VARIATIONS IN THE USE OF ARTIFICIAL WATERHOLES BY MAMMALS AT OKAUKUEJO AND MORINGA IN ETOSHA NATIONAL PARK, NAMIBIA

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ABSTRACT

The presence of artificial waterholes can alter local mammal biodiversity. Research on the impact of artificial waterholes on local mammal biodiversity and studies on the nocturnal patterns of water usage are limited in Namibia. In this study, large mammals that visited Okaukuejo and Moringa artificial waterholes in Etosha National Park were studied in the cool dry season in July 2022 to determine and compare their species richness, patterns of waterhole usage, duration of stay, and behaviors displayed at the waterholes. A total of 14 large mammal species were recorded at both waterholes. Species richness was significantly higher at Okaukuejo than at Moringa waterhole, with cape fox (*Vulpes chama*), blue wildebeest (*Connochaetes taurinus*), giraffe (*Giraffa camelopardalis*) and warthog (*Phacochoerus africanus*) sighted at either Moringa or Okaukuejo waterhole. Zebras (*Equus quagga*) and springboks (*Antidorcas marsupialis*) had the highest abundance at both waterholes and visited at all sampling sessions (03h00- 06h00, 07h00-10h00, 12h00-15h00, 17h00-20h00 and 22h00-01h00). This indicates more water-dependence than other species and may be influenced by the diet and home ranges of these species. There was a temporal differentiation in the use of the waterholes; mammals mostly visited between 12h00-15h00 and least between 03h00-06h00. Low overlap in waterhole visitation times was observed between predators and potential prey, possibly due to predation risk. The duration of mammal stay was significantly higher at Okaukuejo than at Moringa for elephants (*Loxodonta africana*), springboks, and spotted hyenas (*Crocuta crocuta*). Duration of mammal stay was significantly higher between 22h00-01h00 at Okaukuejo, and significantly lower between 03h00-06h00 at Moringa than other sampling sessions. Black rhinos, elephants and giraffes stayed significantly longer at Okaukuejo, while black rhinos and elephants stayed significantly longer at Moringa, compared to other species. Vigilance and aggression were the most frequently observed behaviors among 13 behavior types recorded, possibly driven by the need for water, predation risk and competition for water. Behaviors occurred at a higher frequency at Okaukuejo waterhole due to higher species richness and abundance. This study provides valuable insights on the activity patterns of mammals around artificial waterholes. Repeated and seasonal observations, incorporating water quality tests at waterholes are recommended for year-round assessment of mammal waterhole use and for explaining variations in visitations, species distribution and behaviors of mammals at waterholes.

Key words: mammals, richness, abundance, composition, duration, Okaukuejo, Moringa, competition, predation, predator, herbivores, carnivores, ungulates, vigilance, aggression, Etosha National Park, Namibia.

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LIST OF ABBREVIATIONS AND/ OR ACRONYMYS

ENP	Etosha National Park
HCA	Hierarchical Cluster Analysis
~	Approximately
(α)	Alpha
m	Metres
h	Hours
df	Degrees of freedom
=	Equal to
e.g.	For example
>	Greater than
<	Less than
-	To
%	Percentage
±	Plus-minus
p	Probability
n	Sample size
SEM	Standard Error of the Mean
SPSS	Statistical Software Package for Social Sciences

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DEDICATION

I dedicate this thesis to my wonderful parents: Mr. John Mthethwa and Ms. Zodwa Gama, whose love, encouragement, and support have been the driving force of my academic journey.

DECLARATION

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Name of Student	Signature	Date

CHAPTER 1: INTRODUCTION

1.1 Background of the study

Daily activity patterns of animals provide insight into their overall ecology. These daily activity patterns are shaped by many factors such as the presence or absence of predators, competition for resources such as water and food and phases of the moon (Crosmary *et al*., 2012; Hayward & Hayward, 2012). Water is very essential to the ecology of animals and has implications for their conservation (Hayward & Hayward, 2012) thus making drinking one of the most crucial life activities of an animal. In arid and semi-arid savannas where natural surface water is scarce, most national parks and game reserves provide artificial water sources to supplement natural surface water (Sutherland, Ndlovu & Perez-Rodriguez, 2018).

Namibia is the driest country south of the Sahel (Seely & Jacobson, 1994); as a result, artificial waterholes have been constructed to provide water throughout the year in both national parks and livestock farms (Mukaru & Mapaure, 2012). Smit and Ferreira (2010) discuss the importance of providing water to mammals in enclosed spaces with limited natural perennial water sources. This is necessitated by the fact that animals in conservation areas are enclosed and thus cannot freely migrate in search of water outside the conservation areas.

Etosha National Park (ENP) has many waterholes, some of which are supplied by constructed boreholes while others by natural springs and fountains (Figure 1). Most rivers and watercourses are ephemeral in ENP, and therefore not the main water sources for animals (du Preez & Gobler, 1977). Natural water relies on rainfall, and thus waterholes fed by natural springs and fountains are only available to animals in the wet season in

ENP. In the dry season, low rainfall, and high rates of evaporation lead to low water availability in natural springs (Auer, 1997). Artificial waterholes supplement the few natural springs available in ENP. Since artificial waterholes can be supplied by boreholes, these do not dry up during the dry season when rainfall levels are low.

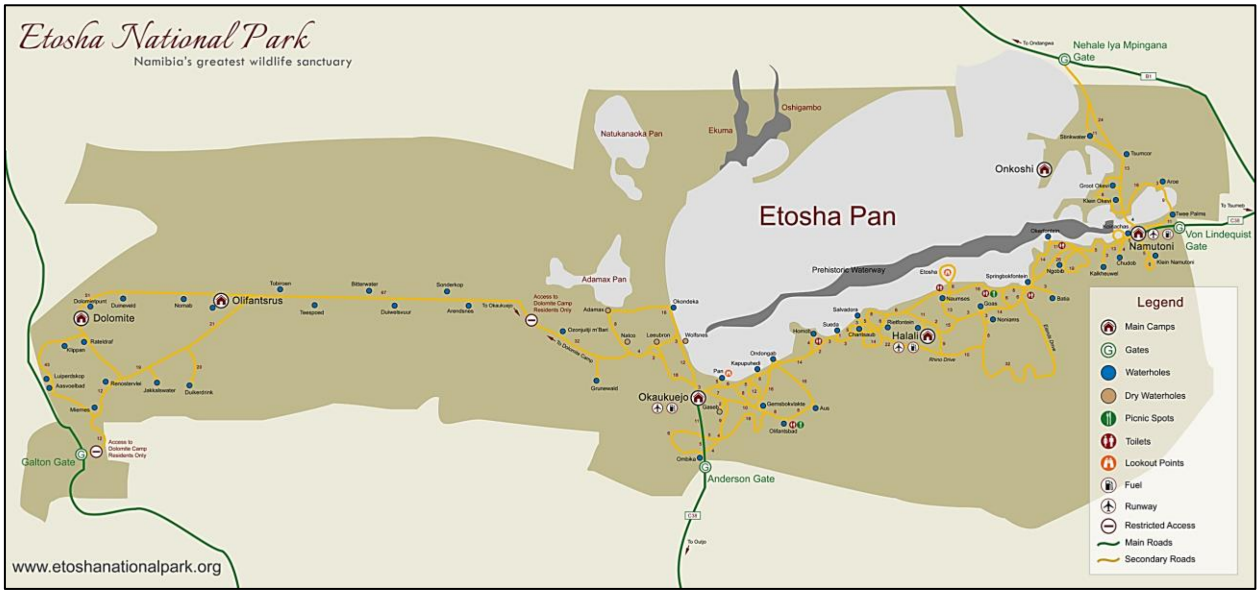

Figure 1: Map of Etosha National Park showing waterholes (blue circles) and other main areas of the park. Downloaded on 20 July 2022 from https://www.etoshanationalpark.org/map

Artificial waterholes play a crucial role in maintaining animal biodiversity. By providing a steady source of water year-round, managing animal densities, and supporting animal populations, they help ensure the survival of various species (Mwakiwa *et al*., 2012). In addition, these waterholes aid in the conservation of animals in protected areas by serving as sites for animal population counts to determine local mammal biodiversity. Moreover, they prevent animals from traveling to external water sources that are not protected. Such migration can cause stress to animals due to the long distances they must travel, as well as increase their risk of being poached (Epaphras *et al*., 2008).

Artificial waterholes have proven to be beneficial in the tourism industry as they attract wildlife to a concentrated area within parks, which increases animal visibility and, consequently, tourism revenue (Mwakiwa *et al.,* 2012). Some artificial waterholes within Etosha National Park are easily accessible from lodges and campsites, providing tourists with designated viewpoints to observe both small and large animals. Waterholes like Okaukuejo and Moringa offer tourists the opportunity to view animals that are active both at daytime and nighttime since they are illuminated at night and accessible 24 hours of each day.

The provision of artificial water sources for conservation management may, however, also yield negative consequences. Prey animals face a higher risk of predation at waterholes (Sirot, Renaud & Pays, 2016). Artificial water sources may also lead to an increase in the population of water-dependent species such as elephants at the expense of water-independent or less water-dependent species like rare antelope species such as the roan antelope (Redfern *et al*., 2005; Valeix *et al*., 2008). Furthermore, due to the congregation of animals around waterholes, there is increased herbivory and trampling of plant species, altering soil properties, and reducing plant species richness and diversity (Mukaru & Mapaure, 2012).

The establishment of an appropriate number of waterholes and their effective distribution is crucial to park managers in their endeavor to ensure sustainable game populations. This approach has been proven to be effective in eliminating challenges of resource over-utilization and under-utilization, particularly around the waterholes.

According to Auer (1997), the proper management of waterholes is key to the success of game population management efforts. By carefully determining the number of waterholes required to support the population of game species in each area, and ensuring that they are distributed effectively, park managers can contribute to maintaining a balance between the available resources and the demands of the wildlife population.

1.2 Statement of the problem

The presence of waterholes may compromise the biodiversity of mammals. The introduction of waterholes can cause a shift in the distribution of animals in the local environment, as observed by Smit, Grant and Devereux (2007). Temporal changes in distribution occur when animals stay permanently in areas where they would have previously stayed for only a short period of time due to the presence of a waterhole. Over time, these changes can lead to an increase in the abundance of water-dependent species such as elephants (Sutherland, Ndlovu & Perez-Rodriguez, 2018) and their predators.

Elephants and large predators can dominate waterholes (Janecke, 2021), and prevent other mammal species from accessing and utilizing them (Sirot, Renaud & Pays, 2016). In addition, increased abundance of these water-dependent species increases grazing pressure, thus altering the vegetation structure. Consequently, this leads to a decrease in the abundance of less water-dependent species because these are sensitive to changes in their habitat structure (Redfern *et al*., 2005; Sutherland, Ndlovu & Perez-Rodriguez, 2018).

Spatial changes in distribution of mammals can also occur due to the presence of waterholes, resulting in increased activity and interaction around waterholes, such as predation and competition. The current body of research on the impact of artificial waterholes on local mammal biodiversity, duration of stay, and behavior at these sites in Namibia is limited. Furthermore, there is a shortage of research on the nocturnal patterns of water usage by large mammals at water provisioning sites in the region. The aim of the study was to determine and compare the diurnal and nocturnal patterns of water usage by large mammals at Okaukuejo and Moringa artificial waterholes at Etosha National Park in Namibia.

1.3 Objectives of the study

The objectives of the study were:

a) To determine and compare species richness of mammals utilizing Okaukuejo and Moringa artificial waterholes.
b) To determine and compare the duration that mammals utilizing Okaukuejo and Moringa artificial waterholes stay and how it varies among waterholes and species.
c) To determine the effect of time of day on the duration that mammals stayed at Okaukuejo and Moringa waterholes.
d) To document and compare the most common behaviours displayed by mammals that visited Okaukuejo and Moringa waterholes.

1.4 Hypotheses of the study

The following null hypotheses (H_0) were tested in the present study:

a) There was no significant difference in the species richness of mammals that visited Okaukuejo and Moringa waterholes.
b) There was no significant difference in the duration that different mammal species stayed at Okaukuejo and Moringa waterholes.

c) Time of day does not significantly affect the duration that mammals stayed at Okaukuejo and Moringa waterholes.
d) The most common behaviours which mammals displayed do not significantly differ between Okaukuejo and Moringa artificial waterholes.

1.5 Significance of the study

Results of this study have contributed to estimation of local mammal biodiversity within the vicinity of Okaukuejo and Moringa waterholes, including daily variations in the utilization of these waterholes by mammals. These are important in the strategic management of these artificial waterholes in ENP, to ensure that the waterholes fulfill the main objective of conservation of animal biodiversity, especially of endemic species. Furthermore, the results of this study contribute to more scientific understanding of the impacts of artificial waterholes on the ecology of large mammals. Such understanding will enhance the development and implementation of specific objectives towards conservation and management of these large mammals.

In addition, this study provides some insights into the daily activity patterns of large mammals at Okaukuejo and Moringa waterholes. This information is crucial in the management of large mammals such as elephants, black rhinos, blue wildebeest, zebra, impala and oryx as most of these species have high water requirements and are essential in the tourism industry (Hayward & Hayward, 2012; Kasiringua, Kopij & Procheş, 2017). Etosha National Park managers will be better informed on how best to supplement current water provisioning guidelines in the park, ensuring that management issues such as over-provision or under-provision of water are mitigated based on data. Moreover, the issue of a high concentration of mammals at the waterholes can be effectively resolved through the implementation of appropriate water provision measures.

1.6 Limitations of the study

Mammals were only studied at three-hour sampling sessions (03h00-06h00, 07h00-10h00, 12h00-15h00, 17h00-20h00 and 22h00-01h00), with periods of rest in between each session. Mammals that visited the waterholes during the resting periods were therefore not included in this study. This is because time and financial constraints did not allow for longer and repeated sessions of data collection. In addition, mammals that were more than 30 metres away from the edge of the water at the two waterholes were not counted. Moreover, mammals that left the waterhole and later returned, if any, were recounted as it was difficult to recognize mammals as returning. Lastly, the exact duration of stay could not be determined for mammals that were already at each waterhole at the start of each sampling session, as well as for those that were left at each waterhole at the end of each sampling session. In such cases, the time when sampling began and the time when sampling ended was recorded as arrival and departure times, respectively, for these mammals.

1.7 Delimitation of the study

The present study was carried out for four consecutive days at each waterhole (Okaukuejo and Moringa) in the dry season and only by direct observation. There were five sampling sessions and four sampling cycles at each waterhole.

CHAPTER 2: LITERATURE REVIEW

2.1 The Utilization of Artificial Water Sources in Conservation Areas

Water accessibility in certain regions marked by aridity has been noted to exhibit seasonal variability and is particularly limited during the dry season (Valeix *et al.*, 2011). Consequently, numerous conservation areas with large mammals have constructed artificial water sources as a management technique to facilitate their conservation in these arid and semi-arid regions (Smit, Grant & Devereux, 2007). Several countries have constructed artificial water sources within conservation areas in Africa e.g. Zimbabwe, South Africa, Tanzania as discussed below, as well as in other continents.

Artificial waterholes are essential for mammal survival during periods of water scarcity, such as during the hot, dry season. Ferry, Dray and Fritz (2016) have reported on the increase of populations of various herbivores in the dry season facilitated by the increase in water supply due to the presence of waterholes. Studies have shown how waterholes play a crucial role in the preservation and protection of biodiversity in Southern African parks. These include Hwange National Park located in Zimbabwe (Valeix, Chamaillé-Jammes & Fritz, 2007), Chobe National Park situated in Botswana (Owen-Smith, 1996), Kruger National Park in South Africa (Sutherland, Ndlovu & Perez-Rodriguez, 2018), as well as Waterberg National Park situated in Namibia (Kasiringua, Kopij & Procheş, 2017). In Hwange National Park, Kruger National Park and the Sahel in northern Africa, waterholes have reportedly positively impacted the biodiversity of certain ungulate species (Sinclair & Byrom, 2006).

Artificial water sources have been deemed indispensable in Ruaha National Park in Tanzania due to the scarcity of natural water in this region (Epaphras *et al.*, 2008).

Namibia’s Waterberg National Park is also characterized by the absence of permanent natural water sources (Kasiringua, Kopij & Procheş, 2017). As a result, measures were taken to construct artificial water sources to aid in the conservation efforts aimed towards the park's wildlife. Waterberg National Park possesses seven waterholes which serve as a guarantee for the continuous availability of water to meet animals' physiological requirements (Kasiringua, Kopij & Procheş, 2017).

Since mammals congregate at waterholes, these waterholes can be used for surveys as well as for conducting research on mammalian behavior and ecology in non-invasive methods (Seeber *et al*., 2019). Waterholes are ideal for research on mammals since they enable easier mammal observation as mammals can be found in large populations around waterholes (Ferry, Dray & Fritz, 2016). This congregation of large populations of mammals at waterholes consequently leads to many interactions at waterholes, which can provide valuable insights into mammal behavioral ecology, such as interference competition and its effects on mammals (Ferry *et al*., 2020).

Predator-prey dynamics and behaviors can also be easily observed and studied at waterholes since the presence of waterholes can influence the behaviour of prey species to avoid predation, as well as lead to changes in the spatial ecology of predators such as lions and hyenas (Makin, Chamaillé-Jammes & Shrader, 2017).

Waterholes can also be used to manage and maintain vegetation in national parks. This is described in Kamanda *et al*. (2008), where waterholes were strategically positioned to facilitate the dispersion of water-dependent species to alternate grazing locations during the dry season and thus reduce grazing pressure in Hwange National Park. The same strategy was used in Tsavo National Park in Kenya, whereby waterholes were constructed to promote the migration of animals from areas in the vicinity of riverbeds to previously unexplored regions of the park (Ayeni, 1975).

Similarly, Chobe National Park shared a common objective of mitigating the impact of grazing pressure on the vegetation of riverine ecosystems within its premises. To achieve this objective, alternative water sources were developed within the park as a strategy to alleviate animal density along these rivers (Owen-Smith, 1996). The pressure exerted on the flora along rivers was mainly attributed to the presence of fauna such as elephants that exhibited strong water-dependence and thus gravitated towards these riverine environments.

2.2 Water Requirement in Mammals

Mammals are categorized as water-dependent, water-independent or less water-dependent, depending on how much water they require and consequently, their frequency of visitation of water sources (Redfern *et al*., 2005). Water-dependent mammals show a higher drinking frequency than less water-dependent species. Water dependency in mammals is impacted by many factors, such as the stage of development. Juveniles have higher water intake requirements compared to adults; pregnant animals also consume more water (Bothma, 2002).

In addition, the dietary habits of organisms play a significant role in their water requirements (Western, 1975; Redfern *et al*., 2005). Browsers are less water-dependent than mixed feeders and grazers (Western, 1975; Redfern *et al*., 2005) since their diet constitutes mostly of browse such as shrubs and trees. Due to its ability to store water during the dry season, this vegetation has been observed to be available throughout most seasons of the year and to have a relatively high water content (Bothma, 2002). Grazers, on the other hand, are water-dependent since they feed mostly on grass which does not store much water during the dry season (Western, 1975). Waterbuck, which is a grazer, has been reported to frequent waterholes as it has very high water requirements (Ayeni, 1975).

Browsers with low water requirements include the greater kudu (Hayward & Hayward, 2012) and giraffe (Ayeni, 1975; Tefempa *et al*., 2008). Findings from Tefempa *et al*. (2008) showed that the giraffe can survive without water for up to four days. Water-dependent mammals include the elephant and impala which are mixed feeders and grazers such as blue wildebeest and zebra (du Preez & Grobler, 1977; Hayward & Hayward, 2012). Carnivores are water-independent, as they can fulfill their water requirements from the flesh and blood of their prey (Ayeni, 1975). Hayward and Hayward (2012) confirmed these results in their report that hyenas and lions require low amounts of water. A study by Kasiringua, Kopij and Procheş (2017) also reported very low sightings of leopard and cheetah at waterholes in Waterberg National Park.

It has also been observed that the species type and hence physiological adaptations of mammals also influences water-dependency. Mammals with larger bodies exhibit a higher consumption of water than those with smaller bodies (Hayward & Hayward, 2012). The fact that elephants visit water sources more frequently than smaller mammals serves as evidence for this assertion (du Preez & Grobler, 1977; Valeix, Chamaillé-Jammes & Fritz, 2007). In a report by Bothma (2002), among a specific set of mammal species, the white rhinos exhibited the greatest intake of water, with the giraffe and black rhino ranking next in order of consumption. The oryx and warthog, on the other hand, exhibited the least water consumption on a daily basis.

The quantity of available water within the habitat can also affect an animal's water requirements (Hayward & Hayward, 2012). Inhabiting a dry habitat typically elicits elevated water requirements in mammals, leading to a heightened water intake during the dry season in contrast to the wet season.

2.3 Mammal species richness and abundance in waterholes

Mammal species richness and abundance at waterholes is influenced by predation, water quality, water dependency of mammals and others (Sutherland, Ndlovu & Perez-Rodriguez, 2018). Elephants (*Loxodonta africana*) usually have a high abundance at waterholes (Sutherland, Ndlovu & Perez-Rodriguez, 2018). Rare antelope species and impala (*Aepyceros melampus*) avoid waterholes when elephants or predators are abundant near waterholes (Sirot, Renaud & Pays, 2016). Moreover, when herbivores assemble in waterholes, it is common for predators to also aggregate in the vicinity (Janecke, 2021).

A study by Hayward and Hayward (2012) reported that the most frequently observed species in different waterholes overlapped with other species in their waterhole utilization time. Grazers showed the greatest overlap with other grazers, followed by browsers with grazers and the least overlap was observed between browsers with other browsers. Large predators such as lions, leopards and hyena, on the other hand, showed the lowest overlap with each other.

Species richness at waterholes can also be influenced by the presence of keystone species such as elephants. Valeix *et al*. (2009) reported that smaller herbivores may avoid waterholes when there are too many elephants. Herbivores such as impala and kudu change their waterhole visitation times in order to reduce the chances of temporal overlap with elephants at waterholes (Valeix, Chamaillé-Jammes & Fritz, 2007). Conversely, wildebeest, waterbuck and giraffe were reported to visit waterholes when elephants were present by Valeix, Chamaillé-Jammes and Fritz (2007).

2.4 Visitation times and duration of mammal stay at waterholes

Physiological needs of animals, such as water, greatly influence how they adjust their seasonal and daily activity patterns, including the allocation of their activity budget (Nasanbat, Ceacero & Samiya, 2021). Although various mammal species may utilize similar waterholes, they partition their waterhole visitation times (temporal partitioning) and differ in their duration of using waterholes (Valeix, Chamaillé-Jammes & Fritz, 2007; Janecke, 2021). Waterhole-use partitioning is as a consequence of interference competition, whereby animals have to compromise between water requirements and conflicts associated with predation and competition, especially in arid environments (Valeix, Chamaillé-Jammes & Fritz, 2007).

Herbivores generally show diurnal overlaps in their utilization of waterholes, while large predators show nocturnal variations (Sutherland, Ndlovu & Perez-Rodriguez, 2018). This partitioning of visitation times helps herbivores reduce competition while daytime visitations helps them to avoid predation (Hayward & Hayward, 2012). Valeix, Chamaillé-Jammes and Fritz (2007) noted a change in the timing of visits to waterholes between elephants and four other herbivorous species (impala, kudu, roan, and sable) at Hwange National Park. This shift led to a decrease in the amount of time that the four species and elephants spent in the same waterhole, resulting in reduced interference competition.

Sutherland, Ndlovu and Perez-Rodriguez (2018) conducted a study that revealed that carnivores and small herbivores visited four waterholes nocturnally, while large herbivores and primates visited the same waterholes during the day. Conversely, a study performed by du Preez and Grobler (1977) at ENP indicated that large herbivores such as rhinoceros and elephants utilized waterholes nocturnally. This finding opposes the previous observation, as large herbivores are not easily preyed on by predators at night because of their size and aggressive behavior (du Preez & Grobler, 1977).

In a study conducted by Nasanbat, Ceacero and Samiya (2021), it was reported that predators and their potential prey exhibited temporal partitioning of waterhole use in the Gobi Desert located in Mongolia. The study revealed that there was only a minor temporal overlap observed between the two groups. The activity patterns of carnivorous animals are primarily influenced by the activity patterns of their prey rather than the availability of water sources. This is because carnivores are able to satisfy their water requirements by consuming their prey, as stated by Nasanbat, Ceacero and Samiya (2021).

Waterhole visitations by mammals also varies at a temporal scale according to the season. More mammals visit artificial water sources in the dry season when natural water sources have dried up (Sutherland, Ndlovu & Perez-Rodriguez, 2018). Conversely, fewer mammals visit artificial water sources in the wet season. This is because they can alternatively use natural water sources which are closer to their areas of refuge and forage and consequently save travelling energy (Valeix *et al*., 2008).

Season also influences the frequency at which animals drink water. During the dry season, ungulates tend to consume water at a higher frequency as compared to the wet season. In cases where water is easily accessible and uniformly dispersed, the majority of ungulate species will consume water at least once per day. Drinking frequency is also greatly influenced by the animal species, habitat and the distribution and number of water sources. This information has been reported by several studies including Hayward and Hayward (2012) and Crosmary *et al*. (2012).

According to Janecke's research (2021), waterholes may be dominated by elephants and big predators, leading to the exclusion of other animal species from accessing them for drinking and other purposes. According to Valeix *et al*. (2009), when mammals display high levels of vigilance at waterholes, they tend to spend more time there. This is because disturbances during the drinking process lead to a lower intake rate, which consequently leads to mammals requiring more time to fulfill their water requirements. This behavior is typically observed in smaller mammal species when sharing waterholes with keystone competitors, such as elephants. The study also suggests that smaller mammals might spend more time at waterholes in the presence of elephants because they feel safer from predators when larger mammals are around (Valeix, Chamaillé-Jammes & Fritz, 2007).

Despite the significance of waterholes as sources of drinking for mammals, the nocturnal usage of these water sources has been largely overlooked by researchers, as noted by Kasiringua, Kopij and Procheş (2017). This study sought to address this gap in knowledge by examining and comparing the patterns of mammalian visitation to waterholes during both daytime and nighttime hours. By shedding light on the nocturnal habits of these animals, the study provides a valuable contribution to the field of mammalian behavioral ecology.

2.5 Mammal behavior at waterholes

Mammals display different types of behaviors when approaching or utilizing artificial waterholes (du Preez & Grobler, 1977). These include vigilance behaviors to avoid predation (du Preez & Grobler, 1977), drinking, thermoregulation, and interactions such as aggression and predation (Hayward & Hayward, 2012). Since more mammals visit artificial water sources in the dry season, this may escalate species interactions such as interspecific competition at these waterholes (Janecke, 2021).

du Preez and Grobler (1977) observed that for increased vigilance, aimed at avoiding predation, most species of mammals such as springbok, eland and wildebeest approach waterholes as a group at ENP. Other interactions such as interspecific competition and fighting normally occur between species such as elephants and other herbivores in waterholes (Janecke, 2021). Other mammal species that show aggressive behavior at waterholes are zebra and gemsbok, especially in small waterholes (du Preez & Grobler, 1977).

Valeix, Chamaillé-Jammes and Fritz (2007) observed and documented various behaviors in the Hwange National Park between elephants and ten other herbivorous species. The results showed that elephants use interactions such as trumpeting, earflaps and aggressive chases to deter other herbivores from using waterholes. Some herbivores also left waterholes when elephants arrived, resulting in temporary shifts in waterhole use. Moreover, it was reported that these behaviors were significantly increased as the number of elephants also increased at the waterholes.

Valeix *et al*. (2009) also confirmed that the presence of elephants around waterholes strongly influences the behaviour of other herbivores. Smaller herbivores were observed to spend time in vigilant activities when elephants were present at waterholes. Moreover, it was suggested that these herbivores may spend more time in other activities such as wallowing when elephants are present at waterholes. The behavior of elephants, themselves, has been reported to be influenced by the availability and quality of water at waterholes (Valeix, Chamaillé-Jammes & Fritz, 2007).

Tefempa *et al.* (2008) state that the behaviour of animals around a waterhole is significantly influenced by meteorological conditions of the site, whereby high temperatures tend to reduce animals' activities. Another factor that greatly influences the behavior of mammals at waterholes is perceived or actual predation risk. In arid environments where mammals aggregate at waterholes during water shortages, predators take advantage of prey's need for drinking, leading to high predation risk around waterholes (Valeix *et al*., 2009; Crosmary *et al*., 2012; Amoroso, *et al*., 2020).

2.6 Data collection methods

Hayward and Hayward (2012) studied seasonal variations of waterhole use by mammals at five southern African reserves using webcams for collecting data. Using webcams for studying mammals visiting waterholes can provide incomplete results since only those mammals within the webcam's field of view are captured, missing those mammals that are outside this field of view. Camera traps, as used by Janecke (2021) can present similar challenges as only mammals in the vicinity of the camera are captured, especially at night when the mammals are too far from the camera to be captured by infrared flashes. Direct observation, which was employed in this study helped in avoiding these challenges.

CHAPTER 3: MATERIALS AND METHODS

3.1 Description of the study area

3.1.1 Location and extent

The study was conducted at Okaukuejo and Moringa artificial waterholes in Etosha National Park (ENP). ENP has an area of 22 915 km^2 in north-central Namibia and lies between 18°30′ S – 19°30′ S and 14°15′ E – 17°10′ E (Ministry of Environment and Tourism., 2011; Figure 2).

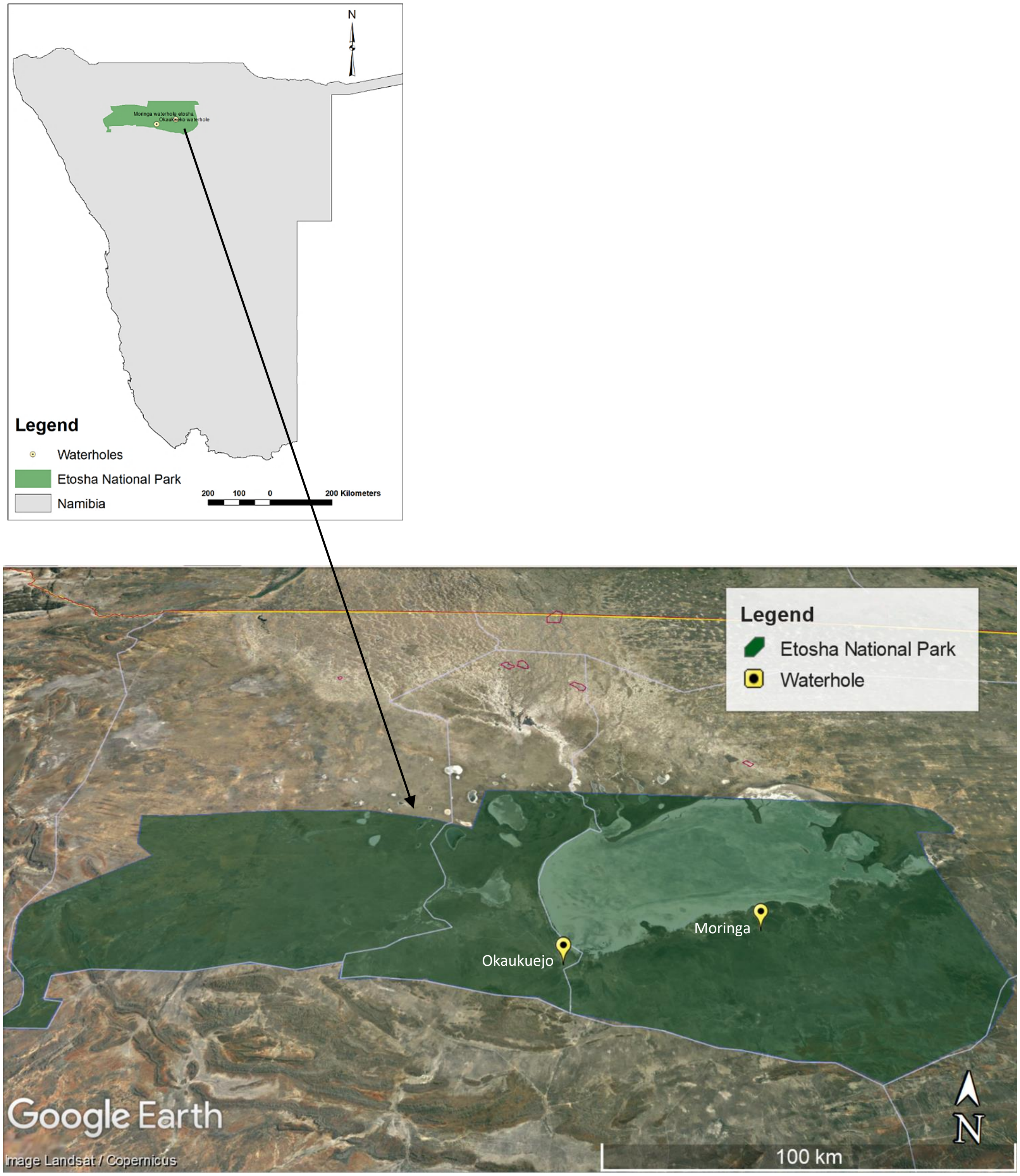

Figure 2: A map of Etosha National Park in northern Namibia with the inset map showing the study sites: Okaukuejo and Moringa waterholes (marked yellow pins) (retrieved from Google Earth).

The park has numerous artificial waterholes and natural springs. Artificial waterpoints are maintained by the park management to supplement the few natural springs available. They are powered by wind or solar energy. Okaukuejo and Moringa artificial waterholes are two of the biggest waterholes in the park; these are illuminated by floodlights at night, enabling the study of nocturnal waterhole utilization by mammals.

3.1.2 Climate

Etosha National Park is a semi-arid savanna, with an average annual rainfall of 358.0 ± 126.7 mm (mean ± s.d.; Okaukuejo station 1954-2020) (Huang *et al*., 2021). Rainfall occurs seasonally between the months of November and April. Rainfall increases from 300 mm in the west to 500 mm in the east (Mendelsohn *et al.*, 2002). The highest rain falls in January and February during the hot wet season that occurs in January to April. The cool dry season occurs in May to August (Engert, 1997). As a result of the seasonal rainfall patterns, water is only found in natural springs at ENP following rainfall.

3.1.3 Fauna

Etosha National Park supports a high density of mammal populations. Most species of large mammals found in southern Africa are found in this park, with exceptions such as African wild dog (*Lycaon pictus*) and buffalo (*Syncerus caffer*) (Wassermann *et al*., 2015). Zebra and springbok are the two most abundant plains ungulate species, with estimated populations of 13,000 zebra and 15,600 springboks (Wassermann *et al*., 2015). Elephants have an estimated population of 2900 (Craig, Gibson & Uiseb, 2021).

3.1.4 Flora

ENP is characterized by arid savanna vegetation such as shrubveld, treeveld and grassland (le Roux *et al.*, 1988). Grassland is found along pans such as along the Etosha pan (le Roux *et al.,* 1988). The most dominant tree species is mopane (*Colophospermum mopane*), with common grass species being *Cynodondactylon, Eragrostis micrantha, Eragrostis rotifer, Diplachnefusca,* and *Chlorisvirgata* (le Roux *et al*., 1988).

3.2 Data collection

3.2.1 Selection of the study sites

The study utilized two artificial waterholes, namely Okaukuejo and Moringa. These waterholes were selected because, unlike other waterholes at Etosha National Park, these two waterholes were floodlit at night, allowing both daytime and nocturnal observations of mammals. Most studies of mammals at waterholes are conducted during the day, ignoring nocturnal behavior and activity patterns of mammals. Okaukuejo waterhole is located at 19.1810° S, 15.9157° E in ENP. This waterhole, which was formerly a natural spring, receives continuous water from surrounding boreholes. The waterhole is illuminated by three floodlights at night (Figure 3).

Figure 3: A night view of Okaukuejo waterhole in Etosha National Park, Namibia, showing floodlights that illuminate the waterhole at night and black rhino (*Diceros bicornis)* species which are easily visible walking around the waterhole at night. A stone wall and fencing that separate the waterhole from the viewpoints are also visible.

Viewpoints are located about 40 meters away from the water, along a semicircular stone wall with fencing that serves as a barrier between the waterhole and the viewpoints (Figures 4 a and b).

Figure 4: Okaukuejo waterhole in Etosha National Park, Namibia showing (a) viewpoints where observers can sit while viewing animals that visit the waterhole and (b) fencing and a stone wall that separates the waterhole from viewpoints.

Okaukuejo waterhole has a large piosphere of greater than 30 metres. There are patches of grass and shrubs, with one big leadwood (*Combretum imberbe*) growing at one side of the waterhole within the piosphere (Figure 5). Dead tree logs are also scattered within the piosphere. Animals can easily be spotted from the viewpoints, more than 30m away from the edge of the waterhole.

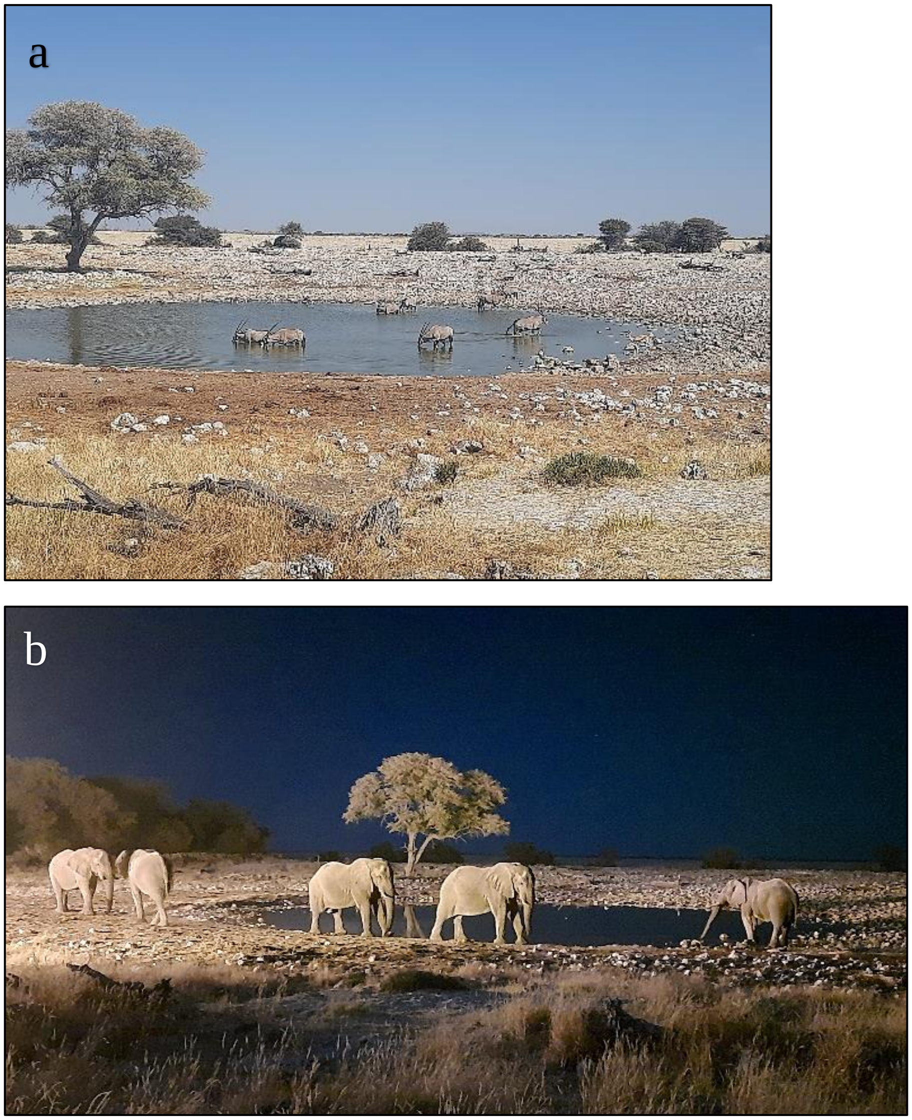

Figure 5: Okaukuejo waterhole in Etosha National Park, Namibia showing the waterhole, patches of grass and tree logs within the piosphere as well as *Combretum imberbe* species growing on the piosphere. Oryx (*Oryx gazelle)* species can be seen drinking in the waterhole during the day in (a) and elephant (*Loxodanta africana)* species can be seen around the waterhole at night in (b).

Moringa waterhole is located at 19.0401° S, 16.4702° E in ENP. This waterhole is illuminated by two floodlights at night, allowing night observation of animals that visit the waterhole (Figure 6). The piosphere is smaller at Moringa waterhole, as the waterhole is surrounded by thick bushes of trees and vegetation growing about 30m away from the waterhole.

Small patches of grass and shrubs grow around the waterhole within the piosphere (Figure 6). Animals within the bushes (more than 30m away from the edge of the waterhole) were not easy to spot within the dense vegetation, especially at night.

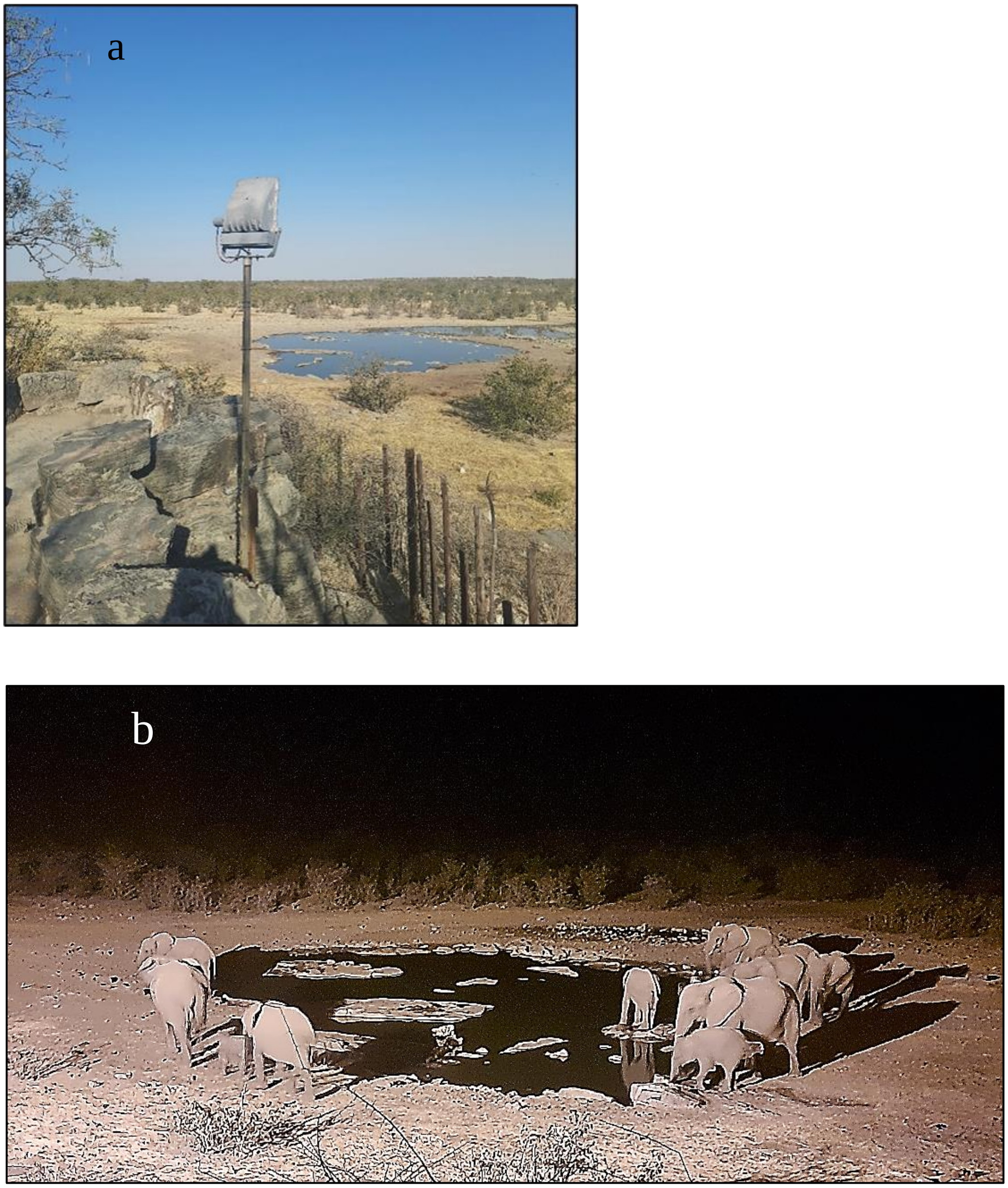

Figure 6: Moringa waterhole in Etosha National Park, Namibia showing (a) one floodlight that illuminates the waterhole at night and (b) elephant (*Loxodanta africana)* species that can be seen at the waterhole at night. Patches of grass and shrubs can also be seen within the piosphere.

The waterhole is separated from viewpoints by a high wall of rocks and fencing. The viewpoint is also elevated, allowing easier sighting of animals (Figure 7 a and b).

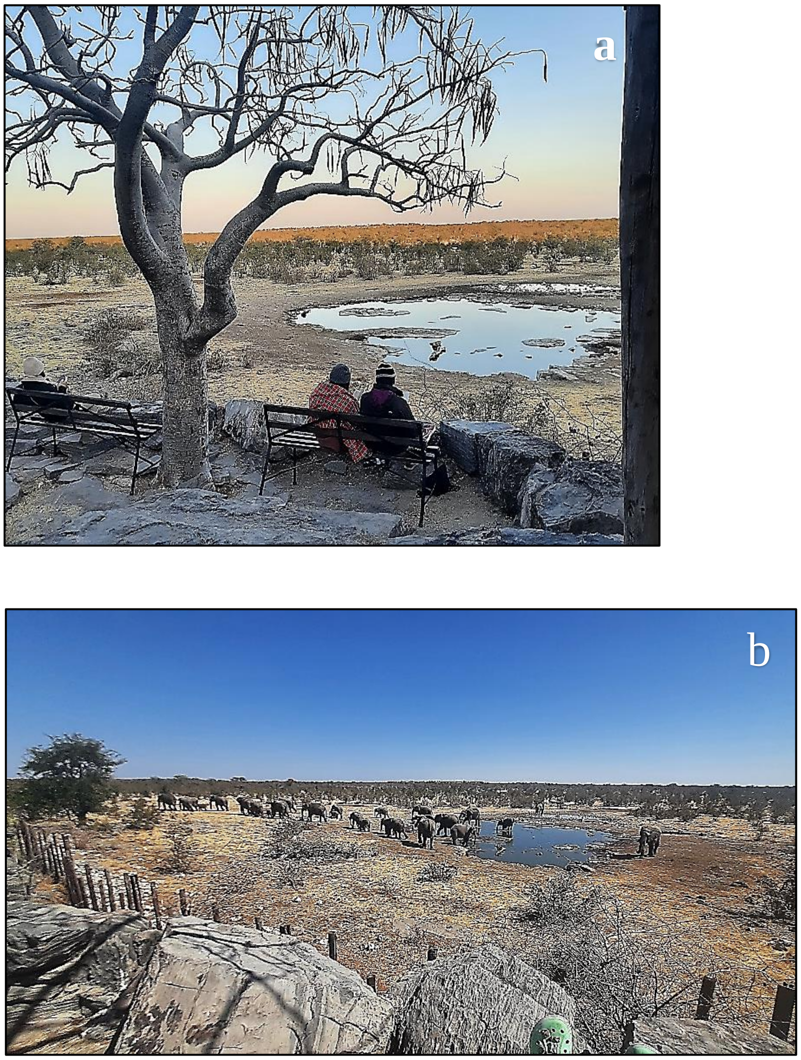

Figure 7: Moringa waterhole in Etosha National Park, Namibia showing (a) elevated viewpoints where observers can sit while viewing animals that visit the waterhole and (b) a high wall and fencing that separate the waterhole from viewpoints. Elephant species can be seen at the waterhole in (b).

3.2.2 Procedure

Data was collected from 13 July 2022 to 22 July 2022 in the cool, dry season. There were twenty sampling sessions at each waterhole, and these were carried out from July 13th to 17th at Okaukuejo waterhole and July 18th to 22nd at Moringa waterhole (Table 1). Observations were done at three-hour sampling sessions at each waterhole: 03h00 – 06h00, 07h00 – 10h00, 12h00 – 15h00, 17h00 – 20h00 and 22h00 – 01h00. Each three-hour period of observation was followed by a period of resting: 06h01 – 06h59, 10h01 – 11h59, 15h01 – 16h59, 20h01 – 21h59 and 01h01 – 02h59. This was done to prevent observer fatigue from interfering with the observations. Collected data was also arranged according to sampling cycle. One sampling cycle was defined as sampling in each waterhole that includes each of all the five consecutive sampling sessions (03h00 – 06h00, 07h00 – 10h00, 12h00 – 15h00, 17h00 – 20h00 and 22h00 – 01h00).

Table 1: Sampling sessions that were used at Moringa and Okaukuejo waterholes in Etosha National Park in this study including their names and periods of rest.

Sampling Session	**Resting Period**
03h00 – 06h00	06h01 – 06h59
07h00 – 10h00	10h01 – 11h59
12h00 – 15h00	15h01 – 16h59
17h00 – 20h00	20h01 – 21h59
22h00 – 01h00	01h01 – 02h59

Mammals were observed using the naked eye and binoculars from the designated viewpoints at each waterhole, and data was recorded by the observer on a field data sheet (Appendix 3). Each large mammal at about 30m from the water was recorded as within the waterhole.

Data collected for each mammal included: common name, time of arrival, number of individuals per species (Tefempa *et al.*, 2008), whether the mammal was drinking at the waterhole or not, behavior at the waterhole (e.g. mud-bathing, grazing, aggression etc.) and time of departure. The time when sampling began was recorded as the arrival time for any mammals that were found already at the waterhole, while the time when sampling ended was recorded as the time of departure for any mammals that remained at the waterhole after the sampling session. The duration of stay for each mammal species was then calculated and recorded.

Mammal behaviors that were recorded in this study were categorized into 13 major categories including vigilance, mud-bathing or sand-bathing, aggression, relaxing, foraging, running in, running out, running off, nurturing, walking around, courtship, playful, and other. These behaviors are shown with their descriptions in Table 2 below.

Table 2: Descriptions of the 13 behavioral activities recorded at Moringa and Okaukuejo waterholes in Etosha National Park during this study.

Behavior	**Description**
Vigilance	Looking around, examining surroundings, standing still with head raised above shoulder height, stopping to listen.
Mud/sand bathing	Rolling inside muddy water, digging underwater to produce mud, splashing mud onto body, covering with mud, immersion of all or part of the body in muddy water or rolling around in sand, throwing sand onto body, covering body with sand.
Aggression	Physical contact, hissing, growling, whining, roaring, trumpeting, chasing, running away, kicking, confronting, charging at another animal, attacking, stomping the ground.
Resting	Lying on the ground, sitting on the ground, standing around waterhole without showing much vigilance.
Foraging	Grazing or browsing on vegetation around waterhole.
Running in	Running into the water.
Running out	Running out of the water but remaining within 30m from the water.
Running off	Running out of the water and leaving the waterhole.
Nurturing	Protecting young, covering/shielding young, splashing young with water/mud, grooming.
Walking around	Walking around the waterhole.
Courtship	Sniffing, licking, following female, raising the tail, attempting to mount.
Playful	Chasing, kicking, jumping, running around, splashing water, spitting water, blowing water.
Other	Urinating, rubbing body against tree.

3.3 Data analysis

All data recorded was summarized using descriptive statistics. In order to analyze the data, all data were first tested for normality using the Shapiro-Wilk test (Shapiro & Wilk, 1965). Results from the Shapiro-Wilk test were used to determine the tests to be used to analyze the data. Parametric tests were used when data were normally distributed ($p > 0.05$) and non-parametric tests were used when data were not normally distributed ($p < 0.05$).

To compare the mammal species richness in Okaukuejo and Moringa waterholes, the sum of species recorded in each sampling session (03h00 – 06h00, 07h00 – 10h00, 12h00 – 15h00, 17h00 – 20h00 and 22h00 – 01h00) was calculated (Appendix 4). This was done for each sampling cycle and waterhole. This species richness data was then tested for normality using the Shapiro-Wilk Test. The test revealed that data were normally distributed [$W(40) = 0.948$, $p = 0.067$]. An independent t-test was therefore used to test for a statistically significant difference between the species richness of mammals that visited Okaukuejo and Moringa waterholes at Etosha National Park.

The duration of mammal stay at the waterholes was not normally distributed [$W(557) = 0.619$, $p < 0.001$]. Therefore, a Mann-Whitney U test was carried out for each mammal species that visited both waterholes to determine if there was a statistically significant difference in the duration of stay of that species between Okaukuejo and Moringa waterholes.

A Kruskal-Wallis H test was also performed for each waterhole to determine if there was a statistically significant difference in the duration of stay among the different mammal species that visited that particular waterhole. To evaluate whether there was a statistically significant difference in the duration of stay of mammals among the different sampling sessions (03h00 – 06h00, 07h00 – 10h00, 12h00 – 15h00, 17h00 – 20h00 and 22h00 – 01h00), a Kruskal-Wallis H test was also performed for each waterhole. All the above statistical analyses were based on algorithms in the Statistical Package of Social Science (SPSS) software programme IBM version 26, with the level of significance set at (α) = 0.05.

Hierarchical Cluster Analysis (HCA) was used to compare similarity in the species composition of mammals that visited waterholes at the different times of the day (visits during sampling sessions 03h00-06h00, 07h00-10h00, 12h00-15h00, 17h00-20h00 and 22h00-01h00) at each waterhole. The HCA was based on the Bray-Curtis Similarity Index, which is useful for comparing the composition of species between different samples (Farooq, Qamar & Panhwar, 2017).

In this study, the Bray-Curtis Similarity Index measured the variation in the similarity in species composition of mammals that visited the waterholes between different sampling cycles and between different sampling sessions, based on the presence or absence of species. The Bray-Curtis similarity expressed the species composition as a percent similarity (Yoshioka, 2008), with 0% being the lowest similarity and 100% being the highest similarity. The results of the HCA were presented in the form of dendrograms which joined samples (sampling cycles or sampling sessions) together in a hierarchical fashion from the closest (most similar) to the furthest (most dissimilar) samples (Aljumily, 2016). HCA was performed using BioDiversity Professional (BioDiversity Pro) software, Version 2 (McAleece *et al*., 1997).

3.4 Research Ethics

Ethical clearance was obtained from the University of Namibia Ethics Committee (REC) (Appendix 1) and research approval from the Centre for Research Services of the University of Namibia (UNAM). A research permit was obtained from the National Commission for Research Science and Technology (NCRST) [Appendix 2; Authorization number AN20200406]. Safety guidelines were adhered to as given by the Etosha National Park management.

CHAPTER 4: RESULTS

4.1 Mammal species richness and abundance at Okaukuejo and Moringa waterholes.

A combined total of 3,552 large mammals visited the two waterholes during the study period (a total of 2,618 individual mammals visited Okaukuejo waterhole and 934 visited Moringa waterhole). There was a combined total of 14 species of large mammals recorded at both waterholes. Of those species, 13 species were recorded at Okaukuejo waterhole and 11 were recorded at Moringa waterhole. Cape fox was exclusively observed at Moringa waterhole, while at Okaukuejo waterhole, exclusive mammal species observed were blue wildebeest, giraffe, and warthog (Table 3). Springboks were the most abundant species at Okaukuejo waterhole, while zebras were the most abundant species at Moringa waterhole.

Table 3: Mammal species abundance and richness recorded at Moringa and Okaukuejo waterholes in Etosha National Park during the study period in July 2022. *n* = number of individuals counted, % = relative abundance.

Common Name	**Species**	**Okaukuejo**		**Moringa**		**Total**	
		n	**%**	***n***	**%**	***n***	**%**
Springbok	*Antidorcas marsupialis*	1180	45.07	10	1.07	1190	33.50
Zebra	*Equus quagga*	814	31.09	380	40.69	1194	33.61
Oryx	*Oryx gazelle*	117	4.47	1	0.11	118	3.32
Blue wildebeest	*Connochaetes taurinus*	116	4.43	0	0.00	116	3.27
Black-faced impala	*Aepyceros melampus petersi*	114	4.35	352	37.69	466	13.12
Elephant	*Loxodonta africana*	111	4.24	95	10.17	206	5.80
Giraffe	*Giraffa camelopardalis*	53	2.02	0	0.00	53	1.49
Kudu	*Tragelaphus strepsiceros*	50	1.91	18	1.93	68	1.91
Black rhino	*Diceros bicornis*	38	1.45	33	3.53	71	2.00
Black-backed jackal	*Canis mesomelas*	15	0.57	10	1.07	25	0.70
Lion	*Panthera leo*	7	0.27	5	0.54	12	0.34
Spotted hyena	*Crocuta crocuta*	2	0.08	16	1.71	18	0.51
Warthog	*Phacochoerus africanus*	1	0.04	0	0.00	1	0.03
Cape fox	*Vulpes chama*	0	0.00	14	1.50	14	0.39
Total		**2618**		**934**		**3552**	
Species richness		**13**		**11**		**14**	

An independent samples t-test showed a significant difference in mammal species richness [t (38) = 4.323; n = 40, $p < 0.001$, (95% confidence interval 1.010 to 2.790)] of mammals that visited Okaukuejo waterhole (Mean 5.2 ± 0.360 SEM) and Moringa waterhole (Mean 3.3 ± 0.252 SEM) (Figure 8).

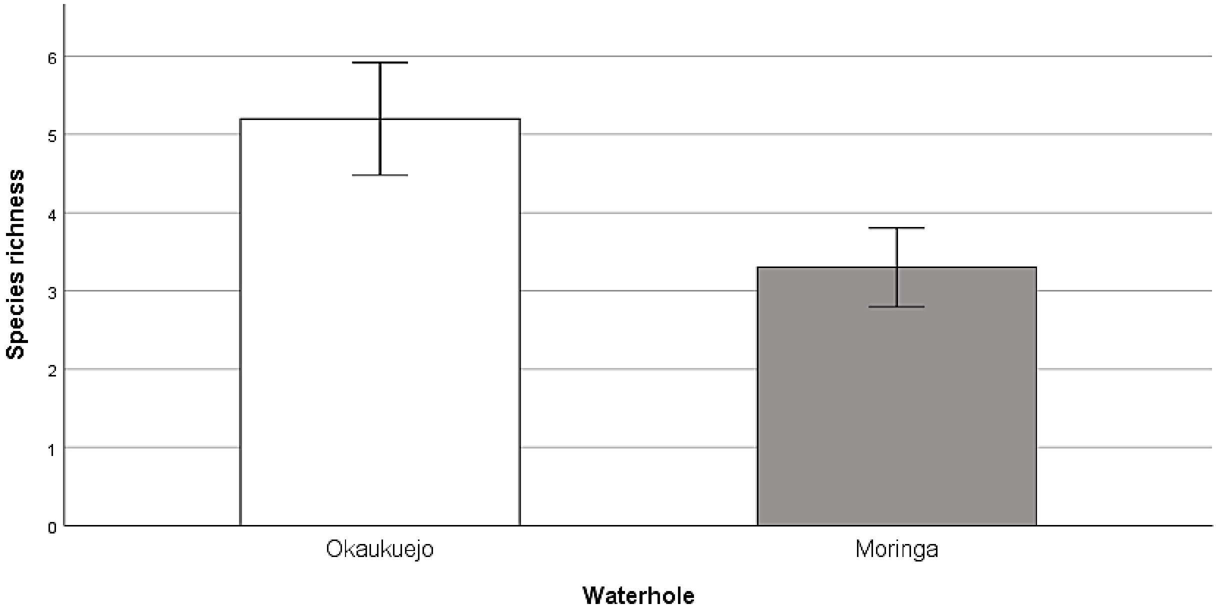

Figure 8: The mean (± Standard Error of the Mean (SEM)) mammal species richness of mammals that visited Okaukuejo and Moringa waterholes in Etosha National Park, Namibia.

4.2 Temporal patterns of waterhole usage by mammals.

At both waterholes, mammals were mostly sighted in the afternoons (12h00 – 15h00) and least sighted at dawn (03h00 – 06h00) (Figure 9). During the study period, 66% of the mammals that visited both waterholes did so in the afternoon, whereas only 3% did so at dawn (Figure 9).

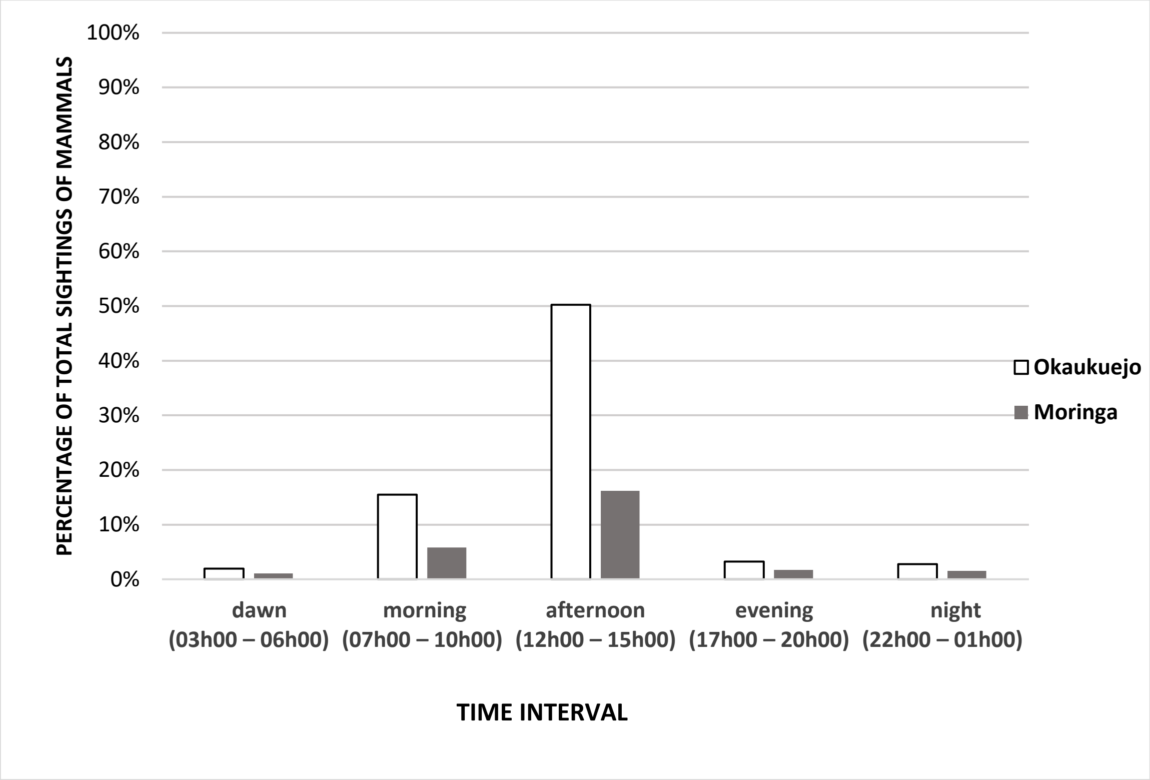

Figure 9: Percentage of total sightings of mammals at Moringa and Okaukuejo waterholes in Etosha National Park at different sampling sessions (times). Percentage of total sightings of mammals was calculated as the percentage of individuals that visited each waterhole in each sampling session out of the total number of individuals that visited both waterholes throughout the data collection period.

4.2.1 Temporal patterns of waterhole usage by mammals at Okaukuejo waterhole.

A dendrogram from a Hierarchical Cluster Analysis (HCA) based on a Bray-Curtis Similarity Index using binary (present-absent) data separated mammal species into three main clusters and six sub-clusters based on visitation times at Okaukuejo waterhole (Figure 10). The three main clusters demarcated between exclusively daytime visitors (A), daytime-nighttime visitors (B) and strictly nocturnal visitors (C) at Okaukuejo waterhole. The dendrogram shows that cluster A (exclusive daytime visitors) was 66% similar to clusters B (daytime-nighttime visitors) and C (strictly nocturnal visitors), while clusters B and C were 75% similar to each other. Clusters 1 to 6 represented species composition at specific sampling sessions (times) throughout the study period.

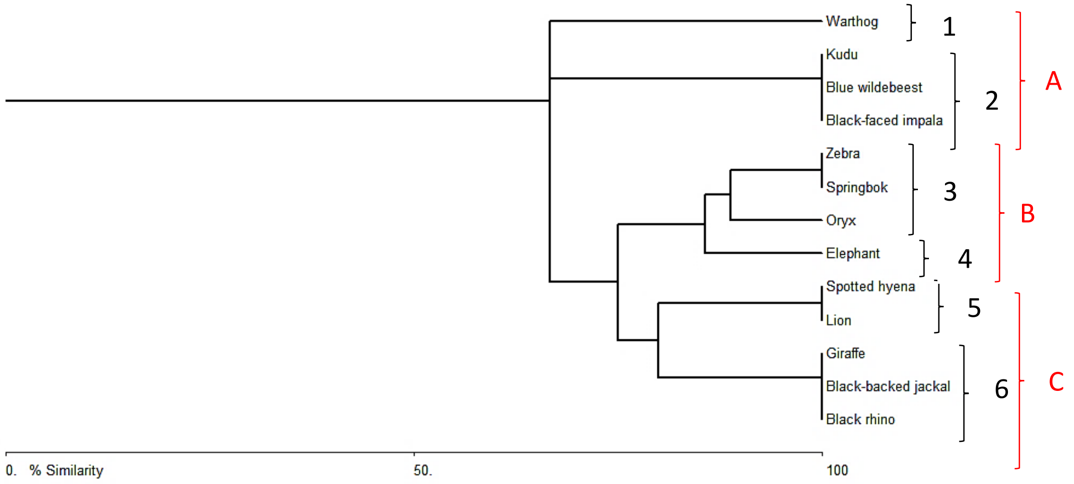

Figure 10: A dendrogram of a Hierarchical Cluster Analysis (HCA) based on Bray-Curtis similarity matrix using binary data showing mammal species composition at Okaukuejo waterhole at different sampling sessions (03h00-06h00, 07h00-10h00, 12h00-15h00, 17h00-20h00 and 22h00-01h00) at Etosha National Park.

In the dendrogram (Figure 10), cluster 1 consisted of just one species: the warthog. This species only visited Okaukuejo waterhole once throughout the study period during the 12h00-15h00 sampling session. Cluster 2 represented strictly daytime visitors that visited Okaukuejo waterhole between 07h00-10h00 and 12h00-15h00 throughout the study period. These species showed 100% similarity in their waterhole visitation times. Cluster 3 represented daytime-nighttime visitors: zebra, springbok and oryx species. Zebra and springbok species visited Okaukuejo waterhole at all sampling sessions (03h00-06h00, 07h00-10h00, 12h00-15h00, 17h00-20h00 and 22h00-01h00) during the study period and showed 100% similarity in their visitation times. Oryx species were also included in this cluster, they showed 89% similarity to zebra and springbok species as they were recorded at Okaukuejo waterhole at all sampling session, besides one (03h00-06h00).

The fourth cluster represented elephants which were the only daytime-nighttime visitors that were recorded at Okaukuejo waterhole only between 12h00-15h00, 17h00-20h00 and 22h00-01h00. Elephants showed 86% similarity in visitation habits to the other daytime-nighttime visitors. Cluster 5 represented strictly nocturnal species (spotted hyena and lion), which showed 100% similarity in their visitations to Okaukuejo waterhole between 03h00-06h00 and 22h00-01h00. The sixth cluster consisted of mammal species that were recorded nocturnally at Okaukuejo waterhole (03h00-06h00, 17h00-20h00 and 22h00-01h00). These mammal species also showed 100% similarity on their waterhole visitation times.

4.2.2 Temporal patterns of waterhole usage by mammals at Moringa waterhole.

A dendrogram from a Hierarchical Cluster Analysis (HCA) based on a Bray-Curtis Similarity Index using binary (present-absent) data separated mammal species composition into three main clusters and five sub-clusters based on visitation times at Moringa waterhole (Figure 11). The three main clusters demarcated amongst strictly daytime visitors (A) (excluding zebra species), strictly nocturnal visitors (B) and daytime-nighttime visitors (C) at Moringa waterhole. The dendrogram shows that cluster A (daytime) was 66% similar to cluster B (nocturnal). Clusters B and C were 80% similar to each other. Clusters 1 to 5 represented species composition at specific sampling sessions (times) throughout the study period.

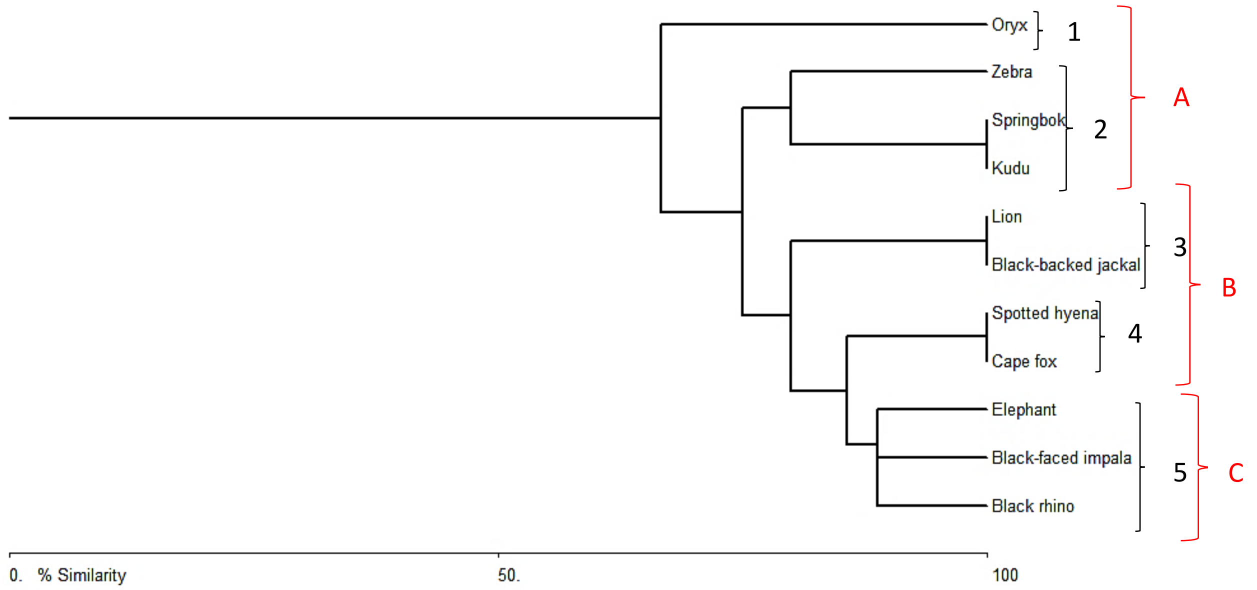

Figure 11: A dendrogram of a hierarchical cluster analysis (HCA) based on Bray-Curtis similarity matrix using binary data showing mammal species composition at Moringa waterhole at different sampling sessions (03h00-06h00, 07h00-10h00, 12h00-15h00, 17h00-20h00 and 22h00-01h00) at Etosha National Park.

Cluster 1 represented oryx species, which were recorded only during 12h00 – 15h00 at Moringa waterhole. Cluster 2 consisted of exclusive daytime mammals (springbok and kudu), which showed 80% similarity to zebra species in their visitation times (07h00 – 10h00 and 12h00 – 15h00). Zebras also visited Moringa waterhole between 17h00 – 20h00, in addition to these times. Strictly nocturnal mammals (lions and black-backed jackals) in cluster 3 were recorded at Moringa waterhole between 03h00 – 06h00 and 22h00 – 01h00. These species were 100% similar to each other and 86% similar in visitation times to other strictly nocturnal species in cluster 4. Cluster 4 consists of mammal species that were sighted at Moringa waterhole nocturnally between 03h00 – 06h00, 17h00 – 20h00 and 22h00 – 01h00. These species (spotted hyena and cape fox) showed 100% similarity in their waterhole visitation times. Cluster 5 consisted of daytime-nighttime visitors, which showed 89% similarity in their visitation times at Moringa waterhole.

4.3 Duration of mammal stay at Okaukuejo and Moringa waterholes.

4.3.1 Duration of mammal stay between the waterholes.

There were 10 similar mammal species that were sighted and recorded at both Okaukuejo and Moringa waterholes. These species were elephant, black rhino, lion, zebra, oryx, kudu, springbok, black-faced impala, spotted hyena and black-backed jackal. The average duration of stay for these species was 17 minutes at Okaukuejo waterhole, whereas the average duration at Moringa waterhole was 11 minutes.

Mann-Whitney U tests revealed statistically significant differences in the duration of stay between Okaukuejo and Moringa waterholes for three species: elephant (z = -2.632, n = 26, p = 0.007); springbok (z = -2.699, n = 152, p = 0.007) and spotted hyena (z = -2.297, n = 14, p = 0.022) (Figure 12). Elephants and springboks stayed significantly longer at Okaukuejo waterhole while spotted hyenas stayed significantly longer at Moringa waterhole. There were no statistically significant differences in the duration of stay between the two waterholes for the other 7 species; black rhino (z = -1.386, n = 56, p = 0.166); lion (z = -0.296, n = 5, p = 0.800); zebra (z = -1.909, n = 87, p = 0.056); oryx (z = -0.972, n = 34, p = 0.471); kudu (z = -1.534, n = 19, p = 0.129); black-faced impala (z = -1.468, n = 87, p = 0.143) and black-backed jackal (z = -0.551, n = 23, p = 0.600) (Figure 12).

4.3.2 Duration of mammal stay among different species at each waterhole.

Elephants spent the longest time at Okaukuejo waterhole compared to other species, with an average duration of 52 minutes. At Moringa waterhole, black rhinos had the highest duration of stay, with an average duration of stay of 27 minutes. Black-backed jackals spent the shortest time at Okaukuejo waterhole, with an average duration of stay of 4 minutes. At Moringa waterhole, spotted hyenas spent the shortest time, with an average duration of stay of 3 minutes (Figure 12).

A Kruskal-Wallis H test showed that there was a statistically significant difference in the duration of stay among the different species at Okaukuejo waterhole, H (12) = 144.180, $p < 0.001$. Post hoc tests were conducted with a Bonferroni correction for multiple tests applied (Appendix 5). These revealed that the statistically significant differences in the duration of mammal stay at Okaukuejo waterhole were between black rhinos, elephants and giraffes with 6 other species: black-backed jackal, springbok, black-faced impala, zebra, blue wildebeest and oryx. Elephants also showed statistically significant differences in the duration of stay at Okaukuejo waterhole with kudu species. Black-backed jackals showed statistically significant differences in the duration of stay at Okaukuejo waterhole with 5 other species; springbok, zebra, blue wildebeest, oryx and kudu (see Appendix 5 for test statistics).

A Kruskal-Wallis H test also revealed a statistically significant difference in the duration of stay among the different species at Moringa waterhole, H (10) = 91.166, $p < 0.001$. Post hoc tests were conducted with a Bonferroni correction for multiple tests applied (Appendix 6). These revealed that the statistically significant differences in the duration of mammal stay at Moringa waterhole were between black rhinos and elephants with 3 other species: spotted hyena, black-backed jackal and cape fox. Black rhinos also showed statistically significant differences in the duration of stay at the waterhole with black-faced impala and zebra species. Cape fox and spotted hyena species showed statistically significant differences in the duration of stay at the waterhole with 2 other species; zebra and black-faced impala (see Appendix 6 for test statistics).

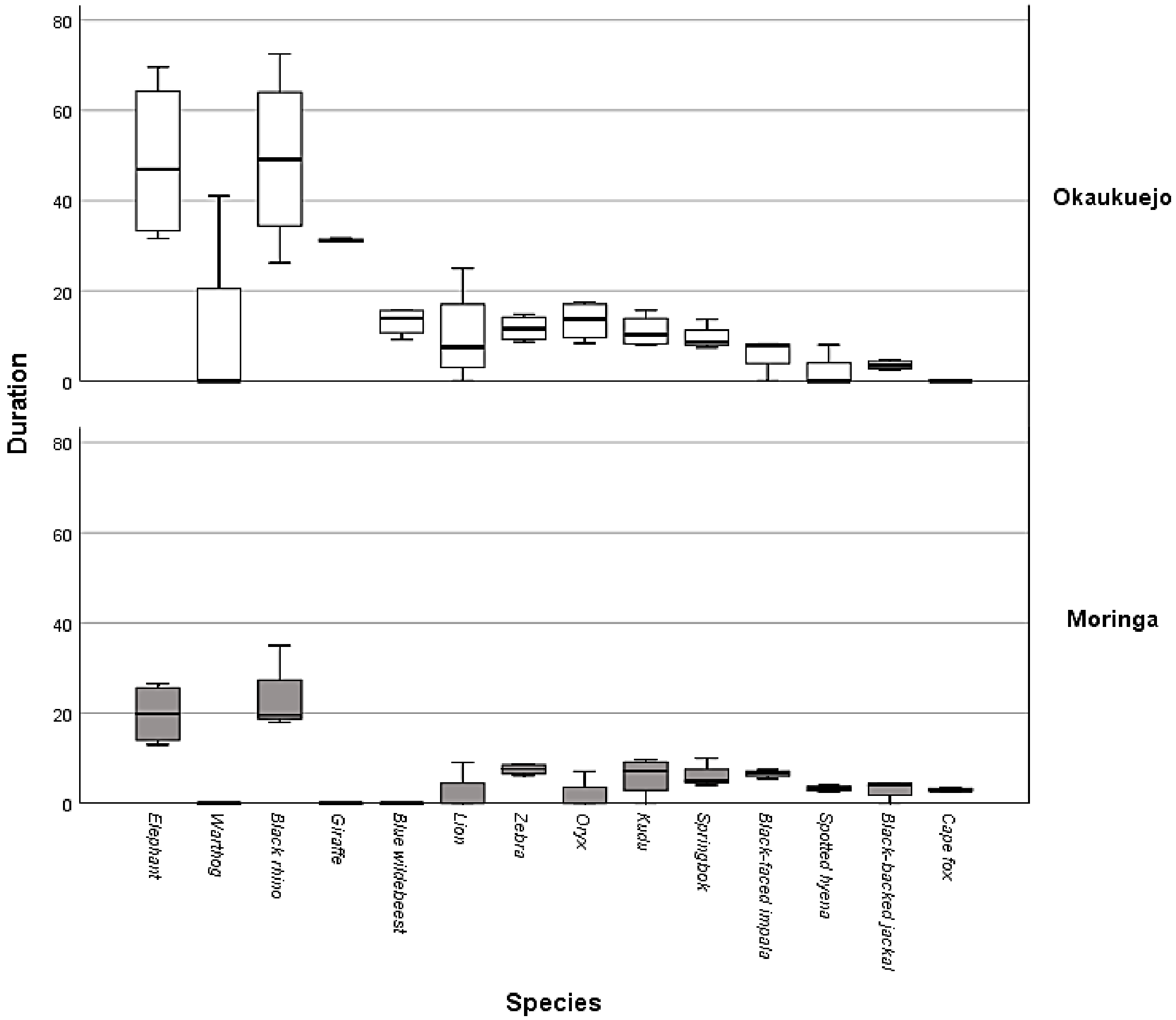

Figure 12: Box and whisker plots comparing the medians of mammal species duration of stay at Okaukuejo and Moringa waterholes at Etosha National Park, Namibia in July 2022. The horizontal line inside each box represents the median. The top part of each box represents the 75th percentile (upper quartile), while the bottom part represents the 25th percentile (lower quartile). The ends of each line above and below the open box indicate the largest and lowest values, respectively, that are not outliers.

4.4 Duration of mammal stay at different times of the day.

Mammals spent the longest time at Okaukuejo waterhole between 22h00 – 01h00, with an average of 31 minutes spent by all mammals collectively at Okaukuejo waterhole at this time (Table 4.1). The longest time spent by all mammals collectively at Moringa waterhole was an average of 17 minutes, also between 22h00 – 01h00 (Table 4.2). The least amount of time spent by all mammals collectively at Okaukuejo waterhole was 12 minutes between 12h00 – 15h00, while the least amount of time spent by mammals at Moringa waterhole was 6 minutes between 03h00 – 06h00 (Tables 4A and 4B).

A Kruskal-Wallis H test showed a statistically significant difference in the duration of stay of mammals among the different sampling sessions (03h00 – 06h00, 07h00 – 10h00, 12h00 – 15h00, 17h00 – 20h00 and 22h00 – 01h00) at Okaukuejo waterhole, H (4) = 12.799, $p = 0.012$. Post hoc tests were conducted with a Bonferroni correction for multiple tests applied (Appendix 7). These revealed that statistically significant differences in the duration of stay at Okaukuejo waterhole were between 12h00 – 15h00 and 22h00 – 01h00 ($p = 0.007$). Other sampling sessions did not show a statistically significant difference in the duration of stay of mammals (see Appendix 7 for test statistics).

A Kruskal-Wallis H test also revealed a statistically significant difference in the duration of stay of mammals among the different sampling sessions (03h00 – 06h00, 07h00 – 10h00, 12h00 – 15h00, 17h00 – 20h00 and 22h00 – 01h00) at Moringa waterhole, H (4) = 17.648, $p = 0.001$. Post hoc tests were conducted with a Bonferroni correction for multiple tests applied (Appendix 8). These revealed that statistically significant differences in the duration of stay at Moringa waterhole were between 03h00 – 06h00 and three other sessions, 07h00 – 10h00 (*p* = 0.010), 12h00 – 15h00 (*p* = 0.007) and 22h00 – 01h00 (*p* = 0.001).

Table 4. 1: Mean duration (minutes) and Standard Error of the Mean (SEM) spent by each mammal species at different sampling sessions in Okaukuejo waterhole in Etosha National Park in July 2022. Where mammals did not visit waterholes, (n/a) is used.

	03h00-06h00		**07h00-10h00**		**12h00-15h00**		**17h00-20h00**		**22h00-01h00**	
Species	**Mean**	**SEM**	**Mean**	**SEM**	**Mean**	**SEM**	**Mean**	**SEM**	**Mean**	**SEM**
Black rhino	33	15	n/a	n/a	n/a	n/a	34	10	44	10
Black-backed jackal	3	0	5	2	n/a	n/a	3	2	4	0
Black-faced impala	n/a	n/a	10	2	8	1	n/a	n/a	n/a	n/a
Blue wildebeest	n/a	n/a	20	4	9	3	n/a	n/a	n/a	n/a
Cape fox	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Elephant	n/a	n/a	n/a	n/a	43	8	39	7	69	13
Giraffe	27	7	n/a	n/a	n/a	n/a	27	4	34	5
Kudu	n/a	n/a	13	3	11	2	n/a	n/a	n/a	n/a
Lion	25	n/a	n/a	n/a	n/a	n/a	n/a	n/a	8	2
Oryx	n/a	n/a	17	3	12	1	4	n/a	9	1
Spotted hyena	n/a	n/a	7	n/a	n/a	n/a	n/a	n/a	9	n/a
Springbok	9	2	11	1	12	1	6	1	6	1
Warthog	n/a	n/a	n/a	n/a	41	n/a	n/a	n/a	n/a	n/a
Zebra	7	1	15	2	12	2	11	7	5	n/a

Table 4. 2: Mean duration (minutes) and Standard Error of the Mean (SEM) spent by each mammal species at different sampling sessions in Moringa waterhole in Etosha National Park in July 2022. Where mammals did not visit waterholes, (n/a) is used.

	03h00-06h00		**07h00-10h00**		**12h00-15h00**		**17h00-20h00**		**22h00-01h00**	
Species	**Mean**	**SEM**	**Mean**	**SEM**	**Mean**	**SEM**	**Mean**	**SEM**	**Mean**	**SEM**
Black rhino	19	12	11	n/a	n/a	n/a	26	7	31	5
Black-backed jackal	4	2	n/a	n/a	n/a	n/a	n/a	n/a	5	1
Black-faced impala	2	0	7	1	7	1	5	n/a	n/a	n/a
Blue wildebeest	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Cape fox	3	0	n/a	n/a	n/a	n/a	3	1	6	2
Elephant	15	n/a	n/a	n/a	35	n/a	25	15	16	3
Giraffe	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Kudu	n/a	n/a	10	n/a	8	2	n/a	n/a	n/a	n/a
Lion	14	n/a	n/a	n/a	n/a	n/a	n/a	n/a	9	n/a
Oryx	n/a	n/a	n/a	n/a	7	n/a	n/a	n/a	n/a	n/a
Spotted hyena	3	1	n/a	n/a	n/a	n/a	3	0	3	0
Springbok	n/a	n/a	5	n/a	6	1	n/a	n/a	n/a	n/a
Warthog	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Zebra	n/a	n/a	9	2	9	1	4	n/a	n/a	n/a

4.5 Behavior of mammals at Okaukuejo and Moringa waterholes.

Mammals displayed various behaviors at waterholes, which were assigned to 13 types (Table 2) and their frequency of occurrence recorded. Frequency of occurrence represented the total number of times that a mammal species visited Moringa and Okaukuejo waterholes during the ten days and nights when data was collected and displayed that behaviour. Ten out of the 13 behaviors recorded occurred at a higher frequency at Okaukuejo than at Moringa waterhole (Figure 13).

Only three behaviors; running in, walking around and courtship had a higher frequency of occurrence at Moringa waterhole. Behaviors that mammal species displayed more frequently at the waterholes included vigilance and aggression (Figure 13; Appendix 9). Vigilance had the highest frequency of occurrence; it accounted for 44% of all behaviors observed at both waterholes. Mammal species that showed the highest vigilance included giraffe, black-backed jackal, spotted hyena and cape fox. Aggression had the next highest frequency of occurrence, and it accounted for 18% of all the observations. Black rhinos showed the highest frequency of aggression, followed by zebras.

The least observed behaviors were nurturing and other types of behaviours, with each behavior type forming 1% of all observations at the waterholes (Figure 13, Appendix 9). Courtship was only observed at Moringa waterhole among black-faced impala species, and among elephants. Sand and mud-bathing was only displayed by elephant species at both Moringa and Okaukuejo waterholes.

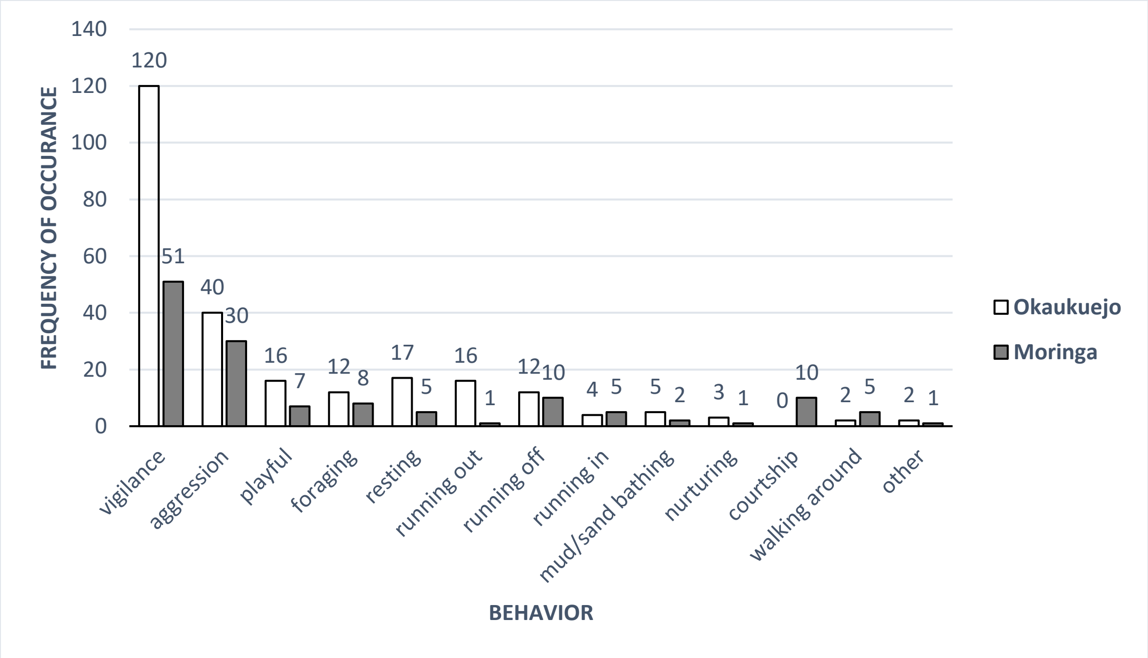

Figure 13: Frequency of occurrence of different types of behaviors at Moringa and Okaukuejo waterholes in Etosha National Park in July 2022.

CHAPTER 5: DISCUSSION OF RESULTS

5.1 Mammal biodiversity at Okaukuejo and Moringa waterholes.

5.1.1 Mammal species richness at the waterholes.

Statistical tests showed a significant difference in mammal species richness between Okaukuejo and Moringa waterholes (Figure 8). Therefore, the null hypothesis that the species richness of mammals that visited the Okaukuejo and Moringa waterholes is not significantly different is rejected. Hence it is concluded that the species richness of mammal that visited Okaukuejo waterhole was higher.

The significant differences in species richness of mammals that visited Okaukuejo and Moringa waterholes may be attributed to many factors, including but not limited to geographical location and size of the waterhole, species and density of surrounding vegetation, the size of the piosphere and predation risk. Okaukuejo waterhole is larger, had a bigger piosphere and had less abundance of surrounding vegetation, with less heterogeneity of plant species growing within the piosphere. Moringa waterhole, on the other hand, had more heterogeneity of plant species and dense vegetation surrounding its smaller piosphere (Figures 5 and 6; personal observation).

Some mammal species were only recorded at one waterhole and not the other, resulting to differences in species richness. It is possible that giraffes and blue wildebeests, which were exclusively sighted at Okaukuejo waterhole in this study, selected Okaukuejo for drinking because it was closer to areas of forage and refuge for these species. This is because mammals avoid travelling over long distances to water sources in order to conserve energy and avoid predation (Smit & Grant, 2009). Sutherland, Ndlovu and

Perez-Rodriguez (2018) have also noted this phenomenon where mammals organize their communities to maintain proximity to resources.

Cape foxes were recorded exclusively at the Moringa waterhole and not at Okaukuejo. This aligns with expectations, as cape foxes are typically associated with habitats that offer greater vegetation cover, including Karoo shrubland, grassland with thickets, and semi-desert shrub (Maxime et al., 2019). The denser vegetation around Moringa may provide better concealment from predators such as lions, spotted hyenas, and black-backed jackals. As cape foxes are occasionally preyed upon by black-backed jackals and can be killed during encounters with these larger carnivores (Maxime *et al*., 2019; Smith, 2023), the availability of cover is likely an important factor influencing their habitat use.

Avoidance of Moringa waterhole by giraffes in this study may be explained with reference to observations by Strauss and Packer (2012) and Sutherland, Ndlovu and Perez-Rodriguez (2018), who reported that giraffes preferred areas with open vegetation. In this study, giraffes were observed showing extensive vigilance behavior, scanning the area for any potential predators while cautiously approaching Okaukuejo waterhole. Due to the open nature of the vegetation, giraffes had a better chance to spot and flee just in time from predators such as lions, which are the main predators of giraffes (Bond *et al*., 2021; Muneza *et al*., 2021) at Okaukuejo rather than Moringa waterhole.

Blue wildebeest are preferred prey for predators such as lions, cheetahs and spotted hyenas at ENP, with lions being their main predators (Berry, 1981). This may explain why they avoided Moringa waterhole and were only sighted at the more open Okaukuejo waterhole during this study, where they could more easily spot any approaching predators. In addition to avoiding Moringa waterhole, blue wildebeests also approached Okaukuejo waterhole in large groups, which is another predator-avoidance strategy (Ripple *et al*., 2014).

With regards to warthogs, research has shown that the presence of warthogs is significantly influenced by environmental factors such as cover, food, and water sources (Adeola *et al*., 2021). It has been documented that warthogs tend to favor open landscapes (Adeola *et al*., 2021; de Jong, d'Huart & Butynski, 2023). This could be another reason to explain why this species was exclusively seen and recorded at Okaukuejo waterhole, which had a more open terrain compared to the densely vegetated surroundings of Moringa waterhole.

5.1.2 Mammal species abundance at the waterholes.

The study revealed the highest mammal species abundance in zebras (n = 1194), followed by springboks (n = 1190) at both waterholes combined. Since zebras and springboks are some of the most abundant species of ungulates at ENP (Wassermann *et al*., 2015), it was expected that they would also have higher abundance than other species at the waterholes. In addition, waterholes were possibly closer to areas of refuge and foraging for these species, enabling the mammals to save energy by traveling a shorter distance to waterholes (Smit & Grant, 2009).

Zebras, which had the highest abundance at both waterholes combined (Table 3) are general, indiscriminate grazers (Owen-Smith, Martin & Yoganand, 2015). They feed on grasses that may have a lower biomass (Havarua, Turner & Mfune, 2014) or water content in the dry season and thus need to frequent waterholes to fulfill their water requirements. This may explain the high abundance of this species at the waterholes. The high abundance of zebras at the waterholes also mirrors other research (Western, 1975; Redfern *et al*., 2005), providing evidence that this species is more water-dependent than other mammal species sighted in this study.

In addition, the frequency of visitation of mammals to both waterholes influenced the abundance of mammals recorded at the waterholes in this study. Zebras and springboks, for instance, were recorded at most sampling sessions at waterholes. This outcome is in line with studies by du Preez and Grobler (1977) and Hayward and Hayward (2012) who reported that zebras and springboks were more water-dependent and thus frequented waterholes more often to meet their water requirements.

Carnivores were recorded at only 2 or 3 sampling sessions in this study, arriving in small groups ($n < 5$) at each visit and thus had an overall low abundance at both waterholes (Table 3). At both waterholes, lions and spotted hyenas were only sighted between 03h00-06h00 and 22h00-01h00. In addition to these sampling sessions, black-backed jackals were also sighted between 17h00-20h00 at both waterholes. Due to their ability to fulfil their water requirements from the body fluids of their prey, carnivores are the subject of numerous papers discussing their water independence (Ayeni, 1975; Hayward & Hayward, 2012). The low frequency of visits to waterholes by carnivores in this study may be explained by their low water-dependence.

The fact that only one individual warthog was spotted at Okaukuejo and their absence at Moringa in this study can be explained by the findings of Butynski and de Jong (2018), who indicated that warthogs have various adaptations to cope with low levels of water. This would mean that warthogs did not need to frequent waterholes to fulfill their water requirements in this study as they can conserve water, for example, by staying in burrows away from the hot sun (de Jong, d’Huart & Butynski, 2023). Bothma (2002) also reported that warthogs consumed low amounts of water daily in his study. In addition, this result could mean that the warthogs around Okaukuejo and Moringa in ENP were less water-dependent, making this observation contrary to Kasiringua, Kopij and Procheş (2017), who reported that warthogs were water-dependent at Waterberg National Park in Namibia.

Giraffes were observed visiting Okaukuejo waterhole every night during this study. Studies have reported that giraffes are less water-dependent as they obtain most of their water from their diet (Skinner & Chimimba, 2005) and that they can survive without drinking for up to four days (Tefempa *et al*., 2008). In line with these studies, it was anticipated that giraffes would not regularly visit waterholes in this study, although this was not the case. Giraffes' daily visits in this study may be due to a decline in browse biomass or low water content of vegetation during the dry season when this study was conducted (Ritter, 1993). A decline in these food sources for giraffes would require them to frequent waterholes more often (Ritter, 1993). In addition, giraffes have been observed to drink more if water is available (Ayeni 1975; du Preez & Grobler 1977), more especially in the dry season.

5.2 Temporal patterns of waterhole usage by mammals.

5.2.1 Diurnal and nocturnal species composition at the waterholes.

There was a temporal differentiation in the use of Okaukuejo and Moringa waterholes by different mammal species. Generally, herbivores in this study mostly visited waterholes during the day (between 07h00-10h00 and 12h00-15h00), with the exception of larger herbivores (Figures 10 and 11). These results are similar to observations reported by Crosmary *et al.* (2012) and Valeix, Chamaillé-Jammes and Fritz (2007). On the contrary, carnivores generally visited waterholes nocturnally (Figures 10 and 11). A similar trend of a low overlap between predators and their prey at waterholes was reported by Sutherland, Ndlovu and Perez-Rodriguez (2018) and Nasanbat, Ceacero and Samiya (2021).

Sutherland, Ndlovu and Perez-Rodriguez (2018) reported an increase in herbivore activity during dusk and dawn hours in their study. Conversely, the only herbivores that were most active during these hours in this study were larger herbivores (elephants and black rhinos). Specifically, small and medium-sized herbivore species (springbok, zebra, oryx, blue wildebeest, black-faced impala, kudu and warthog) mostly visited waterholes during daytime, large herbivores visited both during the day and night (except giraffe), while carnivores visited waterholes nocturnally. These results are similar to observations by du Preez and Grobler (1977) at the same park.

Most small and medium-sized herbivores visited waterholes between 07h00-10h00 and 12h00-15h00, with a peak in activity during 12h00-15h00. This shows that an increase in the levels of activity among these herbivores at the waterholes was during the hottest time of the day. These results are in contrast with those of Kinahan, Pimm and van Aarde (2007) who reported that animals generally spend daytime in shaded areas and avoid being active.

The peak in activity levels observed during hotter daylight hours probably occurred because small and medium-sized herbivores have a higher tolerance for high temperatures, unlike larger herbivores (Ayeni, 1975). Conversely, larger herbivores such as elephants and black rhinos were found to be more active during dusk or nighttime in this study at a time when temperatures were lower, possibly because they are not adapted to withstand high daytime temperatures (Ayeni, 1975).

Herbivores and their potential predators shared the water at the waterholes, significantly increasing the risk of predation at these waterholes. The temporal avoidance of waterholes by prey species at night is probably because of the prey's perceived and actual predation risk, as reported by Valeix *et al*. (2009), Crosmary *et al*. (2012) and Amoroso *et al*. (2020). In this study, predation risk was defined as perceived when there was no sighting of a predator during a sampling session, similar to Embar, Kotler and Mukherjee (2011) and Iranzo *et al*. (2018).

Perceived predation risk was mostly observed at night in this study, when nocturnal predators were most active at waterholes, especially at Moringa waterhole as it was surrounded by taller, thick vegetation. Prey could not easily spot ambush predators due to the dense vegetation (similar to reports by Lima and Dill (1990)) at Moringa waterhole. Predation risk was defined as actual when a predator was sighted during a sampling session, like Creel *et al*. (2017) and Iranzo *et al*. (2018).

In the present study, lions and spotted hyenas were the two main predators at the waterholes. Predators visit waterholes to drink or hunt (Crosmary *et al*., 2012) thereby putting prey, mainly herbivores, at risk of predation. These two carnivores were 100% similar in their strictly nocturnal visitation times to waterholes at Okaukuejo waterhole (Figure 10), and 89% similar at Moringa waterhole (Figure 11). Lions were the largest predator species and they only visited waterholes between 03h00-06h00 and/or 22h00-01h00. Similar findings were reported by Crosmary *et al*. (2012) who recorded 70% to 80% of lion visits at night in their 2012 study in Hwange National Park in Zimbabwe.

Similarities in visitation times between lions and other mammal species were also observed in some nights during the 22h00 – 01h00 sampling session. These similarities only occurred between lions with either elephant, black rhino or cape fox species. Although these mammals visited the waterholes during the same sampling session as lions, they did not overlap in visitation times or share the waterholes with lions. In a study on drinking times and behavior of mammals carried out in ENP, du Preez and Grobler (1977) recorded nocturnal visits to waterholes by rhinos and elephants that occurred during the same time of the night as observed in this study.

Unlike smaller herbivores, larger herbivores have a reduced susceptibility to predation (Valeix *et al*., 2008) and lions, specifically, avoid preying on large herbivores (Dupuis-Desormeaux *et al*., 2015). This explains why nocturnal visits were common among elephants and black rhinos in this study. Elephants visited waterholes during the same sampling session as lions as they are not preyed upon by lions (Hayward *et al*., 2011). Black rhinos, in addition to having large bodies, also displayed aggression at the waterholes, rendering them harder to be preyed on by lions (du Preez & Grobler, 1977; Valeix *et al*., 2009). Although Brain, Forge and Erb (1999) reported on lions killing black rhinos in ENP, this was not observed in this study as these two species only used waterholes during the same sampling session but did not overlap in their actual visitation times.

Where cape fox and lion species visited Moringa waterhole during the same sampling session (22h00-01h00), there was no overlap in the visitation times between these two species. Interestingly, giraffes only visited Okaukuejo waterhole at night during the following times: 03h00-06h00, 17h00-20h00 and 22h00-01h00 in this study. This is despite reports that giraffes are highly vulnerable to lion predation (Ferry, Dray & Fritz, 2016; Muneza *et al*., 2021) especially while drinking at waterholes. This means that the risk of interference competition between giraffes and other herbivores which visited Okaukuejo waterhole in large herds during the day outweighed the risk of predation by lions at night.

Giraffes probably need more space and less disturbance while drinking due to their splay-legged drinking posture, which can render them vulnerable to interference competition with other herbivores during the day when waterholes are crowded (Valeix *et al*., 2008; Ferry, Dray & Fritz, 2016). To avoid this overcrowding, giraffes therefore possibly preferentially chose nocturnal visits, where there was no crowding at the waterhole (Figure 9).

Most animal predation occurs close to a waterhole (Valeix *et al*., 2009). Therefore, other ungulate species perhaps did not visit the waterholes at night when lions were around as a predator-avoidance strategy. In the present study, kudu, a preferred prey for lions (Loveridge *et al*., 2007; Valeix *et al*., 2009) completely avoided nocturnal visitations to both waterholes. Other species that were strictly daytime visitors at the waterholes were blue wildebeest, warthog and black-faced impala (at Okaukuejo), and oryx and springbok (at Moringa). There was only one individual oryx (n = 1) recorded at Moringa waterhole throughout the study, between 12h00-15h00. Hayward and Kerley (2005) report that oryx are among the preferred prey for lions, hence oryx may have avoided Moringa waterhole as it was surrounded by dense vegetation, increasing the predation risk to lions.

The only one individual warthog recorded in this study was sighted between 12h00-15h00 at Okaukuejo waterhole. The fact that this species was sighted only once and during the day is likely attributed to the warthog's tendency to spatially avoid areas that are frequented by its predators, such as lions (Thaker *et al*., 2011). Habitats with a higher risk of predation, including both closed and open riverine areas are typically avoided by warthogs (Thaker *et al*., 2011). Consequently, warthogs are often found in burrows for protection against predators (de Jong, d'Huart & Butynski, 2023).

Spotted hyena, another large carnivore sighted in this study, overlapped with black rhino, black-backed jackal and elephant species in visitation times at Okaukuejo waterhole. These mammal species are possibly not easy prey for spotted hyenas since they are either large-bodied and aggressive (elephants and black rhinos) (Valeix *et al*., 2008; Hayward *et al*., 2011) or also carnivores (black-backed jackal). At Moringa waterhole, spotted hyenas did not overlap with any other mammals in waterhole visitation times. Mammal species avoided this waterhole when spotted hyenas were in the vicinity to avoid these cursorial, pursuit predators (Crosmary *et al*., 2012) who do not show prey species preference (Hayward, 2006). Although Moringa waterhole was surrounded by dense vegetation, other mammal species could probably detect the presence of spotted hyenas due to their loud vocalizations, which can be carried over long distances (Lehmann *et al*., 2022).

The significant time intervals between the spotted hyenas' departure and the arrival of other mammal species at the waterhole indicates that, as spotted hyenas are also cursorial predators (Crosmary *et al*., 2012), potential prey stayed away from the waterhole until these predators were at a considerable distance from it. Spotted hyenas showed 100% similarity in waterhole visitation trends with cape fox species at Moringa waterhole (Figure 11), where both species were observed at night between 03h00-06h00, 17h00-20h00 and 22h00-01h00.

5.2.2 Daytime species overlaps at the waterholes.

Ungulates showed either a differentiation in their visitation time or species overlap in waterhole usage. Kudu, blue wildebeest, and black-faced impala species overlapped at Okaukuejo waterhole and showed 100% similarity in their waterhole visitation times (between 07h00 – 10h00 and 12h00 – 15h00) (Figure 10). These species also overlapped with zebra and springbok species, which visited Okaukuejo waterhole at all the sampling sessions, as well as oryx species, which were sighted at all but one sampling session (03h00 – 06h00).

At Moringa waterhole, kudu and springbok showed 100% similarity in their waterhole visitation times (07h00 – 10h00 and 12h00 – 15h00) (Figure 11), where they often overlapped at the waterhole. These herbivores also overlapped with zebras, which visited Moringa waterhole during the same time periods (80% similarity), although zebras also visited the waterhole between 17h00 – 20h00. Kudu and springbok also overlapped with oryx at Moringa waterhole, although, as already stated, only one individual oryx was sighted.

Compared to the oryx species abundance at Okaukuejo waterhole (*n* = 117), the only individual oryx sighted and recorded at Moringa shows that this waterhole was not frequented by this species. Since there are other waterholes around Moringa waterhole (Figure 1), with the closest waterhole being Naumses about 8 km away (Google Maps), oryx may frequent these other waterholes instead of Moringa. Considering the vegetation surrounding this waterhole, this avoidance of Moringa was possibly driven by predator avoidance.

Overlapping visitation times at the waterholes among herbivores helped the mammals to minimize their risk of predation. Mammal species such as zebra, blue wildebeest, black-faced impala and springbok visited waterholes in large herds in this study, with the largest herd recorded belonging to zebras ($n = 75$). When different herbivorous species with large herds congregate at the waterholes, the "group size effect" comes into play, whereby the predation risk of an individual mammal is reduced (Kamilar, Bribiescas & Bradley, 2010).

In addition, individual herbivores within a large group could use the "selfish herd effect" (Hamilton, 1971; Olson, Knoester & Adami, 2016) at the waterholes, whereby they would position themselves away from predators within the group to reduce their risk of predation. Inter-species group overlaps at the waterholes also yield the benefit of increased vigilance, allowing mammals more time to drink and forage around the waterhole (Ayeni, 1975; Beauchamp, 2019).

A differentiation in the visitation time was also observed among herbivore species, where different species showed a preferred visitation time to waterholes. This temporal partitioning probably was a strategy that helped in reducing interference competition between and among species at the waterholes, as noted by various studies (Edwards, Gange & Wiesel, 2015; Amoroso *et al.*, 2020; Ferry *et al.*, 2020). Interference competition among herbivores probably intensified during afternoon sampling sessions (12h00-15h00), since most mammals (66%) visited both waterholes during this session (Figure 9). Both interspecific and intraspecific aggression behaviors, such as kicking and pursuing, provided evidence for this interference competition. Additionally, some mammals were observed fleeing the waterholes probably because of this competition.

Mammal species that overlapped in their waterhole usage times utilized different sections of the waterhole, probably to avoid interference competition.

Carnivore species in this study also showed temporal partitioning in their waterhole visitation times at night, possibly to avoid encounters and conflict. Edwards, Gange, and Wiesel (2015) observed a similar result between eight carnivore species at waterholes in commercial farmlands in Namibia. These carnivores showed differences in their visitation times to waterholes, where carnivore species with larger differences in body size showed the biggest differences in visitation time.

5.3 Duration of mammal stay at Okaukuejo and Moringa waterholes.

Comparison of differences in the duration of mammal stay between Okaukuejo and Moringa waterholes showed that three out of the ten mammal species that were recorded at both waterholes stayed significantly longer at Okaukuejo waterhole. These species were elephant, springbok and spotted hyena. Therefore, the null hypothesis that the duration which different mammal species stayed at Okaukuejo and Moringa waterholes is not significantly different is rejected. The other 7 species that also visited both waterholes (black rhino, lion, zebra, oryx, kudu, black-faced impala and black-backed jackal) did not show significant differences in their duration of stay between Okaukuejo and Moringa waterholes (Figure 12).

In this study, black rhino, elephants and giraffes stayed significantly longer at the Okaukuejo waterhole than other mammal species (Figure 12). At Moringa waterhole, the duration of mammal stay was significantly higher in black rhinos and elephants than other species (Figure 12). Black rhinos, elephants and giraffes spent an average duration of 40 minutes, 52 minutes and 31 minutes respectively at Okaukuejo waterhole. At Moringa waterhole, black rhinos spent an average of 27 minutes and elephants spent an average of 22 minutes.

Elephants stayed significantly longer than other species at both waterholes drinking, resting, playing with water, mud and sandbathing, nurturing their young and interacting with other elephants, similar to observations by Polansky, Kilian and Wittemyer (2015). In addition, elephants often monopolized waterholes, especially at nighttime. This was possibly to maximize their access to water when other species or even other elephants when not present and thus avoid both interspecific and intraspecific competition for water (Ferry, Dray & Fritz, 2016). The longer stay at Okaukuejo than Moringa waterhole by elephants suggests that elephants were more involved in the various behaviors at Okaukuejo, possibly because more elephants visited Okaukuejo waterhole (Table 3).

In addition, elephants may have spent longer time at waterholes in order to optimize their access to less-contaminated water. It was observed during this study that elephants that stayed longer at waterholes, particularly at night, took their time drinking cleaner water located near the feeding pipes or troughs of the waterholes, rather than from the waterholes themselves. Studies have reported that elephants employ various strategies in order to access less-contaminated water for drinking (Ramey *et al*., 2013; Ndlovu *et al*., 2018).

The artificial waterholes probably had low water quality due to the high populations of mammals that visited throughout the day (Table 3). Some mammal species were seen drinking while immersed inside the water (e.g. oryx and zebra species) or digging inside the waterholes, mud-bathing and swimming (e.g. elephants). According to Ndlovu *et al*. (2018) and Amoroso *et al*. (2019), digging may introduce soil-borne contaminants, while swimming or immersion into water may introduce feacal contaminants.

Black rhinos also spent extensive periods drinking, grazing and resting at the waterholes. In addition, the large body size and feeding guild of elephants, black rhinos and giraffes may require them to consume more water to meet their high-water requirements (Reid *et al*., 2007; Gaugris & Rooyen, 2010; Hayward & Hayward, 2012). Giraffes, on the other hand, spent longer periods at Okaukuejo waterhole in vigilance activities and approaching the waterhole, with minimal time spent drinking since they are more vulnerable to predation while drinking because of their drinking posture (Valeix *et al*., 2008; Ferry, Dray & Fritz, 2016).

At Okaukuejo waterhole, black-faced impala, blue wildebeest, kudu, springbok, oryx and zebra species spent on average 9, 15, 12, 11, 12 and 13 minutes respectively at the waterhole. Black-faced impala and zebra species spent an average of 7 minutes and 9 minutes respectively at Moringa waterhole. The duration spent by these ungulates is probably because of interference competition among the species, resulting in partitioning of the time spent using waterholes (Edwards, Gange, & Wiesel, 2015; Amoroso *et al*., 2020; Ferry *et al*., 2020). This was necessary because many different ungulates visited waterholes during similar sampling sessions as already discussed in section 5.2 above.

When comparing the two waterholes, the significantly longer duration of stay at Okaukuejo than Moringa waterhole for springboks seems to have been influenced by the overall higher species abundance of these species, as well as other mammal species at Okaukuejo (Table 3). This higher species abundance at Okaukuejo meant that some springboks individuals had to wait for their turn to drink as mammals shared the waterhole, and that more time was spent in other activities at the waterhole, such as aggressive behavior.

Carnivorous species: cape fox, spotted hyena and black-backed jackal also showed statistically significant differences in the duration of stay at the waterholes with other species. Black-backed jackals showed statistically significant differences with 5 species at Okaukuejo waterhole: springbok, zebra, blue wildebeest, oryx and kudu. At Moringa waterhole, cape fox and spotted hyena species showed statistically significant differences with zebras and black-faced impalas.

Black-backed jackals spent 4 minutes on average at Okaukuejo waterhole, while cape fox species spent an average of 4 minutes at Moringa waterhole. These carnivorous species were observed rushing to waterholes, drinking quickly, and disappearing into the surrounding vegetation. Cape foxes can be killed by larger carnivores such as black-backed jackals (Kamler *et al*., 2012), while black-backed jackals can be preyed upon or killed by larger carnivores such as lions (Stander, 1992). The short duration of time spent by these carnivores means that they visited waterholes solely to drink, avoiding predation or conflict with larger carnivores.

Spotted hyenas spent short amounts of time at Moringa waterhole (average 3 minutes), which was also the shortest amount of time spent by any species in this study at either waterhole. Conversely, they spent an overall average of 8 minutes at Okaukuejo waterhole, thus showing statistically significant differences in their duration of stay between the two waterholes. Spotted hyenas, which visited waterholes at nighttime, possibly did not stay long at Moringa waterhole due to the physical attributes of this waterhole. Since Moringa waterhole was surrounded by dense vegetation, this increased the risk of intra-guild predation and conflict with lions that could conceal themselves in the vegetation to ambush hyenas. Unlike Okaukuejo waterhole, it was possibly not easy to spot lions approaching the waterhole from a distance at Moringa. Intraguild predation, where lions kill hyenas and conflict between the two species have been reported by several studies (Trinkel & Kastberger, 2005; Périquet, Fritz & Revilla, 2014). As a result, spotted hyenas minimized the amount of time spent at Moringa by running into the waterhole, drinking quickly and fleeing the waterhole.

5.4 Duration of mammal stay at different times of the day.

Statistical tests showed that mammals stayed significantly longer at Okaukuejo waterhole between 22h00 – 01h00 than 12h00 – 15h00. At Moringa waterhole, statistical tests showed a significantly shorter duration of mammal stay between 03h00 – 06h00 than 07h00 – 10h00, 12h00 – 15h00 and 22h00 – 01h00. The null hypothesis that stated that the time of day does not significantly affect the duration which mammals stayed at Okaukuejo and Moringa waterholes is therefore rejected.

Mammals collectively spent the longest time at each waterhole between 22h00 – 01h00. This is probably because this time was favored by elephants, black rhinos and giraffes (at Okaukuejo waterhole), which spent longer time at waterholes. Elephants and black rhinos usually monopolized both waterholes between 22h00 – 01h00 during this study. Elephants, black rhinos and giraffes spent the longest time at Okaukuejo waterhole during 22h00 – 01h00 with an average duration of stay of 69 minutes, 44 minutes and 31 minutes respectively. Black rhinos spent the longest time during 22h00 – 01h00 at Moringa waterhole, with an average duration of stay of 31 minutes.

Elephants and black rhinos spent a lot of time at the waterholes since they did not only visit waterholes for drinking. Elephants displayed other behaviors during 22h00 – 01h00 such as resting, playing with water, and interacting with each other, similar to behaviors observed by Valeix, Chamaillé-Jammes and Fritz (2007). Black rhinos were observed drinking, grazing and resting at the waterholes between 22h00 – 01h00. These primarily nocturnal visits by black rhinos to waterholes are in line with Gurung and Chalise’s (2015) report which stated that black rhinos are more active during the night.

Moreover, black rhinos and elephants probably favored 22h00 – 01h00 for drinking and resting at the waterholes since fewer mammals visited the waterholes at this time (4% of all individual mammals in this study), thus reducing chances of sharing the waterhole with other species. In addition, these two species have been known to assert dominance in waterholes to maximize their access to water (Ogutu & Owen-Smith, 2003; Valeix, Chamaillé-Jammes & Fritz, 2007). Giraffes, as already discussed above, spent the majority of time between 22h00 – 01h00 at Okaukuejo waterhole in vigilance and approaching the waterhole.

Other herbivores who were observed between 22h00 – 01h00 were only observed at Okaukuejo waterhole and not Moringa waterhole. These herbivores did not, on the contrary, spend a long time at this waterhole. These herbivores were oryx, springboks and zebras (spending on average 12 minutes, 6 minutes and 5 minutes) at Okaukuejo waterhole. It is assumed that the physiological needs of these herbivores for drinking water at the waterhole outweighed their need to avoid predation with these nocturnal visits, therefore they ensured that their visits were short, only spending just enough time for vigilance and drinking. Herbivores were observed to shift their visitation time into the night during moonlit nights by Ayeni (1975). Similarly, since Okaukuejo waterhole was open and illuminated at night, herbivores probably had a better chance to detect predators from a distance (Crosmary *et al*., 2012) and thus could risk night visits.

Carnivores also spent minimal time at the waterholes between 22h00-01h00, quickly drinking and leaving the waterholes. It was expected that large carnivores (lions and spotted hyenas) would linger around waterholes for long periods waiting for prey, however this was not the case in this study. As already stated earlier in this paper, these carnivores possibly supplemented their water requirements from the blood of their prey (Ayeni, 1975) and thus did not require much drinking. In addition, lions, which often drank in haste at the waterholes, were probably in a hurry to hunt in the vicinity of the waterholes as reported by Valeix *et al*. (2010) and thus spent minimal time drinking to increase their hunting success. This possible hunting by lions close to the waterhole likely influenced the short time spent drinking by spotted hyenas, in order to prevent intra-guild predation and conflict (Périquet, Fritz & Revilla, 2014).

Mammals collectively spent the least amount of time at Okaukuejo waterhole between 12h00 – 15h00. Since this was the hottest time of the day, mammals probably avoided extensive exposure to the hot sun (like reports by Terrien, Perret and Aujard (2011)) as there was no shade in the piosphere in this waterhole. This observation is also supported by Valeix *et al.* (2008) who reported that mammals reduce exposure to the sunlight by drinking for shorter periods during hotter periods of the day.

In addition, the drinking time for certain species e.g. black-faced impala decreased between 12h00 – 15h00, when they were sharing the waterhole with more aggressive or dominant species such as zebras and elephants, similar to observations by Valeix *et al*. (2008). These results are in contrast with reports by Rispel and Lendelvo (2016), who stated that the length of stay of animals at waterholes increases with a higher population and bigger group sizes.

At Moringa waterhole, mammals collectively spent the least amount of time between 03h00 – 06h00. This was as expected, since this was the sampling session that was least visited by mammals at the waterholes (Figure 9). Mammal species that visited Moringa waterhole between 03h00 – 06h00 during the study were black rhino, black-backed jackal, black-faced impala, cape fox, elephant, lion and spotted hyena (Table 4.2). Of these species, carnivorous species (black-backed jackal, cape fox and spotted hyena) spent the shortest time at the waterhole (an average of 3 or 4 minutes) as shown in Table 4.2. As already discussed in 5.2 above, these carnivores probably spent little time at the waterhole to avoid conflict or ambush by larger carnivores such as lions, which could easily conceal themselves in the dense vegetation surrounding Moringa waterhole.

Black-faced impalas were the only antelopes that visited Moringa waterhole between 03h00 – 06h00, spending an average 2 minutes, sufficient for only vigilance and drinking. Perceived predation risk was probably the biggest factor influencing this short time spent by black-faced impala drinking at Moringa waterhole during this sampling session. This result supports a report by Valeix *et al.* (2008) that stated that perceived predation risk reduces the time spent by mammals at a waterhole.

5.5 Behavior of mammals at Okaukuejo and Moringa waterholes.

Twelve out of the 13 behaviors displayed by mammals were observed at both waterholes, except for courtship behavior, which was observed only at Moringa waterhole. Of the 13 different behaviors, 10 behaviors occurred at a higher frequency at Okaukuejo than at Moringa waterhole (Figure 13, Appendix 9). It is suggested that the need for water, predation risk as well as interspecific and intraspecific competition were the main factors that may have influenced the behaviors of mammals in this study. Vigilance was the most observed behavior among mammals; accounting for 44% of all behaviors in this study (Figure 13, Appendix 9). This behavior was observed in all species in this study, although some species showed more vigilance than others.

More vigilant species at the waterholes included giraffe, black-backed jackal, spotted hyena and cape fox. Members of these species visited waterholes nocturnally and mostly in solitude, only rarely arriving in small groups of 2 – 4 individuals. This shows that vigilance was also influenced by group size in this study, supporting Elgar’s (1989) and Beauchamp’s (2019) reports on "group size effect" on vigilance, which states that individual vigilance increases as the group size of animals decreases. This is because when group sizes are large, individual mammals in the group rely on each other for vigilance (Ayeni, 1975; Fortin *et al*., 2004). Mammal species that visited waterholes in large groups and thus showed less vigilance included springbok and wildebeest (similar to duPreez & Gobler, 1977), zebra and black-faced impala.

Vigilance was observed in herbivorous mammals when they were approaching waterholes, as well as when they were drinking water in this study. Vigilance is crucial in avoiding predators and competitors (Pays *et al*., 2011). As already discussed, giraffes spent more time in vigilance activities than they did drinking at Okaukuejo waterhole, most likely to avoid predation at the waterhole. The highest average duration of stay for giraffes was 34 minutes between 22h00 – 01h00 (Table 4.1) in this study. In certain instances, where the physiological requirements of the giraffes for drinking water was possibly over-ridden by their need to escape predation, giraffes were observed leaving Okaukuejo waterhole without drinking.

Giraffes exhibited vigilant behavior as they cautiously made their way towards the waterhole, advancing slowly with intermittent pauses to survey their surroundings. Once at the water's edge, they continued to scan the area before quenching their thirst. Giraffes spent as long as 40 minutes just scanning the area. This vigilance was then followed by a short period of drinking, the shortest recorded being 4 minutes in this study. Giraffes displayed heightened vigilance at waterholes because their height and splay-legged posture while drinking prevents them from reacting quickly to escape from predators (Valeix *et al*., 2008; Ferry, Dray & Fritz, 2016). Elephants only showed more vigilance at the waterholes in this study when juveniles were present in the herd, like observations by Valeix *et al*. (2008).

Yarnell *et al*. (2013) discuss, in their study, how black-backed jackals are negatively impacted by the presence of large carnivores in their vicinity. This observation is supported by the behavior of black-backed jackals and cape foxes in this study, who were very vigilant, possibly to avoid encounters and attacks by lions and spotted hyenas. Spotted hyenas also showed more vigilance in this study probably to reduce potential confrontations with other carnivores such as lions, as well as to ensure that there were no other species to compete with them while accessing water.

Vigilance behavior in spotted hyenas was also reported by other researchers (Meter *et al*., 2009; Krag *et al*., 2023). Spotted hyenas used vigilance behaviors in combination with vocalizations, which they use when they are threatened or as a signal of the presence of food (Lehmann *et al*., 2022). Lions, which were the biggest predators in this study also showed some vigilance, probably because they were scanning the area for potential prey.

Besides giraffes, other herbivores e.g. springbok and zebra displayed more vigilant behavior at night, since the risk of encountering nocturnal predators such as lions was higher at nighttime. This observation aligns with results reported by Ruble *et al*. (2022) who observed prolonged vigilance by ungulates such as kudu, impala and springbok to waterholes in the presence of a predator.

Studies have shown that vigilance can also increase due to high species diversity (Pallieres & Rose, 2023). This was observed in this study, where some herbivore species e.g. oryx displayed vigilance during the day, especially between 12h00 – 15h00 when many species shared waterholes (Figures 11, 12 and 13). Herbivores displayed high vigilance during the day mostly when arriving at the waterholes alone or in small groups. This vigilance possibly occurred so that competitors would be easier to detect and evade, since species such as springboks and zebras congregated in large herds at waterholes.

Aggression was the behavior with the second highest frequency of occurrence (18%) in this study (Figure 13; Appendix 9). This behavior was observed in black rhino, black-faced impala, elephant, giraffe, oryx, spotted hyena, springbok and zebra species. The species that showed the most interspecific and intraspecific aggression at the waterholes were black rhinos and zebras, while elephants showed interspecific aggression. Among black rhinos, aggression was observed within the same species and with elephants at the waterholes. These solitary animals (Schwabe *et al*., 2015) did not take well to having company at the waterholes, often responding with grunting, stomping the ground, or even charging at other mammals at the waterholes.

The findings of this research align with the report by Ogutu and Owen-Smith (2003), which stated that black rhinos displayed aggression towards other species, particularly elephants and buffalos, at waterholes. Although on a few occasions black rhinos were observed charging at or approaching other species at the waterholes in the present study, this aggressive behavior has been reported as not primarily intended to hinder other mammals from drinking, but rather to establish dominance at the waterholes and ensure sufficient access to water (Ogutu & Owen-Smith, 2003).

Zebras, which often approached waterholes in large herds, were also very aggressive to other species, as well as towards conspecifics. A similar observation where zebras were aggressive at the waterholes was reported by du Preez and Grobler (1977) at the same park (ENP). Zebras were observed running into the waterholes during the day, scattering other ungulates away from the water. While drinking, some zebras kicked or chased after individuals of the same or different species, driving them away from the water. This behavior is influenced by interspecific and intraspecific competition at the waterhole and is seen to maximize the time spent accessing water.

Elephants were also aggressive at the waterholes, especially when in large herds with juveniles and young present. During this study, it was noted that when elephant herds with young made their way to waterholes, the bulls took the lead in approaching the waterholes. On certain occasions, they would also pursue and trumpet, causing other species to flee from the water and the waterhole itself. This behavior was to establish dominance at the waterhole (Ogutu & Owen-Smith, 2003; Valeix, Chamaillé-Jammes & Fritz, 2007), eliminate competition, while also protecting the juveniles in the herd from potential harm. This was essential to increase access to the water due to the overcrowding of waterholes throughout the day, particularly in the afternoon as already discussed. Elephants' aggressive behavior at waterholes was also documented by Valeix, Chamaillé-Jammes and Fritz (2007). Similar to the findings of this study, the presence of elephants was observed to drive certain herbivores away from the waterhole.

Elephants that visited waterholes at night often came in smaller herds or individually, showing less aggression. These elephants were observed drinking mostly closer to the feeding pipe or trough of the waterholes, resting and splashing with water, allowing other mammals to share the waterholes by drinking from other sections. Similar instances of spatial partitioning in waterhole usage between elephants and other species were reported by Valeix *et al*. (2008) and Ferry *et al*. (2020). Aggression observed in other species in this study occurred at a smaller extent.

Although the primary role of waterholes is to provide water for mammals, mammals were also involved in many other activities at and around waterholes that were not related to the acquisition of water (Figure 13). Many social interactions were observed, including nurturing the young, courtship, foraging, as well as playful behavior. Nurturing behavior was among the least observed behaviors at waterholes (1%) (Figure 13, Appendix 9) and it was displayed by black-faced impalas when grooming their young. Elephants also demonstrated nurturing behavior at the waterholes, safeguarding their offspring, splashing them with water or mud and assisting them with rolling on the sand probably for protection against the intense sunlight.

Courtship behavior was observed among herds of black-faced impalas and elephants at Moringa waterhole. Foraging behavior was observed among many herbivore species at the waterholes, including black rhino, black-faced impala, blue wildebeest, elephant, oryx, springbok, warthog and zebra. Most mammals were observed engaging in foraging activities near the waterholes after drinking, with the exception of the single warthog documented in this research. Interestingly, this warthog was observed digging around Okaukuejo waterhole without approaching the water. The consequences of this foraging behavior were clear, resulting in noticeable alterations and depletion of vegetation surrounding the waterholes, similar to observations by Mukaru and Mapaure (2012). This impact was particularly pronounced at the Okaukuejo waterhole, which possessed a substantial piosphere. The extensive vegetation loss in the vicinity of this waterhole was further exacerbated by the fact that it catered to a large number of mammals (Table 3), attracting numerous herds of herbivores simultaneously.

In addition, mammals at the waterholes exhibited playful behavior, engaging in activities like playfully chasing, running around, jumping, and kicking. This behavior was prominently seen at Okaukuejo waterhole, with species such as black rhinos, elephants, oryx, springboks, and zebras partaking in these playful antics. Additionally, at Moringa waterhole, black-faced impalas and zebras were observed engaging in playful behavior as well.

Given the high competition at a shared waterhole and close proximity to conspecifics, play may help to prevent conflict by diffusing aggression in a non-threatening manner (Palagi, Paoli, & Borgognini, 2006). This is particularly relevant for species like elephants and rhinos, who were seen being more aggressive at the waterholes. Among younger individuals, play was likely used to assess competitive ability of others and form dominance relationships in a relatively safe context (Peterson & Flanders, 2005). For mammals that arrived in herds at the waterholes like zebras, springboks, oryx and black-faced impalas, play likely strengthened group cohesion and facilitated smoother interactions during sharing of water (Palagi, 2010).

Black rhinos, blue wildebeests, elephants, lions and springboks were seen resting at Okaukuejo waterhole after drinking, often returning to the waterhole to drink more. The same behavior was observed in black rhinos, black-faced impalas and zebras at Moringa waterhole. This resting behavior at waterholes probably occurred due to various reasons. Firstly, some mammals could have been tired due to travelling for long distances to the waterhole and therefore needed to rest in between or after drinking. Another reason could be that mammals were waiting for their turn to drink (or to drink again), and not necessarily resting, as waterholes were often crowded during daytime (Figure 9). Mammals waiting for their turn to drink at waterholes were observed when more aggressive species, such as elephants, were present at the waterholes. The same behavior of mammal species waiting for elephants to leave before moving in to drink is reported by Castelda *et al*. (2010).

Moreover, mammals may have been waiting at waterholes to maximize their access to water. Elephants are one species that spent extensive periods at Okaukuejo waterhole at dusk and nighttime, drinking, with intermittent periods of resting. This behavior probably helped elephants to also avoid intraspecific competition during daytime, when elephant abundance was high at the waterhole. This behavior by elephants is similar to observations by Ferry, Dray and Fritz (2016).

In addition to these behaviors, elephants were also seen mud-bathing and sandbathing at the waterholes in the afternoon or dusk. Mud-bathing and sandbathing was also observed by Leggett (2009) in elephants in northwest Namibia, while sandbathing was observed by Rees (2002) in captive Asian elephants. Mud-bathing and sandbathing helps elephants with evaporative heat loss (Dunkin *et al*., 2013) and is thus a means of thermoregulation during high temperatures. These behaviors may also yield health benefits for elephants such as skin care and help these mammals avoid ectoparasites (Rees, 2002; Oliveira *et al*., 2020).

Running into the waterhole was a behavior observed among black-backed jackal, black-faced impala, blue wildebeest, spotted hyena and zebra species. This behavior occurred either to avoid predation risk by spending little time at the waterholes; because mammals were very thirsty when they arrived at the waterholes; or to intimidate other species that were already at the waterholes. The first explanation is mostly applicable to black-backed jackals and spotted hyenas in this study, since it correlates to their short duration of stay at the waterholes. The last explanation applied more to zebras, black-faced impalas and blue wildebeest since they usually arrived at waterholes between 12h00-15h00, when waterholes were crowded (Figure 9).

Running out of the waterhole occurred when mammals were disturbed while drinking but did not leave the waterhole and later returned to continue drinking. This occurred mostly within large herds such as zebras, oryx, blue wildebeests and springboks, potentially due to the threat of interference competition e.g. when elephants arrived in big groups at the waterholes. Although in certain instances elephants may cause disturbances at waterholes by intimidating or displacing other species (Ferry, Dray and Fritz, 2016), these species do not intentionally prevent others from drinking (Valeix *et al*., 2008; Ferry *et al*., 2020). This may explain why, in some instances, mammal species that initially ran away when elephants arrived at the waterholes later returned to resume drinking. These species and elephants then shared the waterholes, maintaining spatial partitioning by drinking from different sections.

Running off the waterhole occurred when mammals would flee the waterhole due to disturbance, and not return to the waterhole. This behavior mostly occurred at repeated disturbances, or when a more dominant, aggressive species (e.g. elephants) arrived at the waterhole. Elephants displacing other species was also reported by Valeix *et al*. (2008); Ferry, Dray and Fritz (2016) and Ferry *et al*. (2020). Species that were observed fleeing waterholes included black-backed jackal, black-faced impala, kudu, oryx, spotted hyena, springbok and zebra. Other behaviors displayed by mammals included urinating or rubbing of the body against a tree around the waterhole. These were among the least observed behaviors at the waterholes (1% of behaviors observed).

Out of the 13 behaviors recorded, 10 occurred at a higher frequency at Okaukuejo waterhole since this waterhole was visited by more species, and it also had a higher species abundance. When more mammals congregate in the same area around a shared resource such as water, it is expected that they will engage in a variety of behaviors to maximize their access to the water, while also minimizing the risk of predation. Interestingly, although predation risk seemed to be influencing the behaviors of most mammal species in this study, actual predation was not observed at the waterholes.

CHAPTER 6: CONCLUSIONS AND RECOMMENDATIONS

6.1 Conclusions

This study compared the activity patterns, usage, and behavior of mammals at Okaukuejo and Moringa artificial waterholes. Results showed a significant difference in mammal species richness between the two waterholes with cape fox, giraffe, blue wildebeest, and warthog species showing exclusive visitation to one waterhole. The null hypothesis that the species richness of mammals that visited the Okaukuejo and Moringa waterholes was not significantly different was therefore rejected. Differences in the species richness and composition of mammals sighted at the two waterholes may have been influenced by many factors including but not limited to the differences in size, location, flora and predation risk at each waterhole.

Zebras and springboks were the most abundant species at waterholes, suggesting that these two species were more water-dependent than other mammal species in this study. This also confirmed previous reports of the two species being the most abundant at ENP. Mammals were also more abundant at Okaukuejo waterhole, which was larger in size and hence could accommodate larger herds of mammals at a time.

A low overlap in visitation times was observed between predators and prey mammal species at the waterholes, with prey species mostly visiting during daytime, while predators visited at night. Ungulates visited waterholes mainly during the day, showing either a differentiation in their visitation time or species overlaps in waterhole usage. Overall, mammals mostly favored 12h00-15h00 and least favored 03h00-06h00 in their waterhole visits. Temporal differentiation in waterhole usage among mammals seemed to be driven by predation risk, interference competition and the need for water.

The duration of stay of mammals was significantly higher at Okaukuejo than at Moringa waterhole for elephants, springboks and spotted hyenas. Among the mammal species, the duration of stay was significantly higher in black rhinos, elephants and giraffes at Okaukuejo waterhole than other mammal species. Elephants and black rhinos stayed significantly higher than other mammal species at Moringa waterhole. Therefore, the null hypothesis that the duration which different mammal species stayed at Okaukuejo and Moringa waterholes was not significantly different was rejected. Mammals stayed significantly longer at each waterhole between 22h00 – 01h00, and they stayed significantly shorter between 12h00 – 15h00 at Okaukuejo waterhole and between 03h00 – 06h00 at Moringa waterhole. The null hypothesis that the time of day did not significantly affect the duration which mammals stayed at Okaukuejo and Moringa waterholes was therefore rejected. These differences occurred because of differences in the activities of mammal species at the waterholes at the different times.

In this study, mammals displayed a wide range of behaviors at the two waterholes that included much more than just drinking water. Among 13 different types of behaviors observed, vigilance had the highest frequency of occurrence, followed by aggression. Behaviors observed in this study occurred at a higher frequency at Okaukuejo than at Moringa waterhole. Behaviors of mammals observed were most probably driven by predation risk and competition among and between species.

6.2 Recommendations

This study is important in animal ecology as it provides insights into how environmental factors and ecological pressures shape mammalian activity and behavior at artificial waterholes. The research highlights how variables such as waterhole location, size, surrounding vegetation, predation risk and interference competition influence species-specific visitation patterns and temporal water use.

The observed behaviors, especially vigilance and aggression, reflect key ecological interactions like predation avoidance and competition at waterholes. These findings deepen our understanding of how artificial water sources affect wildlife ecology in arid ecosystems and can inform more ecologically informed waterhole management strategies. The findings are also useful in the conservation of mammal species, such as giraffe, cape fox, blue wildebeest, oryx and spotted hyena who showed preferential visitation to only one waterhole in this study.

It is recommended that future research should be coupled with testing of water quality parameters at each waterhole in order to study the association between variation of water quality and abundance, richness and composition of mammals that visit the waterholes. This will contribute to explaining the observed variations in mammal visitations, species distribution and behaviors at the waterholes.

The period of data collection in the present study was short due to financial constraints and manpower. Future research should include a broader range of waterholes across different habitat types and locations to enhance comparative analysis. Studies carried out over longer periods and with repeated observations of mammals is also recommended. This will generate more representative data that will reflect the reality of activity patterns, abundance, richness and composition of mammal species at waterholes. Additionally, incorporating information on the home ranges, habitat use, and overall abundance of mammal species around waterholes in ENP would help to explain observed variations in species richness and composition more accurately.

Future research should consider the influence of anthropogenic factors such as artificial lighting, human presence, and waterhole proximity to infrastructure on mammalian waterhole usage, particularly for more elusive or shy species. In addition, studies should specifically investigate the effects of tourism by comparing waterholes located near tourism sites with those in more undisturbed areas. Incorporating these variables will provide a more comprehensive understanding of how human activities shape mammal behavior and distribution at artificial water sources.

Moreover, weather parameters such as temperature, humidity, precipitation, air pressure, wind speed and wind direction should also be recorded at each sampling session at waterholes to better explain differences in behaviour and distribution of mammals at the waterholes. Lastly, since artificial waterholes are primarily constructed to provide water to animals during periods of water shortage, it is recommended that data is collected seasonally at waterholes. This will help in determining if there is seasonal variation in the usage of the waterholes and therefore the extent to which these artificial waterholes are required by mammals. ENP managers can then make better informed decisions concerning the construction or closure of artificial waterholes in the park.

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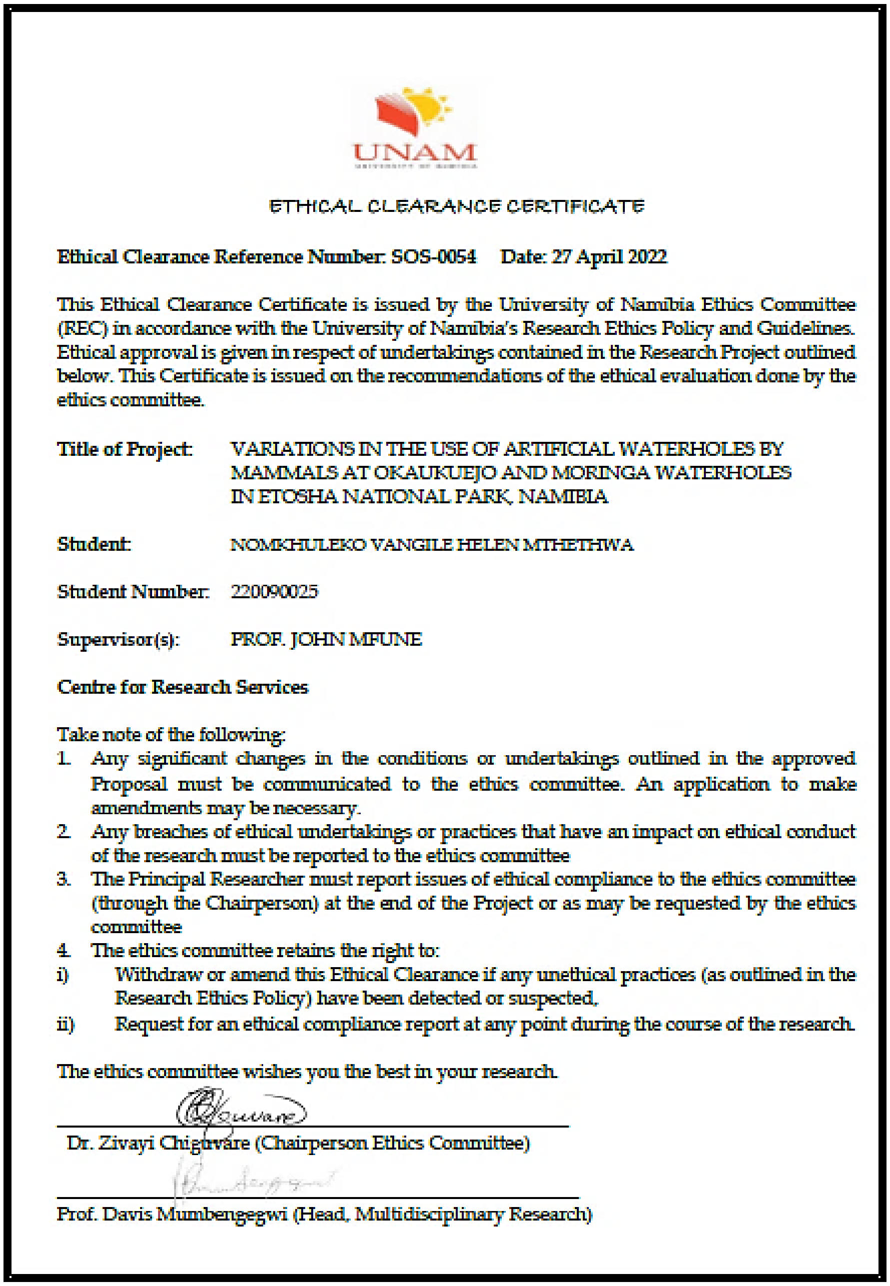
APPENDICES

Appendix 1: Research Project Ethical Clearance Certificate.



UNAM

ETHICAL CLEARANCE CERTIFICATE

Ethical Clearance Reference Number: SOS-0054 Date: 27 April 2022

This Ethical Clearance Certificate is issued by the University of Namibia Ethics Committee (REC) in accordance with the University of Namibia's Research Ethics Policy and Guidelines. Ethical approval is given in respect of undertakings contained in the Research Project outlined below. This Certificate is issued on the recommendations of the ethical evaluation done by the ethics committee.

Title of Project: VARIATIONS IN THE USE OF ARTIFICIAL WATERHOLES BY MAMMALS AT OKAUKUEJO AND MORINGA WATERHOLES IN ETOSHA NATIONAL PARK, NAMIBIA

Student: NOMKHULEKO VANGILE HELEN MTHETHWA

Student Number: 220090025

Supervisor(s): PROF. JOHN MFUNE

Centre for Research Services

Take note of the following:

1. Any significant changes in the conditions or undertakings outlined in the approved Proposal must be communicated to the ethics committee. An application to make amendments may be necessary.
2. Any breaches of ethical undertakings or practices that have an impact on ethical conduct of the research must be reported to the ethics committee
3. The Principal Researcher must report issues of ethical compliance to the ethics committee (through the Chairperson) at the end of the Project or as may be requested by the ethics committee
4. The ethics committee retains the right to:

i) Withdraw or amend this Ethical Clearance if any unethical practices (as outlined in the Research Ethics Policy) have been detected or suspected,

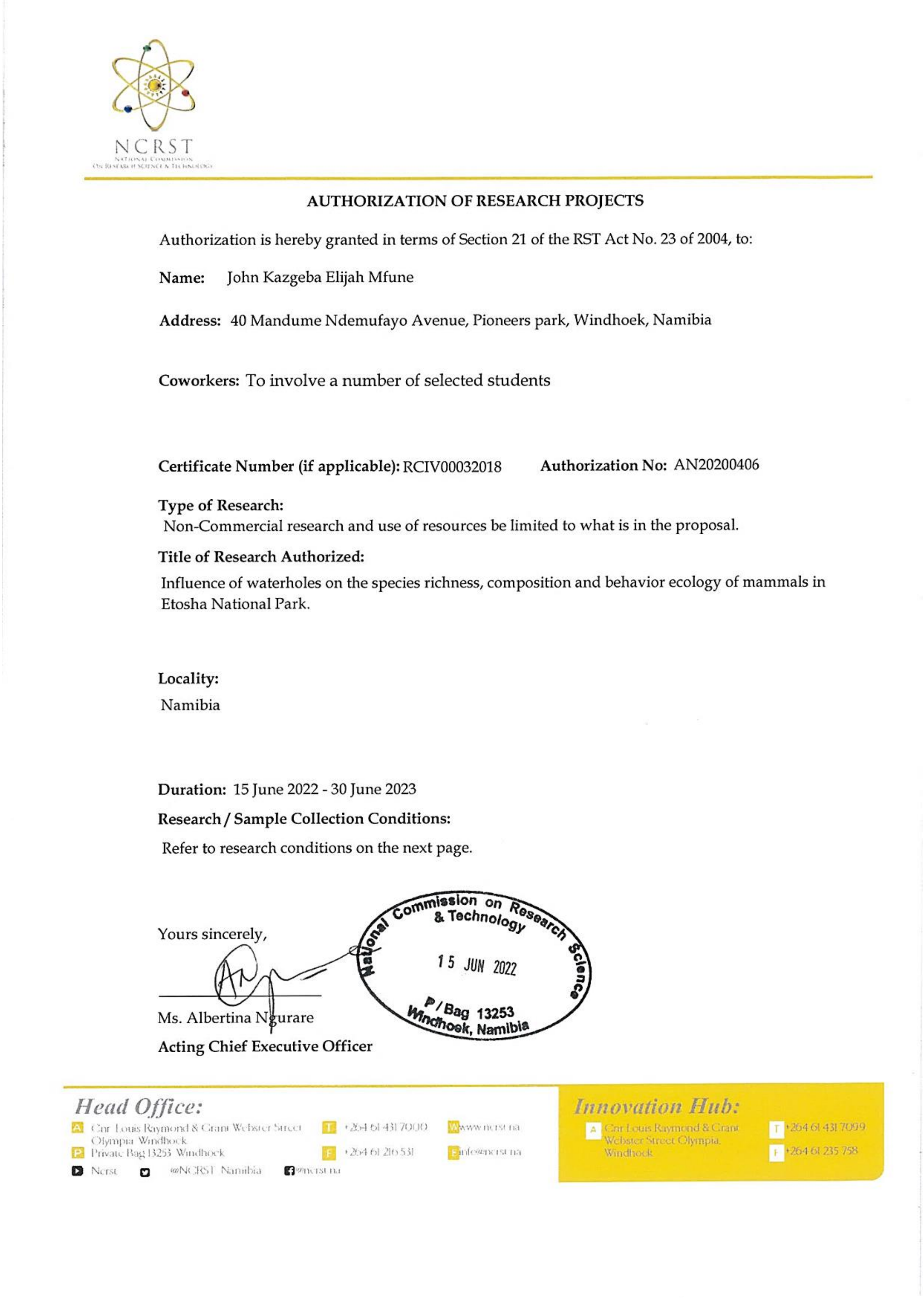
ii) Request for an ethical compliance report at any point during the course of the research.

The ethics committee wishes you the best in your research.

Dr. Zivayi Chiguvare (Chairperson Ethics Committee)

Prof. Davis Mumbengegwi (Head, Multidisciplinary Research)

Appendix 2: Research Permit by National Commission for Research Science and Technology (NCRST).



NCRST
National Commission
on Research Science & Technology

AUTHORIZATION OF RESEARCH PROJECTS

Authorization is hereby granted in terms of Section 21 of the RST Act No. 23 of 2004, to:

Name: John Kazgeba Elijah Mfune

Address: 40 Mandume Ndemufayo Avenue, Pioneers park, Windhoek, Namibia

Coworkers: To involve a number of selected students

Certificate Number (if applicable): RCIV00032018 **Authorization No:** AN20200406

Type of Research:
Non-Commercial research and use of resources be limited to what is in the proposal.

Title of Research Authorized:
Influence of waterholes on the species richness, composition and behavior ecology of mammals in Etosha National Park.

Locality:
Namibia

Duration: 15 June 2022 - 30 June 2023

Research / Sample Collection Conditions:
Refer to research conditions on the next page.

Yours sincerely,

15 JUN 2022
P/Bag 13253
Windhoek, Namibia

Ms. Albertina Ngurare
Acting Chief Executive Officer

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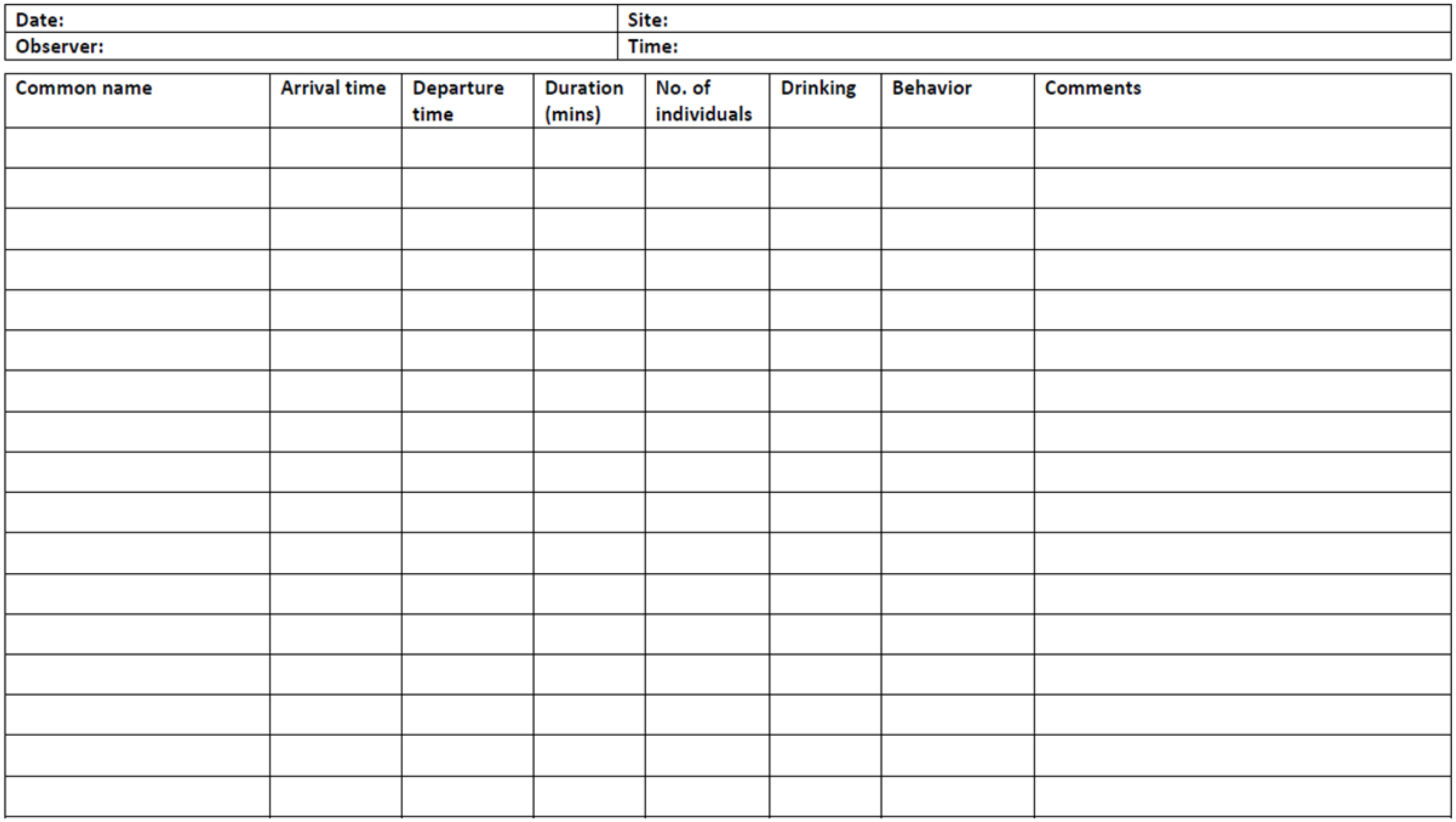
Appendix 3: Field data sheet used to collect data at the waterholes.



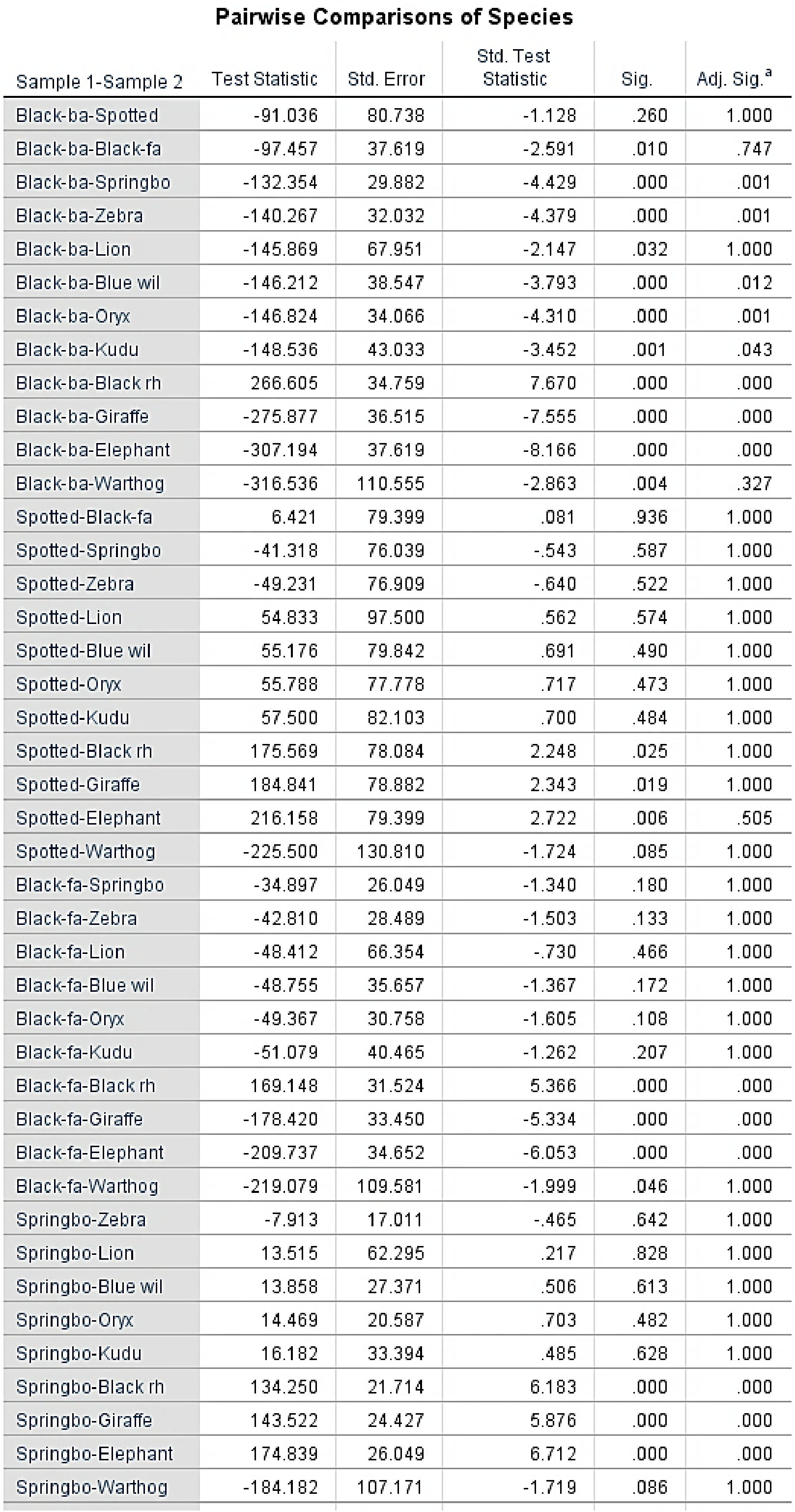
Date:	**Site:**
Observer:	**Time:**

Common name	**Arrival time**	**Departure time**	**Duration (mins)**	**No. of individuals**	**Drinking**	**Behavior**	**Comments**

Appendix 4: Mammal species richness recorded at Moringa and Okaukuejo waterholes in Etosha National Park during the study period in July 2022. Ok 1 – Ok 4 = Okaukuejo sampling cycles 1 to 4, Mor 1 – Mor 4 = Moringa sampling cycles 1 to 4.

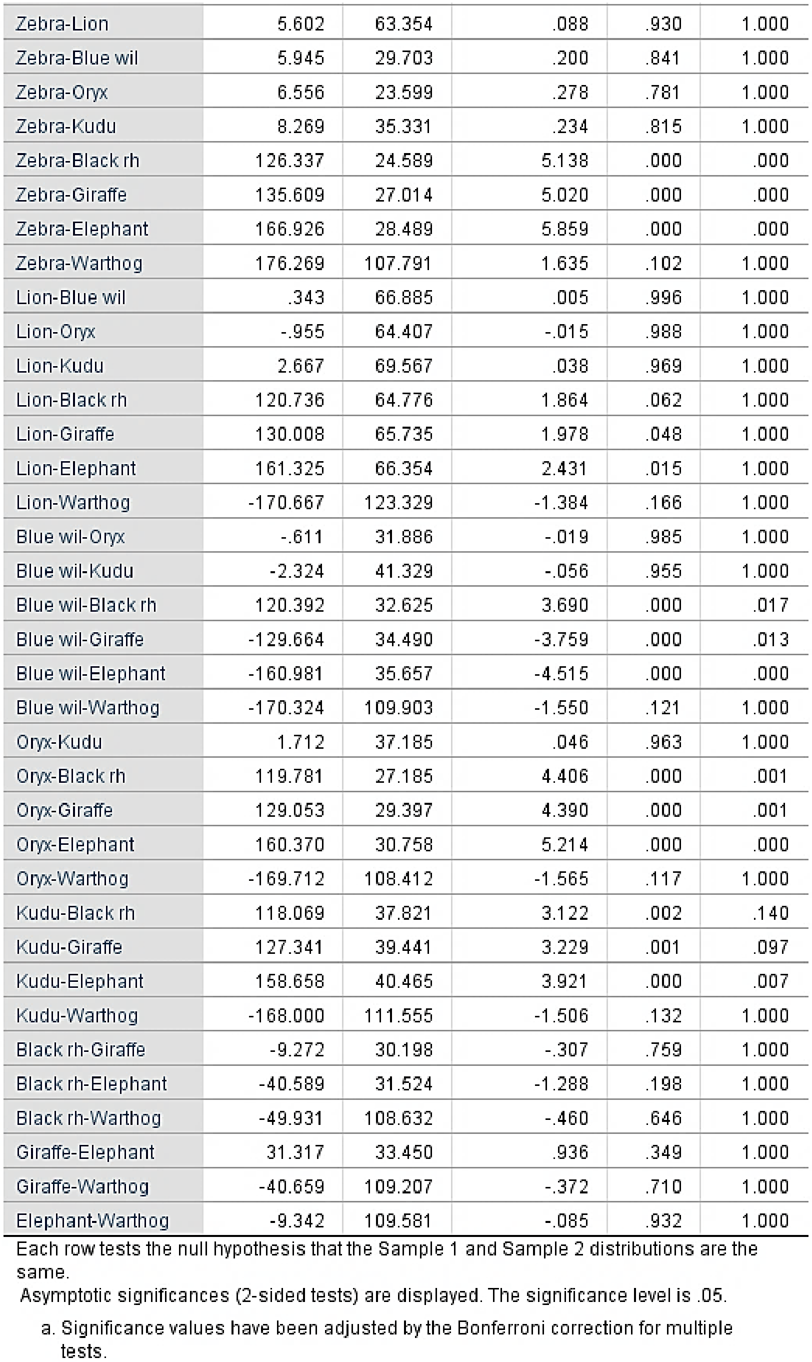
Time session	**Ok 1**	**Ok 2**	**Ok 3**	**Ok 4**	**Mor 1**	**Mor 2**	**Mor 3**	**Mor 4**
03h00-06h00	5	5	6	8	4	4	5	4
07h00-10h00	3	5	4	2	4	3	3	3
12h00-15h00	3	6	6	7	3	3	5	3
17h00-20h00	6	6	8	6	5	3	3	1
22h00-01h00	4	4	6	4	4	2	3	1

Appendix 5: Post hoc test results for duration of mammal stay among different species at Okaukuejo waterhole.



Pairwise Comparisons of Species

Sample 1-Sample 2	Test Statistic	Std. Error	Std. Test Statistic	Sig.	Adj. Sig.^{a}
Black-ba-Spotted	-91.036	80.738	-1.128	.260	1.000
Black-ba-Black-fa	-97.457	37.619	-2.591	.010	.747
Black-ba-Springbo	-132.354	29.882	-4.429	.000	.001
Black-ba-Zebra	-140.267	32.032	-4.379	.000	.001
Black-ba-Lion	-145.869	67.951	-2.147	.032	1.000
Black-ba-Blue wil	-146.212	38.547	-3.793	.000	.012
Black-ba-Oryx	-146.824	34.066	-4.310	.000	.001
Black-ba-Kudu	-148.536	43.033	-3.452	.001	.043
Black-ba-Black rh	266.605	34.759	7.670	.000	.000
Black-ba-Giraffe	-275.877	36.515	-7.555	.000	.000
Black-ba-Elephant	-307.194	37.619	-8.166	.000	.000
Black-ba-Warthog	-316.536	110.555	-2.863	.004	.327
Spotted-Black-fa	6.421	79.399	.081	.936	1.000
Spotted-Springbo	-41.318	76.039	-.543	.587	1.000
Spotted-Zebra	-49.231	76.909	-.640	.522	1.000
Spotted-Lion	54.833	97.500	.562	.574	1.000
Spotted-Blue wil	55.176	79.842	.691	.490	1.000
Spotted-Oryx	55.788	77.778	.717	.473	1.000
Spotted-Kudu	57.500	82.103	.700	.484	1.000
Spotted-Black rh	175.569	78.084	2.248	.025	1.000
Spotted-Giraffe	184.841	78.882	2.343	.019	1.000
Spotted-Elephant	216.158	79.399	2.722	.006	.505
Spotted-Warthog	-225.500	130.810	-1.724	.085	1.000
Black-fa-Springbo	-34.897	26.049	-1.340	.180	1.000
Black-fa-Zebra	-42.810	28.489	-1.503	.133	1.000
Black-fa-Lion	-48.412	66.354	-.730	.466	1.000
Black-fa-Blue wil	-48.755	35.657	-1.367	.172	1.000
Black-fa-Oryx	-49.367	30.758	-1.605	.108	1.000
Black-fa-Kudu	-51.079	40.465	-1.262	.207	1.000
Black-fa-Black rh	169.148	31.524	5.366	.000	.000
Black-fa-Giraffe	-178.420	33.450	-5.334	.000	.000
Black-fa-Elephant	-209.737	34.652	-6.053	.000	.000
Black-fa-Warthog	-219.079	109.581	-1.999	.046	1.000
Springbo-Zebra	-7.913	17.011	-.465	.642	1.000
Springbo-Lion	13.515	62.295	.217	.828	1.000
Springbo-Blue wil	13.858	27.371	.506	.613	1.000
Springbo-Oryx	14.469	20.587	.703	.482	1.000
Springbo-Kudu	16.182	33.394	.485	.628	1.000
Springbo-Black rh	134.250	21.714	6.183	.000	.000
Springbo-Giraffe	143.522	24.427	5.876	.000	.000
Springbo-Elephant	174.839	26.049	6.712	.000	.000
Springbo-Warthog	-184.182	107.171	-1.719	.086	1.000



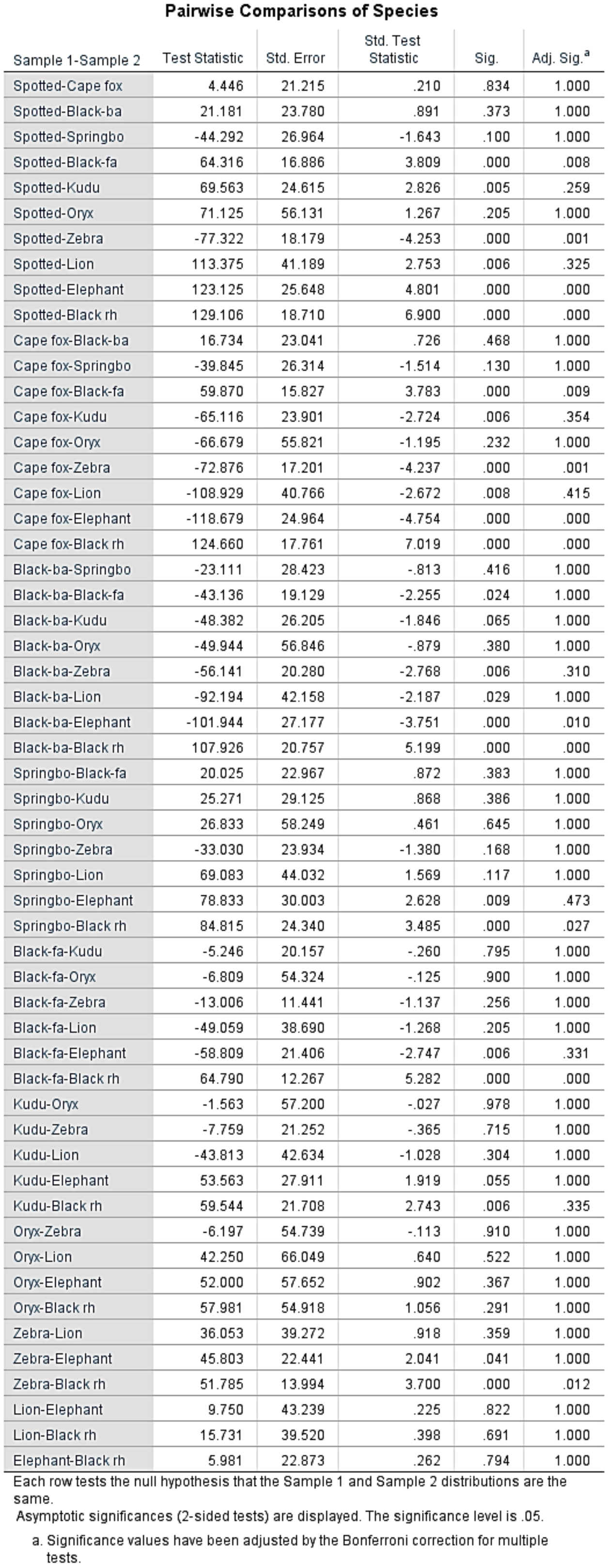
Zebra-Lion	5.602	63.354	.088	.930	1.000
Zebra-Blue wil	5.945	29.703	.200	.841	1.000
Zebra-Oryx	6.556	23.599	.278	.781	1.000
Zebra-Kudu	8.269	35.331	.234	.815	1.000
Zebra-Black rh	126.337	24.589	5.138	.000	.000
Zebra-Giraffe	135.609	27.014	5.020	.000	.000
Zebra-Elephant	166.926	28.489	5.859	.000	.000
Zebra-Warthog	176.269	107.791	1.635	.102	1.000
Lion-Blue wil	.343	66.885	.005	.996	1.000
Lion-Oryx	-.955	64.407	-.015	.988	1.000
Lion-Kudu	2.667	69.567	.038	.969	1.000
Lion-Black rh	120.736	64.776	1.864	.062	1.000
Lion-Giraffe	130.008	65.735	1.978	.048	1.000
Lion-Elephant	161.325	66.354	2.431	.015	1.000
Lion-Warthog	-170.667	123.329	-1.384	.166	1.000
Blue wil-Oryx	-.611	31.886	-.019	.985	1.000
Blue wil-Kudu	-2.324	41.329	-.056	.955	1.000
Blue wil-Black rh	120.392	32.625	3.690	.000	.017
Blue wil-Giraffe	-129.664	34.490	-3.759	.000	.013
Blue wil-Elephant	-160.981	35.657	-4.515	.000	.000
Blue wil-Warthog	-170.324	109.903	-1.550	.121	1.000
Oryx-Kudu	1.712	37.185	.046	.963	1.000
Oryx-Black rh	119.781	27.185	4.406	.000	.001
Oryx-Giraffe	129.053	29.397	4.390	.000	.001
Oryx-Elephant	160.370	30.758	5.214	.000	.000
Oryx-Warthog	-169.712	108.412	-1.565	.117	1.000
Kudu-Black rh	118.069	37.821	3.122	.002	.140
Kudu-Giraffe	127.341	39.441	3.229	.001	.097
Kudu-Elephant	158.658	40.465	3.921	.000	.007
Kudu-Warthog	-168.000	111.555	-1.506	.132	1.000
Black rh-Giraffe	-9.272	30.198	-.307	.759	1.000
Black rh-Elephant	-40.589	31.524	-1.288	.198	1.000
Black rh-Warthog	-49.931	108.632	-.460	.646	1.000
Giraffe-Elephant	31.317	33.450	.936	.349	1.000
Giraffe-Warthog	-40.659	109.207	-.372	.710	1.000
Elephant-Warthog	-9.342	109.581	-.085	.932	1.000

Each row tests the null hypothesis that the Sample 1 and Sample 2 distributions are the same.

Asymptotic significances (2-sided tests) are displayed. The significance level is .05.

a. Significance values have been adjusted by the Bonferroni correction for multiple tests.

Appendix 6: Post hoc test results for duration of mammal stay among different species at Moringa waterhole.



Pairwise Comparisons of Species

Sample 1-Sample 2	Test Statistic	Std. Error	Std. Test Statistic	Sig.	Adj. Sig.^{a}
Spotted-Cape fox	4.446	21.215	.210	.834	1.000
Spotted-Black-ba	21.181	23.780	.891	.373	1.000
Spotted-Springbo	-44.292	26.964	-1.643	.100	1.000
Spotted-Black-fa	64.316	16.886	3.809	.000	.008
Spotted-Kudu	69.563	24.615	2.826	.005	.259
Spotted-Oryx	71.125	56.131	1.267	.205	1.000
Spotted-Zebra	-77.322	18.179	-4.253	.000	.001
Spotted-Lion	113.375	41.189	2.753	.006	.325
Spotted-Elephant	123.125	25.648	4.801	.000	.000
Spotted-Black rh	129.106	18.710	6.900	.000	.000
Cape fox-Black-ba	16.734	23.041	.726	.468	1.000
Cape fox-Springbo	-39.845	26.314	-1.514	.130	1.000
Cape fox-Black-fa	59.870	15.827	3.783	.000	.009
Cape fox-Kudu	-65.116	23.901	-2.724	.006	.354
Cape fox-Oryx	-66.679	55.821	-1.195	.232	1.000
Cape fox-Zebra	-72.876	17.201	-4.237	.000	.001
Cape fox-Lion	-108.929	40.766	-2.672	.008	.415
Cape fox-Elephant	-118.679	24.964	-4.754	.000	.000
Cape fox-Black rh	124.660	17.761	7.019	.000	.000
Black-ba-Springbo	-23.111	28.423	-.813	.416	1.000
Black-ba-Black-fa	-43.136	19.129	-2.255	.024	1.000
Black-ba-Kudu	-48.382	26.205	-1.846	.065	1.000
Black-ba-Oryx	-49.944	56.846	-.879	.380	1.000
Black-ba-Zebra	-56.141	20.280	-2.768	.006	.310
Black-ba-Lion	-92.194	42.158	-2.187	.029	1.000
Black-ba-Elephant	-101.944	27.177	-3.751	.000	.010
Black-ba-Black rh	107.926	20.757	5.199	.000	.000
Springbo-Black-fa	20.025	22.967	.872	.383	1.000
Springbo-Kudu	25.271	29.125	.868	.386	1.000
Springbo-Oryx	26.833	58.249	.461	.645	1.000
Springbo-Zebra	-33.030	23.934	-1.380	.168	1.000
Springbo-Lion	69.083	44.032	1.569	.117	1.000
Springbo-Elephant	78.833	30.003	2.628	.009	.473
Springbo-Black rh	84.815	24.340	3.485	.000	.027
Black-fa-Kudu	-5.246	20.157	-.260	.795	1.000
Black-fa-Oryx	-6.809	54.324	-.125	.900	1.000
Black-fa-Zebra	-13.006	11.441	-1.137	.256	1.000
Black-fa-Lion	-49.059	38.690	-1.268	.205	1.000
Black-fa-Elephant	-58.809	21.406	-2.747	.006	.331
Black-fa-Black rh	64.790	12.267	5.282	.000	.000
Kudu-Oryx	-1.563	57.200	-.027	.978	1.000
Kudu-Zebra	-7.759	21.252	-.365	.715	1.000
Kudu-Lion	-43.813	42.634	-1.028	.304	1.000
Kudu-Elephant	53.563	27.911	1.919	.055	1.000
Kudu-Black rh	59.544	21.708	2.743	.006	.335
Oryx-Zebra	-6.197	54.739	-.113	.910	1.000
Oryx-Lion	42.250	66.049	.640	.522	1.000
Oryx-Elephant	52.000	57.652	.902	.367	1.000
Oryx-Black rh	57.981	54.918	1.056	.291	1.000
Zebra-Lion	36.053	39.272	.918	.359	1.000
Zebra-Elephant	45.803	22.441	2.041	.041	1.000
Zebra-Black rh	51.785	13.994	3.700	.000	.012
Lion-Elephant	9.750	43.239	.225	.822	1.000
Lion-Black rh	15.731	39.520	.398	.691	1.000
Elephant-Black rh	5.981	22.873	.262	.794	1.000

Each row tests the null hypothesis that the Sample 1 and Sample 2 distributions are the same.

Asymptotic significances (2-sided tests) are displayed. The significance level is .05.

a. Significance values have been adjusted by the Bonferroni correction for multiple tests.

Appendix 7: Post hoc test results for duration of mammal stay at Okaukuejo waterhole at different times of the day.

Pairwise Comparisons of Time

Sample 1-Sample 2	Test Statistic	Std. Error	Std. Test Statistic	Sig.	Adj. Sig.[a]
12h00-15h00-03h00-06h00	5.648	21.714	.260	.795	1.000
12h00-15h00-07h00-10h00	16.312	13.864	1.177	.239	1.000
12h00-15h00-17h00-20h00	-33.886	19.658	-1.724	.085	.848
12h00-15h00-22h00-01h00	-56.277	16.578	-3.395	.001	.007
03h00-06h00-07h00-10h00	-10.664	22.526	-.473	.636	1.000
03h00-06h00-17h00-20h00	-28.238	26.489	-1.066	.286	1.000
03h00-06h00-22h00-01h00	-50.629	24.291	-2.084	.037	.371
07h00-10h00-17h00-20h00	-17.574	20.552	-.855	.392	1.000
07h00-10h00-22h00-01h00	-39.966	17.628	-2.267	.023	.234
17h00-20h00-22h00-01h00	-22.391	22.472	-.996	.319	1.000

Each row tests the null hypothesis that the Sample 1 and Sample 2 distributions are the same.

Asymptotic significances (2-sided tests) are displayed. The significance level is .05.

a. Significance values have been adjusted by the Bonferroni correction for multiple tests.

Appendix 8: Post hoc test results for duration of mammal stay at Moringa waterhole at different times of the day.

Pairwise Comparisons of Time

Sample 1-Sample 2	Test Statistic	Std. Error	Std. Test Statistic	Sig.	Adj. Sig.[a]
03h00-06h00-17h00-20h00	-46.004	16.413	-2.803	.005	.076
03h00-06h00-12h00-15h00	-48.075	13.797	-3.485	.000	.007
03h00-06h00-07h00-10h00	-52.240	15.292	-3.416	.001	.010
03h00-06h00-22h00-01h00	-63.995	15.917	-4.021	.000	.001
17h00-20h00-12h00-15h00	2.071	12.394	.167	.867	1.000
17h00-20h00-07h00-10h00	6.236	14.040	.444	.657	1.000
17h00-20h00-22h00-01h00	-17.990	14.718	-1.222	.222	1.000
12h00-15h00-07h00-10h00	4.165	10.866	.383	.702	1.000
12h00-15h00-22h00-01h00	-15.919	11.729	-1.357	.175	1.000
07h00-10h00-22h00-01h00	-11.755	13.456	-.874	.382	1.000

Each row tests the null hypothesis that the Sample 1 and Sample 2 distributions are the same.

Asymptotic significances (2-sided tests) are displayed. The significance level is .05.

a. Significance values have been adjusted by the Bonferroni correction for multiple tests.

Appendix 9: Frequency of occurrence (f) and percentage of observations (%) at each waterhole of different types of behaviors displayed by mammals at Moringa and Okaukuejo waterholes in Etosha National Park in July 2022.

Behavior	**Okaukuejo**		**Moringa**		**Total**
	f	%	f	%	**%**
Vigilance	120	70	51	30	**44**
Aggression	40	57	30	43	**18**
Resting	17	77	5	23	**6**
Playful	16	70	7	30	**6**
running out	16	94	1	6	**4**
Foraging	12	60	8	40	**5**
running off	12	55	10	45	**6**
mud/sand bathing	5	71	2	29	**2**
running in	4	44	5	56	**2**
Nurturing	3	75	1	25	**1**
walking around	2	29	5	71	**2**
Other	2	67	1	33	**1**
Courtship	0	0	10	100	**3**
Total	**249**	65	**136**	35	**100**