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Padayachy, Janiel

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Surface water dependencies and activity patterns of mammalian herbivores in South Africa

Janiel Padayachy

1907756

Submitted in the fulfilment of the requirements for the degree

Master of Science (Dissertation)

School of Animal, Plant and Environmental Sciences

University of the Witwatersrand

Johannesburg

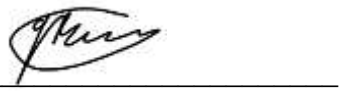
Supervisors:

Robyn Hetem (University of Canterbury & University of the Witwatersrand),

Willem Maartin Strauss (University of Canterbury), Jan Venter (Nelson Mandela University)

Declaration

I declare that this dissertation is my own, unaided work. It is being submitted for the Degree of Master of Science at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other University.



(Signature of candidate)

24th day of October 2024 in Johannesburg

Abstract

An increase in aridity in Africa may make water availability more variable, thus understanding how animals respond to these conditions is important for future wildlife management and conservation. However, mammalian herbivores with varying water requirements may respond differently to changes in water availability and predation. Using camera trap data, I analysed the spatial distribution relative to surface water sources and the 24-hour activity of 16 mammalian herbivores across 10 sites in South Africa. As expected, water dependent herbivores were generally closer to water, but only at sites where lions were absent. Herbivores with low water requirements were more nocturnal, potentially reducing water required to cool themselves evaporatively when active during the heat of the day. But that nocturnal activity was reduced when lions were present, likely reducing predation risk, increasing water requirements to dissipate heat and forcing herbivores to remain close to water. Nocturnal activity increased with body size in mixed-feeders and grazers, but decreased with body size in browsers, potentially reflecting more time spent foraging by large browsers. Using a novel approach of multistate diel occupancy models I showed that herbivores were generally active during both the day and night, and that the presence of lions impacted occupancy of preferred prey species (blue wildebeest, gemsbok and zebra). Diel occupancy of water-dependent prey (blue wildebeest) was influenced by an interaction between lion presence and distance to water sources. Thus environmental factors as well as physiological and morphological features affected the timing of activity and spatial distribution of several mammalian herbivore species in South African wildlife areas, which should be considered for future research and management of these species.

Keywords: mammalian herbivore, surface water dependence, diel activity, diel occupancy, predation risk, camera traps

Acknowledgements

I would like to thank my supervisors, Prof. Robyn Hetem, Dr, Maartin Struass and Prof. Jan Venter for their insight and guidance throughout my degree, as well as presenting opportunities where I could learn and grow as a scientist. Thank you to the instructors and coordinators for the African Field School for Camera Trap Studies hosted by the Nelson Mandela University. Their knowledge and teachings into analyses of camera trap data greatly helped me improve the results of my report.

I would also like to thank the Snapshot Safari team for collecting and providing the data used in my study. I also send further thanks to the team and developers of Zooniverse and Trap Tagger (WildEye Conservation), who are responsible for creating the software responsible for sorting and identifying the data I used before I received it from Snapshot Safari.

I am grateful for the funding provided by the NRF and Post Graduate Merit Award provided by the University of the Witwatersrand, allowing me to conduct my research.

My final acknowledgement goes to the South African Weather Surface (SAWS) for providing the weather data I used in this study.

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Introduction

Many arid and semi-arid regions in Africa are expected to become hotter and drier as a result of climate change (Engelbrecht *et al.*, 2015; Girvetz *et al*., 2019; Greve and Seneviratne, 2015), and understanding how animals will react to these changing conditions is important for management and conservation of species in these regions (Kupika *et al*., 2017; Thuiller *et al*., 2006). With an increase in aridity in arid and semi-arid regions in Africa, surface water availability is expected to become more variable (de Wit and Stankiewicz, 2006; Faramarzi *et al.*, 2013), which is likely to impact the distributions of herbivores that are constrained to surface water sources (Chamaillé-Jammes *et al.*, 2007a; Redfern *et al.*, 2003). Grazing mammalian herbivores in particular are more likely to be impacted by increasing aridity as grazers are considered dependent on surface water sources, while mammalian browsers and mixed-feeders are considered to be less water dependent, because they are able to fully or partially meet water needs through their diet (Kihwele *et al.*, 2020; Redfern *et al.*, 2003; Smit *et al*., 2007; Valeix, 2011; Western, 1975). The differences in water dependencies between herbivores within different guilds may result in different species being impacted in varying ways by climate change. For example, an increase in atmospheric carbon dioxide as a result of climate change, along with fire exclusion management practices, may change the vegetation dynamics (Bond and Midgley, 2012; O'Connor *et al*., 2014), impacting herbivores reliant on specific vegetation types. Increased temperature and aridity may lead to more droughts in southern Africa (Engelbrecht *et al.*, 2015), further shifting vegetation patterns and impacting herbivores. Understanding the reliance of different herbivore species on surface water and how those reliances may differ in conditions of varying heat and aridity is important, especially given the conservation and management importance of mammalian herbivores.

Artificial water sources are often implemented as a management intervention to mitigate water stress. Many wildlife areas in southern Africa make use of artificial water sources (Chamaillé-Jammes *et al*., 2007a; Smit *et al*., 2007; Sutherland *et al*., 2018). The purpose of artificial water sources in wildlife areas was to manage animal densities and allow water availability throughout the year and during water scarce periods (Rosenstock *et al.*, 1999). Within fenced South African reserves such as Kruger National Park, artificial water sources were established with the intention to preserve rare antelope species, provide suitable habitat to confined migratory species, support tourism by increase game viewing opportunities and preventing disease transfer between livestock and game (Pienaar, 1970; Smit and Grant, 2009; Sutherland, *et al.*, 2018). However, a high number of water sources can favour water-dependent species over other species, increasing impacts of predation, vegetation destruction, loss of biodiversity, and decreased ecosystem stability (Harrington *et al.*, 1999; Owen-Smith, 1996; Purdon and van Aarde, 2017). Despite the concerns around artificial water sources, they continue to be used in southern Africa, thus it is important to understand how different herbivores behave in these water abundant spaces. Understanding animal responses to artificial water sources under different environmental conditions may give insight as to how animals may respond to climatic changes in these reserves and how to better manage artificial water sources in the future.

How mammalian herbivores may respond to heat and aridity, in environments with limited water sources, will depend on how reliant the species is on surface water to replenish water used for evaporative cooling in the heat. Yet, water dependency of browsers and mixed-feeders may be more variable than typically proposed. Some non-ruminant browsers and mixed feeders rely on surface water, with black rhinoceros (*Diceros bicornis*) thought to drink once every two days (Buk and Knight, 2012; Emslie and Adcock, 1994; Kiambi *et al.*, 2020), and African elephants

(*Loxodonta africana*) frequently recorded to gather around surface water sources (Abraham *et al.*, 2021; Chamaillé-Jammes *et al.*, 2007b; Valeix, 2011; Western and Lindsay, 1984), suggesting that they are dependent on surface water sources. Both African elephants and impala (*Aepyceros melampus*), a mixed-feeding ruminant, were the most observed species at several water sources across various parks in southern Africa (Hayward and Hayward, 2012). Impala tend to also be the most abundant herbivores in parks and therefore the high frequency of impala at water sources may be linked their wide distribution. Common eland (*Tragelaphus oryx*), another mixed-feeding ruminant, were one of the most frequent visitors of water sources in the Waterberg National Park, Namibia (Kasiringua *et al.*, 2017). Browsers and mixed-feeders in Kruger National Park, South Africa, exhibited no observed response to artificial water sources, but showed a positive relationship to rivers, potentially as a result of the partial cover and better browse quality closer to drainage lines (Smit *et al.*, 2007).

An alternative explanation to browsers and mixed-feeders avoidance of surface water sources is that these herbivores may be avoiding the predation risk associated with water sources. Predation risk tends to be high around water sources because of the concentration of water dependent grazers at water sources, which in turn attracts predators (Cain *et al*., 2012; Valeix *et al.*, 2009b). Predation from lions (*Panthera leo*) in Hwange National Park, Zimbabwe affected the distribution of browsing herbivores in the park, with browsers avoiding risky areas such as watering holes (Valeix *et al.*, 2009b). Similarly, sable antelope (*Hippotragus niger*), a grazer, in the Kruger National Park avoided predators by occupying landscapes further away from water sources, thereby avoiding places frequented by the more common grazing plains zebra (*Equus quagga*) and the predators drawn to the higher concentration of zebra near water sources (Cain *et al*., 2012).

Perceived predation risk by herbivores may be linked to herbivore body size. Across sites in southern Africa, intermediate-sized herbivores (100-550 kg) became more diurnal in the presence of nocturnal predation caused by lions, while large (>550 kg) and small (<100 kg) herbivores remained nocturnal despite the presence of lions (Veldhuis *et al.*, 2020). Similarly, the distribution of African buffalo (*Syncerus caffer*), a large grazer in the system, was relatively unconstrained by predation risk across different landscapes in the Serengeti ecosystem, Tanzania (Hopcraft *et al.*, 2012). Large herbivores are considered difficult for predators to catch thus reducing the impact of predation risk on these species (Hopcraft *et al.*, 2012; Veldhuis *et al.*, 2020). However, while all herbivores in Hwange National Park avoided water sources at night when lions were active, the particularly large herbivores, southern giraffe (*Giraffa giraffa*) and African buffalo, avoided risky water sources altogether presumably because these were preferred prey species for lions (Valeix *et al.*, 2009a); a preference that may have been absent in other sites. Differences in predator community composition and prey preference by predators may also explain why the distribution of small grazing herbivores (20-50kg) were constrained by forage quality and predation risk associated with different landscape types (Hopcraft *et al.*, 2012). The differences in home ranges between small and large herbivores could also act as an explanation for the differences in activity and distribution. Smaller herbivores may have reduced home ranges possibly due to smaller dispersal capabilities, which serves as an explanation as to why small herbivores in Hwange National Park did not avoid risky water sources altogether like the large herbivores did, as risky water sources were the only water source available to small herbivores (Valeix *et al.*, 2009a). There does appear to be a difference in impact by predators on the activity patterns and distributions of herbivores of different sizes, however differences in the

dominant predator and prey preference per site as well as differences in herbivore ranges, diet and water needs could account for some of the apparent discrepancies.

Along with predation risk, herbivore body size may also directly impact experienced heat stress and therefore the degree of water dependency. Larger mammals having a smaller surface area to volume ratio than smaller mammals, resulting in a relatively small area through which to lose heat and thus lose heat at a slower rate compared to small mammals (Kinahan *et al*., 2007; Shrestha *et al.*, 2014). A slower rate of heat loss would make larger mammals more susceptible to heat stress. Alternatively, a larger body size may result in a more stable body temperature due to higher thermal inertia, however this prediction is seldom validated as evident in the dynamic body temperatures seen in mammals of various body sizes (Mitchell *et al*., 2018). In environments where the gradient of heat transfer is from the environment to the animal, small herbivores may at greater risk of overheating (Shrestha *et al.*, 2014), thus may be more likely than large herbivores to rely on evaporative cooling making them more reliant on surface water to replace body water lost by evaporative cooling.

Foraging needs are also impacted by herbivore body size, with larger herbivores predicted to increase their dietary intake to meet higher nutritional needs (Clauss *et al.*, 2013). African ruminant browsers specifically were shown to have a positive relationship between time spent foraging in daylight hours and body mass, thought to be facilitated by the larger rumen of large ruminants, allowing them to eat for longer periods of time (du Toit and Yetman, 2005; Owen-Smith, 1988). Conversely, larger temperate browsing and mixed-feeding ruminants were less active than smaller ruminants, attributed to larger ruminants having a lower-quality diet, resulting in longer rumination time (Demment and Soest, 1985; Mysterud, 1998). If factors such as predation or foraging requirements force herbivores to forage in the heat of the day, these

herbivores may need to rely on access to water sources to replenish body water lost through evaporative cooling.

Alternatively, endotherms may be able to shift their activity patterns between diurnal and nocturnal periods in response to heat stress (Levy *et al.*, 2019). Models created by Levy and colleagues (2019) predicted that in the presence of increased heat stress and reduced water availability, animals may become more nocturnal. Indeed, larger herbivores in Mapungubwe National Park, South Africa showed a greater decrease in diurnal activity in summer compared to smaller herbivores, potentially due to larger herbivores being more susceptible to heat stress (Shrestha *et al.*, 2014). Predation, however, may impact the degree of nocturnality herbivores may display because, as previously mentioned, herbivores tend to switch to more diurnal activities in the presence of predators (Valeix *et al.*, 2009a; Veldhuis *et al.*, 2020), resulting in a potential trade-off between avoiding heat stress and avoiding predation.

Both daily activity patterns as well as spatial distribution within a landscape may be affected by herbivore body size, perceived predation risk and ambient temperature, however studies generally consider daily activity patterns and space use of animals separately (Rivera *et al.*, 2022). For example, occupancy models used to study spatial distributions (MacKenzie *et al.*, 2017), often do not account for variation on a temporal scale (Mayer *et al.*, 2023). A few recent studies have used multistate occupancy models to analyse both spatial and temporal factors on animal occupancy (Mayer *et al.*, 2023; Rivera *et al.*, 2022), showing potential for the use of multistate diel occupancy models in studying animal behaviour. Further research into animal behaviour integrating herbivore responses at a spatial and temporal scale using multistate diel occupancy models would be beneficial to determine the effectiveness of this method in understanding animal behaviour.

Several limitations were present in studies using various methods and analyses that investigated water dependence of herbivores that may have impacted the trends observed. Some studies regarding herbivore water dependencies only used data from the dry season (Smit *et al*., 2007; Western, 1975), most of the studies were conducted in a single site, and all of them were conducted in savanna environments (Kihwele *et al.*, 2020; Redfern *et al.*, 2003; Smit *et al*., 2007; Valeix, 2011; Western, 1975). Another limitation of previous research on herbivore surface water dependency was that several studies were based on direct observations, which were limited to daylight observations, missing potential nocturnal behaviours and visits to water sources (Belovsky and Slade, 1986; Maloney *et al.*, 2005; Mysterud, 1998; Redfern *et al.*, 2003; Smit *et al*., 2007; Valeix, 2011; Western, 1975).

Much of our traditional understanding of species' water dependencies and activity times rely on direct observations of animal behaviour, are often limited to the diurnal period. Camera traps provide an alternative method that may improve our understanding of animal reliance on water sources and activity patterns of animals, because camera traps can record where and when animals are active throughout the day and night, allowing for observations over a full 24 hour period (Rowcliffe *et al.*, 2014). Additionally, camera traps also facilitate the recording of activity and behaviours of elusive species that are difficult to observe directly (Foster and Harmsen, 2012).

Investigating herbivore water use and activity patterns in arid environments may provide an analogue for how herbivores in less arid environments may respond to predicted increased heat and aridity under climate change. By studying activity times of large mammalian herbivores under different vegetation cover, water availability and climatic conditions, as recommended by Levy and colleagues (2019), we can determine how these herbivores may behaviourally respond

to climatic change and potentially identify key resource requirements to facilitate appropriate management interventions in a changing world. While studying varying levels of water availability may not be fully possible in wildlife areas with an abundance of water sources (including artificial ones), understanding these ecosystems would still give insights to improve wildlife management interventions in these environments.

The aim of my study was to analyse the spatial distribution relative to surface water sources and 24-hour activity patterns of selected South African mammalian herbivore species. I focused on how landscape use and activity patterns are impacted by feeding type (browser, mixed feeder or grazer), body size, water requirements, ambient temperatures, vegetation cover (measured through vegetation greenness by means of NDVI (Normalised Difference Vegetation Index)) and presence/absence of lions.

Objectives and hypotheses

Objective 1: Proximity of herbivores to surface water

Determine whether the spatial distribution of herbivores across different landscapes of South Africa is influenced by distance from surface water sources, feeding type, body mass, water requirements, ambient temperature, vegetation greenness and presence/absence of lions.

Hypothesis 1.1: Smaller herbivores will remain in closer proximity to surface water sources than larger herbivores, because smaller herbivores have small home ranges, a relatively larger surface area and are more susceptible to heat stress, therefore needing access to surface water to dissipate heat.

Hypothesis 1.2: Browsing and mixed-feeding herbivores will be in closer proximity to surface water sources in hot seasons and in areas where vegetation greenness is low, whereas grazers will remain near surface water sources year-round regardless of temperature or vegetation greenness. Browsers and mixed-feeders are expected to meet water requirements from diet alone, therefore will only be closer to water sources in periods of higher heat stress and dryness. Grazers are not expected to be able to meet water requirements from diet alone, hence will be close to water sources in all conditions.

Hypothesis 1.3: To reduce the risk of predation by lions associated with water sources, browsing and mixed-feeding herbivores will stay further away from surface water sources in sites where lions are present than sites without lions, whereas grazers will remain near surface water sources regardless of predation risk, since grazers are expected to be more dependent on surface water sources.

Objective 2: Diurnal and nocturnal activity patterns of herbivores

Determine if the timing of activity and the proportion of nocturnal activity of various mammalian herbivores in South Africa are influenced by feeding type, body mass, water requirements, ambient temperature, vegetation greenness and presence/absence of lions.

Hypothesis 2.1: Large African herbivores will shift to be more nocturnal in warmer temperatures to avoid heat stress, whereas smaller African herbivores will not experience a shift in activity times, because they will be able will be able to meet their daily foraging needs within a shorter time window.

Hypothesis 2.2: Browsers and mixed-feeders in sites with higher vegetation greenness will show less of a shift to nocturnal behaviours due to the green vegetation providing shaded refugia in the day and providing dietary water.

Hypothesis 2.3: Herbivores, particularly medium-sized herbivores that are likely to be preferred prey, will show less of a shift to nocturnal behaviours in sites where lions are present to avoid activity overlap with nocturnal predators.

Objective 3: Occupancy during the day and night of different herbivore species

Determine the influence of distance from surface water sources and the presence/absence of lions on the probability of day time occupancy (sunrise to sunset), night time occupancy (sunset to sunrise) and both day and night occupancy of various herbivore species, with different feeding types, body masses and water requirements across different landscapes of South Africa.

Hypothesis 3.1: To reduce the risk of predation by lions in close proximity to water sources, browsing and mixed-feeding herbivores will have a decreased occupancy particularly when

closer to water sources in sites where lions are present than sites without lions, whereas grazers will have a higher occupancy near water sources regardless of predation risk, since grazers are expected to be dependent on surface water sources.

Hypothesis 3.2: Herbivores, particularly medium-sized herbivores that are likely to be preferred prey to lions, will have a decreased night time occupancy and increased day time occupancy in sites where lions are present than sites without lions in order to avoid spatial overlap with lions temporally.

Materials and Methods

Study area

Herbivore photographs that I analysed in this study were provided by Snapshot Safari, a network of camera trap grids distributed across national parks and nature reserves in various African countries, of which I focused on South Africa (Pardo *et al.*, 2021). Snapshot Safari has 31 sites in South Africa, of which eight were selected for use in this study, namely: Kruger National Park, Associated Private Nature Reserves, Pilanesberg National Park, Atherstone Nature Reserve, Madikwe Game Reserve, Molopo Nature Reserve, Tswalu Kalahari Reserve and Samara Private Game Reserve (Figure 1; Table 1; Pardo *et al.*, 2021). The sites I selected were chosen due to the different sites representing a range of climates, having a similar variety of herbivore species with different feeding types and body sizes, and having a large sample size with several seasons' of data to increase confidence in the results. Tswalu Kalahari Reserve and Samara Private Game Reserve are both divided into two fenced sites, one with lions and one without lions, bringing the total number of sites examined in this study to 10 sites. Four of the ten total sites had no lions present, allowing for a good representation of study sites with and without lions.

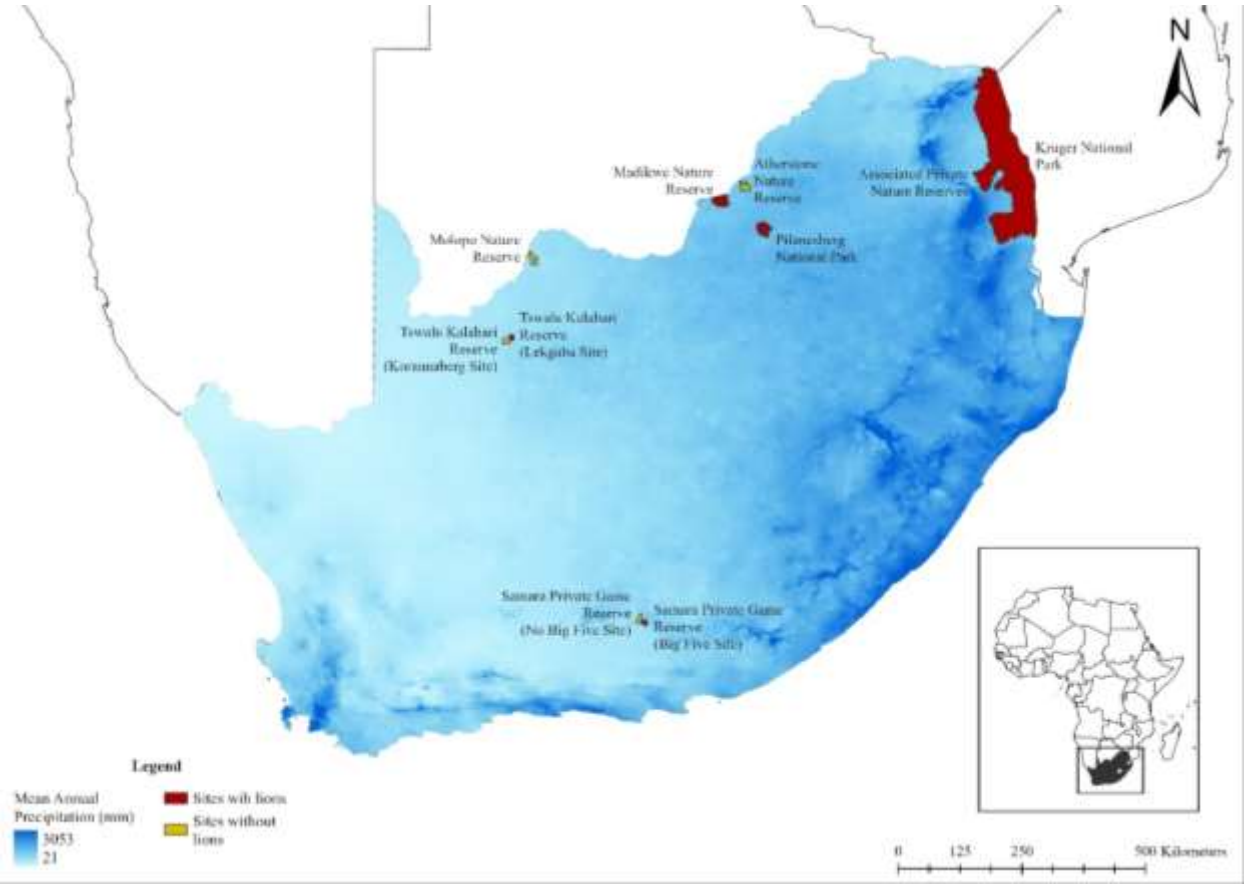

Figure 1. Locations of the 10 Snapshot Safari sites in South Africa used in this study. Sites are coloured based on whether they have lions present (red) or absent (yellow). Mean annual precipitation based on data collected from 1950 to 2007 created by Schulze and Maharaj (2007), demonstrates the variation in aridity found across South Africa and the sites chosen for this study.

Table 1. Study sites where camera trap data for this study were collected with each sites' dominant vegetation type, average annual rainfall, average annual temperature, and average annual NDVI (Normalised Difference Vegetation Index) and the presence or absence of lions in each site. The dominant vegetation type for each site was taken from the South African National Land-Cover dataset for 2020 (SANLC 2020). Average annual rainfall, temperature and NDVI values was calculated for years when camera traps were active during the study period for each site. Rainfall data was extracted and averaged from CHIRPS rainfall estimates, taking the average rainfall for the entire surface area for each site (Funk *et al*., 2014). NDVI values, were extracted and averaged from the MODIS Vegetation Index, specifically the MOD13A2 dataset, taking the average NDVI over the entire surface area of each site (Didan, 2015). Air temperature values were averaged from the closest weather station to each of the sites, with data provided by the South African Weather Service (SAWS).

Study site	Dominant vegetation type	Average annual rainfall (mm)	Average annual NDVI	Average annual air temperature (°C)	Presence of lions
Kruger National Park	Open woodland, grassland and small patches of dense woodland	1.258	3736.884	31.432	Present

Associated Private Nature Reserves	Open and dense woodland	1.604	3791.421	29.371	Present
Pilanesberg Nature Reserve	Open woodland, grassland and small patches of dense woodland	1.674	4459.169	28.880	Present
Atherstone Nature Reserve	Open woodland and grassland	1.847	4280.406	28.015	Absent
Madikwe Game Reserve	Open woodland, grassland and patches of fallow land	1.209	3978.652	26.125	Present
Molopo Nature Reserve	Grassland, low shrubland and patches of open woodland and fallow land	0.983	2422.105	32.038	Absent
Tswalu Kalahari Reserve (Lekgaba Site)	Grassland, low shrubland and patches of open woodland	1.149	2998.860	31.231	Present

Tswalu Kalahari Reserve (Korannaberg Site)	Grassland and low shrubland	0.967	2552.338	31.231	Absent
Samara Private Game Reserve (Big five site)	Grassland, low shrubland and patches of dense woodland	0.954	3271.022	26.983	Present
Samara Private Game Reserve (No big five site)	Grassland, low shrubland and patches of open and dense woodland	0.969	3293.739	26.983	Absent

Study species

Photographic data of 16 mammalian herbivore species were used for this study (Table 2). The herbivore species I selected covered a range of body masses, feeding types and are widely distributed across South Africa, allowing for comparison of responses in different climatic conditions around the country (Table 2). The study species I selected were those that had the highest number of recorded observations over at least five of the ten selected sites.

To quantify water dependence, I used the predicted water requirements and water dependence classifications calculated by Kihwele and colleagues (2020) based on assessments from previous literature. Since Kihwele and colleagues (2020) did not have information on white rhinoceros, I used the predicted water requirements and water dependence classification of black rhinoceros as they are closely related taxa, both are considered dependent on surface water (Buk and Knight, 2012; Emslie and Adcock, 1994; Kiambi *et al.*, 2020; Owen-Smith, 1988; Sinibaldi *et al.*, 2004) and both species have similar renal morphology (Maluf, 1991).

Table 1. Study species examined in the study along with each species' feeding type, body mass (based on average mass values of males and females from different sources), predicted water requirements and category of water dependence taken from Kihwele and colleagues (2020). Water dependence classification based on predicted water requirements were divided into three groups based on classifications by Hempson and colleagues (2015): none - able to obtain needed water from forage or was adapted to survive long periods without drinking; low – irregularly needs access to drinking water with no physiological adaptations to survive long periods without drinking; high – needs almost daily access to drinking water (Kihwele *et al.*, 2020). Herbivore feeding types were taken from Skinner and Chimimba (2005), with the exception of common eland and springbok, which were generally considered mixed-feeders. However both eland and springbok were shown to be primarily browsers in South African ecosystems (Codron *et al.*, 2007; Davies *et al*., 1986; Kerr *et al*., 1970; Watson and Owen-Smith, 2000). Herbivores are listed in order of their feeding type and body mass.

Species		Feeding type	Body mass (kg)	Predicted water requirements (scale from 0-100, with 100 being the highest water requirement)	Category of water dependence
Common name	Scientific name				
Southern giraffe	*Giraffa giraffa*	Browser	816 (Skinner and Chimimba, 2005)	31	low
Common eland	*Tragelaphus oryx*	Browser	340 (Estes, 1999; Posselt, 1963; Skinner, 1967)	36	none

Greater kudu	*Tragelaphus strepsiceros*	Browser	135 (Skinner and Chimimba, 2005; Wilson, 1970)	41	low
Springbok	*Antidorcas marsupialis*	Browser	26 (Kruger *et al*., 1979; Smithers, 1971)	37	low
Common duiker	*Sylvicapra grimmia*	Browser	15 (Rautenbach, 1982; Schmidt, 1984; Smithers, 1971)	30	none
Steenbok	*Raphicerus campestris*	Browser	8 (Smithers, 1971)	25	none
White rhinoceros	*Ceratotherium simum*	Grazer	1500 (Skinner and Chimimba, 2005)	69 (based on black rhinoceros water requirements)	high
African buffalo	*Syncerus caffer*	Grazer	450 (Patterson, 1979; Pienaar, 1969; Taylor, 1985)	43	high
Waterbuck	*Kobus ellipsiprymnus*	Grazer	260 (Skinner and Chimimba, 2005)	52	high
Plains zebra	*Equus quagga*	Grazer	200 (Smuts, 1974)	60	high
Blue wildebeest	*Connochaetes taurinus*	Grazer	165	40	high

			(Attwell, 1982; Braack, 1973; Hitchins, 1968)		
Gemsbok	*Oryx gazella*	Grazer	150 (Skinner and Chimimba, 2005)	30	none
Hartebeest	*Alcelaphus buselaphus*	Grazer	135.20 (Skinner *et al*., 1973; Skinner and Chimimba, 2005; Smithers, 1971)	28	high
Common warthog	*Phacochoerus africanus*	Grazer	45 (Mason, 1985)	57	high
African elephant	*Loxodonta africana*	Mixed-feeder	1725 (Skinner and Chimimba, 2005)	66	high
Impala	*Aepyceros melampus*	Mixed-feeder	45 (Anderson, 1982; Skinner, 1971; Smithers and Wilson, 1979)	28	high

Experimental design and protocol

Snapshot Safari camera traps used for this study, all of which were Cuddeback cameras (models 1231, 1255 and 1347), were placed 0.5 m off the ground (Pardo *et al.*, 2021), being an ideal height to capture pictures of large mammals. The camera traps were triggered by movement or changes in heat perceived by the camera, and were set to capture pictures throughout the day and night, using either a flash or infrared photography at night to ensure the subject can be seen in night time photographs (Pardo *et al.*, 2021). In each of the selected sites used in this study, camera traps were placed on an evenly spread grid five square kilometres in size across a set area over each site to allow for equal capture opportunities across each area (Pardo *et al.*, 2021), Atherstone Nature Reserve had additional cameras stationed at water bodies. Each site had camera traps deployed for different amounts of time, but each site had data that covered all four seasons throughout the years. The study period was from June 2017 to June 2022.

Before November 2019, Snapshot Safari used Zooniverse to identify animals in photographs, which used a mixture of online volunteer identification and machine learning identification based on user feedback to identify animals in photographs (Simpson *et al.*, 2014). After November 2019, TrapTagger, an open-source web application developed by WildEye Conservation, was used to analyse pictures and identify animals in photographs utilising artificial intelligence programs to process data.

In sites that had two species of zebra (*Equus* spp.) and both species of wildebeest (*Connochaetes* spp.), I manually sorted pictures of these genera to ensure the correct study species was identified, as the species are visually similar and have a high likelihood of misidentification.

Further manual cross-checking was done to ensure the dates and time for each camera for each trapping session was correct. Errors included in the data were incorrect dates (either day or month values were inaccurate) and time was shifted by 12 hours (am and pm values were switched when setting up the cameras), which was identified by comparing the date and time in the dataset with the calibration photo which had the correct date and time for each dataset. Incorrect dates or times were corrected in R (R Core Team, 2021) by adding or subtracting the necessary time interval to correct the date or time. Each photograph I identified as having one of the selected study species acted as a herbivore observation, providing information on the species recorded, as well as the date, time and location of the observation.

Data analyses

Once the observations were fully sorted, I analysed the records to determine the proximity to water, temporal activity patterns and spatial occupancy of the various herbivore species. I ran all models in the program R (R Core Team, 2021). For all three objectives, I used weather data in the form of daily rainfall data, NDVI (normalised difference vegetation index) measurements and maximum daily air temperature values in the analysis. Daily rainfall data was extracted from CHIRPS rainfall estimates, which used satellite data to determine rainfall data across Africa (Funk *et al*., 2014). The average daily rainfall values were taken over the surface area for each site over the duration of time camera traps were active in each site. The NDVI values, were extracted from the MODIS Vegetation Index, specifically the MOD13A2 dataset, which provides calculated NDVI values over every 16 days at a scale of one square kilometre across global land surfaces (Didan, 2015). I used NDVI as a measure of vegetation greenness that can be used to infer vegetation quality, and thus potential diet quality of the study herbivores. Both the average daily CHIRPS rainfall and 16 day NDVI values over each site was extracted using

Google Earth engine for the camera trapping period of each site (Gorelick *et al*., 2017). Air temperature values were provided by the South African Weather Service (SAWS), with the air temperature values provided from the closest weather station (ranging from about 1.5 km to 145 km away) to each of the sites that were studied, for the time periods that each site had camera traps deployed. For my analyses, I defined seasons as summer (December to February) autumn (March to May), winter (Jun to August) and spring (September to November).

Proximity to surface water

To determine the proximity to surface water, I first assigned a distance to the nearest water source based on the position of the camera trap to each observation. I removed observations from certain camera traps in Atherstone Nature Reserve that did not follow the standard Snapshot Safari grid setup for this analysis, so that camera traps in each site were set up in evenly spaced grids. Distances to the nearest permanent water source was provided by Snapshot Safari for camera traps in Molopo Nature Reserve, Tswalu Kalahari Reserve and some camera traps in Pilanesberg Nature Reserve, Atherstone Nature Reserve and the Associated Private Nature Reserves. For all camera traps where the distance to the nearest water source was not provided, I calculated the distance from each camera trap to the nearest permanent water source using the South African National Land-Cover dataset for 2020 (SANLC 2020). The SANLC 2020 dataset was provided by the South African department of Forestry, Fisheries and Environment, which included a map of land covers across South Africa, including water sources, at a 20 m scale generated using Sentinel 2 satellite imagery. SANLC 2020 has been confirmed to have user and producer accuracy greater than 90% when measuring water classes (Ngcofe and Nkoana, 2023). Using the provided GPS coordinates of each camera trap and the South African National Land-Cover 2020 dataset I was able to determine the distance from each camera trap to the nearest

surface water source using QGIS, an open source geographic information system (QGIS.org, 2023).

When considering spatial distribution of animals it is important that observations are independent of each other to avoid autocorrelation errors where estimates of spatial distribution, such as home ranges, can be incorrectly estimated (Rooney *et al*., 1998; Swihart and Slade, 1985). Thus to ensure each observation was independent in this study for each species at each camera trap a time to independence of ten minutes was implemented, where all photographs taken after the initial or subsequent photographs within a ten minute interval of each other were removed. A ten minute time to independence was supported by several other camera trapping studies that also used a 10 minute time to independence (Kolowski and Forrester, 2017; Massei *et al*., 2018; Palmer *et al*., 2017; Palmer *et al*., 2018; Thel *et al*., 2021).

I plotted the density of observations against the distance from water for each herbivore species in each site (where the species was present) and season. From each plot, I created records by extracting the distance where the density of observations was highest per species, within each site and season. To avoid records with too few observations skewing the data, I removed any seasons with fewer than 25 observations. I added the feeding type, body mass and predicted water requirements for each species to the dataset along with the average rainfall, air temperature and NDVI values for each season in each site and whether lions were present or not at each site. To check that the data met the criteria for running a GLMM (generalised linear mixed model), I used diagnostic QQ (quantile-quantile) plots integrated in R to check that the residuals were normally distributed when fitted on the plot. I further checked that the data was normally distributed using a Shapiro-Wilk Normality Test in R (Shapiro and Wilk, 1965). I ran a series of

GLMMs, using the package glmmTMB (Brooks *et al.*, 2017), testing combinations of different fixed effects and interactions of these variables against the response variable, using a Gaussian family analysis.

In each GLMM, the response variable I used was the most frequently observed distance to water (calculated as the distance from the nearest surface water source where density was highest) and the random effects variable was the site of each record. The fixed effects I tested were: body mass, feeding type, predicted water requirements, daily rainfall averaged per season, daily maximum air temperature averaged per season, NDVI averaged per season and lion presence/absence. The interactions of fixed effects tested (based on relationships I predicted were the most likely to be impactful) were: body mass*feeding type, body mass*predicted water requirements, body mass*lions present, feeding type*lions present. I tested each combination of fixed effects and fixed effects interactions using the dredge function from the package MuMIn (Bartoń, 2009) to run each GLMM. I selected the simplest model, with the lowest degrees of freedom, that was within two AICs (Akaike Information Criterion) of the model with the lowest AIC as the top model to ensure ease of interpretation (Yates *et al*., 2021).

Proportion of nocturnal activity

To determine the proportion of nocturnal activity engaged by each species, I used the suncalc package (Thieurmel *et al*., 2019) to get the sunrise and sunset times for each observation using the date and coordinates of the camera trap for each observation. I then classified each observation as occurring in the day (sunrise to sunset) or at night (sunset to sunrise). I determined the proportion of observations taken at night (serving as a proxy for nocturnal activity) for each species in each site within each season and compiled the information into a

dataset. For this objective, I included images from all camera traps, including those that did not fall within the standardised Snapshot Safari grid for each site, as this objective is focused on when each species is active, not their distribution within the landscape. Similarly to objective one, I removed any records with fewer than 25 observations from the dataset of nocturnal activity. I did not include a time to independence in this objective following recommendations by Peral and colleagues (2022), which stated that removing data through the application of a time to independence may bias estimates of activity patterns, particularly affecting those of herbivores.

Following a similar procedure as objective one, after using QQ plots and a Shapiro-Wilk Normality Test in R to make sure the data met the criteria for running a GLMM (Shapiro and Wilk, 1965), I ran a series of GLMMs using the glmmTMB package (Brooks *et al.*, 2017), and used the dredge function in the MuMin package (Bartoń, 2009) to test different combinations of variables. In each GLMM, using a Gaussian family, I tested combinations of different fixed effects and interactions of these variables against the response variable, proportion of observations taken at night, with the site set as the random variable. The fixed effects I tested were: body mass, feeding type, predicted water requirements, daily rainfall averaged per season, daily maximum air temperature averaged per season, NDVI averaged per season and lion presence/absence. The interactions of fixed effects tested (based on relationships I predicted were the most likely to be impactful, and did not result in convergence issues) were: body mass*feeding type, body mass*predicted water requirements, body mass*lions present, feeding type*lions present, predicted water requirements*lions present and average rainfall*predicted water requirements. The model I used to predict the most important variables on nocturnal activity was the simplest model run with the lowest degrees of freedom to ensure ease of

interpretation (Yates *et al*., 2021), that was within two AICs of the model with the lowest AIC score.

Diel occupancy

To determine the influence of variables of interest on the day-time and night- time occupancy of different herbivores, I ran multistate diel occupancy models for each species using the unmarked package (Fiske and Chandler, 2011). The unmarked package has been used on camera trap data to determine the occupancy of animals in response to environmental stressors such as anthropogenic changes (Diao *et al.*, 2021) and predation (Steenweg *et al.*, 2023).

I had to calculate the occupancy of each species separately, after which I compared the occupancies and the potential impacts of the traits of each species (body size, feeding type and predicted water requirements). I included all study species except for African buffalo, waterbuck (*Kobus ellipsiprymnus*) and common eland, which had too few observations to predict the probability of occupancy in each model, as well as warthog (*Phacochoerus africanus*), which had predominantly day time observations and thus could not be properly evaluated in a multistate diel occupancy model (i.e. night-time occupancy could not be determined).

Because of the large scale of the data set, spanning multiple years, I summarized the data into weekly events. The mutually exclusive states I defined for each camera trap for each week in the occupancy models were as follows: Camera trap not active (NA), no observations (0), day observations (1), night observations (2), both day and night observations (3). The unmarked package, used to analyse the data, ignored data where the camera trap was inactive (missing data) and only used the rest of the data to predict occupancy. I did not consider camera traps that

did not follow the standard Snapshot Safari protocol (i.e. were not in a standardised grid) in the occupancy models. I did not consider sites without the focal species present for that species' model. I removed sites that had fewer than 16 weekly observations as inclusion of parks with fewer than 16 observations resulted in errors with subsequent models.

In each model the observed covariates, which acted as detection covariates in the model, I used for each camera trap for each week were the rainfall, NDVI and air temperature values for that site. For rainfall, I determined the average precipitation values for each week over the entire site area. For NDVI, since the data given was a 16 day estimate, for each week, I assigned the NDVI value of the date closest to that week for each site. For air temperature, I calculated the maximum daily air temperature averaged per week from the weather station data for each site. In cases where some of the weather stations did not record data over a few weeks (up to two weeks in a month for some sites) over the sampling period, I used the average monthly temperature instead of weekly data. In the sites Kruger National Park and Madikwe Game Reserve, up to four months of weather data was missing, so I used average maximum daily air temperatures from months of following and previous years. The occupancy models of unmarked (Fiske and Chandler, 2011), do not allow for the direct impacts of observed covariates on the occupancy to be evaluated when setting up the model equation, however I still incorporated each of these variables within the model, although no direct effects were able to be calculated.

I tested the following site covariables: distance of each camera trap from the nearest surface water source, presence of lions and interaction between these variables. For each species, I ran 6 multistate models testing different combinations of the site covariates: ~distance from water*lions present, ~distance from water+lions present, ~lions present, ~distance from water

and no site covariates. In some models not all parameters (all states and variables tested) were fully estimated, suggesting certain states occur very rarely or under certain conditions and there is not enough data to predict these parameters. For each species, I used the model with the lowest AIC scores and had estimates for all tested parameters to determine the probability of occupancy and was used to infer the most important variables that impacted the probability of each species occupying an area at different times of day during each week.

Results

Over a period of five years (June 2017 to June 2022), over 200 000 pictures of the 16 selected herbivore species within the 10 sites were captured by Snapshot Safari cameras and analysed in this study. While not all species were present in all 10 sites and not all camera traps in each park were activated for the entire study period, sufficient photographs were gathered to determine the distance from water, timing of activity patterns and occupancy of the study species.

Proximity of herbivores to surface water

By plotting the density of photographs, relative to the nearest surface water source I was able to determine the distance from water that was most frequently occupied for each species in each site for each season (examples in Figure 2). There were 184 camera trapping seasons that had more than 25 observations for each species for each site. After I tested various combinations of fixed effects in GLMMs, the simplest model within two AICs of the top model had the interaction between the presence of lions and the predicted water requirements as significant fixed effects (Table 3).

Herbivores with higher estimated water requirements were generally closer to surface water sources when lions were absent (Figure 3; Estimate = -35.40±12.23m, z-value = -2.894). When lions were present, all herbivore species were generally found within 1.2 km of water, irrespective of their predicted water requirement (Figure 3; Estimate = -2107.73±727.13m, z-value = -2.899).

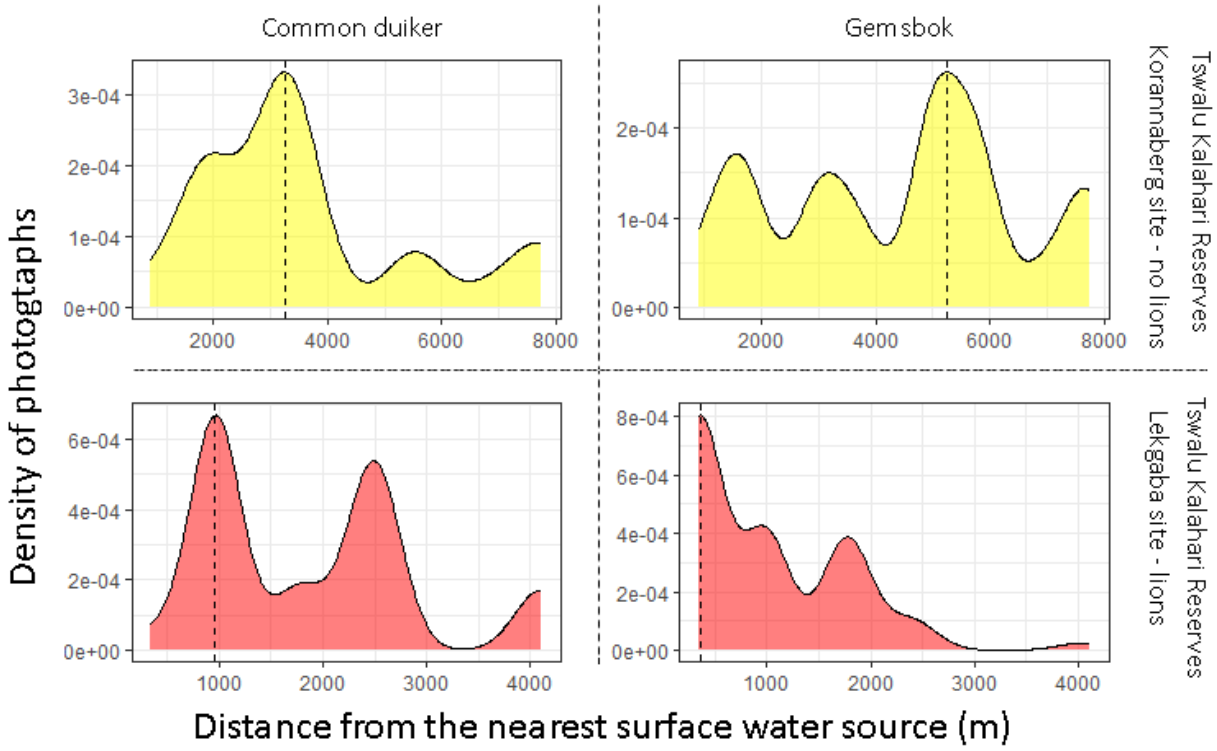

Figure 2. Kernel density plots showing the frequency of common duiker (*Sylvicapra grimmia*) and gemsbok (*Oryx gazella*) photographs relative to the nearest surface water source for each camera trap in Tswalu Kalahari Reserve over summer seasons from 2017 to 2022. The distance from the nearest water source that was most frequently occupied is highlighted by the black dashed vertical line in each plot. Two sites in the Tswalu Kalahari Reserve are represented, Korannaberg which has no lions, and Lekgaba, which has lions present.

Table 3. Model structure, diagnostic values and degrees of freedoms of the top GLMMs (lowest AIC scores) as well as the null model to test the association between variables of interest and the distance from water where the density of observations was the highest for each species in each site and season. The model in bold, was the model selected to be the most informative as the simplest model out of all top models.

Model structure	df	logLik	AIC	deltaAIC	Weight	Conditional R-squared	Marginal R-squared
~Ave. max seasonal temperature + Lions present * Water requirements	7	-1517.64	3049.92	0	1.393e-06	0.528	0.143
~Feeding type + Ave. max seasonal temperature + Lions present * Water requirements	9	-1515.83	3050.69	0.77	1.422e-06	0.534	0.158
~Lions present * Water requirements	**6**	**-1519.32**	**3051.12**	**1.20**	**1.372e-06**	**0.514**	**0.112**
~Ave. max seasonal temperature + Feeding type*Lions Present + Lions present * Water requirements	11	-1513.87	3051.27	1.35	1.422e-06	0.534	0.158
~Rainfall + Lions present * Water requirements	7	-1518.60	3051.83	1.91	1.380e-06	0.520	0.120
~Rainfall + Ave. max seasonal temperature + Lions present * Water requirements	8	-1517.62	3052.06	2.14	1.393e-06	0.528	0.146
~*null*	3	-1523.88	3053.90	3.98	1.336e-06	0.511	0.000

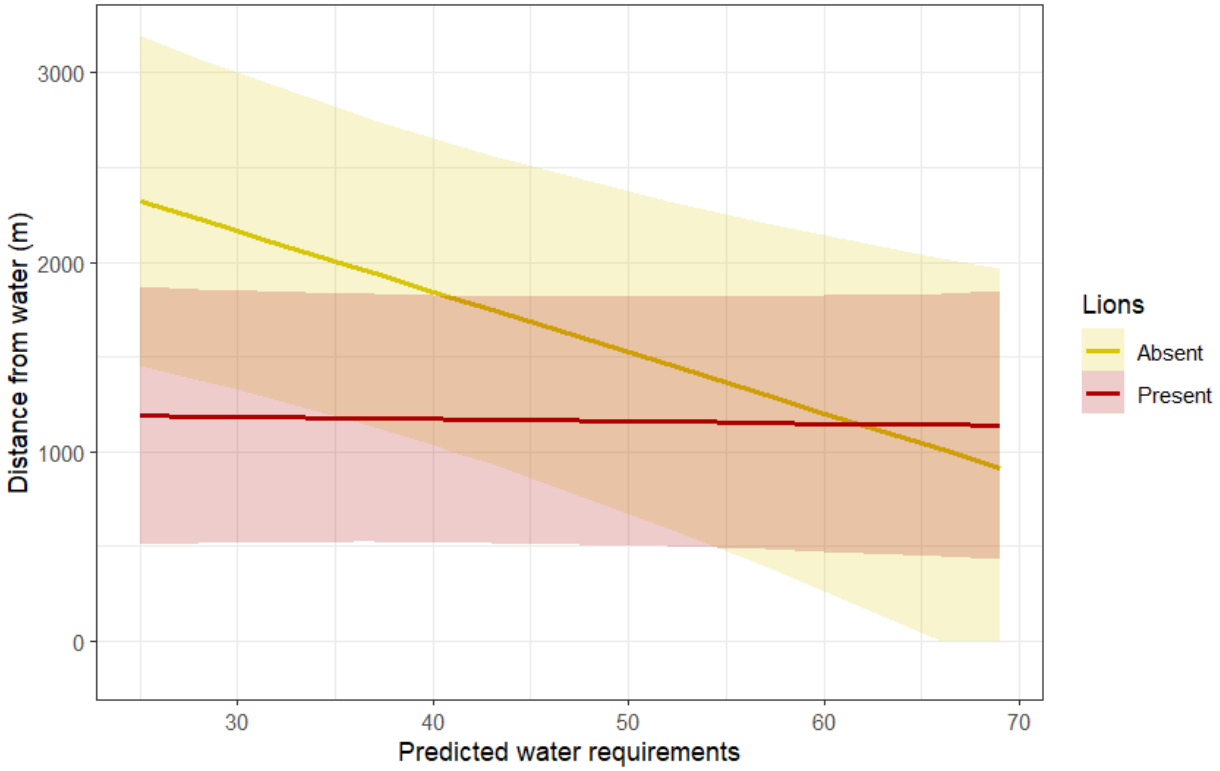

Figure 3. GLMM outputs of the mean distance from water occupied by the mammalian herbivores per season against the predicted water requirements of the herbivore species, in sites that had lions present compared to those sites where no lions were present. Data used in the model was collected by camera traps across 10 sites in South Africa. Mean distances from water were calculated for 16 herbivore species, for each season, in up to 10 sites where the species was present. Predicted water requirements are on a numerical scale from 0 to 100 based on estimates calculated from Kihwele and colleagues (2020).

Nocturnal activity of herbivores

By determining whether each observation occurred during the day or night, I was able to determine the proportion of observations recorded at night for each species in each site for each season (examples in Figure 4). A total of 394 camera trapping seasons that had more than 25 observations for each species for each site were included in my analysis. After testing various combinations of fixed effects in GLMMs, the simplest model within two AICs of the top models had mean season rainfall as a significant factor as well as the interactions between body mass and feeding type, body mass and predicted water requirements, and between predicted water requirements and the presence of lions (Table 4).

The proportion of pictures taken at night decreased with an increase in rainfall (Figure 5; Estimated proportion = -0.0203±0.0069, z-value = -2.944). Body mass also influenced the proportion of nocturnal observations, but the response differed based on the feeding types of herbivores, with the proportion of nocturnal observations of browsers decreasing as body mass increased whereas grazers (browser compared to grazer = -1.192e-03±1.992e-04, z-value = -5.982) and mixed-feeders (browser compared to mixed feeder = -8.637e-04±1.762e-04, z-value = -4.901) increased the proportion of nocturnal observations with increasing body mass (Figure 6). The proportion of nocturnal observations of grazers were more strongly influenced by body mass, with a greater increase in the proportion of nocturnal observations per unit body mass compared to mixed-feeders (Figure 6; grazer compared to mixed-feeder = 3.278e-04±4.933e-05, z-value = 6.646). The influence of body mass on the proportion of nocturnal observations was further influenced by the predicted water requirements of the herbivores. Irrespective of feeding type, herbivores with larger body masses (over 300kg) showed a lower proportion of nocturnal activity as water requirements increased (Figures 7 and 8; Estimated proportion = -1.589e-

05±5.209e-06, z-value = -3.050). The proportion of nocturnal observations decreased with increasing water requirements, particularly within sites where lions were present, yet overall, the proportion of nocturnal observations were lower within sites where lions were present (Figure 9; Estimated proportion = -2.770e-03±1.411e-03, z-value = -1.963).

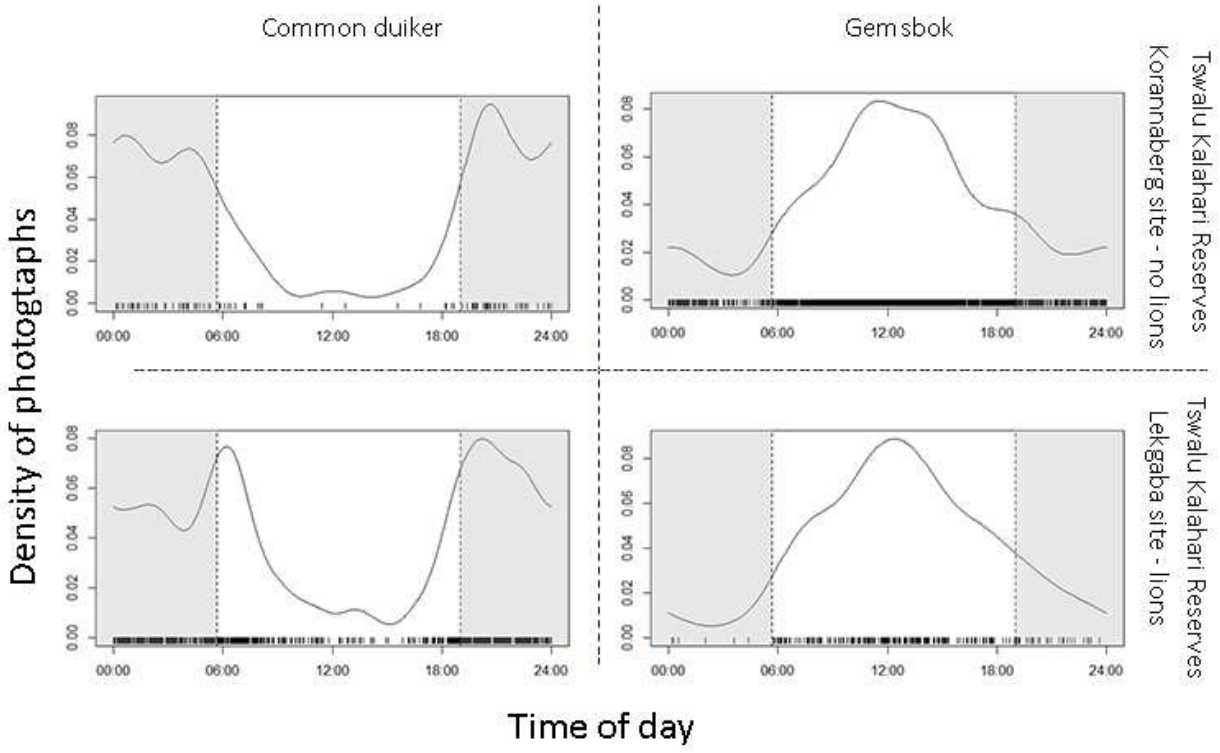

Figure 4. Kernel density plots showing the 24-hour activity patterns of common duiker (*Sylvicapra grimmia*) and gemsbok (*Oryx gazella*) over summer seasons from 2017 to 2022, from the two sites in the Tswalu Kalahari Reserve, Korannaberg which has no lions, and Lekgaba, which has lions present. The shaded area represents night time (sunset to sunrise) calculated using the average respective sunrise and sunset times for each season in the site, using the suncalc package (Thieurmel *et al*., 2019). The black lines at the base of each plot each represent an observation (photograph).

Table 4. Model structure, diagnostic values and degrees of freedoms of the top GLMMs (lowest AIC scores) as well as the null model to test the association between variables of interest and the proportion of night time observations of different herbivore species in each site and season. The model in bold, was the model selected to be the most informative as the simplest model out of all top models.

Model structure	df	logLik	AIC	deltaAIC	Weight	Conditional R-squared	Marginal R-squared
~Rainfall + Body mass * Feeding type + Body mass * Water requirements + Feeding type * Lions present	14	147.08	-265.04	0	36.982	0.386	0.366
~Rainfall + Body mass * Feeding type + Body mass * Water requirements + Lions present * Water requirements	**13**	**145.74**	**-264.52**	**0.527**	**37.310**	**0.392**	**0.371**
~Rainfall + Body mass * Feeding type + Body mass * Water requirements + Water requirements * Lions present + Feeding type * Lions present	15	147.40	-263.53	1.514	37.310	0.392	0.371
~Rainfall + Body mass * Feeding type + Body mass * Water requirements + Feeding type * Lions present	15	147.22	-263.17	1.875	37.166	0.389	0.370
~Rainfall + Body mass * Feeding type + Body mass * Water requirements + Feeding type * Lions present + Rainfall * Water requirements	15	147.21	-263.16	1.86	37.195	0.389	0.371
~Rainfall + Ave. max seasonal temperature + Body mass * Feeding type + Body mass * Lions present + Body mass * Water requirements + Feeding type * Lions present	15	147.15	-263.02	2.020	37.349	0.393	0.370
~null	3	62.10	-118.15	147.37	24.675	0.076	0.000

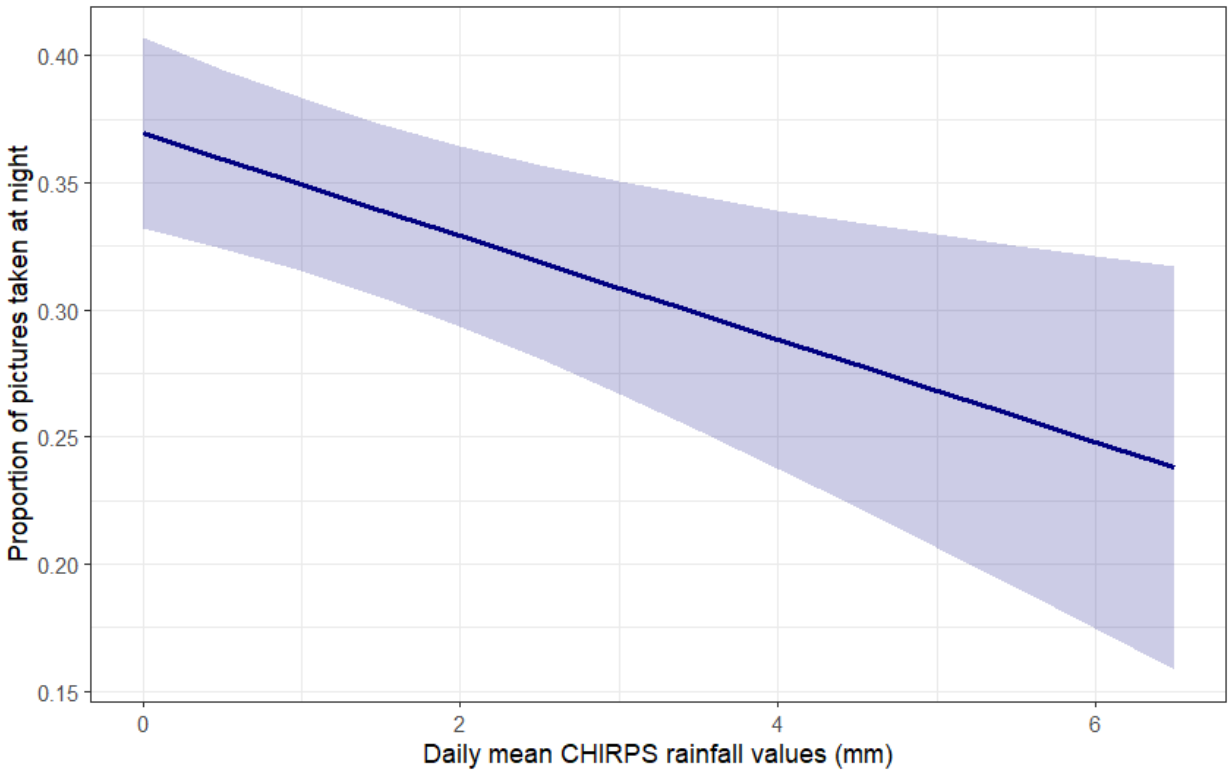

Figure 5. GLMM outputs of the proportion of observations (photographs via camera traps) taken at night of various mammalian herbivore species in different seasons and sites in South Africa against daily mean CHIRPS rainfall values summed for each season for each site. Mean proportions of observations were calculated for 16 herbivore species, per season, in up to 10 sites where the species was present.

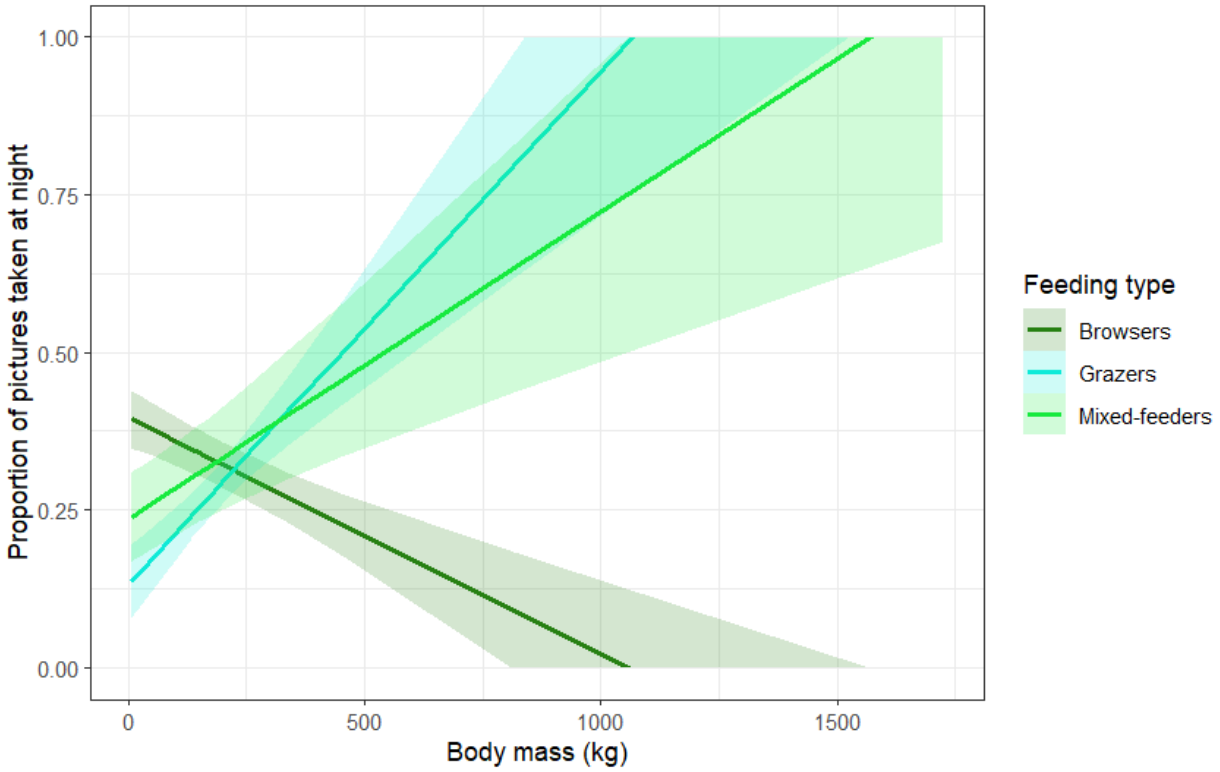

Figure 6. GLMM outputs of the proportion of observations (photographs) taken at night of various mammalian herbivore species in different seasons and sites in South Africa, against their respective body masses. Mean proportions of observations were calculated for 16 herbivore species, for each season, in up to 10 sites where the species was present. Each herbivore species was separated into groups based on their feeding type.

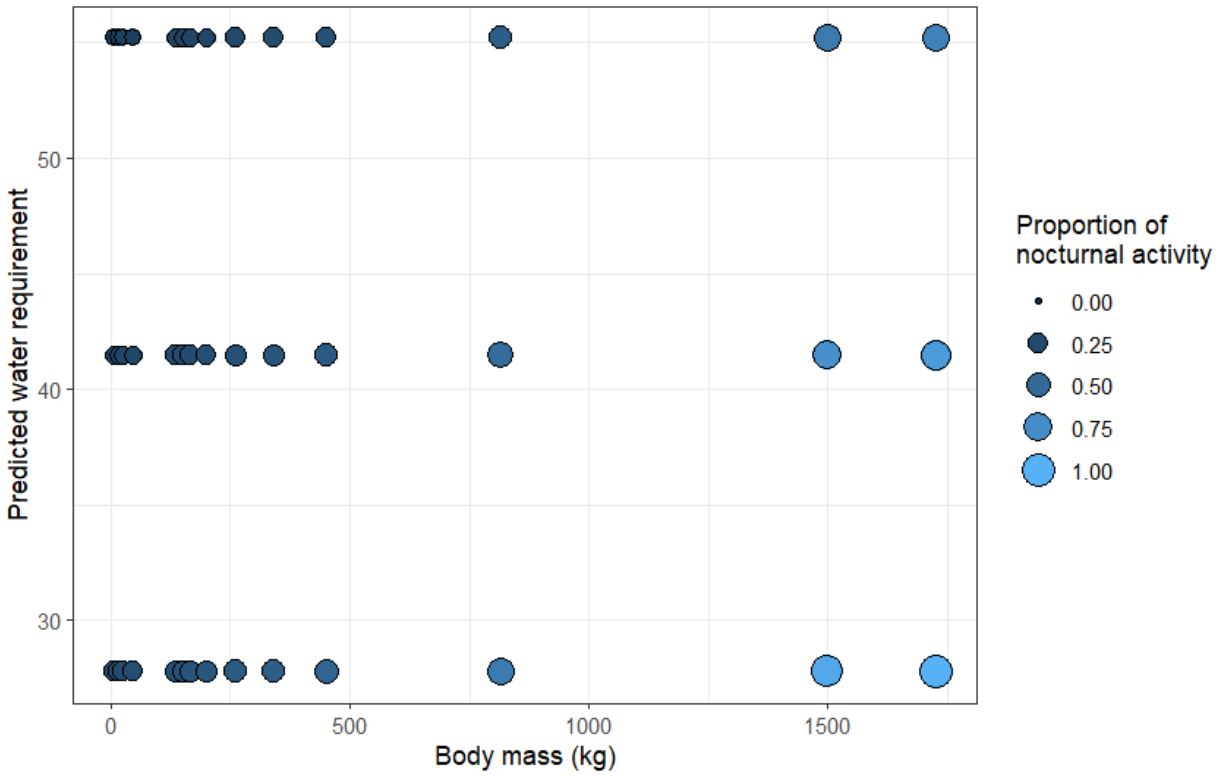

Figure 7. GLMM outputs of the proportion of observations (photographs) taken at night of various grazer and mixed feeder species in different seasons and sites in South Africa, plotted against their respective body masses and water dependency based on their predicted water requirement estimates on a scale from 0 to 100 calculated by Kihwele and colleagues (2020). Mixed feeders and grazers were combined into one plot due to them both having a positive relation between nocturnal activity and body mass (Figure 6).

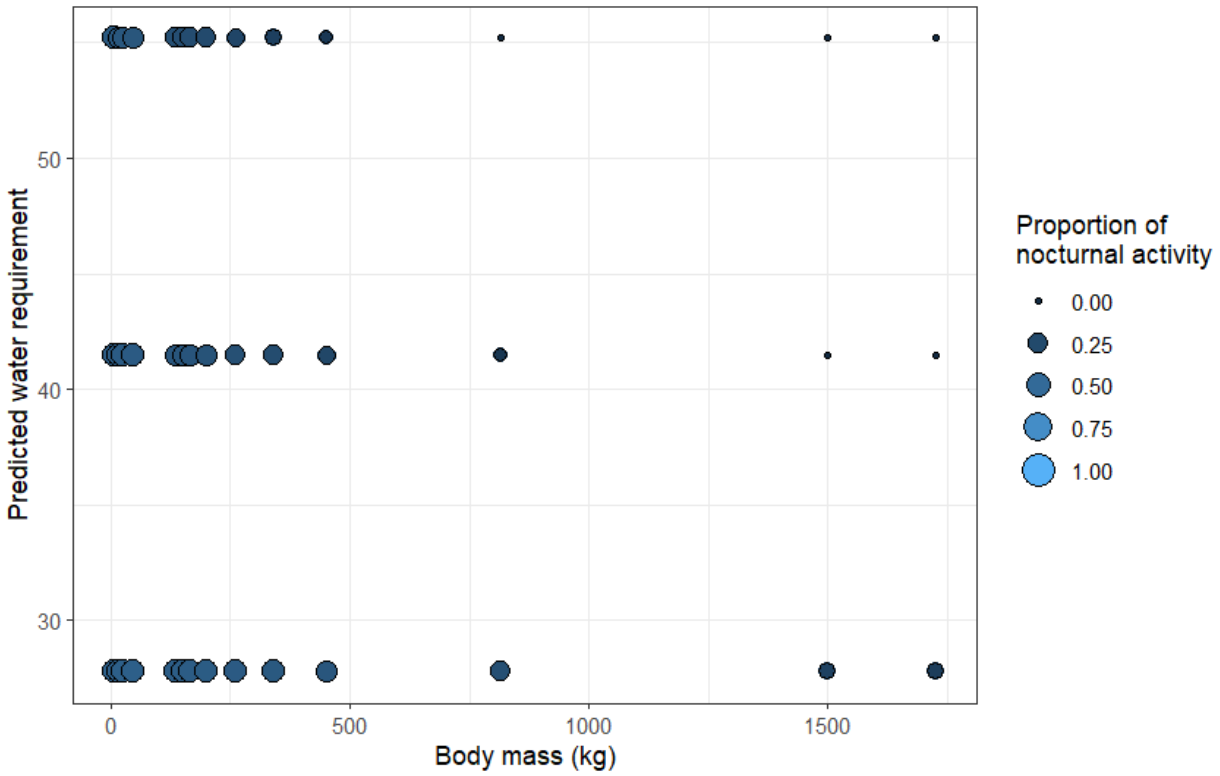

Figure 8. GLMM outputs of the proportion of observations (photographs) taken at night of various browser species in different seasons and sites in South Africa, plotted against their respective body masses and water dependency based on their predicted water requirement estimates on a scale from 0 to 100 calculated by Kihwele and colleagues (2020).

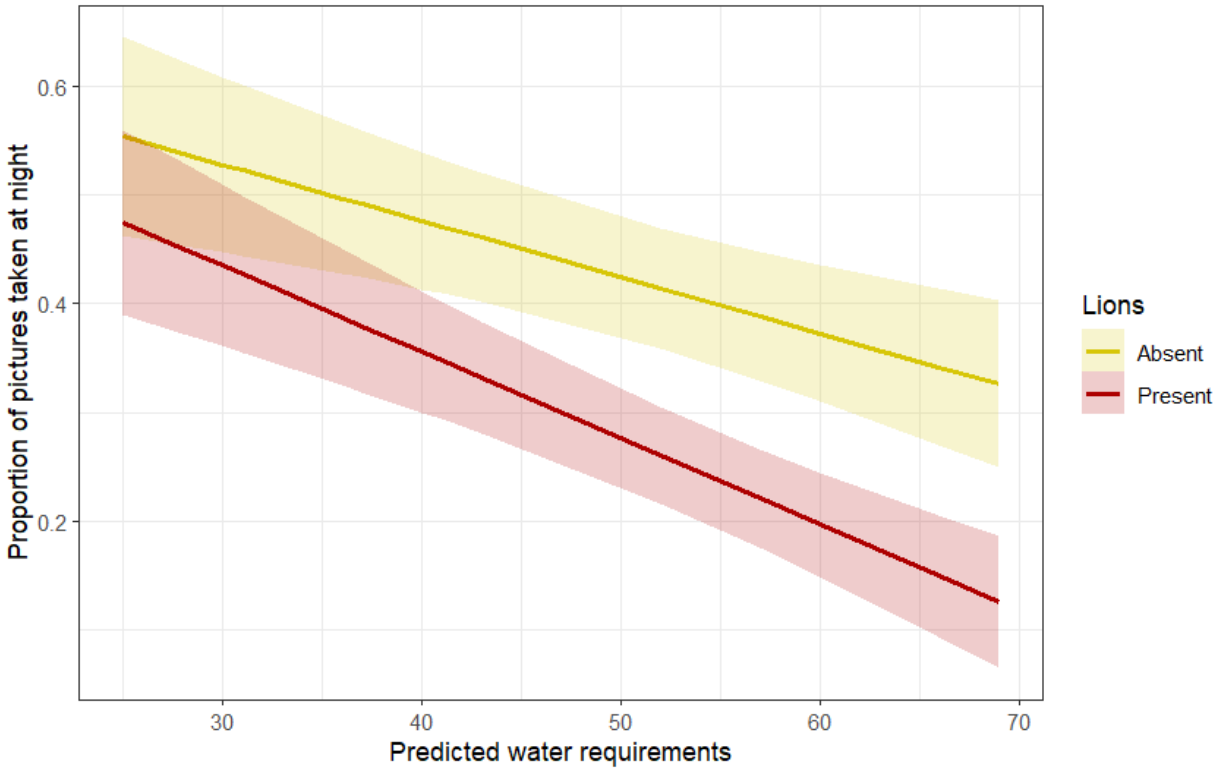

Figure 9. GLMM outputs of the proportion of observations (photographs) taken at night of various mammalian herbivore species in different seasons, plotted against predicted water requirements of each herbivore species, at sites in South Africa with and without lions. Mean proportions of observations were calculated for 16 herbivore species, for each season, in up to 10 sites where the species was present. Predicted water requirements are on a numerical scale from 0 to 100 based on estimates calculated from Kihwele and colleagues (2020).

Diel occupancy

Multistate occupancy models based on weekly observations were conducted on all herbivore species included in the study (Table 2), except for African buffalo, waterbuck, common eland and common warthog. The occupancy states tested were: if the herbivore species was active in the day, at night or both during the day and night for each week. Five multistate models were run for each species testing the influence of the distance from surface water and the presence of lions on the occupancy of the herbivore species. The best model chosen was that with the lowest AIC score and produced estimates for each state tested (Table 5).

One grazer (hartebeest, (*Alcelaphus buselaphus*)), both mixed-feeder species (African elephant and impala) and all but one browsing species (southern giraffe, greater kudu (*Tragelaphus strepsiceros*), springbok (*Antidorcas marsupialis*) and steenbok (*Raphicerus campestris*)) were found to have occupancies that were not impacted by the presence of lions or the distance from surface water (Figure 10). Giraffe, greater kudu, springbok, steenbok and impala were all found to have the greatest probability of occupancy during weeks where they were observed during both day and night, and the lowest occupancy during the daytime state, being close to zero (meaning few observations) for all species except springbok (Figure 10). Elephants also had their highest probability of occupancy during weeks where they were observed during both the day and night, but the probability of occupancy only at night or only during the day was nearly zero (Figure 10). Hartebeest had a similar probability of occupancy for all three states, the highest being during the night and lowest being during the day (Figure 10).

The probability of occupancy of two grazer species, namely plains zebra and gemsbok (*Oryx gazella*) were impacted by the presence of lions, but not the distance to water (Figure 11). For

both species in sites with and without lions, the probability of occupancy was highest in weeks where they were observed during both day and night, and the lowest probability of occupancy being in the day with all probabilities being close to zero (Figure 11).

The probability of occupancy of common duiker (*Sylvicapra grimmia*) and white rhinoceros (*Ceratotherium simum*) were affected by the distance from water, but not the presence of lions (Figures 12 and 13). Both species had their lowest probabilities of occupancy during the day, with the probability decreasing as the distance to water increased (Figures 12 and 13). The probability of occupancy at night was positively associated with the distance from water in both common duikers (Figure 12) and white rhinoceroses (Figure13). In common duiker, the probability of occupancy for weeks where both day and night observations occurred was constant despite changes in distance from water (Figure 12), while white rhinoceroses showed a slight negative relationship between day and night probability of occupancy and distance from water (Figure 13).

Blue wildebeest (*Connochaetes taurinus*) was the only herbivore species that had a probability of occupancy that was impacted by both the presence of lions and the distance from water (Figure 14). In sites where lions were absent, the probability of occupancy in weeks where wildebeest were only seen at night or only seen in the day had a negative relationship with the distance from water (Figure 14). The probability of occupancy for weeks where both day and night observations occurred was higher than both other states in sites without lions and had a positive relationship with distance from water (Figure 14). In sites where lions were present, the probability of occupancy for blue wildebeest in all three states had a negative relationship with

distance from water, however daytime occupancy had the lowest probability of occupancy and the steepest slope (Figure 14).

Table 5. Multistate diel occupancy model structures, AIC values and whether the model produced values for each parameter, for various herbivore species. The interactions between the presence of lions and the distance from water as well as each variable separately was tested for each species. Temporal states used in each model were summarised into weekly observations where animals were observed (photographed by camera trap) only during the day, only at night or both day and night for each week. The model in bold represents the best model selected for each species, having the lowest AIC score and producing occupancy estimates for each tested variable at each temporal state. Four of the study species [African buffalo (*Syncerus caffer*), common eland (*Tragelaphus oryx)*, waterbuck (*Kobus ellipsiprymnus*) and common warthog (*Phacochoerus africanus*)] were excluded from this table due to not producing any models that estimated probability of occupancy for each state in each covariate tested.

Model structure	AIC	Were occupancy estimates generated for all model parameters?
	Steenbok (*Raphicerus campestris*)	
lion present*distance from water	24565.32	No
lion present+distance from water	24561.93	No
lion present	24548.62	Yes
distance from water	24651.48	Yes
None	**21026.4**	**Yes**
	Common duiker (*Sylvicapra grimmia*)	
lion present*distance from water	37676.13	No
lion present+distance from water	37659.67	No
lion present	18448.88	No
distance from water	**37653.67**	**Yes**
None	18322.3	No

Springbok (*Antidorcas marsupialis*)		
lion present*distance from water	4166.877	No
lion present+distance from water	12225.81	No
lion present	4139.548	No
distance from water	12219.81	No
None	**4141.096**	**Yes**
Greater kudu (*Tragelaphus strepsiceros*)		
lion present*distance from water	31654.59	Yes
lion present+distance from water	49410.83	No
lion present	26734.63	Yes
distance from water	49404.83	No
None	**26720.63**	**Yes**
Southern giraffe (*Giraffa giraffa*)		
lion present*distance from water	45971.43	No
lion present+distance from water	45966.59	No
lion present	21445.49	Yes
distance from water	45960.59	No
None	**21429.5**	**Yes**
Hartebeest (*Alcelaphus buselaphus*)		
lion present*distance from water	4980.888	No
lion present+distance from water	14933.51	No
lion present	4694.676	No
distance from water	14927.51	No
None	**4686.47**	**Yes**

Gemsbok (*Oryx gazella*)		
lion present*distance from water	16085.01	No
lion present+distance from water	22285.55	No
lion present	**16056.39**	**Yes**
distance from water	22279.55	No
None	16097.57	Yes
Blue wildebeest (*Connochaetes taurinus*)		
lion present*distance from water	**38582.84**	**Yes**
lion present+distance from water	38599.28	No
lion present	19324.88	No
distance from water	38593.28	No
None	19369.01	No
Plains zebra (*Equus quagga*)		
lion present*distance from water	48684.82	Yes
lion present+distance from water	27401.59	No
lion present	**27344.18**	**Yes**
distance from water	27405.91	No
None	27361.37	Yes
White rhinoceros (*Ceratotherium simum*)		
lion present*distance from water	9194.96	Yes
lion present+distance from water	27573.34	Yes
lion present	8701.615	Yes
distance from water	27567.34	Yes
None	**8699.462**	**Yes**

Impala (*Aepyceros melampus*)		
lion present*distance from water	44141.6	No
lion present+distance from water	44196.7	No
lion present	33105.13	No
distance from water	44190.7	No
None	**33149.16**	**Yes**
African elephant (*Loxodonta africana*)		
lion present*distance from water	Error in model	
lion present+distance from water	24297.03	No
lion present	24284.7	No
distance from water	24303.13	No
None	**24291.81**	**Yes**

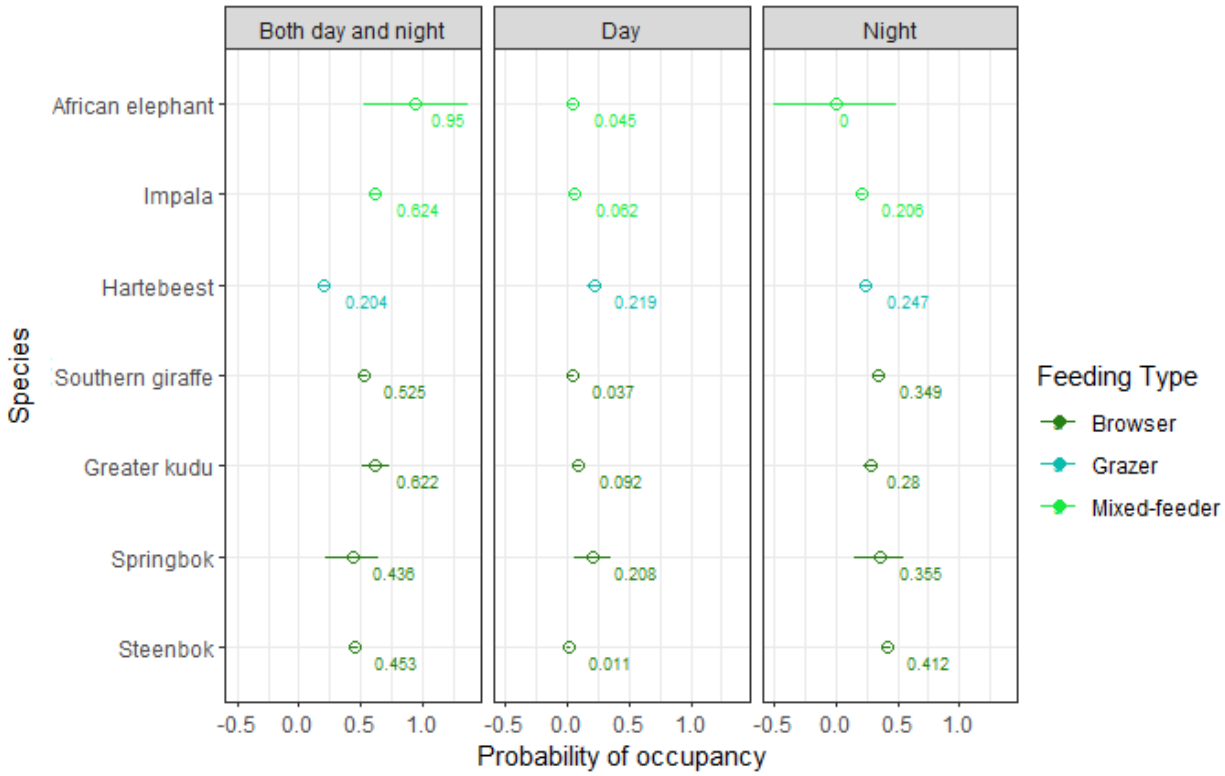

Figure 10. Estimated probability of diel occupancy only during the day, only during the night and during both day and night for each week of mammalian herbivore species whose occupancy was not impacted by the presence of lions or the distance from water. Diel occupancy was estimated based on camera trap data taken across 10 sites in South Africa, with observations from each week summarised into the three occupancy states.

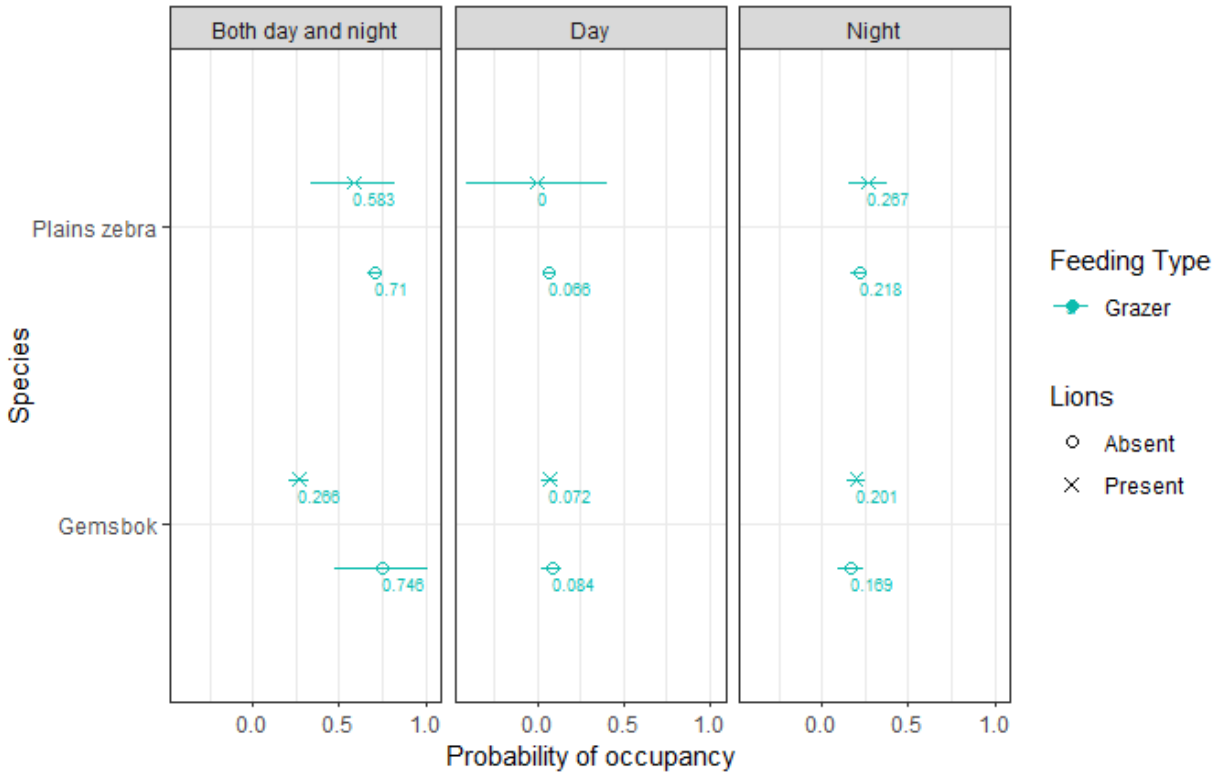

Figure 11. Estimated probability of diel occupancy only during the day, only during the night and during both day and night for each week of mammalian herbivore species whose occupancy was not impacted by the distance from water, but was impacted by the presence of lions. Diel occupancy was estimated based on camera trap data taken across 10 sites in South Africa, with observations from each week summarised into the three occupancy states.

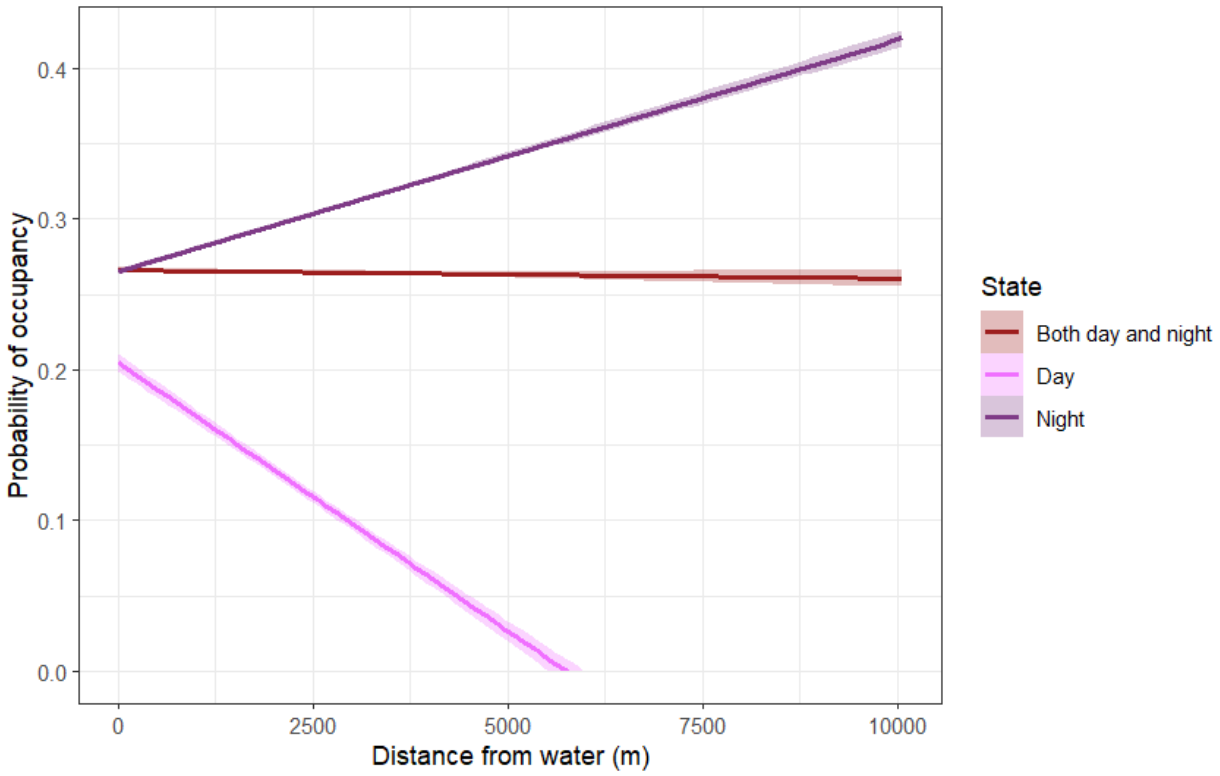

Figure 12. Estimated probability of diel occupancy of common duiker (*Sylvicapra grimmia*) only during the day, only during the night and during both day and night relative to the distance to the nearest surface water source. Diel occupancy was estimated based on camera trap data taken across nine sites in South Africa, with observations from each week summarised into the three occupancy states. Ten sites were examined for the entire study, however one site did not have sufficient observations of common duiker to be analysed and was removed from this analysis.

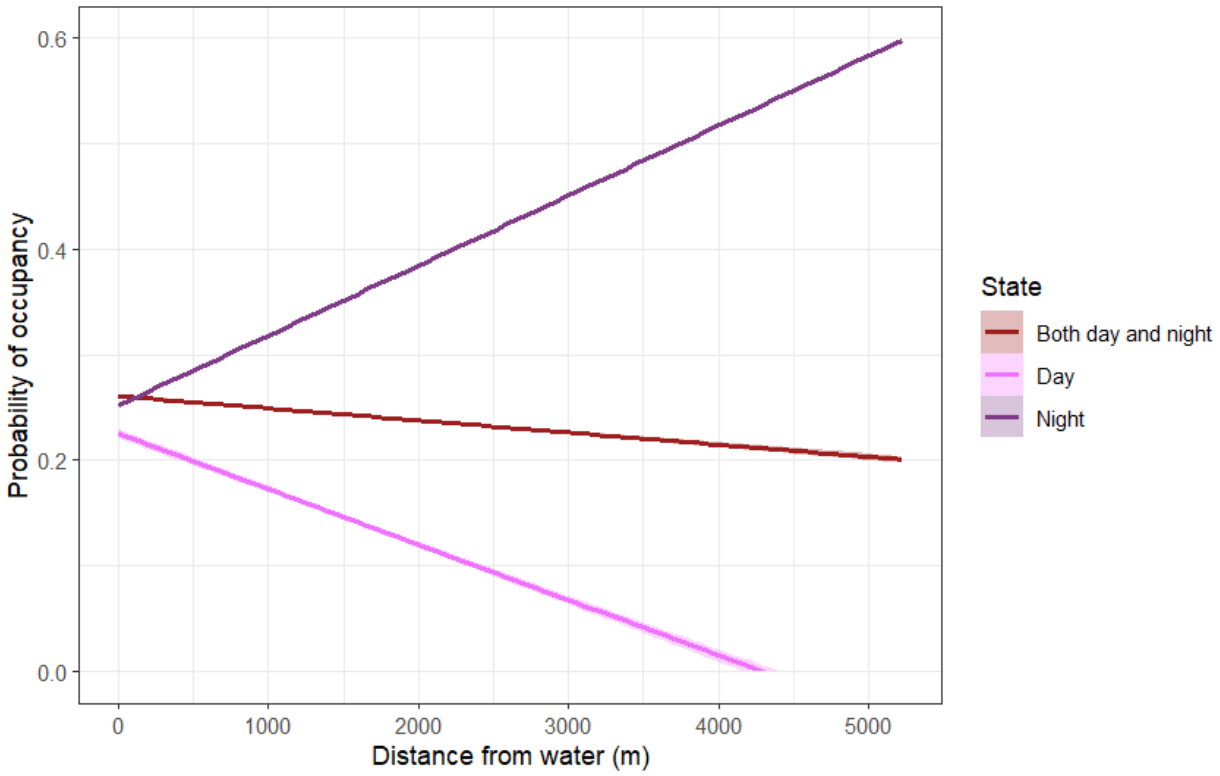

Figure 13. Estimated probability of diel occupancy of white rhinoceros (*Ceratotherium simum*) only during the day, only during the night and during both day and night relative to the distance to the nearest surface water source. Diel occupancy was estimated based on camera trap data taken across five sites in South Africa, with observations from each week summarised into the three occupancy states. Ten sites were examined for the entire study, however only five sites had sufficient observations of white rhinoceros to be analysed.

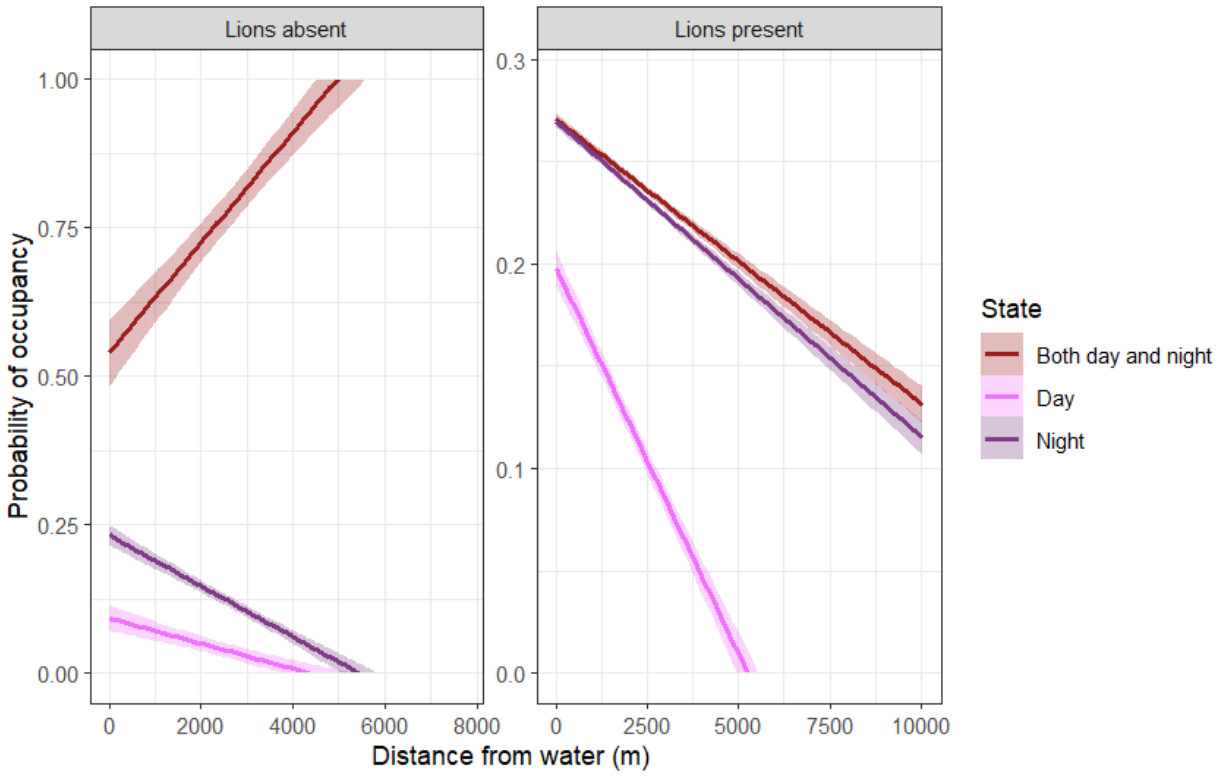

Figure 14. Estimated probability of diel occupancy of blue wildebeest (*Connochaetes taurinus*) only during the day, only during the night and during both day and night relative to the distance to the nearest surface water source, between sites with lions and without lions. Diel occupancy was estimated based on camera trap data taken across eight sites in South Africa, with observations from each week summarised into the three occupancy states. Ten sites were examined for the entire study, however two sites did not have sufficient observations of blue wildebeest to be analysed and were removed from this analysis.

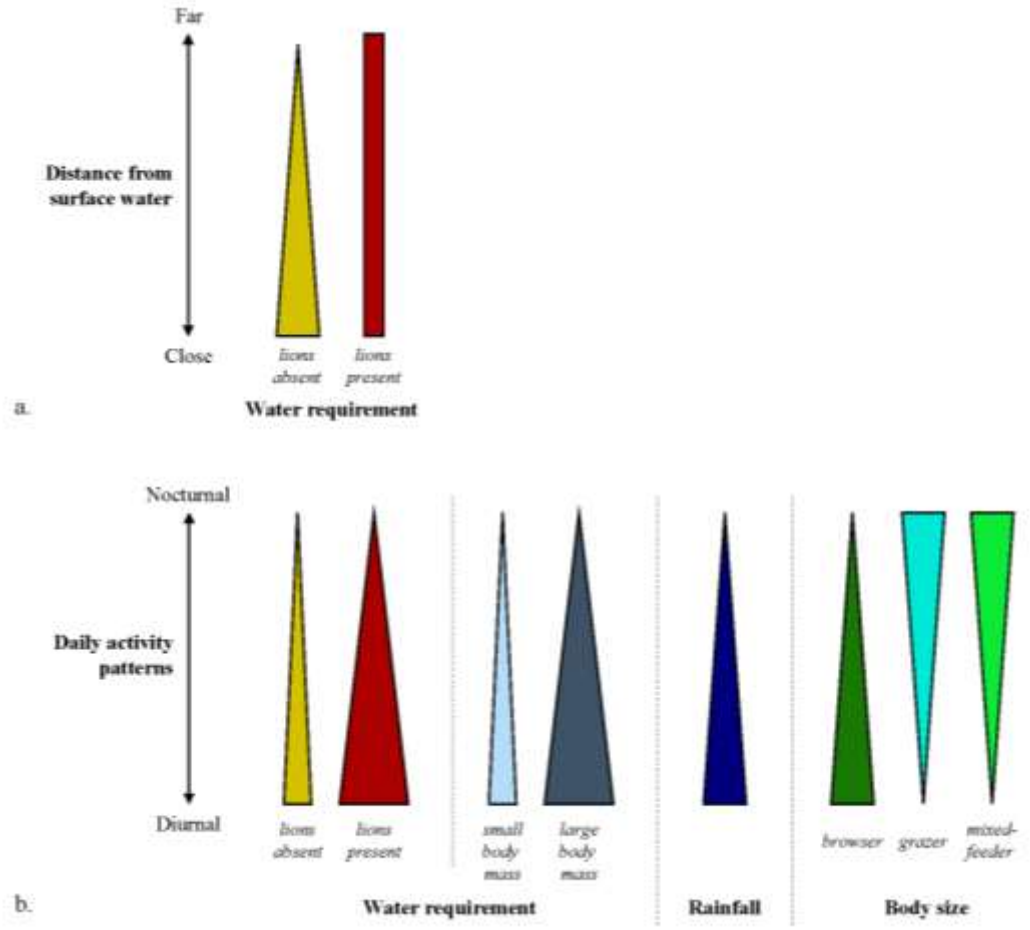

Figure 15. Visual summary of the results of GLMMs (Generalised Linear Mixed-effects Models) looking at the impact of various factors on (a) the distance of herbivores from the nearest surface water source and (b) the daily activity patterns of herbivores. The cones represent a change in variable they represent, with the wider end of the cone representing an increase in magnitude of said variable. Wider cones represent a greater magnitude. The rectangle represents no change in the variable it represents.

Discussion

Proximity of herbivores to surface water

Predicted water requirement and presence/absence of lions impacted the distance herbivores remained from water, while no other variables tested were shown to impact the distance from surface water of herbivore species.

Ideally, group size (the number of individuals recorded in a photograph) would have been included as a factor in data analysis, since herbivore group size may impact the perceived risk of predation (Creel *et al.*, 2014; Périquet *et al.*, 2010). However, it was noted that both Zooniverse and TrapTagger frequently misidentified the number of individuals in a photograph when several animals were present in a photograph, and camera traps also may not capture all individuals in a group. Thus, group size is a limiting factor seen when using camera trap data and current sorting systems used to sort camera trap data. Future developments into animal photograph identification software may produce more accurate estimates of group size making the analysis of group size viable in camera trap studies using a database too large to be sorted by people alone.

Despite the limitation of group size not being accounted for, my study still presented insightful findings on the behaviour of herbivores in South Africa. The interaction between the presence/absence of lion and the distance from water accounted for 51% of the variation of the model. As expected, herbivores with greater water requirements were generally found in close proximity to water, but that relationship disappeared when lions were present, such that all herbivores regardless of their water dependence were frequently found within 1.2 km of the nearest water sources. Indeed water dependent species such as African elephant, white rhinoceros, African buffalo, waterbuck, plains zebra, blue wildebeest, impala and common

warthog are frequently associated with water sources (Cain *et al*., 2012; Chamaillé-Jammes *et al*., 2007b; Hayward and Hayward, 2012; Redfern *et al.*, 2003; Smit *et al*., 2007), whereas less water dependent species like giraffe and greater kudu were not associated with water sources (Hayward and Hayward, 2012; Redfern *et al.*, 2003). However, all of these studies took place on sites where lions are present. My results however, showed that the relationship between water dependence and distance to water disappeared in the presence of lions, with all herbivores, irrespective of their water requirements, remaining ~1.2 km from water in sites with lions. This result is contrary to initial hypothesis (hypothesis 1.3) and, previous studies (Valiex, 2011), which showed that preferred prey species of lions i.e. giraffe, greater kudu and buffalo, avoided water sources in sites where lions were present.

The difference between my results and that of other studies regarding the distance herbivores remain from water may be due to the close proximity of water sources in the study sites included in the current study. The furthest distance predicted by my model (just over 3 km at the highest confidence interval) was shorter than the furthest distances predicted by previous studies. Smit and colleagues (2007) who investigated herbivore distribution in Kruger National Park found that grazers, which are considered dependent on water, had a preferred distance of 4 km from the nearest water source. Western (1975) found that water dependent herbivores in the Amboseli ecosystem, Kenya were found mostly within 10 km of the nearest water source, while some water independent species like giraffe (G*iraffa camelopardalis*) and Grant's gazelle (*Nanger granti*) were found as far as 35 km from the nearest water source. The contrast in the results of my study and previous studies is likely due to the close proximity of Snapshot Safari camera traps used in my study to water sources caused by the high frequency of artificial water points in the sites I studied, causing camera traps to be close to water despite their placement on a

standardised grid. Of the 266 camera traps used in this study to look at the distance of herbivores from surface water sources, only 12.03% of cameras had a distance greater than 4 km from the nearest water source and 27.44% of cameras had a distance greater than 3 km the nearest water source. The results of this study therefore indicate the behaviours of animals in environments with an abundance of water sources and would not reflect how animals may react in a water scarce environment. Artificial water sources are also more likely to be more frequent in areas with lions as these are mostly big five reserves that may priorities setting up artificial water sources to favour wildlife viewing for tourism, as seen in Kruger National Park in the past (Pienaar, 1970; Sutherland *et al*., 2018). The increased amount of water sources in parks with lions may explain why all herbivores here were found at a similar distance from water.

One point of concern with the use of artificial water sources was that predation was more prevalent around water sources (Harrington *et al.*, 1999; Owen-Smith, 1996). Lions in particular were noted to hunt closer to water sources, such as rivers and artificial waterholes (de Boer *et al.*, 2010; Valeix *et al.*, 2009a), however this study has shown that herbivores, particularly those that are less water dependent, tended to be found closer to water sources when lions are present. Instead of avoiding water sources as suggested by previous studies (Valeix, 2011), herbivores in my study may become more diurnal in the presence of lions, in order to avoid lions, which are mostly active at night (Tambling *et al.*, 2015; Valeix *et al.*, 2009a). Thus, herbivores may have moved closer to water sources due to being more reliant on evaporative cooling to overcome heat stress, thus needing easier access to water, when shifting to diurnal behaviours to avoid lions.

While the use of artificial water sources may alleviate climatic stresses for herbivores, it should be noted that when lions were present all herbivores showed a similar average distance from

water, which may result in competition between herbivore species around water sources. Interference competition has been documented at water sources at Hwange National Park, where elephants impacted the behaviour of several smaller herbivore species resulting in these species only visiting water sources at times when elephants are not present in the day (Valeix *et al*., 2007). In Kruger National Park, the addition of artificial water sources in the northern regions allowed water dependent grazers like plains zebra and blue wildebeest to access to region which may have competed with the roan antelope (*Hippotragus equinus*), a specialised grazer in this region, leading to a decline in their population (Harrington *et al.*, 1999; Kröger and Rogers, 2005). Excessive water sources in reserves were shown to potentially favour water-dependent herbivores over rare species (Harrington *et al.*, 1999; Owen-Smith, 1996; Purdon and van Aarde, 2017). Additionally in Kruger National Park, when plains zebras and blue wildebeest moved into areas with newly acquired water sources, lions followed and started preying upon on roan antelope, further showing how artificial water sources may unintentionally impact predation pressures on animals (Harrington *et al.*, 1999). Artificial water sources may also alter the ability of herbivores to survive environmental hardships when water sources become empty as shown in the Central Kalahari Game Reserve, Botswana, where blue wildebeest living in areas without artificial water survived dry seasons whereas those reliant on artificial water sources died when artificial water sources became dry (Selebatso *et al.*, 2018). I therefore advise caution for the use of artificial water sources in fenced reserves, as while artificial water sources may alleviate environmental stresses, they can unexpectedly provide additional stress to the biodiversity of ecosystems.

The high density of water sources in these parks may be another reason why seasonal conditions (temperature and rainfall) were not found to be impactful in my study, contradicting hypothesis

1.2, as herbivores could overcome heat stress by visiting water sources which would always be in close proximity. Drivers such as rainfall may only become impactful on herbivore behaviour under drought conditions, which were not seen in my study. Indeed, rainfall was shown to be an influential factor in water source use by Valeix (2011) in Hwange National Park when rainfall was reduced in periods of drought (362.6 mm annual rainfall), causing animals to aggregate around and use water sources more intensely.

Vegetation greenness (measured through NDVI) not impacting herbivore distance from water, further contradicting hypothesis 1.2, may also be explained by herbivores being able to overcome lower water content in vegetation (potentially indicated by lower NDVI values) by accessing frequently occurring water sources. Alternatively, other measures of vegetation quality not fully quantified in NDVI may explain the proximity of herbivores to water sources. Since forage quality often diminishes closer to water holes (Redfern *et al*., 2003), it may be that the herbivores were prioritizing forage quality and availability over access to water and that my index of vegetation greenness (NDVI) was not sufficiently sensitive to detect those changes. However, giraffe and greater kudu were shown to be associated to rivers presumably due to the preferred vegetation for these browsers found around rivers (Smit *et al*., 2007). Thus, alternative methods looking into vegetation quality may better explain the distribution of herbivores in a landscape.

While I also did not find body mass and feeding type to influence herbivore distance to surface water, contradicting hypotheses 1.1 and 1.2, these factors may be integrated within a species' water dependence (Kihwele *et al.*, 2020; Veldhuis *et al.*, 2019). Both body mass and feeding type are considered impactful on a species' water dependence (Kihwele *et al.*, 2020; Veldhuis *et al.*,

2019), thus the inclusion of predicted water requirement calculated by Kihwele and colleagues (2020) compensates for both these variables by giving a more precise estimate to water dependence than body mass and feeding type.

Nocturnal activity of herbivores

The proportion of nocturnal activity of herbivores was associated with rainfall, body mass, feeding type, predicted water requirement and the presence of lions. Seasonal temperatures and NDVI values were not found to impact nocturnal activity of herbivores.

While the results of this study do provide insight into the broader activity patterns of herbivores, the methods used in this study do not show the finer activity patterns of herbivores. The specific times at which herbivores are active within each day were not seen, meaning behaviours like crepuscular activity could not be determined. While this study was more focused on the broad aspects of animal activity over a large geographic and time scale, future studies could therefore look at activity on a more specific scale.

This study was still able to find important patterns in herbivore activity patterns. The shift in herbivore activity to be less nocturnal when lions were present, partially supporting hypothesis 2.3, explains the relationship mentioned in the previous section where less water dependent herbivores move closer to water sources. Due to being more active in the day, herbivores needed access to water to overcome heat stress by relying on evaporative cooling, thus were found closer to water sources. The shift of herbivore activity to be less nocturnal in the presence of lions was shown in several studies, and was thought to allow herbivores to avoid activity overlap with lions, which are nocturnal (Tambling *et al.*, 2015; Valeix *et al.*, 2009a). Additionally, studies

have shown that the preferred prey species of lions had the greatest shift to diurnal activity (Tambling *et al.*, 2015; Valeix *et al.*, 2009b). While the preferred prey species of lions may differ between different sites, giraffe, gemsbok, African buffalo, plains zebra and blue wildebeest are generally the preferred prey of lions (Hayward and Kerley, 2005), the last three of which are water dependent (Kihwele *et al.*, 2020). Species with a higher predicted water requirement in my study were shown to have a stronger decrease in nocturnal activity when lions were present, supporting the idea that water dependent herbivores may have a greater perceived risk of predation from lions. The diel occupancy modelling discussed in the next section did show that some preferred prey species of lions suggested by Hayward and Kerley (2005) are impacted by the presence of lions, further supporting the preferred prey species of lions being medium-sized water dependent herbivores.

Whether lions were present or absent, a negative relationship between predicted water requirement and nocturnal observations was seen and can be difficult to determine the exact cause. Less nocturnal herbivores having a higher predicted water requirement could be a direct result of being more active in the heat of the day, thus needing more water for evaporative cooling. Alternatively, some water dependent herbivores may possess specific behavioural or physiological adaptations to handle heat stress allowing them to be more active in the day. Elephants, which were considered water dependent (Chamaillé-Jammes *et al*., 2007b; Kihwele *et al.*, 2020; Western and Lindsay, 1984), have several adaptations to heat stress. Adaptations of elephants include large highly vascularised ears that create an area for heat dissipation and wrinkled skin which can retain water, but only external environmental water as elephants have no sweat glands used for evaporative cooling (Domínguez-Oliva *et al.*, 2022). Blue wildebeest and gemsbok in the Kalahari occupy cool micro-climates particularly in drought conditions, with

the more water dependent wildebeest showing a greater use of cool micro-climates (Boyers *et al.*, 2021). Black wildebeest (*Connochaetes gnou*) in environments without shade were shown to change posture throughout the day to reduce exposure to heat and increase heat loss by increasing surface area exposed to the environment when temperatures were high (Maloney *et al.*, 2005). However, adaptations to combat heat stress are also found in species that are not water dependent. Springbok have a relatively thin pelage for its body size and change their orientation to reduce solar radiation, allowing springbok to maintain a constant internal temperature throughout the day (Hofmeyr and Louw, 1987). Selective brain cooling has been displayed on water dependent species such as blue wildebeest and hartebeest as well as in water independent gemsbok (Strauss *et al.*, 2016). Adaptations against heat loss found in herbivores of all feeding groups likely mean that these adaptations are not the sole reason for water dependent species being more active in the day.

When considering herbivore body mass, larger herbivores within their feeding groups (mixed-feeders and grazers separated from browsers) maintained the trend of herbivores with higher predicted water requirements being less nocturnal. However, in smaller herbivores predicted water requirement did not impact the nocturnal activity within their feeding groups. Predicted water requirement not having as great an impact in smaller herbivores as it did large herbivores may potentially be due to the thermal impacts that come with changes in body size. Smaller animals have a higher surface area to volume ratio making heat loss easier than in large animals (Shrestha *et al.*, 2014; Veldhuis *et al.*, 2019). The potentially reduced thermal impact on smaller herbivores may result in these species being able to overcome heat stress without shifting their activity to be more nocturnal to avoid heat despite having differing levels of water dependence. The potentially reduced thermal impact of smaller species may apply to common warthogs as

they are the smallest grazer in the study and are considered mostly diurnal (Deribe *et al*., 2008; Skinner and Chimimba, 2005), thus may be able to overcome heat stress potentially due to their smaller size. Larger herbivores, which may be more susceptible to heat stress would have to shift activity based on their water dependence and survival strategies that come with differences in water dependence.

The relationship between herbivore nocturnal activity and body mass can be further expanded when comparing nocturnal activity between herbivore feeding groups. Browsers in this study showed a trend of decreased nocturnal activity with an increase in body mass, which was also found in browsing ruminants in Kruger National Park (du Toit and Yetman, 2005). Grazers and mixed-feeders showed an opposite trend of increased nocturnal activity with an increased body size. There are no studies looking at the relationship between body mass and activity patterns specifically in grazer or mixed-feeding species. Vallejo-Vargas and colleagues (2022), found that herbivores in tropical regions across the globe showed a trend of increased nocturnal activity with an increase in body mass, potentially due to the thermoregulation costs at larger body masses, resulting in large herbivores being more active in the cooler night, however this study did not separate herbivores of different feeding types and included other orders of smaller sized mammals such as rodentia and hyracoidea. Larger species are predicted to be more susceptible to hyperthermia, due to their smaller surface area to volume ratio making heat loss difficult (Shrestha *et al.*, 2014; Veldhuis *et al.*, 2019). The reduced cost of thermoregulation and risk of heat stress at night may be the reason for increased nocturnality in large grazers and mixed-feeders in this study.

Larger herbivores avoiding the heat during the day is however contradicted by browsers, which show an opposite trend. The difference seen in browser activity patterns may be due to their

foraging behaviours. Large browsers, particularly giraffes, have been suggested to have longer handling times when eating due to the spines and branching patterns of the woody vegetation they eat, further increasing foraging times (du Toit and Yetman, 2005; Owen-Smith, 1982; Pellew, 1984). However, a study on African herbivores of various body sizes, including giraffe, found that larger herbivores had mouthparts that were adapted to increase bite volume, which coupled with selective feeding of soft plants, would allow these herbivores to consume enough vegetation proportional to their body size (Pretorius *et al.*, 2016), meaning forage handling time in giraffes may not be as long as previously predicted. Browsing species of similar sizes do still spend more time foraging than grazing species, likely due to browsers being able to ruminate faster, thus are likely to spend more time foraging (du Toit and Yetman, 2005; Owen-Smith, 1992). Browsers increased foraging time combined with larger herbivores showing a greater time spent active, particularly foraging, due higher dietary requirements (Belovsky and Slade, 1986), may result in large browsers being more active during the day to meet their foraging needs (du Toit and Yetman, 2005).

The activity patterns changing with body mass found in my study and previous activity studies (du Toit and Yetman, 2005; Vallejo-Vargas *et al.* 2022) are contrasted by a camera trap study done in Lake Manyara National Park, Tanzania, where herbivore nocturnal activity did not change with body mass (Clauss *et al.*, 2021). The difference in results between my study and Clauss and colleagues' (2021) study may be due to their study not looking at the diet (feeding type) of herbivores but rather comparing ruminants to non-ruminants, while my study included non-ruminants with ruminants in the same grouping and could have resulted in the differences between the trends we found.

While water dependence, body mass and feeding type each impacted nocturnal activity of herbivores tested, rainfall was the only climatic factor tested found to impact herbivore activity. Proportion of nocturnal activity was lowest during seasons with high rainfall, which may be due to the formation of ephemeral pools and increasing water content of forage, providing herbivores with more access to water. Increased water availability through ephemeral pools and diet may reduce the need of herbivores to shift to nocturnal activities to behaviourally compensate for high heat loads as they may have been able to rely on evaporative cooling to dissipate that heat allowing them to continue foraging during the day. Unfortunately, temporary water sources could not be accounted for in this study due to me using the South African National Land-Cover dataset for 2020 as well as data provided by Snapshot Safari, which only accounts for permanent water bodies.

Vegetation quality may be impacted by rainfall, with water content in forage increasing with greater rainfall, however this was not shown in this study, which used NDVI to measure vegetation greenness and was not shown to impact herbivore activity (contradicting hypothesis 2.2). Instead, only considering seasonal averages, more precise measures of NDVI on a spatial and temporal scale may show the impact of vegetation quality on herbivore behaviour. Other measures of vegetation, such as shade availability alongside forage quality may be able to better infer differences in herbivore activity across different landscapes. If sufficient shade and forage is available, herbivores may forage in shaded areas in the day, as found in Kruger National Park where plains zebras, blue wildebeest and impala were all observed to graze more often underneath the canopy of trees, potentially reducing heat stress experienced in the day (Treydte *et al.*, 2011).

Despite the potential impacts of heat stress on herbivore activity, average seasonal temperature was not shown to impact herbivore nocturnal activity, contradicting hypothesis 2.1. The results of my study contradict several other studies on activity patterns in African buffalo, black wildebeest, southern giraffe, greater kudu, steenbok and impala, which found these species decreased time spent feeding and foraging on hot days (du Toit and Yetman, 2005; Maloney *et al.*, 2005; Winterbach and Bothma, 1998). The lack of a response from herbivore activity to temperature in my study may be due to there being sufficient water available, caused by the abundance of water sources, to facilitate evaporative cooling at higher temperatures, thus herbivores would not shift activity patterns at least on a seasonal scale. Examining temperature values at a smaller temporal scale than done in this study, such as daily or hourly, for each site separately may show impacts of temperature on activity not detectable on the broad seasonal scale used in this study.

Diel occupancy

Most herbivores (African elephants, impala, southern giraffe, greater kudu, springbok and steenbok) had their highest occupancy in weeks they were active throughout the day and night and were not impacted by the presence/absence of lions and distance to water. Hartebeest were the only herbivore with their highest occupancy at night that was not impacted by the distance to water. Three herbivores (gemsbok, plains zebra and blue wildebeest) reduced day and night time occupancy in the presence of lions (partially supporting hypothesis 3.2). Two herbivores (common duiker and white rhinoceros) decreased their day-time occupancy and increased their night-time occupancy with increased distance from water. Blue wildebeest increased their day

and night time occupancy with increased distance from water when lions were absent, but that relationship inversed in the presence of lions.

Unfortunately, because of the categorical nature of each diel state tested, in weeks where herbivores were observed at both day and night, it cannot be quantified what proportion of time was spent active in the day and active at night. This methodological limitation meant that I could not determine if the herbivore activity patterns in these weeks were them being active throughout both the day and night, being crepuscular (active around both sunrise and sunset), being cathemeral or another alternate activity pattern. A finer resolution in time periods (states) used in occupancy models may better show when exactly herbivores are active, however this would require adequate observations in the study species in each state for the model to correctly estimate occupancy. If a time period tested was one where an animal was not active resulting in few observations, occupancy estimates would not be properly calculated. For example, I was unable to estimate common warthog diel occupancy because warthog observations mainly occurred during the day or not during the other two states I tested. The addition of more states could result in fewer species being properly studied using occupancy models, thus only three diel occupancy states were tested in this study. The lack of a multi-species multi-season occupancy models is a further limitation of occupancy models as it demonstrates occupancy models lack complexity at present. While this study was more concerned at the broad activity and spatial patterns over a large geographical and temporal scale of several species, studies examining activity patterns in more detail may find it beneficial to look at activity plots alongside diel occupancy to examine activity patterns on a finer time scale.

Despite limitations on precise activity patterns, diel occupancy models did provide insight into how species changed their broad activity patterns in relation to landscape features, such as

distance to water or presence of predators. Unlike traditional behavioural observations which were biased towards day-time sampling and categorized most herbivores as diurnal (Belovsky and Slade, 1986; Maloney *et al.*, 2005; Mysterud, 1998; Redfern *et al.*, 2003; Smit *et al*., 2007; Valeix, 2011; Western, 1975) or limited to full moon nights for better visibility (Kasiringua *et al.*, 2017). Continuous sampling with camera traps highlighted the flexibility in the timing of activity with most herbivores having higher occupancy throughout the day and night, irrespective of feeding type. Except for the African elephant, all herbivores had higher occupancies at night than during the day despite differences in feeding type and morphology, showing an avoidance of being active solely in the day, likely to avoid heat stress associated with the day. Of the non-grazers not impacted by the presence of lions or distance to water, springbok models had a higher daytime occupancy compared to its other occupancy states. The higher daytime occupancy seen in springbok may be due to the species' arid adaptations allowing springbok to maintain a constant internal temperature throughout the day (Hofmeyr and Louw, 1987). Even herbivore species that were impacted by the presence of lions were unexpectedly less diurnal than expected in the presence of lions, as these species are likely to have a greater perceived risk of predation, thus were expected to shift to be more diurnal to avoid lions (Tambling *et al.*, 2015; Valeix *et al.*, 2009b).

The herbivore species with a diel occupancy impacted by the presence of lions (gemsbok, plains zebra and blue wildebeest), did show a reduced day and night occupancy in the presence of lions, potentially showing a shift in activity potentially to avoid lions although the extent of this relationship cannot be fully determined due to the categorical nature of the diel states in this model. What should be noted is that herbivore species I found to be impacted by the presence of lions are among those most commonly preyed upon by lions (Hayward and Kerley, 2005), with

giraffe being the only preferred prey species not impacted by lions in this study. Three of the four preferred prey species of lions being impacted by the presence of lions does suggest that the results of these models may represent an accurate trend between predator and prey, despite the true relationship of activity patterns not being quantifiable by diel occupancy models. Future studies may be able to further utilise multistate occupancy models to determine the impacts of predation on herbivores. Multistate occupancy models have been done on predators themselves as seen in a study done on predators in Gorno-Badakhshan, Tajikistan to investigate predation risk on livestock (Kachel *et al*., 2022). Occupancy models performed on predators, where data is available, alongside models on herbivores could further show relationships between these two groups.

Of the herbivores impacted by the presence of lions, blue wildebeest, which were considered dependent on water (Kihwele *et al.*, 2020; Redfern *et al.*, 2003; Western, 1975), were the only herbivore with diel occupancy impacted by both the distance from water as well as the presence of lions. The negative relationship between occupancy and distance from water, emphasises the dependence of blue wildebeest to water sources. In sites without lions, a negative relationship is followed for day time weekly occupancy and night time weekly occupancy, however the day and night weekly occupancy shows a positive trend. It is noted however that despite this positive trend, blue wildebeest are predicted to remain within 5 km from the nearest water source, which is close to the preferred distance of 4 km away from water in grazers distance found by Smit and colleagues (2007). Most sites had water sources in close proximity to each other, thus always available to herbivores, so other water dependent herbivores that were expected to be impacted by the distance to surface water did not show this relationship in their diel occupancy model results.

Of the other two species impacted from the distance to water, common duiker, which were not considered reliant on water (Kihwele *et al.*, 2020), were unexpectedly found to be impacted by the distance to water, and showed a similar trend to the water dependent white rhinoceros (Owen-Smith, 1988; Sinibaldi *et al.*, 2004). The negative relationship between distance from surface water and occupancy during the day suggested that these herbivores remained in close proximity to water sources in the day potentially to compensate for water lost using evaporative cooling. At night the opposite relationship was seen with these herbivores occupying spaces further away from water sources when not under the heat stress of the day. It should be noted, that the distance estimates for each species are limited to the maximum distance from water for the camera traps in the sites where the herbivores were found, not necessarily the furthest distance animals will remain from water.

The occupancy results of my study do demonstrate the potential of multistate occupancy models for understanding how animals interact within landscapes and through time. Recent studies have created more complex diel occupancy models, further showing the potential of multistate occupancy models, looking at the influence of human activity and development (Mayer *et al.*, 2023; Rivera *et al.*, 2022). While the specific model I used from the package unmarked (Fiske and Chandler, 2011) did correct for environmental factors, it did not show the impact of these factors. Alternative multistate occupancy models may provide more detail into additional factors giving more complex results.

All the results of this study provide further demonstration on the usefulness of camera traps in studying wildlife. The results of my study were not limited to specific time intervals as shown in direct observational studies (Belovsky and Slade, 1986; Kasiringua *et al.*, 2017; Maloney *et al.*, 2005; Mysterud, 1998), demonstrating how camera traps show a full range in daily activity

patterns. My study also demonstrated how camera trap data can be analysed in a variety of ways, where I was able to use the same set of data to analyse distribution of herbivores in landscapes relative to water, activity patterns (using GLMMs) and diel occupancy models. The diel occupancy predicting lions having an impact on specific species considered to be preferred prey of lions (Hayward and Kerley, 2005) demonstrates how camera trap data may even be able to pick up on relationships between species.

This study also demonstrates the benefits of a standardised camera trap protocol across multiple sites. Most of the camera trap studies mentioned in this report were limited to just one site (Clauss *et al.*, 2021; du Toit and Yetman, 2005; Hayward and Hayward, 2012; Tambling *et al.*, 2015) with the exception of an intercontinental study done by Vallejo-Vargas and colleagues (2022). Due to the standardised grids set up by Snapshot Safari, I was able to analyse thousands of pictures from across the country allowing me to test the impacts between different environments, such as climate or community structure, on animal behaviour.

Conclusion

The predicted water dependence of different species, calculated by Kihwele *et al.*, (2020), has shown to be an important indicator in determining the distances herbivores remain from water sources. Feeding type and body mass along with water dependence, which predicted herbivore activity showed how each of these factors can impact the behaviours of different herbivore species. Vegetation greenness and climatic factors not impacting herbivore behaviour with the exception of rainfall impacting activity, could suggest that changes in climatic factors and vegetation dryness may not have a profound impact on herbivores within South Africa, although

it is possible that the prevalence of water sources in each site allowed herbivores to replenish water used in evaporative cooling to overcome heat stress. Despite the potential of artificial water sources to alleviate pressures that may be seen with climate change, I suggest caution in the use of artificial water sources, as many studies have shown potential negative impacts of artificial water sources to wildlife (Harrington *et al*., 1999; Owen-Smith, 1996; Purdon and van Aarde, 2017). In the presence of lions, herbivores shifted to more diurnal behaviours and remained closer to water sources, showing how lions potentially change the ecosystems they are present in by changing behaviours of prey species and should be considered when managing or introducing lions and mammalian herbivores into an ecosystem. This research demonstrated the usefulness of camera trap data and the various ways such data can be analysed. Multistate occupancy models in particular should be considered more in future studies due to the potential to examine temporal and spatial patterns simultaneously as shown in this study. This study also further showed how environmental factors as well as physiological and morphological features may affect the behaviour of several mammalian herbivore species in South African wildlife areas which could be considered for future research and management of these species.

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