# HUMAN-WILDLIFE CONFLICT AND COEXISTENCE OF BLACK-BACKED JACKAL (*LUPULELLA MESOMELAS*) AND AFRICAN WILD DOG (*LYCAON PICTUS*) IN THE OKAKARARA DISTRICT COMMUNAL AREA, NAMIBIA.

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# Abstract

Human-wildlife conflict is a global phenomenon that occurs wherever humans and wildlife share resources or space. In Namibia, human-wildlife conflict is most severe in communal regions where farmers have fewer financial means to implement mitigation measures against livestock depredation. This study used camera trap data, diet analysis, and questionnaire data to explore distribution, livestock depredation, and coexistence of black-backed jackal (*Lupulella mesomelas*) and African wild dog (*Lycaon pictus*), the highest conflict-causing species in the understudied Okakarara District Communal Area (ODCA). A camera trap survey was conducted in 2018-2019 for 30 days in the dry season and 30 days in the wet season. Black-backed jackal and African wild dog scat was collected both opportunistically and systematically for diet analysis. Using scat locations and questionnaire data, a kernel density of African wild dog - livestock conflict was mapped to determine if African wild dog dens occurred significantly more in regions of high livestock depredation. Black-backed jackal abundance was significantly higher in the dry season in areas of high village density and within 10km of African wild dog dens. Diet analysis revealed that black-backed jackal in the ODCA have a generalist omnivorous diet consisting primarily of ungulates by biomass (74.36%). They preferentially consume greater kudu (*Tragelaphus strepsiceros*), which contributes 19.83% to their diet by biomass. Livestock species made up 29.74% of the biomass in their diet. Black-backed jackal diet did not differ within vs. more than 10km from known African wild dog dens, suggesting that African wild dog function as neither a competitor nor facilitator for black-backed jackal, and both canids select habitat based on concealment and avoidance of persecution. African wild dog dens occurred significantly more in areas of higher African wild dog-livestock conflict, but further research is needed to confirm this preliminary finding. Due to a recent decline in population, African wild dog may be functionally absent from the ODCA, and without top-down pressure from an apex predator, black-backed jackal have experienced mesopredator release. Conservation priorities for the ODCA should focus on capacity building to increase populations of wild prey, implement low-cost predator mitigation solutions, and reduce mesocarnivore dominance by restoring large carnivore populations.

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# Declaration

I, Emma Reasoner, hereby declare that the work contained in this thesis entitled: Human-wildlife conflict and coexistence of black-backed jackal (*Lupulella mesomelas*) and African wild dog (*Lycaon pictus*) in the Okakarara District Communal Area, Namibia, is my own original work and that I have not previously in its entirety or in part submitted it at any university or higher education institution for the award of a degree.

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# Acknowledgements

# Chapter 1: Introduction and Literature Review

## 1.1    Human-wildlife conflict

Human-wildlife conflict (HWC) is an interaction between humans and wildlife that results in a negative outcome for either the humans or wildlife (Pettigrew *et al.*, 2012). HWC is a global phenomenon that manifests virtually everywhere humans and wildlife share space or resources, from elephants raiding crops in southern Africa (Taruvinga and Mushunje, 2014) to orangutan habitat destruction by palm oil plantations in Southeast Asia (Swarna Nantha and Tisdell, 2009) to snow leopards predating on domestic donkeys and horses in India (Bagchi and Mishra, 2006).

Expanding human populations are responsible for increased human-wildlife conflict globally (Woodroffe, 2000; Ogada *et al.*, 2003), but some wildlife species are more equipped than others to adapt to a human-dominated landscape. Carnivores are especially sensitive to anthropogenic pressure because of their space and dietary requirements. Carnivores naturally exist at low densities and have low reproductive rates. They also exhibit wide-ranging behaviour and have high food requirements. Increased development by a growing human population and human carnivory threatens carnivores as humans exploit wild sources of meat and farm livestock, which is associated with agricultural land conversion and persecution due to livestock-carnivore conflict (Ripple *et al.*, 2014).

Carnivores are not only most vulnerable to persecution, but they are typically perceived to present the greatest threat to humans. As a result, they are least likely to be tolerated by humans and face the most severe persecution (Woodroffe, 2000). Over 60% of large carnivores face a high risk of extinction due to inevitable conflict with the growing human population (Ripple *et al.*, 2014).

### 1.1.1    Livestock depredation

Livestock depredation is the principal form of human-carnivore conflict (Chinchilla *et al.*, 2022), and is influenced by multiple factors. Livestock depredation is often exacerbated by low wild prey availability (Bagchi and Mishra, 2006; Linnell *et al.*, 1999) and influenced by habitat type (Miller, 2015). Behavioural characteristics of the predator also play a role (Linnell *et al.*, 1999; Lucherini *et al.*, 2018).

Livestock depredation can be devastating to communities which rely on pastoral livestock farming. Young, inexperienced, or older, sick carnivores (i.e., "problem individuals") are often believed to prey on livestock at a higher rate than prime age adults (Linnell *et al.*, 1999). Rabinowitz (1986) found evidence that sick or injured animals attack livestock, but Linnell's review (1999) emphasized that most livestock-killing individuals are in good health. More recent research supports the concept of problem individuals and suggests that "problem animal profiling" may be a useful conflict mitigation technique (Elbroch and Wittmer, 2013; Moseby, Peacock and Read, 2015; Swan *et al.*, 2017). However, problem individuals are difficult to selectively remove from a population and do not exist in every region where livestock depredation occurs (Linnell, Odden and Mertens, 2012; Melzheimer *et al.*, 2020).

Surplus killing, when a carnivore kills more livestock than it can consume in a short period of time, is fraught with misunderstanding. Lucherini *et al.* (2018) described how the details of surplus killing events were distorted by word-of-mouth information sharing. In their study area in Argentina, farmers believed that surplus killing events were caused by a female puma teaching her kitten to hunt, an explanation that is not likely (Lucherini *et al.*, 2018). Instead, surplus killing is more likely to occur when the "normal" hunting sequence is interrupted as the predator is confronted with many easily caught prey, a situation they would not typically encounter in the wild (Kruuk, 1972; Lucherini *et al.*, 2018). Surplus killing is not proven to be caused by specific problem individuals (Linnell *et al.*, 1999).

Livestock depredation by carnivores may or may not require adaptive or learned behaviours. In grazing systems where livestock roam freely and are unattended, carnivores perceive livestock similarly to wild ungulates. However, where livestock is attended by a herder or guarding dog and confined inside a fence at night, killing livestock requires specialized behaviours to bypass these barriers. It is under these circumstances that problem individuals are more likely to be the cause of depredation. However, more livestock will likely be killed in a more free-roaming system regardless of the presence or not of problem individuals (Linnell *et al.*, 1999).

Improved livestock husbandry practices can prevent livestock loss to predators (Ogada *et al.*, 2003). Using a herder or guarding dog, kraaling livestock at night, and high levels of human activity have been shown to reduce depredation (Ogada *et al.*, 2003). Other effective non-lethal mitigations include land-use zoning to separate livestock grazing areas from critical carnivore habitat (Pettigrew *et al.*, 2012), and increasing wild prey populations (Woodroffe *et al.*, 2005). Farmers often select lethal techniques to address livestock depredation, believing it to be most effective solution

(Mitchell *et al.*, 2004). In reality, lethal control is often unsuccessful at stemming livestock depredation (Avenant and Du Plessis, 2008), and nonlethal controls result in more economic savings (McManus *et al.*, 2015; Miller *et al.*, 2016). Despite this, many farmers still prefer measures that involve removal of carnivores over mitigations that foster coexistence (Whitehouse-Tedd, 2021). Increased livestock depredation is linked to decreased tolerance and increased killing of carnivores (Ogada *et al.*, 2003; Rust and Marker, 2013)

Some farmers cite livestock loss as the reason they do not support conservation efforts (Gebo, Takele and Shibru, 2022). Recognizing the costs of livestock loss to carnivores, NGOs and governments seek to financially incentivize conservation. Carnivore conservation incentives can be categorized into revenue sharing, conservation payments, or compensation schemes (Dickman, 2010). Wildlife tourism has the potential to offset costs of livestock loss if financial benefits are strategically applied through revenue sharing to address HWC (Hemson *et al.*, 2009). Conservation payments include tax incentives for farmers that remove fencing to create more habitat for wildlife (Romañach, Lindsey and Romañach, 2008), direct payments when a camera trap on a farmer's land detects a carnivore species (Nistler, 2007), or financially rewarding a village for each successful carnivore reproduction event (Zabel and Holm-Müller, 2008). HWC compensation schemes offer a financial offset to farmers when they experience livestock loss to carnivores (Gargallo, 2021). Mitigating livestock depredation is critical for both preserving the livelihoods of pastoral communities and for the conservation of carnivore species (Ogada *et al.*, 2003; Khanal, Mishra and Ramesh Suryawanshi, 2020). The key to successful conservation is communities' perception that the economic benefits of conservation outweigh the costs associated with livestock depredation (Gargallo, 2021).

### 1.1.2 Livestock depredation in Namibia

Human-carnivore conflict (HCC) in the form of livestock depredation is considered severe in Namibia. A questionnaire administered across nine communal conservancies and resettled farms found that 96% of participants had experienced livestock loss to predators in the past year. One-third of smallstock (sheep and goats) farmers did not have enough births to replace stock killed by predators, or made no profit (Rust and Marker, 2013). HCC is most severe on communal land, where large predators exist outside of protected areas (Shilongo, Sam and Simuela, 2018). Conflict is also more devastating because communal farmers are less able to cope with the economic losses of livestock depredation than freehold farmers (Rust and Marker, 2013; Shilongo, Sam and Simuela, 2018). Livestock depredation in Namibia also has a complex web of sociocultural underpinnings. Livestock are usually managed by farm workers with no opportunities for advancement due to poverty and

lack of education. Workers have little decision-making ability, are compensated poorly, and are often treated unfairly. Conflict with predators thrives in this environment where farm workers have little personal investment in the care of the farm's livestock. This underlines the importance of solutions that reach beyond practical mitigations or financial incentives for conservation (Rust *et al.*, 2016).

The majority of HCC studies in Namibia rely on data collected from social surveys, but predator diet studies have also found livestock in the scat of brown hyaena and leopard (*Parahyaena brunnea* and *Panthera pardus*; Stein, Fuller and Marker, 2013), cheetah (*Acinonyx jubatus*; Marker *et al.*, 2003), and black-backed jackal (*Lupulella mesomelas*; Goldenberg *et al.*, 2010). It is important to note that diet analysis of scat cannot reliably distinguish between depredation and scavenging (Kaunda and Skinner, 2003; Kamler, Klare and Macdonald, 2012). There have been no published studies on African wild dog (*Lycaon pictus*) diet in Namibia, but livestock depredation by African wild dog is reportedly high (Lines, 2008; Verschueren *et al.*, 2020).

## 1.2     Communal conservancies in Namibia

Namibia is a semi-arid to arid country with the majority of its land suitable only for grazing by wildlife and livestock. Most Namibians practice subsistence agriculture (Forslund, 2007). In 1967, the Nature Conservation Ordinance granted freehold farmers legal rights over the wildlife on their farms, while wildlife use on communal land was illegal (Forslund, 2007). Though communal farmers had little legal control over their wildlife, hunting was still common, and by the 1970s, a decline in wildlife numbers across communal land became obvious (Forslund, 2007; Rust, 2017). The Community Based Natural Resource Management (CBNRM) programme was started in 1995 and led to the formation of communal conservancies, within which communities own the rights to manage and utilize their wildlife (Boudreaux and Nelson, 2011). Today, Namibia has 86 communal conservancies. When successful, these conservancies foster increasing wildlife numbers and experience economic growth from nature-based tourism (Forslund, 2007; Boudreaux and Nelson, 2011). However, conservancies experience increased HWC as communal farmers are more financially disadvantaged and less likely to implement predator mitigations (Forslund, 2007; Rust and Marker, 2013; Shilongo, Sam and Simuela, 2018). In less established conservancies, carnivores may also depredate on livestock as a result of depleted wild prey populations (Rasmussen, 1999; Woodroffe *et al.*, 2005; Gusset *et al.*, 2009).

The four conservancies in the Okakarara District Communal Area (ODCA; Otjituo, Okamatapati, African Wild Dog, and Ozonahi) have a total population estimated at 24,213 in 2021 (NACSO, 2021).

The ODCA is populated primarily by pastoralist livestock farmers of the Herero tribe. Farmers in this region receive little benefit from the conservancy status and suffer severely from HWC (Forslund, 2007; Verschueren, 2020). The region is prey-depleted with abundant mesocarnivores and sparse large carnivores (Lines, 2008). A small population of critically endangered African wild dog inhabits the ODCA, making it an important focus for the species' conservation in Namibia (Hanssen *et al.*, 2022).

## 1.3    Mitigating conflict and the importance of diet studies

Carnivores play vital roles in structuring and maintaining ecosystems, but are some of the most threatened species worldwide (Estes *et al.*, 2011; Ripple *et al.*, 2014). Mitigating HCC is often the most critical action to be taken for carnivore conservation, as reducing persecution has been shown in some regions to be more impactful in restoring large carnivore populations than restoration of prey (Bleyhl *et al.*, 2021). Livestock depredation is the most common form of HCC and is often retaliated with predator persecution.

Predator diet studies can provide baseline information on a species' diet and the extent of livestock depredation in a particular region. They can explore influencing factors such as wild prey availability (Woodroffe *et al.*, 2005; Janeiro-Otero *et al.*, 2020), presence of other large predators (Brassine and Parker, 2012; Yarnell *et al.*, 2013; Codron *et al.*, 2018), and livestock management practices (Ogada *et al.*, 2003). These findings can guide further research, support efforts to reduce livestock depredation where it is shown to be detrimental, and inform recommendations to affected communities to mitigate losses.

The majority of diet studies rely on field identification of scat. However, field identification has proven to be unreliable. Success rate of target species' scat identification is often less than 50% (Janečka *et al.*, 2008; Shehzad *et al.*, 2012; Weiskopf, Kachel and McCarthy, 2016), and often based at least in part on dietary content, leading to a circular argument *(*Glen and Dickman, 2006*;* Lee *et al.*, 2013; Mann *et al.*, 2019). Failure to incorporate a genetic verification of species can result in inaccurate dietary assessments when nontarget scat is included in the analysis (Weiskopf, Kachel and McCarthy, 2016). Especially when analysing the diet of sympatric carnivores whose scat has a similar morphology, genetic confirmation is crucial (Morin *et al.*, 2016).

Mitochondrial DNA (mtDNA) obtained from scat can be used for species identification. Mitochondria are independent cell organelles which contain a separate genome and are abundant in the cell

compared to nuclear DNA, making them useful DNA markers in samples with low and degraded DNA (Chaves *et al.*, 2012). mtDNA also has a fast mutational rate, enabling the study of differences between species by tracing linkages between species (Schmidt-Küntzel *et al.*, 2018). mtDNA contains the ATP6 coding region, which is responsible for energy synthesis in the body. This region has been used for species identification (Chaves *et al.*, 2012). Microsatellite markers can be used to obtain a genetic profile of the individual organism represented (Adams and Waits, 2007; Kumar, 2017). Microsatellites DNA markers are noncoding regions of the nuclear DNA and are short sequence stretches in which a motif of two to six bases is randomly repeated (Ellegren, 2004). They are prone to mutations, which might either increase or decrease the repeat numbers per locus (Merola, 1994; Driscoll *et al.*, 2002; Schmidt-Küntzel *et al.*, 2018). Because microsatellite markers have a lot of variants, they are ideal for identifying individuals.

## 1.4    Focal species

### 1.4.1    Black-backed jackal (*Lupulella mesomelas*)

The black-backed jackal is a slender canid with reddish brown to tan hair and a saddle of black and silver hair across the back. Black-backed jackal are abundant on the African continent with two recognized subspecies. The northern subspecies is *C. m. schmidtii* (Schreber, 1775), which occupies southern Ethiopia, southern Sudan, Somalia, Kenya, Uganda, and northern Tanzania (Van Den Brink, 1973). The range of the southern subspecies, *C. m. mesomelas* (Noack, 1897), is from South Africa to Angola, Zimbabwe, and into southern Mozambique, including all of Namibia (Sheldon, 1992, as cited in Walton and Joly, 2003). Black-backed jackal are highly adaptable and thrive in a variety of habitat types, from mountains to coastal desert to closed woodland regions. Although they are highly persecuted, predator control efforts are largely ineffective against black-backed jackal and may only decrease local numbers temporarily. IUCN assesses the black-backed jackal as a species of least concern (Hoffmann, 2014).

Black-backed jackal are highly territorial and mark their territories by scent marking with urine (Moehlman, 1987). Home range size varies considerably from 1-34 km$^2$ in southern Africa (Kamler *et al.*, 2019) and is largest during the mating season (Loveridge and Macdonald 2001, as cited in Walton and Joly, 2003). Black-backed jackals are monogamous and raise their pups with the help of older offspring from previous litters (Moehlman, 1987). They are not sexually dimorphous in terms of behaviour, and both males and females share roles of hunting, defending territory, and socializing pups.

One reason black-backed jackals are able to thrive in diverse habitats is their flexible diet that allows them to hunt, scavenge, and forage (Walton and Joly, 2003; Goldenberg et al., 2010). While they exhibit a preference for small to medium ungulates from 14-26kg (Hayward et al., 2017), as opportunistic omnivores they are able to exploit many alternative food sources, often exhibiting seasonal diet switching (Klare et al., 2010). Within Namibia, black-backed jackal diet varies widely by food availability. In the Namib desert, they survive on a diet of mostly insects due to the scarcity of mammal prey (Goldenberg et al., 2010). Along the Skeleton Coast, black-backed jackals consume a wide variety of seabirds, penguins, and scavenge on seal carcasses (Avery et al., 1987; Kolar, 2005).

In environments devoid of large predators, black-backed jackal may experience mesopredator release, where removal of an apex predator results in increased abundance of mesopredators (Feit, Feit and Letnic, 2019). Apex predators suffer disproportionately in human-dominated environments due to their large space requirements and sensitivity to persecution (Prugh et al., 2009), but black-backed jackal are better able to cope with persecution and remain widespread in human-dominated landscapes (Klare et al., 2010; Krofel et al., 2017). Mesopredator dominance can increase human-wildlife conflict, including livestock depredation (Prugh et al., 2009).

Black-backed jackal are frequently reported to depredate on livestock across southern Africa (Kamler, Klare and Macdonald, 2012; Humphries et al., 2016; Drouilly, Nattrass and O'Riain, 2018). In Namibia, they are believed to depredate on smallstock more than any other carnivore species (Rust and Marker, 2013; Verschueren et al., 2020). Diet studies often find evidence of cattle in the diet of black-backed jackals (Humphries, Ramesh and Downs, 2016). Due to their size, it is believed that cattle may be scavenged, however, black-backed jackals have been observed killing calves and hunting sick adult cattle (Humphries, Ramesh and Downs, 2016).

Southern Africa has a long history of government-sponsored predator extermination programs (Du Plessis, 2013). In the 19th century, farmers were paid a bounty for each predator killed. In the 20th century, hunting clubs were tasked with removing "declared problem predators" on a regional level (Du Plessis, 2013; Nattrass and Conradie, 2013). Black-backed jackal were among the species most frequently targeted by these hunting clubs (Gunter, 2008; Du Plessis, 2013). From the 1990s to present day, predator control no longer rests in the hands of the government but has been taken on by private landowners (Avenant and Du Plessis, 2008; Du Plessis, 2013). Removal and lethal control of black-backed jackal remains widespread today. In their review of communal and resettled land in Namibia, Rust and Marker found black-backed jackal to be by far the most removed predator (2013).

### 1.4.2    African wild dog (*Lycaon pictus*)

The African wild dog is a slender canid with characteristic large, upstanding ears and a coat with irregular patches of black, brown, red, yellow, and white. They are the only species in the genus *Lycaon* and are isolated from genetic exchange with other canid lineages (Chavez *et al.*, 2019). Historically, their range covered the African continent with the exception of the true desert regions. The species now inhabits approximately 5% of its previous range (Lines, 2008). The global population has most recently been estimated at 6,600 individuals and 1,400 mature adults and is distributed between 39 subpopulations primarily in southern Africa and the southern part of east Africa (Woodroffe and Sillero-Zubiri, 2020).

African wild dogs are highly social and form hierarchical packs of up to 20 adults consisting of an alpha male and female pair along with other reproductively suppressed adults who help to raise the pups of the alpha pair (Rasmussen and MacDonald, 2012). African wild dogs occupy vast home ranges between 423-1218 km$^2$ (Hunter, 2011). During the denning season, their home range was found to contract between 33-76% in previous studies in southern Africa (Darnell *et al.*, 2014; Pomilia, Mcnutt and Jordan, 2015). African wild dogs are cursorial predators that hunt opportunistically and cooperatively in short, moderate to high-speed chases to take down prey (Hubel *et al.*, 2016). Compared to sympatric carnivore species, they predate on the largest prey for their body size, hunting and killing ungulates 120% of their mass (Radloff and Du Toit, 2004; Woodroffe *et al.*, 2007).

African wild dogs' preferred prey is medium-sized ungulates. They typically kill prey around 50kg but up to 200kg. Across most of their range, their most common prey is impala *(Aepyceros melampus),* greater kudu (*Tragelaphus strepsiceros*), Thomson's gazelle (*Eudorcas thomsonii*), and common wildebeest (*Connochaetes taurinus*; Woodroffe, 2020). Their principal prey species is typically the most abundant medium-sized ungulate species in a particular area (Pole *et al.*, 2004; Hayward *et al.*, 2006; Mbizah, Marino and Groom, 2012). However, when prey is scarce, African wild dogs display an adaptability in their diet that allows them to subsist on much smaller prey (Woodroffe *et al.*, 2007). For some populations, common duiker (*Sylvicapra grimmia*) and steenbok (*Raphicerus campestris*) are important prey (Woodroffe, 2020). Some populations predate on warthog *(Phacochoerus africanus*; Pole *et al.*, 2004; Mbizah, Marino and Groom, 2012; Woodroffe, 2020), but they are not preferred when other species are present (Vogel, Somers and Venter, 2018). African wild dogs have been known to prey on scrub hares (*Lepus saxatilis*) and even occasionally consume lizards and eggs, but these food items typically make a small contribution to their diet (Woodroffe, 2020).

African wild dogs are a highly persecuted species because of their "cruel" disembowelment killing method (Lindsey, Du Toit and Mills, 2005) and their conflict with farmers due to livestock depredation. Throughout most of the 20th century, the species was regarded as vermin and state-sanctioned extermination contributed to population decline (Rasmussen, 1999). One survey of South African farmers found African wild dogs were the least popular large predator due to their perceived high costs and minimal benefit (Lindsey, Du Toit and Mills, 2005). Farmers' primary complaint is that African wild dogs reduce their income by killing livestock (Woodroffe *et al.*, 2005). Conflict intensifies in human-dominated landscapes where contact between African wild dogs and livestock increases (Schoener, 2002; Woodroffe *et al.*, 2005). Livestock depredation is more prevalent where wild prey is significantly depleted and livestock is abundant (Woodroffe *et al.*, 2005), as African wild dogs seem to prefer wild game when it is available (Gusset *et al.,* 2009; Rasmussen, 1999; Woodroffe, *et al.,* 2005).

African wild dogs are very wide ranging, meaning they are likely to move out of protected areas (Lindsey, Du Toit and Mills, 2005; Woodroffe *et al.*, 2005). The majority of conflicts with African wild dogs occur outside of protected areas, for example, on communal lands (Lindsey, Du Toit and Mills, 2005; Woodroffe *et al.*, 2005). Therefore, the survival of the species relies on human populations tolerating the presence of African wild dogs outside of protected areas (Lindsey, Du Toit and Mills, 2005).

### 1.5    Objectives of the study

The objectives of this study are:

1. To determine factors influencing black-backed jackal abundance across the Okakarara District Communal Area (ODCA) and how it may be influenced by availability of wild prey, livestock, and proximity to African wild dog territory.

2. To describe black-backed jackal diet and estimate the proportion that consists of livestock and other food item categories.

3. To explore coexistence of black-backed jackal and African wild dog by comparing black-backed jackal diet niche breadth and diet overlap within and outside of African wild dog territory.

4.  To determine if African wild dog-livestock conflict is increased around their denning sites.

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# Chapter 2: Relative abundance of black-backed jackal (*Lupulella mesomelas*) in the Okakarara District Communal Area, Namibia

## 2.1 Abstract

Black-backed jackals (*Lupulella mesomelas*) are a mesocarnivore perceived responsible for the majority of livestock depredation in many regions of Africa. In 2018 and 2019, a camera trap study was carried out in the Okakarara District Communal Area (ODCA) of northeastern Namibia for 30 days in the wet and dry seasons. I modelled black-backed jackal abundance using the Royles-Nichols model (2003), as it can provide more insight than occupancy modelling for widespread species with high naïve occupancy but heterogeneity in detection probability due to variation in abundance. In the dry season, black-backed jackal abundance had a significant positive relationship with village density. Abundance was also significantly higher within 10km of African wild dog (*Lycaon pictus*) dens. This indicates that in the dry season, black-backed jackal may rely on food sources near human settlements, particularly smallstock and potentially human refuse. African wild dogs, an apex carnivore in this system, may act as a facilitator to black-backed jackal, allowing them to access carcasses from African wild dog kills. Black-backed jackal may also prefer habitat where African wild dogs den because of its complex terrain and level of concealment.

## 2.2 Introduction

Mesocarnivores are a diverse group of small to midsized carnivores with body weight <15kg (Roemer, Gompper and Valkenburgh, 2009). They inhabit a variety of habitats, including urban and other human-dominated environments (Roemer, Gompper and Valkenburgh, 2009; Ćirović, Penezić and Krofel, 2016). Mesocarnivores have often been subject to negative perceptions, viewed as vermin or pests and targeted by lethal control programs (Berger, 2006; Roemer, Gompper and Valkenburgh, 2009; Ćirović, Penezić and Krofel, 2016). In reality, mesocarnivores fill an important role in communities and perform ecosystem services such as animal waste removal and seed dispersal (Ćirović, Penezić and Krofel, 2016; Nakashima and Do Linh San, 2022). In areas with low species diversity and absence of large carnivores, mesocarnivores can act as an apex predator, controlling prey populations and inhibiting competitors. Due to anthropogenic extinction and its disproportionate effects on large carnivores, many mesocarnivores now occupy this apex predator role in their respective communities (Roemer, Gompper and Valkenburgh, 2009).

Black-backed jackal (*Lupulella mesomelas*) are a widespread mesocarnivore on the African continent and assessed by the IUCN as a species of least concern (Hoffmann, 2014). They are opportunistic and thrive in a wide range of habitats and human-dominated environments (Klare *et al.*, 2010; Hoffmann, 2014). Black-backed jackal are highly persecuted due to their role in livestock depredation, but predator control efforts are largely ineffective due to their unspecialized, adaptable characteristics (Hoffmann, 2014). Black-backed jackal are reported to be responsible for significant smallstock depredation across southern Africa (Kamler, Klare and Macdonald, 2012; Humphries *et al.*, 2016; Drouilly, Nattrass and O'Riain, 2018; Verschueren *et al.*, 2020).

Estimating species abundance is important for developing conservation strategies, but there is little information on the abundance of mesocarnivores such as black-backed jackal (Hernández-sánchez *et al.*, 2017). Many researchers use camera traps to non-invasively gather data on black-backed jackal and apply occupancy models to estimate their occurrence while accounting for imperfect detection (Thorn *et al.*, 2011; Schuette *et al.*, 2013; James, 2014; Rich *et al.*, 2017; Satterfield *et al.*, 2017; van der Weyde, Mbisana and Klein, 2018; Ehlers Smith *et al.*, 2019; Fink *et al.*, 2020; Verschueren *et al.*, 2021a; Pardo, Swanepoel and Curveira-Santos, 2022). Occupancy ($\psi$) is the probability of a particular species occupying a site, while detection probability (p) is the probability that the species will be detected when present (MacKenzie *et al.*, 2002; Mackenzie and Royle, 2005). By definition, naïve occupancy is the number of sites occupied by a species divided by the total number of sites (Mackenzie and Royle, 2005). Due to imperfect detectability, the number of sites where a species was detected cannot directly predict the occupancy of that species. Therefore, occupancy models estimate species occurrence while accounting for imperfect detectability (Gu and Swihart, 2004). Occupancy models incorporate a history of detection and non-detection of a species at a particular location using repeated survey data (MacKenzie *et al.*, 2002; Mackenzie and Royle, 2005).

Environmental factors, such as season, habitat, or anthropogenic disturbance can be included as covariates in occupancy models to help explain the occurrence of that species (MacKenzie *et al.*, 2002; Mackenzie and Royle, 2005). Previous studies have found opposing effects of season on black-backed jackal, with occupancy either higher in the dry season (Rich *et al.*, 2017) or in the wet season (Verschueren *et al.*, 2021). Similarly, while Masseloux *et al.* (2018), found a positive relationship between percentage cover of woody vegetation and occupancy, recently published studies have found higher black-backed jackal occupancy to be associated with open grassland or reduced cover (Verschueren *et al.*, 2021; Pardo, Swanepoel and Curveira-Santos, 2022). Occupancy of mesocarnivores including black-backed jackal may decrease in the presence of large predators

(Curveira-Santos *et al.*, 2021). Black-backed jackal occupancy has been shown to be higher in livestock farming areas areas (Van der Weyde, Mbisana and Klein, 2018; Ehlers Smith *et al.*, 2019; Fink *et al.*, 2020) and strongly positively associated with increasing livestock abundance (Masseloux *et al.*, 2018; Van der Weyde, Mbisana and Klein, 2018), suggesting a high conflict potential for livestock farmers (Schuette *et al.*, 2013; Masseloux *et al.*, 2018). Although widespread in human-dominated landscapes, black-backed jackals seem to avoid anthropogenic disturbance, with low occupancy reported near human settlements (Schuette *et al.*, 2013; Masseloux *et al.*, 2018) and lower occupancy with increased distance from protected areas (van der Weyde, Mbisana and Klein, 2018).

Royle and Nichols (2003) developed a model within the occupancy modelling framework to estimate local abundance (λ), or the number of individuals of a target species using a given sampling site. Royle and Nichols' abundance model is ideal for modelling detection data of widespread species with high naïve occupancy or when there is heterogeneity uncaptured by the model's covariates (Dorazio, 2007; Royle, 2006; Royle and Nichols, 2003). This heterogeneity in detection is caused by variation in species abundance across the study site. Royle and Nichols' abundance model incorporates heterogeneous detection probabilities induced by variation in animal abundance and allows for extracting information about abundance from detection–non-detection data (Paolino *et al.*, 2018). The model considers that the probability of detecting a species at a sampling station is conditional on abundance based on the following equation:

$$p_i = 1 - (1 - r_i)^{N_i}$$

where $p_i$ is the probability of detection at site $i$ and $r_i$ is the individual-level probability of detection at site $i$. According to this equation, site-level detection probability increases with local abundance ($N_i$) (Royle and Nichols, 2003).

Local abundance values are a function of the effective trapping area for the target species and are not directly comparable between species (Efford and Dawson, 2012; Wearn *et al.*, 2017). Therefore it's important to note that local abundance is distinct from true abundance or density (individuals per unit area). Relative abundance is a more accurate term to describe this model's output. Relative abundance values are spatially comparable and function as a measure of relative density changes across an area (Wearn *et al.*, 2017).

In the Okakarara District Communal Area (ODCA) of Namibia, black-backed jackal are abundant and reportedly responsible for a high amount of livestock loss (Lines, 2008; Verschueren *et al.*, 2020). Understanding what factors influence their distribution will advance understanding of the carnivore guild in this unique region and inform conservation and conflict mitigation priorities. I investigated environmental factors which may influence relative abundance of black-backed jackal in the ODCA. I hypothesized that abundance would be higher at sites with high visibility and reduced canopy cover (Verschueren, Briers-Louw, *et al.*, 2021; Pardo, Swanepoel, Curveira-Santos, 2022) and higher at sites with increased wild prey occupancy (Verschueren, Briers-Louw, *et al.*, 2021) and livestock occupancy (Masseloux *et al.*, 2018; Van der Weyde, Mbisana and Klein, 2018). I also hypothesized that black-backed jackal abundance would be negatively influenced by anthropogenic factors such as distance to village (Schuette *et al.*, 2013; Masseloux *et al.*, 2018) and that abundance would be lower within 10km of African wild dog dens due to competition with a large carnivore (Curveira-Santos *et al.*, 2019).

**2.3 Methods**

**2.3.1 Study Area**

This study occurred in northeastern Namibia in the Okakarara District Communal Area (ODCA), which is part of the Greater Waterberg Landscape. The ODCA consists of four communal conservancies (Okakmatapati, Otjituo, Ozonahi, African wild dog) that span a total area of 18,951 km$^2$. The study area for this research covered 6,720 km$^2$ (Figure 2.1)
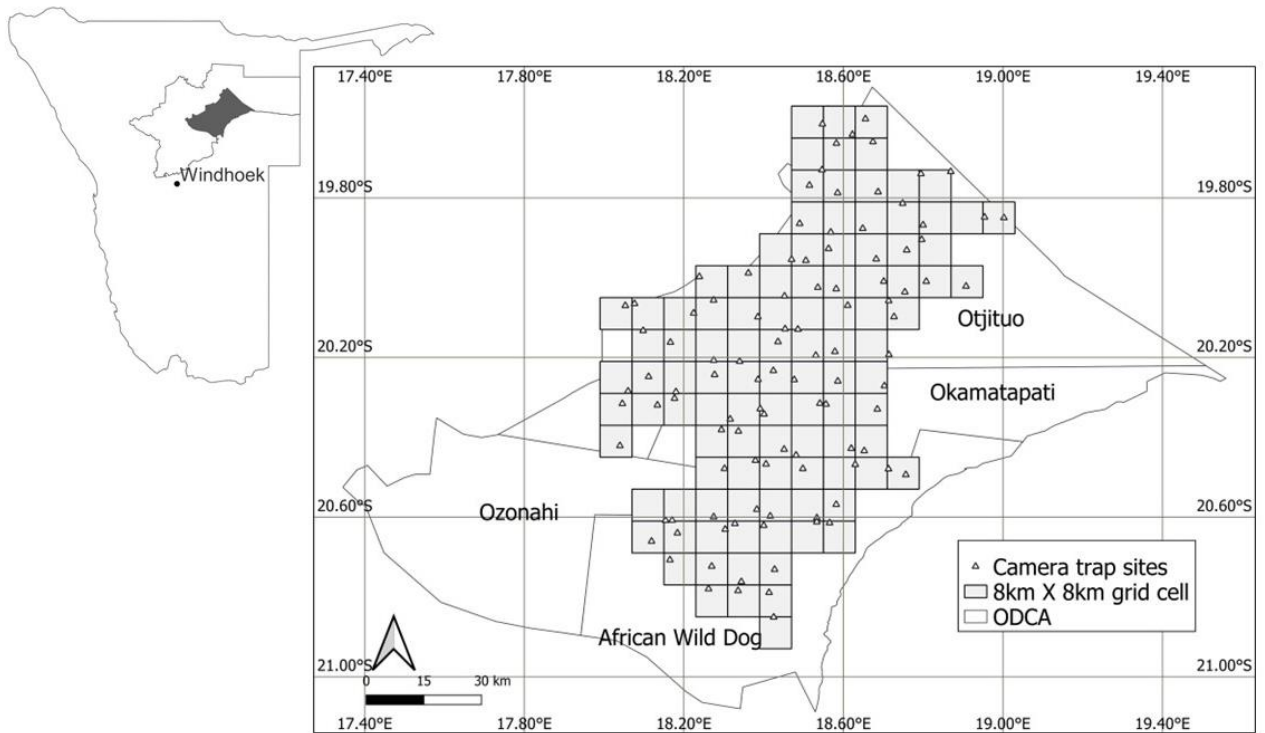
**Figure 2.1.** Grid and camera trap locations in the Okakarara District Communal Area (ODCA) and the study area location in the Otjozondjupa region of Namibia (inset).

The ODCA is situated on the western fringe of the Kalahari basin (Strohbach, 2014). The surface soils are dominated by sandy plains that are flat to rolling with 6°-9° slopes (Strohbach, 2014). Vegetation type is primarily *Terminalia sericea-Combreto collinum* shrub and bushlands (Hüttich *et al.*, 2009; Strohbach, 2014). The ODCA is characterized by three seasons: hot-wet (January-April), cool-dry (May-August), and hot-dry (September-December) (Mendelsohn *et al.,* 2002). The average temperature ranges from 6℃ in the cool-dry season to 31℃ in the hot-dry season (Mendelsohn *et al.,* 2002). Annual rainfall averages from 400-450 mm, with droughts common (Mendelsohn and El Obeid, 2002; Strohbach, 2014).

**Figure 2.2.** Typical landscape and vegetation of the Okakarara District Communal Area (ODCA).

The ODCA is known to be wildlife-depleted compared to other communal conservancies in Namibia and the surrounding freehold farmland, likely as a result of unsustainable hunting (Lines, 2008; Verschueren *et al.*, 2020). Small antelope such as common duiker (*Sylvicapra grimmia*) and steenbok (*Raphicerus campestris*) persist, while greater kudu (*Tragelaphus strepsiceros*) is the only large antelope found in the ODCA and is presumed to be rare (Lines, 2008). Little is known on the carnivore community, but mesocarnivores are assumed to be widespread (Lines, 2008). The region is inhabited by a small population of critically endangered African wild dog (*Lycaon pictus*; Hanssen *et al.*, 2022). Other large carnivores believed present but very sparse are spotted hyaena, brown hyanea, cheetah, and leopard.

The ODCA is populated primarily by the Herero tribe, whose principal livelihood is livestock farming of cattle and smallstock (sheep and goats). Live cattle sales is the primary income of inhabitants (Lines, 2008). Human settlements are concentrated primarily in the western and central regions of the ODCA, with less human impact to the east.

### 2.3.2 Data collection

In January 2018, Cheetah Conservation Fund (CCF) began an extensive camera trap survey of the ODCA. The area of the four communal conservancies was overlaid with an 8 X 8km square grid. From this grid, 105 grid cells were selected to obtain a broad representation of habitats and human

densities across the conservancies. The selected cells were divided into 3 blocks, each block containing 35 cells, and blocks were sampled sequentially.

A single Bushnell camera trap was deployed in each cell of the 3 blocks and was active for 30 days in the wet season (November–April 2018-2019) and 30 days in the dry season (May–October 2018). The location of deployment within each grid cell was selected based on local knowledge with community involvement to increase the probability of wildlife detection. At each farm where a camera trap was to be deployed, the farmer or farm workers were asked to identify areas of high wildlife movement, frequently targeting linear features such as roads or wildlife trails where wildlife was known to travel. The cameras were deployed at a height of approximately 60cm. Additional information was collected at each camera trap site including canopy cover, habitat visibility, and proximity to linear feature.



**Figure 2.3** Black-backed jackal (*Lupulella mesomelas*) image from the Okakarara District Communal Area (ODCA) camera trap study.

Canopy cover was measured using a Bitterlich gauge (Friedel and Chewings, 1988) based on the rough cover estimation method of Zimmerman (2009) modified to Mberirua (2018). The Bitterlich gauge was set to a half angle of 12°55' and pointed at all trees and shrubs over 0.5m tall 360° around the camera at each site. When the canopy of a tree extended beyond the two sighting pins of the Bitterlich gauge, it was recorded. When canopies from multiple overlapping trees extended beyond the sighting pins, they were recorded as one canopy (Zimmerman, 2009). To obtain a relative indication of canopy cover, the number of recorded canopies was divided by the total number of trees and shrubs over 0.5m at the site.

Habitat visibility was recorded using a range finder. The observer crouched at a height of 70cm, assumed to be eye level of large carnivores. The distance at which an object disappeared or was last detectable was recorded for 4 directions (0°; 90°; 180°, and 270°) around the camera. These 4 values were averaged to obtain an average habitat visibility value for each camera trap site.

The distance from the camera trap to the nearest linear feature was recorded in meters. Site proximity features were classified into 4 categories: dirt road (n=43), cutline (n=15), clear wildlife trail (n=12), and fenceline (n=12). Cameras with none of these features present were classified as bush (n=23). Cameras were classified into one of these feature categories when the feature was within the camera's detection range of 20m. When a camera was located at two of these features within the camera's detection range (e.g. at the intersection of a fence and road), the camera was categorized based on the feature assumed to be most influential on wildlife movement. Roads were assumed to be most influential, followed by cutlines, wildlife trails, fencelines, and bush. For example, cameras at the intersection of a road and fenceline were classified in the road category.

### 2.3.3 Data analysis

Images were classified manually to species level following camera retrieval. Relative abundance ($\lambda$) of black-backed jackal was modeled using the Royle-Nichols method, which is ideal for modeling detection data when there is heterogeneity uncaptured by the model's covariates (Royle and Nichols, 2003; Royle, 2006; Dorazio, 2007). Naïve occupancy of black-backed jackal was close to 1, and modeling relative abundance provided more insight into the effects of the covariates on this species' distribution in the study area. The Royle-Nichols model was applied using function *occuRN* in R package *unmarked*.

Camera trapping nights were calculated by multiplying the number of nights a camera was active by the number of camera sites. While 105 cameras were deployed in both seasons, due to camera malfunctions 97 cameras were active throughout the dry season and 99 cameras were active throughout the wet season. The camera trap survey data was separated by wet (November–April) and dry (May–October) seasons and divided into three 10-day survey periods to construct detection histories for black-backed jackal. Relative abundance was modeled in a two-step abundance-detection framework (MacKenzie *et al.*, 2006; Paolino *et al.*, 2018). Detection covariates were tested in the detection function first while holding abundance constant. The covariates from the detection function in the best fitting model were retained in the candidate models which tested covariates for the abundance function.

Three detection or site-level terms were tested: canopy cover, average habitat visibility, and proximity to linear feature. There were 11 abundance covariates tested: canopy cover, average habitat visibility, distance to human settlement, village density, common duiker intensity of use, steenbok intensity of use, ungulate intensity of use (which pools common duiker and steenbok data), scrub hare (*Lepus saxatilis*) intensity of use, smallstock intensity of use, longitude, and proximity to African wild dog den (Table 2.1).

**Table 2.1.** Covariates included in the abundance models for black-backed jackal (*Lupulella mesomelas*) for dry and wet seasons.

| Covariate | Units | Dry season | | Wet season | |
|---|---|---|---|---|---|
| | | Range | Mean | Range | Mean |
| Canopy cover | % | 7.10-100 | 82.20 | 7.10-100 | 83.01 |
| Average habitat visibility | Meters | 6.20-58.90 | 20.19 | 6.20-61.90 | 20.37 |
| Distance to human settlement | Kilometers | 0.34-10.77 | 2.88 | 0.02-10.77 | 2.92 |
| Village density | Mean raster value | 0.06-7.13 | 3.09 | 0.06-7.13 | 3.11 |
| Common duiker intensity of use | Ψ | 0.75-0.87 | 0.81 | 0.68-0.85 | 0.80 |
| Steenbok intensity of use | Ψ | 0.56-0.88 | 0.75 | 0.51-0.64 | 0.55 |
| Ungulate intensity of use | Ψ | 0.68-0.84 | 0.78 | 0.66-0.70 | 0.68 |
| Scrub hare intensity of use | Ψ | 0.27-0.62 | 0.49 | 0.43-0.96 | 0.65 |
| Smallstock intensity of use | Ψ | 0.002-0.74 | 0.34 | 0.12-0.83 | 0.28 |
| Longitude | UTM | 191490.67-290816.82 | 235428.58 | 191065.35-290816.82 | 235952.41 |

For description of how the values for canopy cover, average habitat visibility, and proximity to linear feature were obtained, see Section 2.3.2. Distance to village and village density were included to represent additional human influence. The distance between each camera trap and the nearest human settlement was calculated in QGIS 2.24.1 using a point shapefile for the ODCA villages. Village density was also calculated using the village point shapefile. I used the shapefile to create a raster of village density with a radius or kernel bandwidth of 10km. I created buffers of different sizes around the camera trap locations to represent the average home range size of black-backed jackal and used the zonal statistics tool in QGIS to calculate the mean raster value within each buffer. Black-backed jackal home range has been reported to vary from 1-34 km$^2$ in southern Africa (Kamler *et al.*, 2019) and was not available for the study area. I plotted scatterplots to compare the buffer sizes of the min, max, and mean within this range. The village density raster values were very similar between the tested buffer sizes. Therefore, I used the values from a 17.5 km$^2$ buffer as a covariate in the black-backed jackal abundance models. Prey intensity of use values were calculated by occupancy

modelling. For description of how these values were obtained, see Appendix S1. I included the longitude covariate to account for potential higher density of villages in the west than in the east.

I planned to incorporate African wild dog as a covariate to explore the apex carnivore's influence on black-backed jackal abundance, but the camera trap study recorded only 5 detections of African wild dog between the two seasons, precluding occupancy or abundance modeling. Therefore, I used the locations of known African wild dog dens to estimate African wild dog den proximity as a categorical variable indicating if a camera trap was within 10km of an identified African wild dog den. African wild dog dens have been identified from 2017-2022 as a result of CCF's ongoing human-wildlife conflict work in the ODCA. Dens are discovered by farmers and their locations shared with CCF. These locations are visited by CCF's ecology team and confirmed before their coordinates are recorded as African wild dog dens. Although the home range of the African wild dogs in the ODCA is unknown, the 10km buffer size reflects approximate home range contraction during the denning season, during which movement is restricted to close to the den (Darnell *et al.*, 2014; Pomilia, Mcnutt and Jordan, 2015). I used QGIS 2.24.1 to create buffers around den locations and the camera traps were categorized accordingly if they were within or outside 10km of a den.

The continuous covariates (canopy cover, average habitat visibility, distance to village, and longitude) were standardized to z-scores. I included quadratic terms for canopy cover and average habitat visibility to account for potential non-linear relationships. Prior to constructing candidate models, the covariates were tested for correlation within each season. Where two covariates were strongly correlated ($r > |0.7|$), I included only one covariate in the candidate models for abundance. In such situations, I retained for analysis the covariate with better goodness-of-fit and ΔAICc < ΔAICc of the null model when tested univariately.

All models with ΔAICc <2 were averaged (Oberosler *et al.*, 2017; Zeller *et al.*, 2017; Wevers *et al.*, 2021) using function *modavg* from R package *AICcmodavg* to interpret relationships between black-backed jackal abundance and covariates with confidence intervals that did not overlap zero (Burnham and Anderson, 2002). To obtain per-site abundance estimates, models with ΔAICc <2 were averaged using function *modavgPred* from R package *AICcmodavg* (Burnham and Anderson, 2002).

To assess model fit, I applied McKenzie and Bailey's goodness-of-fit test to the global model for each season using 1,000 simulations. An estimate of the overdispersion or variance inflation parameter ($ĉ$;

Burnham and Anderson, 2002) was also obtained and used as an indicator of lack-of-fit where $\hat{c} > 1$ indicates overdispersion (O'Brien *et al.*, 2020)

## 2.4 Results

### 2.4.1 Black-backed jackal abundance dry season

This camera trap study detected 1,003 independent records of black-backed jackal over 2,910 camera trapping nights in the dry season. Naïve occupancy for black-backed jackal in the dry season was 0.742. Detection probability was 0.348. There were no significant covariates for detection, and the null model was highly ranked (ΔAICc <2) and only 0.2 units away from the top ranked model, which included average habitat visibility as a detection covariate. Therefore, no detection covariates were included in abundance model candidates.

For the black-backed jackal dry season abundance models, the covariates smallstock and scrub hare intensity of use were negatively correlated with distance to village (-0.890 and -0.730, respectively). Steenbok, ungulate, and scrub hare intensity of use were positively correlated to village density (0.976, 0.834, and 0.841, respectively). Steenbok was positively correlated to ungulate and scrub hare intensity of use (0.864 and 0.874, respectively).

I retained smallstock intensity of use and village density as covariates in the abundance candidate models. Table 2.2 includes model outputs for the top-ranked detection and abundance models (ΔAICc <2). For a full list of all candidate models, see Appendix S2.

**Table 2.2.** Top-ranking (ΔAICc <2) model selection procedure for factors influencing black-backed jackal (*Lupulella mesomelas*) site detectability (p) and relative abundance (λ) in the dry season. Covariates considered are canopy cover (CC), average habitat visibility (AH), proximity feature (PF), village density (VD), smallstock intensity of use (SS), AWD den proximity (AWD), and longitude (L). The number of parameters in the model (k); AICc values; the relative difference in AICc values between each model and the model with the lowest AICc (ΔAIC); AICc model weights (w); č, variance inflation factor (overdispersion). (.) indicates the parameter is constant.

| Model | k | AICc | ΔAICc | w | Goodness-of-fit | ĉ |
|---|---|---|---|---|---|---|
| **Detection models** | | | | | | |
| λ(.)p(AH) | 3 | 379.83 | 0.00 | 0.21 | 0.30 | 1.19 |
| λ(.)p(.) | 2 | 380.03 | 0.20 | 0.19 | 0.27 | 1.28 |
| λ(.)p(AH,CC) | 4 | 380.23 | 0.41 | 0.17 | 0.28 | 1.24 |
| λ(.)p(CC) | 3 | 380.49 | 0.66 | 0.15 | 0.28 | 1.26 |
| λ(.)p(PF) | 3 | 381.62 | 1.79 | 0.08 | 0.28 | 1.28 |
| λ(.)p(AH,PF) | 4 | 381.80 | 1.98 | 0.08 | 0.26 | 1.28 |
| **Relative abundance models** | | | | | | |
| λ(AWD,SS,VD)p(.) | 5 | 374.30 | 0.00 | 0.24 | 0.30 | 1.23 |
| λ(AWD,SS)p(.) | 4 | 375.59 | 1.29 | 0.13 | 0.30 | 1.24 |
| λ(AH,CC,AWD,L,SS,VD)p(.) | 10 | 375.86 | 1.56 | 0.11 | 0.35 | 1.13 |
| λ(AH,CC,L,SS,VD)p(.) | 9 | 376.04 | 1.74 | 0.10 | 0.33 | 1.14 |

Per-site relative abundance estimates ranged from 0.919-4.13 (x̄= 2.10). The covariates included in the top models were average habitat visibility, canopy cover, African wild dog den proximity, longitude, smallstock, and village density. Goodness-of-fit for the top abundance models ranged from 0.30-0.35, indicating no evidence of lack of fit. Variance inflation parameters (ĉ) ranged from 1.13-1.24, indicating slight overdispersion.

Black-backed jackal abundance was significantly higher in areas of low smallstock occupancy ($\hat{\beta}$ = -1.251, SE = 0.604, Figure 2.4). Abundance was significantly higher in areas of higher village density ($\hat{\beta}$ = 0.213, SE = 0.111, Figure 2.5). Abundance was also significantly higher at camera traps within 10km of an African wild dog den ($\hat{\beta}$ = 0.509, SE = 0.230, Figure 2.6).
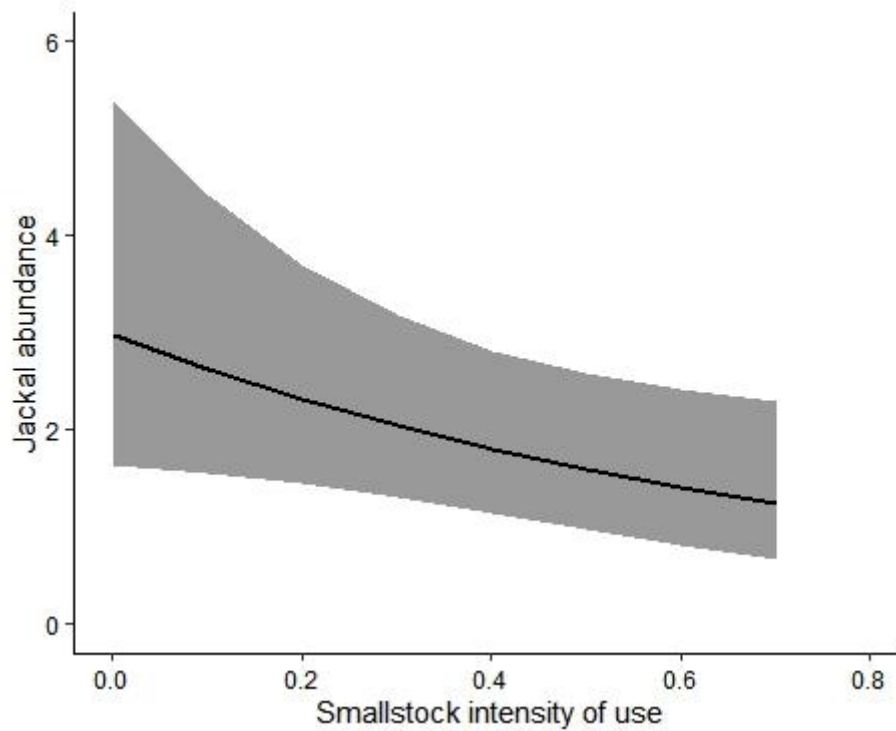
**Figure 2.4.** Black-backed jackal (*Lupulella mesomelas*) abundance and smallstock intensity of use in the dry season. Ribbon envelops 95% confidence intervals. Supported models ΔAICc <2 averaged to plot relationship between smallstock intensity of use and abundance.
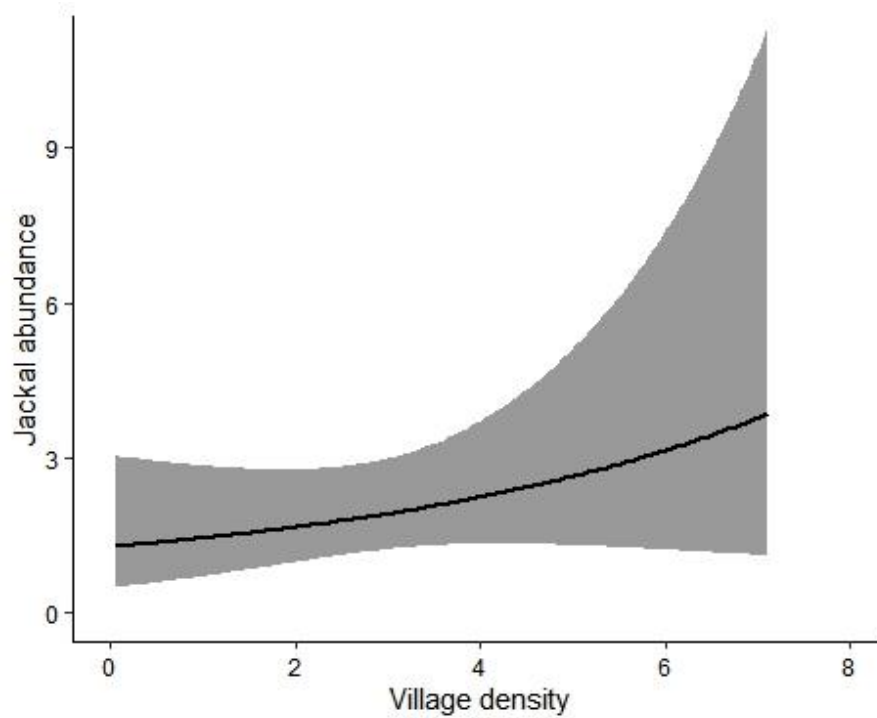


**Figure 2.5.** Black-backed jackal (*Lupulella mesomelas*) abundance and village density in the dry season. Ribbon envelops 95% confidence intervals. Supported models ΔAICc <2 averaged to plot relationship between village density and abundance.
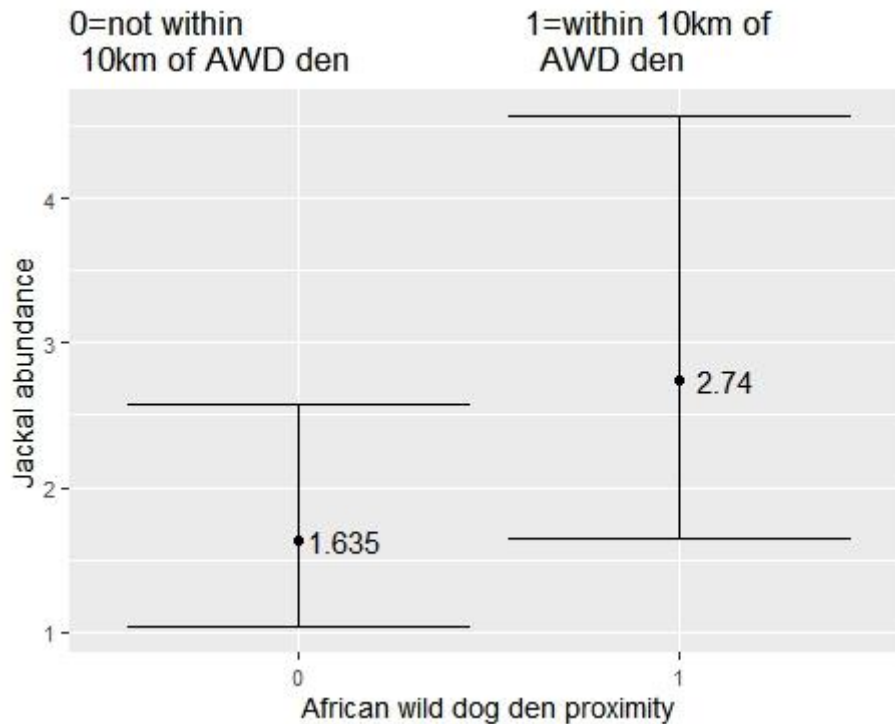
**Figure 2.6.** Black-backed jackal (*Lupulella mesomelas*) predicted abundance for cameras traps within 10km of African wild dog (*Lycaon pictus*) dens in the dry season. Error bars represent 95% confidence intervals.

**2.4.2 Black-backed jackal abundance wet season**

This camera trap study detected 592 independent records of black-backed jackal over 2,970 camera trapping nights in the wet season. Naïve occupancy for black-backed jackal in the wet season was 0.788. Detection probability was 0.313, but detectability was significantly higher with increasing average habitat visibility ($\hat{\beta}$ = 0.316, SE = 0.156, Figure 2.7) and this model was more than 2 ΔAICc units away from the null model (Table 2.3). Therefore, average habitat visibility was maintained as a covariate for the abundance model candidates.

For the black-backed jackal wet season abundance models, the covariates common duiker and ungulate intensity of use were positively correlated with each other (0.792) and both were negatively correlated with longitude (-0.810 and -0.978, respectively). Scrub hare and steenbok intensity of use were positively correlated with each other (0.978) and both were positively correlated with distance to village (0.966 and 0.998, respectively). Smallstock intensity of use was also positively correlated with canopy cover quadratic term (0.717).

I retained ungulate, scrub hare, and smallstock intensity of use as covariates in the abundance candidate models. Table 2.3 includes model outputs for the top-ranked detection and abundance models (ΔAICc <2). For a full list of all candidate models, see Appendix S3.

**Table 2.3.** Top-ranking (ΔAICc <2) model selection procedure for factors influencing black-backed jackal (*Lupulella mesomelas*) site detectability (p) and relative abundance (λ) in the wet season. Covariates considered are canopy cover (CC), average habitat visibility (AH), proximity feature (PF), scrub hare intensity of use (H), and ungulate intensity of use (U). The number of parameters in the model (k); AICc values; the relative difference in AICc values between each model and the model with the lowest AICc (ΔAIC); AICc model weights (w); č, variance inflation factor (overdispersion) (.) assumes the parameter is constant.

| Detection models | | | | | | |
|---|---|---|---|---|---|---|
| Model | k | AICc | ΔAICc | w | Goodness-of-fit | ĉ |
| λ(.)p(AH) | 3 | 393.24 | 0.00 | 0.38 | 0.21 | 1.38 |
| λ(.)p(AH,PF) | 4 | 394.62 | 1.38 | 0.19 | 0.22 | 1.40 |
| λ(.)p(AH,CC) | 4 | 395.21 | 1.97 | 0.14 | 0.21 | 1.39 |
| Relative abundance models | | | | | | |
| λ(U)p(AH) | 4 | 391.15 | 0.00 | 0.30 | 0.24 | 1.37 |
| λ(H)p(AH) | 4 | 392.88 | 1.73 | 0.13 | 0.23 | 1.39 |
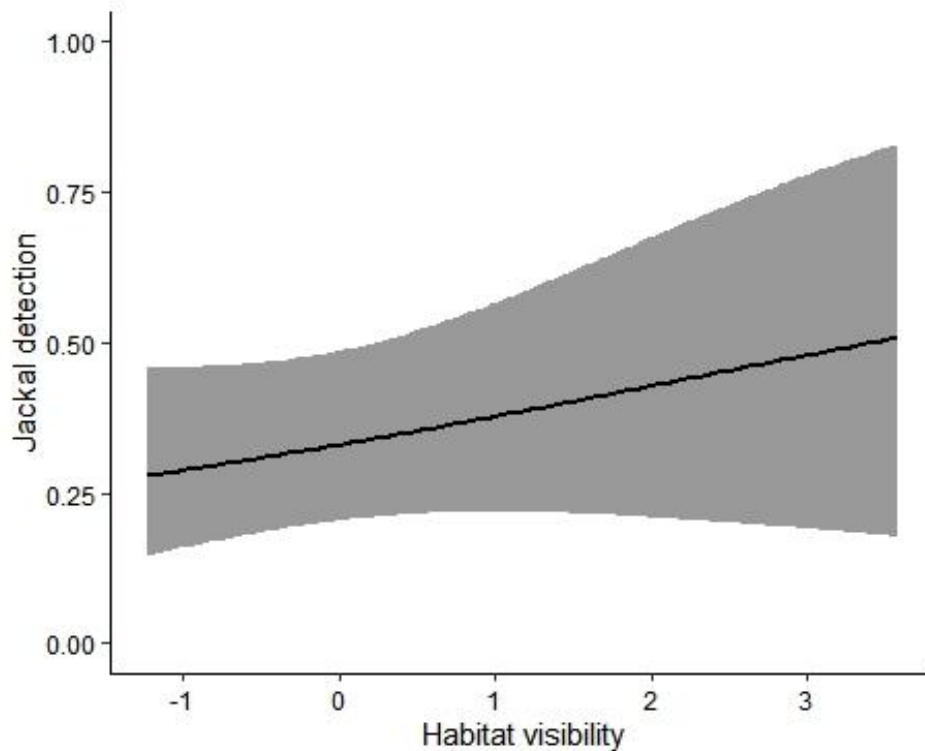


**Figure 2.7.** Black-backed jackal (*Lupulella mesomelas*) detection and average habitat visibility in the wet season. Ribbon envelops 95% confidence intervals. Supported models ΔAICc <2 averaged to plot relationship between habitat visibility and detection.

Per-site abundance estimates ranged from 1.62-3.37 (x̄= 2.38). The covariates included in the top

models (ΔAICc < 2) were scrub hare and ungulate intensity of use. Goodness-of-fit for the top

abundance models were 0.24 and 0.23, indicating no evidence of lack of fit. The variance inflation parameters (ĉ) were 1.37 and 1.39, indicating slight overdispersion.

Black-backed jackal abundance was significantly higher with decreasing ungulate intensity of use ($\hat{\beta}$ = -19.582, SE = 9.669, Figure 2.8).
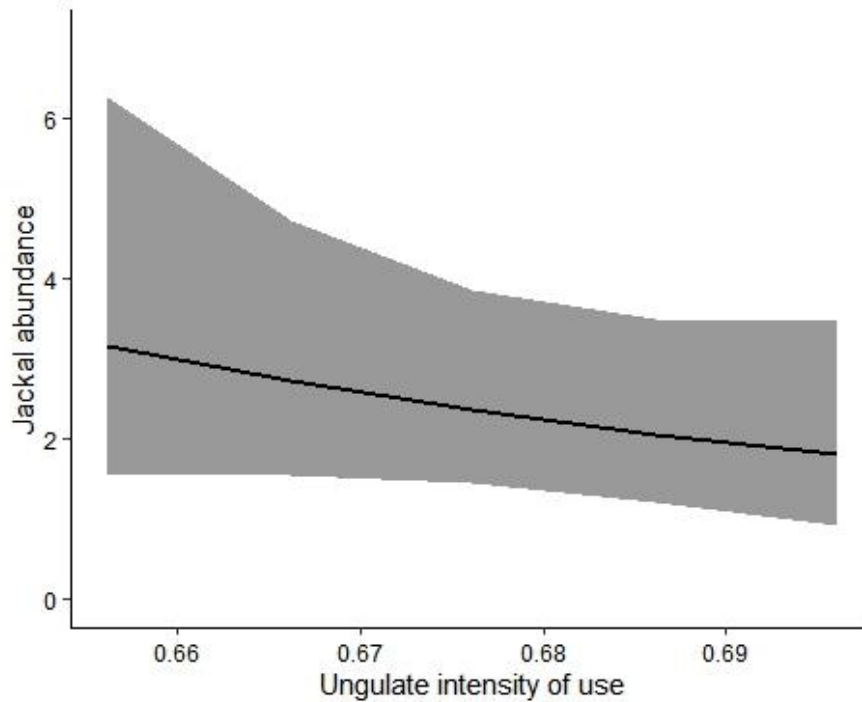


**Figure 2.8.** Black-backed jackal (*Lupulella mesomelas*) abundance and ungulate intensity of use in the wet season. Ribbon envelops 95% confidence intervals. Supported models ΔAICc <2 averaged to plot relationship between ungulate intensity of use and abundance.

**2.5 Discussion**

Black-backed jackal are a wide-ranging mesocarnivore in the ODCA with high naïve occupancy. Detection of black-backed jackal was significantly increased by higher habitat visibility in the wet season, likely due to vegetation growth which reduced visibility at camera sites in the wet season (Nghikembua *et al.*, 2016).

Black-backed jackal abundance was significantly higher in the dry season in areas of higher village density and within 10km of an African wild dog den. Reduced food availability in the dry season may influence black-backed jackals to rely more on livestock and other food resources of human origin in more village-dense areas, as well as scavenging from African wild dog kills (Verschueren *et al.*, 2021).

While typically avoiding human settlements, previous studies have found black-backed jackal to have higher occupancy in livestock farming areas (Van der Weyde, Mbisana and Klein, 2018; Ehlers Smith *et al.*, 2019; Fink *et al.*, 2020). Areas closer to villages may represent increased food resources for black-backed jackal in the form of livestock and potentially human refuse (Kaunda and Skinner, 2003; Loveridge and Macdonald, 2003). In this study, one black-backed jackal scat sample collected for diet analysis contained plastic, potential evidence of consumption of human refuse. Canid mesocarnivores including golden jackal (*Canis aureus*; Jaeger *et al.*, 2007), coyote (*Canis latrans*; Lukasik and Alexander, 2011), and red fox (*Vulpes vulpes*; Lewis, Sallee and Golightly, 1993) have been found to rely on human refuse as a food source. Although this is typically associated with urban areas, rural areas may also produce a significant amount of waste (Bateman and Fleming, 2012), which may be exploited seasonally when other resources are low (Lewis, Sallee and Golightly, 1993; Jaeger *et al.*, 2007). Carnivores often avoid large human settlements (Nellemann *et al.*, 2007; Schuette *et al.*, 2013; Masseloux *et al.*, 2018). However, the villages in the ODCA are very small and represent additional food sources for black-backed jackal, which may increase black-backed jackal abundance in village-dense areas in the dry season.

Mesocarnivores can interact with apex predators through competition, where the apex predator prevents access to food resources, or facilitation, where mesocarnivores benefit from scavenging on prey obtained by the larger carnivore (Codron *et al.*, 2018). The 10km buffer around African wild dog dens reflects hunting activity and home range contraction during the denning season (Darnell *et al.*, 2014; Pomilia, Mcnutt and Jordan, 2015). In the ODCA system, black-backed jackal may be more abundant closer to African wild dog dens because the African wild dogs' hunting near their dens facilitates increased food intake by black-backed jackal through scavenging carcasses from African wild dog kills. Although some studies found that apex predator presence did not impact black-backed jackal diet (Brassine and Parker, 2012; Yarnell *et al.*, 2013), other research found that black-backed jackal niche breadth was increased by the presence of an apex predator (Codron *et al.*, 2018).

Black-backed jackal may also be more abundant within 10km of African wild dog dens because den sites are selected by African wild dogs based on risk avoidance factors (Jackson *et al.*, 2014) including dense vegetation (Davies-Mostert, Mills and Macdonald, 2013; Alting *et al.*, 2021), rugged terrain (Davies-Mostert, Mills and Macdonald, 2013; O'Neill, Durant and Woodroffe, 2020; Alting *et al.*, 2021), and concealment (Van der Meer *et al.*, 2014). Although black-backed jackal can be abundant in human-dominated areas (Klare *et al.*, 2010; Hoffmann, 2014), they have been shown to

preferentially select habitat with high concealment to avoid conflict with humans (Kaunda, 2001; Humphries, Ramesh and Downs, 2016). This risk avoidant behaviour has also been described in other canid mesocarnivores such as red fox (Murdoch *et al.*, 2016) and golden jackal (Selimovic *et al.*, 2021), which prefer highly concealed habitat due to hunting pressure. Black-backed jackal may independently choose to occupy the same habitat in which African wild dogs den, indicating they do not face direct predation or competition from African wild dogs, as has been observed in other systems (Kamler *et al.*, 2007). It's important to consider that while the camera trapping study was completed in 2018-2019, the dataset of African wild dog dens included dens identified as active between 2017-2022. As it is not possible to verify if all of these dens were occupied by African wild dogs during the duration of the camera trapping study, this could introduce a bias to conclusions on black-backed jackal abundance.

In the wet season, black-backed jackal relative abundance was not significantly related to village density or proximity to African wild dog dens. Black-backed jackals' diet is known to vary seasonally depending on available food resources (Kaunda and Skinner, 2003; Klare *et al.*, 2010; Kamler, Klare and Macdonald, 2012; Van de Ven, Tambling and Kerley, 2013). In the wet season, black-backed jackals in the ODCA may capitalize on alternative food sources such as small mammals and berries (Moehlman, 1987; Kamler, Klare and Macdonald, 2012; Nattrass and Conradie, 2013). Due to the abundance of these seasonal resources in the wet season, livestock, other resources of human origin, and scavenging from African wild dog kills may be less important food sources.

Black-backed jackal abundance significantly increased with decreased smallstock intensity of use in the dry season and ungulate intensity of use in the wet season. However, the smallstock intensity of use model for the dry season had evidence of lack of fit, as did the common duiker intensity of use model for the wet season, which was combined with the steenbok model to obtain the ungulate intensity of use estimates (see Appendix S1 Table 1). Furthermore, the intensity of use model for smallstock may underrepresent smallstock density across the study area. Cameras were deployed to maximize wildlife detections and not near villages, where smallstock are likely more abundant. Unlike cattle, which were highly detected by the camera trap study, smallstock in the ODCA graze in the veld during the day and are kraaled in the villages at night (Verschueren *et al.*, 2020). Their probability of detection is therefore lower than cattle and wildlife species, which may have influenced the low intensity of use estimate. Village density, which was significantly positively influential on abundance in the dry season, may be a better indication of smallstock prey availability and its influence on black-backed jackal abundance.

**2.6 Conclusion**

Black-backed jackal are abundant in the ODCA, but may face pressure of reduced food availability in the dry season, driving them to rely more heavily on scavenging and livestock as food sources.

African wild dog potentially function as a facilitator to black-backed jackal in the ODCA system. Black-backed jackal abundance is higher close to African wild dog dens, indicating the two canids display a limited competitive relationship. Black-backed jackal animal protein intake may be increased by scavenging on kills made by African wild dogs, and they may also prefer habitat where African wild dogs den due to concealment and avoidance of human-derived risk. Black-backed jackals also occur more abundantly in areas that are more village dense. This is likely due to increased food resources around villages, especially smallstock availability, and should be explained further through investigation of black-backed jackal diet.

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**2.8 Appendices**

**Appendix S1. Black-backed jackal (*Lupulella mesomelas*) prey intensity of use modeling**

Using R packages *unmarked* and *AICcmodavg*, I modelled intensity of use for the mammalian prey species which were determined to be within the prey range of black-backed jackal and which were detected at >10% of the camera trap sites. I estimated intensity of use instead of true occupancy, because the home ranges of all prey species were smaller than the size of a given grid cell sampled. Intensity of use values per site were estimated for the dry and wet seasons and these values were included as covariates in black-backed jackal abundance models.

I used a two-step method and the same process as the black-backed jackal abundance models described in Section 2.3.3 to generate detection histories and create intensity of use models for

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common duiker, steenbok, scrub hare, and sheep and goats, which were combined in one smallstock category.

Canopy cover, average habitat visibility, and proximity feature were included as detection covariates for detection model selection. For description of how these values were obtained, see Section 2.3.2. The continuous detection covariates (canopy cover and average habitat visibility) were standardized to z-scores to have a mean of 0. Intensity of use covariates included were canopy cover, average habitat visibility, longitude, distance to village, and village density.

Distance to village and village density were calculated using the same process as described in Section 2.3.3. For the home range size of scrub hare, I used 0.0825 km$^2$, the published home range size of the cape hare (*Lepus capensis*), the other hare species found in Namibia, as the home range of scrub hare has not been reported (Wessels, 1978). For common duiker, average home range size for an adult female is between 0.03-0.17 km$^2$ (Furstenburg, 2018). For steenbok, home range is between 0.12-0.3 km$^2$ for both sexes (Furstenburg, 2008). I plotted scatterplots to compare the min, max, and mean home range buffer sizes for common duiker and steenbok and found the raster values were very similar between the tested buffer sizes. Therefore, I used the values from the buffer size representing the mean home range size of the species. This was 0.1 km$^2$ for common duiker and 0.21 km$^2$ for steenbok. For the smallstock covariate, I considered their "home range" to be the average distance from the camera trap locations to the nearest village, which was 2.88 km$^2$, or an area of 26 km$^2$.

In addition to canopy cover and average habitat visibility, distance to village and longitude were standardized to z-scores. Quadratic terms were included for canopy cover and average habitat visibility to account for potential non-linear relationships. All models with ΔAICc <2 were averaged to plot relationships among covariates for which confidence intervals did not overlap zero and intensity of use, as well as to calculate per site use values, using the same process described in Section 2.3.3. For the ungulate intensity of use values per site, the per-site use values of common duiker and steenbok were averaged. To assess model fit, McKenzie and Bailey's goodness-of-fit tests and variance inflation parameter (č; Burnham and Anderson, 2002) were obtained for the prey global models as described in Section 2.3.3.

**Appendix S1 Table 1.** Summary of top-ranking prey intensity of use models. Covariates considered are canopy cover (CC), average habitat visibility (AH), proximity feature (PF), distance to village (D), and longitude (L). Ψ indicates mean intensity of use probability; p, species detection probability; č, variance inflation factor (overdispersion). Signs inside parentheses indicate direction of significant covariates.

| Species | Season | ψ | p | Covariates in top detection models | Covariates in top intensity of use models | Goodness-of-fit | ĉ |
|---|---|---|---|---|---|---|---|
| **Common duiker** (*Sylvicapra grimmia)* | Dry | 0.810 | 0.598 | — | AH,CC,D,VD,L | 0.043 | 2.25 |
| | Wet | 0.804 | 0.683 | — | D,VD,L | 0.048 | 2.22 |
| **Steenbok** (*Raphicerus campestris*) | Dry | 0.754 | 0.438 | AH(-) | D,VD | 0.585 | 0.79 |
| | Wet | 0.550 | 0.403 | — | D,VD,L | 0.121 | 1.71 |
| **Scrub hare** (*Lepus saxatilis*) | Dry | 0.492 | 0.54 | — | CC,D,VD | 0.173 | 1.51 |
| | Wet | 0.646 | 0.494 | AH(+) | D,VD | 0.175 | 1.53 |
| **Smallstock** (*Capra hircus* and *Ovis aries*) | Dry | 0.340 | 0.501 | AH(+) | AH,CC,D(-) | 0.011 | 2.89 |
| | Wet | 0.280 | 0.483 | — | AH,CC,D(-),VD | 0.003 | 3.36 |

**Appendix S2.** Model selection procedure for factors influencing black-backed jackal (*Lupulella mesomelas*) site detectability (p) and relative abundance (λ) in the dry season. Covariates considered are canopy cover (CC), average habitat visibility (AH), proximity feature (PF), scrub hare intensity of use (H), ungulate intensity of use (U), smallstock intensity of use (SS), village density (VD), longitude (L), and African wild dog den proximity (AWD). The number of parameters in the model (k); AICc values; the relative difference in AICc values between each model and the model with the lowest AICc (ΔAIC); AICc model weights (w). (.) assumes the parameter is constant.

| Model | k | AICc | ΔAICc | w |
|---|---|---|---|---|
| **Detection models** | | | | |
| λ(.)p(AH) | 3 | 379.83 | 0.00 | 0.21 |
| λ(.)p(.) | 2 | 380.03 | 0.20 | 0.19 |
| λ(.)p(AH,CC) | 4 | 380.23 | 0.4 | 0.17 |
| λ(.)p(CC) | 3 | 380.49 | 0.66 | 0.15 |
| λ(.)p(PF) | 3 | 381.62 | 1.79 | 0.08 |
| λ(.)p(AH,PF) | 4 | 381.80 | 1.98 | 0.08 |
| λ(.)p(CC,PF) | 4 | 381.97 | 2.15 | 0.07 |
| λ(.)p(AH,CC,PF) | 5 | 382.18 | 2.36 | 0.06 |
| **Relative abundance models** | | | | |
| λ(AWD,SS,VD)p(.) | 5 | 374.30 | 0.00 | 0.24 |
| λ(AWD,SS)p(.) | 4 | 375.59 | 1.29 | 0.13 |
| λ(AH,CC,AWD,L,SS,VD)p(.) | 10 | 375.86 | 1.56 | 0.11 |
| λ(AH,CC,L,SS,VD)p(.) | 9 | 376.04 | 1.74 | 0.10 |
| λ(AWD,L,SS)p(.) | 5 | 377.27 | 2.96 | 0.05 |
| λ(SS,VD)p(.) | 4 | 377.42 | 3.11 | 0.05 |
| λ(AWD,VD)p(.) | 4 | 377.44 | 3.13 | 0.05 |
| λ(AH,CC,AWD,L,VD)p(.) | 9 | 377.59 | 3.28 | 0.05 |
| λ(AH,CC,VD)p(.) | 7 | 377.64 | 3.34 | 0.05 |
| λ(AWD)p(.) | 3 | 377.90 | 3.59 | 0.04 |
| λ(VD)p(.) | 3 | 378.98 | 4.68 | 0.02 |
| λ(CC)p(.) | 4 | 379.26 | 4.95 | 0.02 |
| λ(SS)p(.) | 3 | 379.29 | 4.98 | 0.02 |
| λ(AWD,L)p(.) | 4 | 379.59 | 5.29 | 0.02 |
| λ(.)p(.) | 2 | 380.03 | 5.72 | 0.01 |
| λ(L,VD)p(.) | 4 | 380.04 | 5.74 | 0.01 |
| λ(AH,CC,SS)p(.) | 7 | 380.82 | 6.51 | 0.01 |
| λ(AH)p(.) | 4 | 380.89 | 6.58 | 0.01 |
| λ(AH,CC,L)p(.) | 7 | 381.15 | 6.85 | 0.01 |
| λ(L)p(.) | 3 | 381.37 | 7.06 | 0.01 |

**Appendix S3.** Model selection procedure for factors influencing black-backed jackal (*Lupulella mesomelas*) site detectability (p) and relative abundance (λ) in the wet season. Covariates considered are canopy cover (CC), average habitat visibility (AH), proximity feature (PF), scrub hare intensity of use (H), ungulate intensity of use (U), smallstock intensity of use (SS), village density (VD), and African wild dog den proximity (AWD). The number of parameters in the model (k); AICc values; the relative difference in AICc values between each model and the model with the lowest AICc (ΔAIC); AICc model weights (w). (.) assumes the parameter is constant.

| Model | k | AICc | ΔAICc | w |
|---|---|---|---|---|
| **Detection models** | | | | |
| λ(.)p(AH) | 3 | 393.24 | 0.00 | 0.38 |
| λ(.)p(AH,PF) | 4 | 394.62 | 1.38 | 0.19 |
| λ(.)p(AH,CC) | 4 | 395.21 | 1.97 | 0.14 |
| λ(.)p(.) | 2 | 396.49 | 3.24 | 0.08 |
| λ(.)p(PF) | 3 | 396.50 | 3.26 | 0.08 |
| λ(.)p(AH,CC,PF) | 5 | 396.55 | 3.31 | 0.07 |
| λ(.)p(CC,PF) | 4 | 398.31 | 5.07 | 0.03 |
| λ(.)p(CC) | 3 | 398.40 | 5.16 | 0.03 |
| **Relative abundance models** | | | | |
| λ(U)p(AH) | 4 | 391.15 | 0.00 | 0.30 |
| λ(H)p(AH) | 4 | 392.88 | 1.73 | 0.13 |
| λ(.)p(AH) | 3 | 393.24 | 2.10 | 0.11 |
| λ(U,H,VD)p(AH) | 6 | 393.79 | 2.64 | 0.08 |
| λ(U,H,AWD)p(AH) | 6 | 393.89 | 2.74 | 0.08 |
| λ(U,H,SS)p(AH) | 6 | 394.56 | 3.41 | 0.05 |
| λ(AWD)p(AH) | 4 | 395.07 | 3.92 | 0.04 |
| λ(VD)p(AH) | 4 | 395.14 | 4.00 | 0.04 |
| λ(SS)p(AH) | 4 | 395.15 | 4.01 | 0.04 |
| λ(H,SS,U,VD,AWD)p(AH) | 8 | 396.65 | 5.50 | 0.02 |
| λ(AH,H,U)p(AH) | 7 | 396.66 | 5.51 | 0.02 |
| λ(SS,AWD)p(AH) | 5 | 397.01 | 5.86 | 0.02 |
| λ(VD,AWD)p(AH) | 5 | 397.01 | 5.87 | 0.02 |
| λ(SS,VD)p(AH) | 5 | 397.04 | 5.89 | 0.02 |
| λ(AH)p(AH) | 5 | 397.17 | 6.02 | 0.01 |
| λ(AH,H,SS,U,VD)p(AH) | 9 | 398.79 | 7.65 | 0.01 |
| λ(AH,AWD)p(AH) | 6 | 399.01 | 7.87 | 0.01 |
| λ(AH,VD)p(AH) | 6 | 399.07 | 7.93 | 0.01 |
| λ(AH,SS)p(AH) | 6 | 399.10 | 7.96 | 0.01 |
| λ(AH,H,SS,U,AWD)p(AH) | 9 | 399.23 | 8.08 | 0.01 |
| λ(AH,H,SS,U,VD,AWD)p(AH) | 10 | 400.03 | 8.88 | 0.00 |

# Chapter 3: Diet of black-backed jackal (*Lupulella mesomelas*) and diet facilitation by African wild dog (*Lycaon pictus*) in the Okakarara District Communal Area, Namibia

**3.1 Abstract**

Many widespread mesocarnivores have extremely flexible diets which allow them to thrive in a wide variety of habitat types. In many parts of their range, canid mesocarnivores are perceived as responsible for the majority of smallstock depredation. I collected suspected black-backed jackal (*Lupulella mesomelas*) scat both opportunistically and systematically between 2019-2022 in the Okakarara District Communal Area (ODCA) of northeastern Namibia and confirmed the species genetically before analysing black-backed jackal diet. By frequency of occurrence, small mammals and insects of the Coleoptera order were most consumed (9.80% and 9.39%). By biomass, ungulate species contributed the most to black-backed jackal diet (74.36% by biomass), especially greater kudu (*Tragelaphus strepsiceros*; 19.83% by biomass), which was also highly preferred (D=0.93). Livestock contributed 29.74% of the total biomass of black-backed jackal diet. Niche breadth of black-backed jackal was similar between areas within vs. more than 10km from African wild dog (*Lycaon pictus*) dens and diet overlap was very high between these two regions (α=0.97). There was no significant difference in frequency of occurrence of large mammals in the scat of black-backed jackal within vs. more than 10km from African wild dog dens. This suggests that African wild dog may neither facilitate nor compete with black-backed jackal in the ODCA.

**3.2 Introduction**

The presence of a large carnivore can influence a mesocarnivore's diet through facilitation or competition. Facilitation allows mesocarnivores to scavenge on prey obtained by larger carnivores, while inter-specific competition can prevent access to food resources (Codron *et al.*, 2018). Because of this dichotomous interaction, it is difficult to predict how a mesocarnivore's diet will be impacted by an apex predator in a given system. In North America, grey wolves (*Canis lupus*) are the dominant canid over coyotes (*Canis latrans*), limit the growth of the coyote population, and frequently kill coyotes (Berger and Gese, 2007; Merkle, Stahler and Smith, 2009). However, grey wolves also act as facilitators to coyotes by providing scavenging opportunities (Wilmers *et al.*, 2003). In Europe, grey wolves and golden jackals (*Canis aureus*) have a primarily competitive relationship, with wolves driving golden jackals away from their kills and even killing them (Giannatos *et al.*, 2005; Mohammadi, Kaboli and López-Bao, 2017).

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Africa supports the richest assemblage of large predators in the world, which compete with each other and with abundant mesocarnivores through both interference and exploitative competition (Hayward and Kerley, 2008). Interference is direct conflict such as black-backed jackals (*Lupulella mesomelas*) being killed by African wild dogs (*Lycaon pictus*; Kamler *et al.*, 2007), while exploitation is indirect competition as a result of shared resources (Hayward and Kerley, 2008). The density of dominant predators such as lion (*Panthera leo*) is typically correlated with prey density (Vinks *et al.*, 2021), while the density of subordinate large predators such as African wild dog typically declines with an increase in the density of the dominant predator (Creel and Creel, 1996; Groom, Lannas and Jackson, 2017). There is uncertainty on if the presence of large carnivores is beneficial or detrimental to mesocarnivores such as black-backed jackal and brown hyaena (*Parahyaena brunnea*; Kamler *et al.*, 2020). Black-backed jackal frequently come in conflict with large carnivores and have reportedly been killed or consumed by lions (Stander, 1992), spotted hyaenas (*Crocuta crocuta*; van Lawick and van Lawick-Goodall, 1970) brown hyaenas (Mills, 1982), leopards (*Panthera pardus*; Kamler *et al.*, 2020), cheetahs (*Acinonyx jubatus;* Hayward *et al.*, 2006), and African wild dogs (Kamler *et al.*, 2007). However, large carnivores may provide mesocarnivores with access to scavenge on large ungulate prey they would otherwise not have access to (Codron *et al.*, 2018). For example, the presence of lion has been found to increase diet niche breadth of black-backed jackal (Codron *et al.*, 2018) and the presence of lion and African wild dog has been found to increase the diet niche breadth of brown hyaena (Yarnell *et al.*, 2013). However, other studies did not find any impact of large carnivore presence on black-backed jackal diet (Brassine and Parker, 2012; Yarnell *et al.*, 2013). It is likely that different large carnivore species at different densities may have differing effects on mesocarnivore diet (Kamler *et al.*, 2020).

The majority of carnivore species are in decline worldwide, primarily due to human-wildlife conflict (Ripple *et al.*, 2014). Most of this conflict stems from livestock depredation (Chinchilla *et al.*, 2022), which threatens farmers' livelihoods (Ogada *et al.*, 2003; Khanal, Mishra and Ramesh Suryawanshi, 2020) and puts carnivores at increased risk for persecution and lethal predator control (Ogada *et al.*, 2003; Rust and Marker, 2013). In Namibia, where the majority of the population depends on agriculture as the main source of income, livestock depredation is a severe problem (Forslund, 2007; Shilongo, Sam and Simuela, 2018). Conflict is particularly challenging on communal farmlands, where farmers are less able to tolerate the economic losses of livestock depredation in comparison to freehold farmers (Rust and Marker, 2013; Shilongo, Sam and Simuela, 2018). Black-backed jackal is

reported responsible for the majority of smallstock (sheep and goat) losses in Namibia (Rust and Marker, 2013; Verschueren *et al.*, 2020).

Black-backed jackal are a mesocarnivore which occur across the African continent and are adaptable to a wide range of habitat types (Hoffmann, 2014). In Namibia they are found on pastoral farmlands (Verschueren *et al.*, 2020), the Namib Desert (Goldenberg *et al.*, 2010), and coastal Namibia (Avery *et al.*, 1987; Kolar, 2005). In the Okakarara District Communal Area (ODCA) of northeastern Namibia, they are perceived by livestock owners to be responsible for 73% of smallstock losses (Verschueren *et al.*, 2020). As opportunistic predators, black-backed jackal may rely on livestock as a food source in areas where wild ungulates are scarce, as has been observed in many carnivore species (Rasmussen, 1999; Woodroffe *et al.*, 2005; Gusset *et al.*, 2009; Valeix *et al.*, 2012).

I focused on a population of black-backed jackal in the ODCA to understand the diet of this mesocarnivore on land used for raising livestock and diet interactions with a dominant competitor, the African wild dog. I hypothesized that black-backed jackal diet niche breadth would expand with African wild dog presence due to increased scavenging opportunities from African wild dog kills (Codron *et al.*, 2018). I also hypothesized that black-backed jackal would have a diverse omnivorous diet with smallstock as a significant contributor, as has been reported from similar land use types (Kamler, Klare and Macdonald, 2012) and is consistent with farmer perception of high smallstock depredation from the area (Verschueren *et al.*, 2020). However, I hypothesized that black-backed jackal would exhibit a preference for wild ungulates <30kg over smallstock prey (Kamler, Klare and Macdonald, 2012; Hayward *et al.*, 2017).

### 3.3 Methods

### 3.3.1 Study area

This study was conducted in northeastern Namibia on communal farmland designated as a conservancy. The area was located in the Okakarara District Communal Area (ODCA), which covers a total of 18,951 $km^2$. Scat was collected from within a 6,720 $km^2$ area that was gridded for a camera trap survey on wildlife distribution (Figure 3.1). For a full description of the study area, see Chapter 2 Section 2.3.1.
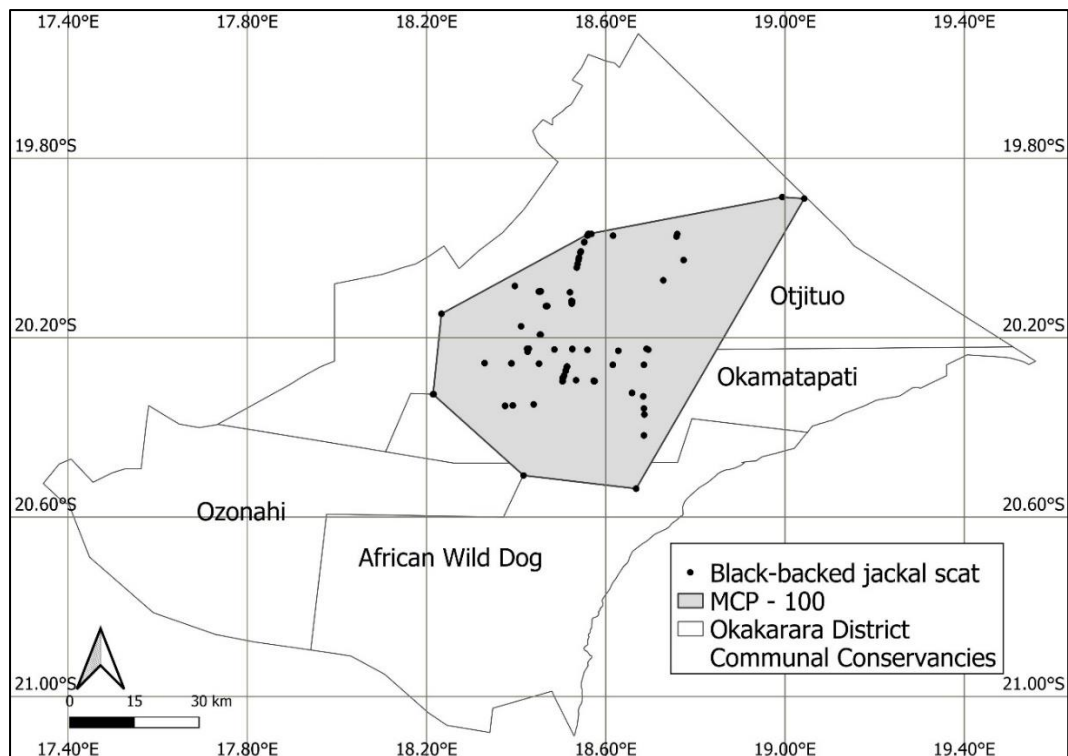
**Figure 3.1.** Locations of black-backed jackal (*Lupulella mesomelas*) scat (n=101) in the Okakarara District Communal Area (ODCA). Calculated minimum convex polygon containing 100% of scat locations is shown.

### 3.3.2 Data collection

Black-backed jackal scats were collected from June 2019-Sep 2022. Scats were collected opportunistically during human-wildlife conflict (HWC) work in the ODCA. Systematic surveys were also completed in which scats were collected on road transects. Cheetah Conservation Fund's (CCF) scat detection dog team completed a survey of the study area in 2022 which covered road transects and area searches around waterpoints. In the field, scat was attributed to black-backed jackal morphologically by size, shape, and location. Black-backed jackal are known to defecate on elevated conspicuous objects such as tufts of grass or large rocks (Kamler, Klare and Macdonald, 2020). Scats were collected in a small plastic or paper bag for storage using an object from the surrounding environment (i.e., stick) to avoid contamination of the sample. Only half of each scat was collected, as carnivores use scat for territorial marking (Jansen *et al.*, 2019). Scat samples were labelled with date, species field ID, location description, and GPS coordinates. Samples were frozen at -20°C for storage immediately after field teams returned to the research centre at CCF, Namibia.

As described in Chapter 2 Section 2.3.3, African wild dog dens have been identified in 2017-2022 through CCF's ongoing human-wildlife conflict work in the ODCA.

### 3.3.3 Laboratory analysis

### 3.3.3.1 DNA extraction and amplification

To confirm field identification of scat as black-backed jackal, DNA was extracted from scat samples at CCF's genetics laboratory using the QIAamp® Fast DNA Stool Mini Kit (QIAGEN) following manufacturer's protocol, with the following modifications: initial volume was reduced to 0.10g, and final elution to recover the isolated DNA was reduced from 200ul to 100ul to increase the concentration of the obtained DNA (Appendix S4). A scalpel blade was used to scrape off the outer surface of the sample, which contains epithelial cells from the gastrointestinal tract of the carnivore. For the first extraction of a sample, 0.10g of scat was used. If samples did not perform successfully, subsequent second, and if necessary third extractions were performed using double (0.20g) and half (0.05g) the amount of scat, respectively. After pelleting the dirt from the samples through centrifugation, the DNA was separated from the supernatant by filtration through a filter column and eluted after purification.

Two primers, ATP6-DF3 and ATP6-DR1, were utilized in PCR reactions to amplify the ATP6 gene (Appendix S5). The ATP6 coding region of mitochondrial DNA (mtDNA) is known to differ between different species and its sequencing allowed for species identification of scat (Kim and Kim, 2006). The PCR touch down cycling process starts with the initial denaturation, which activates the thermosensitive DNA polymerase and separates the DNA strands, at 90˚C for 10 minutes. The denaturation is followed by 40 cycles of exponential amplification, which starts with 10 cycles of denaturation at 94˚C for 10 seconds, annealing of primers at 60-51˚C for 30 seconds, lowering the temperature with 1˚C per each cycle (known as touch down), and elongation at 72˚C for 45 seconds. This is followed by 30 cycles of denaturation at 94˚C for 15 second, annealing at 50˚C for 30 seconds, and elongation at 72˚C for 45 seconds. PCR 1 used 1.5µl of DNA. PCR 2 used 3.0µl of DNA and was done for all samples which did not show bands after gel electrophoresis following PCR 1 (Appendix S6). When a sample did not show a band in either PCR 1 or PCR 2, the sample was subjected to a second, and if necessary third extraction.

The DNA molecules contained in the PCR products were separated according to size using a 1% agarose gel electrophoresis. Each well contained 10µl PCR product, 2µl heavy loading dye (to make the PCR products denser than the buffer, allowing them to settle at the bottom of the wells), and 2µl DNA stain (which binds to the DNA and is visible under UV light). The gel was run for 45 minutes at 75 V. Amplicons were visualized on a Kodak Digital Science™ Image Station 440CF (IS440CF) system.

Samples that showed bands in gel electrophoresis were included in an enzymatic purification step to eliminate non-integrated primers, which would interfere with sequencing results. To each sample tube was added 2µl of ExoSAP-IT reagent (Applied Biosystems). ExoSAP-it reagent contains 0.1µl Exo, 0.2µl Sap, and 1.7µl $H_2O$ (Appendix S7). Exonuclease was activated by incubating the mix in a thermocycler at 37°C for 45 minutes. After treatment, the ExoSAP-IT reagent was inactivated by heating the mix to 80°C for 15 minutes.

### 3.3.3.2 Sequencing reaction

Following the ExoSAP-IT step, cleaned samples were set up for the sequencing reaction with the ATP6-DR1 primer (Appendix S8).

Sequence reactions were cleaned up using ethanol precipitation to remove non-integrated dyes and primers (Appendix S9). This was done by the addition of 10µl of sequencing product to 2µl of EDTA and 10µl of water (master mix I). To the same 1.5ml tube, 2µl of NaOAc and 50µl 95% ethanol was added (master mix II). The mixture was incubated for 15 minutes at room temperature. The mixture was then centrifuged for 20 minutes at 600 rpm using a 36.5 mm diameter centrifuge and then the supernatant was decanted from the pellets. The pellets were washed two times with 250µl of 70% ethanol and centrifuged at 600 rpm for 10 minutes. Following the last decantation, the pellets were air dried at room temperature.

### 3.3.3.3 Denaturation and electrophoresis

Following ethanol precipitation, the DNA pellets were resuspended in 13ul of formamide and loaded in a 96-well PCR plate for genetic analysis on a 3130 ABI Genetic Analyser or 3500 ABI Genetic Analyser. Before loading in the analyser, the samples were denatured at 95°C for 4 minutes to obtain single stranded DNA. The genetic analyser performs capillary electrophoresis, which separates DNA fragments by size. The fluorescent dye characterizing each DNA fragment (and corresponding to the last integrated nucleotide) is detected by the laser of the analyser, and the electropherogram of colourful peaks representing the nucleotide sequence is transferred to the computer.

### 3.3.3.4 Electropherogram clean-up and sequence alignment

Obtained sequences were analysed with the ABI software Sequence Analysis Software v6.0 (SeqA 6) for base calling and quality control. Sequences were then imported into Geneious Prime 2020.2.3. The calling of bases was verified visually and bases that were not called correctly were corrected. In addition, missing bases were assigned to chromatogram peaks as needed.

Sequence alignment allows for the comparison of nucleotide bases between sequences. Global multiple alignments with free end gaps alignment was performed with Geneious Prime with a cost

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matrix of 65% similarity (5.0/-4.0) for the sample sequences and reference sequences of all Namibian carnivores. The obtained alignment was used to assign samples to species.

### 3.3.4 Data analysis

### 3.3.4.1 Food item categorization and cuticular hair imprint identification

Following genetic confirmation of species, the samples were removed from the lab and prepared for diet analysis. Samples were sterilized in aluminium trays in a Sturdy SA-232X manual autoclave for 30 minutes at 134 °C. After autoclaving, samples were placed inside 36 DEN nylon stockings and carefully washed to remove all organic material, leaving only undigestible material (Marker *et al.*, 2003; Klare *et al.*, 2010). Samples were air dried and 10ml of scat were measured from each sample in a graduated centrifuge tube to standardize the analysed volume.

The indigestible scat remains were spread out in a transparent square dish. Using tweezers and a dissecting microscope, food items were grouped into categories. Categories included mammal material (hair, bone, hoof, etc.), bird (feathers or eggs), reptile (reptile scales), berries or fruit, miscellaneous vegetation, and insects which were categorized to the taxonomic rank of Order.  A grid of 0.75 X 0.75cm was placed below the dish to estimate the proportion of each food category relative to the total sample. Excluding non-dietary items such as sand, this allowed estimation of proportion of food items per standardized sample volume (Schwab *et al.*, 2011; Cristescu, Stenhouse and Boyce, 2015).

From each sample, 20 hairs were selected randomly (Davies-Mostert *et al.*, 2010; Ramnanan, Swanepoel and Somers, 2013). Hairs were placed on a plastic cover slide between two glass slides and heated at 100°C for 5 minutes in an oven. This left a cuticular imprint of the hair on the plastic cover slide which could be viewed microscopically (Marker *et al.*, 2003). Hairs that were completely fragmented were replaced, since it is very difficult to distinguish some species without the tip or follicle of the hair present. Hairs that were completely intact or contained at least the tip or follicle were included for analysis.

After being trained by an CCF staff member who is experienced in diet analysis, I read all whole hair cuticular imprints on an Omax M82E Series 40X-2000X microscope. Reference materials used to identify the cuticular imprints included CCF's hair reference library and the photographic references published by Keogh (1983, 1985). To ensure reading accuracy, a blind test of 100 hairs was administered using reference hair samples from all potential prey species found in the ODCA (Davies-Mostert *et al.*, 2010). All hairs included in the test contained at least the distal (tip) or

proximal (follicle) end of the hair, which mimicked the conditions of the study. Hairs were identified correctly 95% of the time in this blind test.

### 3.3.4.2 Frequency of occurrence and corrected frequency of occurrence

Microscopic hair scale identification results of black-backed jackal scat were converted to frequency of occurrence per scat (OccST), frequency of occurrence per food item (OccIT), and corrected frequency of occurrence (CFO). OccST was the percentage of scats containing a particular food item. OccIT was expressed as a percentage and was the occurrences of a particular food item relative to the total number of occurrences (Breuer, 2005; Kamler, Klare and Macdonald, 2012). Using frequency of occurrence calculations alone can overestimate small food items such as invertebrates, as they weigh the presence of small and large food items in the scats equally (Weaver 1993, as cited in Kamler, Klare, and MacDonald 2011). To address this, CFO was calculated in which each scat has a total weighting of 1. Food items have a decreasing weight when more than one food item is present in a sample. For example, in a scat that contains two food items, each would receive a weighting of 0.5. This weighted number of occurrences is expressed as a percentage of the total number of scats (Klare *et al.*, 2011; Jansen *et al.*, 2019).

### 3.3.4.3 Biomass calculation

Klare *et al.* (2011) recommend calculating the percentage biomass of food items in order for diet study results to be ecologically relevant, as biomass calculation models (BCM) are likely to provide the closest estimation to true diet. BCM incorporate correction factors from linear regression based on feeding trials. While frequency calculations include rare food items which may diminish in importance when BCM are applied, BCM better represent the true importance of a food item in a predator's diet (Jansen *et al.*, 2019).

Weights of prey species were taken from southern African mammal guides by Stuart and Stuart (2015) and Skinner and Chimimba (2005). I used Goszczyński's correction factors developed for red fox (*Vulpes vulpes*) (1974) supplemented by additional correction factors compiled by Jedrzejewska and Jedrzejewski (1998). Goszczyński's model is frequently used for black-backed jackal diet studies rather than correction factors obtained from side-striped jackal (Loveridge and Macdonald, 2003), which did not account for food items larger than a hare (Goldenberg *et al.*, 2010; Klare *et al.*, 2010; Kamler *et al.*, 2012; Van de Ven *et al.*, 2013; Jansen, 2016). In this study area, where black-backed jackal is reported to frequently predate on livestock (Verschueren *et al.*, 2020), it was important to consider larger ungulates. Red fox have a relatively similar body mass to black-backed jackal and a comparable prey range (Klare *et al.* 2010).

Goszczynski's model uses correction factors to convert the share of the different prey species as found in the scats into their share of the biomass ingested. OccST was multiplied by the correction factor (kg/scat) for food item to calculate the biomass consumed of each food item. The biomass consumed of each prey species was divided by the total biomass consumed to express relative biomass contribution of each prey species as a percentage (Jansen, 2016).

**3.3.4.4 Prey abundance and prey preference of black-backed jackal**

Prey intensity of use was modelled using data from a camera trap survey conducted in the dry season (May-October) of 2018 in the study area. I used R packages *unmarked* and *AICcmodavg* to estimate intensity of use instead of true occupancy, because the home ranges of prey species were smaller than the size of grid cells sampled, which were 8km X 8km. I modelled intensity of use for mammalian prey species which were detected at >10% of the camera trap sites and were within the prey range of black-backed jackal. I was not able to estimate intensity of use for small mammal species because they were not detected reliably in the camera trap survey. I was not able to model intensity of use for greater kudu (*Tragelaphus strepsiceros*) and warthog (*Phacochoerus africanus*) due to their low number of detections in the camera trap survey.

As an alternative measure of abundance for greater kudu and warthog, the relative abundance index (RAI) of the mammal species was also calculated by multiplying the useable camera trap captures by 100 and dividing by the camera trap nights (Jenks *et al.*, 2011). This also allowed exploration of how using two different metrics of relative abundance may impact the index of preference.

I calculated prey preference of black-backed jackal using Jacobs' index, which provides a measure of preference defined as consuming a prey species more than expected given the prey's relative abundance (Jacobs, 1974). Jacobs' index uses the following equation:

$$D = r_i - p_i/(r_i + p_i - 2r_ip_i)$$

where $r_i$ is the proportion of all scats containing species *i* extracted from the results of the biomass models, and $p_i$ is the relative abundance of species *i* as determined by the camera trap-based intensity of use or RAI values. The resulting values range from 1 (complete preference) to -1 (complete avoidance), with values -0.2<$D$<0.2 indicating that prey was used according to its availability (Jacobs, 1974).

**3.3.4.5 Diet breadth and overlap of black-backed jackal with African wild dog dens**

To explore how black-backed jackal diet may be influenced by presence of African wild dog, I created 10km buffers around previously identified African wild dog dens to represent their restricted home ranges during the denning season (Darnell *et al.*, 2014; Pomilia, Mcnutt and Jordan, 2015). I compared black-backed jackal diet from scats that were collected within the region of these 10km buffers and those that were collected more than 10km from an African wild dog den. To make this comparison, I applied Levins' index of niche breadth:

$$B \; = \; 1/(\sum p_i{}^2)$$

where *B* is the dietary diversity of predator *p* and $p_i$ is the relative frequency of the ingested food item *i* in the diet of predator *p* (Levins, 1968). Levins' index of niche breadth varies from 0-*n*, where *n* is the number of prey categories in the diet. I also applied Levins' standardized index of niche breadth, which standardizes the index value to 0-1 using the following equation:

$$B_a = (B - 1)/(n - 1)$$

where $B_a$ is the standardized niche breadth, *B* is the degree of niche breadth, and *n* is the number of prey categories (Levins, 1968). Lower values indicate a specialist carnivore diet, and higher values indicate a generalist carnivore diet.

The dietary overlap between scats collected within and more than 10km from an African wild dog den was calculated as:

$$\alpha = \sum p_i q_i \sqrt{\sum p_i{}^2 \sum q_i{}^2}$$

where α is the dietary overlap of the 2 species, $p_i$ is the relative frequency of food item *i* in the diet of predator *p* and $q_i$ is the relative frequency of food item *i* in the diet of predator *q* (Pianka, 1973, 1975).

A nonparametric Kruskal–Wallis test by ranks was performed to determine differences between frequency of occurrence of large mammal (greater kudu and warthog) in scats within vs. outside of 10km from an African wild dog den.

**3.4 Results**

**3.4.1 General black-backed jackal diet**

Overall, 101 genetically confirmed black-backed jackal scat samples were collected in a period from June 2019-Sep 2022. Of all scats field identified as black-backed jackal, 90.77% were genetically confirmed to be black-backed jackal. However, 35.64% of the genetically confirmed black-backed jackal scats were identified as another carnivore in the field, indicating low field identification accuracy for other carnivore species. Six of the 101 jackal samples were collected opportunistically by CCF's HWC team in 2019. Twenty-two samples were collected during surveys by CCF's scat detection dog team in 2020 (n=9) and 2022 (n=13). In 2021, 73 scat samples were collected by CCF's ecology team (n=63) and veterinary team (n=10).

Mammal items occurred in 83.17% of black-backed jackal scats. Berries occurred in 58.42% of samples. The berries were from the *Grewia flava* bush which produces spherical berries also called velvet raisins. Other vegetation occurred in 92.08% of samples. Coleoptera (beetles) occurred in 40.59% of samples (Table 3.1).

Mammal hair averaged the largest proportion of the sample volume (46.65%), followed by berries (33.79%). While present in 40.59% of samples, Coleoptera on average made up just 2.00% of sample volume. Other insects as well as birds and lizards occurred at percentages of <1% sample proportion (Table 3.1).

**Table 3.1.** Food item occurrence and proportion of volume per sample for black-backed jackal (*Lupulella mesomelas*) scat collected in the Okakarara District Communal Area (ODCA).

| | Occurrence in samples (%) (n=101) | Mean proportion of volume in sample (%) |
|---|---|---|
| **Vertebrates** | | |
| Mammal | 83.17 | 48.52 |
| Birds | 7.92 | 0.54 |
| Lizards | 3.96 | 0.07 |
| **Invertebrates** | | |
| Coleoptera | 40.59 | 2.00 |
| Scorpions | 7.92 | 0.15 |
| Orthoptera | 6.93 | 0.11 |
| Hymenopterans | 4.95 | 0.04 |
| Odonata | 3.96 | 0.04 |
| Spirostreptida | 0.99 | 0.13 |
| Cicadae | 0.99 | 0.03 |
| **Vegetation** | | |
| Berries | 58.42 | 33.79 |
| Other vegetation | 92.08 | 18.36 |

From the 84 scat samples which contained mammal hair, 7 samples did not contain 20 hairs to read as per the methodology outlined in Section 3.3.4.1. For these samples, between 2-15 hairs were read, according to how many intact hairs could be found in each sample. Ten mammal species were identified from cuticular hair pattern analysis including a small mammal category which primarily included species from the rodent families Muridae and Cricetidae. By CFO, small mammals (9.80%) were the most frequently occurring food item, followed by greater kudu (5.14%) and goat (3.91%). The CFO of black-backed jackal hair was 7.26% (Table 3.2).

The total extrapolated biomass corresponding to all food items analysed from black-backed jackal scats was 11784.16kg (Appendix S10). The prey which made up the highest percentage of the total biomass consumed were greater kudu (19.83%), common duiker (*Sylvicapra grimmia*; 15.86%), sheep (*Ovis aries*; 11.90%), and goat (*Capra hircus*; 11.90%) (Table 3.3). Food items including vegetation and fruit/berries, lizards, and all insect orders contributed <1% to the total biomass

consumed before CFs were applied. After CFs were applied, however, these food items contributed between 0.04-6.94% of the total biomass consumed (Appendix S10).

**Table 3.2.** Food items recorded in black-backed jackal scat (*Lupulella mesomelas*) (n=101) collected in the Okakarara District Communal Area (ODCA). Frequency of occurrence per scat (OccST) (%) was calculated as the number of scat containing each food item divided by the total number of scats (n=101). Frequency of occurrence per food item (OccIT) (%) was calculated as the number of occurrences of each food item divided by the total number of occurrences (n=379). Corrected frequency of occurrence (CFO) (%) was calculated as the weighted number of occurrences of each food item divided by the total number of scats collected (n=101).

| Food item | Number of occurrences (food items) | OccST (%) (n=101) | OccIT (%) (n=379) | Weighted number of occurrences | CFO (%) |
|---|---|---|---|---|---|
| **Large mammals (>40kg)** | | | | | |
| Greater kudu (*Tragelaphus strepsiceros*) | 20 | 19.80 | 5.28 | 5.19 | 5.14 |
| Common warthog (*Phacochoerus africanus*) | 2 | 1.98 | 0.53 | 0.48 | 0.47 |
| **Medium to large mammals (10-40kg)** | | | | | |
| Common duiker (*Sylvicapra grimmia*) | 16 | 15.84 | 4.22 | 3.92 | 3.88 |
| Steenbok (*Raphicerus campestris*) | 7 | 6.93 | 1.85 | 1.91 | 1.89 |
| **Medium mammals (1-10kg)** | | | | | |
| Scrub hare (*Lepus saxatilis*) | 4 | 3.96 | 1.06 | 0.99 | 0.98 |
| **Small mammals (<1kg)** | 39 | 38.61 | 10.29 | 9.90 | 9.80 |
| **Livestock** | | | | | |
| Goat (*Capra hircus*) | 12 | 11.88 | 3.17 | 3.95 | 3.91 |
| Sheep (*Ovis aries*) | 12 | 11.88 | 3.17 | 3.22 | 3.19 |
| Cattle (*Bos taurus*) | 6 | 5.94 | 1.58 | 1.76 | 1.74 |
| **Birds** | 10 | 9.90 | 2.64 | 1.28 | 1.27 |
| **Lizards** | 4 | 3.96 | 1.06 | 0.69 | 0.69 |
| **Invertebrates** | | | | | |
| Coleoptera (beetle) | 41 | 40.59 | 10.82 | 9.48 | 9.39 |
| Scorpiones (scorpion) | 8 | 7.92 | 2.11 | 1.74 | 1.73 |
| Orthoptera (locust) | 7 | 6.93 | 1.85 | 1.49 | 1.47 |
| Hymenopterans (ant) | 5 | 4.95 | 1.32 | 0.94 | 0.93 |

| | | | | | |
|---|---|---|---|---|---|
| Odonata (dragon fly) | 4 | 3.96 | 1.06 | 0.79 | 0.79 |
| Cicadae (cicada) | 1 | 0.99 | 0.26 | 0.10 | 0.10 |
| Spirostreptida (millipede) | 1 | 0.99 | 0.26 | 0.10 | 0.10 |
| **Vegetation** | | | | | |
| Berries | 59 | 58.42 | 15.57 | 17.22 | 17.05 |
| Other vegetation | 93 | 92.08 | 24.54 | 28.47 | 28.19 |
| **Self (allo-grooming or infanticide)** | | | | | |
| Black-backed jackal (*Lupulella mesomelas*) | 28 | 27.72 | 7.39 | 7.33 | 7.26 |

**Table 3.3.** Biomass consumed calculated from black-backed jackal (*Lupulella mesomelas*) scat (n=101) collected in the Okakarara District Communal Area (ODCA). Only food items that contributed >5% to the biomass consumed are indicated. For a full list of food items analysed from scats and their biomass contributions, see Appendix S10.

| Food item | Prey weight (kg)[a] | Correction factor (kg/scat)[b] | Number of occurrences (n=101) | OccST (%) | Total biomass consumed (kg)[c] | Relative biomass consumed (%) |
|---|---|---|---|---|---|---|
| **Greater kudu** (*Tragelaphus strepsiceros*) | 130 | 118 | 20 | 19.80 | 2336.63 | 19.83 |
| **Common duiker** (*Sylvicapra grimmia*) | 16 | 118 | 16 | 15.84 | 1869.31 | 15.86 |
| **Goat** (*Capra hircus*) | 50 | 118 | 12 | 11.88 | 1401.98 | 11.90 |
| **Sheep** (*Ovis aries*) | 40 | 118 | 12 | 11.88 | 1401.98 | 11.90 |
| **Small mammals** | 0.06 | 23 | 39 | 38.61 | 888.12 | 7.54 |
| **Steenbok** (*Raphicerus campestris*) | 11.1 | 118 | 7 | 6.93 | 817.82 | 6.94 |
| **Fruits/berries** | 0.002 | 14 | 59 | 58.42 | 817.82 | 6.94 |
| **Cattle** (*Bos taurus*) | 123 | 118 | 6 | 5.94 | 700.99 | 5.95 |

[a]From Stuart and Stuart (2015) and Skinner and Chimimba (2005)

[b]From Goszczyński (1974) and Jedrzejewska and Jedrzejewski (1998)

[c]Correction factor x OccST (%)

### 3.4.2 Prey preference of black-backed jackal

Jacobs' index calculated using prey intensity of use indicated strong avoidance of common duiker, steenbok, cattle, scrub hare, and slight avoidance of smallstock. Using RAI, cattle and scrub hare were still strongly avoided, but steenbok and common duiker were consumed consistent with their abundance ($-0.2 > D < 0.2$), and smallstock was preferred. Jacobs' index using RAI indicated strong preference for greater kudu and warthog (Figure 3.2, Appendix S11).
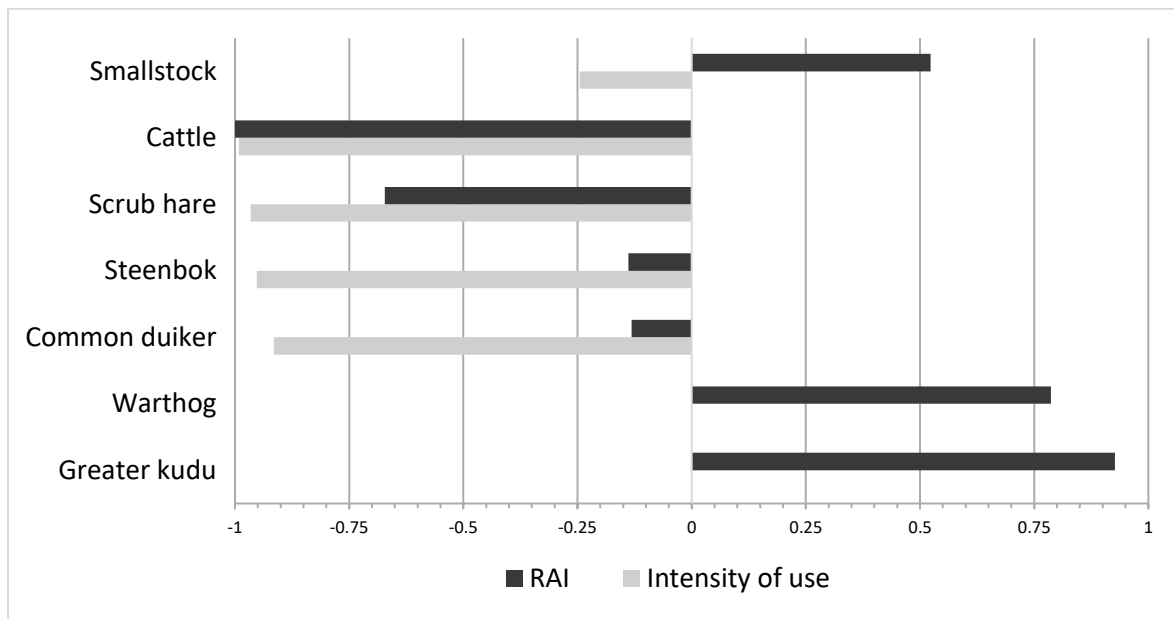


**Figure 3.2** Jacobs' index (Dvalue) showing preference and avoidance for ungulates and leporids by black-backed jackal (*Lupulella mesomelas*) in the Okakarara District Communal Area (ODCA).

### 3.4.3 Diet breadth and overlap of black-backed jackal in relation to African wild dog denning areas

Levins' niche breadth of black-backed jackal diet in regions within 10km of an African wild dog den was 7.05 ($B_a=0.605$). Niche breadth of black-backed jackal more than 10km from an African wild dog den was slightly lower (B= 6.44, $B_a=0.544$). Based on Pianka's dietary overlap index, the overlap between these two regions is 0.97 (Table 3.4).

**Table 3.4.** Dietary niche, standardized dietary niche, and dietary overlap of black-backed jackal (*Lupulella mesomelas*) samples within 10km of an African wild dog (*Lycaon pictus*) den vs. more than 10km from an African wild dog den.

| | Dietary niche (B) | Standardized dietary niche (B$_a$) | Dietary overlap (α) |
|---|---|---|---|
| Within 10km from AWD den | 7.05 | 0.605 | |
| | | | 0.97 |
| More than 10km from AWD den | 6.44 | 0.544 | |

A Kruskal-Wallis test revealed there was no significance in the frequency of occurrence of large mammals in black-backed jackal scat within vs. outside of 10km from African wild dog dens (H = 0.12231, 1 df, p=0.7265).

**3.5 Discussion**

Twenty food items were found in black-backed jackal scat from the ODCA in northeastern Namibia, ranging from large ungulate prey to insects and berries. This supports the conclusions of many other studies that black-backed jackals are generalist omnivores (Kaunda and Skinner, 2003; Loveridge and Macdonald, 2003; Klare *et al.*, 2010; Kamler, Klare and Macdonald, 2012; Van de Ven *et al.*, 2013). It's important to consider that this study's results represent black-backed jackal diet only in the dry season, as scat samples were collected between the months June-October. These months coincide with black-backed jackal pupping season (Moehlman, 1987), which is when their diet may be more likely to be dominated by animal food items due to the increased protein requirements of raising pups (Kaunda & Skinner, 2003).

By biomass, medium to large ungulates, including livestock, contribute the most to the black-backed jackal diet in the ODCA. Greater kudu and common duiker contribute the most biomass to the black-backed jackal diet. Common duiker is within the ungulate prey size range of 14-26kg reported to be the preferred prey by black-backed jackal (Hayward *et al.*, 2017) and are commonly occurring in the ODCA (Lines, 2008). Black-backed jackal have also been reported to consume large ungulates including eland, wildebeest, and greater kudu (Van de Ven, Tambling and Kerley, 2013; Hayward *et al.*, 2017). Black-backed jackal exhibit a preference for greater kudu and warthog, which exist in the study area in low abundance (Appendix S11). Cattle, which are abundant in the study area, are avoided as a food item by black-backed jackal, likely due to their large size. Duiker and steenbok may be consumed as expected or avoided and smallstock may be consumed as expected or preferred. Estimates of prey preference changed depending on which metric of prey proportional abundance

was used. The majority of carnivore diet studies use RAI to estimate prey abundance (Jansen, 2016; Henrici, 2018; Steenkamp, 2018; Shao *et al.*, 2021). However, RAI has been shown to be severely biased by ecological and sampling-related factors. For example, species with larger home ranges will be detected more frequently, inflating their RAI. Camera trap setup can bias RAI ratios, as certain species will be detected more often on cameras placed on roads, while others may be detected more often on off-road cameras. For these reasons, use of RAI as an estimation of density is not recommended (Sollmann *et al.,* 2013). Indeed, our results reveal that using a more robust technique for estimating prey abundance (i.e., intensity of use or occupancy) can result in significantly different values for index of prey preference. Our findings emphasize the importance of using alternative techniques to estimate prey abundance and help interpret diet results.

Smallstock species made up 23.8% of black-backed jackal diet by biomass in the ODCA. This is not surprising as farmers in the study area attributed 73% of smallstock losses to black-backed jackal (Verschueren *et al.*, 2020). Cattle also contributed over 5% of the total biomass. Unfortunately, with scat analysis there is no way to determine if prey was hunted and killed or scavenged. Prompt field identification of carcasses would be required to differentiate predation from scavenging (Cristescu *et al.*, 2022). Black-backed jackal have been recorded killing calves and even sick adult cattle (Humphries, Ramesh and Downs, 2016). However, in their questionnaire with communities, Verschueren *et al.* found that farmers in the ODCA attributed no cattle losses to black-backed jackal (2020), which points to the likelihood of scavenging. When depredating on livestock, black-backed jackal are most likely to prey on smallstock lambs and kids, and if they are killing cattle, it is likely they would kill young calves. Livestock breeding is largely uncontrolled in communal regions of Namibia with no structured breeding season (Hangara, 2011; Marius, Shipandeni and Togarepi, 2021). However, influenced by annual climatic variations, breeding often occurs at the beginning of the wet season and kidding and lambing at the end of the wet season or early dry season in the ODCA (CCF unpublished data). This indicates there was likely an abundance of smallstock lambs and kids in the dry season months when the scat samples were collected for this study. Because the CFs do not take age structure into account, the biomass contribution of livestock, as well as other ungulates such as kudu, may be overestimated. However, the data confirm that livestock are an important part of black-backed jackal diet in this prey-depleted region.

While they did not contribute as much biomass as the ungulates, small mammal species were the mammal item most frequently occurring in black-backed jackal scat. This finding reinforces outputs of black-backed jackal diet studies in South Africa which reported rodents as an important

component of black-backed jackal diet (Van der Merwe *et al.*, 2009; Brassine *et al.*, 2012; Humphries, Ramesh and Downs, 2016). Hayward *et al.*'s review (2017) concluded that small mammals may be unable to satisfy black-backed black-backed jackal's daily energy requirements, explaining why they typically prefer ungulate prey. Nonetheless, small mammals are likely a primary prey source for black-backed jackal in habitats where other prey are not available (Kok and Nel, 2004). This study's findings indicate that small mammals are an important part of black-backed jackal diet in the ODCA, but black-backed jackal rely on ungulate prey for the majority of the biomass they consume.

Birds and lizards were present in the diet of the black-backed jackal in the ODCA, but contributed <5% to the total biomass consumed. Many other diet studies also report low contribution of birds to black-backed jackal diet (Brassine *et al.*, 2012; Humphries, Ramesh and Downs, 2016; Jansen, 2016), although in coastal regions seabirds and penguins are important dietary components (Avery *et al.*, 1987; Kolar, 2005). Birds are difficult to catch, and black-backed jackals have a high catch failure rate, meaning hunting birds is often an inefficient use of time and energy (Kaunda and Skinner, 2003). Lizards are a supplemental and not a primary food source for black-backed jackal, as supported by previous diet studies of black-backed jackal in diverse locations and habitat (do Linh San *et al.*, 2009; Brassine *et al.*, 2012; Humphries, Ramesh and Downs, 2016; Jansen, 2016).

Invertebrates occurred frequently in the diet of black-backed jackal in the study area, especially Coleoptera species. However, all invertebrate orders combined contributed <5% to the biomass consumed. Previous studies have found that arthropods occur frequently in black-backed jackal diet where they are abundant in a study area (Kaunda and Skinner, 2003; Loveridge and Macdonald, 2003; Brassine and Parker, 2012; Van de Ven, Tambling and Kerley, 2013). However, as in this study, black-backed jackal need to supplement their diet with richer energy sources. For example, black-backed jackals consume primarily insects in the Namib Desert, but supplement with small mammals and scarcely occurring ungulates, which contribute the most biomass to their diet (Goldenberg *et al.*, 2010). Invertebrates are a frequent food item for black-backed jackals in the ODCA but not an important diet item in terms of biomass.

Berries were present in over half the scat samples and contributed significantly to the biomass of black-backed jackal diet in the ODCA. Black-backed jackal are omnivorous, preferring ungulate prey when it is available but able to exploit other resources when it is not (Hayward *et al.*, 2017). A number of studies report low biomass contribution of fruit (do Linh San *et al.*, 2009; Kamler, Klare

and Macdonald, 2012; Jansen, 2016), but other research found that fruits and berries can be an important food source, especially when other food items are scarce. For example, the !Nara fruits (*Acanthosicyos horridus*) contribute significantly to black-backed jackal diet in the Namib Desert (Goldenberg *et al.*, 2010). In this study, 16.8% of the scat samples analysed did not contain any mammal hair at all but consisted predominantly or completely of *Grewia flava* seeds. Klare *et al.* also found *Grewia flava* to be an important seasonal food source exploited by black-backed jackal in South Africa (2010). Nattress *et al.* described how black-backed jackal birth their pups between June and November, in large part due to the abundance of rodents and fruiting bushes (Moehlman, 1987; Nattrass *et al.*, 2017). The scat samples analysed for this research were collected between the months of June-October. During the dry season, fruits and berries, specifically *Grewia flava* berries, appear to be a key component of black-backed jackal diet in the ODCA.

Other miscellaneous vegetation occurred in nearly every sample and made up 18.36% proportion of the sample on average. Vegetation could be ingested for bulk and roughage purposes (Smithers, 1983), but since carnivore stomachs do not digest plant matter well, vegetation may be overestimated in scat samples (Jones, Archer, and Dickman, 2003; Brassine *et al.*, 2012). Although occurring frequently, vegetation contributed <5% to the total biomass consumed, indicating it is not a food source for black-backed jackals in the ODCA but may be ingested accidentally or for roughage purposes. The CFO of black-backed jackal hair was 7.26%, which is likely from allo grooming or infanticide (Moehlman, 1987).

The dietary niche breadth of black-backed jackal was similar between areas within 10km of African wild dog dens and areas more than 10km from dens. The dietary overlap between the two regions was near 1, indicating the diet is very similar in both regions. There was also no significant difference in the frequency of occurrence of large mammals in scat between the regions. This supports findings of studies in South Africa that black-backed jackal diet did not differ between regions where large predators were present or absent (Brassine and Parker, 2012; Yarnell *et al.*, 2013). These results suggest that either black-backed jackal predate on ungulates instead of relying on scavenging, or that ungulate carcasses are available for scavenging across the landscape irrespective of large predator presence. The black-backed jackal scats analysed for this study were collected in 2019-2022 during the dry season, which coincides with the denning season for the ODCA African wild dog population (CCF unpublished data). However, the dataset of African wild dog dens includes dens identified as active between 2017-2022. As there was not a large enough number of dens to

complete an annual analysis considering only confirmed active dens for each year, it is possible active and non-active dens were grouped together in the analysis, which may have biased results.

This diet study provides more context to the results of Chapter 2 which found higher black-backed jackal abundance in areas within 10km of African wild dog dens. Comparison of black-backed jackal diet revealed that it does not differ within and more than 10km from African wild dog dens. Black-backed jackal may occupy these areas for other reasons than dietary facilitation by African wild dog. Den site selection by African wild dogs is driven by risk avoidance (Jackson *et al.*, 2014), including avoidance of large predators (Davies-Mostert, Mills and Macdonald, 2013; Jackson *et al.*, 2014; Groom, Lannas and Jackson, 2017; Alting *et al.*, 2021), preference for dense vegetation (Davies-Mostert, Mills and Macdonald, 2013; Alting *et al.*, 2021), and rugged terrain (Davies-Mostert, Mills and Macdonald, 2013; O'Neill, Durant and Woodroffe, 2020; Alting *et al.*, 2021). Even where the risks of other predators are low, African wild dogs still select dens in highly concealed habitat (van der Meer *et al.*, 2014). They also avoid areas of high human density during denning season (O'Neill, Durant and Woodroffe, 2020).

Although black-backed jackal can thrive in human-dominated environments, they have also been shown to preferentially select habitat with high concealment to avoid hunting pressure and other conflict with human populations (Kaunda, 2001; Humphries, Ramesh and Downs, 2016). Black-backed jackal diet does not differ in areas within 10km of African wild dog dens, so they may be more abundant in these areas because, like African wild dogs, they are risk avoidant and seeking concealed habitat.

It is also possible that our use of 10km den buffers did not accurately reflect higher African wild dog presence. Perhaps, due to their large home ranges, African wild dogs impact black-backed jackal diet across the entire the study area, which is why there was no significant dietary differences within portions of the study area.

**3.6 Conclusion**

Black-backed jackals in the ODCA display an opportunistic omnivorous diet. The most frequently occurring food items in their diet were vegetation, berries of the *Grewia flava* bush, small mammals, and Coleoptera insects. When CFs were applied, mammal species contributed 74.36% of the biomass to the black-backed jackal diet, with greater kudu and common duiker contributing the highest amount of relative biomass. Livestock species made up 29.74% of black-backed jackal diet by biomass.

These findings underline black-backed jackal's high adaptability and ability to exploit a variety of food resources to survive. In an area that is predominantly depleted of large prey (Appendix S11), greater kudu, one of only two remaining large ungulates, has become a key component of their diet. Medium to large ungulate species such as common duiker and steenbok are also primary diet components. Black-backed jackal incorporate livestock into their diet, but it is not their primary food source. In comparison, some studies in South Africa have encountered black-backed jackal populations whose diet is specialized to livestock consumption (Kamler, Klare and Macdonald, 2012; Humphries, Ramesh and Downs, 2016).

Black-backed jackal is believed by farmers to be responsible for most smallstock loss in the ODCA (Verschueren *et al.*, 2020). This study confirms that a substantial proportion of black-backed jackal diet is livestock, but that by biomass they consume primarily wild ungulate prey and supplement with non-mammal food sources, especially *Grewia flava* berries. While livestock is a part of black-backed jackal diet, it is not the principal component. Communal farmers employ less predator prevention methods than freehold farmers, despite experiencing significant depredation (Rust and Marker, 2013). If improved livestock husbandry and depredation mitigation methods were employed, black-backed jackal may shift hunting efforts from livestock to wild ungulates or non-mammal food sources. They may not put in the effort to pursue livestock due to the availability of other food resources, which could reduce conflict with black-backed jackal.

This study found no evidence for dietary facilitation of black-backed jackal by African wild dog. I was not able to obtain a large enough sample size of African wild dog scat to statistically analyse diet. To further explore the dietary niches of both canids, additional African wild dog samples should be analysed to determine the dietary overlap of African wild dog and black-backed jackal. This can be challenging in areas such as the ODCA where African wild dogs are intensely persecuted and locating their scat is difficult.

### 3.7 References

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**3.8 Appendices**

**Appendix S4.** DNA extraction reagents and volume per sample.

| Reagent | Volume (µl) |
|---|---|
| Buffer InhibitEX | 1000 |
| Buffer AL | 600 |
| Proteinase K | 25 |
| Ethanol | 600 |
| Buffer AW1 | 500 |
| Buffer AW2 | 500 |
| ATE Buffer | 100 |

**Appendix S5.** ATP6 primers and sequences.

| Primer names | Primer sequences |
|---|---|
| **ATP6-DF3** | AACGAAAATCTATTCGCCTCT |
| **ATP6-DR1** | CCAGTATTTGTTTTGATGTTAGTTG |

**Appendix S6.** ATP6 PCR 1 and PCR 2 reagents and volume per reaction.

| Reagents | Concentration | Volume per reaction (µl) | |
|---|---|---|---|
| | | Normal PCR | Max DNA PCR |
| Taq Gold 360 MM | 10x | 7.5 | 7.5 |
| ATP6—DF3 | 10MM | 0.6 | 0.6 |
| ATP6—DR1 | 10MM | 0.6 | 0.6 |
| BSA | 20 mg/ml | 0.3 | 0.3 |
| dH2O | | 3.0 | 4.5 |
| DNA | Unknown | 1.5 | 3.0 |
| Total volume used | | 15 | 15 |

**Appendix S7.** ExoSAP-IT reagents and volume per reaction.

| Reagents | Volume per reaction (µl) |
|---|---|
| Exo | 0.1 |
| Sap | 0.2 |
| PCR product | 5 |
| dH20 | 1.7 |
| Total | 7 |

**Appendix S8.** Sequencing reagents and volume per reaction.

| Reagents | Volume per reaction (µl) |
|---|---|
| Big Dye Buffer | 2 |
| Sequencing primer (0.2uM) | 1 |
| Big Dye (v.1.1) | 1 |
| Cleaned PCR product | 1 |
| dH20 | 5 |
| Total | 10 |

**Appendix S9.** Ethanol precipitation reagents and volume per reaction.

| Reagents | Volume per reaction (µl) |
|---|---|
| EDTA | 2 |
| dH20 | 10 |
| Ethanol | 50 |
| Sodium acetate (NaOAc) | 2 |
| Sequencing product | 10 |
| Total | 74 |

**Appendix S10.** Biomass consumed calculated from black-backed jackal (*Lupulella mesomelas*) scat (n=101) collected in the Okakarara District Communal Area (ODCA).

| Food item | Weight (kg)[a] | Correction factor (kg/scat)[b] | Number of occurrences (n=101) | OccST (%) | Total biomass consumed (kg)[c] | Relative biomass consumed (%) |
|---|---|---|---|---|---|---|
| **Greater kudu** (*Tragelaphus strepsiceros*) | 130 | 118 | 20 | 19.80 | 2336.63 | 19.83 |
| **Common duiker** (*Sylvicapra grimmia*) | 16 | 118 | 16 | 15.84 | 1869.31 | 15.86 |
| **Goat** (*Capra hircus*) | 50 | 118 | 12 | 11.88 | 1401.98 | 11.90 |
| **Sheep** (*Ovis aries*) | 40 | 118 | 12 | 11.88 | 1401.98 | 11.90 |
| **Small mammals** | 0.06 | 23 | 39 | 38.61 | 888.12 | 7.54 |
| **Steenbok** (*Raphicerus campestris*) | 11.1 | 118 | 7 | 6.93 | 817.82 | 6.94 |
| **Fruits/berries** | 0.002 | 14 | 59 | 58.42 | 817.82 | 6.94 |
| **Cattle** (*Bos taurus*) | 123 | 118 | 6 | 5.94 | 700.99 | 5.95 |
| **Vegetation** | 0.001 | 4 | 93 | 92.08 | 368.32 | 3.13 |
| **Birds** | 1.57 | 35 | 10 | 9.90 | 346.53 | 2.94 |
| **Common warthog** (*Phacochoerus africanus*) | 43 | 118 | 2 | 1.98 | 233.66 | 1.98 |
| **Coleoptera** | 0.004 | 5 | 41 | 40.59 | 202.97 | 1.72 |
| **Scrub hare** (*Lepus saxatilis*) | 2.35 | 50 | 4 | 3.96 | 198.02 | 1.68 |
| **Lizards** | 0.006 | 18 | 4 | 3.96 | 71.29 | 0.60 |
| **Scorpiones** | 0.004 | 5 | 8 | 7.92 | 39.60 | 0.34 |
| **Orthoptera** | 0.004 | 5 | 7 | 6.93 | 34.65 | 0.29 |
| **Hymenopterans** | 0.004 | 5 | 5 | 4.95 | 24.75 | 0.21 |
| **Odonata** | 0.004 | 5 | 4 | 3.96 | 19.80 | 0.17 |
| **Cicadae** | 0.004 | 5 | 1 | 0.99 | 4.95 | 0.04 |
| **Spirostreptida** | 0.004 | 5 | 1 | 0.99 | 4.95 | 0.04 |

| | | |
|---|---|---|
| **Total** | 11784.16 | 100 |

[a]From Stuart and Stuart (2015) and Skinner and Chimimba (2005)

[b]From Goszczynski (1974) and Jedrzejewska and Jedrzejewski (1998)

[c]Correction factor x OccST (%)

**Appendix S11.** Prey biomass proportion in diet, intensity of use, RAI, and Jacobs' index (D-value).

| Prey species | Biomass proportion in diet (%) | Intensity of use | RAI | Jacobs' index using intensity of use (D) | Jacobs' index using RAI (D) |
|---|---|---|---|---|---|
| **Smallstock** (*Capra hircus* and *Ovis aries*) | 23.80 | 0.34 | 8.90 | -0.25 | 0.52 |
| **Common duiker** (*Sylvicapra grimmia*) | 15.86 | 0.81 | 19.73 | -0.92 | -0.13 |
| **Steenbok** (*Raphicerus campestris*) | 6.94 | 0.75 | 8.97 | -0.95 | -0.14 |
| **Cattle** (*Bos taurus*) | 5.94 | 0.94 | 113.61 | -0.99 | -1.00 |
| **Scrub hare** (*Lepus saxatilis*) | 1.68 | 0.49 | 8.01 | -0.97 | -0.67 |
| **Greater kudu** (*Tragelaphus strepsiceros*) | 19.83 | - | 0.93 | - | 0.93 |
| **Warthog** (*Phacochoerus africanus*) | 1.98 | - | 0.24 | - | 0.79 |

# Chapter 4: African wild dog (*Lycaon pictus*) livestock conflict in relation to denning sites in the Okakarara District Communal Area, Namibia

**4.1 Abstract**

African wild dogs (*Lycaon pictus*) are a critically endangered canid that, due to their very large home ranges, are not likely to be contained by protected areas. The small population of African wild dogs in Namibia is highly persecuted due to conflict with farmers in the form of livestock depredation. Farmers believe that African wild dogs kill livestock near their denning sites, which influences farmers to destroy dens and kill African wild dogs when they encounter them on their farms. I collected African wild dog scat both opportunistically and systematically from 2019-2021 in the Okakarara District Communal Area (ODCA) of northeastern Namibia and found evidence of livestock depredation, which I pooled with reports of livestock depredation from human-wildlife conflict questionnaires administered in 2018 and 2019 to create a kernel density conflict map. Using Fisher's exact testing, I found that African wild dog dens occurred significantly more frequently in regions of high livestock conflict. These preliminary findings suggest that livestock depredation may be increased close to dens, emphasizing the need for developing conflict mitigation strategies for communities in this area.

**4.2 Introduction**

African wild dogs (*Lycaon pictus*) are a wide-ranging, critically endangered canid whose population has declined 98% over the past 100 years (Hanssen *et al.*, 2022). African wild dogs frequently come into conflict with humans due to livestock depredation (Rasmussen, 1999). Because African wild dogs' large home ranges are unlikely to be contained by protected areas, most conflict occurs outside of protected areas (Lindsey, Du Toit and Mills, 2005; Woodroffe *et al.*, 2005). Therefore, the survival of the species depends on human populations tolerating the presence of African wild dogs outside of protected areas (Lindsey, Du Toit and Mills, 2005). Creel and Creel (2002) explained that African wild dogs may hunt intensively in the area around their dens due to range contraction during the denning season (Hunter, 2011). Farmers also believe that African wild dogs deplete prey in the areas surrounding where they den (Mbizah *et al.*, 2014). However, several studies have found no negative impact on prey populations around dens during the denning season (Romañach, Lindsey and Stephanie Romañach, 2008; Mbizah *et al.*, 2014).

The Okakarara District Communal Area (ODCA) African wild dog population was perceived responsible for 71% of cattle losses and 6% of smallstock losses and is highly persecuted as a result (Verschueren *et al.*, 2020). Farmers in the ODCA believe that African wild dogs denning near their farms presents an increased threat to their livestock, and they are quick to destroy African wild dog dens when they discover them. Destroyed dens and killed adult dogs led to the confiscation of three litters of pups from the ODCA by MET in 2017 and 2018 (Marker *et al.*, 2022). There have been no studies published on the ODCA African wild dog diet or spatial conflict related to their denning sites in the ODCA.

This study will help determine if African wild dog conflict is higher near dens, which will guide development of conservation priorities and conflict mitigation strategies. I hypothesized that African wild dog dens will be located significantly more in regions of high conflict due to range contraction and hunting intensively around dens (Creel, 2002; Hunter, 2011).

## 4.3 Methods

### 4.3.1 Study area

This study was conducted in the Okakarara District Communal Area (ODCA) in northeastern Namibia. The ODCA covers a total of 18,951 km$^2$. Scat was collected from within the 6,720 km$^2$ area where camera traps were deployed for an occupancy survey in 2018-2019. For a full description of the study area, see Chapter 2 Section 2.3.1.

### 4.3.2 Data collection

African wild dog scats were collected opportunistically and near confirmed or suspected kills and around African wild dog dens. Scat samples were collected in the period from June 2019-Oct 2021. Scat was collected and stored using the same methodology as described in Chapter 3 Section 3.3.2.

As described in Chapter 2 Section 2.3.3, African wild dog dens have been identified in 2017-2022 as a result of CCF's ongoing human-wildlife conflict work in the ODCA.

### 4.3.3 Laboratory analysis

#### 4.3.3.1 DNA extraction and amplification

DNA was extracted from scats following the protocols outlined in Chapter 3 Section 3.3.3.1. However, the ATP6 primer used for species verification did not reliably amplify DNA for African wild dog samples.

I identified that the African wild dog sequence has several base-template mismatches in the primer binding site of ATP6 DR-1, including 2 mismatches in the 3' end region, where mismatches are more detrimental (Stadhouders *et al.*, 2010). Therefore, I used microsatellite analysis to assign African wild dog scat to species. Microsatellite DNA markers are noncoding regions of nuclear DNA where a motif of two to six bases is randomly repeated (Ellegren, 2004), which can be used to obtain a genetic profile of the individual organism represented (Adams and Waits, 2007; Kumar, 2017). The primer pairs are labeled with a fluorescent dye which is detected by the laser of the genetic analyser to output an electropherogram (peaks representing the amplified DNA fragment).

I amplified the microsatellite repeats from the extracted DNA using a combined primer mix (multiplex) for six microsatellite loci identified in domestic dog and previously used for a genetic study of African wild dog (Appendix S12, Miller-Butterworth *et al.*, 2019).

DNA amplification was done using the same PCR touch down cycling process as for the ATP6 sequencing laboratory workflow described in Chapter 3 Section 3.3.3.1.  PCRs 1 and 2 used 1.0µl of DNA. Subsequent max DNA PCR used 3.0µl of DNA and was done for samples which were not confirmed as African wild dog following the first two PCRs (Appendix S13).

**4.3.3.2 Denaturation and electrophoresis**

For electrophoresis in the genetic analyser, each well contained 13µl consisting of 12µl of formamide/size standard premix and 1µl of PCR product. Denaturation and electrophoresis used the same process described in Chapter 3 Section 3.3.3.3.

**4.3.3.3 Size standard and allele calling**

The data from the genetic analyser was imported into GeneMapper software for allele calling. The size standard was corrected for each sample, which gives the accurate position of the alleles relative to the size standard peaks. GeneMapper's calling of alleles was verified visually, corrected if needed, and recorded in an Excel spreadsheet, where a genetic profile for each sample was determined.

**4.3.4 Data analysis**

**4.3.4.1 Diet analysis**

African wild dog scats were analysed using the same methodology outlined in Chapter 3 Section 3.3.4.1. Because of the small sample size, I was unable to complete quantitative diet analysis. The scats containing livestock material were used to spatially map conflict with African wild dog in the study area.

### 4.3.4.2 Livestock conflict density and den locations map

I pooled the diet analysis results with questionnaire data collected by the Cheetah Conservation Fund (CCF) in the ODCA in 2018 and 2019. In 2018, at the farms where cameras were deployed for this project, CCF administered questionnaires in which respondents were asked to report livestock losses to specific predator species from the previous year. CCF administered follow-up questionnaires in 2019 which collected the same information on livestock loss. Along with the locations of livestock-containing scat, I plotted the village points where African wild dog had been reported to predate on livestock in 2018 and 2019.

In QGIS 2.24.1, I used these conflict points to create a kernel density raster of livestock conflict with a radius or kernel bandwidth of 10km based on African wild dog home range contraction during the denning season (Darnell *et al.*, 2014; Pomilia, Mcnutt and Jordan, 2015). I classified the raster to its 50% and 100% volume contours. I plotted 14 African wild dog den locations identified by CCF's prior work in the ODCA and categorized them according to their location within the 100% or 50% contours of the conflict raster or outside of the raster. I used Fisher's exact test to determine if the African wild dog dens occurred significantly more frequently than expected in regions of high livestock conflict (Fisher, 1992). I used pairwise Fisher's exact tests with Bonferroni p-value correction to make pairwise comparisons. To calculate the expected distribution of dens across the contours of the conflict raster, I determined the number of pixels in each contour category (100% conflict, 50% conflict, and no conflict) and used the percentage to predict how many dens would be within each category based on their relative sizes.

### 4.4 Results

### 4.4.1 African wild dog diet

Seventeen African wild dog scats were collected in a period from June 2019-October 2021 (Figure 4.1).
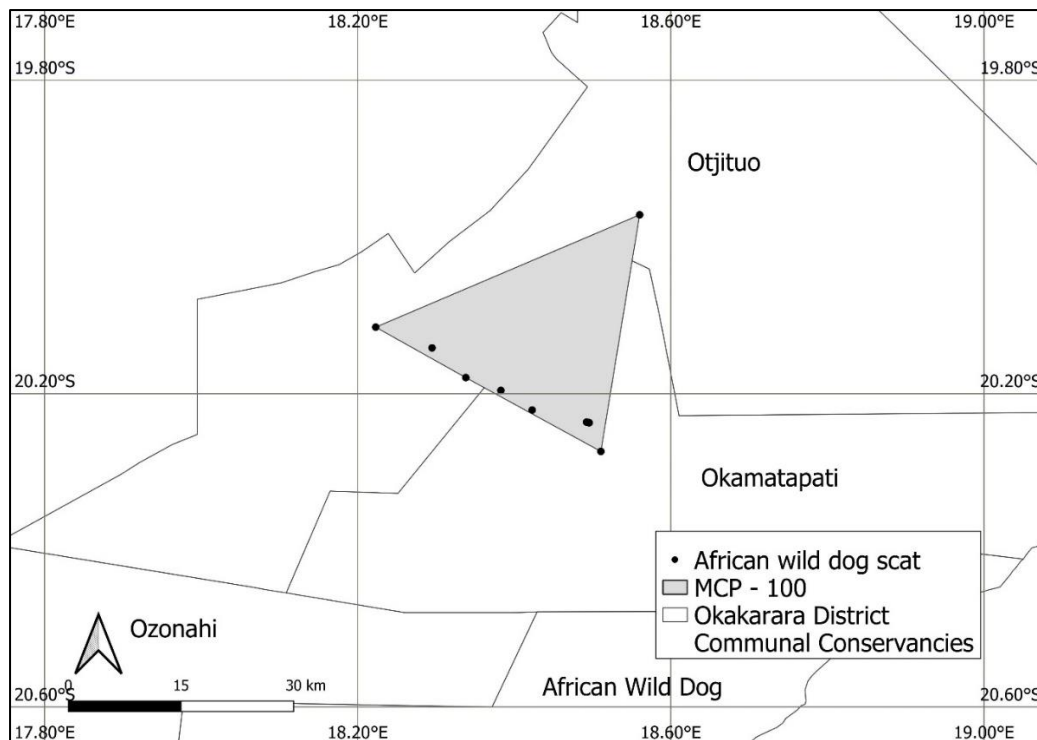
**Figure 4.1.** African wild dog (*Lycaon pictus*) scat locations in the Okakarara District Communal Area (ODCA). Calculated minimum convex polygon containing 100% of scat locations is shown.

Fifteen of these samples were collected opportunistically by CCF's HWC team in 2019 (n=7) and 2020 (n=8). One sample was collected by CCF's scat detection dog team during a survey of the study area in 2020. CCF's ecology team collected 1 sample in 2021 while completing a targeted search for carnivore scat in the study area.

On average, the African wild dog scats contained 63.66% vegetation and 36.67% mammal food items by proportion. One sample contained fruit from the *Grewia flava*. 5 samples contained Coleoptera, which made up 0.54% of sample volume on average. All 17 scats contained mammal hair. Six species were recorded: greater kudu (*Tragelaphus strepsiceros*), common duiker (*Sylvicapra grimmia*), steenbok (*Raphicerus campestris*), cattle (*Bos taurus*), sheep (*Ovis aries*), and African wild dog (*Lycaon pictus*).

**4.4.2 Livestock conflict density and den locations**

Five of the 17 scats analysed contained livestock material. The GPS coordinates of these scat were pooled with 56 reports of African wild dog livestock depredation from 2018 and 2019 to create a kernel density raster of conflict. Of the 14 known African wild dog dens, 4 occurred within the 50% kernel density, 8 within the 100% kernel density, and 2 dens occurred outside the conflict raster (Figure 4.2). There was a significant difference in the distribution of these dens compared to their

expected distribution in the three raster categories (p = < 0.01). Pairwise Fisher's tests found there were significantly more dens in the 50% conflict raster category and significantly fewer dens in the no conflict region of the raster (p = <0.03).
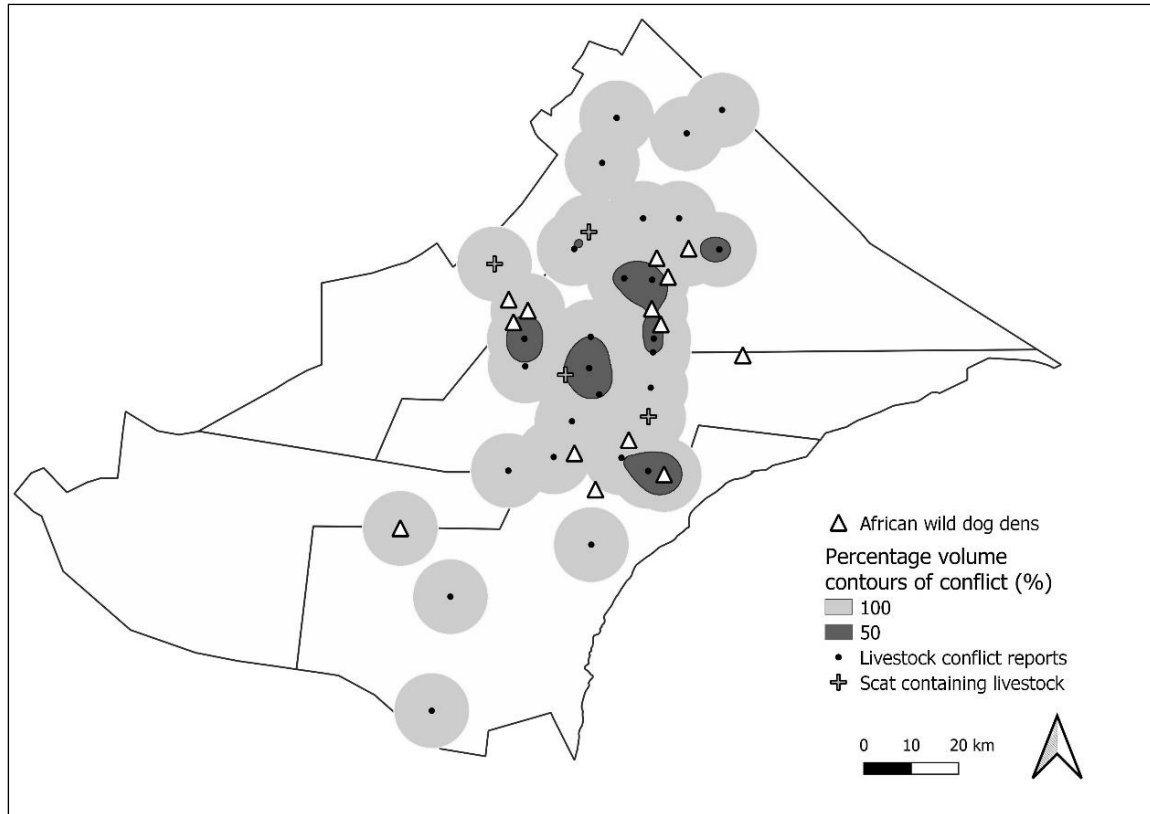


**Figure 4.2.** African wild dog (*Lycaon pictus*) livestock conflict kernel density and locations of dens, livestock conflict reports, and scat containing livestock in the Okakarara District Communal Area (ODCA).

## 4.5 Discussion

This study found evidence of livestock depredation through presence of cattle and sheep hair in African wild dog scat. Although not a large enough sample size to make conclusions about diet, the scat results support farmer reports that livestock depredation is problematic in the ODCA. However, it is important to note that due to the difficulty of finding African wild dog scat in the study area, scats were collected non-randomly including at kills, which is likely to bias the sample set. Combining the coordinates of livestock-containing scats with questionnaire reports of livestock conflict, a kernel density map revealed that African wild dog dens were significantly more located in areas of high livestock conflict, suggesting that livestock loss may increase around dens.

These results have practical applications in the ODCA because of farmers' low tolerance for African wild dog and their willingness to destroy dens and kill African wild dogs if they believe they are causing livestock loss (Mbizah, Marino and Groom, 2012b; Marker *et al.*, 2022). African wild dogs

undergo home range contraction during the denning season, which has been shown to shrink their hunting area to a smaller radius around their dens (Creel, 2002; Hunter, 2011; Darnell *et al.*, 2014; Pomilia, Mcnutt and Jordan, 2015). African wild dogs may also return to den in the same area year after year (Mbizah *et al.*, 2014b), which is observed in the ODCA (CCF unpublished data). Although other research did not find decreased prey around African wild dog dens despite range contraction (Romañach, Lindsey and Romañach, 2008; Mbizah, Marino and Groom, 2012), my findings suggest livestock depredation is higher in regions around dens in the ODCA, which may reflect the high energetic intake requirements needed to raise pups (Van den Berghe *et al.*, 2012).

However, it is important to consider that livestock losses recorded by the questionnaires were self-reported, and farmers are likely to rate a carnivore species as more of a problem when they are sighted frequently (Rust and Marker, 2013). Livestock loss reports could be biased because in areas near African wild dog dens, farmers may assume they are responsible for livestock losses due to their increased visibility (Marker, 2002). Furthermore, this study used a dataset of African wild dog dens which were identified from 2017-2022. The African wild dog scats analysed were collected between 2019-2021, and the questionnaires on livestock loss were administered in 2018 and 2019. As it was not possible to verify that all dens were active when scats were collected and when farmers reported livestock losses, it is possible that active and non-active dens were grouped together in the analysis, potentially biasing conclusions regarding livestock conflict and den locations.

## 4.6 Conclusion

The ODCA African wild dog population is highly persecuted because of the perceived threat they present to farmer's livestock. This study's findings that dens occur significantly more in regions of high livestock conflict may tentatively offer support to this perception.

These results emphasize the need for more comprehensive research on African wild dog depredation to inform development of conflict mitigation strategies for communities in the ODCA. More African wild dog scat from the ODCA should be collected from a wider area across the conservancies and analysed to enable more robust conclusions about diet and livestock depredation in relation to den location. Annual verification of active and non-active African wild dog dens should be done to ensure non-active dens are not being considered in analyses. It is also possible that there are additional African wild dog dens which have not been discovered or shared with CCF from 2017-2022 during the period of data collection.

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**4.8 Appendices**

**Appendix S12.** PCR Primers and forward and reverse sequences (Miller-Butterworth *et al.*, 2019).

| AWD 1 | Marker | Primer sequences |
|-------|--------|------------------|

| FH3965 | F: GTCGCTCAGCAGTTAAGCTC |
| | R: GAATCCTGGCTCTGCTACTTAC |
| | |
| FH2054 | F: GCCTTATTCATTGCAGTTAGGG |
| | R: ATGCTGAGTTTTGAACTTTCC |
| | |
| FH2658 | F: TCTTAGAAATTGCTGGTGGG |
| | R: TAAGAAACTGCCAGTCTGTGG |
| | |
| FH3399 | F: TCTCTATGCCTGCAGTTTCC |
| | R: TTCTGATGCCCTCATAAAGC |
| | |
| FH2611 | F: GAAGCCTATGAGCCAGATCA |
| | R: TGTTAGATGATGCCTTCCTTCT |
| | |
| PEZ12 | F: GTAGATTAGATCTCAGGCAG |
| | R: TAGGTCCTGGTAGGGTGTGG |

**Appendix S13.** PCR reagents, concentration, and the volume per rection for normal and max DNA PCR.

| Reagents | Concentration | Volume per reaction(µl) | |
| --- | --- | --- | --- |
| | | normal PCR | max PCR |
| **Taq Gold 360 MM** | 2x | 7.5 | 7.5 |
| **Primer mix** | 8 µM | 0.5 | 0.5 |
| **BSA** | 20 mg/ml | 0.2 | 0.2 |
| **dH2O** | | 3.3 | 1.3 |
| **DNA** | unknown | 1 | 3 |
| **Total** | | 10 | 10 |

# Chapter 5: Integrated Discussion and Recommendations

**5.1 Coexistence of black-backed jackal and African wild dog**

This study confirmed that black-backed jackal (*Lupulella mesomelas*) have an opportunistic generalist diet in the Okakarara District Communal Area (ODCA). I found no evidence of either competition or facilitation between African wild dog and black-backed jackal. While black-backed jackal are more abundant within 10km of an African wild dog (*Lycaon pictus*) den, I did not find evidence that their diet was influenced by increased African wild dog den presence. It is most likely that black-backed jackal select habitat based on human risk avoidance, which is also the driving factor behind den selection for African wild dogs (Jackson *et al.*, 2014).

An analysis of questionnaires administered in 2015, 2016, and 2018 indicated that farmers believe African wild dogs to be responsible for devastating livestock losses (Verschueren *et al.*, 2020). This study found that livestock loss may be increased within 10km of African wild dog dens, but more research is needed to strengthen this conclusion. Over the past three years, however, farmers have reported less livestock loss to African wild dogs, likely due to a further decrease in the already small population of African wild dog in the area (CCF unpublished data). African wild dog may be functionally absent from the ODCA, where leopard and brown hyaena, other large carnivores, are also scarce, but black-backed jackal are widespread (Verschueren *et al.*, 2020).

In the absence of any suppressive large carnivore, black-backed jackals may be experiencing mesopredator release, where removal of an apex predator results in increased abundance of mesopredators (Feit, Feit and Letnic, 2019). Top-down effects of apex carnivores regulate mesopredators through direct competition, predation, and a "landscape of fear" (Laundré, Hernández and Ripple, 2010) which influences mesopredators to avoid interactions with an apex predator (Ritchie and Johnson, 2009). Apex predators face disproportionate challenges in human-altered landscapes due to their large space requirements, low tolerance by humans, and sensitivity to persecution (Prugh *et al.*, 2009). Mesopredators, on the other hand, can thrive in human-dominated environments (Krofel *et al.*, 2017). Although Pardo *et al.* (2022), concluded that black-backed jackal occupancy is shaped at a large scale by habitat structure and not large predator presence, it is likely that in the absence of an apex predator, black-backed jackal may increase (Taylor, 2015). This phenomenon may have occurred in the ODCA, leading to the high abundance of black-backed jackal and the severity of their livestock depredation.

Mesopredator release involving canids has been well documented in North America between the grey wolf (*Canis lupus*) and coyote (*Canis latrins*). In Europe, persecution of the grey wolf has led to release of the golden jackal (*Canis aureus*). However, there has been little research into comparable canid relationships in Africa. Gusset *et al.* found that black-backed jackal in Botswana depredated on livestock more in areas absent of African wild dog and suggested they could be experiencing mesopredator release (2009). In the Eastern Cape, South Africa, black-backed jackal abundance was higher in the absence of apex predators (Taylor, 2015).

Our study indicates that African wild dog may not be exerting top-down effects on black-backed jackal in the ODCA, allowing the mesopredator to multiply and exploit a variety of food resources including livestock. Mesopredator dominance results in an unbalanced system which has negative impacts on vulnerable prey species (Ritchie and Johnson, 2009; Letnic and Dworjanyn, 2011; Taylor, 2015) and may increase human-wildlife conflict due to mesopredators' tendency to thrive in human-dense environments (Prugh *et al.*, 2009). Restoration of an apex predator may moderate the harmful effects of black-backed jackal dominance (Ritchie and Johnson, 2009), however, this study also found preliminary evidence that African wild dog livestock depredation may be increased around their denning sites.  Therefore, more investigation is needed into livestock depredation by African wild dog and the top-down control of black-backed jackal by African wild dog.

### 5.2 Management recommendations

Black-backed jackal is the predator perceived as responsible for the majority of smallstock losses in the ODCA (Verschueren *et al.*, 2020). This study confirmed that livestock makes up approximately 30% of black-backed jackal diet by biomass. Livestock depredation by black-backed jackal likely has multiple causes: availability of livestock, lack of apex predator top-down pressure (mesopredator release), and lack of wild prey.

The ODCA is dominated by livestock farming, and inexpensive predator mitigation methods are needed to address the issue of livestock depredation. Farmers often use lethal techniques to address livestock depredation, believing it to be most effective solution (Mitchell *et al.*, 2004). However, lethal control of black-backed jackal has been proven unsuccessful in reducing livestock depredation (Avenant and Du Plessis, 2008; Nattrass and Conradie, 2013; Du Plessis, Avenant and De Waal, 2015). Nonlethal controls can more effectively solve conflict and result in more economic savings when compared to lethal controls (McManus *et al.*, 2015; Miller *et al.*, 2016). Based on self-reported questionnaires, Verschueren *et al.* (2020) found that 96% of ODCA farmers kept their smallstock in a

kraal at night, 75% used livestock guarding dogs, and 44% used herders. However, they found livestock depredation increased with herd size, and that the presence of local livestock guarding dogs was associated with increased livestock loss. The dogs used to guard livestock in the ODCA are often small, poorly trained, and not bred to guard livestock (Verschueren *et al.*, 2020). Careful management of smaller herds of smallstock with larger and well-trained dogs could reduce livestock depredation. Use of a vigilant herder along with a livestock guarding dog can also improve the effectiveness of the dog (Marker *et al.*, 2020). In a pilot study conducted in the ODCA, CCF found that flashing Foxlights© were also effective at reducing livestock depredation (Verschueren, Torres-Uribe, *et al.*, 2021). Farmers' lack of knowledge and/or financial means to improve longstanding livestock husbandry practices is a significant challenge (Rust and Marker, 2013; Verschueren *et al.*, 2020).

Livestock depredation by black-backed jackal may also be exacerbated by the effects of mesopredator release. Conservation of African wild dog in the ODCA has been recognized as a priority for several years (Verschueren *et al.*, 2020), but this study emphasizes the potential of African wild dog restoration as an apex predator to reduce HWC with black-backed jackal. However, tolerance of African wild dog is very low in the ODCA due to perceived high depredation (Lines, 2008; Verschueren *et al.*, 2020; Marker *et al.*, 2022) and this study's preliminary findings suggest that farmers may suffer from increased livestock loss around African wild dog dens. Therefore, restoration of African wild dog as an apex predator will likely not reduce the livestock conflict in the ODCA without a substantial increase in wild prey, as African wild dogs typically prefer wild prey over livestock when it is available (Rasmussen, 1999; Woodroffe *et al.*, 2005; Gusset *et al.*, 2009).

The ODCA is known to be prey-depleted, (Lines, 2008; Verschueren *et al.*, 2020), which may drive carnivores to depredate on livestock as an alternative food source (Bagchi and Mishra, 2006). Given the scarcity of large ungulates, reintroduction of prey may support the recovery of large carnivore populations, decrease mesocarnivore dominance, and reduce livestock depredation. Currently unsustainable hunting is widespread in the ODCA and believed to be the reason that wildlife prey populations have been depleted (Lines, 2008). Management priorities for these conservancies should include restoring populations of wild prey through reintroduction and a reduction in hunting. Capacity building and educational efforts in the ODCA are needed to address human-wildlife conflict, improve attitudes towards carnivores, and develop toward conservation priorities.

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