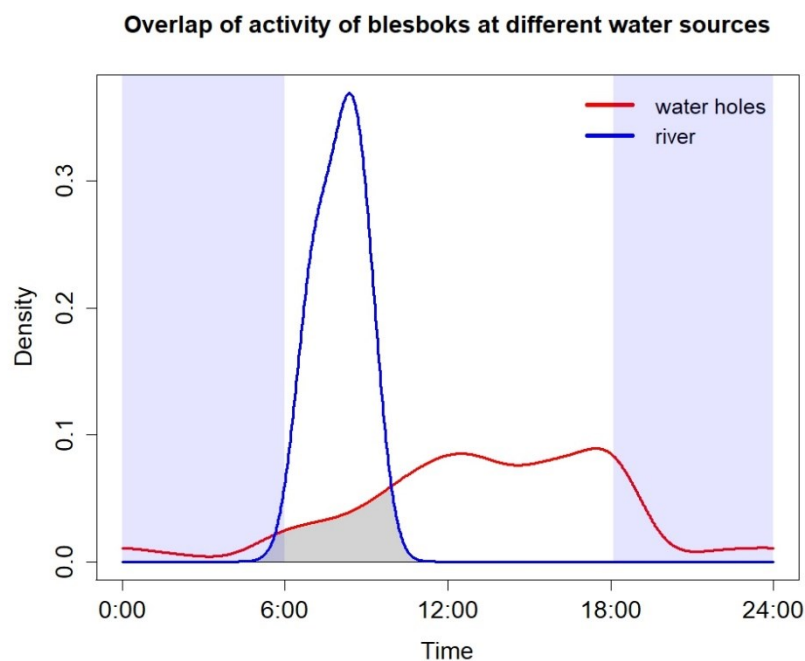


Figure S2: Plot of overlap of activity of blesboks at different water source types.

Table S4: Overlap estimates of activity of individual species at water sources during dry and wet season with corrected 95% confidence intervals. Overlap larger than 0.75 marked boldly, overlap lower than 0.25 marked boldly and in red. Confidence intervals exceeding these values for estimates >0.25 and <0.75 marked similarly. Values rounded up to two decimals.

| Species    | Overlap estimate | Lower 95% CI (basic0) | Upper 95% CI (basic0) |
|------------|------------------|-----------------------|-----------------------|
| impala     | <b>0.89</b>      | 0.85                  | 0.93                  |
| wildebeest | 0.73             | 0.63                  | 1.03                  |
| blesbok    | <b>0.88</b>      | 0.81                  | 0.94                  |
| zebra      | <b>0.77</b>      | 0.68                  | 0.86                  |
| giraffe    | <b>0.86</b>      | 0.82                  | 0.91                  |
| waterbuck  | 0.69             | 0.64                  | 0.74                  |
| gemsbok    | 0.41             | <b>0.16</b>           | 0.68                  |
| warthog    | <b>0.89</b>      | 0.83                  | 0.94                  |
| steenbok   | <b>0.85</b>      | 0.66                  | 0.97                  |
| duiker     | <b>0.86</b>      | 0.79                  | 0.93                  |
| eland      | 0.67             | 0.54                  | <b>0.79</b>           |
| nyala      | <b>0.77</b>      | 0.71                  | 0.84                  |
| bushbuck   | <b>0.89</b>      | 0.83                  | 0.95                  |
| kudu       | <b>0.83</b>      | 0.76                  | 0.90                  |
| bushpig    | <b>0.83</b>      | 0.54                  | 1.00                  |

Overlap of activity of gemsboks at water sources based on season

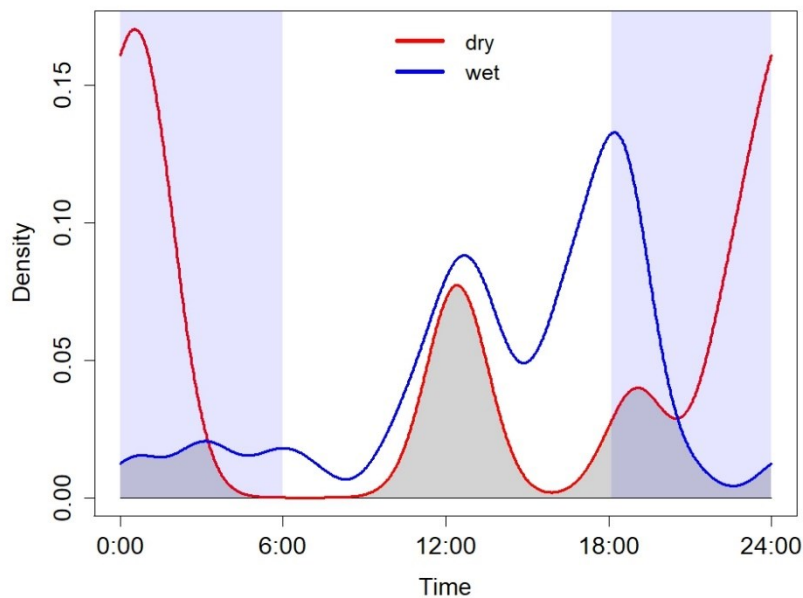


Figure S3: Plot of overlap of activity of gemsbok at water sources during dry and wet season.

Table S5: Overlap estimates of activity of individual species at water sources with and without juveniles with corrected 95% confidence intervals. Overlap larger than 0.75 marked boldly. Confidence intervals exceeding these values for estimates >0.25 and <0.75 marked similarly. Values rounded up to two decimals.

| Species    | Overlap estimate | Upper 95% CI (basic0) | Lower 95% CI (basic0) |
|------------|------------------|-----------------------|-----------------------|
| impala     | <b>0.85</b>      | 0.80                  | 0.90                  |
| wildebeest | 0.67             | 0.55                  | <b>0.77</b>           |
| blesbok    | <b>0.90</b>      | 0.83                  | 0.97                  |
| zebra      | <b>0.91</b>      | 0.82                  | 0.97                  |
| giraffe    | <b>0.88</b>      | 0.79                  | 0.93                  |
| waterbuck  | <b>0.78</b>      | 0.72                  | 0.84                  |
| warthog    | <b>0.88</b>      | 0.83                  | 0.92                  |
| nyala      | <b>0.89</b>      | 0.81                  | 0.95                  |
| bushbuck   | <b>0.81</b>      | 0.71                  | 0.91                  |
| kudu       | <b>0.86</b>      | 0.78                  | 0.94                  |

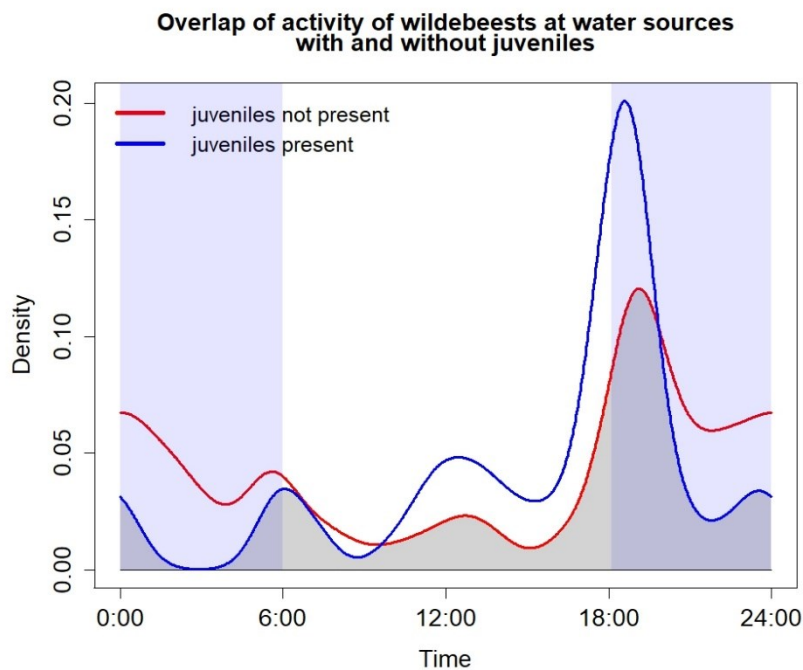


Figure S4: Plot of overlap of activity of wildebeests at water sources with and without juveniles present.

Table S6: Overlap estimates of activity of individual species at water sources during maximum daily temperatures  $>30\text{ }^{\circ}\text{C}$  and  $<30\text{ }^{\circ}\text{C}$  with corrected 95% confidence intervals. Overlap larger than 0.75 marked boldly, overlap lower than 0.25 marked boldly and in red. Confidence intervals exceeding these values for estimates  $>0.25$  and  $<0.75$  marked similarly. Values rounded up to two decimals.

| Species    | Overlap estimate | Upper 95% CI (basic0) | Lower 95% CI (basic0) |
|------------|------------------|-----------------------|-----------------------|
| impala     | <b>0.91</b>      | 0.88                  | 0.95                  |
| wildebeest | 0.72             | 0.64                  | <b>0.81</b>           |
| blesbok    | <b>0.87</b>      | 0.75                  | 0.96                  |
| zebra      | <b>0.89</b>      | 0.81                  | 0.94                  |
| giraffe    | <b>0.88</b>      | 0.85                  | 0.91                  |
| waterbuck  | <b>0.88</b>      | 0.83                  | 0.93                  |
| gemsbok    | 0.41             | 0.18                  | 0.57                  |
| warthog    | <b>0.91</b>      | 0.84                  | 0.97                  |
| steenbok   | 0.74             | 0.53                  | <b>0.89</b>           |
| duiker     | <b>0.77</b>      | 0.66                  | 0.87                  |
| eland      | <b>0.80</b>      | 0.70                  | 0.89                  |
| nyala      | <b>0.91</b>      | 0.85                  | 0.96                  |
| bushbuck   | <b>0.92</b>      | 0.84                  | 0.97                  |
| kudu       | <b>0.82</b>      | 0.75                  | 0.91                  |
| bushpig    | 0.54             | <b>0.21</b>           | <b>0.80</b>           |

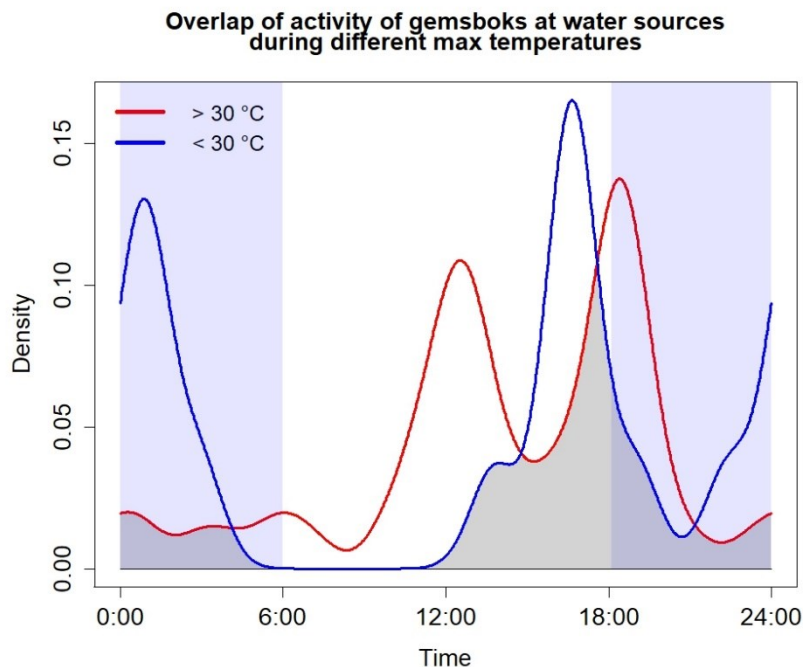


Figure S5: Plot of overlap of activity of gemsboks at water sources during different maximum daily temperatures.

Table S7: Overlap estimates of activities of all pairs of species of ungulates at water sources with corrected 95% confidence intervals. Overlap larger than 0.75 marked boldly, overlap lower than 0.25 marked boldly and in red. Values rounded up to two decimals.

| Species 1  | Species 2  | Overlap estimate | Upper 95% CI (basic0) | Lower 95% CI (basic0) |
|------------|------------|------------------|-----------------------|-----------------------|
| wildebeest | impala     | 0.48             | 0.44                  | 0.52                  |
| blesbok    | impala     | <b>0.91</b>      | 0.88                  | 0.94                  |
| blesbok    | wildebeest | 0.46             | 0.41                  | 0.51                  |
| zebra      | impala     | 0.59             | 0.54                  | 0.63                  |
| zebra      | wildebeest | <b>0.82</b>      | 0.78                  | 0.86                  |
| zebra      | blesbok    | 0.59             | 0.54                  | 0.64                  |
| giraffe    | impala     | <b>0.85</b>      | 0.83                  | 0.88                  |
| giraffe    | wildebeest | 0.48             | 0.45                  | 0.52                  |
| giraffe    | blesbok    | <b>0.91</b>      | 0.88                  | 0.94                  |
| giraffe    | zebra      | 0.62             | 0.57                  | 0.66                  |
| waterbuck  | impala     | 0.64             | 0.62                  | 0.67                  |
| waterbuck  | wildebeest | <b>0.79</b>      | 0.76                  | 0.83                  |
| waterbuck  | blesbok    | 0.64             | 0.61                  | 0.68                  |
| waterbuck  | zebra      | <b>0.90</b>      | 0.86                  | 0.93                  |
| waterbuck  | giraffe    | 0.67             | 0.64                  | 0.69                  |
| gemsbok    | impala     | 0.74             | 0.66                  | 0.81                  |
| gemsbok    | wildebeest | 0.65             | 0.54                  | 0.74                  |
| gemsbok    | blesbok    | <b>0.75</b>      | 0.66                  | 0.83                  |
| gemsbok    | zebra      | <b>0.75</b>      | 0.65                  | 0.86                  |
| gemsbok    | giraffe    | <b>0.75</b>      | 0.66                  | 0.83                  |
| gemsbok    | waterbuck  | <b>0.82</b>      | 0.74                  | 0.89                  |
| warthog    | impala     | 0.73             | 0.70                  | 0.76                  |
| warthog    | wildebeest | 0.26             | 0.23                  | 0.30                  |
| warthog    | blesbok    | <b>0.76</b>      | 0.72                  | 0.81                  |
| warthog    | zebra      | 0.40             | 0.36                  | 0.45                  |
| warthog    | giraffe    | <b>0.77</b>      | 0.74                  | 0.79                  |
| warthog    | waterbuck  | 0.45             | 0.42                  | 0.48                  |
| warthog    | gemsbok    | 0.55             | 0.45                  | 0.66                  |
| steenbok   | impala     | <b>0.82</b>      | 0.76                  | 0.88                  |
| steenbok   | wildebeest | 0.52             | 0.44                  | 0.61                  |
| steenbok   | blesbok    | <b>0.81</b>      | 0.73                  | 0.88                  |
| steenbok   | zebra      | 0.63             | 0.55                  | 0.70                  |

|          |            |             |      |      |
|----------|------------|-------------|------|------|
| steenbok | giraffe    | <b>0.81</b> | 0.73 | 0.88 |
| steenbok | waterbuck  | 0.65        | 0.57 | 0.72 |
| steenbok | gemsbok    | 0.69        | 0.60 | 0.77 |
| steenbok | warthog    | 0.63        | 0.54 | 0.71 |
| duiker   | impala     | 0.45        | 0.40 | 0.49 |
| duiker   | wildebeest | 0.70        | 0.64 | 0.75 |
| duiker   | blesbok    | 0.42        | 0.37 | 0.46 |
| duiker   | zebra      | 0.66        | 0.62 | 0.71 |
| duiker   | giraffe    | 0.46        | 0.42 | 0.50 |
| duiker   | waterbuck  | 0.62        | 0.56 | 0.68 |
| duiker   | gemsbok    | 0.48        | 0.39 | 0.57 |
| duiker   | warthog    | <b>0.24</b> | 0.20 | 0.28 |
| duiker   | steenbok   | 0.54        | 0.45 | 0.63 |
| eland    | impala     | 0.50        | 0.44 | 0.57 |
| eland    | wildebeest | <b>0.82</b> | 0.76 | 0.87 |
| eland    | blesbok    | 0.50        | 0.44 | 0.58 |
| eland    | zebra      | <b>0.82</b> | 0.76 | 0.88 |
| eland    | giraffe    | 0.50        | 0.44 | 0.57 |
| eland    | waterbuck  | <b>0.79</b> | 0.74 | 0.86 |
| eland    | gemsbok    | 0.69        | 0.58 | 0.78 |
| eland    | warthog    | 0.28        | 0.22 | 0.34 |
| eland    | steenbok   | 0.55        | 0.43 | 0.64 |
| eland    | duiker     | 0.61        | 0.52 | 0.68 |
| nyala    | impala     | <b>0.89</b> | 0.86 | 0.92 |
| nyala    | wildebeest | 0.41        | 0.37 | 0.45 |
| nyala    | blesbok    | <b>0.89</b> | 0.85 | 0.92 |
| nyala    | zebra      | 0.52        | 0.48 | 0.57 |
| nyala    | giraffe    | <b>0.87</b> | 0.84 | 0.90 |
| nyala    | waterbuck  | 0.57        | 0.53 | 0.59 |
| nyala    | gemsbok    | 0.67        | 0.58 | 0.76 |
| nyala    | warthog    | <b>0.76</b> | 0.72 | 0.80 |
| nyala    | steenbok   | <b>0.80</b> | 0.73 | 0.87 |
| nyala    | duiker     | 0.45        | 0.41 | 0.50 |
| nyala    | eland      | 0.42        | 0.36 | 0.48 |
| bushbuck | impala     | <b>0.87</b> | 0.83 | 0.90 |
| bushbuck | wildebeest | 0.45        | 0.40 | 0.49 |
| bushbuck | blesbok    | <b>0.82</b> | 0.78 | 0.87 |
| bushbuck | zebra      | 0.55        | 0.51 | 0.60 |
| bushbuck | giraffe    | <b>0.84</b> | 0.79 | 0.88 |
| bushbuck | waterbuck  | 0.59        | 0.55 | 0.62 |
| bushbuck | gemsbok    | 0.65        | 0.56 | 0.74 |

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|          |            |             |       |      |
|----------|------------|-------------|-------|------|
| bushbuck | warthog    | 0.72        | 0.67  | 0.76 |
| bushbuck | steenbok   | <b>0.81</b> | 0.71  | 0.88 |
| bushbuck | duiker     | 0.52        | 0.47  | 0.56 |
| bushbuck | eland      | 0.44        | 0.37  | 0.49 |
| bushbuck | nyala      | <b>0.90</b> | 0.85  | 0.94 |
| kudu     | impala     | <b>0.82</b> | 0.80  | 0.85 |
| kudu     | wildebeest | 0.61        | 0.57  | 0.65 |
| kudu     | blesbok    | <b>0.85</b> | 0.81  | 0.90 |
| kudu     | zebra      | 0.74        | 0.69  | 0.78 |
| kudu     | giraffe    | <b>0.85</b> | 0.81  | 0.89 |
| kudu     | waterbuck  | <b>0.79</b> | 0.76  | 0.83 |
| kudu     | gemsbok    | <b>0.82</b> | 0.74  | 0.89 |
| kudu     | warthog    | 0.62        | 0.58  | 0.67 |
| kudu     | steenbok   | <b>0.80</b> | 0.71  | 0.87 |
| kudu     | duiker     | 0.54        | 0.48  | 0.59 |
| kudu     | eland      | 0.65        | 0.59  | 0.71 |
| kudu     | nyala      | <b>0.77</b> | 0.73  | 0.81 |
| kudu     | bushbuck   | <b>0.75</b> | 0.70  | 0.79 |
| bushpig  | impala     | <b>0.15</b> | 0.07  | 0.23 |
| bushpig  | wildebeest | 0.59        | 0.47  | 0.70 |
| bushpig  | blesbok    | <b>0.16</b> | 0.08  | 0.23 |
| bushpig  | zebra      | 0.56        | 0.46  | 0.65 |
| bushpig  | giraffe    | <b>0.21</b> | 0.15  | 0.28 |
| bushpig  | waterbuck  | 0.49        | 0.46  | 0.52 |
| bushpig  | gemsbok    | 0.34        | 0.26  | 0.41 |
| bushpig  | warthog    | <b>0.04</b> | -0.01 | 0.08 |
| bushpig  | steenbok   | <b>0.22</b> | 0.14  | 0.30 |
| bushpig  | duiker     | 0.50        | 0.44  | 0.55 |
| bushpig  | eland      | 0.50        | 0.44  | 0.56 |
| bushpig  | nyala      | <b>0.10</b> | 0.06  | 0.15 |
| bushpig  | bushbuck   | <b>0.15</b> | 0.06  | 0.23 |
| bushpig  | kudu       | 0.31        | 0.23  | 0.39 |

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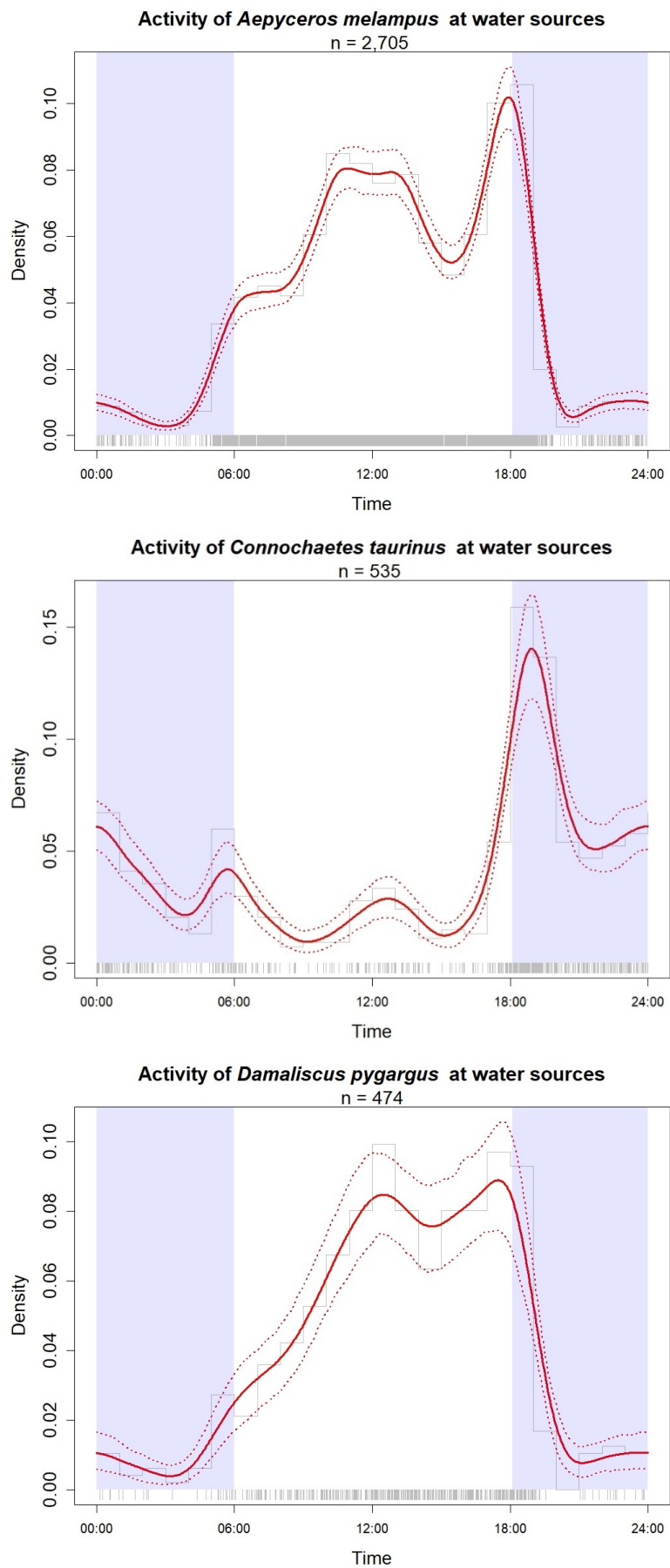


Figure S1a: Plots of activity of impalas, wildebeests, and blesboks (top to down order) at all water sources in the Mogalakwena River Reserve during the whole study season (27<sup>th</sup> September 2021 to 2<sup>nd</sup> December 2022).



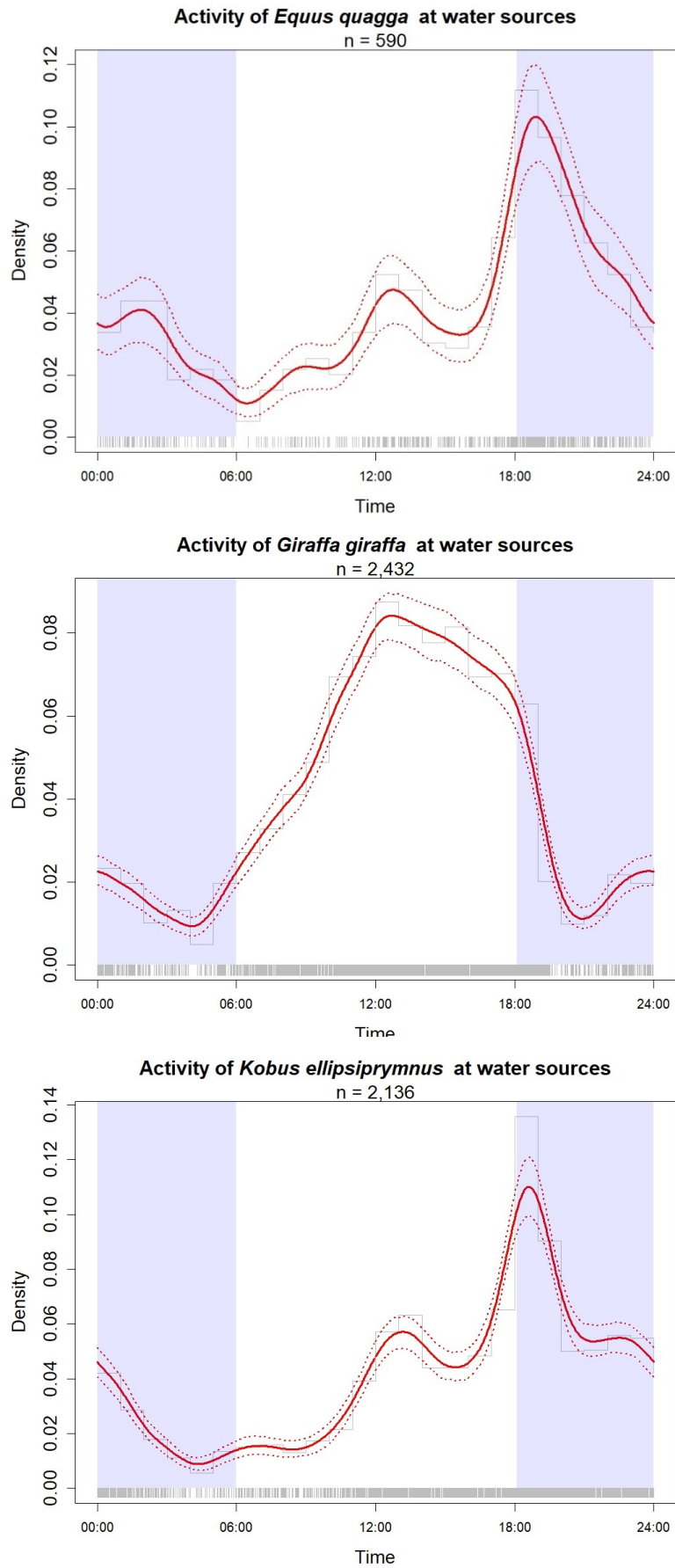


Figure S1b: Plots of activity of zebras, giraffes, and waterbucks (top to down order) at all water sources in the Mogalakwena River Reserve during the whole study season (27<sup>th</sup> September 2021 to 2<sup>nd</sup> December 2022).

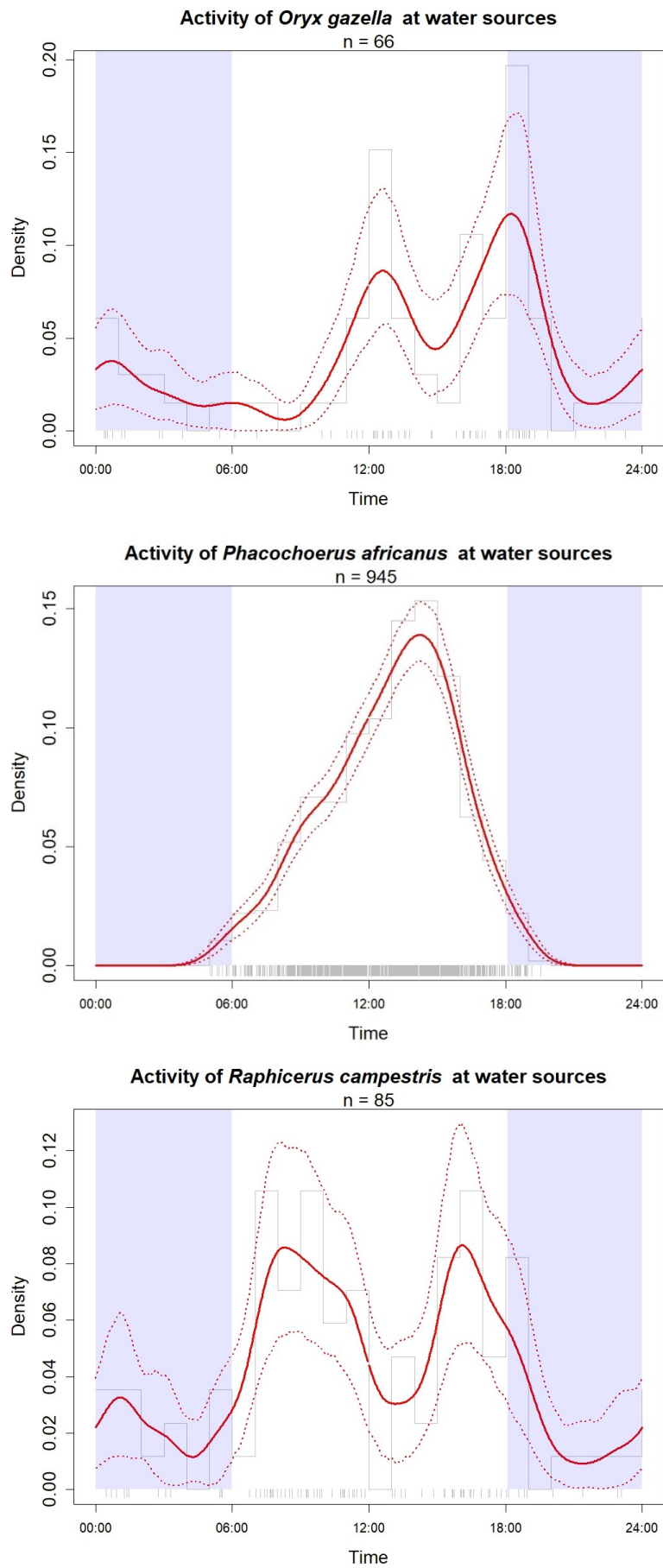


Figure S1c: Plots of activity of gemsboks, warthogs, and steenboks (top to down order) at all water sources in the Mogalakwena River Reserve during the whole study season (27<sup>th</sup> September 2021 to 2<sup>nd</sup> December 2022).

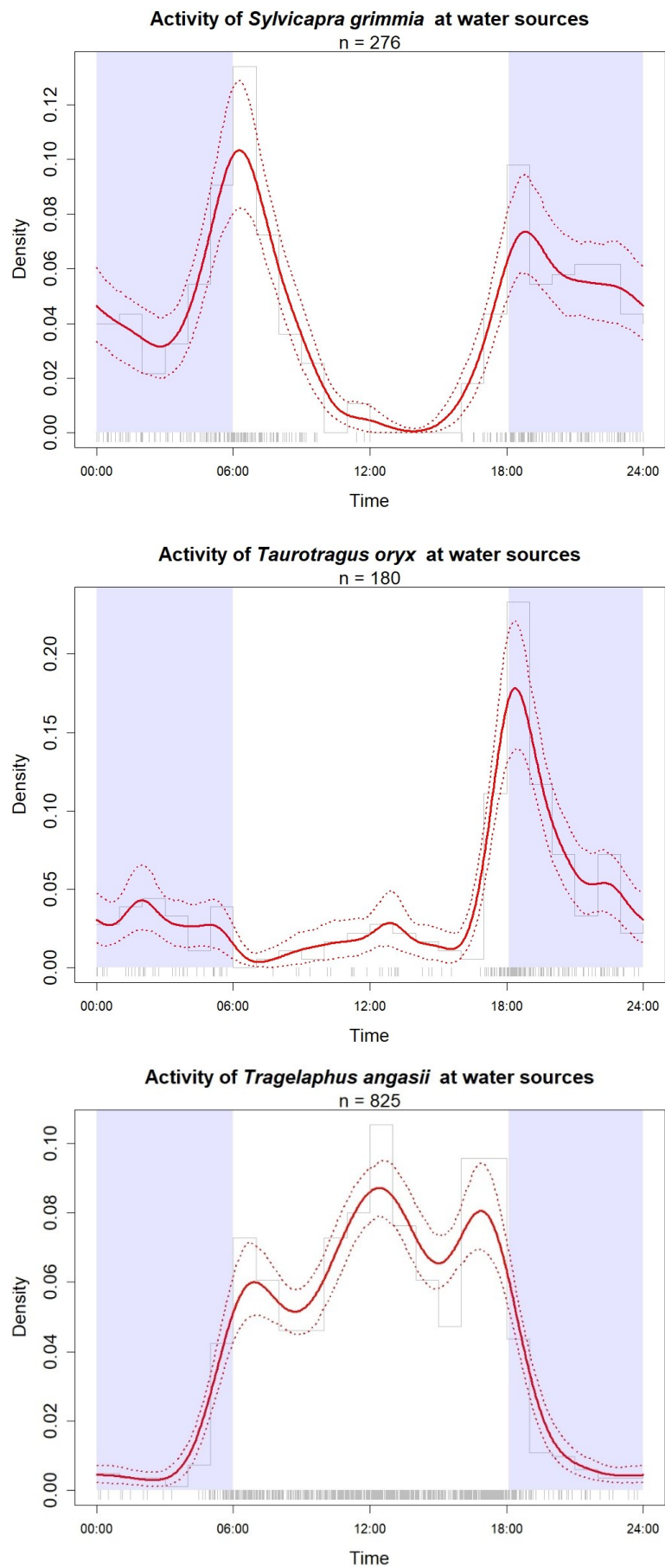


Figure S1d: Plots of activity of duikers, elands, and nyalas (top to down order) at all water sources in the Mogalakwena River Reserve during the whole study season (27<sup>th</sup> September 2021 to 2<sup>nd</sup> December 2022).

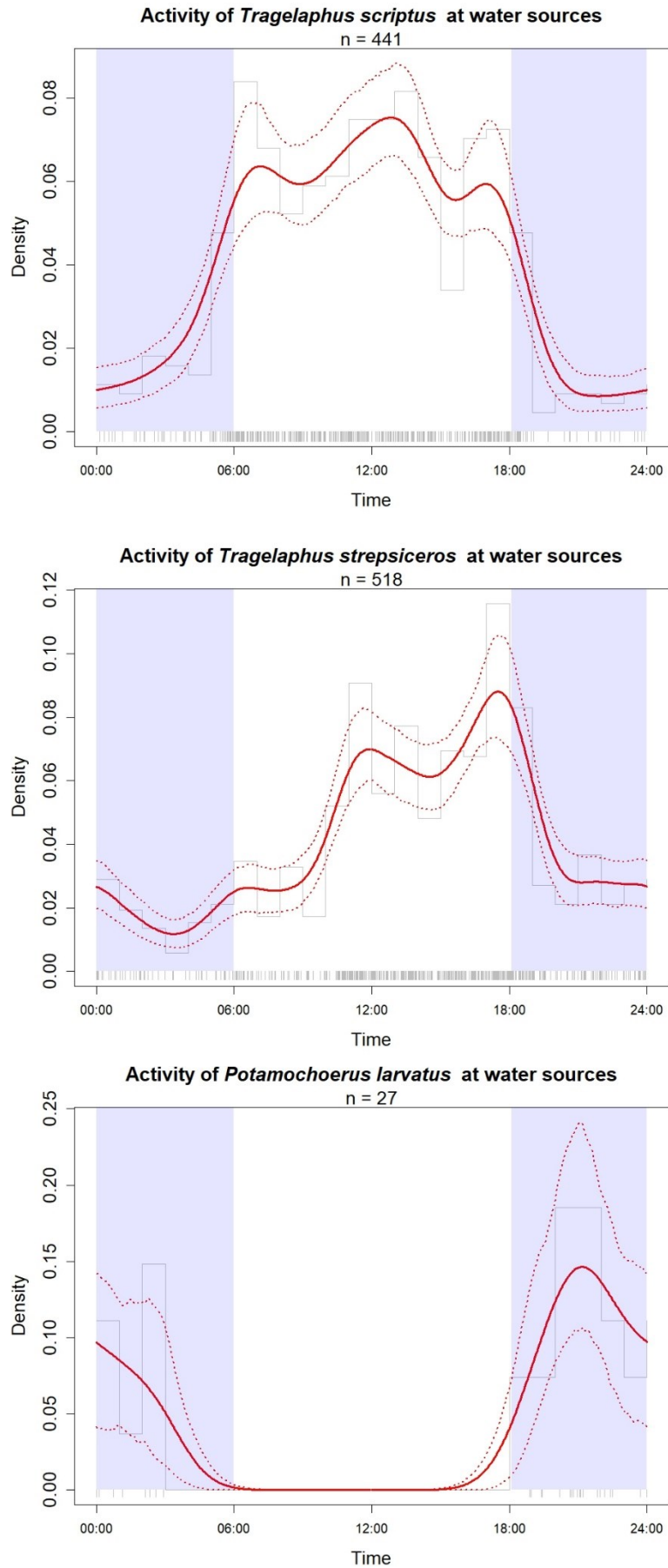


Figure S1e: Plots of activity of bushbucks, kudus, and bushpigs (top to down order) at all water sources in the Mogalakwena River Reserve during the whole study season (27<sup>th</sup> September 2021 to 2<sup>nd</sup> December 2022).