

**Impact of interspecific competition on African wild dogs
(*Lycaon pictus*) in an ecosystem with artificial
perennial water provision**



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“This special moment when you see African wild dogs in the wild for the first time in your life, and they are in a waterhole!”

(Zimbabwe, 12 of May 2021)

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Abstract

Interspecific competition with large predators affects African wild dogs through food resource competition, exclusion from prey rich areas, kleptoparasitism, injury, mortality, den site selection, and human landscape exposure. Waterhole distance and density can work as surrogates on prey aggregation and abundance, which in turn these resources attract large dominant predators. Subordinate smaller predators, such as African wild dogs, have to balance the trade-off between resource acquisition and the risk of encountering large predators. My aim is to determine how African wild dogs cope with the competition with larger dominant predators (mainly lions and spotted hyaenas - hyaenas) in a semi-arid ecosystem with artificial water provision: Hwange National Park (HNP), Zimbabwe. In HNP, during the dry season the only water available for animals is mainly found in artificial waterholes, which makes this area ideal to perform this research. First, I evaluated the food resource competition of African wild dogs with competing predators (cheetahs, leopards, lions and hyaenas) in different seasons and across areas with different waterhole densities, using predators scats to analyse diet composition, diet comparisons, diet overlap, niche breadth, and prey preference (Chapter 2). Secondly, I assessed the level of kleptoparasitism risk for African wild dogs from lions and hyaenas in areas with different waterhole densities and at different distances from waterholes (0 and 5 km away), using playback experiments simulating African wild dog kills and analysing the data with hurdle models (Chapter 3). Thirdly, I evaluated if African wild dogs avoid large competing predators (leopards, lions and hyaenas) reactively or proactively in space and time

at different spatial and temporal scales, using camera trap data to perform generalized linear mixed models, activity pattern overlap and time-to-event analyses (Chapter 4). Finally, I discussed water management strategies to help decrease the level of interspecific competition on African wild dogs and assist in their conservation (Chapter 5). My main results show that: a) prey conservation mainly in low waterhole density areas is crucial to decrease food resource competition between African wild dogs with large predators (Chapter 2); b) areas with too high waterhole densities increased the kleptoparasitism risk on African wild dogs and hence the risk of agonistic encounters with dominant predators through an increase on the number of dominant predators arriving at playback locations (Chapter 3); c) African wild dogs preferred temporal partitioning over spatial partitioning to avoid large predators, and African wild dogs were able to co-occur in areas (rich in prey) with high aggregation and density of dominant predators as long as there were enough permanent waterhole densities (at least ~ 0.01 waterholes per km^2) and not too high hyaena densities (above ~ 14 hyaenas/100 km^2) (Chapter 4). Specifically to decrease the interspecific competition intensity of African wild dogs with larger predators, it is important that there are areas with enough permanent waterholes (at least ~ 0.01 waterholes per km^2) during the late dry season, but to also limit the number of artificial waterholes created in high waterhole density areas (above ~ 0.03 waterholes per km^2) (Chapter 5). A heterogeneous water management system is recommended. This study is relevant to the overarching conservation work in areas with water provisioning as a conservation management tool.

Declaration of authorship

I declare that this thesis was composed by myself and that it is primarily my work (analyses and writing are my own). The conception was collaborative and the individual authors are specified in each chapter.

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Chapter 1

General introduction

Interspecific competition

Competition involves direct or indirect interaction between co-occurring organisms that share a common and limited resource (e.g. water, food, shelter), and that through this interaction lowers the fitness of the organisms involved (Begon et al. 2006). When competition occurs between different species it is called interspecific competition (Tilman 1987; Begon et al. 2006; Lourenço et al. 2014). This competition can affect population dynamics, community structure and ecosystem functioning (Linnell & Strand 2000; Clare et al. 2016; Davis et al. 2018). Interspecific competition can be divided in exploitative (i.e. indirect competition for a common resource through depletion of this resource) and interference competition (i.e. direct competition, including aggressive encounters, kleptoparasitism, competitive killing and intraguild predation) (Amarasekare 2002; Lourenço et al. 2014; Tilman 1982).

Sympatric species have evolved behavioural and morphological adaptations to reduce interspecific competition (Turner 1990; Hunter & Caro 2008). An example of this is that carnivores that overlap the most in their geographical range are more different in their carnassial tooth length, which is an indicator of resource partitioning (Davies et al. 2007). To promote coexistence and reduce interspecific competition, animals can adjust their ecological requirements through behavioural changes (e.g. diet choice, habitat use, activity patterns), and consequently, reduce their niche overlap with competitive species in one or more dimensions (e.g. diet, space, time) (Schoener 1974; Amarasekare 2003; Davis et al. 2018).

Additionally to interspecific competition, resource availability (e.g. water, food, shelter) has an influence on species behavioural adaptations (Dupuch et al. 2009; Carter & Linnell 2016). Exploitative and interference competition are widespread interactions that occur in a large number of carnivores species (Linnell & Strand 2000; Caro & Stoner 2003; Donadio & Buskirk 2006; Davis et al. 2018), and especially interspecific competitive killing is common among carnivores as they are well adapted to kill vertebrate prey (Donadio & Buskirk 2006). Relative body size can influence the dynamics of interspecific competition among carnivores; for instance, occurrence of interactions is more common in carnivores with intermediate differences in their body size (2-5.4 times the mass of the victim) and with similar diet (Polis et al. 1989; Donadio & Buskirk 2006). As such, competition with or predation by larger carnivores (dominant species) affects the distribution, behaviour, and ultimately abundance of smaller carnivores (subordinate species), which have to balance resource availability with the risk of encountering larger competing carnivores (Woodroffe et al. 1997; Vanak et al. 2013).

The risk of encountering larger dominant carnivores carry costs (e.g. physical injury, stress) for subordinate carnivores even when the interspecific competition killing is null (Creel & Christianson 2008; Ritchie & Johnson 2009). Thus, subordinate carnivores need to choose the best behavioural adaptation strategy that maximizes benefits and reduces costs (Carter & Linnell 2016; Creel 2018; Sévêque et al. 2020). For example in canids, coyotes and red foxes (both subordinate species) can fluctuate their behavioural adaptations depending on the

level of prey availability and risk of encounters with wolves (dominant species) (Atwood & Gese 2010; Haswell et al. 2018).

Besides balancing prey availability with the risk of encountering dominant carnivores, subordinate carnivores also need to outweigh the risk of human disturbances (Carter & Linnell 2016; Sévêque et al. 2020). Due to anthropogenic impacts, there is a reduction in habitat availability for animals, and in turn, a reduction in spatial niche overlap among carnivores which can affect their interspecific competition dynamics (Woodroffe & Ginsberg 1998; Van der Meer et al. 2013a; Sévêque et al. 2020).

Interspecific competition with larger dominant carnivores can reduce the density of subordinate species or even exclude them completely from specific areas, and in turn, influence their population viability (Linnell & Strand 2000; Swanson et al. 2014). Therefore, interspecific competition knowledge should be incorporated into conservation planning (Harihar et al. 2011; Boron et al. 2023; Strampelli et al. 2023). This is especially important for subordinate and endangered carnivores (Caro & Stoner 2003; Woodroffe & Sillero-Zubiri 2012; Vanak et al. 2013).

The case of the African wild dog

One carnivore that suffers a high level of interspecific competition with larger carnivores is the African wild dog (*Lycaon pictus*) (hereafter: wild dog) (~22 kg), especially African lions (*Panthera leo*) (hereafter: lions) (150-250 kg), and spotted hyaenas (*Crocuta crocuta*) (~70 kg) (hereafter: hyaenas) (Woodroffe & Sillero-Zubiri 2012; Vanak et al. 2013). Wild dogs have disappeared from most of their original range (extirpated from ~93% of their original range). Once distributed across most of the sub-Saharan Africa, except probably absent from lowland rainforest and driest deserts, they are now mainly found in the south and west of Africa, with the largest populations remaining in southern Africa (IUCN 2024). Thus, wild dogs are an endangered species whose population is in decline worldwide (with only 1,409 mature individuals left) (Woodroffe and Sillero-Zubiri 2012, IUCN 2024). They are particularly vulnerable to habitat loss, retaliatory killing and killing from snares, road kills, diseases (such as rabies and canine distemper), prey depletion, and interspecific competition (Woodroffe & Sillero-Zubiri 2012; Creel et al. 2024).

Wild dogs are social canids that form packs of 3 to 30 individuals, and live in low densities with home ranges ranging from 260 to 950 km² (Mills & Gorman 1997; Creel & Creel 1998, 2002; Woodroffe 2011; Pomilia et al. 2015). They live in a variety of habitat types, from savannahs, forests, bushlands, and grasslands from 0 to 4000 m.a.s.l. (Woodroffe & Sillero-Zubiri 2012). They are excellent hunters that are able to hunt large prey (~160 kg) due to their cooperative hunting system (Creel & Creel 2002). Their diet across the continent mainly includes Greater kudu

(*Tragelaphus strepsiceros*) (~160 kg), Thomson's gazelle (*Gazella thomsonii*) (~25 kg), impala (*Aepyceros melampus*) (~60 kg), bushbuck (*Tragelaphus scriptus*) (~35 kg), and nyala (*Tragelaphus angasii*) (~65 kg) (Creel & Creel 2002; Hayward et al. 2006).

Wild dogs are obligatory cooperative breeders and hunters, where normally only the alpha pair reproduces and all the other members of the pack help to rear the pups by babysitting and regurgitating food (Malcolm & Marten 1982; Creel & Creel 2002). They breed once a year (normally in April-July), giving birth to 1 to 15 pups (Malcolm & Marten 1982; Fuller et al. 1992; Creel & Creel 2002). Offspring are born in a den at the onset of the dry season, and stay at the den for around 3 months (Malcolm & Marten 1982; Fuller et al. 1992). After reaching sexual maturity (~ 2 years old), some members of the group disperse from their natal pack to form new packs and establish new territories (McNutt 1996; Creel & Creel 2002; Woodroffe et al. 2019).

Interspecific competition in wild dogs

African wild dog overlap in more than 33% of its range with a high number (~17) of other African carnivores (Caro & Stoner 2003). One of the biggest natural threats to wild dogs is interspecific competition, especially with dominant larger predators such as lions and hyaenas (Woodroffe & Sillero-Zubiri 2012). High interspecific competition pressure can decrease wild dog density inside protected areas, especially in areas with a high lion density (Swanson et al. 2014). Although wild dogs have evolved with larger predators (Turner 1990), shrinking

environments due to anthropogenic factors has resulted in most of large dominant predator populations occurring within protected areas (Loveridge et al. 2010). This could have implications on the level of interspecific competition, and especially affect subordinate predators, such as wild dogs (Woodroffe & Ginsberg 1998; Van der Meer et al. 2013a). Interspecific competition with lions and hyaenas has been found to affect wild dogs through different mechanisms:

1 – Competition for prey and exclusion from prey rich areas - Interspecific competition with larger carnivores excludes wild dogs from high prey density areas (Mills & Gorman 1997; Creel 2001). The reduced prey availability (food depletion competition) due to exclusion from rich resource patches may reduce hunting efficiency and herewith increase pup mortality due to lower food intake (Malcolm & Marten 1982; Moehlman & Hofer 1997; Marneweck et al. 2019).

2 – Kleptoparasitism – Although hyaenas seldom directly kill wild dogs, they often steal wild dogs' kills (kleptoparasitism) (presence of hyaenas at wild dog kills in different ecosystems: from 6% to 85%) (Creel & Creel 2002; Van der Meer et al. 2011). This mainly occurs when hyaena densities are high, kill sites are in open habitat, and wild dog hunting-packs are small and can therefore not defend their kills successfully (Carbone et al. 1997, 2005; Courchamp et al. 2002; Van der Meer et al. 2011). In contrast, as lions impose a higher mortality threat, wild dogs never defend their kills against kleptoparasitism by lions, which are rarely present at wild dog kills (3%) (Van der Meer et al. 2011). Energy budget models indicate that wild dogs need to forage 12 hours a day (compared to 3.5 hours) to cope with 32.5% of

their kills being kleptoparasitized; thus, kleptoparasitism can impose significant energetic losses (Gorman et al. 1998; Speakman et al. 2016).

3 – *Direct mortality due to intraguild predation* - Intraguild predation is a major cause of adult and pup mortality in wild dogs (Creel & Creel 1998; Woodroffe & Ginsberg 1999), especially within protected areas (Woodroffe et al. 2007). Over different study populations of wild dogs, predation by lions accounts for 12% of adult (range: 0-46%) and 31% of pup mortality (range: 11-69%); whereas predation by hyaenas accounts for 4% of adult (range: 0-10%) and 6% of pup deaths (range: 0-29%) (Van Heerden et al. 1995; Mills & Gorman 1997; Woodroffe & Ginsberg 1999; Groom et al. 2017). Wild dog populations are extremely vulnerable to intraguild predation by lions and even affect wild dog population persistence (Swanson et al. 2014).

4 – *Impact on den site selection* - The selection of den sites is crucial for pup survival (Malcolm & Marten 1982; Van der Meer et al. 2013b; Davies et al. 2016). Even when lion population abundance is low (Van Dyk & Slotow 2003), wild dogs select dens in rugged terrain and high vegetation cover, away from waterholes (>2km) and roads to avoid predators (Van der Meer et al. 2013b; Jackson et al. 2014; Davies et al. 2016; O'Neill et al. 2020). Reducing the danger of predation by larger carnivores seems to be a more important den selection criterion than proximity to prey and water (Van der Meer et al. 2013b; Mbizah et al. 2014; Alting et al. 2021). However, when waterhole density is too high, denning wild dogs might not be able to den far away from water (Comley et al. 2023). Furthermore, the denning season means the movement of the pack is restricted to a den site and

the pack faces a trade-off between time spent at the den babysitting the pups, and time spent away from the den while foraging (Courchamp et al. 2002).

5 – *Wild dogs moving outside protected areas and facing anthropogenic threats* - When dominant predator densities are lower outside protected areas than inside protected areas, competition with larger predators can result in wild dogs moving outside protected areas or moving at the border of protected areas where they face higher anthropogenic threats, such as road kills or snaring (Mills 1991; Woodroffe & Ginsberg 1998; Van der Meer et al. 2013a). For instance, outside Hwange National Park (HNP) in Zimbabwe, anthropogenic landscapes result in wild dog mortality exceeding natality (Van der Meer et al. 2013a). This occurs despite the fact that outside HNP the risk of encountering lions and hyaenas is lower (Van der Meer et al., 2011), wild dogs' hunting success is higher (Van der Meer et al. 2013c), their per capita energetic intake is higher (Van der Meer et al. 2015), and wild dogs give birth to larger litters and have better access to suitable den sites (Van der Meer et al. 2011, 2013a).

Besides lions and hyaenas, which are the most dominant predators in the African carnivore guild, wild dogs also compete with other larger predators such as leopards (*Panthera pardus*) (23-31 kg) and cheetahs (*Acinonyx jubatus*) (34-64 kg) (Hayward & Kerley 2008; Vanak et al. 2013). The overlap in diet, time and space between wild dogs with leopards and cheetahs can be higher than with lions and hyaenas (Hayward & Kerley 2008; Vanak et al. 2013; Strampelli et al. 2023).

To reduce interspecific competition and promote coexistence, some form of niche partitioning is required between competing species. For example, diet choice

segregation, temporal separation or spatial partitioning (Amarasekare 2003; Owen-Smith & Mills 2008; Hayward & Slotow 2009; Vanak et al. 2013). Species have developed different behavioural mechanisms to avoid larger predators (Lima & Dill 1990; Kozłowski et al. 2011; Vanak et al. 2013). Subordinate carnivores respond to short and long-term risks of encountering dominant predators by reducing encounter risk and, thus, the associated competition and/or intraguild predation. Such avoidance response can be reactive (short-term: after detection of an immediate threat) or proactive (in response to *a priori* assessment of the risk level) (Broekhuis et al. 2013; Vanak et al. 2013; Creel 2018). Previous studies showed that wild dogs normally use a proactive strategy mainly to avoid lions but also hyaenas and leopards (Vanak et al. 2013; Swanson et al. 2014; Davies et al. 2021), and use a reactive strategy to avoid predators during the wet season (when visibility was low and hiding was easier) (Vanak et al. 2013). These avoidance strategies can reduce the risk of encountering larger predators but also incur costs for subordinate species, proactive strategies are associated to food-related costs (e.g. nutritional costs due to prey rich areas deprivation) and reactive strategies are associated with stress-related costs (e.g. glucocorticoids secretion due to predator encounter) (Rasmussen & Macdonald 2012; Swanson et al. 2016; Creel 2018).

In addition, living in groups plays an important role in coping with interspecific competition (Gittleman 1989; Palomares & Caro 1999). Hence, wild dogs' coping mechanisms towards larger carnivores can be affected by the size of a wild dog pack. Wild dog pack size is important for wild dog reproduction and foraging success (Courchamp et al. 2002; Carbone et al. 2005; Marneweck et al. 2019), especially in areas with high densities of lions and hyaenas. Larger packs

are more efficient at hunting, catching larger prey, eating a carcass faster and defending their kills from kleptoparasitism (Carbone et al. 1997; Courchamp et al. 2002). Intermediate-sized hunting groups (5 to 10 individuals) may be most effective at meeting energy intake demands (Carbone et al. 1997; Rasmussen et al. 2008). The reliance on helpers for cooperative hunting, defence from predators, pup feeding and babysitting makes small packs (<5 individuals) more vulnerable to interspecific competition with lions and hyaenas (Courchamp & Macdonald 2001; Courchamp et al. 2002).

The role of water

In arid and semi-arid ecosystems, such as the Hwange ecosystem (Zimbabwe), the use of water pumping is a common management practice (Owen-Smith 1996; Redfern et al. 2003; Valeix 2011). Waterholes are key areas for animals, especially during the dry season, and have implications on carnivore interactions (Chamaillé-Jammes et al. 2009; Valeix et al. 2010; Périquet 2014).

Interspecific competition can potentially be amplified at artificial waterholes also because they are fixed key resources (Brawata & Neeman 2011; Edwards et al. 2015; Rich et al. 2019). Water availability affects herbivore distribution (Redfern et al. 2003; Valeix et al. 2009a), which in turn affects predator distribution (Valeix et al. 2010) and ultimately predator-prey interactions (Valeix et al. 2009a, 2009b; Courbin et al. 2016) and predator-predator interactions (Périquet 2014). Lions and hyaenas use areas within a 2 km radius from waterholes to increase search efficiency while hunting for prey (Valeix et al. 2010; Périquet 2014). Despite an

increased risk of encountering larger carnivores, a large percentage (73%) of wild dog kills is also made within 2 km from waterholes (Van der Meer 2011) which may increase the risk of interspecific competition with lions and hyaenas. This can play a role during the nomadic season (when wild dogs are not breeding and are not restricted to a den), as it means wild dogs may have to avoid prey rich areas around waterholes to reduce competition. However, in the denning season (when the movement of the pack is confined to a den), this trade-off between foraging efficiency and predation risk can become particularly intense. In theory, the further the den is situated from the waterhole, the lower the risk of predation. However, with prey aggregating around waterholes, this could increase foraging distance and herewith the time spent away from the den, leaving the pups more vulnerable to predators even when there is a baby-sitter. Thus, especially in an ecosystem with limited water availability during the dry season (which overlaps with the wild dogs breeding season), wild dogs face a trade-off not only between reproduction and predation risk but also between foraging efficiency and predation risk. Wild dogs take higher risks to spatio-temporally overlap with dominant predators when they need to access resources such as water and prey, as well as, when they are not denning (Vanak et al. 2013; Marneweck et al. 2021; Pretorius et al. 2021).

Although it is well understood that larger predators negatively affect wild dogs (Creel & Creel 1996; Mills & Gorman 1997) and that wild dogs thus avoid larger predators (Vanak et al. 2013), the mechanisms linking water availability with interspecific competition between wild dogs and their larger competitors is not yet well researched (Darnell et al. 2014). Furthermore, as the link between ecological factors and individual fitness is important for canid conservation (Moehlman &

Hofer 1997; Courchamp et al. 2002; Davies et al. 2016), studying how wild dogs survive in areas with a high risk of interspecific competition and different levels of water availability can bring important insights for their conservation.

Study area

The study site is located in Hwange National Park (HNP), an unfenced protected area without human settlements or main roads, which covers ca. 15,000 km² in the northwest of Zimbabwe (19:00'S, 26:30'E) (Fig. 1 and 2). HNP is the largest protected area in Zimbabwe, and part of the Kavango Zambezi (KAZA) Transfrontier Conservation Area, which is the largest transfrontier conservation area in the world (PPF 2018). The altitude in HNP varies from 800 m to 1100 m. HNP is semi-arid with a mean annual rainfall of ~600 mm and approximately 98% of this annual rainfall occurs from October to April. The park's habitat comprises mainly woodlands and, bushlands with some patches of open areas of grassland mainly associated with waterholes (Davidson et al. 2013; Van der Meer et al. 2013a; Arraut et al. 2018). HNP has hardly no natural perennial water sources; thus, in the dry season animals mainly depend on artificial waterholes (pumped from groundwater) (Valeix et al. 2010). Depending on funding to fill in the artificial waterholes and the amount of rain received per year to keep the natural waterholes full, there can be around 79 to 117 waterholes (including natural and artificial) that tend to keep water the whole year round (ZIMPARKS 2015; WEZ Reports 2012-2022). The wet season (November-February) has ~380 mm of mean rainfall, the

early dry season (March-June) has ~111 mm of mean rainfall, and the late dry season (July–October) is characterized by a mean rainfall of ~25 mm, water being mainly restricted to artificial waterholes (between 50 to 66 in years 2012 to 2017 and between ~75 in years 2018-2022), deciduous trees losing their foliage, and grazing being on the lowest quality (Valeix et al. 2010; Davidson et al. 2013; Van der Meer et al. 2013a; Périquet 2014; WEZ Reports 2012-2022). Waterholes are mainly found in the north of HNP. The northwest has the most fertile soil and highest terrain ruggedness, it is mainly characterized by woodland and grassland, it has a seasonal river and a high number of waterholes (~0.019 waterholes/km²), as well as a high abundance of dominant predators (Arraut et al. 2018; Loveridge et al. 2022). The northeast is characterized by open wooded savannahs on Kalahari sands with the maximum number of waterholes (~0.036 waterholes/km²). The south west is the driest part (~0.006 waterholes/km²), as it is characterized by Kalahari sand soil with almost no water provisioning during the dry season, and it also has the least abundance of dominant predators and prey (Rogers 1993; Chamaillé-Jammes et al. 2009; Arraut et al. 2018; Loveridge et al. 2022).

African wild dogs' main prey species present include impala (*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*) and duiker (*Sylvicapra grimmia*) (Van der Meer et al. 2013c). On average from years 2013 to 2019 the density of dominant predators in HNP has been 2.9 (± 2.2 sd) lions/100 km², and 10.7 (± 6.1 sd) hyaenas/100 km² (unpublished data; Loveridge et al. 2022). The total number of adult wild dogs estimated in the network of protected areas in Zimbabwe (including private conservancies) is around 450 adults (ZIMPARKS 2009). In HNP, it has been estimated that there are around 196 adults in 32 packs at an average

of 6 adults per pack (PDC 2018). With the world's largest population of wild dogs remaining in southern Africa (IUCN 2024), the Hwange wild dog population is not only important for Zimbabwe but also for the African continent.

The main aims to pump artificial waterholes in HNP are to provide water for wildlife and sustain animal populations during the dry season for conservation and tourism purposes (ZIMPARKS 2015). Outside the border of HNP there are human villages, and areas for trophy hunting areas and photographic safari (Loveridge et al. 2017). As during the dry season the only water available in HNP is through artificially pumped waterholes, HNP is an ideal ecosystem to study the role of water management in the dynamics of species interactions.

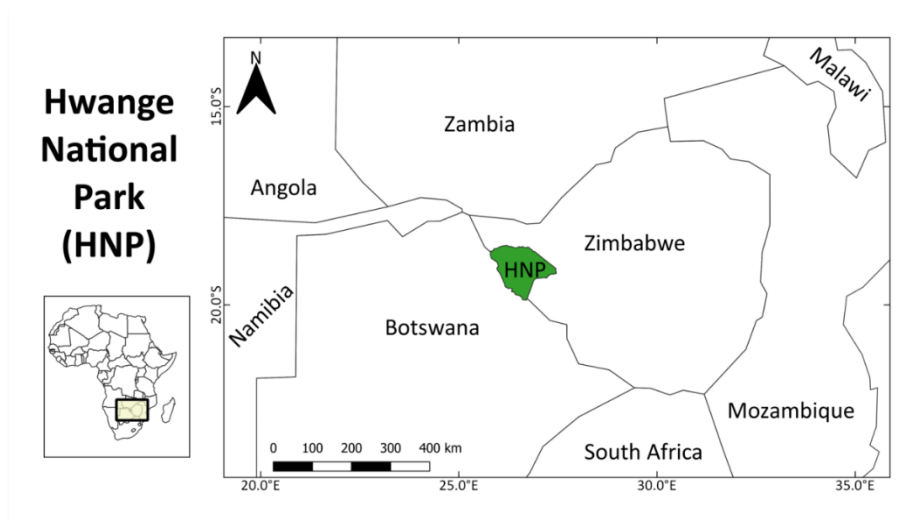
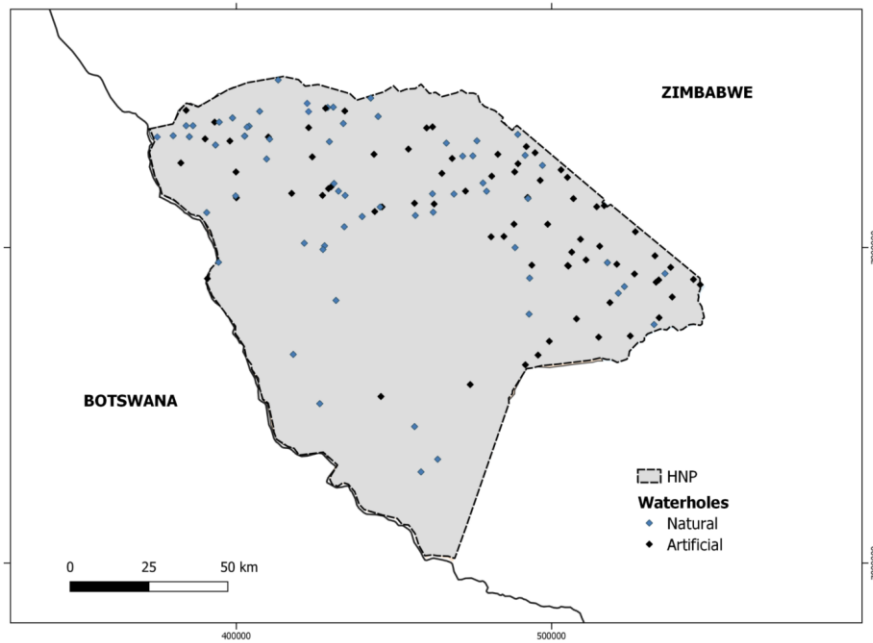


Figure 1. Location of Hwange National Park (HNP), Zimbabwe.

a)



b)

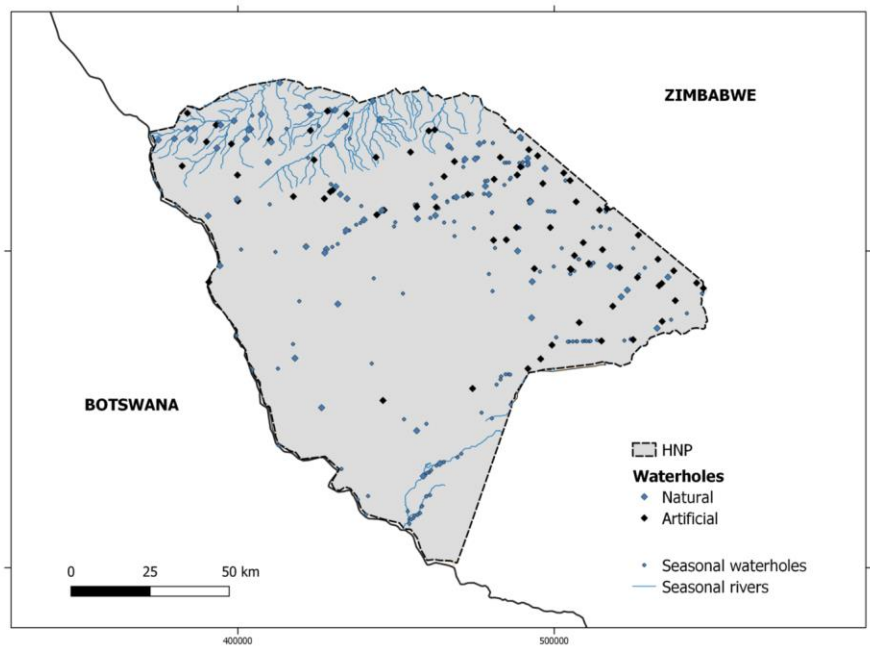


Figure 2. Location of waterholes within HNP: a) map with only waterholes that can remain with water during the late dry season; b) map including seasonal rivers and waterholes that dry up during the late dry season.

Thesis overview

I aimed to determine how African wild dogs (hereafter: wild dogs) cope with the competition with larger dominant predators (lions and spotted hyaenas – hereafter: hyaenas) in a system with limited (artificial) surface water availability and how the distribution and abundance of surface water influence the intensity of this competition (Diagram 1).

Specifically, I aimed:

- a) To evaluate the dynamics of food resource competition between wild dogs and four competing predators (cheetahs, leopards, lions and hyaenas) in different seasons and across areas with different waterhole densities (Chapter 2).
- b) To determine the level of kleptoparasitism risk from dominant predators (lions and hyaenas) to wild dogs in relation to distance to waterholes and in areas characterized by contrasting waterhole densities (Chapter 3).
- c) To determine if wild dogs avoid large predators (leopards, lions, hyaenas) reactively and/or proactively in time and space, and assess if environmental covariates are affecting the avoidance strategy of wild dogs towards large predators in space and time (Chapter 4).

Ultimately, I provide insights into how artificial water provisioning, and therefore water management, affects the level of intraguild competition for wild dogs, and

propose water management recommendations to reduce predator competition and assist wild dogs conservation (Chapter 5).

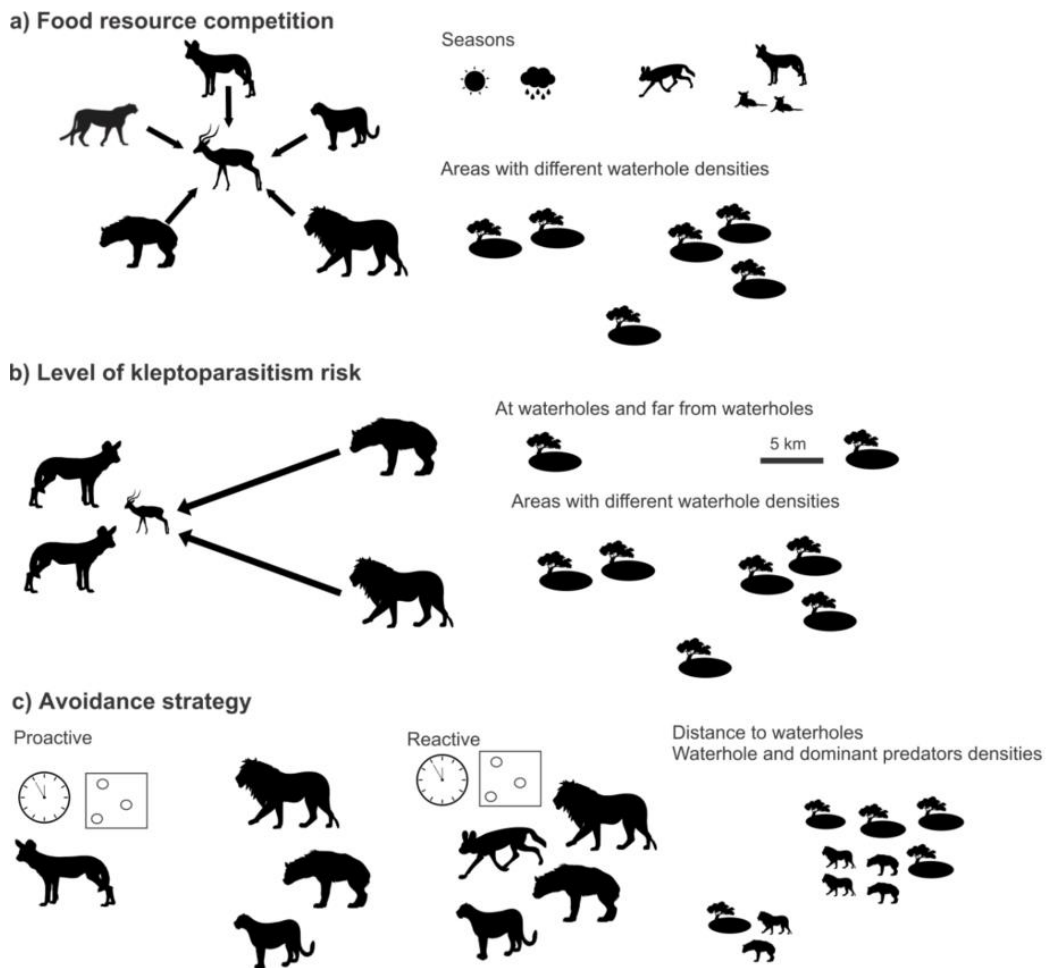


Diagram 1 Interspecific competition between African wild dogs and larger predators in an ecosystem with artificial perennial water provision: a) level of food resource competition of wild dogs with larger predators (Chapter 2); b) level of kleptoparasitism risk from dominant predators to wild dogs (Chapter 3); c) proactive and reactive risk avoidance in time and space of wild dogs in response to larger predators (Chapter 4).

Chapter 2: “*Food resource competition between African wild dogs and larger carnivores in an ecosystem with artificial water provision*”

In this chapter, I evaluated the dynamics of food resource competition between wild dogs and four competing predators (cheetahs, leopards, lions and hyaenas) in different seasons (weather: wet-early dry and late dry; wild dogs’ behavioural seasons: nomadic [non-breeding] / breeding) and across areas with different waterhole densities (maximum, high and low) in Hwange National Park, Zimbabwe. I used the frequency of occurrence and biomass of prey found in predators’ scats to analyse diet composition (statistical comparisons using PERMANOVA), diet overlap (Pianka’s index), niche breadth (Levin’s index), and prey preference (Jacob’s index). Additionally, I categorized the predators’ diet depending on the level water dependency of their prey. This chapter shows the diet niche partitioning of wild dogs with other predators in relation to waterhole availability and distribution. Finally, I discuss how to reduce food resource competition for wild dogs in a semi-arid ecosystem with artificial water provision. This chapter is published in *Ecology and Evolution*.

Chapter 3: “*Water availability affects the risk of kleptoparasitism of African wild dogs by larger dominant predators*”

In this chapter, I determined the level of kleptoparasitism risk for wild dogs by dominant predators (lions and hyaenas) in areas with different waterhole densities and at different distances from waterholes (0 and 5 km away). I tested the level of kleptoparasitism risk by performing playbacks of a soundtrack of wild dogs killing and eating an impala at waterholes and 5 km away from waterholes. I

performed hurdle model analyses to test whether a dominant predator arrived at a playback location, as well as to test the number of dominant predators present at the playback location when they arrived. Additionally, I used generalized linear models to determine the lapse time that it took dominant predators to arrive at a playback location. Dominant predators arriving at wild dog kills imposes a high threat to wild dogs not only through kleptoparasitism risk but also through the risk of agonistic encounters. In this chapter, I discussed water management solutions to lower kleptoparasitism risk towards wild dogs and in turn the risk of for wild dogs to encounter dominant predators at kills in ecosystems with artificial water provisioning. This chapter is submitted to *Oecologia*.

Chapter 4: “Spatio-temporal dynamics of African wild dogs with larger carnivores in an ecosystem with artificial water provisioning”

In this chapter my first aim was to evaluate if wild dogs avoided larger competing predators (leopards, lions and hyaenas) reactively or proactively in space and time at different spatial and temporal scales. Secondly, I aimed to determine (taking vegetation characteristics into account) whether seasonality (early dry and late dry), waterhole density at different spatial scales, waterhole distance and dominant predator density affected the avoidance strategy of wild dogs towards large predators in space and time. I analysed camera trap data and I used generalized linear mixed models (spatial dimension), activity pattern overlap (temporal dimension), and time-to-event analyses (spatio-temporal dimension). Finally, I discussed waterhole-provisioning schemes as tools in conservation management that can facilitate interspecific coexistence by potentially increasing

niche-partitioning opportunities. This chapter shows the spatial and time related niche partitioning of wild dogs with larger predators in an ecosystem with artificial water provision. This chapter is submitted to *Biological Conservation*.

Chapter 5: *General discussion*

In this last chapter, I synthesized the main aims of this study and summarised the main results. I also discussed future improvements and limitations of this research. Subsequently, based on the results of this study, I discussed how water management could help conservation practitioners and policy makers to develop water management strategies that can assist in lowering wild dogs interspecific competition with dominant larger predators. I also discussed how this study can contribute to the conservation work in other areas where water management is crucial for wildlife conservation. Finally, I ended by highlighting the main findings of this study for wild dogs conservation. (This section will directly contribute with knowledge to the Water Management Policy brief in Hwange National Park and surroundings – project from ZPWMA [Government of Zimbabwe] in collaboration with the Public Policy Challenge Fund and WildCRU [University of Oxford]).

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Chapter 2

Food resource competition between African wild dogs and larger carnivores in an ecosystem with artificial water provision

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Abstract

Predators of similar size often compete over prey. In semi-arid ecosystems where water is a limiting resource, prey availability can be affected by water distribution, which further increases resource competition and exacerbate conflict among predators. This can have implications for carnivore dietary competition. Hence, we evaluated the dynamics of food resource competition between African wild dogs and four competing predators (cheetahs, leopards, lions and spotted hyaenas) in different seasons and across areas with different waterhole densities in Hwange National Park, Zimbabwe. We used the frequency of occurrence of prey items found in predators' scats to analyse diet composition, overlap and prey preference. For most predators, kudu was most frequently consumed and preferred. Low and medium water-dependent prey (medium and small-sized) were mostly consumed by wild dogs, leopards and cheetahs. Wild dog diet overlap was high with all predators, particularly with hyaenas and lions. There were no seasonal differences in the predators diet. The diet overlap of wild dogs with lions was highest in the low waterhole density area, and wild dog diet composition did not differ significantly from the diet of lions and hyaenas. In the low waterhole density area, wild dogs and hyaenas broadened their niche breadth, and predators diet had a higher proportion of low water-dependent prey. A low density of waterholes increased food resource competition. However, high density of waterholes, where there is more prey availability, can increase the aggregation and density of predators, and hence, increase the risks involved in interspecific competition on

wild dogs. To reduce food resource competition on wild dogs, we propose to conserve larger-bodied prey that are less dependent on water (e.g. kudu, reedbuck, eland, gemsbok). As the use of water pumping is common practice, we propose maintaining water management heterogeneity where prey which is less dependent on water can also thrive.

Keywords: Diet, waterholes, interspecific competition, carnivores, resource partitioning

Introduction

Large predators help maintain stable ecological processes as they exert top-down effects (Dalerum et al. 2008). Thus, their conservation is crucial to maintain healthy ecosystem functioning (Martinez-del-Rio et al. 2001). Among mammals, large predators (> 21 kg) are a distinct functional group on top of the food chain that can feed on a wide range of prey sizes (Radloff and Du Toit 2004). As large predators belong to the same carnivorous guild, their ecological niches overlap, which results in competition (Amarasekare 2003; Radloff and Du Toit 2004).

To promote coexistence among competing species, a form of niche separation is necessary; this can be temporal, spatial or through diet partitioning (Amarasekare 2003). Diet separation can reduce exploitative competition, which is when species indirectly compete for common resources through depletion of these resources (Tilman 1982; Ghoddousi et al. 2017). Thus, species need to adapt their foraging strategies to maximize their fitness (Schoener 1971). As predators of similar size compete over prey (Cupples et al. 2011; Harihar et al. 2011), a subordinate predator (smaller in size) may change its diet due to the presence of a dominant predator (larger in size), especially when food is scarce (Hayward and Kerley 2008; Mbizah et al. 2012). In such a situation, prey selection could depend more heavily on competition among predators than on predator-prey characteristics (Jones and Barmuta 1998; Radloff and Du Toit 2004).

Diet overlap serves as an indication of resource competition (Du Preez et al. 2017). A high degree of diet overlap, which can indicate the potential for a high level of resource competition, can exacerbate conflict among predators (Fedriani et

al. 2000; Donadio and Buskirk 2006; Du Preez et al. 2017). One way to reduce interspecific competition is through diet segregation, particularly when competing species overlap spatio-temporally (De Almeida Jácomo et al. 2004; Gerber et al. 2012; Balme et al. 2017). Subordinate predators can reduce interspecific competition by feeding on different prey groups (e.g. prey water dependency, or prey size) (Hayward and Kerley 2005; Davis et al. 2018); as well as, through segregating their diet seasonally (Jones and Barmuta 1998; Carvalho and Gomes 2004; Azevedo et al. 2006) and spatially (different habitats and areas) (Jones and Barmuta 2000; Tsunoda et al. 2019). However, it is possible that the options for diet segregation are reduced when prey abundance decreases, in which case subordinate predators will be affected more heavily than dominant ones (Schoener 1971; Creel et al. 2018; Ferretti et al. 2020; Steinmetz et al. 2020).

The African wild dog (*Lycaon pictus*) (~22 kg) (referred to as wild dog throughout the manuscript) is an endangered, social and subordinate carnivore within Africa's large carnivore guild (IUCN 2023). It suffers from interspecific competition with lions (*Panthera leo*) (150-250 kg) and spotted hyaenas (referred to as hyaenas throughout the manuscript) (*Crocuta crocuta*) (~70 kg). These two dominant predators affect wild dogs through direct killing, exploitative competition, exclusion from prey rich areas, and kleptoparasitism (Creel 2001; Van der Meer et al. 2011, 2013b; Vanak et al. 2013). Wild dog diet overlaps not only with the diet of lions and hyaenas, but also with the diet of leopards (*Panthera pardus*) (23-31 kg) and cheetahs (*Acinonyx jubatus*) (34-64 kg) (Hayward and Kerley 2008; Mbizah et al. 2012).

In arid and semi-arid ecosystems, water becomes a limiting resource in the dry season and is therefore, in some areas, actively pumped to provide water to animals (Owen-Smith 1996). Variation in water availability affects the abundance and distribution of herbivores (Redfern et al. 2003; Valeix 2011), which in turn affects the abundance and distribution of predators (Valeix et al. 2010, 2012), and ultimately the level of intraguild competition between predators (Périquet et al. 2021). The widespread use of artificially supplied water in African savannahs (Owen-Smith 1996; Edwards et al. 2015; Sutherland et al. 2018) can impact carnivore interactions and potentially affect the fate of endangered species such as wild dogs. Although food competition between large African predators has been widely studied (Hayward and Kerley 2008; Mbizah et al. 2012; Creel et al. 2018), the role of water on the dynamics of this competition has never been assessed.

Here, we aim to identify the level of food competition (diet composition, diet overlap, and prey preference) between wild dogs and the four competitive predators (cheetahs, leopards, lions and spotted hyaenas) in different seasons (weather seasons: wet-early dry [November-June] / late dry [July-October]; wild dogs' behavioural seasons: nomadic (non-breeding) [September-April] / breeding (restricted in movement due to denning) [May-August]) across areas characterized by contrasting water availability to assess the role of water availability, and hence provisioning, on the potential exploitative competition between wild dogs and other large carnivores. As water can have an impact on prey species distribution and abundance, our main hypothesis is that food resource competition between wild dogs with larger predators would differ between seasons and between areas with different waterhole densities due to differences in prey distribution and availability.

We predict that the potential for resource competition, i.e. diet overlap, is higher between wild dogs and the other predators during the dry and breeding season and in areas with a lower density of waterholes, as prey would likely be less available there.

Methods

Study site

The study site is situated in Hwange National Park (HNP), an unfenced protected area without human settlements or paved roads and used for photographic tourism. The park covers ca. 15,000 km² in western Zimbabwe (19:00'S, 26:30'E) (Fig. 1), with altitudes between 800 m and 1100 m. The habitat comprises of woodland, bushland and open areas of grassland mainly associated with waterholes (Arraut et al. 2018). HNP does not have natural perennial water sources; thus, in the dry season, animals depend on artificially provisioned waterholes. The wet-early dry season (November-June) has a mean rainfall of ~540 mm, and the late dry season (July-October) has a mean rainfall of ~12 mm (Wilderness Safaris Zimbabwe, unpublished data for 2010-2017). During the late dry season, deciduous trees lose their foliage, and pasture is of the lowest quality. Waterholes are mainly found in the northern area of HNP (both in the North West (NW) and North East (NE) areas - Fig. 1 - where waterhole density is 2.0 and 4.6 per 100 km², respectively – Table 1). The NW area has the most fertile soil (basalt soil) and is characterized by woodland and bushland; while woodland and open grassland in Kalahari sands characterize the NE area. Moreover, in the NW area

there are rivers that carry water during the wet season (Chamaillé-Jammes et al. 2007). The South West (SW) area is the driest part of the park (waterhole density is 0.5 per 100 km²; Table 1), and characterized by bushy grassland on Kalahari sand soil with almost no water provisioning during the dry season (Rogers 1993; Arraut et al. 2018). Areas adjacent to HNP include human settlements, trophy hunting areas and photographic safari areas (Loveridge et al. 2017). During the study period in HNP (2013-2019), the density of dominant predators was estimated to be: 2.9 (± 2.2 sd) lions/100 km², and 10.7 (± 6.1 sd) hyaenas/100 km² (Table 1; Loveridge et al. 2022).

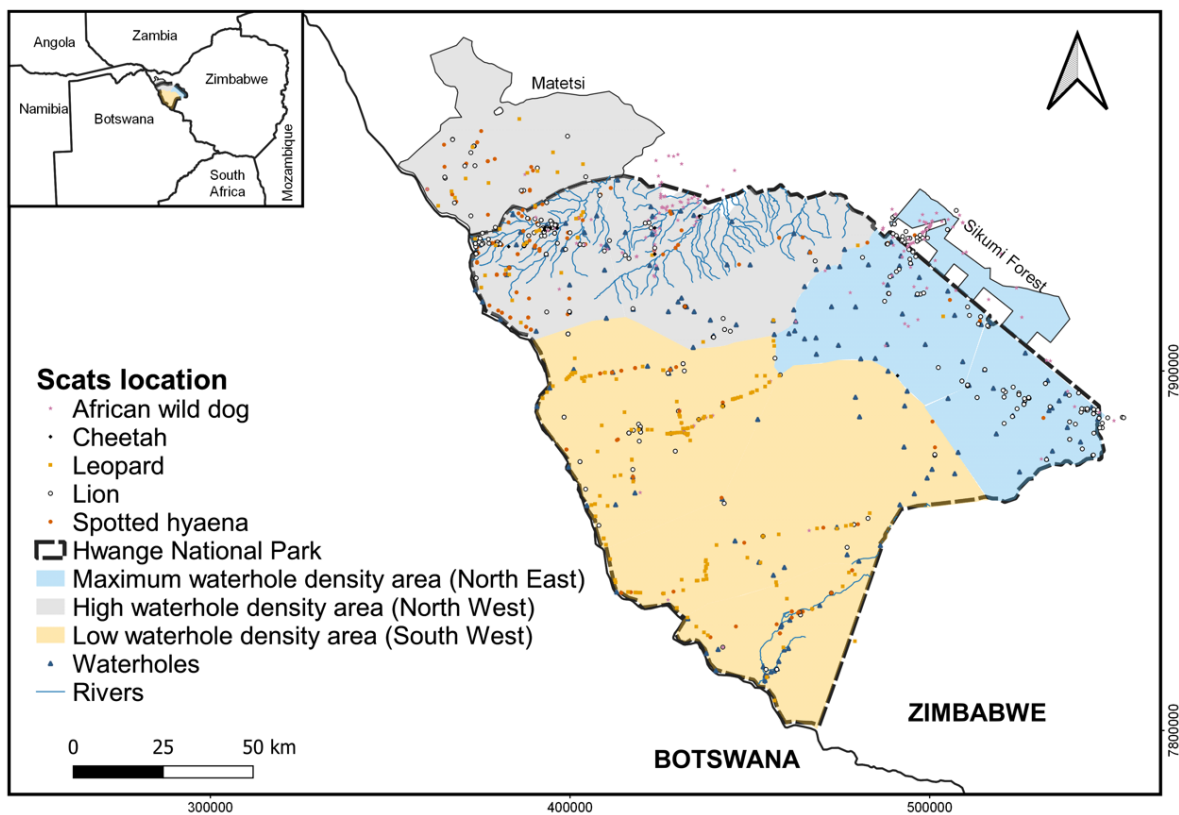


Figure 1 Map of the study area, Hwange National Park, Zimbabwe, with locations of scat samples per predator within the three areas of the park with contrasting waterhole densities.

Table 1. Characteristics of the study areas in Hwange National Park, Zimbabwe.

Areas	North East	North West	South West
Waterhole density per 100 km ²	~3.25	~1.4 + seasonal rivers	~0.2
Vegetation types and soil	Woodland, open grassland, bushed grassland on Kalahari sand soil.	Woodland, grassland, and bushland on basalt soil (most fertile).	Bushed grassland on Kalahari sand soil.
Average abundance of African wild dogs (2014-2020) (±SE standard error)	Pack size = 7.5 (±0.6) Pack number = 10.0 (±1.3)	Pack size = 10.9 (±1.0) Pack number = 7.9 (±1.3)	Pack size = 8.3 (±2.3) Pack number = 2.2 (±0.7)
Average densities (2013-2019) per 100 km ² (±SD standard deviation)	Leopard 2.3 (±1.0) Lion 2.3 (±1.3) Spotted hyaena 8.4 (±2.1)	3.0 (±1.5) 6.5 (±0.3) 19.1 (±5.4)	2.0 (±0.1) 1.8 (±1.1) 6.1 (±1.1)
Summary of prey species abundances[#]	Highest for: duiker, steenbok, wildebeest, sable, kudu, elephant, and zebra.	Highest for: impala, buffalo, bushbuck, kudu, warthog.	Low, except for gemsbok, bushpig and reedbuck.

Vegetation and soil taken from Arraut et al. (2018).

African wild dogs' abundance including pups less than 1-year-old (PDC Annual Reports).

Predator densities taken from Loveridge et al. (2022).

[#]Prey density and relative abundance index taken from Supporting information, Table 3 and 4.

Data collection

Faecal samples of cheetahs, leopards, lions and hyaenas were collected opportunistically along roads, trails, kills, and latrines from 2012 until 2015. Faecal samples for wild dogs were collected while following packs from 2012 to 2020. The identification of the faeces of predators was based on morphology, colour, odour and associated tracks (Mbizah et al. 2012) or by directly observing defecation. Following Mbizah et al. (2012), samples were photographed, washed in acetone,

dehydrated in 100% ethanol, and dried on filter paper. For prey species identification, 6 to 8 hairs from the washed hair sample were selected from different parts of the prey species' pelage. Hair cross-sections and scale pattern imprints made on wood glue were photographed through a microscope and each hair was identified to species level using photographic reference guides (Buys and Keogh 1984; Kent 2004; Seiler 2010; Taru and Backwell 2014). To limit the probability of pseudo-replication, for lion and hyaena scats, we considered only one sample collected per 24 hours per location (location was considered the same if ≤ 1 km apart). For wild dog's scats, we considered only one sample collected per 24 hours from the same pack, regardless of location. We acknowledge that there could still be some pseudo-replication by only considering 24h, as complete digestion can take longer, however, in order to keep a good sample size we used 24h based on Mbizah et al. 2012.

To calculate prey abundance, we used data from line-transect surveys carried out in the north of HNP in September/October (late dry season) and in May/June (early dry season) each year from 2012 until 2019. Further details of line-transect survey methodology in HNP can be found in Chamailié-Jammes et al. (2009). A total of 492 camera trap stations (Cuddeback models 1125, 1149 and C1, Non-Typical, WI, USA; Panthera V4, Panthera, NY, USA; Stealthcam G42NG, Grand Prairie, TX, USA) were deployed between 2013 and 2020 across nine surveyed sectors (three surveyed sectors per area) (total effort: 23,319 trap days). Camera trap stations were placed along trails or roads and spaced in a grid of 5 km apart (Fig. 1) (Loveridge et al. 2022).

Analyses

Diet composition and comparisons

To determine the diet of each predator, we analysed the faecal data as a whole (including all samples: “All” category), as well as, per area (NW, NE and SW areas), and per season over all years. One limitation of dividing the park into three areas was that we were not able to control for instances where consumption and defecation took place in different areas. However, scats collection at the margin between these areas was minimal (Fig. 1). For the seasonal analyses, we took the following categories into account: “wet-early dry” season (November-June) “late dry” season (July-October); and “nomadic” season (September-April) when wild dogs are nomadic versus “breeding” season (May-August) when wild dogs are denning and therefore restricted in their movement (packs that were not denning during the breeding season were excluded from this analysis: 12 scats). We categorized prey species by level of water dependency (high, medium, low) and diet (mixed feeder [browser and grazer], browser, grassland grazer, woodland grazer, omnivorous, carnivore, other) (based on Redfern et al. 2003; De Boer et al. 2010; Hayward & Hayward 2012; Supporting information, Table A1). In cases where we found carnivore species in the diet, they were included in the analyses because even though they can be killed as part of interspecific competition, they are also sometimes preyed upon by predators (Rasmussen 1996; Breuer and Breuer 2005; Du Preez et al. 2017). We used prey size based on mean female weight as described by Cumming & Cumming (2003) and Kingdon (2004) (XS extra-small <5 kg, S small 6-24 kg, M medium 25-99 kg, L large 100-349 kg, XL extra-large >350 kg) (Mbizah et al. 2012; Balme et al. 2017) (Supporting

information, Table A1). Wild dogs hunt together as a pack which allows them to increase hunting efficiency and to hunt for larger prey (Creel and Creel 1998). To determine if there was any correlation of wild dog pack size with prey size, we performed a Cumulative Link Mixed Model - CLMM (*ordinal* package; Christensen 2022), using prey size as the dependent variable, pack name as a random factor, and pack hunting size (excluding pups) as a fixed factor. As the distribution of prey weights was clumped, we used prey weight class, a categorical variable, and hence used ordinal regression: CLMM.

To determine if we collected the minimum number of scats needed to adequately describe the diet of predators, we calculated prey-species accumulation curves using the function *specaccum* in the *vegan* package (Oksanen et al. 2018) (Supporting information, Fig. A1). Because of a small sample size (< 21) neither cheetah's diet (information only available for the NW area) nor leopard diet in NE and seasonally were included in statistical comparisons, as we did not perform any analysis when there were fewer than 21 scats within a category (Supporting information, Table A2a).

For each area and season, we calculated the frequency of occurrence (Klare et al. 2011). For the "All" category, we also estimated the relative biomass intake. Following Woodroffe et al. (2007), we used the Weaver's equation derived from the grey wolf (*Canis lupus*): prey mass per scat (kg) = 0.439 + (0.008 * prey species' mean female weight) to estimate the biomass intake for wild dogs (Weaver 1993). Following Briers-Louw (2017) and Du Preez et al. (2017), we used the Ackerman's equation derived from pumas (*Puma concolor*) for the other predators: prey mass per scat (kg) = 1.980 + (0.035* prey species' mean female

weight) (Ackerman et al. 1984). As these formulas are not specific for the species of our study, the biomass results are only indicative representations of the proportions of biomass consumed and not necessarily the accurate biomass value. When calculating biomass, we corrected for the maximum stomach capacity of each predator, which were corrected at a maximum of 10 kg for leopards, 24 kg for hyaenas and 50 kg for lions (Kruuk 1972; Bertram 1975). As the highest biomass consumed per scat for wild dogs and cheetahs (4 kg) did not exceed maximum stomach capacity (~9 kg) (Creel and Creel 1995), there was no need to correct their biomass calculations. For seasonal and spatial comparisons on predators diet composition, we performed a permutational analysis of variance (PERMANOVA) of prey species found in the predators' scats with 1000 permutations and controlling for "year" using the *adonis2* function of the *vegan* package (Oksanen et al. 2018). We used PERMANOVA analysis because it is a non-parametric test that compares groups' differences where it is possible to stratify the permutations performed (Oksanen et al. 2018). This meant that we were able to control for "year" in our comparisons. When comparing prey species composition, we used the Jaccard index (presence/absence data: prey species in each scat): $= \frac{A+B-2J}{(A+B-J)}$; where A and B are the numbers of species in compared predator scats, and J is the number of species shared in predator scats (Jaccard 1908). When comparing prey categories (prey water dependency, prey diet and prey size), we used the Bray-Curtis dissimilarity index (using abundance data, as more than one prey species could be found in each category): $= \frac{\sum_{i=1}^n |X_{ij}-X_{ik}|}{\sum_{i=1}^n (X_{ij}+X_{ik})}$; where X_{ij} and X_{ik} are the numbers of prey

species per category i found in predator scats j and k ; n is the number of categories (Bray and Curtis 1957).

As this is a study using scats and not direct observations, we were not able to determine the proportion of prey consumed through scavenging or hunting; however, it is mainly lions and hyaenas that scavenge or kleptoparasitize if the opportunity appears, wild dogs very rarely scavenge (Creel and Creel 2002; Périquet et al. 2015).

Diet overlap and niche breadth

To determine the diet overlap of wild dogs with the other predators, we used

Pianka's index (Pianka 1973): $O_{jk} = \frac{\sum_i^n p_{ij} p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}}$; where O_{jk} is the diet overlap

between predators j and k ; p_{ij} is the prey proportion i of the total prey used by predator j ; p_{ik} is the prey proportion i of the total prey used by predator k ; and n is the total number of prey items. This index ranges between 0 (no overlap) and 1 (complete overlap). For seasonal diet overlap, we only included the samples collected in the northern part of HNP, as in the SW no wild dog samples were collected in the wet-early dry seasons and there was no breeding information on wild dogs available. We evaluated statistical significance of Pianka's index with a null model in which diet items are reshuffled randomly and independently (with 10,000 iterations) while maintaining the observed prey species richness. For this, we used the *EcoSimR* package (Gotelli et al. 2015). To determine the diet niche breadth of each of the three predators, we used the standardized Levin's index

(Levins 1968; Krebs 1999): $B = \frac{1}{\sum p^2}$, and $Bs = \frac{B-1}{n-1}$, where B is niche breadth; p is the proportion of prey items; Bs is standardized niche breadth; and n is the total number of prey species. Both diet overlap and niche breadth indices were calculated taking into account all consumed prey by all predators.

Prey preference

To determine whether prey consumption was based on prey availability or prey preference, we used Jacobs' index: $D = (r - p)/(r + p - 2rp)$, where r is the proportion of prey species in the diet and p is the proportion of prey available. A Jacobs' index value of -1 indicates maximum avoidance and a value of +1 maximum preference (Jacobs 1974). We calculated Jacobs' index using two different measurements for prey availability (that we calculated): 1) prey density, and 2) prey relative abundance index (RAI). Prey density is a more accurate measure for prey abundance, however RAI was also used, as prey density was not available in the SW of HNP. To coincide with the sampling period of scat collection of predators, we calculated prey abundance data from all years (2012-2019) to calculate prey preference of wild dogs, and prey abundance data of 2012 to 2015 to calculate prey preference of the other predators. To calculate prey density, we used distance sampling methods (Buckland et al. 2001) using the *Distance* package (Miller 2020). We used 5% truncation, and ran models using half-normal, uniform, and hazard-rate key-functions with cosine/polynomial series expansion, both including and excluding vegetation type as a covariate for detection function. We selected the model with the smallest Akaike Information Criterion (Burnham

and Anderson 2002), and checked the goodness of fit with a chi-square test (results of p-value were above 0.20). To calculate prey RAI, we used camera trap data and calculated RAI as follows: independent records / trap-days. We used as independent records, consecutive photographs of different individuals (appearing on the same picture together) of the same species taken more than 30 minutes apart (O'Brien et al. 2003). We calculated RAI indices per survey sector and then averaged the indices per area. Prey densities can be found in Supporting information, Table A3; and prey RAI can be found in Supporting information, Table A4. We considered that there was statistical evidence of a difference when a p-value was under 0.05; and we performed all our analyses using R 4.1.2 (R Core Team 2022).

Results

Diet composition and comparisons

In total, for wild dogs, there were 225 food items sampled in 209 scats with 20 prey species identified; for cheetahs, 27 items in 26 scats and 7 species; for leopards 246 items in 204 scats and 25 species; for lions there were 351 items in 342 scats and 33 species; and for hyaenas there were 337 items in 317 scats and 33 species (Supporting information, Table A2a). Main results are summarized in Table 2.

Table 2. Predators diet results summary.			
Most common and preferred prey species (Fig. 3 and 5).			
	Maximum waterhole density area	High waterhole density area	Low waterhole density area
African wild dog main prey	Kudu, Impala , bushbuck and waterbuck.	Impala and bushpig.	Duiker and steenbok .
Cheetah main prey	No data.	Bushbuck, duiker and scrub hare.	No data.
Leopard main prey	No data.	Impala , kudu and squirrel.	Duiker , bushbuck, steenbok and birds.
Lion main prey	Impala , buffalo and sable.	Buffalo and bushpig.	Kudu and duiker .
Spotted hyaena main prey	Impala and sable.	Kudu, impala and wildebeest.	Duiker and steenbok .
Diet overlap of African wild dogs with lions within areas	0.59	0.63	0.77
Diet overlap of African wild dogs with spotted hyaenas within areas	0.60	0.88	0.68

In bold = shared prey species between African wild dogs and other predators per area, and the highest diet overlap.

There was no evidence of seasonal differences (either in wet-early dry vs. late dry [pseudo- $F_{2,839} = 1.14$, $p = 0.59$], or in nomadic vs. breeding; [pseudo- $F_{1,815} = 0.64$, $p = 0.16$]) in the diet of wild dogs, lions and hyaenas (Supporting information, Table A5a). However, there was evidence that predators diet differed in different areas of the park (Table 3; Supporting information, Table A5b).

Table 3. Differences on prey water dependency in the diet of predators in areas with contrasting waterhole densities in Hwange National Park, Zimbabwe.

(Fig. 3 and Supporting information Fig. A2)

	Maximum vs. High waterhole density area	High vs. Low waterhole density area	Maximum vs. Low waterhole density area
African wild dog	pseudo- $F_{1,167} = 4.65$ p = 0.0012* $r^2 = 0.027$	pseudo- $F_{1,99} = 4.35$ $p = 0.51$ $r^2 = 0.042$	pseudo- $F_{1,108} = 0.92$ $p = 0.25$ $r^2 = 0.008$
Leopard	NA	pseudo- $F_{1,199} = 14.56$ $p = 0.26$ $r^2 = 0.068$	NA
Lion	pseudo- $F_{1,285} = 0.41$ $p = 0.62$ $r^2 = 0.0014$	pseudo- $F_{1,191} = 19.74$ p = 0.012* $r^2 = 0.094$	pseudo- $F_{1,202} = 23.23$ p = 0.048* $r^2 = 0.103$
Spotted hyaena	pseudo- $F_{1,205} = 1.32$ $p = 0.34$ $r^2 = 0.0064$	pseudo- $F_{1,131} = 19.74$ $p = 0.081$ $r^2 = 0.094$	pseudo- $F_{1,292} = 17.73$ p = 0.002* $r^2 = 0.057$

NA = not applicable due to lack of data.

*In bold = statistical evidence for significant results ($p < 0.05$)

Overall, the most frequent prey species (by occurrence) for wild dogs were impala (*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*), duiker (*Sylvicapra grimmia*) and bushbuck (*Tragelaphus scriptus*) (~94% of total diet;

where kudu and impala encompassed ~66% of the diet). In terms of biomass, kudu was the prey species with the highest contribution to the wild dog diet (~40%) followed by impala (~33%). For cheetahs, the most common prey were scrub hare (*Lepus saxatilis*), impala, duiker (*Sylvicapra grimmia*) and bushbuck (~80%), and impala the most important in terms of biomass (~37%). For leopards, the most common prey were duiker, bushbuck and steenbok (*Raphicerus campestris*) (~51%), and kudu the most important in terms of biomass (~20%). For lions, impala, kudu, buffalo (*Syncerus caffer*) and sable (*Hippotragus niger*) were the most common prey species (~42%), while the prey with the highest biomass contributions were buffalo, eland (*Taurotragus oryx*) and elephant (*Loxodonta africana*) (~42%). For hyaenas, the most important prey species both in terms of frequency and in terms of biomass were impala, kudu and sable (~42%); and in addition to these species, buffalo was important in terms of biomass (~16%) (Fig. 2; Supporting information, Fig. A2).

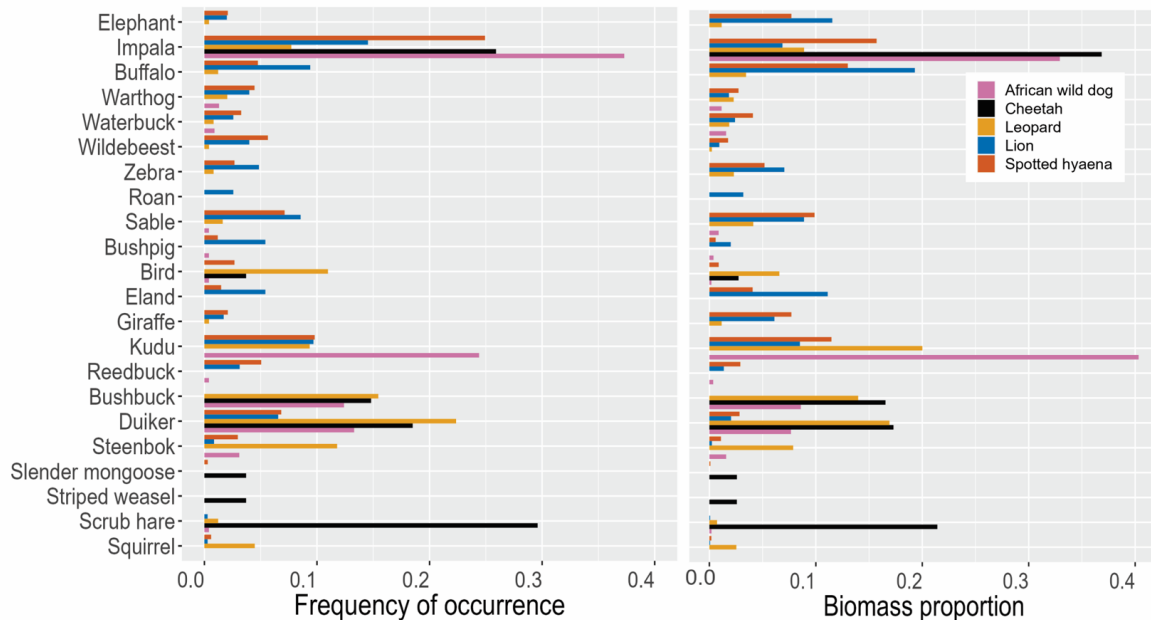


Figure 2 Frequency of occurrence and biomass proportion of prey species for the five large carnivores in Hwange National Park, Zimbabwe. Only including species with either frequency of occurrence or biomass larger than 0.03. Supporting information, Fig. A2 includes all species. Order from high water-dependent prey to low water-dependent prey.

Only in the low waterhole density area there was no statistical evidence that wild dog diet differed from the diet of both lions and hyaenas, this was consistent in terms of diet composition (lion: pseudo- $F_{1,74} = 1.079$, $p = 0.33$; hyaena: pseudo- $F_{1,129} = 1.56$, $p = 0.068$), in terms of prey water dependency (lion: pseudo- $F_{1,483} = 6.91$, $p = 0.70$; hyaena: pseudo- $F_{1,461} = 7.91$, $p = 0.25$) and prey size (lion: pseudo- $F_{1,74} = 1.54$, $p = 0.21$; hyaena: pseudo- $F_{1,129} = 1.62$, $p = 0.20$). Contrarily, in the high waterhole density area, wild dog diet differed significantly from the diet of the other

three predators in terms of diet composition, prey diet and prey size, but not in prey water dependency. Leopard diet composition was different from the diet of wild dogs in the areas tested (NW and SW), except in terms of prey diet and prey size in the low waterhole density area (Table 4, Supporting information, Tables A5b and A6).

Table 4. Differences between the diet of African wild dogs with the diet of other predators in Hwange National Park, Zimbabwe.
(Fig. 3 and Supporting information Fig. A2)

African wild dog vs.			
	Maximum waterhole density area	High waterhole density area	Low waterhole density area
Leopard	NA	pseudo-F _{1,113} = 5.66 p = 0.0019* r ² = 0.048	pseudo-F _{1,185} = 3.15 p = 0.0059* r ² = 0.017
Lion	pseudo-F _{1,236} = 12.77 p < 0.001* r ² = 0.051	pseudo-F _{1,216} = 13.89 p < 0.001* r ² = 0.06	pseudo-F _{1,74} = 1.079 p = 0.33 r ² = 0.014
Spotted hyaena	pseudo-F _{1,110} = 4.96 p = 0.24 r ² = 0.043	pseudo-F _{1,262} = 6.99 p < 0.001* r ² = 0.026	pseudo-F _{1,129} = 1.56 p = 0.072 r ² = 0.012

NA: not applicable due to lack of data.

*In bold = statistical evidence for significant results (p < 0.05)

Wild dog diet differed significantly between the high waterhole density area (NW) and the maximum waterhole density area (NE) in composition (pseudo-F_{1,167}= 4.14, p = 0.004), prey water dependency (pseudo-F_{1,167}= 4.65, p = 0.0012), and prey size (pseudo-F_{1,167}= 4.61, p = 0.015) (Supporting information, Table A5b, and A6). Wild dogs had a higher proportion of impala (medium mixed feeder) in their diet in the maximum waterhole density area (NE), a higher proportion of kudu

(large browser) in the high waterhole density area (NW), and a more diverse diet in the low waterhole density area (SW), including duiker and steenbok (Fig. 3). For lions there was some evidence that they had differences in their diet between the different areas ($p = 0.057$), for the other predators there was no evidence for differences in their diet in the different areas (Supporting information, Table A5b). However, when comparing prey water dependency in their diet, lions and hyaenas had a higher proportion of less water-dependent prey in the low waterhole density area (lion: pseudo- $F_{1,191} = 19.74$, $p = 0.012$; hyaena: pseudo- $F_{1,292} = 17.73$, $p = 0.002$), such as kudu and duiker for lion diet and duiker for hyaena diet (Table 3, Fig. 3; Supporting information, Fig. A3, Tables A7 and A8).

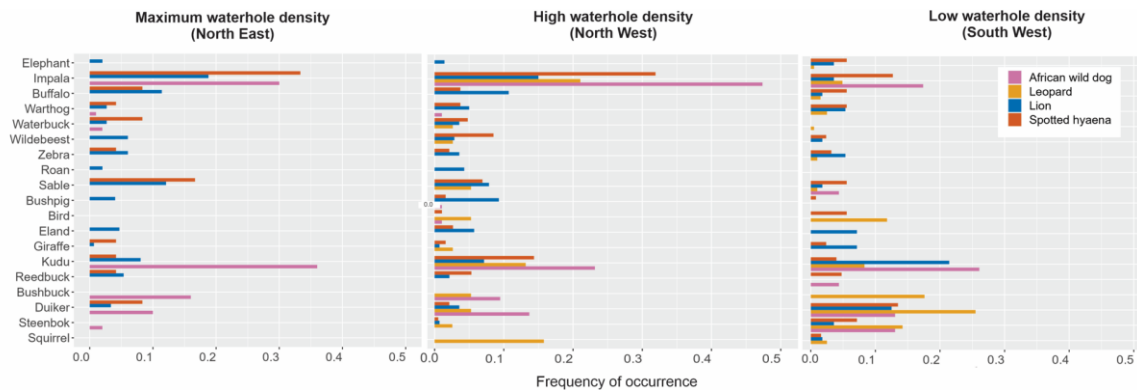


Figure 3 Frequency of occurrence per area of the proportions of the main prey in the diet of four predators in three different areas of Hwange National Park, Zimbabwe. Prey species are ordered by size. Only including species with the frequency of occurrence larger than 0.03. Supporting information, Fig. 3 includes all species. Order from high water-dependent prey to low water-dependent prey.

Overall, wild dogs had a high frequency of high and low water-dependent species (which also are medium mixed and browsing feeders) in their diet. We did not find any correlation of wild dog pack size with prey size (estimate = -0.02 (SE = 0.027); $p = 0.45$). Cheetahs and leopards consumed the highest proportion of low water dependent prey species (which also are small and medium mixed and browser species); whereas lions and hyaenas consumed a high frequency of water-dependent species (which also are large and medium grassland grazers and mixed feeders) in their diet (Supporting information, Fig. A4).

Diet overlap and niche breadth

In total, wild dog diet overlap was high with all predators (>0.55), but higher with hyaenas (0.85) and lions (0.71) (Supporting information, Table A2b; Fig. 4). There was more diet overlap between wild dogs and predators in the high and low waterhole density areas than in the maximum waterhole density area. In the low waterhole density area, wild dog and lion diet overlapped the most, while in the high waterhole density area wild dog and hyaena diet overlapped the most (Fig. 4). All Pianka's indices were significantly different from null models ($p < 0.05$). Overall, wild dogs had the narrowest niche breadth of the five predators. However, in the low waterhole density area, wild dogs had the broadest diet niche (Fig. 4).

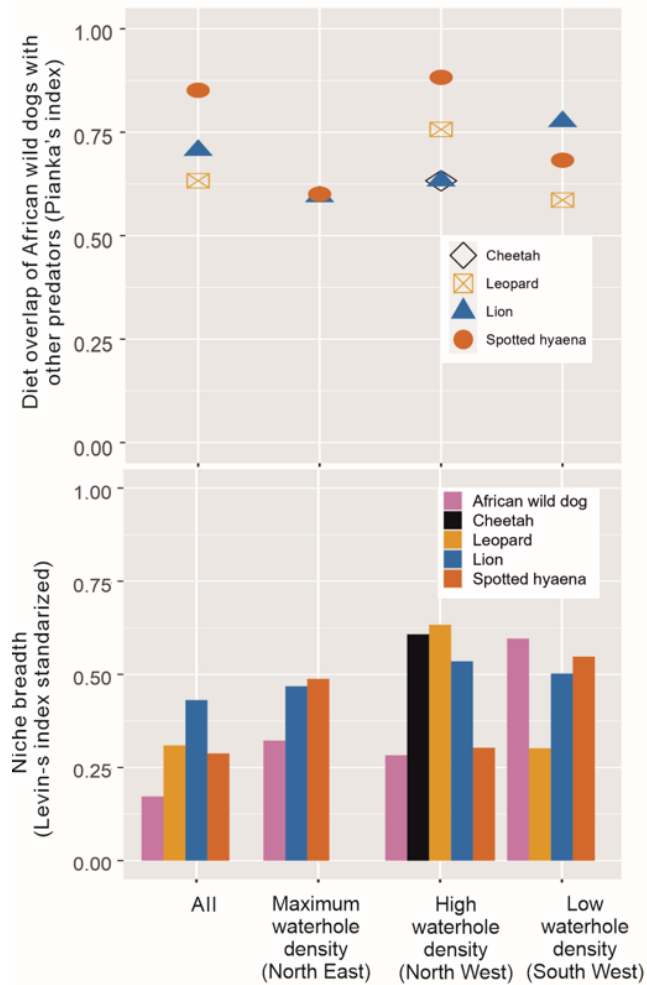


Figure 4 Diet overlap and dietary niche breadth of five predators in three different areas of Hwange National Park, Zimbabwe. Indices are calculated including carnivores in the predators diet. Data on cheetahs only in North West, no data of leopards in North East.

Prey preference

Kudu (medium water-dependent prey), duiker and bushbuck (low water-dependent prey) were preferred by wild dogs, cheetahs and leopards in all areas. In addition, leopards preferred impala, steenbok, sable, waterbuck (*Kobus*

ellipsiprymnus), wildebeest (*Connochaetes taurinus*) and giraffe (*Giraffa camelopardalis*). Lions and hyaenas preferred duiker, wildebeest, waterbuck, sable, eland, reedbuck (*Redunca arundinum*) and warthog (*Phacochoerus africanus*); and hyaenas also preferred kudu and giraffe. Only in the maximum waterhole density area wild dogs preferred waterbuck. In general, prey density and prey RAI gave similar results. Prey RAI results showed that most prey were less abundant in the low waterhole density area (Table 1, Supporting information, Table A4a). However, when we calculated Jacobs' index using prey density, buffalo was not preferred, and impala was only preferred in the maximum waterhole density area; but when using prey RAI both prey species were preferred (density values were higher than RAI values for both species) (Fig. 5; Supporting information, Fig. A5).

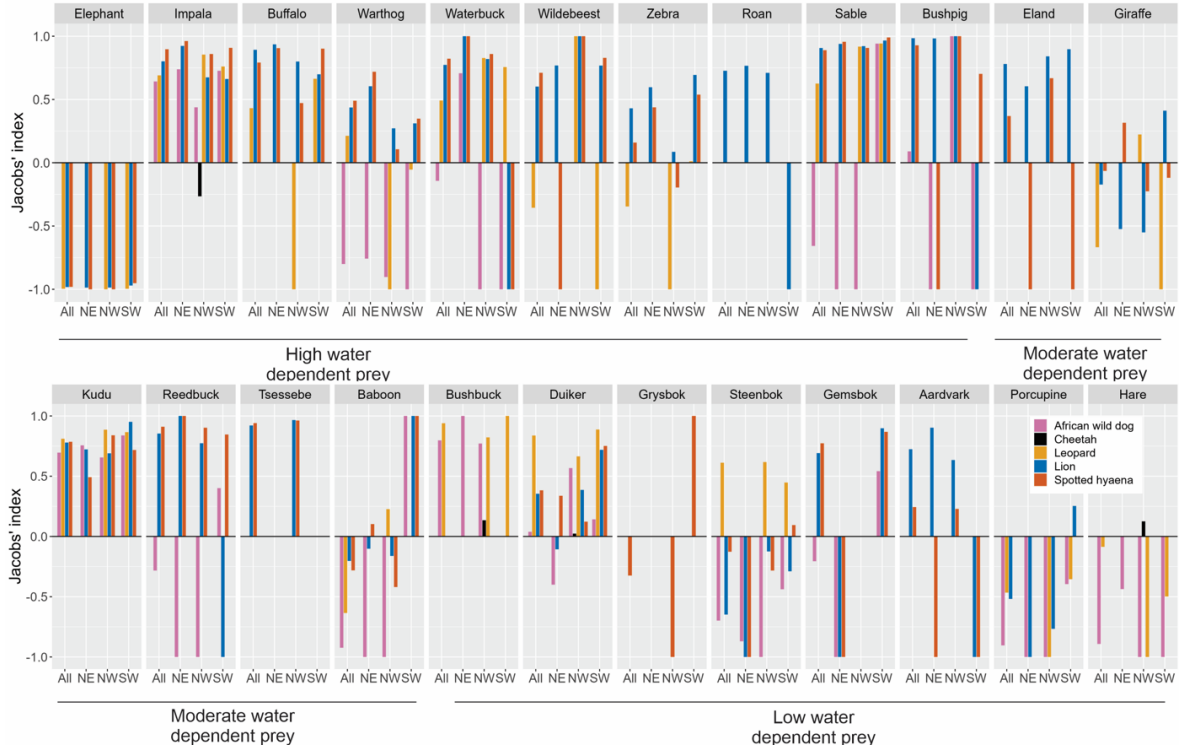


Figure 5 Diet preference (Jacobs' Index calculated with RAI – relative abundance index) of five predators in three different areas of Hwange National Park, Zimbabwe. NE = North East (Maximum waterhole density area); NW = North West (High waterhole density area); SW = South West (Low waterhole density area). Supporting information, Fig. A5 has the diet preference with Jacobs' Index calculated with prey density.

Discussion

Artificial water provisioning in arid and semi-arid ecosystems is a common practice throughout Africa (Owen-Smith 1996; Edwards et al. 2015; Sutherland et al. 2018). As water distribution can affect herbivores availability and abundance (Redfern et al. 2003; Valeix 2011), the competition level of predators over prey can

also be affected. In HNP, competition over prey was high between wild dogs and larger predators (cheetahs, leopards, lions, hyaenas), and the levels of food resource competition between wild dogs with dominant predators (lions and hyaenas) differed between areas with different waterhole densities associated to different levels of resource availability.

Diet composition

Wild dog diet overlap was high with all predators. Overall, it was highest with hyaenas, similar to findings from Breuer and Breuer (2005) and Mbizah et al. (2012), and lowest with leopard and cheetah diet. This contrasts with other studies where wild dog diet overlapped more with cheetah and leopard diet than with lion and hyaena diet (Hayward and Kerley 2008; Vogel et al. 2019). This might indicate that wild dogs are subjected to higher levels of dietary competition with the two most dominant predators (lions and hyaenas) in HNP than in other parts of Africa. This could add competition pressure of dominant predators to wild dogs in HNP.

Wild dogs, cheetahs and leopards preyed more upon less water-dependent species (which are mixed, browser, medium and smaller species). While, lions and hyaenas preyed more frequently upon high water-dependent species (which are grazers and larger sized species). These differences in prey categories could facilitate coexistence.

Contrary to our predictions that food resource competition was going to be different between seasons, season did not influence diet composition of predators nor the level of resource competition between wild dogs with lions and hyaenas. In HNP, Davidson et al. (2013), also found that overall there were no seasonal

differences in lion diet. In other carnivores and ecosystems, there were seasonal foraging differences that depended on seasonal food availability (Padial et al. 2002; Lanszki et al. 2020; Vissia et al. 2022). Our results demonstrate that the level of resource competition did not depend on prey fluctuation due to seasonality, as waterholes are also pumped in the dry season. Perhaps, instead of seeking different prey in different seasons, wild dogs focused on different age and sex classes of the same species (Pole 2000), depending on the breeding season of their main prey.

The main prey of wild dogs were impala, kudu, duiker and bushbuck. These results are consistent with other studies in HNP (Childes 1988; Van der Meer et al. 2013b) and other areas (Pole et al. 2004; Hayward et al. 2006; Mbizah et al. 2012). However, impala was not always preferred by wild dogs, but consumed according to availability. Prey size tends to increase with wild dog pack size (Creel and Creel 1995), but we did not find a correlation with pack size and prey size. This result could be because we did not consider prey age classes, or because even only one individual wild dog can kill large prey species such as a kudu (PDC unpublished data). In densely vegetated areas, wild dogs hunting success is higher (Creel and Creel 2002), and the risk of kleptoparasitism is lower (Creel and Creel 1996, 1998). Therefore wild dogs may prefer to make their kills in dense vegetation where kudus, bushbucks and duikers (as strict browsers) are commonly found (Valeix et al. 2009).

Resource competition in areas with different waterhole densities

In the low waterhole density area, the level of resource competition of wild dogs with lions and hyaenas was higher. This was mainly due to both dominant predators shifting their diet (lion and hyaena diet had a higher proportion of wild dogs preferred prey species in this area). Only in this area, wild dogs diet did not differ from lion and hyaena diet, nor did it differ in terms of prey diet and size with leopard diet (browsers were consumed more by the four predators). Browsers are less dependent on water than grazers (Redfern et al. 2003; Valeix 2011), which could also explain why browsers were consumed more in the low waterhole density area. In this area, wild dogs and leopards had a higher proportion of duiker and steenbok in their diet; hyaenas consumed proportionally more duikers compared to other areas; and lions consumed a significantly higher proportion of low water-dependent species (kudu, duiker, steenbok) than in other areas of HNP. For both dominant predators, in the driest area, there is less abundance of preferred prey, which are mainly large sized, grazers, and high water-dependent prey; this can explain why lions and hyaenas consume more prey preferred by wild dogs (prey smaller in size and less water dependent) in that area. All this potentially indicates a high level of resource competition between wild dogs with both dominant predators (especially with lions) in the area with the lowest waterhole density.

Wild dogs had the largest niche breadth in the low waterhole density area. In this area, wild dogs preferred prey included a wider range of prey species (i.e. sable, reedbuck, gemsbok [*Oryx gazelle*] and baboon [*Papio ursinus*]), which were avoided in the high and maximum density areas, possibly because these species are more dangerous to hunt (Van der Meer et al. 2019). Wild dogs would tend to

evade hunting these species to avoid any potential fitness costs imposed by hunting dangerous prey. Carnivores need to become more generalist when there is lower prey abundance (MacArthur and Levins 1967; Lanszki et al. 2019), especially subordinate carnivores competing with dominant ones for food (Dröge et al. 2017; Petroelje et al. 2021). Consequently, wild dogs might have had to broaden their niche breadth in this area to compensate for a high diet overlap with the dominant predators, as well as, due to a lower relative prey abundance.

Conservation implications

It is important to conserve complete predator guilds to preserve ecological processes (Dalerum et al. 2008). Although wild dogs are adapted to coexist with other predators as they have evolved with them for millennia (Turner 1990), water provisioning could potentially aggravate the interspecific competition of wild dogs by reducing areas to escape competition inside protected areas with high dominant predator densities and outside protected areas with high anthropogenic threats (Van der Meer et al. 2013a).

Wild dogs might not necessarily need an exclusive prey species to survive, as kudu, impala and duiker are also important prey for the four other predators, and bushbuck is a species also preferred by leopards and cheetahs. However, a reduction of prey abundance can increase food resource competition (Karanth and Sunquist 1995; Creel et al. 2018; Sévêque et al. 2020), which is what seems to be happening in the low waterhole density area in HNP.

Although wild dogs do not seem to be limited by prey availability (Creel and Creel 1998; Woodroffe et al. 2007), reducing prey availability can affect wild dogs

by increasing intraguild competition (Creel et al. 2018). Moreover, low prey abundance could affect wild dogs' reproduction (Marneweck et al. 2019b), potentially increase intraspecific competition between African wild dog packs (Marneweck et al. 2019a), and increase the probability of packs consuming livestock herewith provoking conflict with humans (Woodroffe et al. 2005).

It is crucial to conserve both density and diversity of prey, especially prey preferred by threatened predators (Hayward and Kerley 2008; Davidson et al. 2019). Kudu is an important species because it was preferred, and had frequency and high biomass contribution in the diet of most predators (especially in wild dog diet). In the low waterhole density area with high resource competition, and where lions and hyaenas were consuming a higher proportion of smaller prey less dependent on water (possibly because there was less abundance of large bodied prey), conserving large sized prey preferred, like eland and gemsbok, by lions and hyaenas, would most likely decrease the food competition on wild dogs. Hence, we emphasise not only to prioritize the conservation of kudu, but also the conservation of other large prey species moderately dependent on water, such as reedbuck, eland and gemsbok, mainly in areas with low waterhole density. This is consistent with Creel et al. 2018 who found that a lack of large bodied prey leads to more dietary competition. Hence, we propose to conserve these prey species by keeping their populations stable but not necessarily increasing their abundance. To prioritize the conservation of these prey species we recommend to avoid the culling of them, as well as to have enough spaces without too many waterholes: either by closing waterholes in the maximum waterhole density area, or by not creating more waterholes in areas with high waterhole densities.

In high waterhole density areas, there is a higher density of dominant predators (Loveridge et al. 2022), which means that there is a higher number of competitors for food in those areas. Moreover, if prey abundance is high (such as in high waterhole density areas), dominant carnivores' density can increase (Carbone and Gittleman 2002; Hayward et al. 2007), and have negative effects on wild dogs (Creel and Creel 1996, 1998), such as excluding them from prey rich areas (Creel 2001), or even through direct mortality (Prugh and Sivy 2020). When food resource competition is high, diet partitioning might not play a major role in predators' niche segregation for coexistence. Instead, in those cases, spatiotemporal dimensions might be the main mechanisms allowing coexistence, such as wild dogs hunting in crepuscular times and dominant predators hunting at night, or by wild dogs avoiding areas highly used by lions (Bruno et al. 2003; Dröge et al. 2017; Tsunoda et al. 2019; Vissia et al. 2022).

Low waterhole density in the ecosystem increases food resource competition (especially with lions); but high waterhole density in the ecosystem (where there is more prey availability), can increase the density of predators (Macdonald 2016), and hence, increase the risks involved in interspecific competition on wild dogs (Creel 2001). Thus, we emphasize the need to maintain heterogeneity in water management actions.

Conclusion

Resource competition between wild dogs with larger predators, driven by fluctuations of prey availability and abundance, differed between areas with different waterhole densities, but not between seasons. Dietary competition of wild

dogs with dominant predators (especially with lions) was highest in the low waterhole density area. To reduce food resource competition (exploitative competition) on wild dogs, we propose to conserve larger-bodied prey that are less dependent on water. As food resource competition was high between wild dogs with the four larger predators, spatiotemporal partitioning might be playing a major role to allow coexistence.

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Conflict of Interest

None declared.

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Authors' contributions

E.S.S., M.V., E.M., E.D. and A.J.L. conceived the idea; M.M.M., S.P. and S.P.C. collected and processed the scat samples; E.S.S. processed the data, did the analyses, and led the writing of the manuscript; D.M, H.M and P.B supervised data collection. All authors gave feedback to the drafts and final approval for publication.

Data Availability Statement

The data is available in:

https://figshare.com/articles/dataset/Sandoval_Seres_et_al_2024_Food_resource_competition_between_African_wild_dogs_and_larger_carnivores_in_an_ecosystem_with_artificial_water_provision_csv/25112936

doi: 10.6084/m9.figshare.25112936

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Supporting information Chapter 2

Food resource competition between African wild dogs and larger carnivores in an ecosystem with artificial water provision

Supporting information

Table A1. Prey categories in the diet of African wild dogs, lions and spotted hyaenas in Hwange National Park, Zimbabwe.

Prey (Common name)	Prey (Scientific name)	Prey water dependency	Prey diet	Adult female weight (kg)	Prey size	In predators diet AWD = African wild dog. CH = Cheetah. LE = Leopard. LI = Lion. SH = Spotted hyaena.
Aardvark	<i>Orycteropus afer</i>	Low	Other	50	M	LI SH
African wild dog	<i>Lycaon pictus</i>	Low	Carnivore	23	S	LI SH
Baboon	<i>Papio ursinus</i>	Moderate	Omnivorous	21	S	AWD LI SH
Banded mongoose	<i>Mungos mungo</i>	Low	Carnivore	1.8	XS	LI SH
Bat-eared fox	<i>Otocyon megalotis</i>	Low	Carnivore	4	XS	AWD LE
Bird		High	Other	1	XS	AWD CH LE SH
Buffalo	<i>Syncerus caffer</i>	High	Grassland grazers	450	XL	LE LI SH
Bushbuck	<i>Tragelaphus scriptus</i>	Low	Mixed	35	M	AWD CH
Bushpig	<i>Potamochoerus larvatus</i>	High	Omnivorous	59	M	AWD LE LI SH
Caracal	<i>Caracal caracal</i>	Low	Carnivore	10.5	S	LE LI
Cheetah	<i>Acinonyx jubatus</i>	Low	Carnivore	50	M	LE LI SH
Common genet	<i>Genetta genetta</i>	Low	Carnivore	1.5	XS	LE
Domestic cow	<i>Bos taurus</i>	High	Grassland grazers	306	L	AWD SH
Domestic sheep	<i>Ovis aries</i>	High	Grassland grazers	42	M	LE LI
Duiker	<i>Sylvicapra grimmia</i>	Low	Browser	20	S	AWD CH LI SH

Prey (Common name)	Prey (Scientific name)	Prey water dependency	Prey group/diet	Adult Female weight (kg)	Prey size	In predators diet
Eland	<i>Taurotragus oryx</i>	Moderate	Mixed	450	XL	LE LI SH
Elephant	<i>Loxodonta africana</i>	High	Mixed	2275	XL	LI SH
Fox		Low	Carnivore	4	XS	AWD
Gemsbok	<i>Oryx gazella</i>	Low	Woodland grazers	225	L	AWD LE LI SH
Giraffe	<i>Giraffa camelopardalis</i>	Moderate	Browser	825	XL	LE LI SH
Honey badger	<i>Mellivora capensis</i>	Low	Carnivore	11.5	S	LE SH
Impala	<i>Aepyceros melampus</i>	High	Mixed	60	M	AWD CH LI SH
Jackal		Low	Carnivore	9	S	SH
Klipspringer	<i>Oreotragus oreotragus</i>	Low	Mixed	13.2	S	AWD LI
Kudu	<i>Tragelaphus strepsiceros</i>	Moderate	Browser	160	L	AWD LE LI SH
Marsh mongoose	<i>Atilax paludinosus</i>	Low	Carnivore	3.7	XS	LE LI SH
Mice		Unknown	Other	0.5	XS	AWD LE SH
Pangolin	<i>Smutsia temminckii</i>	Low	Other	9	S	LE
Porcupine	<i>Hystrix africaeaustralis</i>	Low	Other	17	S	AWD LI
Reedbuck	<i>Redunca arundinum</i>	Moderate	Grassland grazers	50	M	AWD LI SH
Roan	<i>Hippotragus equinus</i>	High	Woodland grazers	250	L	LI
Sable	<i>Hippotragus niger</i>	High	Woodland grazers	200	L	AWD LE LI SH

Prey (Common name)	Prey (Scientific name)	Prey water dependency	Prey group/diet	Adult Female weight (kg)	Prey size	In predators diet
Scrub hare	<i>Lepus saxatilis</i>	Low	Other	3	XS	AWD CH LI
Sharpe's grysbok	<i>Raphicerus sharpei</i>	Low	Browser	7.5	S	SH
Slender mongoose	<i>Galerella sanguinea</i>	Low	Carnivore	0.6	XS	CH SH
Snake		Low	Other	1	XS	LE
Spotted hyaena	<i>Crocuta crocuta</i>	Low	Carnivore	65	M	LI
Squirrel		Low	Other	0.7	XS	LE LI SH
Steenbok	<i>Raphicerus campestris</i>	Low	Browser	11	S	AWD LE LI SH
Striped polecat	<i>Ictonyx striatus</i>	Low	Carnivore	1.1	XS	SH
Striped weasel	<i>Poecilogale albinucha</i>	Low	Carnivore	0.5	XS	LI SH
Tsessebe	<i>Damaliscus lunatus</i>	Moderate	Grassland grazers	126	L	CH
Vervet monkey	<i>Chlorocebus pygerythrus</i>	Moderate	Omnivorous	4.2	XS	LE LI SH
Warthog	<i>Phacochoerus africanus</i>	High	Grassland grazers	57	M	AWD LE LI SH
Waterbuck	<i>Kobus ellipsiprymnus</i>	High	Grassland grazers	175	L	AWD LI SH
White-tailed mongoose	<i>Ichneumia albicauda</i>	Low	Carnivore	3.5	XS	LI
Wildebeest	<i>Connochaetes taurinus</i>	High	Grassland grazers	180	L	LE LI SH
Zebra	<i>Equus quagga</i>	High	Grassland grazers	302	L	LE LI SH

Table A2a. Number of samples and species in the diet of five predators in Hwange National Park, Zimbabwe.

Predator	Season or Region	Number of items	Number of scats	Number of species
African wild dog	Early Dry Wet	130	105	9
	Late Dry	113	104	17
	Nomadic	138	121	17
	Denning	72	63	8
	North East	100	89	10
	North West	95	80	9
	South West	23	21	11
	Total*	225	209	20
		(64 in years 2012-2015)	(53 in years 2012-2015)	(14 in years 2012-2015)
Cheetah	Early Dry Wet	14	15	4
	Late Dry	11	11	6
	North West	25	26	7
Leopard	Early Dry Wet	14	14	9
	Late Dry	28	190	10
	Nomadic	15	12	8
	Breeding	26	26	22
	North East	4	3	4
	North West	39	35	13
	South West	203	166	21
	Total	246	204	25
Lion	Early Dry Wet	99	98	26
	Late Dry	243	241	30
	Nomadic	79	76	20
	Breeding	207	207	27
	North East	149	149	23
	North West	140	138	25
	South West	56	55	21
	Global*	351	342	33
Spotted hyaena	Early Dry Wet	40	38	15
	Late Dry	296	278	33
	Nomadic	125	122	19
	Breeding	86	81	16
	North East	24	23	11
	North West	188	184	20
	South West	125	110	27
	Total*	337	317	33

Total numbers do not necessarily match the sum of the other categories because some scat samples had missing information on location or seasonality. Numbers in red: scat samples with less than a minimum of 59 scats to describe a site species diet containing 12 or more species (Trites and Joy 2005). Analyses were not performed when there were less than 21 scats. To perform any analyses species accumulation curves needed to arrive almost to an asymptote (Appendix A, Figure A1b). Nomadic refers to wild dogs' nomadic season (not breeding), and breeding refers to wild dogs' denning. Both seasons only include data on the North West and North East of Hwange National Park.

Table A2b. Diet overlap (Pianka's index) of African wild dogs with four predators in Hwange National Park, Zimbabwe.

	In years 2012-2015	In years 2012-2019
Cheetah	0.59	0.63
Leopard	0.61	0.63
Lion	0.74	0.71
Spotted hyaena	0.89	0.85

Table A3a. Prey density (individuals / km²) in the north of Hwange National Park, Zimbabwe (2012-2015).

Density used to calculate the diet preference of cheetahs, leopards, lions, and spotted hyaenas.

Prey species	North			North East			North West		
	Density	Lci	Uci	Density	Lci	Uci	Density	Lci	Uci
Baboon (2012-2019)	0.51	0.29	0.89	0.40	0.18	0.90	0.61	0.30	1.23
Buffalo (2012-2017)	3.05	1.82	5.12	2.09	1.21	3.62	4.01	1.97	8.16
Duiker	0.07	0.05	0.10	0.13	0.09	0.20	0.01	0.00	0.03
Eland (2012-2019)	0.02	0.01	0.04	0.04	0.02	0.08	0.0003	0.000	0.001
Elephant	3.84	3.40	4.33	5.16	4.49	5.93	2.52	2.07	3.05
Giraffe	0.35	0.29	0.43	0.46	0.37	0.58	0.24	0.18	0.33
Impala	6.40	5.39	7.62	2.09	1.48	2.95	11.2	9.18	13.67
Kudu	1.53	1.28	1.83	1.42	1.18	1.70	1.65	1.29	2.12
Reedbuck (2012-2016)	0.08	0.05	0.13	0.00	0.00	0.00	0.17	0.11	0.27
Roan	0.11	0.06	0.19	0.12	0.06	0.25	0.10	0.05	0.22
Sable (2012-2016)	0.06	0.04	0.09	0.09	0.06	0.15	0.03	0.01	0.07
Steenbok (2012-2019)	0.98	0.86	1.11	1.87	1.65	2.12	0.07	0.05	0.11
Warthog	0.70	0.59	0.83	0.39	0.30	0.50	1.01	0.83	1.24
Waterbuck (2012-2017)	0.11	0.08	0.15	0.08	0.05	0.13	0.14	0.09	0.21
Wildebeest (2012-2016)	0.22	0.14	0.35	0.43	0.27	0.67	0.01	0.01	0.03
Zebra	1.02	0.85	1.23	1.31	1.08	1.60	0.73	0.52	1.03

Lci = lower confidence interval; Uci = upper confidence interval.
All densities include both seasons.

Table A3b. Prey density (individuals / km²) in the north of Hwange National Park, Zimbabwe (2012-2019).

Density used to calculate the diet preference of African wild dogs.

Prey species	North			North East			North West		
	Density	Lci	Uci	Density	Lci	Uci	Density	Lci	Uci
Baboon	0.51	0.29	0.89	0.40	0.18	0.90	0.61	0.30	1.23
Duiker	0.08	0.06	0.09	0.13	0.11	0.17	0.02	0.01	0.03
Impala	6.32	5.52	7.23	1.63	1.34	2.00	10.94	9.42	1.27
Kudu	1.12	0.99	1.27	1.18	1.04	1.34	1.07	0.89	1.28
Reedbuck	0.07	0.05	0.11	0.00	0.00	0.01	0.15	0.10	0.21
Sable	0.08	0.05	0.12	0.14	0.10	0.21	0.02	0.01	0.05
Steenbok	0.98	0.86	1.11	1.87	1.65	2.12	0.07	0.05	0.11
Warthog	0.71	0.62	0.80	0.38	0.32	0.46	1.03	0.89	1.19
Waterbuck	0.10	0.07	0.14	0.09	0.06	0.13	0.12	0.08	0.18

Lci = lower confidence interval; Uci = upper confidence interval.

All densities include both seasons.

Table A4a. Average of relative abundance index (RAI) (independent records/ trap-days) of prey in Hwange National Park, Zimbabwe (2013-2015).

RAI used to calculate the diet preference of cheetahs, leopards, lions, and spotted hyaenas.

Prey species	Total	North East (Max whd) (2014, 2015)	North West (High whd) (2013, 2014)	South West (Low whd) (2013, 2017)
Aardvark	0.35	0.16	0.56	0.22
Baboon	7.95	7.52	8.38	
Buffalo	1.11	0.99	2.28	0.46
Bushbuck	1.36		1.36	
Bushpig	0.09	0.09		0.21
Duiker	6.08	9.47	2.77	3.30
Eland	1.32	2.77	0.90	0.60
Elephant	124.28	166.26	112.17	90.24
Gemsbok	0.29	0.17		0.43
Giraffe	4.51	4.86	4.15	4.44
Impala	3.49	2.12	5.74	1.07
Kudu	2.48	3.21	2.40	1.01
Porcupine	4.96	2.09	8.84	3.07
Reedbuck	0.48		0.48	0.62
Roan	0.78	0.62	1.29	0.17
Sable	0.86	0.99	0.60	0.04
Sharpe's grysbok	1.11		1.11	
Steenbok	7.27	10.34	1.57	8.88
Tsessebe	0.18		0.18	
Warthog	3.01	1.55	5.03	4.12
Waterbuck	0.63		0.63	0.10
Wildebeest	1.92	1.92		0.34
Zebra	3.74	3.68	5.19	1.45

RAI average of surveys performed in nine different sites shown in Figure A1.

For South West 2017 year was added to include more than only one survey in the region.

whd = waterhole density.

Blank spaces mean that there were no observations to calculate RAI.

Table A4b. Average of relative abundance index (RAI) (independent records/ trap-days) of prey in Hwange National Park, Zimbabwe (2013-2019).

RAI used to calculate the diet preference of African wild dogs.

Prey species	Total	North East (Max whd) (2014, 2015, 2018)	North West (High whd) (2013, 2014, 2019)	South West (Low whd) (2013, 2017)
Baboon	8.29	8.45	8.02	
Bat-eared fox	0.58	0.76	0.61	0.19
Bushbuck	0.72		0.72	
Bushpig	0.17	0.15		0.21
Duiker	5.64	8.40	2.25	3.30
Gemsbok	0.30	0.11		0.43
Impala	5.26	2.50	14.06	1.07
Kudu	2.50	2.99	3.17	1.01
Porcupine	3.67	1.88	7.27	3.07
Reedbuck	0.36	0.29	0.26	0.62
Sable	0.96	1.37	0.37	0.04
Scrub hare	3.28	1.03	3.87	6.63
Steenbok	6.90	9.24	1.81	8.88
Warthog	4.90	2.79	9.21	4.12
Waterbuck	0.53	0.14	0.81	0.10

RAI average of surveys performed in nine different sites shown in Figure A1.

Blank spaces mean that there were no observations to calculate the relative abundance index.

whd = waterhole density.

Table A5a. Seasonal diet comparisons of African wild dogs, lions and spotted hyaenas in Hwange National Park, Zimbabwe.

	Weather season	Behavioural season
Season	pseudo-F _{1,839} = 2.31	pseudo-F _{2,815} = 4.95
A difference in diet of predators between seasons	p = 0.79 r ² = 0.0027	p = 0.14 r ² = 0.012
Predator	pseudo-F _{2,839} = 11.76 p < 0.001* r ² = 0.0027	pseudo-F _{2,815} = 8.83 p < 0.001* r ² = 0.021
Season*Predator a difference in diet for each predator between seasons	pseudo-F _{2,839} = 1.14 p = 0.59 r ² = 0.0026	pseudo-F _{1,815} = 0.64 p = 0.16 r ² = 0.0017

PERMANOVA results. * significant differences: p < 0.05

Table A5b. Regional diet differences of predators in Hwange National Park, Zimbabwe.

	Maximum whd (NE) vs. High whd (NW)	High whd (NW) vs. Low whd (SW)	Maximum whd (NE) vs. Low whd (SW)
African wild dog	pseudo-F _{1,167} = 4.14 p = 0.0039* r ² = 0.024	pseudo-F _{1,99} = 3.59 p = 0.35 r ² = 0.035	pseudo-F _{1,108} = 2.036 p = 0.52 r ² = 0.018

All areas compared

(as results were also non-significant when compared one area against another one)

Leopard	pseudo-F _{2,201} = 3.27 p = 0.13 r ² = 0.031
Lion	pseudo-F _{2,339} = 2.67 p = 0.057 r ² = 0.016
Spotted hyaena	pseudo-F _{2,314} = 3.63 p = 0.32 r ² = 0.023

PERMANOVA results.
whd= waterhole density.

Table A6. Differences between the diet of African wild dogs with the diet of other predators per area and per prey category in Hwange National Park, Zimbabwe.

	African wild dogs vs.		
	Leopard	Lion	Spotted hyaena
Prey water dependency			
Maximum whd (NE)	NA	No differences in any areas.	No differences in any areas.
High whd (NW)	pseudo-F _{1,113} = 61.37 p = 0.081 r ² = 0.012	pseudo-F _{1,483} = 6.91 p = 0.70 r ² = 0.014	pseudo-F _{1,461} = 7.91 p = 0.25 r ² = 0.017
Low whd (SW)	pseudo-F _{1,185} = 5.27 p = 0.0069* r ² = 0.028		
Prey diet			
Maximum whd (NE)	NA	pseudo-F _{1,236} = 25.92 p = 0.0019* r ² = 0.099	pseudo-F _{1,110} = 7.38 p = 0.14 r ² = 0.063
High whd (NW)	pseudo-F _{1,113} = 11.28 p = 0.0029* r ² = 0.091	pseudo-F _{1,216} = 29.36 p < 0.001* r ² = 0.12	pseudo-F _{1,262} = 20.57 p = 0.0019* r ² = 0.073
Low whd (SW)	pseudo-F _{1,185} = 0.14 p = 0.65 r ² = 0.0026	pseudo-F _{1,74} = 0.069 p = 0.92 r ² = 0.0009	pseudo-F _{1,129} = 2.69 p = 0.021* r ² = 0.024
Prey size			
Maximum whd (NE)	NA	pseudo-F _{1,236} = 4.95 p = 0.042 r ² = 0.021	pseudo-F _{1,110} = 0.86 p = 0.57 r ² = 0.0078
High whd (NW)	pseudo-F _{1,113} = 9.98 p < 0.001* r ² = 0.081	pseudo-F _{1,216} = 10.95 p = 0.002* r ² = 0.048	pseudo-F _{1,262} = 8.53 p = 0.0069* r ² = 0.031
Low whd (SW)	pseudo-F _{1,185} = 2.55 p = 0.071 r ² = 0.014	pseudo-F _{1,74} = 1.54 p = 0.21 r ² = 0.020	pseudo-F _{1,129} = 1.62 p = 0.20 r ² = 0.012

whd = waterhole density.

NA = not applicable, not tested due to lack of data.

Table A7. Differences on prey categories in the diet of predators in Hwange National Park, Zimbabwe.

	Maximum whd (NE) vs. High whd (NW)	High whd (NW) vs. Low whd (SW)	Maximum whd (NE) vs. Low whd (SW)
Prey diet			
African wild dog	pseudo-F _{1,167} = 2.87 p = 0.048 r ² = 0.017	pseudo-F _{1,99} = 6.68 p = 0.52 r ² = 0.061	pseudo-F _{1,108} = 2.39 p = 0.26 r ² = 0.021
Leopard	NA	pseudo-F _{1,199} = 7.37 p = 0.13 r ² = 0.036	NA
Lion	No differences in regions. pseudo-F _{2,339} = 5.52, p = 0.11, r ² = 0.031		
Spotted hyaena	No differences in regions. pseudo-F _{2,314} = 2.66, p = 0.53, r ² = 0.017		
Prey size			
African wild dog	pseudo-F _{1,167} = 4.61 p = 0.015* r ² = 0.027	pseudo-F _{1,99} = 7.99 p = 0.29 r ² = 0.074	pseudo-F _{1,108} = 4.52 p = 0.20 r ² = 0.040
Leopard	NA	pseudo-F _{1,199} = 6.27 p = 0.46 r ² = 0.031	NA
Lion	No differences in regions. pseudo-F _{2,339} = 2.83, p = 0.17, r ² = 0.016		
Spotted hyaena	No differences in regions. pseudo-F _{2,314} = 8.00, p = 0.37, r ² = 0.048		

NA = not applicable, not tested due to lack of data.
whd = waterhole density.

Table A8. Percentage of prey water dependency in the diet of four predators in three different regions of Hwange National Park, Zimbabwe.

Prey water dependency	African wild dog			Leopard		Lion			Spotted hyaena		
	Max whd NE	High whd NW	Low whd SW	High whd NW	Low whd SW	Max whd NE	High whd NW	Low whd SW	Max whd NE	High whd NW	Low whd SW
High	32%	49%	23%	45%	25%	59%	63%	26%	63%	50%	47%
Moderate	37%	23%	36%	26%	9%	23%	27%	40%	17%	31%	14%
Low	31%	28%	41%	29%	66%	18%	10%	34%	21%	19%	39%

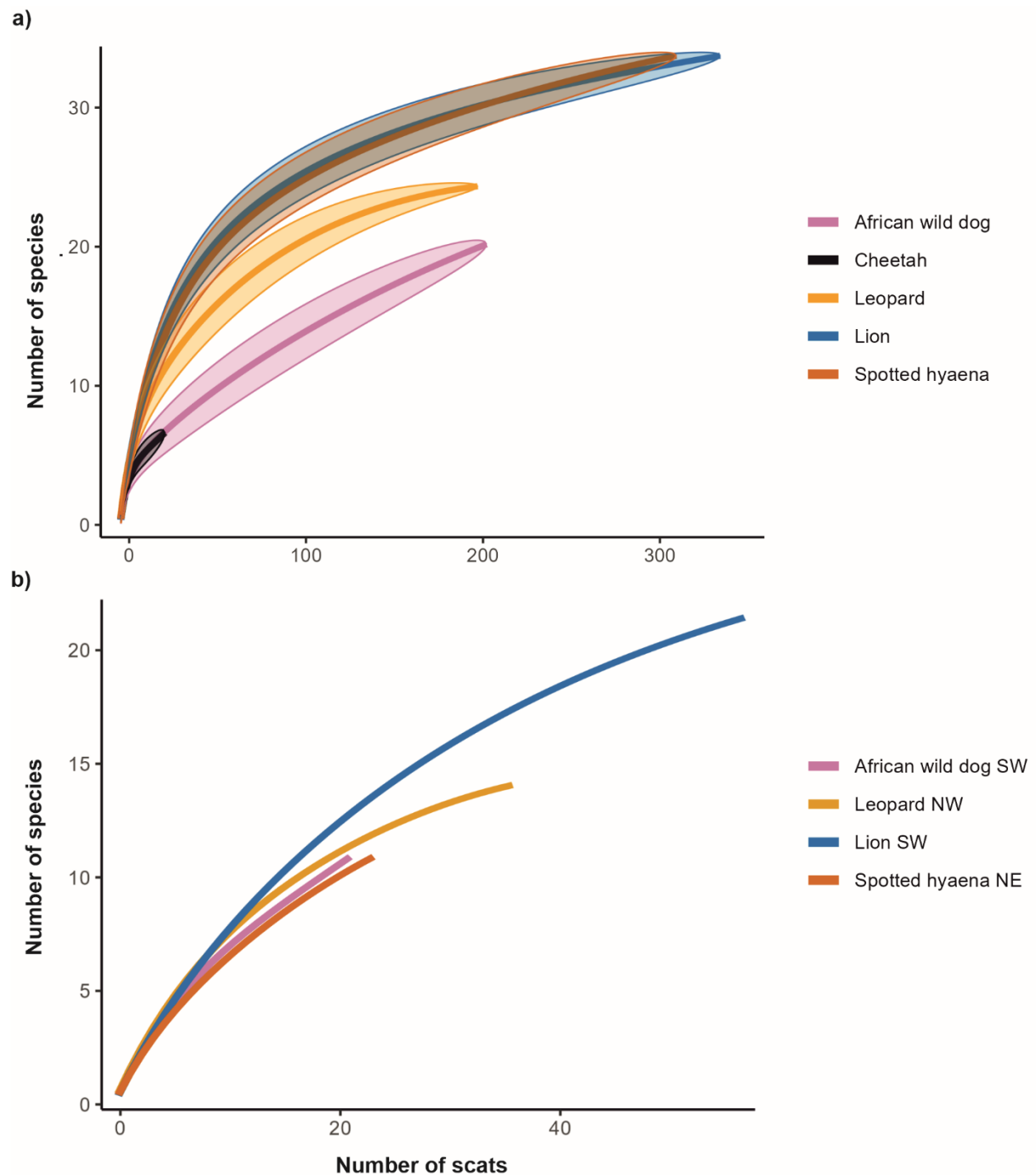


Figure A1 a) Species accumulation curve of expected mean prey richness from five predator scats collected in Hwange National Park, Zimbabwe, 2012– 2019. The shadow area represents 95% confidence intervals based on 10,000 permutations. b) Species accumulation curve of expected mean prey richness from four predator scats collected in three specific areas of Hwange National Park, Zimbabwe, 2012– 2019. Areas: SW = South West; NW = North West; NE = North East.

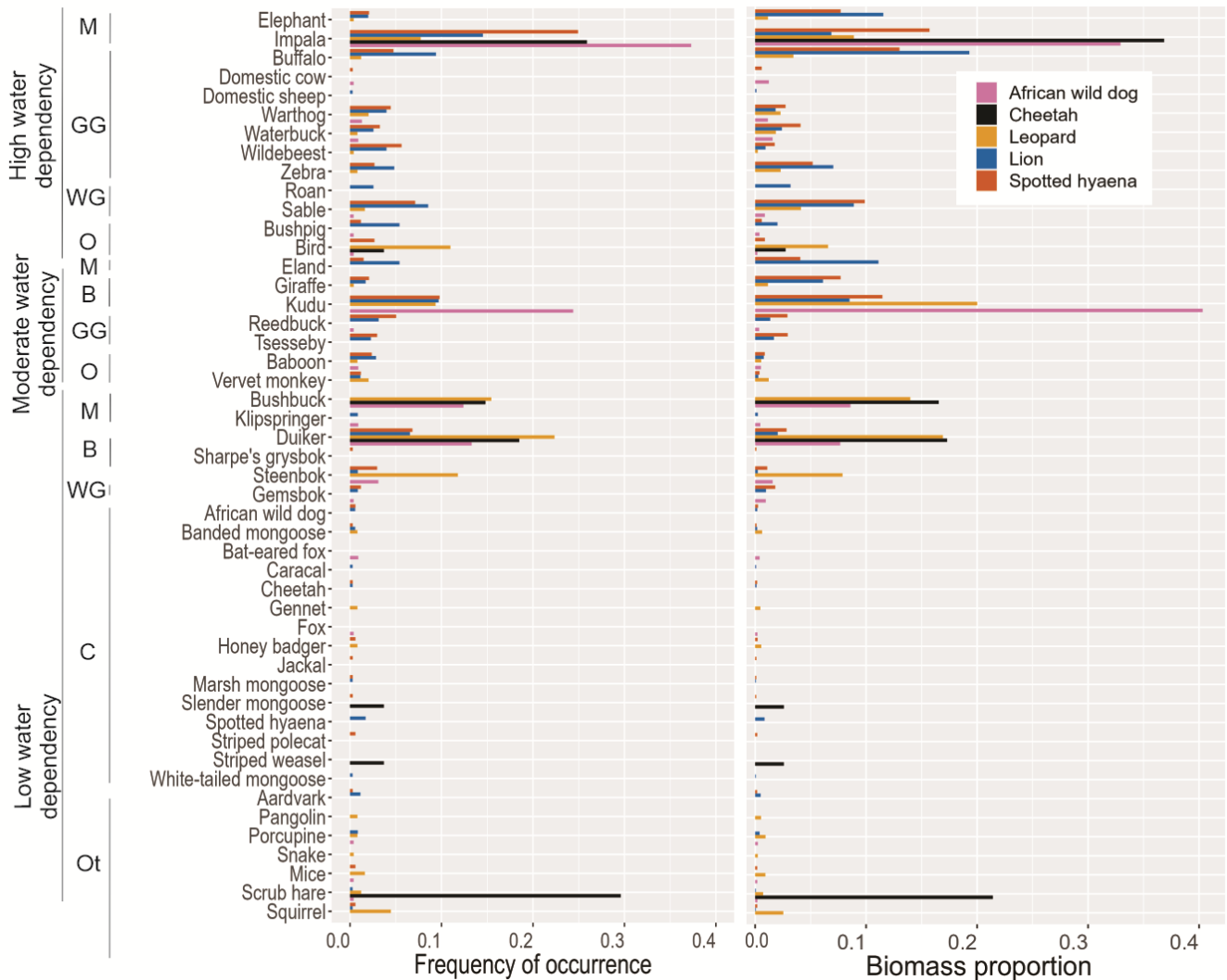


Figure A2 Frequency of occurrence and biomass proportion of the diet of five predators in Hwange National Park, Zimbabwe. Prey species are ordered first by water dependency and then by prey diet: M = mixed (browser, grazer), B = browser, GG: grassland grazer, WG = woodland grazer, O = omnivorous, C = Carnivore, Ot = other.

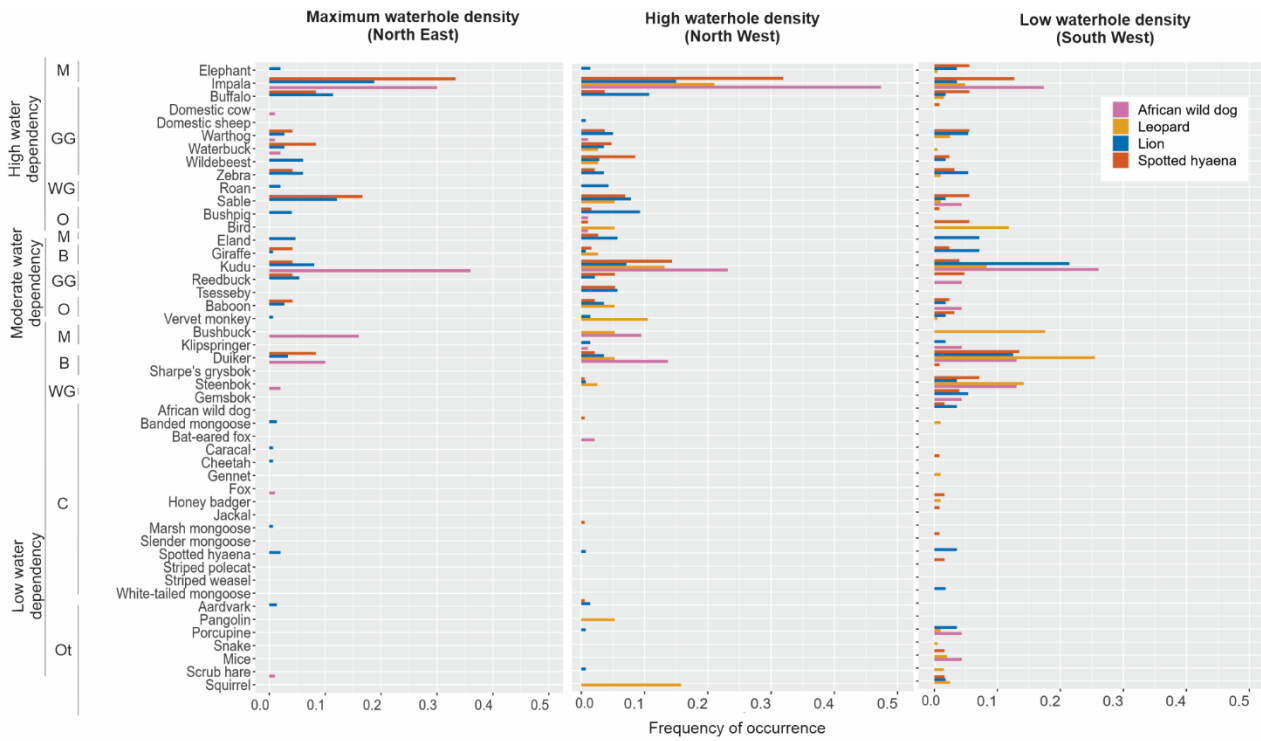


Figure A3 Frequency of occurrence per area of the diet of five predators in three areas of Hwange National Park, Zimbabwe. Prey species are ordered first by water dependency and then by prey diet: M = mixed (browser, grazer), B = browser, GG: grassland grazer, WG = woodland grazer, O = omnivorous, C = Carnivore, Ot = other.

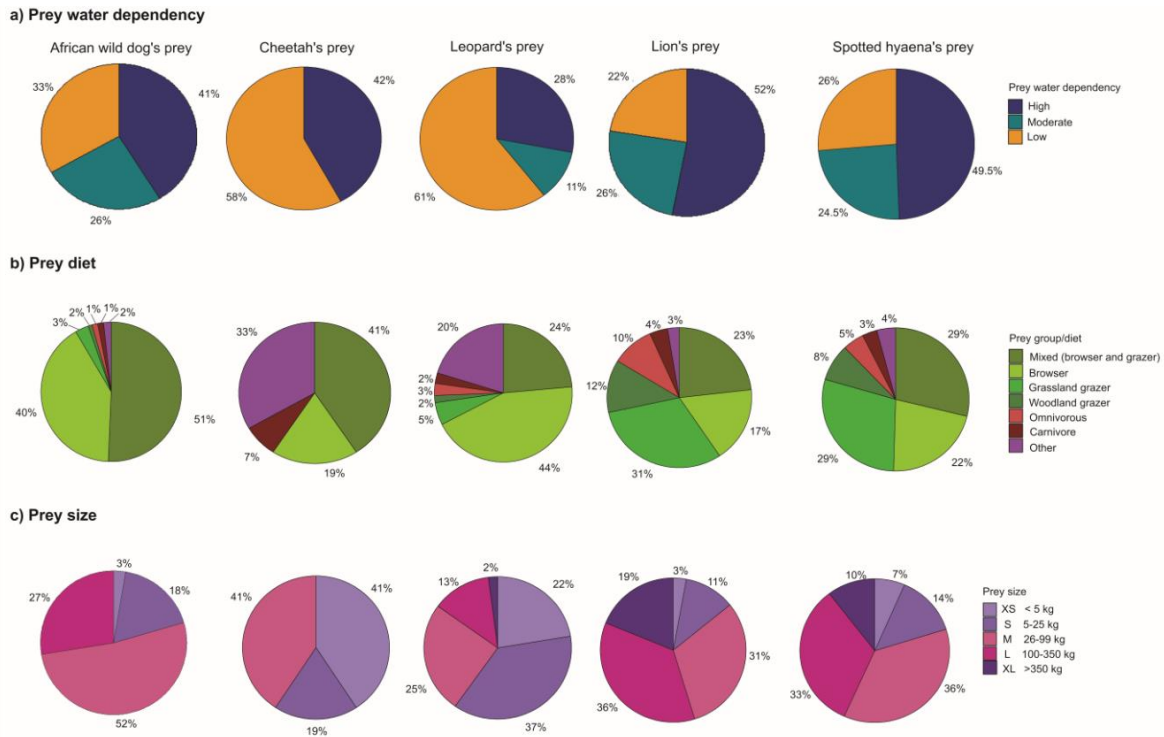


Figure A4 Distribution of a) Prey water dependency, b) prey diet, and c) prey size of the five large predators in Hwange National Park, Zimbabwe.

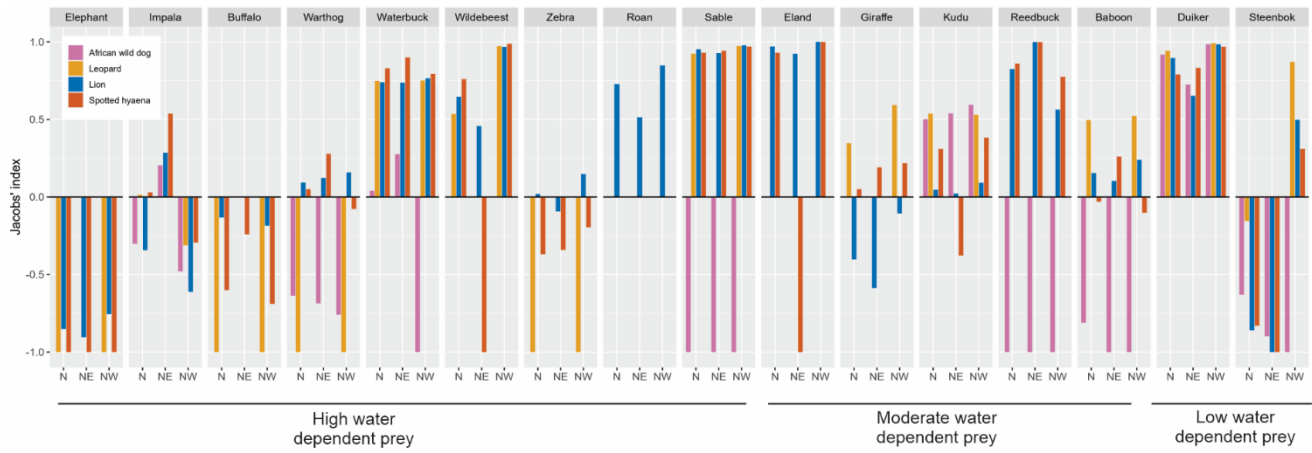


Figure A5 Diet preference (Jacobs' Index calculated with prey density) of five predators in Hwange National Park, Zimbabwe. N = North (only including NE and NW); NE = North East (Maximum waterhole density area); NW = North West (High waterhole density area). Cheetah not included due to little sample size.

Supplementary references:

Trites AW, Joy R (2005) Dietary Analysis From Fecal Samples: How Many Scats Are Enough? *J Mammal* 86:704–712.

Chapter 3

Water availability affects the risk of kleptoparasitism of African wild dogs by larger dominant predators

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Abstract

Dominant predators can steal food from smaller and subordinate predators. We experimentally assessed whether the availability of surface water, influenced by water provisioning management, affects the risk of kleptoparasitism by dominant predators (lions and spotted hyaenas) on African wild dogs in Hwange National Park, Zimbabwe. We performed playbacks of a soundtrack of African wild dogs killing an impala at waterholes and 5 km away from them, and performed hurdle model analyses. The probability of dominant predators arriving at a playback location and the time it took them to arrive (median: 13 and 21 minutes for hyaenas and lions, respectively) did not depend on water distribution, however the number of dominant predators arriving at a playback location was lower far from waterholes, and in low waterhole density areas. A high number of dominant predators arriving at wild dog kills imposes a high threat to wild dogs not only through kleptoparasitism but also through the risk of agonistic encounters. We propose water management solutions to lower kleptoparasitism and the risk to wild dogs of agonistic encounters with dominant predators in ecosystems with artificial provisioned waterholes: i.e. by limiting new artificial waterholes in high waterhole density areas, and avoiding spatially homogeneous water provisioning.

Key words: dominant carnivores, interspecific competition, kleptoparasitism, *Lycaon pictus*, playback experiments, subordinate carnivores, waterholes, water management.

Introduction

Among processes to acquire food resources in carnivore species, kleptoparasitism (i.e. stealing food from another species) occurs in situations where the success of hunting is not as high as the success of stealing food, or the cost of hunting (i.e. searching for and handling food) is higher than the cost of kleptoparasitism (i.e. searching for kleptoparasitism opportunities and confronting the victim of kleptoparasitism) (Broom & Ruxton 1998; Hamilton 2002). When competitive differences are large between predator species, then it is more likely that larger predators successfully steal the food from smaller predator (Hamilton 2002). This is the case with the African wild dog (*Lycaon pictus*; ~22 kg; hereafter: wild dogs), an endangered species, which suffers from kleptoparasitism by African lions (*Panthera leo*; 150-250 kg; hereafter: lions) and spotted hyaenas (*Crocuta crocuta*; ~70 kg, hereafter: hyaenas), both bigger and dominant over wild dogs (IUCN 2023; Creel 2001; Carbone et al. 2005). The risk of kleptoparasitism does not only imply losing a kill but it also implies the risk of agonistic interactions with dominant predators, which could result in injury or mortality of the subordinate predator (Creel 2001; Van der Meer et al. 2011, 2013a; Jordan et al. 2023). Besides kleptoparasitism, competition for prey, intraguild predation and exclusion from good quality habitat (e.g. prey rich areas close to water, protected areas away from human threats) are other ways in which competition with dominant predators can affect wild dogs (Creel 2001; Van der Meer et al. 2011, 2013a). Thus, as a way to promote coexistence and reduce interspecific competition, wild dogs have adapted to temporally and spatially avoid dominant predators, even if that involves

avoiding prey rich areas (Dröge et al. 2017; Van der Meer et al. 2013b; Vanak et al. 2013).

Wild dogs are obligatory cooperative breeders and hunters (Malcolm & Marten 1982). In packs, wild dogs are highly efficient hunters (44% up to almost 100% hunting success; Creel & Creel 1998; Hayward et al. 2006), compared to lions (30–73%; Schaller 1972; Funston et al. 1998) and hyaenas (25–75%; Holekamp et al. 1997). Throughout its distribution, wild dogs' preferred prey species size ranges from 16 to 140 kg (Hayward et al. 2006). Cooperative hunting allows wild dogs to predate on large prey relative to their body weight (Creel & Creel 1995). For a pack of wild dogs, hunting large prey can impose a higher risk of kleptoparasitism, as the handling time of large prey may be higher (Griffiths 1980; Ruxton & Moody 1997).

Hyaenas have found to be present at wild dog kills up to 86% of the time, and eat from all of the kills (Creel & Creel 1998, 2002). Kleptoparasitism mainly occurs when hyaena densities are high, kill sites are in open habitats where wild dogs are easier to detect, or when wild dog packs are small and therefore unable to defend their kill successfully (Carbone et al. 1997, 2005; Courchamp et al. 2002; Van der Meer et al. 2011). Hyaenas tend to use kleptoparasitism as a foraging strategy, and therefore regularly trail wild dog packs closely when they are hunting, whereas lions use an opportunistic approach and do not tend to follow packs (Carbone et al. 2005; Van der Meer et al. 2011). However, whenever lions appropriate a kill, wild dogs rarely defend it, as lions impose a high mortality threat to wild dogs (Creel & Creel 1998; Webster et al. 2012; Van der Meer et al. 2011).

The energy wild dogs use for cursorial hunting is extremely high (Gorman et al. 1998; Rasmussen et al. 2008; Speakman et al. 2016). Energy budget models indicate that wild dogs need to forage 12 hours a day to cope with 32.5% of kleptoparasitism, compared to 3.5 hours a day when there is no kleptoparasitism; thus, kleptoparasitism can impose significant energetic losses (Gorman et al. 1998; Speakman et al. 2016). The victim of kleptoparasitism does not only lose the intake energy of the food lost, but also the energy and time spent searching for and handling prey (Garay et al. 2020). Furthermore, when kleptoparasites arrive at wild dog kills, there is the potential cost of injury or even mortality of wild dogs due to encountering and confronting dominant predators (Mills & Gorman 1997; Groom et al. 2017).

When water is scarce, water management is a common practice in natural protected areas across African savannas (Edwards et al. 2015; Smit & Grant 2009). This practice aims at managing the distribution and densities of large herbivores (Owen-Smith 1996; Smit & Grant 2009), which in turn also affects the distribution of large carnivores (Valeix et al. 2010). During the dry season in arid ecosystems, large herbivores, and hence large carnivores, tend to aggregate around waterholes (Redfern et al. 2003; Valeix et al. 2010; Périquet 2014). Lions, hyaenas and wild dogs seem to prefer areas within a 2 km radius from waterholes to hunt for prey (Valeix et al. 2009; 2010; Van der Meer 2011; Périquet 2014). This potentially means that wild dogs have a high probability to encounter both dominant predators and suffer from interspecific competition close to waterholes.

The repercussions of kleptoparasitism to wild dogs by larger competing predators is well understood (Carbone et al. 1997, 2005; Gorman et al. 1998; Van der Meer et al.

2011; Speakman et al. 2016), however the role of water distribution on risk of kleptoparasitism has not been studied before. We experimentally assessed the level of kleptoparasitism risk on wild dogs by larger predators in relation to water availability. Our aim was to determine the level of kleptoparasitism risk from dominant predators (lions and hyaenas) to wild dogs in relation to distance to waterholes in areas characterized by contrasting waterhole densities. We hypothesized that the risk of kleptoparasitism (and associated agonistic encounters) would be higher near waterholes and in areas with higher waterhole densities. We therefore expected a higher probability of response of larger predators, a higher number of dominant predators responding, and a shorter time of response when near waterholes and in areas with higher waterhole densities. Furthermore, we hypothesized that hyaenas would present a higher kleptoparasitism risk (higher probability of response, higher number of individuals responding, and shorter time to arrive) than lions. This study gives an insight on water management strategies to lower the risk of kleptoparasitism and agonistic encounters of dominant predators to wild dogs. This, in turn, can help wild dogs' conservation in ecosystems with artificial water provisioning.

Methods

Study site

This study was undertaken in Hwange National Park (HNP), an unfenced protected area (ca. 14,600 km²) without human settlements in northwest Zimbabwe (19:00'S, 26:30'E) (Fig. 1). The altitude in HNP ranges between 800 and 1200 m.a.s.l. Vegetation consists of wooded bushland, woodland, bushland, bushed grassland and

open grassland mainly associated with waterholes (Arraut et al. 2018). Mean annual rainfall is ca. 600 mm with most rainfall occurring during the wet season (November to April). During the dry season (May to October), animals depend on artificially pumped waterholes, as HNP has no meaningful perennial surface water sources. Artificial waterholes are mainly found in the North East (NE) and North West (NW) of the park (waterhole density: 3.6 and 2.0 per 100 km², respectively). The NW area has a seasonal river, most fertile soils covered by wooded bushland (mainly mopane trees); while the NE area is characterized by bushy grassland on Kalahari sands. The South West (SW) area has the lowest waterhole density of the park (0.5 per 100 km²), and is characterized by wooded bushland on Kalahari sands (Rogers 1993; Arraut et al. 2018). Predator surveys undertaken between 2013 and 2020, showed that the density of hyaenas and lions is highest in the NW and lowest in the SW of the park (in the NW 19.1 hyaenas per 100 km², and 6.5 lions per 100 km²; in the NE 10.4 hyaenas per km², and 2.3 lions per 100 km², in the SW 6.7 hyaenas per 100 km², and 1.8 lions per 100 km²) (unpublished data; Loveridge et al. 2022). Main large and medium herbivore species in HNP are buffalo (*Syncerus caffer*), elephant (*Loxodonta africana*), impala (*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*), and zebra (*Equus quagga*) (Chamaillé-Jammes et al. 2009; Sandoval-Serés et al. 2024).

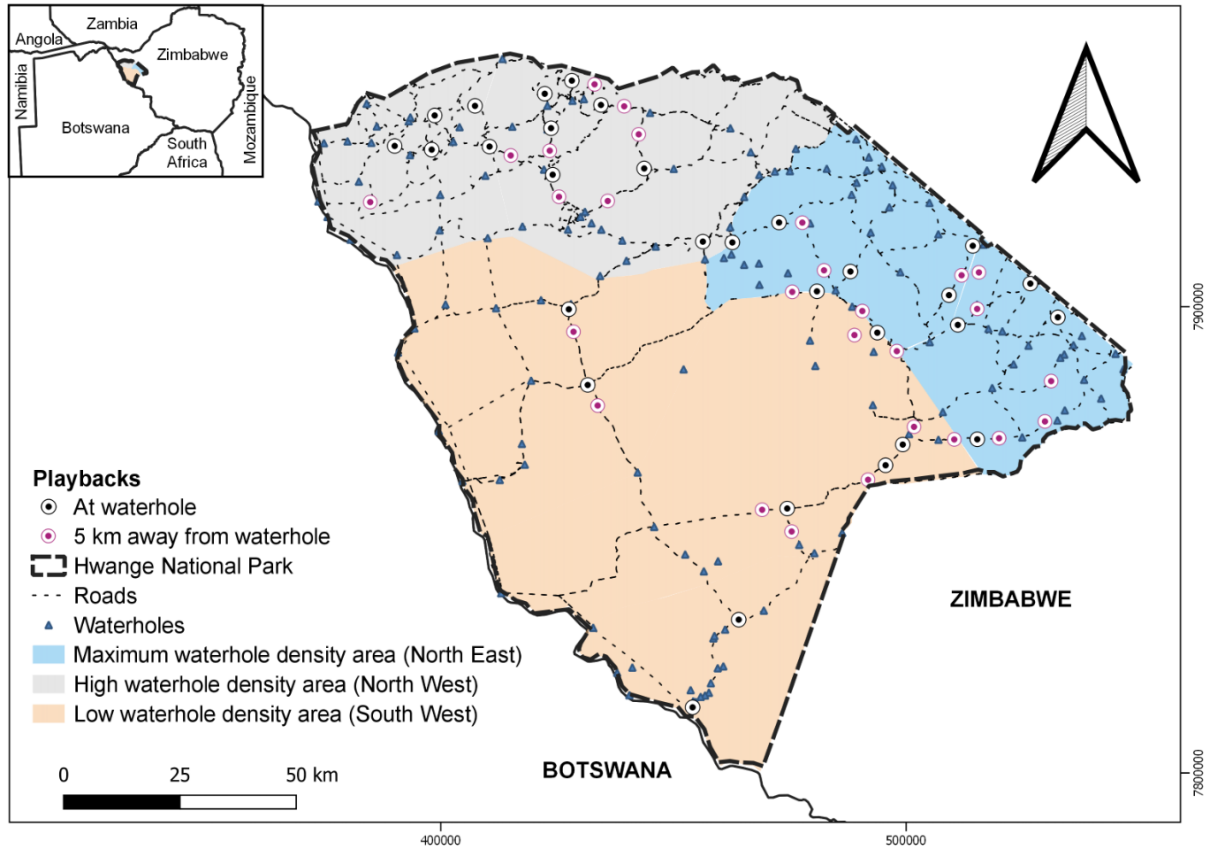


Figure 1. Map of Hwange National Park, Zimbabwe, and location of playback experiments. (When performing a playback experiment, we always checked that there was water in the waterhole for playbacks at waterholes and that there was no water within 5 km for playbacks 5km away from waterholes).

Data collection

We performed audio playbacks, using the recording of a wild dog pack (consisting of two or four individuals depending on the playback sound broadcasted) killing and eating an impala (PDC audio playback), at two distances from water: at the waterhole, and 5 km away from a waterhole. We performed playback experiments during the dry season (June-October) of 2021 and 2022. We performed the playback

experiments either at sunrise or one hour before sunset, as this is normally the time wild dogs are hunting (Cozzi et al. 2012). Each experiment lasted one hour using the methodology of Van der Meer et al. 2011; where a 2-minute audio was repeated in four directions (N, E, S, W), and then this session was repeated 3 times with a 5-minute pause between sessions; subsequently 26 minutes were spent in silence to allow for late responses (Van der Meer et al. 2011). The audio was played with one speaker (MEGAVOX PRO, 22 watts) on top of the car. Sound from audio playbacks can usually be heard by predators up to 2 to 3 km from the playback location (Ogutu & Dublin 1998; Mills et al. 2001). To avoid habituation of animals and to minimize the possibility that one soundtrack conveys a specific message, we used two different audio recordings (2-minutes each) from different packs of wild dogs, both eating an impala. We randomly picked one type of audio per playback experiment without ever using the same audio at adjacent sites (< 7km) in the same month. To avoid sound attenuation due to wind, we never performed playbacks experiments when the wind was strong (estimated categorically by the same person). We were sitting on the top of the vehicle using binoculars to lower the chance of missing individuals. We measured the time of first arrival of lions and hyaenas at the playback location (lapse time), and recorded the number of individuals present. We did not include dominant predators vocalizing if we could not see them. This was because we could not differentiate between dominant predators vocalizing by chance or as a response to the playback experiments, nor could we differentiate the exact distance of the predators vocalizing. Furthermore, we saw all predators that vocalized next to the playback locations. We used an ethogram to record general behaviours of the hyaenas and lions that we were able to observe during the

playback experiment (Supporting information, Table S1). Additionally, we recorded all other animals with a carnivorous diet that responded to the audio playbacks, plus the elephants that reacted to playbacks (arriving at the playback location displaying aggressive behaviour) (Supporting information, Figure S2a). At each location, we recorded the closest dominant vegetation type (wooded bushland, bushed grassland, grassland, bushland, woodland), and visibility (never less than 80m): medium (>80 m and < 600 m) and open (>600 m).

Analyses

First, to analyse both whether a larger predator arrived at a playback experiment and the number of larger predators present at the playback location when they responded, we performed hurdle models. Hurdle models consist of two parts, the first part (presence-absence data) is a binomial logit-link process, and the second part (count data without zeros, only fitting positive counts) is a truncated Poisson or Negative Binomial log-link procedure (Zuur et al. 2009). The dependent variable was the number of individual predators (either lions or hyaenas) arriving at the playback experiment (including zeros). Based on the lowest corrected Akaike information criterion (AICc) (for small sample sizes) of the full model (Zuur et al. 2009), we selected a Poisson distribution for lion counts, and a Negative Binomial distribution for hyaena counts. Then, to analyse the lapse time (in minutes) that dominant predators took to arrive at the playback locations, we used Generalized Linear Models (GLM) (using a Gaussian distribution for lapse time of lions [data normally distributed using Shapiro-Wilk Test: $p >$

0.05], and a gamma distribution with log-link for lapse time of hyaenas) (Zuur et al. 2009).

Preliminary analysis of the covariate “year” using GLMs, showed no evidence that this covariate was correlated with the dependent variable (non-significant $p > 0.14$), we therefore did not include it in the final analyses. We did not include the covariate “vegetation type” as a Chi-squared test showed that it was correlated to visibility ($X^2 = 25.14$, $df = 4$, $p < 0.001$). For model selection, in each of the following models, we included “audio type” as a covariate, and used a combination of the following categorical covariates: distance to a waterhole (at a waterhole, far, 5 km, from a waterhole), area (maximum, high, low waterhole density), visibility (medium, open), and time of the day (morning, evening). We also included a null model (intercept only). Models used for model selection are found in Supporting information, Table S2. We selected the model with the lowest AICc (Burnham & Anderson 2002). We did not perform model averaging, as it is not recommended (Cade 2015). For the hurdle models, we used rootograms as goodness-of-fit tests (Supporting information, Fig. S1) (Kleiber & Zeileis 2016). Following O’Brien (2007), as we had categorical variables, we used a Variance Inflation Factor < 10 as a cut-off. We ran the hurdle models in *pscl* package (Tahk et al. 2023) and graphed the results of the best models in the *sjplot* package (Lüdecke 2020) in R (R Core Team 2023).

Results:

We performed a total of 92 playback experiments: 50 at waterholes and 42 far from waterholes (5 km away) (Supporting information, Table S3). A summary of lions

and hyaenas responses to playback experiments is shown in Table 1. The best hurdle model for lions included the variables: time, distance class to waterhole and area; and the best model for hyaenas included the variables: time and area (Table 2; Supporting information, Table S2). All selected models had a satisfactory goodness-of-fit (Supporting information, Fig. S1).

Table 1. Summary of lions and spotted hyaenas responses to African wild dog playback experiments performed in Hwange National Park, Zimbabwe, in 2021 and 2022.

	Waterhole density area			Distance to waterhole		Overall
	Maximum (North East)	High (North West)	Low (South West)	0 km	5 km	
Lions						
Responded	12.1%	15.6%	7.4%	14.0%	9.5%	12.0%
Mean	8.50	4.40	3.50	7.29	3.00	5.73
number	(±3.2)	(±1.48)	(±2.5)	(±2.15)	(±1.08)	(±1.52)
Median						
lapse time	31 (±3.45)	21	18.5	16	39	21
(min)		(±3.40)	(±12.30)	(±2.15)	(±13.00)	(±2.25)
Spotted hyaenas						
Responded	60.6%	56.2%	40.7%	56.0%	50.0%	53.3%
Mean	6.55	5.00	1.91	5.46	4.24	4.94
number	(±1.41)	(±1.11)	(±0.41)	(±1.23)	(±0.58)	(±0.74)
Median						
lapse time	20 (±3.48)	13.5	9 (±1.25)	15	13 (±2.00)	13
(min)		(±1.85)		(±1.68)		(±1.20)

Means are shown with standard error.
Medians are shown with first quartile (Q₁).

Probability of response

We did not find any evidence that the probability of lions arriving at playbacks at waterholes compared to those far from waterholes was different (lions: $p = 0.51$, 95% CI = -1.76, 0.88; hyaenas: “distance to waterhole” covariate was not selected in the best model], nor did we find any evidence that the probability of predators arriving at playbacks in areas with different waterhole densities was different ($p > 0.05$; lions: 95% CI NW = -1.24, 1.63, and 95% CI SW = -2.58, 1.10; hyaenas: 95% CI NW = -1.33, 0.89, and 95% CI SW = -1.95, 0.37) (Table 2).

Table 2. Best hurdle models of lions and hyaenas arriving at playback experiments

Dependent variable		Estimate	Standard error	Z-value	Pr (> z) significance $p < 0.05^*$	
Lions responding to playbacks Fig. 2a	<u>Zero hurdle (Binomial)</u>					
		Intercept	-1.73	0.76	-2.27	0.02*
		Audio 2	-0.65	0.71	-0.92	0.36
		Time Morning	0.70	0.73	0.96	0.34
		Distance Far	-0.44	0.67	-0.65	0.51
		Area High waterhole density (NW)	0.19	0.73	0.26	0.79
		Area Low waterhole density (SW)	-0.74	0.94	-0.79	0.43
		<u>Count model (Truncated Poisson)</u>				
		Intercept	2.43	0.26	9.42	< 0.001*
		Audio 2	-1.35	0.39	-3.45	< 0.001*
		Time Morning	1.74	0.46	3.77	< 0.001*
		Distance Far	-1.60	0.56	-2.84	< 0.005*
		Area High waterhole density (NW)	-1.81	0.41	-4.43	< 0.001*
		Area Low waterhole density (SW)	0.16	0.69	0.24	0.81
Spotted hyaenas responding to playbacks# Fig. 2b	<u>Zero hurdle (Binomial)</u>					
		Intercept	-0.97	0.53	-1.81	0.07
		Audio 2	1.42	0.49	2.90	< 0.005*
		Time Morning	0.97	0.48	2.01	0.04*
		Area High waterhole density (NW)	-0.18	0.56	-0.33	0.74
		Area Low waterhole density (SW)	-0.80	0.59	-1.34	0.18
		<u>Count model (Truncated Negative Binomial)</u>				
		Intercept	0.98	0.44	2.22	0.03*
		Audio 2	0.07	0.43	0.17	0.86
		Time Morning	0.96	0.37	2.58	< 0.01*
		Area High waterhole density (NW)	-0.22	0.33	-0.66	0.51
	Area Low waterhole density (SW)	-1.89	0.48	-3.96	< 0.001*	
	Log(theta)	0.36	0.45	0.80	0.42	

NW = North West; SW = South West.

#Additional best models ($\Delta AICc < 2$) for spotted hyaenas found in Supporting information Table S2b. Best additional models had similar results (same significant results and same estimate trend).

Number of dominant predators responding

Overall, more dominant predators arrived at playbacks at waterholes than far from waterholes, and more arrived at playbacks in areas with high waterhole densities (the northern areas) than in those with low waterhole density (Table 1). When lions arrived at the playback locations, there was statistical evidence that a higher number responded at waterholes than far from waterholes ($p < 0.005^*$, 95% CI = -2.70, -0.50), and that lower number of lions responded in the high waterhole density area (NW) compared to the maximum waterhole density area (NE) ($p < 0.001^*$; 95% CI = -2.61, -1.01). Due to a small sample size of lions in the low waterhole density area (SW), the confidence intervals were too large to show any conclusive results ($p = 0.81$; 95% CI = -2.58, 1.10) (Table 2, Fig. 2a). When hyaenas arrived at the playback locations there was strong evidence that a smaller number of them responded in the low waterhole density area (SW) than in the maximum waterhole density area (NE) ($p < 0.001^*$; 95% CI = -2.70, -0.94) (Table 2, Fig. 2b).

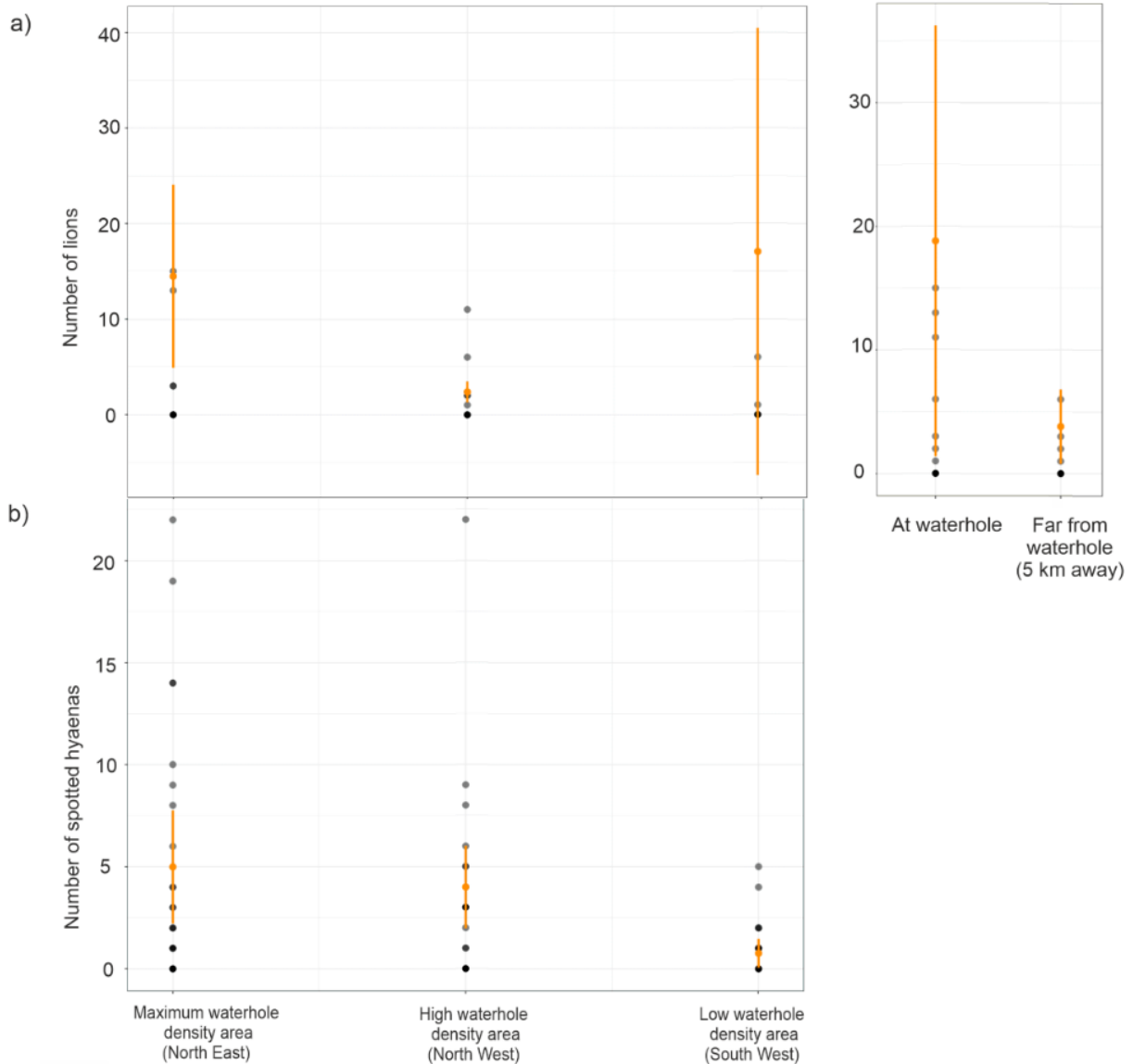


Figure 2. Plots of the marginal effects of the best Hurdle models. a) Number of lions arriving at playback sessions depending on distance to waterhole and areas with different waterhole densities. b) Number of hyaenas arriving at playback sessions depending on areas with different waterhole densities. Black and grey dots are the observed values (several grey dots form a black dot). Orange lines represent 95% confidence intervals. Due to small sample size for lions, confidence intervals are large in the low waterhole density area (South West).

Lapse time

Overall, the median lapse time for lions was 21 minutes (First quartile, $Q_1= 2.25$) and 13 minutes for hyaenas ($Q_1= 1.20$). Despite the fact that the median lapse time for lions was 16 minutes ($Q_1= 2.15$) at waterholes and 39 minutes ($Q_1= 13.00$) far from waterholes; and for hyaenas 9 minutes in the low waterhole density area and 20 minutes in the maximum waterhole density area (Table 1); for both species, the null model was the best model (lions: null model weight = 0.97; next $\Delta AIC = 6.84$; hyaenas: null model weight = 0.32; next $\Delta AIC = 0.51$ with still no evidence of any significant effect). Thus, we did not find any evidence that the distance to waterholes or the density of waterholes had an effect on lapse time of lions and hyaenas arriving at the playbacks.

Differences between lions and hyaenas

Overall, lions were attracted to 12% of the playbacks, and hyaenas to 53% (Table 1). In general, the probability of lions appearing at a playback session was lower than for hyaenas ($p < 0.001^*$, 95% CI = 1.38, 2.88), but once they arrived at the playback location, there was no difference between the number of lions and hyaenas responding ($p = 0.66$; 95% CI = -0.43, 0.13) (Table 3). Additionally, there were no differences in lapse time between lions and hyaenas ($p = 0.16$; 95% CI = -0.80, 0.00006).

Table 3. Hurdle model to test differences between lions and spotted hyaenas arriving at playback locations.

Dependent variable		Estimate	Standard error	Z-value	Pr (> z) significance p < 0.05*
Predators responding to playbacks	<u>Zero hurdle (Binomial)</u>				
	Intercept	-2.00	0.32	-6.21	< 0.001*
	Species Hyaena	2.13	0.38	5.55	< 0.001*
	<u>Count model (Truncated Negative Binomial)</u>				
	Intercept	1.38	0.45	3.05	< 0.01*
	Species Hyaena	-0.19	0.45	-0.43	0.66
	Log (theta)	-0.56	0.54	-1.02	0.31

Discussion

Scientific knowledge on how management decisions impacts ecosystems and ecological interactions in protected areas is crucial for the development of successful conservation policies and practices (Ferraro & Pressey 2015). Species interactions can be altered by management decisions of natural areas (Gaylard et al. 2003; Hadwen et al. 2007; Rich et al. 2019) and by human imprint (Smith et al. 2017). For example, non-well managed tourist pressure can degrade natural areas (Hadwen et al. 2007), or on the other hand, the presence of tourists can reduce predation pressure of sea turtle nests from carnivores (Leighton et al. 2010). Additionally, human sound can cause pumas to reduce their feeding time and possibly alter puma-prey interactions (Smith et al. 2017).

Management decisions on artificial water provisioning can alter ecosystems processes by transforming and regulating landscape heterogeneity (Chamaillé-Jammes

et al. 2007). This because surface-water availability drives the distribution and abundance of herbivores, carnivores' aggregation, plus distribution grazing/browsing pressure affecting vegetation (Gaylard et al. 2003; Chamaillé-Jammes et al. 2007; Valeix et al. 2010). A complete stop of water provisioning can have detrimental effects on the ecosystem through landscape homogenization (Gaylard 2015); however, an over-provisioning of water can also have detrimental consequences on the ecosystem through vegetation degradation and ecosystem instability (Owen-Smith 1996; Gaylard et al. 2003). Furthermore, interspecific competition between dominant and subordinate predators can be intensified at artificial waterholes (Rich et al. 2019).

Therefore, in this study, we show how water distribution, influenced by water provision management, affects the risk of kleptoparasitism on wild dogs. We found that although the probability of encountering a dominant predator as a potential kleptoparasite and their arrival time at a playback session was not associated to distance to water and waterhole density, we found evidence that a higher number of dominant predators arrived at a playback at waterholes and in areas with a higher density of waterholes. Kleptoparasitism success increases with the number of dominant predators arriving at a kill because subordinate carnivores are less likely to successfully defend their kill (Carbone et al. 1997, 2005). A higher number of lions arriving at playbacks at waterholes and the higher number of both lions and hyaenas responding in high waterhole density areas suggests a higher risk for wild dogs to get kleptoparasitized when water is more abundant. Thus, we found some evidence for water affecting the risk of a kleptoparasitism attempt, as there was an increased risk of losing the carcass if an attempt occurred

Prey abundance and distribution can play a role in the risk of kleptoparasitism (Hamilton 2002). As prey tend to aggregate close to water, there is also an aggregation of predators in those places (Valeix et al. 2010); herewith increasing the potential of kleptoparasitism opportunities close to water. This could explain why there was a higher number of lions arriving at playback sessions at waterholes than 5 km away from them. However, contrary to our expectation, the number of hyaenas arriving at playback sessions was not associated with distance to waterhole, possibly because foraging group size of hyaenas is not influenced by prey abundance (Périquet 2014). Even though lions and hyaenas are not pure kleptoparasites (Davidson et al. 2013; Périquet 2014), the fact that kleptoparasitism on wild dogs mainly occurs when hyaena density is high (Carbone et al. 2005) and hyaena density is higher in the maximum and high waterhole density areas (the north of HNP, Loveridge et al. 2022) could explain why the number of hyaenas appearing at playback sessions was higher in those areas of the park. The number of lions appearing at a playback session was higher in the maximum waterhole density area (NE) than in the high waterhole density area (NW) (the area with the highest lion density and the highest buffalo density, the main prey of lions in the area - Chamaillé-Jammes et al. 2009; Loveridge et al. 2022; Sandoval-Serés et al. 2024). The fact that buffalo density was lower in the maximum waterhole density area (NE) compared to the high waterhole density area (NW) could explain why the mean number of lions arriving at playback sessions in the maximum waterhole density area (NE) was higher, despite this not being the area with the highest lions' density. Perhaps when there is less buffalo to hunt, more lions prefer to use kleptoparasitism as a strategy to feed.

Conservation implications

Anthropogenic factors have negatively affected the survival of wild dog populations (IUCN 2023; Woodroffe & Sillero-Zubiri 2012). One coping mechanism of wild dogs to lower competition with dominant predators is avoiding them in space (Vanak et al. 2013, Davies et al. 2021). As dominant predators, such as lions, mainly survive within protected areas and pristine environments of high prey densities (Loveridge et al. 2010), wild dogs are selecting areas with lower density of dominant competitors normally at the boundary of protected areas, where conflict with people aggravates (Woodroffe & Ginsberg 1998; Van der Meer et al. 2013a). Water provisioning could increase the interspecific competition of wild dogs inside protected areas and force them to select areas outside the park.

Wild dogs have several behavioural adaptations to reduce the risk of kleptoparasitism and resulting encounters with dominant predators. Hunting medium size prey can be a strategy to decrease the feeding time at a carcass (Hubel et al. 2016), and decrease the chances of kleptoparasitism (Carbone et al. 1997; Courchamp et al. 2002). Besides the strategy of eating their food fast, wild dogs move away from their kill to rest to avoid the threat of encountering dominant predators at their kills (Jordan et al. 2023).

The amount of time that wild dogs can retain their kills decreases with the number of hyaenas arriving at the kill (Carbone et al. 2005). Wild dog packs consume ~90% of the carcass within 20 minutes (4–6 kg/dog; 12-30 kg prey weight) (Carbone et al. 2005). In this study, lions took a median time of 21 minutes to arrive at the playback

sessions (in theory enough time for wild dogs to consume most of the carcass). However, in 25% of the playback sessions, dominant predators arrived within 3 minutes at the playback locations, which could translate into losing nearly their whole kill in 25% of the times. The high hunting energetic cost of wild dogs can leave them with a low margin in their energy budget (Hubel et al. 2016), which makes them more susceptible to the costs imposed by kleptoparasitism (Gorman et al. 1998; Speakman et al. 2016). They would have to make up for this energy loss by allocating more time to hunting, or by leaving for lower quality habitats. Less time to consume a carcass for wild dogs before a dominant predator arrives does not only mean the potential to lose a carcass, but also a higher risk of being involved in aggressive interactions.

Thus, avoiding kleptoparasitism also means avoiding the threat of encountering dominant predators that can injure them, especially encountering lions, which can impose a bigger mortality threat for wild dogs than hyaenas (lions can kill up to 46% of wild dog adults, and hyaenas up to 10% of adults) (Woodroffe & Ginsberg 1999). Although hyaenas rarely kill wild dogs directly, they often steal their kills, kleptoparasiting them from 0 and 2% in Kruger and Selous, to 60 and 86% in Ngorongoro and Serengeti, respectively (Creel & Creel 2002). In HNP, Van der Meer et al. (2011) also performed playback experiments of wild dogs' sounds, and found 29% of lions response and 37% of hyaenas response. However, following wild dog packs, they found low kleptoparasitism rates of dominant predators on wild dogs (lions: 3%; hyaenas: 6%) (Van der Meer et al. 2011). In our study, we also found that the probability of hyaenas arriving at a playback session (53% of the times) was higher than for lions (12%). This could be because in HNP hyaenas' density is almost three times

higher than lions' density (Loveridge et al. 2022), and hyaenas tend to use kleptoparasitism as a foraging strategy more often than lions (Carbone et al. 2005; Van der Meer et al. 2011). However, once dominant predators arrived at the playback location, there was no difference between the number of lions and hyaenas responding. This could be because the foraging group size of both predators is similar in HNP (2 to 10 lions - Mbizah 2017; 1 to 8 hyaenas - Périquet 2014). Hence, it seems that hyaenas impose a higher threat in terms of kleptoparasitism attempts (energetic costs for wild dogs), but lions impose a higher threat in terms of encountering wild dogs if an attempt of kleptoparasitism occurs (both in terms of energy and injury costs for wild dogs).

As lions impose a higher mortality threat, wild dogs never defend their kills from lions, whereas wild dogs defend their kills from hyaenas in half of the occasions that hyaenas are present (Van der Meer et al. 2011). The size of wild dog packs is extremely important to avoid the negative effects of kleptoparasitism. This is because large packs of wild dogs can benefit from being more efficient at hunting, consuming their prey faster, and better defending their kills from hyaenas (Carbone et al. 1997; Courchamp et al. 2002; Fanshawe and Fitzgibbon 1993). Moreover, small wild dog packs, catching larger prey could increase the risk of kleptoparasitism as it would increase the handling time of the prey (Hamilton 2002). In HNP, wild dog packs tend to be small (~ 6 individuals) (PDC 2021), which can impose a challenge when facing kleptoparasites.

Conclusion

Overall, the probability of dominant predators arriving at a playback session simulating a wild dog kill and the time for a dominant predator to arrive do not depend

on water distribution at the landscape scale; however, the number of dominant predators arriving at a wild dog kill is higher at waterholes and in areas with high waterhole densities. In our study, we found that there are some areas in HNP (areas with low waterhole density, and far from water - at least 5 km away - in areas with high waterhole densities) that can facilitate wild dogs' spatial avoidance from kleptoparasitism and avoid dominant predator encounters at their kills.

In Africa, especially in protected areas with active water management, it should be important to create more favourable conditions for wild dogs. One way to achieve this could be by implementing a heterogeneous artificial water management, which would provide more "refuge" areas for wild dogs to avoid the risks of kleptoparasitism and hence the risks of encountering dominant predators. A heterogeneous waterhole system could be accomplished by not creating more waterholes especially in high waterhole density areas (> 2 waterholes per 100 km²), as well as leaving some areas without water provisioning. Particularly in HNP, it has been identified that there is a need to implement a science-informed water management plan (ZIMPARKS 2015). Therefore, in this study we intend to contribute knowledge on how water management could lower kleptoparasitism and the risk to wild dogs of agonistic encounters with dominant predators. This to help conservation practitioners and policy makers to develop water management strategies that can help with the conservation of wild dogs, a species of conservation concern. In addition, this could potentially have further implications in other national parks with water management for wildlife where there is interspecific competition between dominant and subordinate carnivores.

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Conflict of Interest

None declared.

Data Availability Statement

The data will be available in <https://figshare.com/>

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Authors' contributions

E.S.S., E.M., E.D. M.V. and A.J.L. conceived the idea; E.S.S., G.N., W.M., and A.A. collected the data; E.S.S. processed the data and did the analyses; E.S.S., E.M., E.D. M.V. and A.J.L. interpreted the results; E.S.S. led the writing of the manuscript; D.M,

H.M and P.B supervised data collection. All authors gave feedback to the drafts and final approval for publication.

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Supporting information Chapter 3

Water availability affects the risk of kleptoparasitism of African wild dogs by
larger dominant predators

Supporting information:

Table S1. Ethogram of lions and spotted hyaenas used on playback experiments

Behaviour	Description	Sample size Lions	Sample size Spotted hyaenas
Vigilant	Standing with a head up with both ears up	53	154
Vigilant resting	Lying down with head up	20	12
Call	Any sound made	13	62
Smelling	Using their nose to find odours either on air or floor	1	16
Resting	Sitting down or lying down	6	12
Exploring	Walking or trotting around the playback location (looking for carcass)	33	202
Running	Moving in a very rapid pace	0	96
Marking	Defecating and urinating	1	0
Socializing	Any intraspecific interaction	3	4
Ignore playback	Just passing by	3	1
Other	Drinking, interacting with other species	1	4

Table S2a. Models used for model selection

	Models of Lions responding to playbacks (AICc)	Models of Spotted hyaenas responding to playbacks (AICc)
Null model	149.68	375.72
Audio + Distance to waterhole	145.10	369.21
Audio + Area	153.32	361.52
Audio + Distance to waterhole + Area	146.73	364.89
Audio + Visibility + Distance to waterhole	137.43	369.61
Audio + Visibility + Area	142.07	363.83
Audio + Visibility + Distance to waterhole + Area	146.37	365.40
Audio + Time + Distance to waterhole	148.43	367.15
Audio + Time + Area	142.19	356.32
Audio + Time + Distance to waterhole + Area	<i>134.67</i>	359.90
Audio + Time + Visibility + Distance to waterhole	137.46	365.77
Audio + Time + Visibility + Area	138.19	357.18
Audio + Time + Visibility + Distance to waterhole + Area	139.41	357.77

In italics is the best model (lowest AICc)

Table S2b. Additional best hurdle models of spotted hyaenas arriving at playback experiments

Dependent variable		Estimate	Standard error	Z-value	Pr (> z) significance $p < 0.05^*$	
Spotted hyaenas responding to playbacks	<u>Zero hurdle (Binomial)</u>					
		Intercept	-0.96	0.53	-1.8	0.07*
		Audio 2	1.42	0.49	2.89	0.004*
		Time Morning	0.96	0.48	2.01	0.045*
		Area High waterhole density (NW)	-0.18	0.56	-0.33	0.74
		Area Low waterhole density (SW)	-0.79	0.59	-1.34	0.18
		<u>Count model (Truncated Negative Binomial)</u>				
		Intercept	0.98	0.44	2.22	< 0.027*
		Audio 2	0.07	0.43	0.17	0.86
		Time Morning	0.96	0.37	2.58	< 0.009*
		Area High waterhole density (NW)	-0.22	0.33	-0.66	0.51
		Area Low waterhole density (SW)	-1.89	0.48	-3.96	< 0.001*
		Log(theta)	0.36	0.45	0.80	0.42
	Spotted hyaenas responding to playbacks	<u>Zero hurdle (Binomial)</u>				
		Intercept	-0.49	0.58	-0.85	0.39
		Audio 2	1.45	0.50	2.88	0.003*
		Time Morning	1.20	0.51	2.34	0.02*
		Visibility (Open)	-1.06	0.53	-2.0	0.04*
		Area High waterhole density (NW)	-0.53	0.61	-0.87	0.38
		Area Low waterhole density (SW)	-0.95	0.60	-1.57	0.11
		<u>Count model (Truncated Negative Binomial)</u>				
		Intercept	0.90	0.46	1.94	0.051
		Audio 2	0.06	0.43	0.14	0.88
		Time Morning	0.96	0.37	2.59	0.009*
		Visibility (Open)	0.16	0.34	0.48	0.62
		Area High waterhole density (NW)	-0.15	0.35	-0.43	0.67
		Area Low waterhole density (SW)	-1.88	0.47	-3.96	< 0.001*
	Log(theta)	0.38	0.45	0.83	0.40	

NW = North West; SW = South West.

Table S3. Number of playback experiments performed in Hwange National Park, Zimbabwe (years: 2021-2022) and sample size of dominant predators arriving at playback sessions

Area	Number of playbacks		Total number of dominant predators arriving at playback locations	
	At waterholes	Far from waterholes (5 km away)	Lions	Spotted hyaenas
North West	15	14	34	131
North East	21	15	22	90
South West	14	13	7	21
Total	50	42	63	242

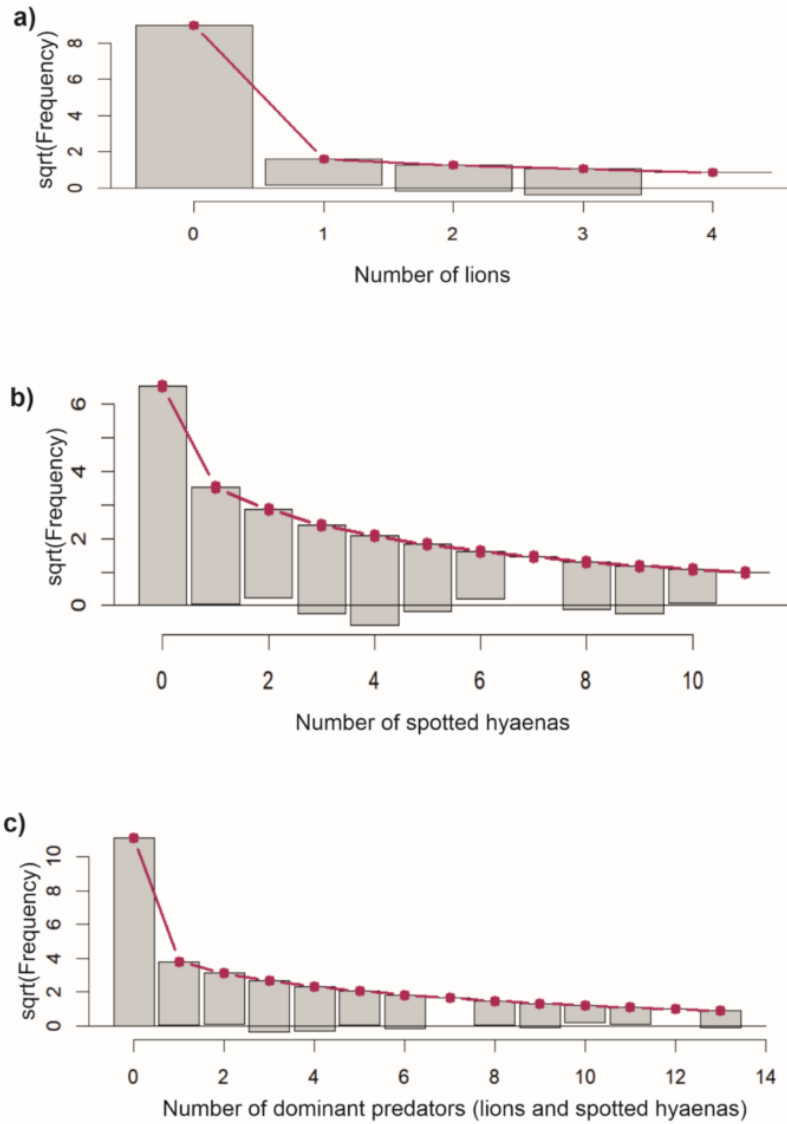
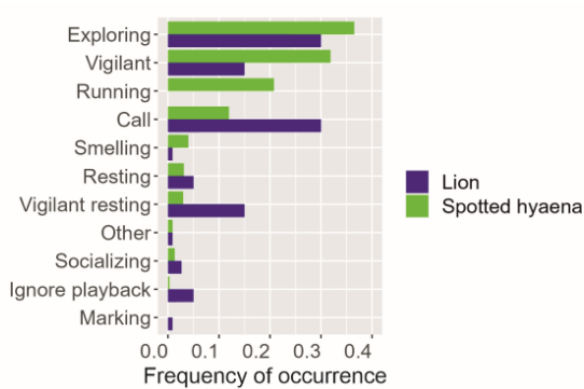


Figure S1. Rootograms to check goodness-of-fit in the Hurdle models from Tables 2 and 3. Red line: expected counts, given the model. Bars: observed counts. a) Lion model (Table 2). b) Spotted hyaena model (Table 2). c) Dominant predators model (Table 3).

a)



b)

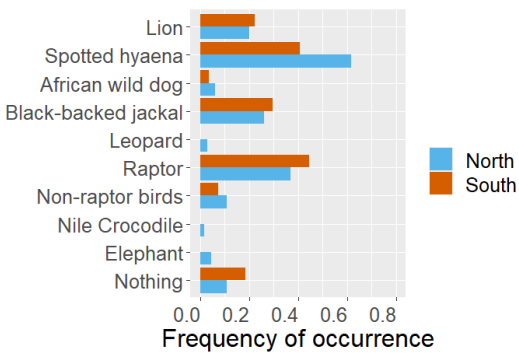


Figure S2. a) Frequency of occurrence of different behaviours of spotted hyaenas and lions responding to playback experiments (number of individuals performing a behaviour, in proportion to other behaviours). b) Frequency of occurrence of different species responding to playback experiments (number of times species or group of species appeared in one playback session, in proportion to the other species) in areas with high density of waterholes (North) and low waterhole density area (South) of Hwange National Park, Zimbabwe.

Chapter 4

Spatio-temporal dynamics of African wild dogs in response to larger carnivores in an ecosystem with artificial water provisioning

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Abstract

Temporal and spatial partitioning are forms of niche segregation between sympatric carnivores to reduce interference competition. Subordinate carnivores face a trade-off between accessing resources and avoiding larger predators. Avoidance strategies can be reactive (small-scale: after detecting an immediate threat) or proactive (large-scale: in response to a priori assessment of the risk). We aimed to evaluate if African wild dogs avoid larger competing predators (leopards, African lions and spotted hyaenas) reactively or proactively in space and time at different spatial and temporal scales in an ecosystem with artificial water provisioning. In addition, we aimed to determine (taking vegetation characteristics into account) whether seasonality, permanent waterhole density at different spatial scales, waterhole distance and dominant predator density affected the avoidance strategy of wild dogs towards the larger predators in space and time in Hwange National Park, Zimbabwe. To test our predictions, we used camera-trapping data collected over the whole park and generalized linear mixed models (spatial dimension), activity pattern overlap (temporal dimension), and time-to-event analyses (spatio-temporal dimension). In general, wild dogs used the same space as the other three larger predators, but at different times. In general, wild dogs did not avoid the larger predators in space, but temporal avoidance of all three predators was especially strong close to waterholes. Spatio-temporally, wild dogs used a reactive strategy to avoid hyaenas, and most likely a proactive strategy towards lions and leopards. Wild dogs were able to coexist at different times in areas (rich in prey) with high aggregation and density of predators (but lower than ~14 hyaenas/100km²) as long as there was closed vegetation (e.g. bushland), and enough

permanent waterholes (approximately above 0.01 waterholes per km², waterholes being a surrogate for prey aggregation and abundance). Conservation management tools should implement heterogeneous waterhole-provisioning schemes that facilitate interspecific coexistence which potentially help to keep a heterogeneous landscape that increases niche-partitioning opportunities.

Key words: niche partitioning, avoidance strategies, species interactions, waterholes.

Introduction:

Sympatric carnivores with similar ecological traits (i.e. functional, nutritional) often compete over habitat, space and resources (Davis et al. 2018; Li et al. 2021). When one species actively prevents another species from accessing a resource (interspecific interference competition), a form of niche partitioning needs to occur to be able to coexist (Amarasekare 2002). Temporal and spatial partitioning are forms of niche segregation between competing species that reduce interference competition and promote coexistence (Vanak et al. 2013; Karanth et al. 2017).

Competition with larger carnivores that are able to dominate smaller ones can shape carnivore communities (Davis et al. 2018; Monterroso et al. 2020). Smaller subordinate carnivores have to balance the trade-off between avoiding dominant carnivores with the need to access key resources (e.g. water, food) (Broekhuis et al. 2013; Li et al. 2021). Hence, balancing this trade-off is crucial for subordinate species to avoid the reduction of fitness caused by the ecological suppression exerted by dominant carnivores (Kozłowski et al. 2011; Li et al. 2021).

Interspecific interactions can depend on scale (Broekhuis et al. 2013; Monterroso et al. 2020; Strampelli et al. 2023), as well as biotic and abiotic traits (Vanak et al. 2013; Pretorius et al. 2021). When the density of dominant carnivores increases, subordinate carnivores can diminish the use of prey rich habitats to reduce spatial overlap (St-Pierre et al. 2006), and in low prey densities areas, temporal and spatial partitioning can diminish (Karanth et al. 2017). As such, spatio-temporal partitioning can be dynamic and flexible; when there is an increase in temporal overlap, a decrease in spatial overlap can occur, and vice versa (Karanth et al. 2017; Zhao et al. 2020). Overall,

landscape and habitat heterogeneity both at local and regional scales tend to promote coexistence (Manlick et al. 2020; Davies et al. 2021).

In arid and semi-arid environments, water is a crucial resource where prey aggregates (Redfern et al. 2003). Consequently, areas close to water (< 2 km) are the preferred hunting grounds for carnivores (Valeix et al. 2010; Van der Meer 2011; Périquet 2014). As subordinate carnivores face a trade-off between accessing water areas, and the associated prey, and interference competition, spatio-temporal dynamics are key for carnivore coexistence around water (Atwood et al. 2011; Edwards et al. 2015).

Among large African predators, one of the most subordinate carnivores is the African wild dog (referred to as wild dog hereafter) (*Lycaon pictus*), which is a social, endangered canid (Vanak et al. 2013; IUCN 2024). Large dominant carnivores, such as lions (*Panthera leo*) and spotted hyaenas (*Crocuta Crocuta*), impact wild dogs through intraguild predation, kleptoparasitism, and exclusion from high-quality habitats (Creel 2001). Wild dogs show strong avoidance both spatially and temporally towards lions (Swanson et al. 2014; Davies et al. 2021), as lions pose a direct mortality risk to wild dogs (Woodroffe & Ginsberg 1999). Conversely, the strength of avoidance of wild dogs towards spotted hyaenas (hereafter hyaenas) and leopards (*Panthera pardus*) is not as evident (Dröge et al. 2017; Strampelli et al. 2023).

Subordinate carnivores can avoid dominant predators through reactive (small-scale: after detection of an immediate threat) or proactive (large-scale: in response to a *priori* assessment of predictable and controllable risk) strategies (Broekhuis et al. 2013; Creel 2018). These avoidance strategies incur costs for subordinate species; proactive

strategies will have food-related costs and reactive strategies will have stress-related costs (Swanson et al. 2016; Creel 2018). Previous studies showed that wild dogs tend to use a proactive strategy mainly to avoid lions but also hyaenas and leopards (Vanak et al. 2013; Swanson et al. 2014; Davies et al. 2021), and wild dogs use a reactive strategy only during the wet season when visibility is low (Vanak et al. 2013).

As niche partitioning can be crucial for the coexistence of wild dogs with dominant predators (Darnell et al. 2014; Dröge et al. 2017) especially around water (Pretorius et al. 2021; Krag et al. 2023), we aimed to evaluate if wild dogs avoid larger competing predators (leopards, lions and hyaenas) reactively or proactively in space and time at different spatial and temporal scales in an ecosystem with artificial water provisioning. In addition, we aimed to determine (taking vegetation characteristics into account) whether seasonality, waterhole density at different spatial scales (as a surrogate covariate of prey abundance), waterhole distance (as a surrogate of prey aggregation) and dominant predators' density affected the avoidance of wild dogs towards large predators in space and time. We expected that wild dogs would neither have attraction nor avoidance towards leopards spatially, but a proactive response (large scale) temporally; that wild dogs would avoid lions using a proactive strategy (large scale) both spatially and temporally; and finally, wild dogs would avoid hyaenas using a reactive response spatially and a proactive response temporally. Furthermore, we expected that wild dogs would have a higher strength of spatial and temporal avoidance (i.e. proactive avoidance or a stronger effect of an avoidance) with the three other predators when there is more water availability in the system (i.e. in the early dry

season, close to water, and in areas with higher density of waterholes and large predators).

Methods:

(a) Study area

The study area is in Hwange National Park (HNP), an unfenced protected area in western Zimbabwe (19:00'S, 26:30'E) that covers approximately 15,000 km² (Fig. 1). The main habitat types are woodland, bushland and open areas of grassland (this last habitat type is associated to artificial waterholes) (Chamaillé-Jammes et al. 2009a; Arraut et al. 2018). The wet season (November-March) has a mean rainfall of ~380 mm, the early dry season (April-June) has a mean rainfall of ~123 mm, and the late dry season (July-October) has a mean rainfall of ~10 mm (Wilderness Safaris Zimbabwe, unpublished data for 2010-2020). During the dry season (April-October), animals depend mainly on artificial waterholes (which tend to have water the whole year round). Permanent artificial and natural waterholes (containing water even in the late dry season) are predominantly found in the northern area of HNP (North: ~1.69 permanent waterholes / 100 km²; South West: ~0.18 permanent waterholes / 100 km²) (Fig. 1, Supporting information, Table S1). During the study period in HNP (2013-2020), the density of predators was estimated to be in the north of HNP (high waterhole density area): 2.6 (± 1.2 s.d.) leopards/100 km², 3.5 (± 2.2) lions/100 km², and 14.1 (± 6.0) hyaenas/100 km²; and in the south west of HNP (low waterhole density area): 2.1 (± 0.1 s.d.) leopards/100 km², 1.3 (± 1.1) lions/100 km², and 6.7 (± 1.4) hyaenas/100 km²

(unpublished data, Loveridge et al. 2022). Abundance of prey is also higher in the northern part of HNP (Sandoval-Serés et al. 2024).

(b) Camera trap survey

A total of 487 camera trap stations (two camera traps per station: Cuddeback models 1125, 1149 and C1, Non- Typical, WI, USA; Panthera V4, Panthera, NY, USA; Stealthcam G42NG, Grand Praire, TX, USA) were deployed during the dry season between 2013 and 2020 across seven surveyed areas within HNP (total effort: 26,030 trap days). Each survey consisted of a mean of 49 (SD±14; min 38 to max 78) camera trap stations, and 2527 (SD±1133; min 1670 to max 5483) trap days. Camera trap stations were placed on game trails or roads and spaced in a grid of 4 to 5 km apart (Fig. 1; Supporting information, Table S1).

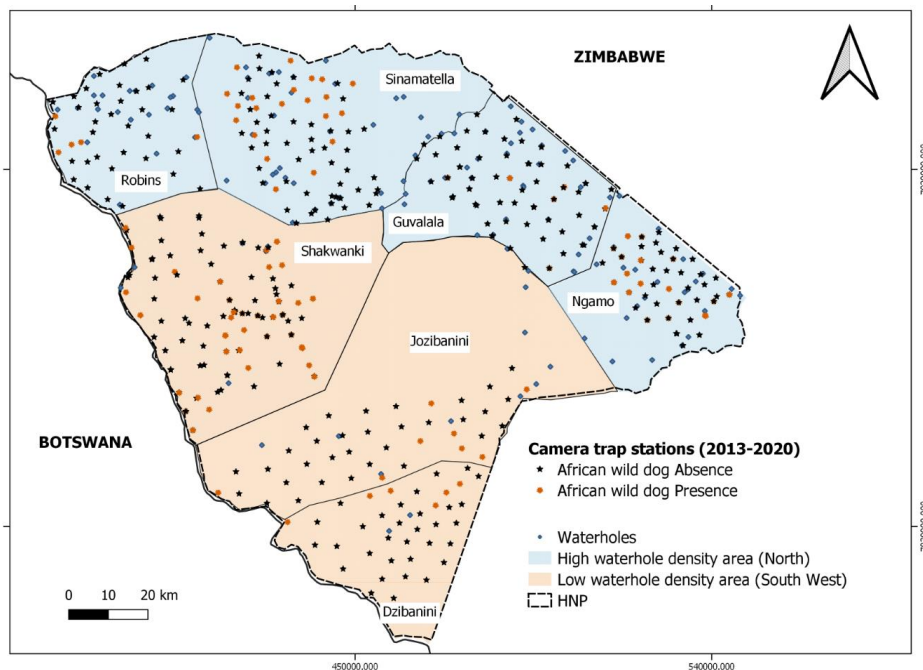


Fig. 1 Map of presence/absence of African wild dogs in the camera trap stations in Hwange National Park, Zimbabwe. Lines divide the surveyed areas of the park.

(c) Analyses

Covariates tested

We took the following covariates: season (early dry, late dry), year (2013-2020), vegetation visibility (closed, medium, open), ruggedness of the terrain, Euclidian distance to the closest waterhole, permanent waterhole densities (number of waterholes within buffer) during the dry season at four different scales (2, 9, 14 km buffer, and per surveyed area), number of individuals of leopards, lions and hyaenas identified in each camera trap station (small scale), and lion and hyaena densities per the seven surveyed areas (large scale) (Fig. 1). Furthermore, in all models we included trap effort (number of days that a camera trap station was working).

Low visibility due to dense vegetation and rugged terrain can help wild dogs avoid detection from dominant predators (Davies et al. 2021). We therefore included vegetation visibility and terrain ruggedness as covariates. We attributed a vegetation visibility class to each camera trap station. To do so, we used the vegetation layer from Arraut et al. 2018 (30 m resolution), and categorized grassland and bushed grassland as 'open vegetation', woodland as 'medium vegetation', and bushland and mopane scrub as 'closed vegetation' (Davidson et al. 2012; Périquet 2014; Arraut et al. 2018). We calculated terrain ruggedness using the Vector Ruggedness Measure in QGIS 3.12 using a digital elevation layer of 15-arc-second (~450 m resolution) from ETOPO 2022 (NOAA 2022).

As natural pans highly depend on rainfall to keep having water during the dry season (Chamaillé-Jammes et al. 2007a), for each surveyed area, we checked which

waterholes (regardless of artificial or natural) had water during the year when the camera trap survey was performed (Fig. 1; Supporting information, Table S1). To check this, we used the information gathered by the Wildlife and Environment Zimbabwe, who undertake an aerial assessment of waterholes which contain water at the end of the late dry season (WEZ Reports 2013-2020). To calculate waterhole densities of the dry season (i.e. permanent waterholes), we used four different scales: 2 km radius buffer (as predators prefer to hunt within 2 km of waterholes - Valeix et al. 2010; Van der Meer 2011; Périquet 2014), 9 and 14 km radius buffer (as the area under the circle would approximate to the minimum and maximum home range of wild dogs: 260-633 km² - Pomilia et al. 2015), and per the seven surveyed areas (average area: 2079 km² ; range: 1330 km²-3712 km²) (Fig. 1).

The dominant predator densities per surveyed area and per year were taken from Loveridge et al. 2022. Lions were identified through unique whisker spots patterns, leopards and hyaenas were identified through unique pelage patterns, and blurred images were discarded (Loveridge et al. 2022). We checked for collinearity among all covariates with either Pearson or Spearman correlation test (we did not use leopard density as it was correlated to lion density: $r > 0.70$; $p < 0.01$), and we z-standardized all continuous covariates. We performed all our analyses in R programme (R Core Team 2023).

Spatial

To answer our question about spatial avoidance we fitted a Generalized Linear Mixed Model (GLMM) (family Poisson, log link) (Bolker et al. 2009) with R package *lme4* package (Bates et al. 2023). We included year (n = 6) and survey session (n = 8) as random covariates (Fig. 1; Supporting information, Table S1). We used the number of wild dogs identified per camera trap station as the response variable. We identified wild dogs through unique pelage patterns following the same methodology of identifying leopards and hyaenas. Additionally, we only took into account the number of wild dogs that were seen on the camera trap regardless of pack size.

Regarding the fixed covariates, we first tested which scale of waterhole density was the best to use in the global model. To do so, we performed four GLMMs, attesting for different spatial scales of waterhole density (2, 9, 14 km, and the surveyed area) as the only covariate. We then selected a 14 km buffer scale as the model with this scale of waterhole density had the lowest Akaike Information Criterion (AIC). Additionally, to avoid overfitting the global model by including too many covariates and to assure a good sample size, we tested each environmental covariate separately, and only included in the global model those significant environmental covariates with p-value lower than 0.05 (vegetation visibility). Finally, as we had a good sample size (n = 366 observations), we built a global and final model also including the fixed covariates of interest: individuals of leopards, lions and hyaenas per camera trap station (small scale), lion and hyaena densities per surveyed areas (large scale), distance to the closest waterhole and waterhole density within a 14 km buffer. We compared this global model with a null model (the global model had a lower AIC) and performed a goodness-of-fit test of this global model using the pseudo-R² (marginal pseudo-R² encompasses

the variance explained by only the fixed covariates; and conditional pseudo-R² encompasses the variance explained by both random and fixed covariates) (Nakagawa & Schielzeth 2013).

Temporal

To assure independence, we excluded those records that were from the same species in the same camera trap station within a period of one hour (Sample sizes: Supporting information, Table S2) (Niedballa et al. 2019). We estimated the coefficient of overlap Δ (Δ_1 for fewer than 75 independent records, and Δ_4 for larger sample sizes) of activity pattern of wild dogs with the other three predators (the higher the coefficient number the higher overlap of activity between species) (Ridout & Linkie 2009; Meredith & Ridout 2018), and performed 10,000 bootstraps to obtain 95% confidence intervals using the R package *overlap* (Meredith & Ridout 2020). To test for statistical differences in the activity pattern of wild dogs and other predators, we calculated the Watson's Two-Sample Test of Homogeneity (Landler et al. 2021) using the R package *circular* (Lund et al. 2017). We classified activity patterns in three different categories: season, area (high waterhole density area located in the North of HNP, against low waterhole density area in the South of HNP: <0.01 waterholes per km²), and distance to waterholes (close < 2 km; medium 2-5 km; far > 5 km).

Spatio-temporal (time-to-event models and indices)

We fitted time-to-event models (Parsons et al. 2016; Niedballa et al. 2019). We calculated the time difference between different predators detected at each camera trap

station within 1 and 8 days (1 day only for wild dogs with hyaenas, as there was not enough data for wild dogs with the other two predators). We fitted Generalized Linear Models (GLMs) (gamma family, log link) using the time difference in hours between a wild dog and a larger predator passing by at the same camera trap station as the dependent variable. In each model, we included number of independent records of wild dogs per camera trap station (to control for differences in wild dogs abundance per site). We did not include the number of independent records of the larger predators (lions and hyaenas) per camera trap station as this was correlated with the number of independent records of wild dogs (Pearson test >0.95 ; $p < 0.05$). We also included in each model the order of the species appearing on the camera trap (two options: wild dog appearing first or afterwards). Moreover, to test if any covariate had an effect on the time appearance of wild dogs after a hyaena we fitted GLMs with a subset of the dataset of a hyaena appearing first and then a wild dog (we did not subset data of wild dogs with other predators due to sample size restrictions).

We tested the effect of each covariate of interest separately. We selected the models which had covariates with $p < 0.05$. We compared the selected models with a null model (null models had lower AICc than the selected models). We used the McFadden's R^2 as a measure of goodness-of-fit, which encompasses the variance explained by the covariates used (McFadden 1987). When the models purpose is to explain and not to predict the effect of specific covariates on the outcome, R^2 value is not as crucial for the analyses and can be considered a descriptive and heuristic tool (Hagquist & Stenbeck 1998; Rafiq et al. 2023).

Additionally, we calculated attraction-avoidance ratios: index AB/BA, and index BAB/BB (Parsons et al. 2016; Niedballa et al. 2019), where: A = other predator, and B = wild dog. We calculated the median of the time intervals of BA (wild dog appears first and then the other predator), AB (other predator appears first and then wild dog), BB (wild dog appearing after a wild dog independent record), and BAB (wild dog appears first, then a predator and then a wild dog again). Values above 1 of both indices indicate non-random movements between the two species. High values of index AB/BA could be due to either a wild dog avoiding a predator, or a predator attracted to a wild dog. However, attraction of a predator to a wild dog would also result in low BAB/BB values plus high AB/BA values ($AB/BA > 1$) (Parsons et al. 2016). We only calculated indices per category (season, area, and distance to waterholes) for wild dogs with hyaenas (as wild dogs with other predators had a sample size which was too small per category). All analyses had an adequate sample size of at least 10 records per combination (Supporting information, Table S4) (Niedballa et al. 2019). To compare the observed indices to indices obtained under the null hypothesis, we generated random records per predator (except for wild dogs) (Karanth et al. 2017; Niedballa et al. 2019). While conserving the actual records of wild dogs, we generated 1000 random records of leopards, lions and hyaenas (random times accounting for the diel activity pattern of the predator and random dates within the period of activity of the camera trap in the area). We then compared the observed indices with the indices generated with random records, and calculated the 2.5% and 97.5% percentile of the random indices distribution.

Results:

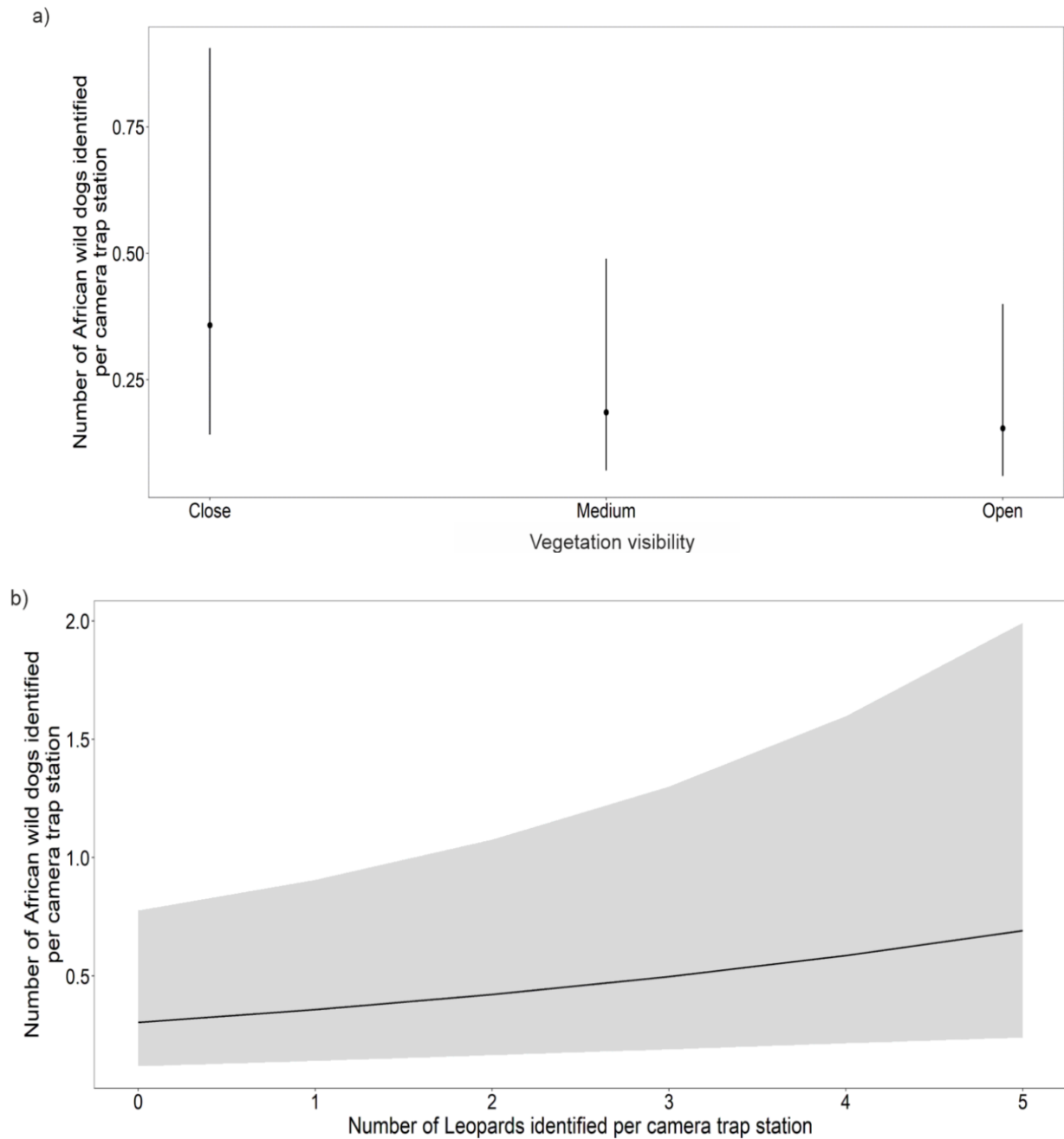
We summarized the main results in Tables 1 and 2.

Spatial

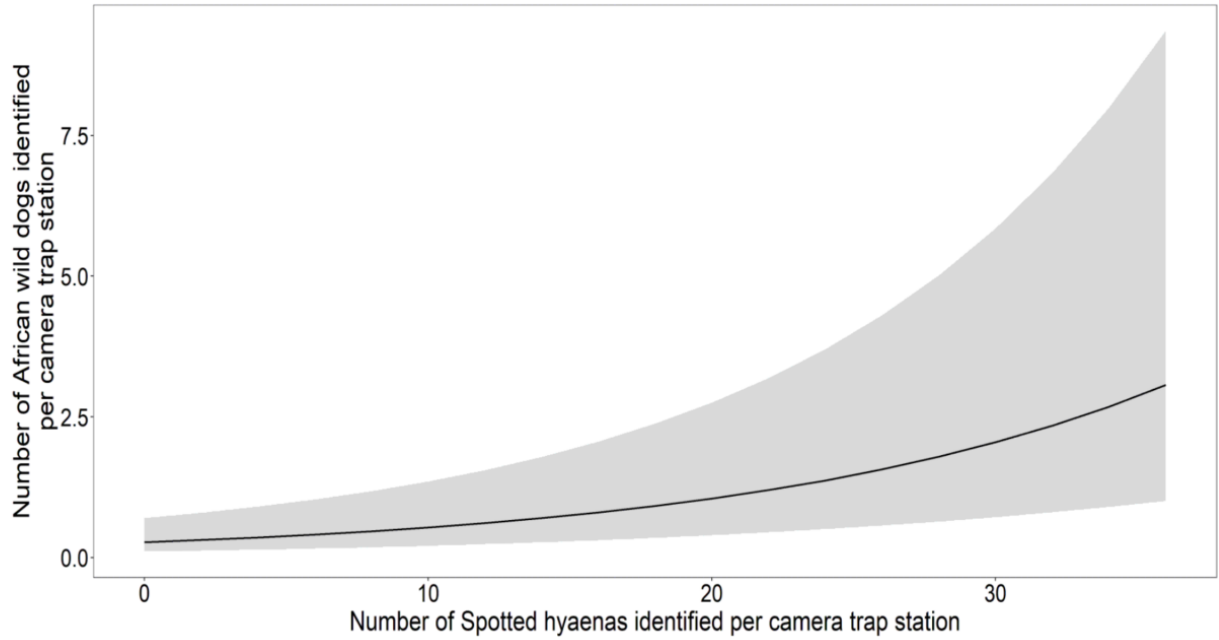
We found very strong statistical evidence that vegetation visibility (medium vs closed: estimate = -0.66 [SE = 0.20]; z-value < -3.26; p = 0.001; open vs closed: estimate = -0.85 [SE = 0.19]; z-value = -4.48; p < 0.001; Fig. 2a), number of hyaenas per camera trap station (estimate = 0.067 [SE = 0.011]; z-value = 6.053; p < 0.001; Fig. 2c), hyaena density in surveyed areas (estimate = -0.73 [SE = 0.20]; z-value = -3.62; p < 0.001; Fig. 2d) were the covariates that were associated with the number of individual wild dogs identified per camera trap station. Furthermore, we found strong statistical evidence that number of leopards per camera trap station (estimate = 0.16 [SE = 0.07]; z-value = 2.46; p = 0.01; Fig. 2b), waterhole distance (estimate = -0.42 [SE = 0.13]; z-value = -3.10; p = 0.002; Fig. 2e), and waterhole density within a 14 km buffer (estimate = 0.60 [SE = 0.21]; z-value = 2.91; p = 0.003; Fig. 2f) were the covariates that were associated with the number of wild dogs identified per camera trap station (conditional pseudo- $R^2 = 0.57$). There were more wild dogs in areas with closed vegetation visibility (bushy vegetation) than in areas with medium and open vegetation visibility (woodland and grassland). There were also more wild dogs with an increase in leopard and hyaena individuals at a camera trap station (small scale), a decrease in hyaena densities (especially above ~14 hyaenas / 100 km²) in surveyed areas (large scale), closer to waterholes and with higher waterhole densities (Fig. 2; Supporting information, Table S4).

On the other hand, we did not find statistical evidence that the number of lions in each camera trap station (estimate = -0.01 [SE = 0.027]; z-value = -0.24; p = 0.81), nor lion density in the surveyed areas (estimate = 0.57 [SE = 0.47]; z-value = 1.20; p = 0.23) were associated with the wild dog numbers per camera trap station (Supporting information, Table S4).

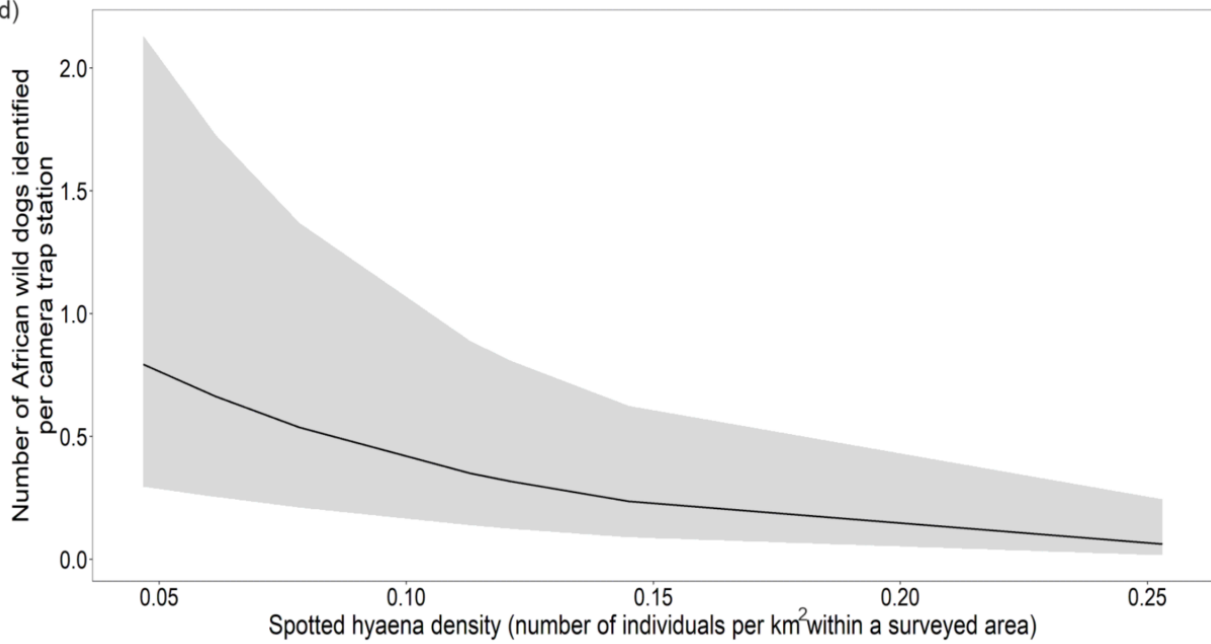
Figure 2. Results of the spatial model. Marginal back-transformed effects with 95% confidence intervals of the best GLMM of the number of African wild dogs identified per camera trap station per respective covariate (marginal pseudo- $R^2 = 0.31$; conditional pseudo- $R^2 = 0.57$). (Model results are in Supporting information, Table S4).

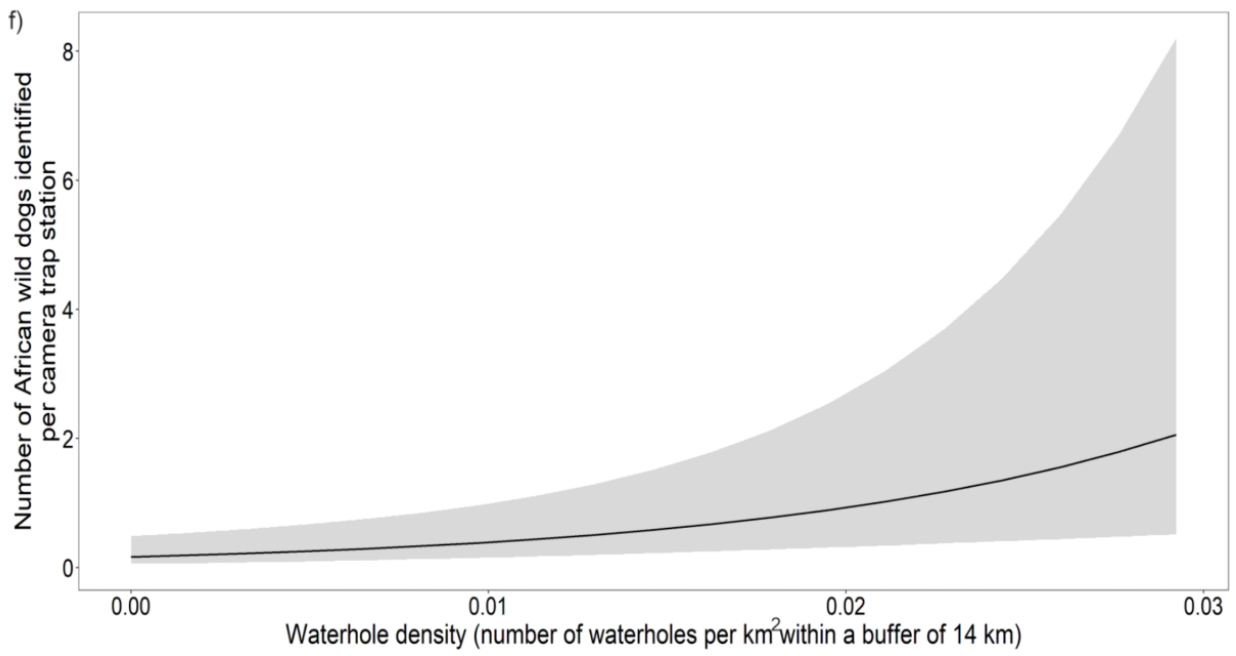
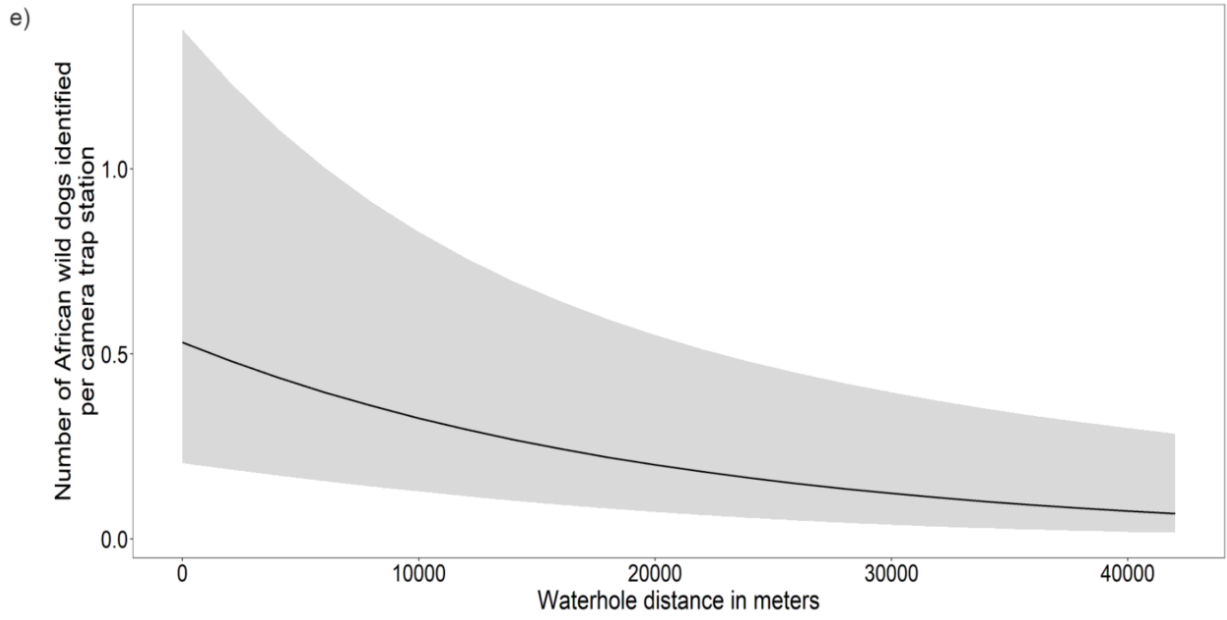


c)



d)





Temporal

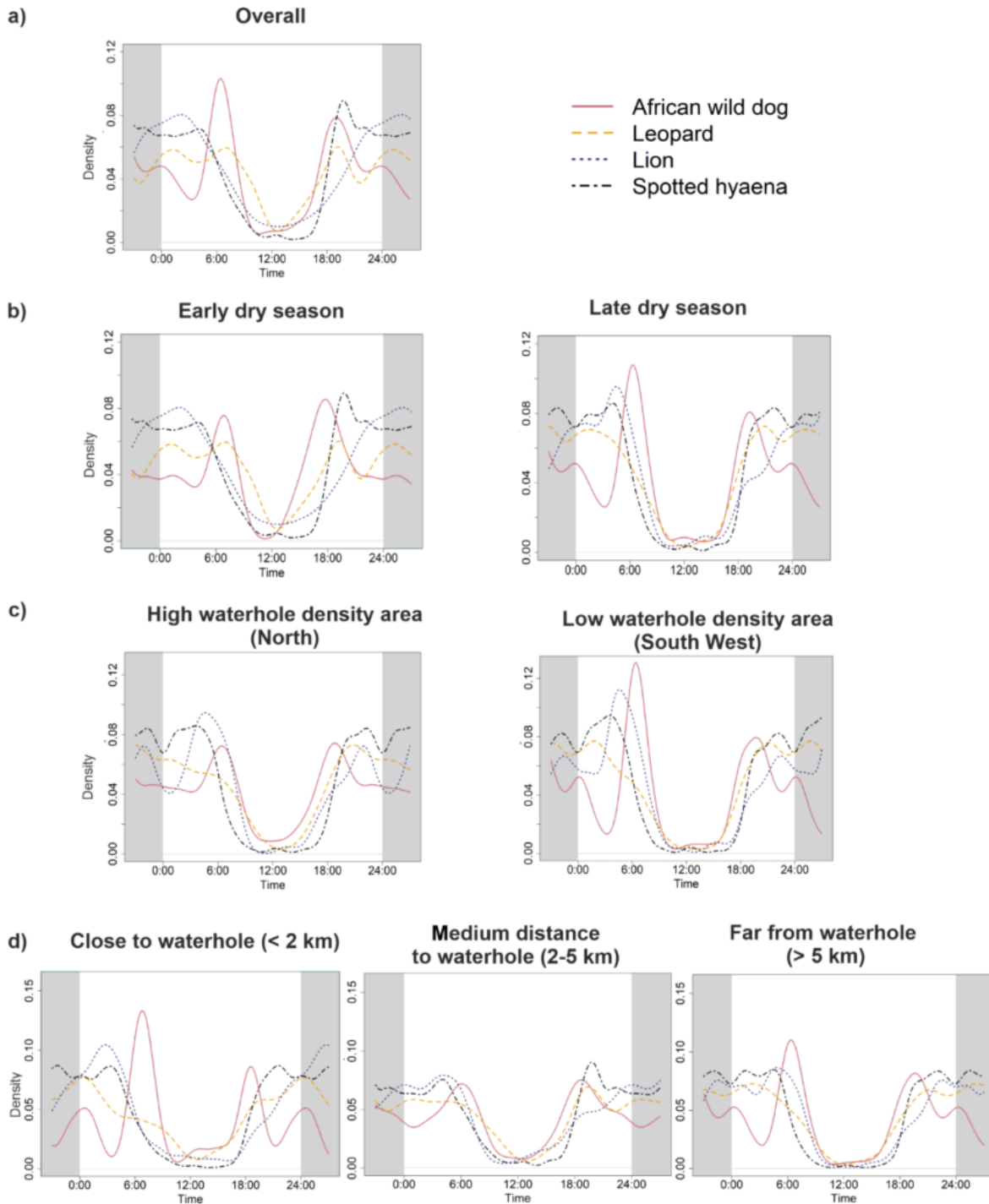
All predator activity patterns had two main peaks; wild dog activity peaked in crepuscular times (around 06:00 and 18:00); while other predators were more nocturnal with peaks before 06:00 and after 18:00. The wild dog activity pattern did not change with season, waterhole density nor waterhole distance ($p > 0.10$) (Fig. 3; Supporting information, Table S5).

Wild dog activity pattern overlapped the most with leopards ($\Delta_4 = 0.79$ [CI: 0.73, 0.86]) and the least with hyaenas activity ($\Delta_4 = 0.68$ [0.63, 0.74]). We found moderate evidence that wild dog activity pattern was different from the other predators ($p < 0.05$); except with leopards in the early dry season, in the high waterhole density area, and in a medium distance from waterholes ($p > 0.10$), where leopards and wild dogs activities overlapped the most (early dry season: $\Delta_4 = 0.81$ [0.69, 0.91]; high waterhole density area: $\Delta_4 = 0.87$ [0.79, 0.93]; medium distance to waterholes: $\Delta_4 = 0.88$ [0.79, 0.95]). Leopard activity pattern changed with seasons and waterhole distribution ($p < 0.01$). In the early dry season and in areas with high waterhole density leopard activity peaks were more crepuscular than nocturnal (more closely resembling wild dogs activity peaks) (Fig. 3; Supporting information, Table S5 and S6).

Wild dog activity overlap with the three other predators activity was the lowest closer to waterholes (leopards: $\Delta_1 = 0.67$ [0.49, 0.83]; lions: $\Delta_1 = 0.54$ [0.37, 0.70]; hyaenas: $\Delta_1 = 0.53$ [0.37, 0.70]). In these areas close to waterholes, there was hardly any wild dogs activity when dominant predators were the most active (before 06:00 and after 18:00). In contrast, in medium distance to waterholes wild dog activity overlap with lions and hyaenas activity was the highest (lions: $\Delta_4 = 0.80$ [0.69, 0.89]; hyaenas: $\Delta_4 =$

0.78 [0.69, 0.86]); and these differences in the activity overlap of wild dogs with lions and hyaenas between close and medium distance to waterholes were statistically significant (as 95% confidence intervals did not overlay). On the other hand, we did not find any evidence that wild dog activity overlap with lions and hyaenas activity differed between seasonality and waterhole density (95% confidence intervals overlapped). However, the tendency was that wild dog activity overlapped more with lion activity in the late dry season (late dry: $\Delta_4 = 0.73$ [0.66, 0.80]; early dry: $\Delta_4 = 0.67$ [0.54, 0.79]) and in the high waterhole density area (high waterhole density: $\Delta_4 = 0.75$ [0.66, 0.83]; low waterhole density: $\Delta_4 = 0.71$ [0.61, 0.80]). Additionally, wild dog activity overlap with hyaenas was almost equal between seasons ($\Delta = \sim 0.68$), but it was highest in the high waterhole density area ($\Delta_4 = 0.74$ [0.62, 0.88]) and lowest in the low waterhole density area ($\Delta_4 = 0.62$ [0.53, 0.70]) (Fig. 3; Supporting information, Table S7).

Figure 3. Activity pattern of African wild dogs and other predators depending on different categories: a) Overall; b) Seasons; c) Areas with different waterhole densities; d) Distance to waterhole. (Activity overlaps are in Supporting information, Table S6).



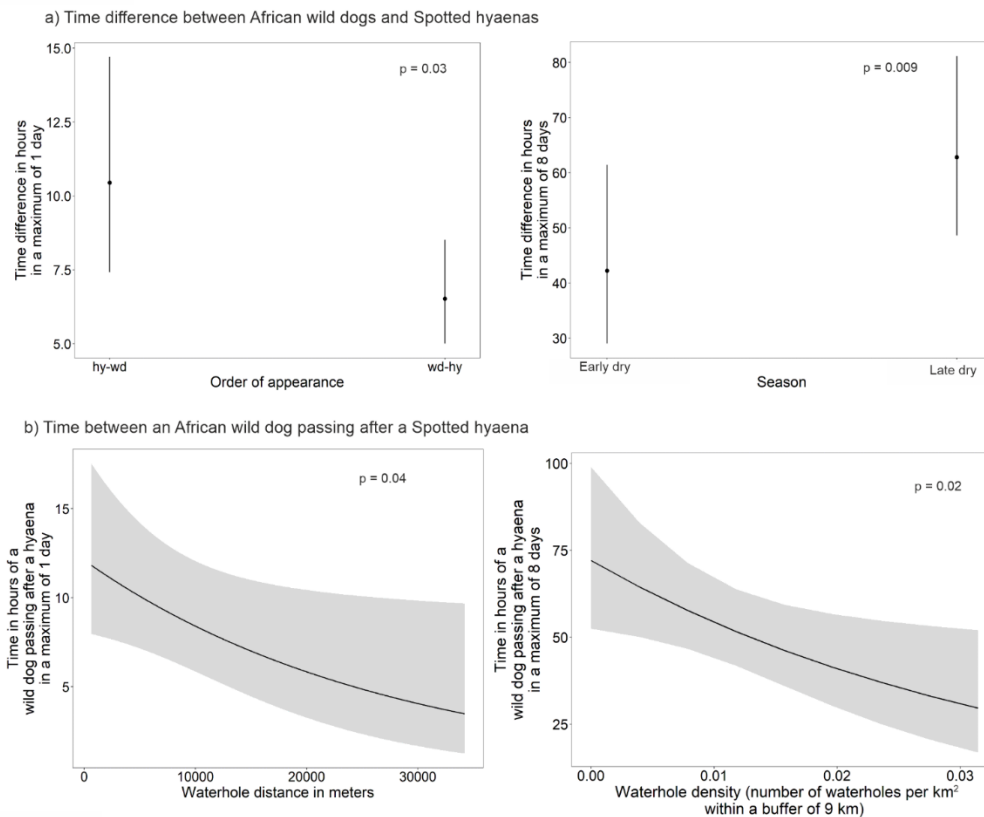
Spatio-temporal (time-to-event models and indices)

We did not find any evidence that season, waterhole density or predator density had an effect ($p > 0.14$) on the spatio-temporal dynamics of wild dogs with leopards and lions. However, predator density was the most important one to explain the time difference between wild dogs with leopards and lions. Nor did we find any evidence of attraction or avoidance of wild dogs with leopards and lions ($p > 0.24$). The fact that we did not find any statistical evidence could be due to a small sample size of wild dogs with lions and leopards occurring in the same camera trap station within 8 days (leopards: $n = 69$; lions: $n = 37$). This is especially the case for wild dogs and lions (lions and wild dogs appearing on the same location had the smallest sample size), which in itself might indicate that wild dogs avoid lions (Supporting information, Table S3).

When considering a maximum of 1-day difference, hyaenas passed a camera trap station an estimated average (both from the model and calculated from the data) ~6 hours after a wild dog; and wild dogs passed by an estimated average ~10 hours after a hyaena; and this difference was significant (estimate = -0.47 [SE = 0.21]; t-value = -2.20; $p = 0.03$) (Fig. 4a). However, using a maximum of 8-days difference, there was no evidence of attraction or avoidance of wild dogs with hyaenas (estimate = -0.28 [SE = 0.16]; t-value = -1.74; $p=0.08$). In a maximum of 1-day difference, there was no effect of any covariates influencing the appearance of a wild dog after a hyaena. In contrast, in a maximum of 8-days difference, wild dogs and hyaenas passed closer in time during the early dry season (estimate = -0.48 [SE = 0.18]; t-value = -2.64; $p = 0.009$) (Fig. 4a). Within 1-day difference, wild dogs took longer to pass after hyaenas when distant from waterholes increased (estimate = -0.35 [SE = 0.16]; t-value = -2.13; $p = 0.04$), and

waterhole density within a buffer of 9 km decreased (estimate = -0.24 [SE = 0.11]; t-value = -2.31; p = 0.02) (Fig. 4b) (Supporting information, Table S7).

Figure 4. Marginal effects with 95% confidence intervals of the generalized linear models from the time-to-event analyses of African wild dogs (wd) with Spotted hyaenas (hy). a) Including both order of appearance between wild dogs and hyaenas (in 1 day maximum time: McFadden's $R^2 = 0.04$; in 8 days maximum time: McFadden's $R^2 = 0.05$); b) spotted hyaenas appear first then African wild dogs (in 1 day maximum time: McFadden's $R^2 = 0.07$; in 8 days maximum time: McFadden's $R^2 = 0.06$). (Model results are found in Supporting information, Table S7).



Regarding the attraction/avoidance indices, all results fell inside the 2.5% and 97.5% percentile of the random indices, which indicates that any evidence of wild dog avoidance of predators was not strong (Supporting information, Fig. S1a). However, the tendency was that, as expected, wild dogs avoided the two largest dominant predators: lions and hyaenas ($AB/BA > 1$; lions = 1.04; hyaenas: 1.7), whereas, there was no attraction nor avoidance of wild dogs and leopards ($AB/BA = 0.97$). Hyaenas were the species most attracted to wild dogs (low values of BAB/BB index [3.23] and values of $AB/BA > 1$) as compared to the other two predators, and wild dogs avoided lions the most (high value of BAB/BB index [24.52]) as compared to the other two predators (BAB/BB index in leopard: 6.41; in hyaena: 3.23). In addition, in a maximum of both 1-day and 8-days difference, wild dogs tended to use areas previously used by hyaenas in the early dry season (as the observed value of the BAB/BB index was outside of the 2.5% percentile to the left of the random distribution) (Supporting information, Fig. S1b,c,d).

Table 1. Summary of results: African wild dog avoidance strategy towards predators in a an ecosystem with artificial water provision

Dimension	Scale	Method	Species	Avoidance	Result
Space	Small	GLMM (wild dog number of individuals with predators number of individuals on same location) (Fig. 2)	Leopard	No	Positive correlation between wild dog abundance and leopard abundance at the same location.
			Lion	No effect	
			Spotted hyaena	No	Positive correlation between wild dog abundance and hyaena abundance at the same location.
	Large	GLMM (wild dog individuals with predators densities on surveyed areas) (Fig. 2)	Leopard	No effect	Negative correlation with hyaena density in surveyed areas
			Lion	No effect	
			Spotted hyaena	Yes	
Time	Large	Activity overlap (Δ) (Fig. 3)	Leopard	Sometimes ($\Delta = 0.79$)	Avoidance (different activity pattern) only in the late dry season, in low waterhole density areas, and close to water (< 2 km) ($\Delta = \sim 0.70$) Avoidance (different activity pattern) especially close to water (< 2 km) ($\Delta = 0.54$)
			Lion	Yes ($\Delta = 0.73$)	
			Spotted hyaena	Yes ($\Delta = 0.68$)	
Spatio-temporal	Small	Time-to-event (same location within 1 day) and indices (Fig. 4)	Leopard	Not enough data	Wild dogs detected after longer period after hyaenas than hyaenas after wild dogs (especially closer to water)
			Lion	Not enough data	
			Spotted hyaena	Yes	
	Large	Time-to-event (same spot within 8 days) and indices (Fig. 4)	Leopard	No effect	Wild dogs detected after longer period after hyaenas in the late dry season, and the lower the waterhole density
			Lion	No effect	
			Spotted hyaena	Sometimes	

	Leopard	Lion	Spotted hyaena
Space	No avoidance	No evidence of an effect	No avoidance at small scale. Proactive avoidance at large scale.
Time	Proactive in late dry season, in low waterhole density areas, and close to water.	Proactive (different activity pattern)	Proactive (different activity pattern)
Spatio-temporal	Most likely proactive* but there was not enough data to test	Most likely proactive* but there was not enough data to test	Reactive, although proactive in the late dry season, closer to water and with lower waterhole densities.

*small sample size to test it in a big survey (26,030 trap days; Supporting information, Tables S1, S2 and S3), which in itself most likely indicates avoidance from wild dogs.

Discussion:

Avoidance behaviours towards predators are favoured by subordinate predators when the information gathered about the threat is reliable, the threats fluctuate and when the fitness benefits of avoidance are higher than the costs of encounters, provided the avoidance behaviour is effective (Harvell 1990; Creel 2018). Depending on different ecological circumstances (e.g. prey abundance, seasonality, vegetation) the avoidance strategies of subordinate predators can vary spatially and temporarily (Vanak et al. 2013; Karanth et al. 2017; Zhao et al. 2020).

Our main finding was that wild dogs overall used the same space as the other three larger predators, but at different times. When the risk is predictable in time but not space, proactive temporal avoidance is expected and the costs are on the limited time spent in habitat rich in resources, such as water and prey (Palmer et al. 2022). In our

study, wild dogs were mainly using a proactive temporal avoidance strategy (different activity pattern) with all three predators. On the other hand, when the risk is predictable in space but not in time, proactive spatial avoidance is expected (costs are on the deprivation of prey-rich areas) (Palmer et al. 2022). In our study, when only considering spatial avoidance, wild dogs were not avoiding larger predators at a small scale (same location), and wild dogs were only avoiding hyaenas proactively at a large scale (surveyed area). In addition, even though the strength of avoidance of wild dogs towards larger predators was not always strong, we found moderate evidence that wild dogs were using a spatio-temporal proactive avoidance strategy with lions and leopards and a reactive avoidance strategy (same location within 1 day) towards hyaenas. When the risk of predator encounters is unpredictable in both space and time, then reactive behaviours are expected (Creel 2018; Palmer et al. 2022).

In various ecosystems, wild dogs actively avoid lions both spatially and temporally at different scales (Hayward & Slotow 2009; Darnell et al. 2014; Dröge et al. 2017). In our study, wild dogs probably (untested due to a small sample size) avoided lions proactively at a small spatial scale (same location) and time (1 day). This is consistent with most other studies where reactive spatial avoidance behaviours from wild dogs towards lions are less common than proactive behaviours (Vanak et al. 2013; Swanson et al. 2014; Davies et al. 2021). However, Strampelli et al. (2023) found reactive spatial avoidance by wild dogs towards lions at a small-scale (within home range: ~2 km grid); and little evidence of proactive spatial avoidance (at the home range scale: 225 km² grid). On the other hand, wild dogs do not always exhibit spatial or temporal avoidance towards hyaenas or leopards at different scales (Darnell et al. 2014;

Dröge et al. 2017; Strampelli et al. 2023). This could be because the threat hyaenas and leopards pose to wild dogs is not as high as threats posed by lions, especially in terms of wild dog mortality risk (Woodroffe & Ginsberg 1999; Comley et al. 2023). Perhaps, this is why wild dogs did not avoid leopards and hyaenas spatially on a small scale (same location). When spatial avoidance does not occur, subordinate species tend to avoid using the same space at the same time (temporal avoidance) as the dominant competitor; this was for example found for pumas and jaguars (Harmsen et al. 2009) and is in line with our finding that wild dogs avoided the three predators temporally. Conversely, this can also occur when an increase of temporal overlap is associated to a decrease in spatial overlap, which has been shown for mesocarnivores avoiding leopards (Zhao et al. 2020).

Influence of covariates

At a large temporal scale, wild dogs were active at different times of the day than lion and hyaenas and to a lesser extent leopard. This temporal proactive avoidance was especially evident close to water with all three competing predators (as expected in our predictions), and with hyaenas and leopards during the late dry season and in low waterhole density areas (contrary to our predictions).

In our study the activity overlap of wild dogs with the other predators was slightly higher than in other studies, especially in regard to the activity pattern of wild dogs and leopards (Hayward & Slotow 2009; Krag et al. 2023). This could cause a higher probability of leopards and wild dogs encounters (Rafiq et al. 2020), especially in the high waterhole density area where leopards were more crepuscular than nocturnal and

therefore showed a higher activity overlap with wild dogs. Although leopards are larger than wild dogs, wild dogs in a pack outnumber solitary leopards (Creel & Creel 1996; Bailey 2005); thus, leopards do not necessarily impose a high threat to wild dogs (Comley et al. 2023).

When subordinate species are constrained (e.g. due to resource access or denning restrictions, or periodic increases in competition), they might not be able to strongly avoid the risk of larger predators, and in turn, be forced to use a reactive avoidance strategy over a proactive strategy (Darnell et al. 2014; Palmer et al. 2022). In addition, when strong spatial (proactive) avoidance is not possible reactive spatial avoidance occurs, and wild dogs can implement stronger temporal avoidance instead (Darnell et al. 2014; Palmer et al. 2022). Close to water (a crucial resource), wild dogs were using stronger proactive temporal partitioning to avoid the three large predators. Temporal partitioning is commonly seen at waterholes among other African carnivores (Edwards et al. 2015) and between herbivores and carnivores (Valeix et al. 2009; Courbin et al. 2016). For instance, wild dog activity pattern in Maremani Nature Reserve (South Africa) differed between artificial waterholes and roads: at waterholes wild dogs activity overlapped more with hyaenas than at roads (Krag et al. 2023). We show the opposite in our study, the highest activity overlap of wild dogs with hyaenas was at medium distances from waterholes. In Maremani Nature Reserve, lions are absent (Krag et al. 2023), thus wild dogs do not need to avoid them temporally at waterholes. This is not the case in HNP, where wild dogs activity overlap with lions was the lowest close to water.

In the late dry season and in the low waterhole density area, wild dogs used a strong avoidance towards hyaenas and leopards. When there is high visibility due to little vegetation to hide during the dry season (in our case late dry season), wild dogs tend to use a stronger avoidance strategy (proactive strategy) towards predators. However, when there is low visibility due to dense vegetation during the wet season (in this case early dry season), wild dogs tend to use a reactive strategy to avoid predators (Vanak et al. 2013). As the risk is difficult to predict (hard to detect potential threats) in low visibility (e.g. early dry season, or closed vegetation), reactive avoidance strategies are favoured. This is also the case in other species, where for example seals use reactive behaviours to avoid sharks in rookeries as the risk is unpredictable (Hammerschlag et al. 2006), or when dholes and leopards restrict small-scale avoidance behaviours towards tigers in locations with open vegetation and high visibility (Karanth et al. 2017).

Wild dogs tend to evade dominant predators in space by using habitat structure and altering habitat selection (Davies et al. 2021). In HNP, lions prefer grassland, leopards prefer woodland, and hyaenas prefer both woodland and grassland (Valeix et al. 2010; Davidson et al. 2012; Périquet 2014; Loveridge et al. 2022). In our study, we found that wild dogs abundance was higher in closed vegetation (bushland), and lower in medium and open vegetation (woodland and grassland). In other studies wild dogs also preferred dense vegetation, except in areas of high lion-encounter risk where they use temporal partitioning and open vegetation to facilitate lion detection (Davies et al. 2021; Pretorius et al. 2021). In dense vegetation, predator encounter risk can be higher due to the risk of ambush (Webster et al. 2012; Rafiq et al. 2020; Davies et al. 2021).

However high visibility in open vegetation can also facilitate detection of subordinate species by predators (Janssen et al. 2007), and increase the risk of kleptoparasitism (especially from hyaenas) of wild dog kills (Creel & Creel 1998). Thus, it appears that wild dogs are dynamic in their habitat use and need landscape heterogeneity to successfully avoid predators (Dröge et al. 2017; Shumba et al. 2018; Davies et al. 2021). There are other species that also alter their habitat use to avoid dominant predators, such as kit foxes avoiding coyotes (Kozłowski et al. 2011) or leopards and dholes avoiding tigers (Steinmetz et al. 2013).

As wild dogs are cursorial hunters (Creel & Creel 2002), it could be expected that they select open vegetation (Vanak et al. 2013; O'Neill et al. 2020); however, low visibility in dense vegetation can reduce chase distance and increase wild dogs hunting success (Krüger et al. 1999; Creel & Creel 2002). Wild dogs in HNP, feed primarily on browsers and mixed feeders, which are prey species found in dense bushland vegetation; and dominant predators select both browsers and grazers, which are found in grassland (Sandoval-Serés et al. 2024). This dietary separation can also enable wild dogs to select habitats where some of their primary prey is found but dominant predators are less likely to occur (e.g. bushland) (Vanak et al. 2013; Davies et al. 2021).

Despite the fact that the risk of kleptoparasitism towards wild dogs from hyaenas is lower in low waterhole density areas (Chapter 3, Sandoval-Serés et al. *in review*), wild dogs avoided hyaenas more strongly in the low waterhole density area. This could be because as lions are less abundant in the low waterhole density area, wild dogs had more opportunity to avoid hyaenas in this area because they did not have to strongly avoid lions in the low waterhole density areas. Similarly, the density of leopards is

higher than the density of lions in low waterhole areas (Loveridge et al. 2022) which could explain why wild dogs had a stronger temporal avoidance (lower activity overlap) with leopards in this area than in the high waterhole density area. It is also in this low waterhole density area, where there is less prey abundance (Sandoval-Serés et al. 2024), and it was in these areas where wild dogs did not show strong avoidance towards larger predators. This is consistent with other studies, where subordinate predators showed stronger avoidance towards other larger predators (decrease in temporal and spatial partitioning) in low prey densities areas (Karanth et al. 2017).

In our study, and opposite to our predictions, wild dogs used a proactive spatial strategy to avoid hyaenas. In HNP lion densities (~ 3.5 lions/100km²) are not as high as in other ecosystems (~ 12 to 26 lions/100km²) (Davies et al. 2021; Marneweck et al. 2021), whereas hyaena densities in HNP (~ 14.1 hyaenas/100 km²) are not low compared to other ecosystems averaged (~ 39 hyaenas/100km²) (Périquet, 2014). Perhaps this explained why in our study wild dogs at a large scale spatially avoided hyaenas and not lions. Moreover, lions and hyaenas tend to aggregate close to waterholes (Valeix et al. 2010; Davidson et al. 2012; Périquet 2014), and their densities tend to be higher in areas with high waterhole densities (in the north part of HNP) (Loveridge et al. 2022; Sandoval-Serés et al. 2024). Despite this, wild dog abundance in HNP was higher closer to water and in higher waterhole densities. As prey and dominant predators concentrate close to waterholes (Redfern et al. 2003; Chamailé-Jammes et al. 2009b; Valeix et al. 2010), wild dogs in HNP also tend to hunt close to water (Van der Meer 2011). Additionally, as prey abundance is higher in the north of HNP where more waterholes are found (Sandoval-Serés et al. 2024), then most likely

wild dogs are prioritizing prey encounter over the risk of encountering larger predators. It could be that wild dogs can afford to use the same areas that dominant predators use (i.e. areas with high prey abundances associated to high waterhole densities), because they can hide in dense vegetation and use a temporal avoidance strategy when they need to approach a waterhole. Thus, it seems that wild dogs are able to cope with predators as long as there is a heterogeneous landscape (in terms of both waterhole density and vegetation) to be able to hide from larger predators.

When a proactive spatial avoidance strategy is used, wild dogs are excluded from prey rich areas (Mills & Gorman 1997; Creel 2001; Swanson 2014). This has nutritional-related costs which lowers their fitness (e.g. decreasing their reproductive success) (Creel 2018; Marneweck et al. 2019). These costs might be the reason why wild dogs in HNP did not normally use a spatial proactive strategy, and preferred to use a temporal strategy to avoid predators instead. As hyaena densities in HNP are higher than the densities of the other larger predators and hyaenas tend to be evenly distributed across habitats (unpublished data, Cozzi et al. 2013; Loveridge et al. 2022), wild dogs might not be able to spatially avoid hyaenas at small scales, and thus try to avoid them in a large scale (wild dog individuals increasing in areas with less hyaena densities).

Limitations

Due to the nature of our data (camera trap data) and the nature of the study species (wild dogs, lions and leopards living in lower densities than hyaenas and appearing less in camera trap pictures than hyaenas), we were unable to test very small

spatio-temporal scales of avoidance (e.g. less than 1-day time differences on the same location, or home ranges and core-areas of wild dog packs, or exact distances of wild dog individuals to dominant predators in simultaneous events). Thus, in our study, the reactive avoidance behaviours of wild dogs towards competing predators referred to a 24h scale at the same location. Small-scale spatio-temporal avoidance (less than 8 days) towards lions and leopards was only inferred indirectly due to small sample sizes. This small sample size could indicate either low abundances, or strong avoidance by wild dogs. As our data set was large (26,030 trap days) and the sample size was small even in areas with higher abundances of wild dogs and dominant predators, the most probable explanation is that a small sample size indicated that wild dogs actively spatio-temporally avoided lions and leopards at scales of less than 8 days. This study shows that it is also possible to infer reactive and proactive behaviours with camera trap studies as long as the scale is specified. Specification of scale is highly important as reactive and proactive strategies can vary depending on the scale used (e.g. it is not the same to use a 2 to 24 hours difference than to use a 1 to 8 days difference to test reactive against proactive behaviours).

Conservation implications

Spatial and temporal overlap of subordinate predators with dominant predators can increase due to human pressure (Rasmussen & Macdonald 2012; Sévêque et al. 2020; Strampelli et al. 2023). Although wild dogs have evolved together with larger predators (Turner 1990), decreased habitats due to anthropogenic factors has provoked that most of large carnivore populations occur within protected areas (Loveridge et al.

2010). This could aggravate interspecific competition especially for subordinate predators, which can in turn result in high levels of anthropogenic mortality at the edge of protected areas; for example, wild dogs select areas at the border of protected areas where they face less competition from lions and hyaenas but higher anthropogenic threats (Woodroffe & Ginsberg 1998; Van der Meer et al. 2013). Thus, it is important to understand the dynamics of interspecific competition and create or maintain suitable habitat for wild dogs which assists the species in coping with dominant predators.

Habitat and prey are main drivers of predator interactions and coexistence (Vanak et al. 2013; Karanth et al. 2017; Davies et al. 2021). Habitat heterogeneity at different spatial scales is highly important for wild dogs to thrive and to be able to spatially avoid dominant predators (Dröge et al. 2017; Davies et al. 2021). In HNP, wild dogs prefer to use areas with a mixture of different vegetation types (Shumba et al. 2018), which could be due to habitat use alternation and adaptation to avoid larger predators (Davies et al. 2021). In our study, wild dogs were able to coexist in space in the areas with high lion densities (highest lion density: ~ 6.9 lions/100 km² - unpublished data, Loveridge et al. 2022). This was most likely thanks to temporal avoidance and the landscape heterogeneity (probably influenced by waterhole density and distribution) and the availability of dense vegetation. However, wild dogs tend to avoid areas where hyaena densities were high (especially higher than ~ 14 hyaenas/100 km²).

Wild dogs take higher risks to overlap with dominant predators when they need to access critical resources (i.e. water and prey) and when they are not denning (Vanak et al. 2013; Marneweck et al. 2021; Pretorius et al. 2021). As prey is crucial for wild dog survival and reproduction (Marneweck et al. 2019; Creel et al. 2024), encountering prey

can outweigh the risk of encountering dominant predators (Cozzi et al. 2012; Vanak et al. 2013; Creel et al. 2024). Highly structured habitat and with high prey densities, are therefore both crucial for wild dogs to thrive and to offset the risks of interspecific competition (Davies et al. 2021; Marneweck et al. 2021). Furthermore, habitat heterogeneity also helps conserve different prey species (Janssen et al. 2007).

We show that very high hyaena densities do not favour wild dogs, especially when there is little water in the system (i.e. in the late dry season and in areas with low waterhole densities). Low water availability can increase food resource competition of wild dogs with lions and hyaenas, and reduce prey abundance (Sandoval-Serés et al. 2024). This can potentially contribute to lower numbers of wild dogs when permanent waterhole densities are low. The creation of more artificial waterholes (increasing waterhole density) could potentially help increase the abundance of prey and potentially also lower food resource competition (increasing diet niche partitioning opportunities) of wild dogs with other competitors. However, the creation of new artificial waterholes could also have negative impacts to other species, such as plant species (Wilson et al. 2021).

Waterhole distribution can potentially have an indirect impact on the landscape by the creation of vegetation changes due to herbivores distribution and aggregation. For example, elephant densities are higher in areas of higher waterhole densities (Chamaillé-Jammes et al. 2007b; Sandoval-Serés et al. 2024), and elephants highly concentrate around artificial waterholes especially during the dry season (Chamaillé-Jammes et al. 2007b); as elephants are landscape architects they can impact herbivores feeding areas and increase the pressure on vegetation around waterholes

(e.g. vegetation around waterholes tends to be open grassland) (Chamaillé-Jammes et al. 2007a; Valeix et al. 2011; Landman et al. 2012). Thus, a homogeneous waterhole distribution in the ecosystem could become counterproductive for wildlife conservation by potentially provoking habitat homogeneity in the landscape and decreasing niche-partitioning opportunities. Thus, a water management plan in natural protected areas should avoid provoking that different areas of the park resemble each other.

Coexistence among intraguild competitors is possible without population repercussions as long as there is a balance in the ecosystem, and specifically for wild dogs, as long as there is a heterogeneous landscape (Miller et al. 2018; Davies et al. 2021). Water provisioning, as a conservation management tool, should be planned in accordance to favour wildlife, and especially endangered species. Very low waterhole densities in the landscape may not benefit wild dogs by not helping increase the prey abundance. However, creating waterholes without a planned strategy and having the same densities of waterholes everywhere would not help create a heterogeneous landscape essential for wild dogs to thrive and be able to cope with interspecific competition. To sum up, we propose a heterogeneous water management provisioning scheme that potentially could help keep enough prey abundance and aggregation and a heterogeneous landscape that increases niche partitioning opportunities. This can have further implications in the wide range ecosystems where water provisioning occurs.

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Conflict of Interest

None declared.

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Authors' contributions

E.S.S., E.D., M.V., E.M., and A.J.L. conceived the idea; J.S.S., A.S., and L.S. collected and processed the camera trap data; E.S.S. processed the data, did the analyses, and led the writing of the manuscript; E.D., L.S. E.Say-S., D.N, L.C. assisted in the analyses; D.M, R.M and A.J.L. supervised data collection. All authors gave feedback to the drafts and final approval for publication.

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Supporting information Chapter 4

Spatio-temporal dynamics of African wild dogs in response to larger carnivores in an ecosystem with artificial water provisioning

Supporting information

Table S1. Camera trap survey from 2013 to 2020.

N = North (high waterhole density area)

SW = South West (low waterhole density area)

Area	Surveyed areas (Fig. 1 in manuscript)	Year	Camera trap stations	Start date	End date	Total effort (days)	Water-hole density during the dry season (per 100 km ²)	Ratio* and % of artificial waterholes with water that year
N	Guvalala	2015	51	May	July	2325	1.29	20/21 95%
N	Guvalala	2018	44	May	July	2364	2.27	23/37 62%
N	Ngamo	2014	41	Sept	Nov	2133	0.82	9/11 82%
<i>N</i>	<i>Ngamo</i>	<i>2018</i>	<i>41</i>	<i>May</i>	<i>July</i>	<i>2103</i>	<i>1.57</i>	<i>19/21</i> <i>90%</i>
N	Robins	2013	40	Sept	Nov	1670	1.18	5/15 33%
N	Sinamatella	2019	73	June	Ago	4112	0.67	9/16 56%
SW	Dzibanini	2017	38	Sept	Oct	1932	0.076	0/1 0%
SW	Jozibanini	2017	40	Sept	Nov	2229	0.19	5/7 71%
SW	Shakwanki	2013	41	Aug	Sept	1679	0.035	1/1 100%
<i>SW</i>	<i>Shakwanki</i>	<i>2020</i>	<i>78</i>	<i>July</i>	<i>Oct</i>	<i>5483</i>	<i>0.035</i>	<i>1/1</i> <i>100%</i>

*Ratio = artificial waterholes with water in the dry season / total number of waterholes with water in the dry season that year.

In italics surveys that were not included in the GLMMs due to a lack of lion and hyaena densities information.

Table S2. Sample size of independent records (> 1 hr).

	Category	African wild dog	Leopard	Lion	Spotted hyaena
	Overall	234	763	658	3443
Season	Early dry	45	163	162	921
	Late dry	189	600	496	2522
Area	High waterhole density (North)	129	430	499	2335
	Low waterhole density (South West)	105	333	159	1108
Distance to waterhole	Close (< 2 km)	21	77	136	529
	Medium	80	187	202	1603
	Far (> 5 km)	114	415	186	940

Table S3. Sample size of African wild dogs with other predators.

A = predator; Wd = wild dog.

	Leopard	Lion	Spotted hyaena	
Combination	8 days	8 days	1 day	8 days
A-Wd	37	18	43	102
Wd-A	32	19	62	118
Wd-Wd	71	79	36	56

Table S4. Results of the Generalized Linear Mixed Model (GLMM) of the number of African wild dogs identified per camera trap station

(Fig. 2 in Main manuscript)

Fixed effects	Estimate	Standard error	Z-value	P-value
Intercept	-1.18	0.60	-1.98	0.047*
Trap effort (days)	-0.005	0.007	-0.75	0.45
Medium vegetation visibility	-0.66	0.20	-3.26	0.001*
Open vegetation visibility	-0.84	0.19	-4.48	< 0.0001*
Number of lion individuals	-0.006	0.03	-0.24	0.81
Number of spotted hyaena individuals	0.067	0.01	6.053	< 0.0001*
Number of leopard individuals	0.16	0.067	2.46	0.014*
Lion density	0.57	0.48	1.20	0.23
Spotted hyaena density	-0.73	0.20	-3.62	0.0003*
Waterhole distance	-0.42	0.13	-3.10	0.0019*
Waterhole density in 14 km buffer	0.60	0.21	2.91	0.004*

*significant differences ($p < 0.05$).

Random effects: Survey session: SD = 0.35; Year: SD = 1.05

Table S5. Watson's two-sample test of homogeneity of the activity pattern of predators depending on different categories.

	African wild dog	Leopard	Lion	Spotted hyaena
Seasons (Early dry vs Late dry)	Statistic: 0.14 P-value > 0.10	Statistic: 0.47 *P-value < 0.001	Statistic: 0.12 P-value > 0.10	Statistic: 0.65 *P-value < 0.001
Area (High vs Low waterhole density)	Statistic: 0.075 P-value > 0.10	Statistic: 0.43 *P-value < 0.001	Statistic: 0.17 P-value > 0.10	Statistic: 0.83 *P-value < 0.001
Distance to waterhole (Close vs Medium)	Statistic: 0.12 P-value > 0.10	Statistic: 0.062 P-value = 0.19	Statistic: 0.21 *P-value < 0.05	Statistic: 0.51 *P-value < 0.001
Distance to waterhole (Close vs Far)	Statistic: 0.14 P-value > 0.10	Statistic: 0.068 P-value = 0.19	Statistic: 0.21 *P-value < 0.05	Statistic: 0.05 P-value > 0.10
Distance to waterhole (Medium vs Far)	Statistic: 0.065 P-value > 0.10	Statistic: 0.20 P-value = 0.187	Statistic: 0.046 P-value > 0.10	Statistic: 0.94 *P-value < 0.001

*significant differences of activity patterns ($p < 0.05$).

Table S6. Overlap and Watson's two-sample test of homogeneity of the activity pattern of African wild dogs with other predators depending on different categories.

CI = 95% confidence interval.

(Fig. 3 in Main manuscript)

	African wild dog vs Leopard	African wild dog vs Lion	African wild dog vs Spotted hyaena
Overall	$\Delta_4 = 0.79$, CI: 0.73–0.86 Statistic: 0.70 P-value < 0.001	$\Delta_4 = 0.73$, CI: 0.66–0.79 Statistic: 1.60 P-value < 0.001	$\Delta_4 = 0.68$, CI: 0.63–0.74 Statistic: 2.69 P-value < 0.001
Early dry season	$\Delta_1 = 0.81$, CI: 0.69–0.91 Statistic: 0.01 P-value > 0.10	$\Delta_1 = 0.67$, CI: 0.54–0.79 Statistic: 0.43 P-value < 0.001	$\Delta_1 = 0.67$, CI: 0.54–0.78 Statistic: 0.57 P-value < 0.001
Late dry season	$\Delta_4 = 0.78$, CI: 0.71–0.85 Statistic: 0.72 P-value < 0.001	$\Delta_4 = 0.73$, CI: 0.66–0.80 Statistic: 1.25 P-value < 0.001	$\Delta_4 = 0.68$, CI: 0.62–0.74 Statistic: 2.30 P-value < 0.001
High waterhole density area	$\Delta_4 = 0.87$, CI: 0.79–0.93 Statistic: 0.139 P-value > 0.10	$\Delta_4 = 0.75$, CI: 0.66–0.83 Statistic: 0.73 P-value < 0.001	$\Delta_4 = 0.74$, CI: 0.62–0.88 Statistic: 1.01 P-value < 0.001
Low waterhole density area	$\Delta_4 = 0.70$, CI: 0.61–0.79 Statistic: 0.74 P-value < 0.001	$\Delta_4 = 0.71$, CI: 0.61–0.80 Statistic: 0.79 P-value < 0.001	$\Delta_4 = 0.62$, CI: 0.53–0.70 Statistic: 1.88 P-value < 0.001
Close to waterhole	$\Delta_1 = 0.67$, CI: 0.49–0.83 Statistic: 0.21 P-value < 0.05	$\Delta_1 = 0.54$, CI: 0.37–0.70 Statistic: 0.48 P-value < 0.001	$\Delta_1 = 0.53$, CI: 0.37–0.70 Statistic: 0.56 P-value < 0.001
Medium distance to waterhole	$\Delta_4 = 0.88$, CI: 0.79–0.95 Statistic: 0.096 P-value > 0.10	$\Delta_4 = 0.80$, CI: 0.69–0.89 Statistic: 0.37 P-value < 0.01	$\Delta_4 = 0.78$, CI: 0.69–0.86 Statistic: 0.51 P-value < 0.001
Far to waterhole	$\Delta_4 = 0.76$, CI: 0.67–0.84 Statistic: 0.52 P-value < 0.001	$\Delta_4 = 0.67$, CI: 0.59–0.75 Statistic: 0.66 P-value < 0.001	$\Delta_4 = 0.62$, CI: 0.51–0.73 Statistic: 1.60 P-value < 0.001

In red the highest overlap within a different category.

In grey activity pattern did not differ significantly ($p > 0.05$).

Table S7. Results of the time-to-event models (GLMs) (Fig. 4 in Main manuscript)

*Time difference of Spotted hyaena and African wild dogs passing on the same spot
(1 day maximum)* (Fig. 4a in Main manuscript)

Covariate	Estimate	Standard error	t-value	P-value
Intercept	2.45	0.21	11.57	< 0.001*
Number of independent records of wild dogs	-0.11	0.075	-1.41	0.16
Combination first wild dog passes then hyaena	-0.47	0.21	-2.20	0.03*

*Time difference of Spotted hyaena and African wild dogs passing on the same spot
(8 days maximum)* (Fig. 4a in Main manuscript)

Covariate	Estimate	Standard error	t-value	P-value
Intercept	3.92	0.19	20.93	< 0.001*
Number of independent records of wild dogs	-0.12	0.038	-3.16	0.002*
Combination first wild dog passes then hyaena	-0.28	0.16	-1.74	0.08
Late dry season	0.48	0.18	2.64	0.009*

*Spotted hyaena appears first then African wild dog
(1 days maximum)* (Fig. 4b in Main manuscript)

Covariate	Estimate	Standard error	t-value	P-value
Intercept	2.07	0.26	7.83	< 0.001*
Number of independent records of wild dogs	0.08	0.12	0.68	0.50
Waterhole distance	-0.35	0.16	-2.13	0.04*

Spotted hyaena appears first then African wild dog

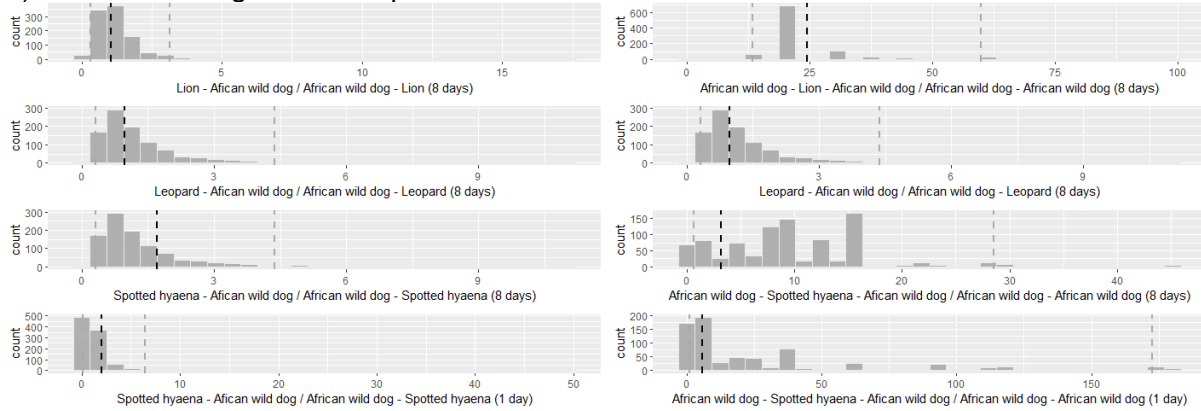
(8 days maximum) (Fig. 4b in Main manuscript)

Covariate	Estimate	Standard error	t-value	P-value
Intercept	4.24	0.16	26.33	< 0.001*
Number of independent records of wild dogs	-0.12	0.049	-2.36	0.021*
Waterhole density in 9 km buffer	-0.24	0.10	-2.31	0.023*

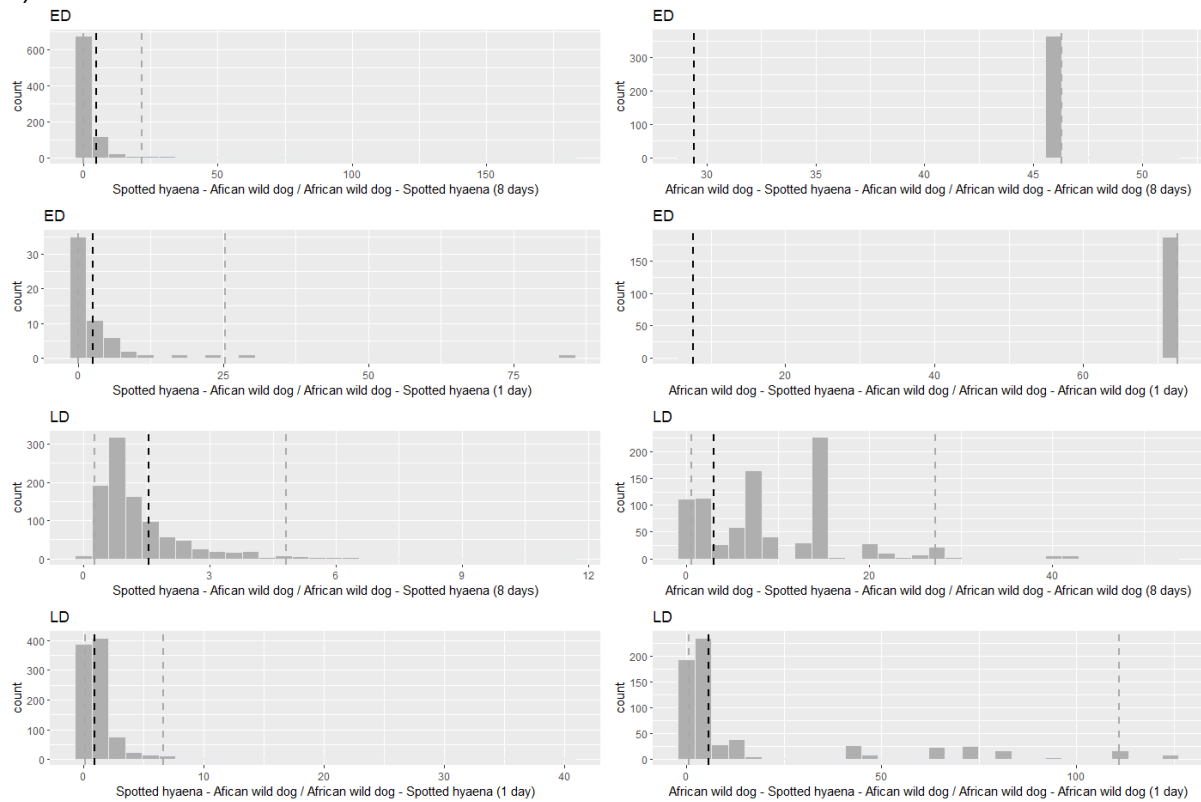
*significant differences ($p < 0.05$).

Figure S1. Attraction-avoidance indices (AB/BA and BAB/BB) values (black-dotted vertical line showing the real observed value) versus the distribution of the random simulated indices (grey-dotted vertical lines showing 2.5% and 97.5% percentile of the random indices distribution), for a) African wild dog with other predators (using a maximum of 8-days difference); and African wild dog with spotted hyaena per category (using a maximum of 1 and 8-days difference): b) Season (ED = early dry; LD = late dry), c) area with different waterhole densities, and d) distance to waterholes.

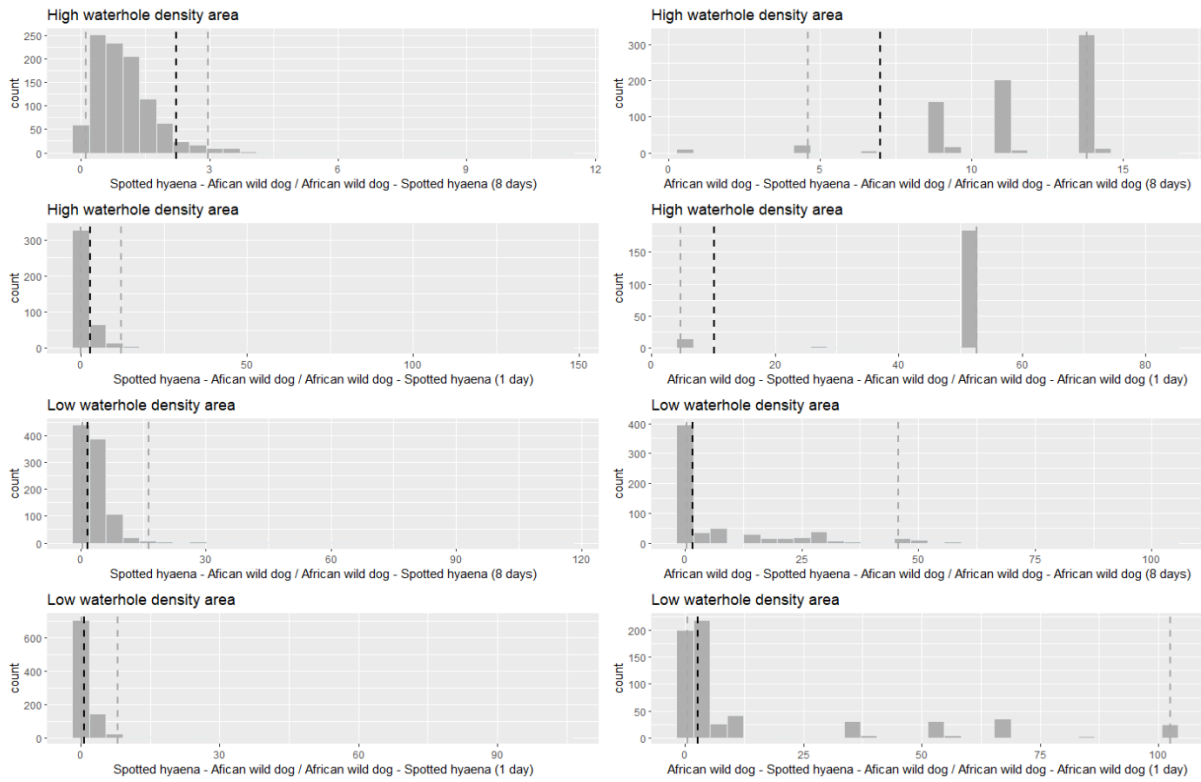
a) African wild dog with other predators



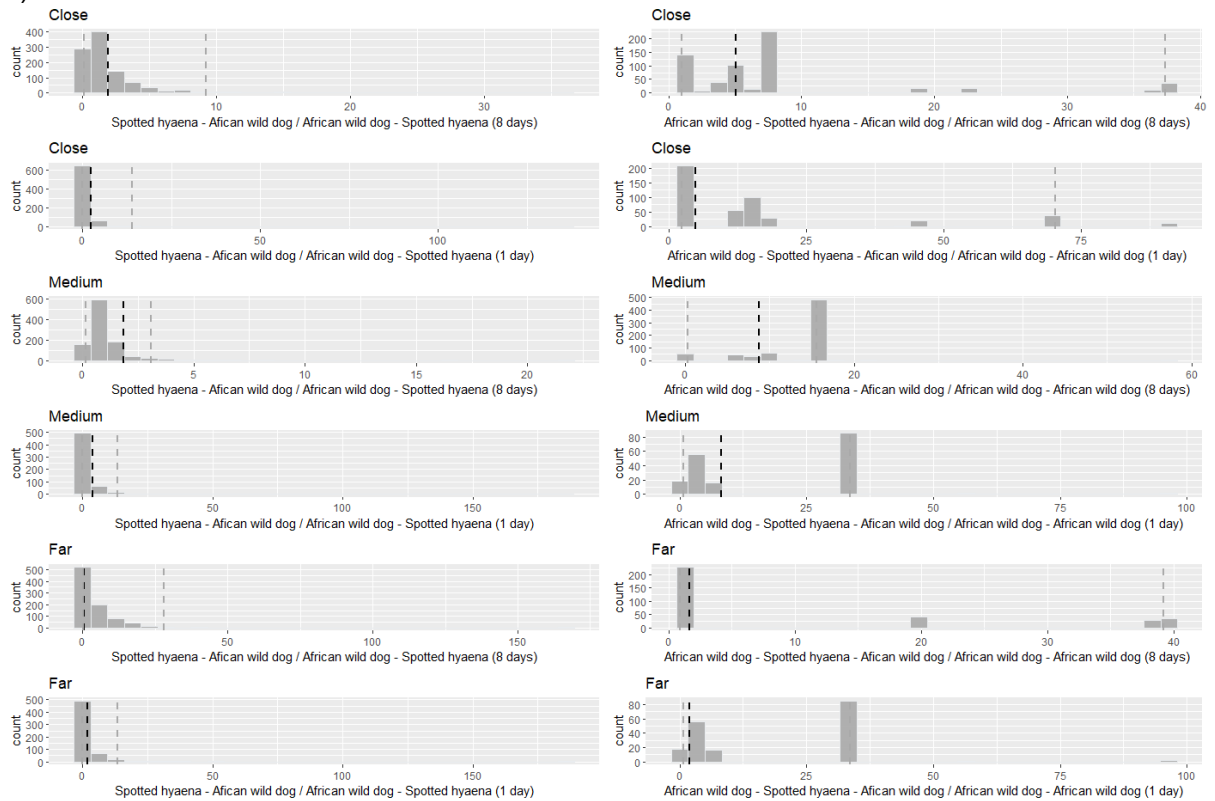
b) Season



c) Area



d) Distance to waterhole



Chapter 5
General discussion

Aims and motivations

The main aim of this thesis was to evaluate how African wild dogs cope with the competition with larger dominant predators (mainly lions and spotted hyaenas) in an ecosystem with artificial perennial water provisioning. The main motivation to perform this research was that even though it is well known that interspecific competition with larger dominant predators affects wild dogs negatively (Creel & Creel 1996; Mills & Gorman 1997; Swanson 2014), the role of artificial permanent water availability in the dynamics of interspecific competition between wild dogs and their larger competitors was not yet well researched.

Based on this research it was intended to propose water management strategies to decrease interspecific competition on wild dogs and assist with their conservation. Science-based management decisions in natural protected areas are essential for wildlife conservation (Ferraro & Pressey 2015), especially for endangered species such as wild dogs. Moreover, water is an essential resource for wildlife, and its availability and distribution affects prey availability and distribution (Chamaillé-Jammes et al. 2009b; Sandoval-Serés et al. 2024), and in turn, have implications on the dynamics of interspecific competition (Périquet 2014; Sandoval-Serés et al. 2024). Moreover, the topic of this thesis can help address one of the research and conservation priorities of the African wild dog Action Plan in the KAZA Transfrontier Conservation Area (KAZA-TFCA Secretariat 2014) and in the National Conservation Action Plan in Zimbabwe (where Hwange National Park [HNP] the study area is located) (ZIMPARKS 2009),

which is to understand how to limit wild dog competition with dominant predators through management decisions.

Subordinate species, such as wild dogs, need to balance the trade-off between accessing key resources, such as prey and water, versus facing and avoiding interspecific competition with larger dominant predators (Vanak et al. 2013; Rich et al. 2017). Nowadays, large predators, such as lions, mainly survive within natural protected areas and in the least human-dominated ecosystems (Loveridge et al. 2000). This imposes a new challenge for subordinate species such as wild dogs that not only have to cope with human activities outside protected areas but also with interspecific competition with dominant predators inside the protected areas. Bordering areas of reserves can work as ecological traps and population sinks for wild dogs (Woodroffe & Ginsberg 1998; Creel et al. 2004; ZIMPARKS 2009; Van der Meer et al. 2013). Thus, the fact that higher densities of lions and hyaenas are found within protected areas can bring extra challenges for wild dogs to survive inside protected areas.

As such, the main focus of this research was to understand how wild dogs are able to cope with large predators inside a protected area with artificial water provisioning. To address this, I specifically aimed to evaluate how water availability and distribution affected: (i) the dynamics of food resource competition between wild dogs and larger predators (Chapter 2); (ii) the level of kleptoparasitism risk from dominant predators to wild dogs (Chapter 3); and (iii) the avoidance strategy of wild dogs towards large predators in space and time at different spatial and temporal scales (Chapter 4).

To evaluate food resource competition (Chapter 2), I used wild dogs' and larger predators' scats to analyse and compare diet composition, diet overlap and prey

preference in different seasons and in areas with different waterhole densities. To evaluate kleptoparasitism risk (Chapter 3), I performed playback experiments (simulating wild dogs killing and eating an impala) at waterholes and 5 km away from waterholes in areas with different waterhole densities. To evaluate wild dogs spatio-temporal avoidance strategies (Chapter 4), I used camera trap data from different seasons, and located at different distances from waterholes and in areas with different waterhole and larger predator densities.

Key findings

The main findings of each data chapter are summarized in Diagram 2.

In Chapter 2 (food resource competition, Diagram 2a), I found that wild dogs diet overlap was high with the diet of all the other larger predators (cheetahs, leopards, lions and hyaenas), especially with hyaenas. In general, lions and hyaenas tended to consume larger-bodied prey than wild dogs. Water availability due to seasonality did not have an effect on the diet and food competition of predators. However, water availability and distribution due to areas with contrasting waterhole densities did have an effect on the level of food competition between wild dogs and larger predators. In the low waterhole density areas, food resource competition between wild dogs and larger dominant predators (lions and hyaenas) increased. This increase in food competition was especially evident with lions, as lions tended to hunt prey preferred by wild dogs in these drier areas. In the low waterhole density areas, where prey are less abundant,

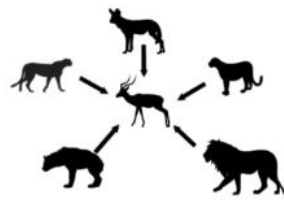
predators diet included a higher proportion of prey less dependent on water. Therefore, to conclude, it is important to conserve larger-bodied prey less dependent on water (e.g. kudu, reedbuck, eland and gemsbok) especially in these drier areas. This with the intention increase prey abundance preferred by all large predators which would likely decrease the food resource competition on wild dogs with larger predators.

In Chapter 3 (kleptoparasitism risk, Diagram 2b), I found that the level of kleptoparasitism risk and hence the probability of agonistic encounters with larger dominant predators (lions and hyaenas) increased at waterholes with lions, and increased in higher waterhole density areas with both lions and hyaenas. This increase of kleptoparasitism risk was due to a higher number of larger predators arriving at playback locations and not due to the time it took them to arrive nor the probability of arriving at the playback locations. As areas with high waterhole densities increase the level of kleptoparasitism risk on wild dogs, I proposed to limit the creation of new artificial waterholes in high waterhole density areas with the aim to avoid a higher number of larger predators arriving at wild dog kills. Assuming an equal pack size of wild dogs, a lower number of larger predators arriving at wild dog kills would decrease the risk of injury, mortality and kleptoparasitism on wild dogs.

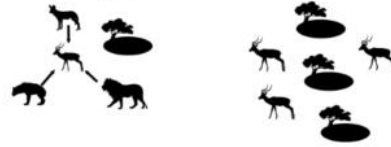
In Chapter 4 on the avoidance strategy of wild dogs towards large predators in space and time (Diagram 2c), I found that wild dogs used the same space as the other three larger predators (leopards, lions and hyaenas), but at different times. Temporal avoidance of all three predators was especially evident close to waterholes (< 2 km). At a small spatial scale, wild dogs did not avoid leopards and hyaenas. However, at a large spatial scale, wild dog individual numbers lowered when hyaena densities were high

(especially above ~ 14 hyaenas/100km²); which could indicate a proactive avoidance of wild dogs with hyaenas at a large spatial scale. Spatio-temporally, wild dogs used a reactive strategy to avoid hyaenas, although a proactive strategy was also detected in the late dry season, closer to water, and in areas with low waterhole density. Contrarily, wild dogs most likely used a proactive strategy to avoid lions and leopards spatio-temporally. Wild dogs were able to coexist spatially in areas (rich in prey) with high aggregation (close to water) and density of predators (areas with higher density of both predators and waterholes), but lower than ~ 14 hyaenas/100km², as long as there was closed vegetation (e.g. bushland), and enough permanent waterholes (> 0.01 waterholes per km², waterholes being a surrogate for prey aggregation and abundance). Therefore, landscape heterogeneity as well as a heterogeneous water management provisioning scheme (with areas with enough permanent waterholes: above ~ 0.01 waterholes per km²) is necessary in the ecosystem to facilitate the coexistence of wild dogs with larger predators by increasing niche-partitioning opportunities.

a) Food resource competition is higher at



Low waterhole density areas
where there is less prey abundance



b) The level of kleptoparasitism risk is higher at:

At waterholes



High waterhole density areas



c) Avoidance strategy in space, time and spatio-temporal

In Time: Proactive avoidance of all predators



In Space and Time: Proactive avoidance of lions and leopards



In Space:
In a small spatial scale: No avoidance
of leopards and hyenas



In Space and Time: Reactive avoidance of hyenas



In a large spatial scale: Proactive avoidance of
hyaenas



In Space and Time: Proactive avoidance of hyenas, in
the late dry season, close to water and in low waterhole
density areas



Diagram 2 Main results of interspecific competition between African wild dogs and larger predators in an ecosystem with artificial perennial water provision: a) level of food resource competition between wild dogs and dominant predators is higher in low waterhole density areas (Chapter 2); b) level of kleptoparasitism risk of wild dogs is higher at waterholes by lions, and higher at high waterhole density areas by both dominant predators (Chapter 3); c) avoidance strategy (proactive or reactive) in time, space and spatio-temporally of wild dogs with leopards, lions and hyenas (Chapter 4).

Future improvements and limitations

Prey preference is an important tool to understand food resource competition, as prey preference indices consider prey availability, and thus, these indices can indicate if a prey species is consumed due to its availability or due to the actual consumption preference of the predator (Jacobs, 1974). Prey density is a more accurate measure for prey availability than relative prey abundance calculated from camera trap data. However, in the low waterhole density area (in the South west [SW] of HNP), there are no line-transects performed to monitor prey. Thus, I was not able to analyse prey densities in this area of the park, and I had to use relative abundance indices instead to calculate prey availability (Chapter 2). Even though it is logistically more challenging to access the SW of HNP due to remoteness and limited road access, it would be extremely valuable for conservation as a whole to better monitor prey in the SW of HNP. It would be extremely valuable for wildlife conservation to monitor prey abundance and availability through the performance of road transects in the SW of HNP, just as prey is monitored twice a year through road transects in the northern areas of HNP (thanks to the Hwange Zone Atelier [consortium CNRS, CIRAD, IRD], PDC, Hwange Lion Research Project and ZPWMA). This especially because it was in this area of the park where there was a higher food competition of wild dogs with other predators (mainly with lions). Additionally, in the SW (where there is less water availability), prey populations might also be more vulnerable as their abundances are not as high as in other areas of the park with higher waterhole densities. In addition to the recommendation to also monitor prey abundance in the SW of HNP, it would also be

valuable to keep monitoring the diet of predators (especially lions and wild dogs) in this low waterhole density area where food resource competition was higher.

The ideal way to monitor the level of kleptoparasitism risk (Chapter 3) would be to actually record lions and hyaenas appearing and kleptoparasiting wild dogs at real kills. However, at times in the field due to the nature of the study area (e.g. HNP being very extensive, with some areas difficult to access due to either high ruggedness terrain or very closed vegetation) and the nature of the study species (e.g. wild dogs being elusive and living in low densities) it can be logistically very difficult to witness and record a large amount of cases of kleptoparasitism of wild dog kills. Thus, playback experiments simulating a wild dog killing and consuming prey can be a very useful and more pragmatic tool to measure the level of kleptoparasitism risk on this subordinate species, especially in a very extensive area such as HNP. A useful complementary study to this one could be to perform playback experiments at random distances from the closest waterholes, or to perform playback experiments in the wet season as well. A complementary study of this research could also be to perform playback experiments and measure the risk of kleptoparasitism in areas with similar densities of waterholes but with different prey and predator densities.

Regarding wild dogs' strategies to avoid large predators in time and space (Chapter 3), due to the nature of the data I used (camera trap data) and the nature of the study species (wild dogs, lions and leopards living in lower densities than hyaenas and appearing less in camera trap pictures than hyaenas), I was unable to test very small spatio-temporal scales of avoidance (e.g. less than 1-day time differences on the same location). Thus, in Chapter 3, due to small sample sizes, I was only able to infer

small-scale spatio-temporal avoidance (less than 8 days) towards lions and leopards indirectly. To test for avoidance strategies of wild dogs towards larger predators at a small spatio-temporal scale, it would be ideal to monitor wild dogs and large predators simultaneously in the same areas using GPS collars combined with the direct observation of wild dog packs. However, as GPS collars are logistically more difficult and expensive to use, and direct observations of wild dog packs for long periods of time can sometimes be challenging, camera trap data might be a more feasible tool to use. This especially in the case of monitoring predators (normally living in low densities and being elusive species) in extensive areas (e.g. thousands of km²) and for long periods of time (e.g. years). As a future complementary study, it could be beneficial for wild dog conservation to monitor both wild dogs and hyaenas closely (e.g. using GPS collars) in areas of high hyaena densities in order to gain a better understanding of why wild dogs are not coping well in areas with high hyaena densities.

Water management recommendations

Historically in the region of Hwange, which is mainly covered by Kalahari sands with barely any natural permanent water sources, animals in the dry season moved outside HNP to the north-east where permanent water sources from the Gwayi river system can be found (ZIMPARKS 2015). However, in 1928 (when HNP was established), these permanent water sources were excluded from the park through a railway line that delimited the boundary of HNP. Thus, in 1935 to provide and supplement permanent water sources for wildlife inside HNP, a programme on artificial

water provisioning started (ZIMPARKS 2015). Through a scheme on artificially-pumped waterholes, the availability of permanent water inside HNP has allowed to sustain animal populations during the dry season, especially the elephant population which has grown due to the increase of artificial water provisioning (Chamaillé-Jammes et al. 2008; ZIMPARKS 2015). Currently, in HNP, the water management system (besides being performed for the need to sustain animals) is especially done due to tourism pressure (ZIMPARKS 2015). However, managing waterholes without proper planning can have implications on wildlife and indirectly affect the conservation of endangered species, such as wild dogs. Surface-water availability drives the distribution and abundance of herbivores (Smit et al. 2007; Chamaillé-Jammes et al. 2008; Valeix et al. 2008), and in turn aggregation of carnivores (Valeix et al. 2010; Van der Meer 2011; Périquet 2014), plus distribution of grazing/browsing pressure which affects vegetation (Chamaillé-Jammes et al. 2007a, 2009a; Valeix et al. 2011). Thus, understanding how water management decisions ecologically affect species is crucial for conservation practice.

In this study, I intended to contribute knowledge on how water management can help conservation practitioners and policy makers to develop water management strategies that assist with the conservation of wild dogs (an endangered species of conservation concern), by helping lower the intensity of interspecific competition on wild dogs with dominant predators. As water provisioning is a common practice in wildlife reserves (Owen-Smith 1996; Gaylard et al. 2003), this work performed in Zimbabwe could contribute to the overarching conservation work in other areas where water management is crucial for wildlife conservation. For instance, artificial waterholes are

also found in other African natural reserves, such as Ruaha National Park in Tanzania (Epaphras et al. 2008), Etosha National Park in Namibia (Franz et al. 2010), Kruger National Park (Owen-Smith 1996; Gaylard et al. 2003) and Karongwe Game Reserve (Vanak et al. 2013) in South Africa (in the Great Limpopo Transfrontier Conservation Area -PPF 2018).

Water management strategies for wild dogs

In this thesis, I intend to contribute to knowledge on water provisioning strategies specifically in relation to favouring African wild dogs. Based on the results of this thesis, very low waterhole densities in the landscape (i.e. less than 0.01 waterholes per km²) do not benefit wild dogs (Chapter 4) most likely due to the decrease of prey abundance in these low waterhole density areas (Chapter 2), where there is an increase in food resource competition of wild dogs with larger predators (Chapter 2). However, a high density of waterholes increases the risk of kleptoparasitism on wild dog kills by larger dominant predators (Chapter 3). A homogenization of waterhole provisioning could potentially decrease niche partitioning opportunities and intensify interspecific competition (Chapter 4). Thus, specifically to decrease interspecific competition on wild dogs with larger predators, I propose heterogeneous management of water provisioning. More specifically, I propose 1) to limit the creation of artificial waterholes in areas with high waterhole densities (above ~0.03 waterholes per km²); 2) to prioritize the creation of artificial waterholes in areas with few permanent waterholes (especially during drought years) but, in order to prevent homogeneity, not to the same extent as the high waterhole density areas (above ~0.02 waterholes per km²), and 3) not to have

waterholes at equal distances in areas with high waterhole densities, but at different distances in km from each other to allow for the existence of patches of dense (refuge) vegetation.

Water management strategies for ecosystem functioning

It is important to acknowledge that this waterhole management recommendations are specifically for wild dog species conservation (which is a high conservation priority as it is an endangered species). However, the consideration of other species conservation is also important for a healthy ecosystem functioning. Thus, the creation and increase of artificial waterholes in low waterhole density areas could also have negative unintended consequences for other species that are affected by an increase of waterhole densities. For example, a high density of waterholes can increase the aggregation and density of elephants (Chamaillé-Jammes et al. 2007b), which could increase vegetation pressure around waterholes (Chamaillé-Jammes et al. 2007a; Landman et al. 2012), and be counterproductive for ecosystem functioning (Owen-Smith 1996; Gaylard et al. 2003). This is why, if more waterholes are going to be created in areas of low waterhole densities, there should still be some areas with few artificial permanent waterholes. This would be to mainly allow areas of vegetation recovery during the dry season from herbivores pressure (Owen-Smith 1996; Gaylard et al. 2003).

An overprovisioning of water can provoke ecosystem instability (Owen-Smith 1996; Gaylard et al. 2003). Excessive water provisioning could a) decrease biodiversity by favouring only high water-dependent species over rarer low water-dependent

species; b) increase dominant predator impacts on prey and subordinate predator species; c) increase vegetation degradation (e.g. due to intense herbivory pressure around waterholes; or loss of herbivores migratory behaviour due to being in areas with at present enough water in the dry season compared to no water in the past); and d) increase animal mortality during drought years due to an excessively large population size of high water-dependent species such as elephants (Owen-Smith 1996; Chamaillé-Jammes et al. 2007a; Valeix et al. 2008; Sandoval-Serés et al. 2024). However, a complete stop on water provisioning can also have detrimental effects on the ecosystem through landscape homogenization (Gaylard 2015), and artificial water provisioning can become crucial to help animal population survive during drought episodes (Chamaillé-Jammes et al. 2007a; Smit & Grant 2009; Gaylard 2015). This emphasizes that a heterogeneous balance on water provisioning is important for wildlife conservation and ecosystem functioning.

Climate implications

Hot temperatures and climate change can accentuate how crucial water becomes for wildlife (Beschta et al. 2013; Perkins 2019, 2020). Natural water pans depend on rain to hold water in the late dry season, hence, artificial water provisioning can reduce the variability on surface available water over time (Chamaillé-Jammes et al. 2007a). Ideally to resemble natural circumstances, artificial waterholes should be pumped in natural pans during drought episodes in areas of natural historical water availability (Perkins 2019, 2020).

Artificial waterholes strategically planned may alleviate interspecific interactions through compensating for the low availability of water during years with little rain (Chamaillé-Jammes et al. 2007a; Ockendon et al. 2014; Ochoa et al. 2021). The negative effect of low rainfall can impact a species through disrupting the balance of interspecific interactions with its prey and predators rather than through water stress alone (Ockendon et al. 2014). Although higher ambient temperatures can reduce the distance over which wild dog pursuit prey (Creel et al. 2016) and leave prey more vulnerable due to lack of enough available water (Mills 1995), high diurnal temperatures (due to climate change) causes wild dogs to reduce daytime hunting and forces them to hunt more at night (Woodroffe et al. 2017; Rabaiotti & Woodroffe 2019). Episodes of high temperature could have negative effects on wild dogs by potentially decreasing their ability to: a) overcome food resource competition in areas with low prey abundance (as in the low waterhole density area - Chapter 2); or b) to compensate for the loss of energy due to kleptoparasitism risk (especially in the high waterhole density area - Chapter 3); or to have a higher probability to encounter large dominant predators at night (lowering the possibilities for temporal avoidance, the preferred avoidance strategy used by wild dogs - Chapter 4). By compensating for the decrease of natural available water in the dry season through artificial waterhole provisioning during very dry years can potentially assist in the survival of prey species and lower the interspecific competition intensity of wild dogs with larger predators.

Conservation implications

Coexistence of subordinate predators with large dominant predators is possible without population repercussions as long as the conditions in the ecosystem are balanced (Miller et al. 2018; Davies et al. 2021; Creel et al. 2024). Specifically for wild dogs, as long as there is a heterogeneous landscape (Dröge et al. 2017; Miller et al. 2018; Davies et al. 2021) (including close vegetation - Chapter 3), sufficient prey (Creel et al. 2023, 2024), enough permanent waterholes (at least ~ 0.01 waterholes per km^2) as surrogates of prey abundance and aggregation (Chapter 4), and not an extremely high density of lions (e.g. above ~ 12 to 26 lions/ 100km^2) (Davies et al. 2021; Marneweck et al. 2021), and hyaenas (Chapters 3 and 4), wild dogs can cope well with interspecific competition with dominant large predators (mainly lions and hyaenas) in a natural protected area.

Landscape heterogeneity in vegetation and other habitat characteristics (i.e. heterogeneous water distribution – this thesis) can promote intraguild predator coexistence through niche partitioning and refuge opportunities (Mills & Funston 2003; Groom et al. 2017; Miller et al. 2018; Davies et al. 2021). Additionally, food resource renewal, prey abundance and diversity are critical for predators' coexistence and species subsistence (Risk 1972; Andheria et al. 2007; Périquet et al. 2015; Creel et al. 2024). Therefore, it is extremely important to conserve a wide range of prey species especially those prey species preferred by threatened predators (Hayward & Kerley 2008).

If prey abundance is too low to sustain wild dog populations, the benefits to wild dogs of low dominant predator abundance in areas of low prey abundance cannot be sufficient (Creel et al. 2023, 2024). This might explain why despite lower dominant predator densities at low waterhole densities in HNP (which have low prey abundances - Chapter 2), there was more food resource competition of wild dogs with larger predators (Chapter 2) and less occurrence of wild dogs in these low waterhole density areas (Chapter 4). Conversely, if prey abundance and biomass are too high, dominant predator density could also increase (Carbone & Gittleman 2002; Hayward et al. 2007; Périquet 2014), which can have negative effects on wild dogs (Creel & Creel 1996, 1998). Thus, there is a tipping point where the benefits to wild dogs of high prey abundance do not outweigh the costs of high densities of dominant predators (Creel et al. 2023, 2024). This might explain why in high waterhole density areas where there is a higher density of dominant predators (and more prey abundance – Chapter 2), the kleptoparasitism risk for wild dogs was higher (Chapter 3), and the likelihood of occurrence of wild dogs decreased with an increase in hyaena densities (Chapter 4). Therefore, there should be a balance in the number of waterholes (as surrogates of prey abundance and aggregation) in order to sustain enough prey numbers without resulting in an extreme increase of dominant predators.

Studies on management become more relevant as national protected areas become more dependent on wildlife management for conservation, and water provisioning is regarded as a key management tool for wildlife conservation (Ferraro & Pressey 2015; Perkins 2019). Holistic management is crucial for biodiversity conservation and maintenance of ecosystem functioning (Owen-Smith 1996; Harihar et

al. 2011; Ferraro & Pressey 2015), management authorities of protected areas should therefore take into account the conservation of not only flagship species (e.g. lions) but also the conservation of less charismatic other (subordinate) species (e.g. wild dogs).

Large connected networks of protected areas are crucial for wildlife conservation to allow animals to move from dry areas to wet areas during the dry season (Perkins 2019) to allow for genetic exchange (Creel et al. 2019) and to provide enough refuge opportunities to cope with interspecific competition (Marneweck et al. 2021). HNP is the largest protected area in Zimbabwe and is found in KAZA, the largest Transfrontier Conservation Area in the world (PPF 2018). This makes HNP an important area for wild dog conservation as well as for the conservation of other emblematic African animals. As water provisioning is an important management tool which can have different implications for different species, water management planning in areas with water provisioning, such as HNP, is essential for conservation success.

Final conclusions

Waterhole distribution affects prey aggregation and abundance. Prey abundance conservation, especially in low waterhole density areas, is essential to decrease food resource competition between wild dogs and larger dominant predators (Chapter 2). Areas with lower waterhole densities can serve as refuges to decrease kleptoparasitism risk for wild dogs (Chapter 3). Wild dogs preferred temporal partitioning over spatial partitioning to avoid large predators, and wild dogs were able to occur in areas (rich in prey) with high aggregation and density of dominant predators as long as there were enough permanent waterholes and not high hyaena densities (Chapter 4). Water management should be holistic and heterogeneous; and to decrease interspecific competition of wild dogs with larger predators, artificial waterhole pumping should be a priority especially during the late dry season, when there is less water availability in the system.

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Thesis Appendix

Long distance African wild dog dispersal within the Kavango-Zambezi Transfrontier Conservation Area

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Introduction

For spatially separated populations, dispersal is essential to facilitate gene flow and colonization (Creel et al., 2019; Woodroffe et al., 2019). This is especially true for the wide-ranging African wild dog (*Lycaon pictus*), an endangered species, whose global population currently consists of ca. 6,600 adults, scattered across 39 sub-populations and is vulnerable to habitat loss and fragmentation, infectious diseases and anthropogenic mortality (Woodroffe & Sillero-Zubiri, 2012).

Wild dogs are cooperative breeders living in packs of up to 30 individuals (Creel & Creel, 2002). Both sexes disperse from their natal pack, over distances of 2 (Woodroffe et al., 2019) to 476 km (Davies-Mostert et al., 2012), to find unrelated mates or packs, and colonise new territories (McNutt, 1996; Creel & Creel, 2002). Although valuable observations for conservation management, long distance dispersals (>80 km straight linear distance) of wild dogs are rarely recorded (Davies-Mostert et al., 2012; Cozzi et al., 2020). Here, we describe a long distance cross-boundary dispersal of an African wild dog female (FEMALE146.02) within the Kavango–Zambezi Transfrontier Conservation Area (KAZA-TFCA).

Methods

Study Area:

The KAZA-TFCA covers 520,000 km² across five African countries (PPF, 2018) and is home to ca. 25% of the global African wild dog population (Woodroffe, 2013).

FEMALE146.02's natal pack (which dissolved) lived in Hwange National Park (HNP), Zimbabwe: a 14,651 km² unfenced protected area with woodland, bushland and open

grassland (Valeix et al., 2010). She settled in the unfenced 1,200 km² Wildlife Management Area Linyanti NG15 (Linyanti), Botswana, which consists of riparian woodland, sandveld and grassland (Fynn, 2017) (Fig. 1).

Fieldwork

FEMALE146.02 (a 3-year-old subordinate female in a pack of 16 individuals) was fitted with a GPS-collar (Tellus/Followit, Sweden). From 12 June to 25 September 2021, this collar provided fixes at 08:20, 16:20 and 00:20 h. FEMALE146.02 was immobilized by qualified veterinarians using butorphanol/medetomidine, reversed with atipamezole. Independently, our Trans-Kalahari Predator Programme deployed a camera trap survey at Linyanti (October-December 2021, 63 stations, 4x4km grid).

Analyses

To identify departure, transience, and settlement phases of dispersal, we calculated the net squared displacement (NSD), which is the square of the Euclidian distance (dE) (Börger and Fryxell, 2012). For each phase, we calculated the mean, maximum and minimum dE between 8 and 24h fixes; the total dE (from first to last fix per phase), total path length (L) (cumulative distance), straightness index (ST = total dE/L, 1 = straight line, 0 = tortuous path - Almeida et al., 2010); plus the straight line between the furthest two dispersal locations (maximum straight distance). Using QGIS 3.8.2 (2019, qgis.org) we calculated, per phase, the percentage of time FEMALE146.02 spent in each land use type (PPF; <https://www.peaceparks.org/>) and land cover (ESA-CCI-LC 2016;

<http://2016africalandcover20m.esrin.esa.int/>). We performed Fisher's exact tests to compare land cover proportions from random proportions (Table 1).

Results and discussion

Based on NSD (Figure A1) and field observations, FEMALE146.02's transience phase lasted from 27 June to 29 July in which she travelled 430 km in 32 days with a straight linear distance of 252 km (Table 1) (Fig. 1). This is comparable to a previously recorded dispersal from the Okavango Delta, Botswana, to HNP (Cozzi et al., 2020), but shorter than the dispersal from southwest Botswana to HNP reported by Davies-Mostert et al. (2012) (Table 2). Throughout Africa, dispersal distances of wild dogs vary widely (Table 2), possibly due to terrain and overall wild dog densities (potential of locating mates) (Cozzi et al., 2020).

In accordance with observations by Woodroffe et al. (2019) and Cozzi et al. (2020), FEMALE146.02 travelled in a straighter line during transience than departure and settlement. FEMALE146.02's mean daily distance travelled (DDT) during departure and settlement in HNP and Linyanti respectively, was comparable to DDT of established packs (Pomilia et al., 2015). However, compared to departure and settlement, FEMALE146.02's maximum DDT was larger during transience. Although not different from random proportions (p -value > 0.05), FEMALE146.02 travelled in grassland more during transience (Table 1), possibly because it presents less resistance to movement. This is in line with Klarevas-Irby et al. (2021), who showed that transient individuals travel farther, faster and straighter to reduce energetic costs of long distance dispersals.

FEMALE146.02's dispersal followed the disappearance of the natal pack's alpha female, resulting in a pack of related members with no pups, which is a known cause of pack dissolution through dispersal (Masenga et al., 2015; Behr et al., 2020). Wild dogs usually disperse in same sex aggregations (McNutt, 1996; Somers et al., 2008; Woodroffe et al., 2019) and occasionally in mixed sex coalitions (Masenga et al., 2015). As two females and three males disappeared on the same date as FEMALE146.02, both options are possible. However, only FEMALE146.02 was detected during the camera trap survey at Linyanti, along with an unrelated male detected four days later and 4 km away from where FEMALE146.02 had appeared. It therefore seems that, despite the high anthropogenic mortality risk related to dispersal (Woodroffe et al., 2019; Cozzi et al., 2020), five months after dispersing, FEMALE146.02 was still alive and could potentially breed in Linyanti.

During dispersal, FEMALE146.02 did not cross the Zambezi River and crossed one highway three times (Botswana's A33) (Fig. 1). Dispersing wild dogs avoid large water bodies and human infrastructures (Cozzi et al., 2020; Hofmann et al., 2021), which may be dispersal barriers. During transience, the majority of FEMALE146.02 fixes were in wildlife designated areas, while 30% were in non-protected areas (Table 1). This is testament to the high permeability of the KAZA-TFCA to wildlife movements, which consists of ~70% intact protected natural habitat (KAZA TFCA, 2015; Hofmann et al., 2021), and the area's importance in facilitating dispersal, and therewith gene-flow, between wildlife populations (Elliot et al., 2014; Brennan et al., 2020; Hofmann et al., 2021). Wild dogs are a strong indicator species for connectivity across the KAZA-TFCA (Brennan et al., 2020), as such, the dispersal described here can assist in locating and

protecting more wildlife dispersal areas within the KAZA-TFCA (Munthali, et al., 2018), and confirms the significance of international transboundary conservation efforts.

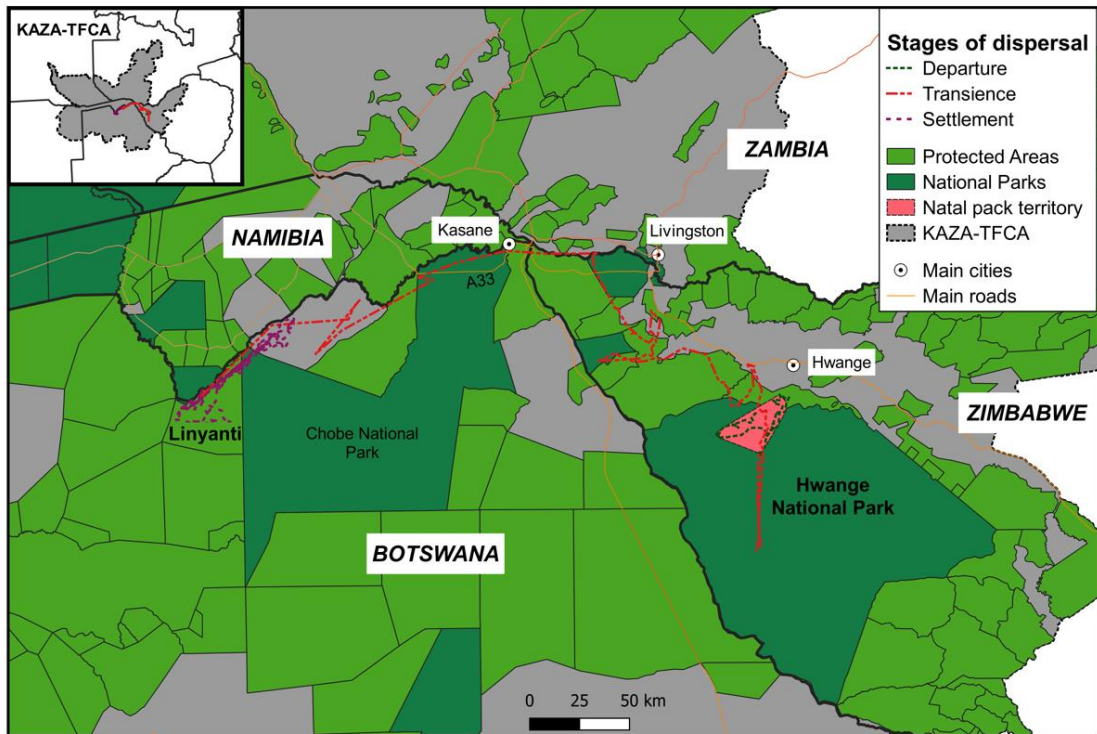


Figure 1. Dispersal movement of African wild dog female FEMALE146.02, which dispersed from Hwange National Park (Zimbabwe) to Linyanti (Botswana), situated within the Kavango–Zambezi Transfrontier Conservation Area (KAZA-TFCA). (Natal pack territory using 100% Minimum Convex Polygon in QGIS).

Table 1. Summary of the African wild dog female trajectory from Hwange National Park (HNP), Zimbabwe, to Linyanti, Botswana.

	Departure from HNP	Transience	Settlement at Linyanti
Dates	12 ^{ve} June 2021	27 th June 2021	29 th July 2021
Days	15	32	58
In 24 h window			
Mean dE	7.47 (SE = 0.96)	17.95 (SE = 2.89)	8.72 (SE = 0.95)
Maximum dE	13.31	52.64	29.85
Minimum dE	3.21	2.83	0.003
In 8 h window			
Mean dE	3.08 (SE = 0.37)	6.17 (SE = 1.01)	4.06 (SE = 0.26)
Maximum dE	11.44	39.17	14.62
Minimum dE	0.067	0.002	0.026
Total dE	20.00	252.62	51.95
L in 24h window for the total number of days	97.10	430.84	479.51
ST = total dE / L	0.21	0.59	0.11
Land cover ^{NS}			
Woodland	7%	7%	0%
Bushland	50%	33%	68%
Grassland	36%	41%	30%
Cropland	7%	19%	2%
Land Use			
National Parks	86%	30%	16%
Protected Areas	14%	41%	61%
†			
Not protected ‡	0%	30%	23%

SE= Standard error;

dE = Euclidian distance in km between first and last position;

L = total path length in km; and

ST = straightness index (where 1 indicates a straight line and 0 a tortuous path).

† Protected Areas: all natural areas with legal protection other than National Parks.

‡ Not protected: all areas without any category of protection, including communal land with livestock and settlements.

NS: all land cover proportions of the three phases were not significantly different from random proportions (p-value > 0.05 in Fisher's exact test). Random proportions were calculated from 1000 random points per phase inside a buffer with an equivalent distance to the mean dE in a 24-window of each phase.

Table 2. African wild dogs' dispersal trajectories from different studies.
(Distances in km)

Starting location	Final location	Sample size	Days	Straight linear distance to settlement	Cumulative distance	Max. straight distance during the whole trajectory	Max. DDT in 24 h during transience	Study
HNP, Zimbabwe	Linyanti, Botswana	One female	32	252	430	307	52	Our study
Okavango delta, Botswana	HNP, Zimbabwe	One coalition of four females	9	311	614	345	54	Cozzi et al., 2020.
HNP, Zimbabwe	southeast Zimbabwe	One coalition of two males	-	-	-	199	-	Davies-Mostert et al., 2012.
southwest Botswana	HNP, Zimbabwe	One coalition of three males	-	-	-	476	-	Davies-Mostert et al., 2012.
Okavango delta, Botswana	Okavango delta, Botswana	Average data of 16 coalitions	48	54	597	103	35	Cozzi et al., 2020; Hofmann et al., 2021.
Okavango delta, Botswana	Long distance‡ dispersal within KAZA-TFCA	Average data of 7 coalitions	32	110	465	137	43	Cozzi et al., 2020.
Laikipia, Kenya	Laikipia, Kenya	Average data of 44 coalitions	19	37	487	-	-	Woodroffe et al., 2019.
Serengeti, Tanzania	Border of Tanzania and Kenya	Average data of 2 coalitions	250	361	4713	-	-	Masenga et al., 2015.

HNP: Hwange National Park; KAZA-TFCA: Kavango–Zambezi Transfrontier Conservation Area. DDT: Daily distance travelled. ‡Long distance: outside Okavango Delta study area: 3,000 km² (Cozzi et al., 2020).

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Conflict of Interest

The authors declare that they have no conflict of interest.

Data Availability Statement

The data is available from the authors upon reasonable request.

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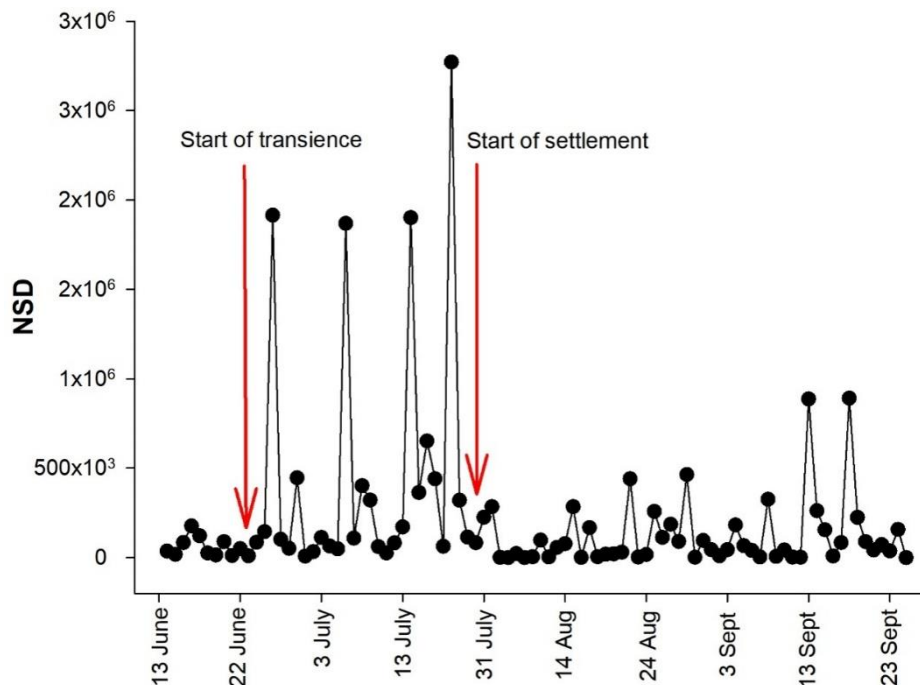
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Appendix A

Figure A1: Depiction of the net squared displacement (NSD) for the movement of FEMALE146.02, an African wild dog female which dispersed from Hwange National Park (Zimbabwe) to Linyanti (Botswana) in 2021. During the departure and settlement phase, the NSD will vary around a constant value, and during the transience phase the NSD is expected to increase linearly over time (Börger & Fryxell, 2012). The pronounced variation of the NSD indicates the change to a dispersal stage (Börger & Fryxell, 2012; Cozzi et al., 2020). The red arrows specify the inflection points of NSD, which indicate transitions from the different dispersal stages: departure, transience, settlement.



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“Through a collaborative network, combining research with conservation actions, we can help wildlife conservation.”