SCENT MARKING AND DIETARY PATTERNS OF AFRICAN WILD DOGS (*LYCAON PICTUS*, TEMMINCK 1820) IN NORTHERN BOTSWANA

By

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ABSTRACT

African wild dogs are endangered and their populations continue to decline in many African reserves. These declines have been largely associated with a variety of anthropogenic biotic and abiotic dynamics. The conservation and sustainable management of the African wild dogs requires proper scientific understanding of its basic ecology. Better scientific knowledge on the scent marking behaviour and dietary habits of African wild dogs is likely to help scientists' strategic management of the species. This thesis discusses the scent marking characteristics and dietary patterns of African wild dogs in parts of northern Botswana. Scan sampling and all occurrences sampling methods were used to observe 24 (16 adult and 8 sub adult) African wild dogs from three packs between August 2010 and April 2012. The mean scent marking rates of individuals were compared by age, social status and sex using the General Linear Model. The results showed no significant difference in the scent marking rates of adults and the young. Sex also did not significantly relate with an individual's scent marking rates. However, social status had a significant association with the scent marking rates of individuals, as dominants scent marked at significantly higher rates than subordinates. African wild dogs scent mark densities were significantly higher within their home range 'cores' zones compared to the 'intermediate' and 'edge' zones of home ranges. Wild dogs also significantly marked more on grass than on other substrates. Results on diets showed impala as the most common prey; however, other medium sized ungulates were also preferred prey while large ungulates were generally not utilised. Their diet did show any significant variation to between the dry and wet seasons. These findings are consistent with previous studies on the scent marking behaviour of other carnivores. Future research should investigate the role of scent marking in spatial ecology and its ultimate prospects in management intervention strategies of this endangered species. Studies on how wild dogs use their scent marks to protect food resources would provide better insights into wild dog space habits.

Key words: African wild dog, scent marking rate, diet, Vumbura, Linyanti- Selinda

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Dedication

I dedicate this thesis to my favorite women: my late mother Goitseone Tshimologo and grandmother Violet Motsatsing**.** I love them very much and hope to meet them in another life.

Disclaimer

The work contained in this thesis/dissertation was completed by the author at the University of Botswana between 20/08/2010 to 23/04/2014. It is original work except where due reference is made and neither has been nor will be submitted for the award of any other University.

Signature..

Date signed: ………………………………

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Thesis outline

Chapter 1 discusses the general theoretical research developments on the scent marking behavior and diets of African wild dogs. Chapter1 is preceded by a brief background on the ecology of the study animals; African wild dogs. Chapter 2 discusses demographic scent marking characteristics of African wild dogs. The spatiotemporal scent marking patterns are further discussed in chapter 3.Since the scent marking behavior has been largely linked to territorial behavior, hence resource defense definitely become a fundamental biotic factor. Hence Chapter 4 describes the dietary composition of African wild dogs in the Vumbura, Linyanti and Selinda parts of Northern Botswana, exploring similarities and prey preferences among the study packs. The thesis is finally synthesized in Chapter 5. The subject of scent marking behaviour is discussed in light of its theoretical functions and the demographic, spatial and temporal aspects associated with the behaviour. Chapter 5 goes further and discusses the ecological and management implications of the dietary characteristics of wild dog populations in these Northern parts of Botswana. Limitations and recommendations on issues of concern for the future studies, as far as behavioural ecology and conservation, of African wild dogs are made too.

Chapter One

1.0 Introduction

1.1 Importance of carnivores in ecosystems

Predators are very important to large mammalian communities as they keep population checks on herbivores communities (Mills and Shenk, 1992; Brown *et al.*, 1999; Creel and Creel, 2002; Hebblewhite *et al.*, 2005). Carnivores are trophically aboveherbivores, and herbivore populations dynamics are considerably infliuenced by the impact of predation by large carnivores. For instance, lion (*Panthera leo*) predation significantly influenced populations of wildebeest (*Connochaetes taurinus*), plains zebra (*Equus burchellii*) and buffalo (*Syncerus caffer*) (Funston *et al.*, 2001; Hayward and Kerley, 2005). In North America (Creel *et al.*, 2005; Fawcett *et al.*, 2013) and Europe (Meriggi and Lovari, 1996; Sand *et al.*, 2008) *Canis lupus* are essential to controlling populations of moose (*Alces alces*) and elk (*Cervus canadensis*). Large carnivores also offer a greater aestetic value for nature enthusiasts. Apart from their potential source of ecotourism attraction (Lindsey *et al.*, 2005a), large predators also influence the behavior, structure and distributions of herbivore communities in natural systems (Brown *et al.*, 1999; McIntyre and Wiens, 1999; Hebblewhite *et al.*, 2005). However, many large carnivores are disappearing from their natural habitats due to a variety of threats associated with environmental, ecological and anthropogenic factors or a combination of such.

1.2 Threats to wild carnivores

There are several documented threats faced by wild canids in general that affect their populations. Habitat loss, fragmentation and degradation due to human encroachment are chief amongst them (Creel, 1992; Woodroffe and Ginsberg, 1999b; Ogada *et al.*, 2003). Persecution and poaching for animal parts and conflicts with human and their livestock represents another important possible threat (Woodroffe *et al.*, 2005). For example, illegal trading of tiger (*Panthera tigris*) fur threatened their populations in the past, but has since been curbed recently. However, a new trade of tiger meat and bones for the illegal markets of traditional Asian medicine practioners has caused concern in recent years (Gurung *et al.*, 2008). In Africa, human wildlife conflict increases as carnivore predation on livestock outside of protected areas thus raising serious conservation concerns (Woodroffe *et al.*, 2005), and calls for proactivemitigation strategies (Gusset *et al.*, 2008). North American large carnivores such as grizzly bears (*Ursus arctos horribilis*), wolves and coyotes (*Canis latrans*) have endured similar human wildlife-conflicts over the past century (Mech, 1995). Diseases such as rabies, distemper and parvovirus amongst others, are difficult to detect and control in wild carnivore populations, hence posing serious extinction threats, especially for social and group living speciessuch as African wild dogs, hyaenas and lions (Woodroffe and Ginsberg, 1999b; Creel and Creel, 2002; Woodroffe *et al.*, 2012).

The disppearance of large mammalian carnivores from their natural habitats has a long history. In the 1930s, wolveswere actively extarminated by wildlife authorities from Yellowstone National Park and its sorrounding, including many northern states in United States of America and provinces in southern Canada (Mech, 1995). This wolve extarmination programmeswere done to protect the interests of the livestock farming industry. Such extarminationprogrames caused local extinctions of wolves throughout most of the United States of America (U.S.A) until they were reintroduced in the mid-1990s. In Ethiopia, Ethiopian (*Canis simensis*) are also suffer human persecution. They were pushed into hostile habitats by human enchroachment (Sillero-Zubiri and Laurenson, 2001). Asian tigers have in recent history lost a great amount of their natural habitats most likely due to deforrestation and human clearing the land for agriculture (Ramakrishnan *et al.*, 1999; Ranganathan *et al.*, 2008). This wildlife habitat loss is very common in the South American Amazon forests too, where not only local carnivores but a wide variety of wild mammalian species are losing their natural habiats due to human enchroachment (Cardillo *et al.*, 2004). The African lion, leopard (*Panthera pardus*) and cheetah (*Acinonyx jubatus*) often move out of protected areas to pastoral lands and prey on livestock (Woodroffe *et al.*, 2005)which exposes them to fierce human-carnivore conflicts. The African wild dog is no exception and causes greater concernthan larger competitors as an endangered species. The African wild doghas been percieved as savageous throughout history and demonised in local traditional myths(Creel and Creel, 2002). From the early 20th century into the 1970s, African wildlife rangers culled them for various reasons such as dislike for their method of killing prey and disrupting prey in plains when hunting (Creel and Creel, 2002).

For these reasons, African wild dogs have become so rare that the International Union on Conservation of Nature (IUCN) lists them as Endangered (Woodroffe *et al.*,1997; Creel and Creel, 2002; Woodroffe and Sillero-Zubiri, 2012)

1.3. Description of the study Species

Possessing large, rounded black ears, with a deep chest and long legs (Estes, 1991), an average adult wild dogs stands 60cm to 75 cm at shoulder height (Creel and Creel, 2002).Average adult body mass ranges from 20kg to25 kg in east Africa (Estes, 1991; Creel and Creel, 2002) and up to 30 kg in southern Africa (Creel and Creel, 2002). There is evidence suggesting size variations exist across the species's geographic range. It is the only carnivore species that has only four toes on the foreleg and lack the vestigial dewclaw found in other canid species (Estes, 1991; Creel and Creel, 2002). There is limited sexual dimorphism within this African wild dogs as males have been reported to be only 3-7% larger than females (Creel and Creel, 2002). African wild dogs are group living social carnivores. Wild dog groups are known as packs and a pack usually comprises a breeding pair and other related individuals of various age groups and different sexes. Pack size can range from two to 20 individuals (Creel and Creel, 1995; Creel and Creel, 2002), though some reports up to forty individuals (Estes, 1991).

1.4. Distribution and Conservation status

The IUCN (2012) estimated a total population of 6600 individuals, mostly found in east and southern Africa in several small sub-populations (Woodroffe *et al.*, 1997) (Figure 1.1). This is an increase from Woodroffe and Ginsberg (1999)'s estimate of about 3500 to 5000. African wild dogs can occur in different biogeographic regions of Africa(Estes, 1991). Wild dogs are found over a wide range of habitats in sub-Saharan landscapes, including semi-deserts such as the Kalahari. They also range in mountainous areas as high as the summit of Mount Kilimanjaro (Estes and Goddard, 1967), the open grassland savannas of the Serengeti (Creel and Creel, 2002), and the marshy swamps of the Okavango Delta (McNutt, 1996b). However, they are absent from lowland rainforests (Creel and Creel, 2002) and the most arid of deserts in Namibia (Goss, 1986).

The number of African wild dogs has been declining over the past half century (Mills and Gorman, 1997; Woodroffe and Ginsberg, 1999b). There are several factors attributed to this declines, amongst them diseases (Creel, 1992; Creel and Creel, 1998), fragmented and lost habitats due to expanding human settlements (Creel and Creel, 2002), and human-wild dog conflict outside protected areas (Ogada *et al.*, 2003). Even inside protected areas, interspecific competition with lions and spotted hyaenas (*Crocuta crocuta*) causes mortalities among juveniles (Creel, 1992). Wild dogs are the second most endangered large African carnivore after the Ethiopian wolf (Sillero-Zubiri and Laurenson, 2001). Endemic only to Africa, they have since disappeared from 25 of the 39 countries where they formerly ranged (Woodroffe and Ginsberg, 1999b). The species is virtually extinct in West Africa (Creel and Creel, 2002). This decline has led conservationists in other parts of Africa to set wild dogs as a flagship species to demonstrate the negative effects of human expansions into wildlife areas (Romanach *et al.*, 2007).

It is very rare to find African wild dogs outside protected areas, most likely as a result of fragmented, degraded and lost habitats, and human-wild dog conflicts. Several southern African countries, among them Botswana, Zimbabwe and South Africa, have fairly good and genetically viable populations of African wild dogs in their protected areas (Creel and Creel, 2002).Kruger

National Park (South Africa), Northern Botswana, including the Okavango Delta, Chobe National Park, and Hwange National Park in Zimbabwe, hosts a considerably proportion of the total population of African wild dogs extant today (Creel and Creel, 2002). In east African countries of Kenya and Tanzania, there are considerably viable populations of wild dogs (Woodroffe and Ginsberg, 1999a). These protected areas also harbour a diverse assemblage of ungulate species that serve as prey for wild dogs. Humans have almost completely eliminated these native ungulates from outside of protected areas.

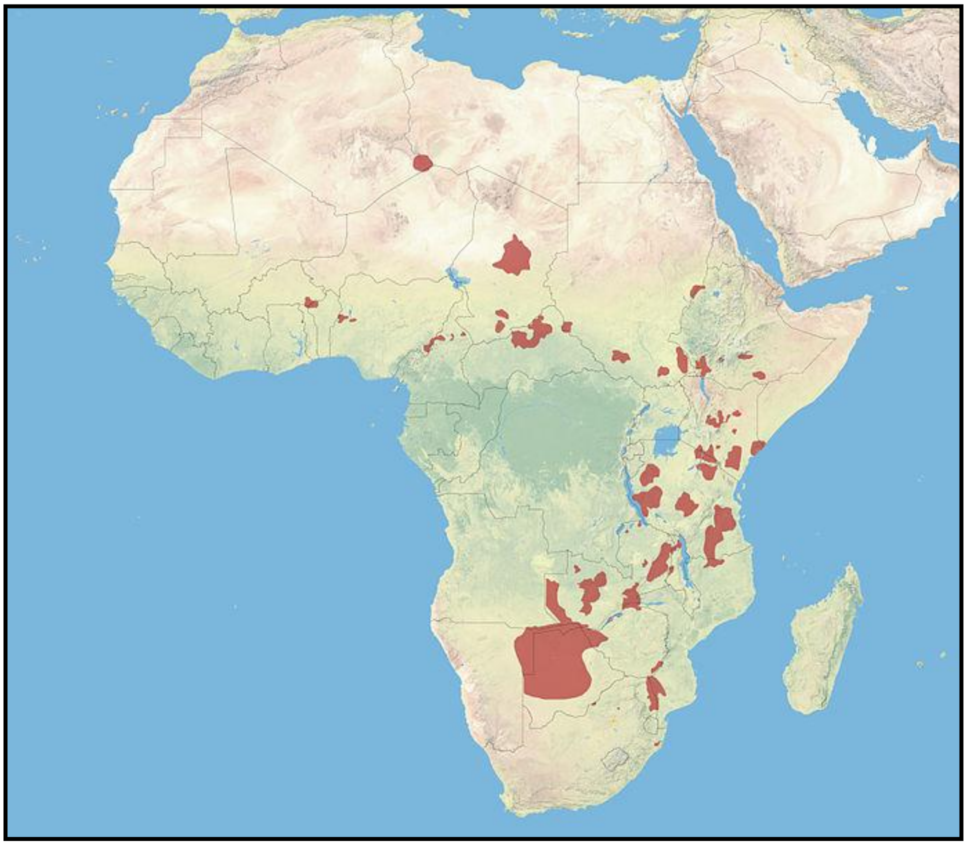

Figure 1.1: A historical global distribution of African wild dogs (*Lycaon pictus*) as of July 2011. (http://en.wikipedia.org/wiki/File:African_Wild_Dog_Distrbution.jpg)

1.5 Feeding behavior

African wild dogs are gregarious, generalist feeders, hunting cooperatively in packs (Creel, 1997), with highly specialized hunting skills that affords them about 60% or more hunting success rate (Estes and Goddard, 1967; Creel and Creel, 1995; Creel and Creel, 2002). They are crepuscular as they spend most the day resting between the hunts (Creel and Creel, 2002). They prey on a wide range of small and medium-sized mammals (Creel and Creel, 2002; Hayward *et al.*, 2006; Hayward *et al.*, 2007; Woodroffe *et al.*, 2007). Wild dogs seem to avoid large prey, probably because they pose seriously fatal risks for them to appropriate. Most of their preferred medium-sized antelopes are also less dangerous to pursue as their anti-predation defense mechanisms of sharp hooves and horns, and outrunning their predators do not seem to deter wild dogs (Creel and Creel, 2002). Gemsbok (*Oryx gazelle*), wildebeest (*Connochaetes taurinus*), Thomson’s gazelles (*Eudorcas thomsonii*), impala (*Aepyceros melampus*), steenbok (*Raphicerus campestris*), kudu *(Tragelaphus strepsiceros*), dik dik (*Madoqua guentheri*) and springbok (*Antidorcas marsupialis*) are amongst common ungulates species commonly hunted by African wild dogs in southern and east African ranges (Fanshawe and Fitzgibbon, 1993; Creel and Creel, 2002; Hayward *et al.*, 2006; Woodroffe *et al.*, 2007). In southern Africa, impala and kudu form a considerable proportion of the African wild dog diet (Radloff and Du Toit, 2004; Hayward and Kerley, 2005; Hayward, 2011). However, carnivore diets are not easy to quantify, especially in their natural systems due to the nocturnal and elusive nature of most carnivores. As such, field researchers have over decades used scat analysis techniques to bridge the knowledge gap on wild carnivore diets.

1.5.1 The use of scat analysis in determining carnivore diets

Scat analysis has been widely embraced not only in carnivore diet studies, but across various taxa (Gamberg and Atkinson, 1988; Farrell *et al.*, 2000; Andheria *et al.*, 2007; van Dijk *et al.*, 2007; Klare *et al.*, 2011). The method explores gastric indigestibility of some ingested food items and uses the identification of such food items to quantify the diet of a species. However, there is still insufficient research into inter-carnivore gastric acidity variations, and how that affects the digestibility of ingested hairs and feathers; hence the accuracy of scat analysis remains doubtful (Quadros and Monteiro-Filho, 1998). That is, a particular ‘food item’ might be completely digestible for a certain carnivore species, but indigestible for another.

To conduct scat analyses, researchers examine fecal samples from the field at different locations of the animal’s home range, usually from accumulations at denning and resting sites, along trails and at latrines (Gorman and Trowbridge, 1989; Woodmansee *et al.*, 1991). Various species have their own ways of depositing scats. For instance, cheetahs defecate at specific trees, perhaps so that they function as scent marks (Stuart, 2000). African wild dogs seem less particular and defecate almost anywhere along their movement tracks, but most of their scats are found at resting sites where they spend most of the day when not hunting (*Pers. Observ.*). During the ‘pep rally ritual’ (pre-hunting greetings and gathering of pack members that often precedes hunting), subordinates defecate and urinate as they ready themselves for the hunt.

African wild dogs also use extensive ranges to avoid competition with sympatric carnivores, such as lions, leopards and hyaenas (Creel and Creel, 2002). Kruuk and Turner (1967) reported that African wild dogs rarely scavenge and suspected that to be a way of avoiding risky encounters with the much larger lions, hyaenas and leopards. Like many other large predators ranging over vast habitats, African wild dogs communicate through spatially and temporally distributed olfactory messages known as scent marks (Creel and Creel, 2002). The spatial and temporal distribution of scent marks is not well understood in African wild dogs. Temporal, spatial and social patterns exist in the scent marking behavior of other large carnivores such as brown hyaenas (*Hyaenea brunnea*) (Maude, 2010) aardwolves (*Proteles cristatus*) (Sliwa, 1996), Black footed cat (*Felis nigripes*), coyotes (Bowen and Cowan, 1980), honey badgers (*Meles meles)* (Begg *et al.*, 2003, 2005) and wolves (Paquet, 1991). A basic understanding of fundamental factors underlying scent marking behavior of wild dogs could hold the key to breakthroughs in adaptive management of this territorial, scent marking species. However, communication in mammals, including carnivores, has proven complex and variable (Johnson, 1973; Gosling, 1982; Gosling and Roberts, 2001).

1.6 Communication mechanisms and territorial behaviour

The most common and probably most effective form of communication in African wild dogs is olfactory. Unlike larger and more competitively superior lions and hyaenas, African wild dogs rarely vocalise over long distances presumably to minimise chances of being detected by their competitors (Creel and Creel, 2002). Rather, they use scent secretions with chemical signals to communicate amongst themselves. Although scent marking has been fairly well studied in other canids (Richardson, 1991; Woodmansee *et al.*, 1991; Gese and Ruff, 1997; Sillero-Zubiri and Macdonald, 1998), there is still a scarcity of published information on African wild dogs scent marking behaviour. Scent marking behaviour is difficult to study in wild carnivores, and the challenges are not just limited to the difficulty of carrying out field observations (Peters and Mech, 1975; Verberne and Leyhausen, 1976). Many researchers find it difficult to define a scent mark and the context for when any particular 'scent mark' is relevant (Kleiman, 1966; Thiessen and Rice, 1976; Gosling and Roberts, 2001; Jordan *et al.*, 2013). The difficulty in separating what serves a scent mark from simple urination or defecations for purely eliminatory purposes remains problematic (Raymer *et al.*, 1984; Gorman and Trowbridge, 1989; Jordan *et al.*, 2013).

1.6.1 Definition of Scent Mark

Scent mark definitions vary among scientists, resulting in an ambiguous meaning (Kleiman, 1966; Gorman and Trowbridge, 1989; Jordan *et al.*, 2013). This ambiguity is due to the various purposes that scent marks may serve (Gosling and Roberts, 2001). The earliest studies by Kleiman (1966); and reviewed by Thiessen and Rice (1976) and Gosling and Roberts (2001) were not very clear in their definition of a scent mark. Other studies (Ralls, 1971; Johnson, 1973; Peters and Mech, 1975; Verberne and Leyhausen, 1976) followed and also lacked in proposing a universal definition of a scent mark. Bowen and Cowan (1980) defined scent marking as the application of scented secretions and excretions by an animal on areas or objects in the environment. This definition was also adopted by other researchers (Carpenter and Duvall, 1995; Gosling and Roberts, 2001). Barrette and Messier (1980) reported that a scent mark is often placed on objects in the absence of the receiver and detected much later. Gosling (1982) purported that scent marking is a common form of signalling by male mammals, without implying that females do not scent mark. Alberts (1992) casted doubt on the efficiency of scent marks as olfactory communication agents since they run the risk of degradation by rain or veldt fires before the intended receiver can detect them. Complex as the behaviour is, scent marks must serve specific purposes by the signaller. Hence, scientists have proposed several hypotheses.

1.6.2 Scent marking hypotheses

Different species scent mark in different ways, with the physical and chemical constituents of each scent mark communicating specific messages (Johnson, 1973; Gosling, 1982; Raymer *et al.*, 1984; Gosling and Roberts, 2001).Thus, understanding the communicative purposes of a scent marks is difficult. Scent marks may serve one or a combination of the following purposes: 1) intimidation, 2) territory boundary demarcation, 3) orientation, 4) labelling resources, 5) synchronizing reproductive processes, 6) attracting mates, and 7) synchronizing social structures(Geist, 1964; Johnson, 1973; Lazaro-Perea *et al.*, 1999; Lledo-Ferrer *et al.*, 2011).

1.6.2.1 Intimidation hypothesis

The intimidation hypothesis suggests that scent marking indicates to other animals that an area is occupied and thus an intruder risks an agonistic confrontation if it is noticed by the territory holder (Richardson, 1991). According to this hypothesis, residents should attack intruders to reinforce the meaning of their scent marks. However, Pryor (1985) questioned the hypothesis because it requires a short time interval between depositing the scent mark, detection of the intruder, and ultimately reinforcement for the intruder to realise the true meaning of the scent mark. This ‘time lag problem’ between deposition of the scent by the signaller and reaction by the recipient leaves doubt on the efficiency of scent marking for intimidation purposes (Alberts, 1992). This doubt led to proposition of a mechanism known as *scent matching*; in which territory holders repeatedly counter-matches their odours with the scents of their competitors or intruders (Gosling, 1982; Pryor, 1985; Gosling and McKay, 1990b).

1.6.2.2. Territorial demarcation hypothesis

The territorial demarcation hypothesis or scent fence, which suggests that animals demarcate their territories using scent marks to create a ‘scent fence’ surrounding their territories. In the territorial demarcation hypothesis, the scent marker uses scents as land marks to demarcate its territory and act as advertisements for ownership. As such, scent marks announce occupancy of the territory and intruders must willingly avoid aggressive confrontations by not crossing into a foreign territory (Gosling, 1986; Cafazzo *et al.*, 2012; Stockley *et al.*, 2013). This hypothesis predicts high scent marking intensity at the territory perimeter (Gosling and Roberts, 2001; Ausband *et al.*, 2013). The hypothesis has been suggested for several primate species such as Callitrichid primates (Roberts, 2012a) and carnivore species, like badgers (*Meles meles*) (Roper *et al.*, 1993), and red foxes (*Vulpes vulpes*) (Fawcett *et al.*, 2013). The scent fence informs potential intruders about the presence of the territory holder, thereby deterring them from risking agonistic and possibly fatal encounters (Welsh and Muller-Schwarze, 1989). This hypothesis appears to have developed from ideas of two other hypotheses – *intimidation* (see above) and *orientation* (Gosling, 1982; Johansson and Olof, 1996).

1.6.2.3 Orientation hypothesis

The orientation hypothesis suggests that animals leave scent marks on their environments to help them navigate through the area at a later time. This hypothesis is insufficient because it assumes that animals base their movements only on scent marks, oblivious to other environmental, ecological factors, stochastic events, and competitors (Johnson, 1973). This hypothesis assumes that scent markers move around their territories using systematic and routine paths, as if patrolling or monitoring.

1.6.2.4 Resource labelling hypothesis

Proponents of the resources labelling hypothesis propose that animals identify, label and guard food resources using their scent marks (Ralls, 1971; in Gosling and Roberts, 2001). This hypothesis, is also known as the Ownership hypothesis, suggests that animals label resources within a known home range and that the labelled resources indicate priority of use by the scent marker (Kruuk, 1991; Lazaro-Perea *et al.*, 1999). This hypothesis might be applicable to primates and herbivores, but not carnivore species as they cannot directly label prey(Gosling, 1982; Gosling and Roberts, 2001).

1.6.2.5 Mate attraction hypothesis

The mate attraction hypothesis has been highly associated with females advertising their reproductive state to potential reproductive mates (Lledo-Ferrer *et al.*, 2011). This hypothesis should thus be able to predict high scent marking rates during the mating season as opposed to non-mating seasons when estrous cycles favor copulation.

1.6.2.6 Synchronization of reproductive processes

These synchronization of reproductive cycle hypothesis purports that male odours have a potential to synchronize female's oestrus cycles, and even induce abortion (Gosling and Roberts, 2001). Gosling and Roberts (2001) continue to note that little research has been conducted on this hypothesis.

1.6.2.7 Synchronizing social structure

In this hypothesis, dominant individuals are expected to use scent marking patterns and postures to express their superiority over subordinates. This hypothesis predicts different scent marking patterns for dominants and lower ranking group members.

1.7 Problem statement

In many African countries African wild dogs do survive outside of protected areas, however with very potentially fatal challenges (Woodroffe *et al.*, 2005). Even inside protected areas, ecological factors such as competition with larger and more competitively successful carnivores often drive them to the edges of the parks. This result in African wild dogs suffering edge effects, such as direct and high human induced mortalities due to human-carnivore conflicts, lack of reproductive mates, increased infant mortality and scarcity of natural prey at peripheries of protected areas. Difficulty in accessing scientific information and even baseline data on various aspects of the African wild dog ecology makes it difficult to manage their populations. In the Okavango Delta, lack of published information on the dietary relationship of the wild dogs and their seasonal prey availability dynamics exists. Few published studies quantitatively examined the scent marking behaviour of African wild dogs (but see Jordan et al. 2013). Other previous studies did not address the social, demographic and spatiotemporal aspects of the scent marking behaviour of African wild dogs. Instead, they focused on other factors, such as population ecology (Fuller *et al.*, 1992; Ginsberg *et al.*, 1995b; Lindsey *et al.*, 2004). genetics (Girman *et al.*, 2001), disease (Prager *et al.*, 2012; Woodroffe *et al.*, 2012), human-wild dog conflict (Ogada *et al.*, 2003; Lindsey *et al.*, 2005b), diet (Hayward *et al.*, 2006; Woodroffe *et al.*, 2007) and conservation issues (Moehrenschlager and Somers, 2004; Gusset *et al.*, 2008; Somers *et al.*, 2008).Jordan *et al.* (2013) and Parker (2010) had not adequately described demographic, spatial and temporal scent marking patterns in wild dogs but rather focused on defining the scent marking and its functionality respectively. A study by Parker (2010) experimentally evaluated the functional scent marking properties of African wild dog scent odours, but did not address the ecological and social patterns of this behaviour. However, the study successfully found that wild dogs respond to both foreign and local scents, suggesting that scent marks could be used in maintaining territories. Parker (2010) also elaborated on the biochemical properties of wild dog scents. On the other hand Jordan *et al.* (2013) was limited to redefining the scent marking and differentiating genuine scent marks from eliminatory excreta as attempted earlier by Kleiman (1966). For a group living, social and most importantly endangered species as African wild dogs, a scientific understanding of all fundamental factors underlying scent marking behaviour could be crucial to solving the species' often unharmonious relationship with people resulting from its propensity to range over vast areas. Intrinsic biological factors, including behaviour, can played a critical role in a species's exposure to extinction risk (Cardillo *et al.*, 2004). A sound understanding of the scent marking behaviour coupled with space use habits might aid comprehension of resources use within the context of space and temporal scales. We therefore also require good knowledge on seasonal dietary patterns of African wild dogs and diet's relationship with prey availability. The present study examined demographic scent marking, and dietary patterns and prey availability dynamics of African wild dogs in Vumbura plains (northeastern Okavango Delta) and Linyanti-Selinda areas of northern Botswana

1.8. Research Questions

1. How do demographic factors relate to scent marking behaviour of African wild dogs in the Vumbura and Linyanti-Selinda areas of Botswana?

2. What are the spatial and temporal scent marking patterns of African wild dogs in the Vumbura and Linyanti-Selinda areas of Botswana?
3. How do African wild dog diets relate to prey availability in the Vumbura and Linyanti-Selinda areas of Botswana?

1.8.1 Hypotheses

1. Age, sex, and social rank have a significantly correlate with the scent marking rates of African wild dog individuals in a pack.
2. Wild dogs scent mark more on the territory exterior than the home range interior and mark more during denning than non denning seasons.
3. Season does not significantly correlate with the African wild dogs' diet and relative seasonal prey availability does not have a significant correlation with wild dogs' preference for impala.

1.9 Aim of the study

To contribute to the knowledge of scent marking and dietary patterns of African wild dogs in the northern Botswana.

1.9.1 Specific Objectives

1. To establish which, if any, demographic factors relate to scent marking rates in African wild dogs.

2. To determine temporal and seasonal variations in scent marking rates of African wild dogs in the Vumbura and Linyanti-Selinda areas of Botswana.
3. To determine the seasonal dietary patterns of African wild dogs in the Vumbura Plains and the Linyanti-Selinda areas of Botswana and compare those patterns to prey availability.

1.10 Study areas

1. 10.1 Location

The study was conducted in two study sites, 1) Vumbura Plains and 2) the Linyanti-Selinda Reserves. Vumbura lies on the eastern side of the Okavango Delta panhandle from whence the Selinda spillway joins the Kwando-Linyanti Rivers system from the northeast. Like the Savuti channel, the Selinda spillway sequentially dries and floods as it sustains the contiguity of the Mababe and the Kwando-Linyanti river systems with the Okavango Delta ecosystems respectively (Thomas and Shaw, 1991). The two study sites are characterized by seasonal flood plains that dry up on the edges of permanent swamps and rivers, eventually blending with vast mopane (*Colophospermum mopane*) and Kalahari apple leaf (*Philenoptera nelsii*) woodlands. Permanent swamps are dominated by *Phragmites australis*, *Cyperus papyrus and Imperata cylindrical* communities while seasonal floodplain grasslands are usually characterized by *Panicum repens* and *Setaria sphacelata* communities on shallower waters (Mendelsohn *et al*., 2010).

Vumbura (NG 22) is located between 18 ° 55’48” S and 22° 45’ 07” E, and 18°55 ’49”S and 22° 58’ 26” E (Figure 1.2), while Linyanti-Selinda (NG 15 and 16) is located between18° 38’ 14” S and 23° 27’ 24” E, and 18° 08’ 15” S 24° 05’ 38” E (Figure 1.2). The Linyanti-Selinda area is bordered by Chobe National Park on the east, Moremi Game Reserve to the south past controlled hunting areas, and Namibia to the north. All study sites are privately operated photographic tourism concessions that employ several hundred local residents.

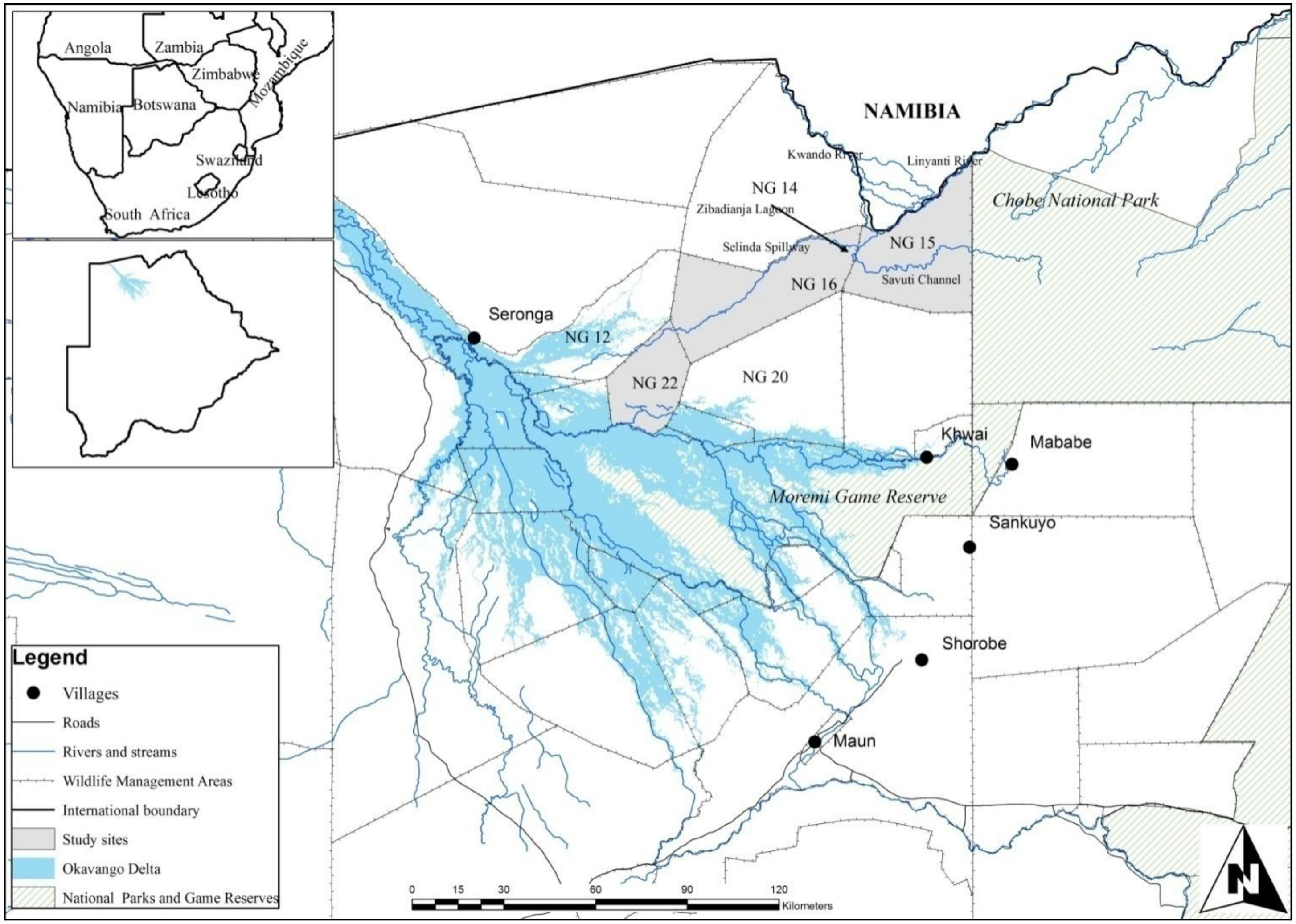

Figure 1.2: The Okavango Delta and the Kwando-Linyanti river systems of northern Botswana. Note the Selinda spillway connecting the Okavango Delta near Vumbura area (NG 22) with the Kwando-Linyanti Rivers systems and the Savuti channel at Zibadianja Lagoon splitting the Selinda (NG 16) and Linyanti (NG 15) areas

1. 10.2 Topography and climate

The Linyanti area (NG 15, Figure 1.2) is generally flat and is separated from the Caprivi strip, Namibia by a fault line of the East African Rift Valley that runs across the Linyanti –Selinda study area as the Linyanti River (Ellery and McCarthy, 1998; McCarthy and Ellery, 1998). The Vumbura study site, like the Linyanti and the rest of the Okavango Delta, sits on a tectonically active intercontinental fault that is slightly tilted. Vumbura receives flood water from channels radiating from the Okavango River (Figure 1.2). In the process the water spreads across the dry seasonal floodplains during the non rainy season and recedes as the next rainy season approaches (McCarthy and Ellery, 1998).

Vumbura site received an annual rainfall of 500mmin 2009 and 436mm in 2010 accordingly (Hensman *et al.*, 2013b). Both study sites experience similar mean minimum and maximum summer temperatures of 30.5° C to 40° C and 14.8° C to 19.2° C, respectively. Winter temperatures range between 25.3C and 28.7 C and night temperatures can fall to 8°C (Ellery *et al.*, 1990). Rainfall in the Okavango is spatially and temporally variable. The rainy season runs from November to March or April, with an average annual amount of 500 mm (Mccarthy *et al.*, 1993). The Okavango Delta's local precipitation is thought to contribute only a third of the annual total water to the ecosystem as almost 10,000 $x10^9$ m^3 (66%) of the water comes from the Angolan highlands as annual inflow through the Okavango River. However, most of this water is soon lost (McCarthy 1993), as evapotranspiration in the Okavango Delta far exceeds precipitation throughout the year (Mccarthy *et al.*, 1992a). These large amounts of water support a variety of floral and faunal communities.

1. 10.3 Fauna

Hippopotamus (*Hippopotamus amphibius*), buffalo, Plains zebra, rhinos (*Diceros bicornis*), giraffe (*Giraffa cameleopardalis*), eland (*Taurotragus oryx*), Blue wildebeest and African elephant (*Loxodonta africana*) represent mega fauna in both study sites. The largest herds of African elephants and other ungulates are found in northern Botswana from the Chobe- Linyanti river systems to the Okavango Delta (Bartlam-Brooks *et al.*, 2011). These large herds, including of zebra, buffalo and wildebeest, seasonally migrate in and out of the Okavango Delta and the Chobe River to Savuti, Mababe, and the Makgadikgadi Pans(Bonyongo, 2004; Brooks and Harris, 2008). *Aepyceros melampus*, red Lechwe (*Kobus lechwe*), Greater kudu (*Tragelaphus strepsiceros*), warthog (*Phacochaerus africanus*), Duiker (*Sylvicapra grimmia*), and Waterbuck (*Kobus ellipsiprymnus*) are common ungulates in the study sites. These medium-sized antelopes are found across a variety of habitat types in the wet season. These and other herbivores congregate in the floodplains during the dry season (May-October), as these areas often get flooded by runoff from the Angolan highlands. Other medium-sized antelopes, such as Tsesebe (*Damaliscus lunatus*) and Sable antelopes (*Hippotragus nigger*) are often found in Vumbura, but rarely so in Linyanti-Selinda.

Leopards, cheetahs, lions, spotted hyaenas, black backed jackals (*Canis mesomelus*) and African wild dogs are the major predators inhabiting both study areas. Several other, smaller carnivores inhabit both study areas as well. Common primates include Vervet monkeys (*Chlorocebus pygerythrus*), Chacma baboons (*Papio ursinus*) and Lesser Bush babies (*Galago senegalensis*).

1. 10.4 Vegetation and Soil

Vumbura site is characterised by a variety of woodland, floodplain and riparian vegetation communities. These communities are well described in (Hensman, 2012; Hensman *et al.*, 2013a). The vegetation types include amongst others Mopane(*Colophospermum mopane*) woodlands, silver cluster-leaf (*Terminalia sericea*) woodlands, Kalahari apple-leaf (*Lonchocarpus nelsii*) woodlands, mixed woodlands, floodplain grasslands, dryland grasslands and open savannah (Mendelsohn *et al.*, 2010).

The Linyanti-Selindasite shows similar vegetation structure to the Vumbura site, but also contains riparian woodlands, permanent and seasonal floodplain grasslands around the Savuti channel and the Kwando and Linyanti rivers (Mendelsohn *et al.*, 2010). Soils adjoining the Vumbura site are mainly composed of Aeolian clay sands on which *Colophospermum mopane* woodlands occur (Wolski and Murray-Hudson, 2005)and alluvial clay soils on the edges of permanent water channels and *Terminalia* woodlands (McCarthy *et al.*, 1992b).

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Chapter Two

Demographic scent marking rate variations of African wild dogs, in Vumbura and Linyanti-Selinda areas, northern Botswana.

2.0 Introduction

Globally, scent marking behaviour has received considerable attention in research projects on many carnivore species e.g. (Bowen and Cowan, 1980; Mills and Gorman, 1987; Kruuk, 1991; Sliwa, 1996; Roberts and Lowen, 1997; Crooks, 2002; Parker, 2010). Territorial scent marking occurs across taxa, (including carnivores and herbivores; solitary and group living animals; and nocturnal, diurnal, and crepuscular species). For example, primates use scent marks to synchronize their intra-sexual interest in opposite sex mates (Heymann, 2000). Even though scent marking is widely used among territorial species, Lledo-Ferrer *et al.* (2011) observed that wild saddleback tamarins (*Saguinus fuscocillis*) used scent marking to facilitate extra-group exchange of reproductive information rather than for territoriality purposes.

Earlier studies that addressed scent marking behaviour in mammals date back to the 1930s (reviewed in Gosling and Roberts, 2001, and Thiessen and Rice, 1976). Those earlier studieswere not clear on their definition of scent marks, but focused on scent mark functionalities.Kleiman (1966)was one of the earliest researchers who attempted to define a scent mark and postulated that scent marks are only those marks that are direct at a conspicuous object and received a response from conspecifics. Ralls (1971), Johnson (1973) and, Verberne and Leyhausen (1976) also studied the scent marking behaviour in mammals. Bowen and Cowan

(1980) later redefined a scent mark as any bodily excretion, or its derivative, deposited by an individual for the purpose of imparting a specific message(s) to conspecifics, such as intruders to deter them from occupying a territorial range. ()Other researchers (Gosling, 1982; Carpenter and Duvall, 1995) redefined this definition to include a temporal component after observing that animals often place scent marks on objects so that they can be detected later in time. The present study adopted the definition provided by Bowen and Cowan (1980) in which scent marking is defined as the application of scented secretions and excretions by an animal on areas or objects in its environment to signal a message to other conspecifics. Thus the present study considered any act of urinating, defecating, back rolling and ground scratching to constitute acts of scent marking.

Like most other large and several smaller carnivores, African wild dogs have evolved an olfactory system to communicate among conspecifics (Creel and Creel, 2002; Jordan *et al.*, 2013). Like lions, leopards, Ethiopian wolves (Sillero-Zubiri and Macdonald, 1998), brown hyaenas (*Hyaenea brunnea*) (Maude, 2010) and spotted hyaenas (Mills and Gorman, 1987) that can communicate through a combination of visual and vocal displays together with scent marking, wild dogs also have a greater tendency for the latter(Creel and Creel, 2002; Parker, 2010; Jordan *et al.*, 2013). Like most other carnivores that use scent marking and vocalizations for territorial maintenance(Kleiman, 1966; Ralls, 1971; Sillero-Zubiri and Macdonald, 1998),African wild dogs rarely vocalize except when making contact calls to others after scattering during a hunt (Creel and Creel, 2002). There is limited understanding of the scent marking behaviour of African wild dogs creates an important scientific knowledge gap worth of exploring.

The subject of scent marking is relatively well understood for some large canids across the world. However, previous studiesfor example, Creel and Creel (2002) elsewhere focused on other behavioural aspects of African wild dogs, but not scent marking behaviour. Except for Parker (2010) and Jordan et al. (2013), the scent marking behaviour of African wild dogs in the northern Botswana, remains poorly studied. Limited published information on this behavioural aspect of the species might be attributed to the logistical difficulty of studying wild carnivores in their natural habitats (Peters and Mech, 1975; Kruuk, 1991; Woodroffe *et al.*, 1997). Yet it is imperative to understand the underlying behavioural ecology of scent marking in African wild dogs by conducting rigorous scientific studies to help fill the current knowledge gap. This chapter contributes to the understanding of the fundamental demographic scent marking behaviour of African wild dogs.

2.1 General Objective

To describe scent marking patterns of African wild dogs among different demographic groups.

2.1.1 Research questions

1. Do dominants and subordinates differ in their scent marking rates?
2. Do adults and young individuals differ in their scent marking rates?
3. Do males and females differ in their scent marking rates?

2.1.2 Hypotheses

1. Dominant individuals scent mark at higher rates than subordinates.
2. Adult individuals scent mark at higher rates than younger individuals in a wild dog pack.
3. Males scent mark at higher rates than females in a wild dogs pack.

2.1.3 Specific Objectives

1. To compare the scent marking rates of dominant and subordinate African wild dogs.
2. To compare the scent marking rates of adult and young African wild dogs.
3. To compare the scent marking rates of male and female African wild dogs.

2.2 Materials and Methods

2.2.1 Study sites

The study was conducted on three wild dog packs in Vumbura Plains, the Okavango Delta and Linyanti and Selinda Reserves in the northern fringes of Botswana (Figure 1.2, Chapter 1). Located between 18°38’00’’ S and 23°27’24’’ E, and 18°08’00’’S 24°00’00’’ E, the study sites occur predominantly in wetland ecosystems. The Linyanti-Selinda areas are on the Kwando Linyanti river confluence and surroundings (Figure 1.2). See Chapter 1 for more details.

2.2.2 Captures: Anaesthesia and Collaring

A total of eight wild dogs were collared, two of which died and collars were replaced onto other live members of the respective packs after refurbishments. A total of four Botswana registered and highly experienced wildlife veterinarians (Dr.Bruce Whittles, Dr. Rob Jackson, Dr Larry Patterson and Dr Eric Verreynne) were used to capture wild dogs following standard protocols. Different combinations of anaesthetic drugs were used in the present study. This comprised of medatomidine, ketamine, atipamezole and telazole. The quantities of drug combinations were variable depending the circumstances of the animal of interest. 1.75mg/kg Meditomedine and 30mg/kg of Ketamine were used to immobilize the animals. Approximately 0.20mg/kg of Atipamazole was used to reverse anaesthesia. The veterinarians used different types of pressure dart guns. In each of the three study packs, two adults were tagged with Very High Frequency (VHF) and global positioning system (GPS PLUS Globalstar-3 VECTRONICS) collars for tracking and GPS data recording and storage, respectively (http://www.vectronic-aerospace.com). Except in the Zib pack , only non-dominant males were tagged because they were less likely to disperse than females (McNutt, 1996b). Telemetry tracking was used to locate the pack for observational data collection.

2.2.3 Behavioural observations

Wild dogs were sampled from the Golden (Vumbura plains), Linyanti (Linyanti-Selinda) and Zibadianja (Linyanti-Selinda) packs. A total of 24 wild dogs from the three study packs were observed for a cumulative total of 2697. 5 hours from August 2010 to April 2012. Focal observations were carried out as described in (Altmann, 1974). These methods have been widely used in behavioural studies of many large carnivores and primates (Altmann, 2001). All study individuals were identified by their individual coat patterns, as no two dogs are ever identical (Creel and Creel, 2002), and were given names. Other physical features, such as torn ears and scars on the body, were also used to identify and differentiate individuals. Scent marking activities of study individuals (all adults, sub adults and yearlings members of the pack) were observed and recorded. This scent marking activities comprised all events of urinations of various gestures, defecations, back rolling and ground scratching. Due to differences on accessibility of terrain and time spent tracking before locating the study animals, observation ‘windows’ varied temporally. To avoid bias due to different total observation times for each individual (i.e., pseudo-replication) that led to compromises interpretation of results in other studies (c.f. Jordan et al. 2013), the individual dog was used as the unit of analysis and data were standardized as marking rates (number of scent marks/hr) for each individual. The study animals were observed between sunrise and sunset (diurnal). Nocturnal observations were not practical to carry out due to logistic, safety and ethical reasons. It would compromised the safety of the study animals to observe them under spot lights at night as that could make them vulnerable to intraguild aggressive (even fatal) interactions with lions and hyaenas. Since the study areas were mesic and largely populated with potentially dangerous animals, tracking and observing wild dogs at night was too risky.

The study animals were easy to closely observe even at less than 10m without them fleeing (*Pers observ*). Whenever necessary, binoculars were used to positively identify individuals. Habituation also permitted close contact with study packs as they moved through their habitats and hunted, although the dogs were often lost during hunts due to thick untraversable vegetation.

Study animals belonged to various demographic groups (adults, sub-adults, yearlings and pups). All pups (< 6 months) were excluded demographic scent marking analysis, as they were highly susceptible to mortalities and presumed to be too immature to functionally participate in scent marking. In addition, sub-adults and yearlings were grouped into a single category, ‘young,’ for the present study. All sampled individuals were profiled by keeping records of their pictures (Appendix 1) and particular activities (i.e. dispersal, death, injuries, etc.) for identification purposes. Mortalities, dispersals and emigrations events were noted throughout the study period. Each individual was further categorised by sex and social rank, either as 1) dominant or 2) subordinate class. Dominant females of each pack were determined based on the last breeding season. Pilot observations helped to determine dominant males whom were found on close associations with the dominant females. The alpha male was determined from the rest other males as the individual which occasionally sniff the genitals of the alpha female and repelled other males from the alpha female. Dominant males were usually recognised by their relatively larger body stature. The reproductive history and intra pack interactions of the alpha pair confirmed by resident, experienced and professional safari guides.

The ages of all individual were recorded and kept; these records were periodically updated during successive sightings over the course of the study period. This permitted updating data on animals as they matured from pups to yearlings, and yearlings to sub adults and ultimately to full adults.

2.2.4 Scent marking sampling

A GPS Unit (Garmin 267C model) was used to record GPS coordinates and time of every observed scent mark. A waypoint was taken at the beginning and the end of an observation window to store GPS coordinates. Observed scent markings and other social interactions during an observation window were recorded. When the study animal(s) were out of view for a particular observation window (i.e., sight of the animal lost during a hunt as they run fast into the vegetation or for any other reason) a waypoint was recorded and another when that particular individual(s) was back in view. The time when the animal(s) were out of view was excluded for scent marking analyses.

A total of 16 adults (66.7 %) and 8 young (33.3%) (≥ 6 months and ≤ 2 years) were observed in the present study for observations. Fourteen males (48.3%) and ten females (41.7%) were observed. Except for the Linyanti pack, where one dominant male was displaced by another as dominant male in the breeding season of 2011, there were 2 dominants (one dominant male and one dominant female) in each of the other packs. The rest of the 17 (70.8%) other dogs were subordinates in their respective packs. Scent marks were considered as any observed event of urination, defecation, back rolling, ground scratching or a combination of two or more of these.

2.3 Data analysis

IBM SPSS Statistics 20 (Field, 2005) was used to analyse scent marking behavioural data. Individuals were grouped by *age, sex* and *social rank.* Dogs were considered adults when they were >2 years old and young when they were < 6months > 2 years old. Each individual's mean scent marking rate was calculated by computing its total number of scent marks against total observations time. Rates of specific forms of scent marking were also calculated. The mean rates of scent marking for each demographic group were calculated and compared. A General Linear Model (GLM) was used to compare mean rates of scent marking among different demographic groups while controlling for other demographic variables. GLM was used because it accommodated unequal sample sizes of my dependent variable (scent marking rates), unlike ANOVA, which is an 'omnibus' test. GLM afforded the ability to tell which predictor variable(s) (sex, social rank and age) were significantly correlated with the dependent variable (Field, 2005).

The test was performed at 95% confidence level and all assumptions of the GLM were met. All results are presented as ± 1 standard error (SE).

2.4 Results

A total of four forms of scent markings (urination, defecation, back rolling and ground scratching) were observed amounting to 857 scent marking events (Table 2.1).The form of scent marks observed with the highest frequency were of urines (57%), followed by defecations (scats,21%), back rolling (20.4%) and lastly ground scratches (1.6%) (Table 2.1). There was no significant difference in the frequency counts of all forms of scent marks by pack ($X^{2} = 11.09$, df = 9, $p > 0.05$) (Table 2.1). After categorically analysing the data by demographic groups , it was found that the highest and lowest mean scent marking rates by a young dogs was 0.41 marks/hr and 0.05 marks/hr respectively (Table 2.2). The highest mean scent marking rate was calculated for a dominant adult male (0.98 marks/hr). While the lowest was of a young subordinate female (0.05 marks/hr) (Table 2.2)

Table 2.1: Various forms of scent marks from the Golden, Linyanti and Zibadianja packs in Vumbura and Linyanti –Selinda areas.

		Wild dog Pack				
	Form of scent mark	**Golden**	**Linyanti**	**Zib**	**Total number of scent marks**	**% Total scent marks**
1	Urinations	227	156	112	495	57.8
2	Defecations	80	75	32	187	21.8
3	Back rolling	76	53	46	175	20.4
4	Ground scratching	12	2	0	14	1.6
5	**Total**	**383**	**284**	**190**	**857**	**100**

Table 2.2: Scent marking rates for individual African wild dogs (*Lycaon pictus*) in the Vumbura Plains and Linyanti-Selinda regions of Botswana. F = female, M = male; Lin = Linyanti pack, Zib = Zibadianja lagoon pack. ** = dog was observed from birth to end of the study. As of between August 2010 to April 2012.n=871 (scent marks).Rate of scent marking in descending order.

Dog Name	**Pack**	**Age**	**Sex**	**Status**	**Observation time (hours)**	**Urinating**	**Defecating**	**Back rolling**	**Ground scratching**	**Mean scent marking rate (marks/hr)**
Gauta	Golden	Adult	F	Dominant	160.2	0.26	0.03	0.08	0.01	0.38
Cally	Golden	Adult	M	Dominant	134.3	0.64	0.10	0.23	0.01	0.98
Motsumi	Golden	Adult	M	Subordinate	142.3	0.04	0.01	0.04	0.02	0.11
SM3**	Golden	Young	M	Subordinate	102.5	0.07	0.07	0.02	0.00	0.16
SF2**	Golden	Young	F	Subordinate	80.1	0.05	0.00	0.00	0.00	0.05
SF1**	Golden	Young	F	Subordinate	98.2	0.06	0.04	0.07	0.02	0.19
Dennis	Golden	Young	M	Subordinate	104.2	0.02	0.06	0.00	0.02	0.10
Browny**	Golden	Young	M	Subordinate	98.1	0.11	0.07	0.04	0.00	0.22
Mokoka	Lin	Adult	M	Dominant	152.4	0.13	0.08	0.03	0.00	0.24
Madame	Lin	Adult	F	Dominant	287.9	0.07	0.02	0.00	0.00	0.09
Comet	Lin	Adult	M	Dominant	128.8	0.21	0.04	0.01	0.00	0.26
Vitali	Lin	Adult	M	Subordinate	144.2	0.06	0.08	0.01	0.00	0.15
Vienna	Lin	Adult	F	Subordinate	58.8	0.48	0.07	0.19	0.00	0.73
Margie	Lin	Adult	F	Subordinate	91.9	0.03	0.01	0.01	0.00	0.05
Zico**	Lin	Young	M	Subordinate	111.4	0.11	0.04	0.03	0.00	0.17
SM1**	Lin	Young	M	Subordinate	96.3	0.17	0.12	0.09	0.02	0.41
Oscar**	Lin	Young	M	Subordinate	96.6	0.12	0.04	0.03	0.00	0.20
Queen	Zib	Adult	F	Dominant	101.0	0.30	0.05	0.06	0.00	0.41
Ngwenya	Zib	Adult	M	Dominant	103.7	0.47	0.09	0.12	0.00	0.68
VHF	Zib	Adult	F	Subordinate	86.4	0.10	0.03	0.14	0.00	0.28
Rhumba	Zib	Adult	M	Subordinate	67.4	0.01	0.04	0.04	0.00	0.10
Nicky	Zib	Adult	M	Subordinate	74.0	0.09	0.00	0.01	0.00	0.11
Hearty	Zib	Adult	F	Subordinate	102.2	0.04	0.05	0.03	0.00	0.12
Blackie	Zib	Adult	F	Subordinate	74.8	0.12	0.01	0.07	0.00	0.20

The mean scent marking rate of adults was 0.30 ± 0.26 marks/hour, while the mean scent marking rate of the young was 0.19 ± 0.09 marks/hour. Although substantially higher, the mean scent marking rate of adults (n = 16) was not significantly higher ($F_{1,\ 23} = 0.36$, $p = 0.58$) than that of the young (n = 8) (Figure 2.1). Similarly, the rates of adult scent marking with urine, feaces-, back rolling and ground scratching was not significantly different ($p > 0.05$) (Figure 2.1)

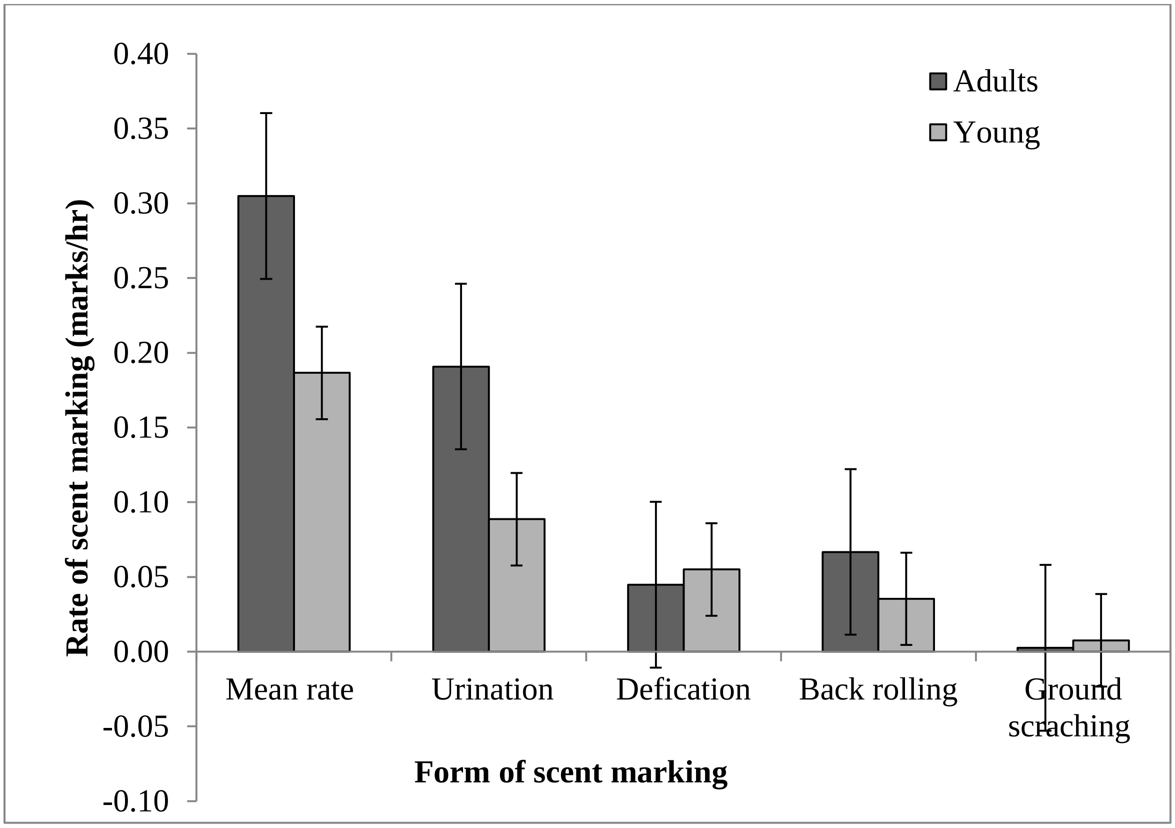

Figure 2.1: Mean (+SE) rates of different forms of scent marking for adult and young African wild dogs (*Lycaon pictus*) in the Vumbura Plains and Linyanti-Selinda regions of northern Botswana.

Dominant individuals scent marked at a significantly higher mean rate than subordinates ($F_{1, 23}$ = 4.74, p = 0.04). Dominants (n =7) scent marked at mean rate of 0.43 ± 0.12 marks/hour, while subordinate dogs (n = 17) scent marked at a mean rate of 0.20 ± 0.03 marks/hour (Figure 2.2). The mean rate of urine marking by dominant dogs was significantly higher than that of subordinates (p = 0.03). However, adults' mean rates of scat marking, back rolling and ground scratching was not significantly higher (p> 0.05) than that of young dogs (Figure 2.2).

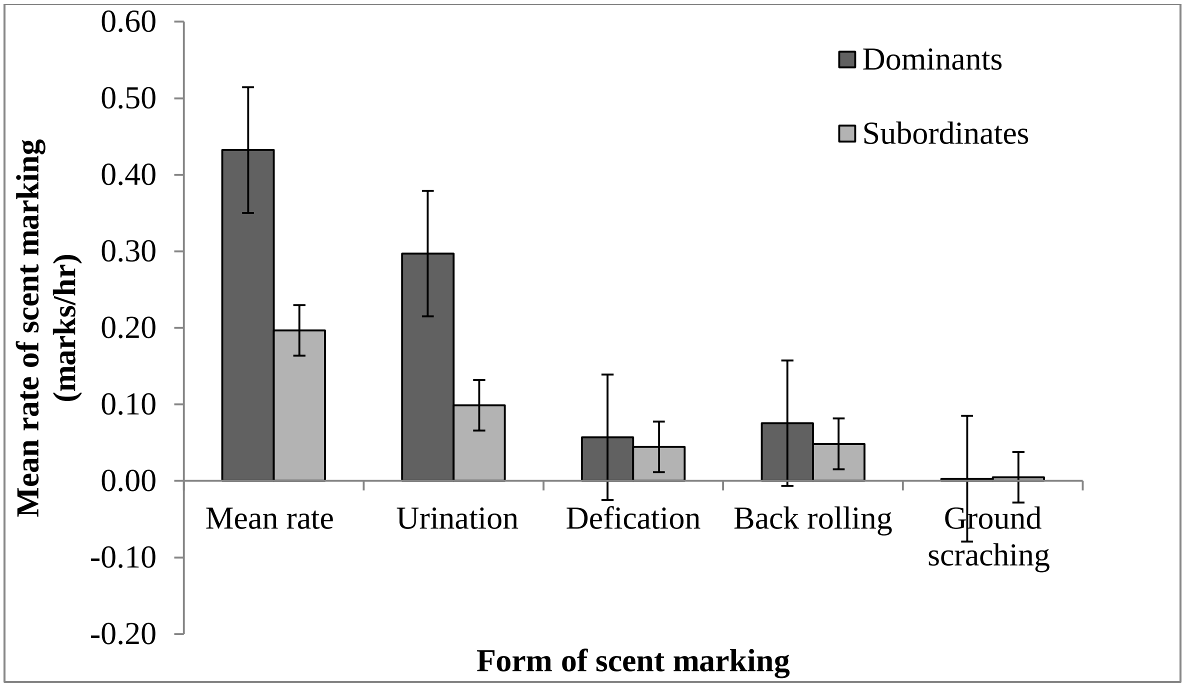

Figure2.2: Mean (+SE) scent marking rates using different forms of scent marks of dominant and subordinate African wild dogs (*Lycaon pictus*) in the Vumbura Plains and Linyanti-Selinda regions of northern Botswana.

Male wild dogs scent marked at higher rates than females. The mean scent marking rate of males (n = 13) was 0.40± 0.15 marks/hour, while that of females (n = 10) was 0.25 ± 0.08 marks/hour. The difference was not significant ($F_{5, 18}$ =1.18 $p = 0.29$) (Figure 2.3). Similarly, there were no significant differences between males and females ‘s rate of urine marking , scat marking, back rolls and ground scratching ($p > 0.05$).

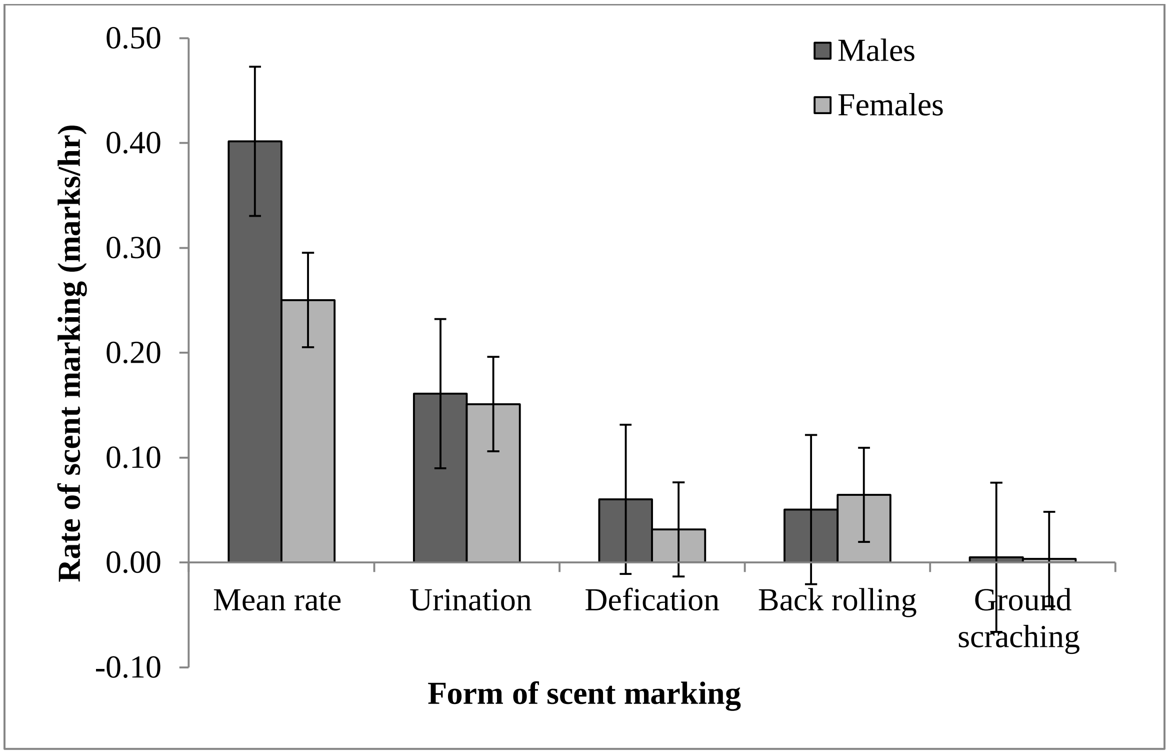

Figure 2.3: Mean (+SE) scent marking rates using different forms of scent marks, of males and females African wild dogs (*Lycaon pictus*) in the Vumbura Plains and Linyanti-Selinda regions of northern Botswana.

2.5 Discussion

As is common among members of the family Canidae, African wild dogs use urine marks more than other forms of scent marks (Table 2.1) (Bekoff and Wells, 1986; Gese and Ruff, 1997; Pal, 2003). Jordan *et al.* (2013) also found that wild dogs significantly urine marked more than they marked with other forms of scent marking. On the other hand, very few (1.6%) ground scratches were observed (Table 2.1). This contrasts with a conclusion on *Canis familiaris* (Cafazzo *et al.*, 2012) study, where 18.3% (n = 782) ground scratches were observed. In the presence of adequate drinking water, greater urine marking makes intuitive sense. In the present study, wild dogs had access to drinking water almost constantly. Observations of wild dog populations in more arid environments like the Kalahari might find different results.

The high frequency of urinating may also have been for primarily eliminatory purposes. Similarly the problem of differentiating urines and defecations deposited for eliminatory and genuine signalling has been noted by many past studies on the scent marking behaviour of mammals (Ralls, 1971; Bowen and Cowan, 1980; Bekoff and Wells, 1986; Boydston *et al.*, 2006). Nonetheless, the present study adopted a broader definition of what constituted a scent mark. In the present study, adult wild dogs scent marked at higher rates than younger members of the pack, though the difference was not significant. Though also not significantly different, adults also urine marked and back rolled at higher rates than younger dogs. The opposite was true for defecations and ground scratching (Figure 2.1).This was possibly because younger dogs did not necessarily urinate to confer a communicative gesture as mature older individuals might, but rather more for eliminatory purposes (Blaustein, 1981). Adults probably used urinations (as described in Jordan et al. 2013) to place a scent mark and not simply for excretory purposes. Given their relatively longer experience, adult wild dogs were likely much better at understanding the purpose and functions of scent marking compared with younger individuals. In addition, adults may use scent marking to signal specific messages to the young than vice versa; for instance, to synchronize intra-pack sociality or express sexual or reproductive status among themselves (Lledo-Ferrer *et al.*, 2011).Hence, the lack of a significant difference in the mean scent marking rates of young and adults could have resulted from my inability to differentiate between simple excretory eliminations and scent marking. Another possible explanation for lack of significance in the scent marking rates of the two age groups could be the small sample size, as the Zibadianja pack had no young individuals for the two study years due to mortality. The loss of pups to lion kills (n = 4) and other unrecorded infanticide events could have influenced the pack's sociality and hence its scent marking behaviour. The findings of the present study did not support the hypothesis that adults scent mark at significantly higher rates than younger dogs. The hypothesis originated from studies that linked scent marking to territorial behaviour in other canids(Gosling and Roberts, 2001; Roberts, 2011), and the expectation that young dogs would be least expected to express territoriality against conspecifics.

When comparing scent marking rates by social status, dominant dogs' mean scent marking rates were significantly higher than those of subordinates (Figure 2.2). Dominants also urinated at significantly higher rates than subordinates. This was probably because dominants signal their superiority to the latter using scent marks and physical gestures. Another possible reason for the higher scent marking rates of dominants could imply sexual and reproductive status signals between each other using urinary and scats scents. Since reproduction is usually exclusive to the dominant pair (Creel and Creel, 2002), sexual messages might have been packaged in scent marks. The lack of a significant difference in the rates of other scent mark forms (Figure 2.2) could be attributed to the smaller sample sizes (Table 2.1) and higher standard errors (Figure 2.2). The present study's finding suggests support for the hypothesis that increased scent marking rates may signal good health to opposite sex members and sexually suppress subordinates as found in house mice (*M.misculus domesticus*; Zala et al. 2004). In the present study, dominant pairs appeared relatively well nourished, displayed good body statures and probably in good health throughout the study period, except for the dominant male in the Linyanti pack (Mokoka, Table 2.1, and Appendix 1). Previous studies found that sexual receptivity by females and a male's good health are often indicated by increased scent marking rates (Creel and Creel, 2002; Zala *et al.*, 2004). Creel and Creel (2002) also found a relationship between endocrine levels and sexual suppression of subordinates by dominants. Richardson (1991)andSliwa (1996) also found that that dominance correlated positively with scent marking patterns of *Proteles cristatus,* as patrolling dominant males scent marked more frequently, especially at their territory boundaries.

The sexual variations can be manifested in morphology, physiology and behavioural activities of animals. The present study found no significant difference between the mean scent marking rates of males and females. Lack of statistically significant difference in scent marking rates for all forms of scent marks might be attributed to the tight social bonds among pack members. Sexes are less likely to compete for resources at the pack level. In other species scent marking rates varied by sex**.** For example, female house mice noticed and were attracted to a frequently scent marking male as an indication of good health (Zala *et al.*, 2004). House mice, (*Mus musculus*) show mating preference for healthy individuals and differentiate healthy and diseased individuals through odours (scents) (Zala *et al.*, 2004). Female *Mus musculus* also tend to avoid inbreeding with related males through odours triggered in the major histocompatibility genes (Yamazaki *et al.*, 1976). However, the present study's findings contrasted with those for aardwolves, where males scent marked more frequently than females at territory boundaries (Richardson, 1991; Sliwa, 1996). Nonetheless, aardwolves are largely solitary, so males increase their scent marking intensity when foraging at territories boundaries to advertise their presence to potential intruders and reproductive mates (Richardson, 1991). Male wild dogs did not need to intensify scent marking rates to attract potential reproductive mates at territory boundaries since potential reproductive mates could occur within the pack (except for potential dispersers).

2.5.1 Summary

Dominance status correlated significantly with the scent marking rates of wild dogs, but age and sex did not. Begg et al. (2003) and Sillero-Zubiri andMacdonald (1998) also found that dominance and age influenced scent marking patterns in honey badgers (*Mellivora capensis*) and *Canis simensis*, respectively. The findings of the present study partially supported the hypothesis that demographic factors relate to the scent marking behaviour of African wilds dogs as:

- There was a significant relationship between social rank or status and scent marking rates of individual wild dogs within a pack.
- Dominant individuals' scent marked at significantly higher rates than subordinates.

- Dominant dogs‘s urine marked at significantly higher rates than subordinates.
- Adults did not scent mark at significantly higher rates than young dogs.
- Males and females did not significantly differ in their scent marking rates.

2.6 Link with next Chapter

Territoriality and scent marking behaviours are usually related in carnivore species (Bekoff and Wells, 1986; Mills, 1993; Roberts and Lowen, 1997; Lazaro-Perea *et al.*, 1999; Gosling and Roberts, 2001; Lledo-Ferrer *et al.*, 2011). The present study provides some support for this as the Zibadianja and Linyanti packs were reported fighting on the overlap zone of their home ranges on two different occasions. The two packs were also observed scent marking on the overlap area. Although this chapter did not focus on movement and space use, the territorial defence hypothesis with respect to scent marking may be connected to the fights on the packs' home range boundaries. During these antagonistic encounters, aggression was sex-biased, with same sex counterparts attacking each other from the two packs (*e.g.,* the Zib pack dominant female fatally injured the Linyanti pack dominant female).This led to the serious ill deterioration of the Linyanti dominant female's health. This behaviour has also been found in east African wild dog populations (Creel, 2001; Creel and Creel, 2002). Thus, the next chapter discusses the spatiotemporal context of African wild dog scent marking.

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Chapter Three

Spatial and temporal variation in African wild dogs scent marking rates in northern Botswana.

3.1 Introduction

Scent marking is a common form of communication mechanism in many mammals (Ralls, 1971; Johnson, 1973; Verberne and Leyhausen, 1976; Lledo-Ferrer *et al.*, 2011), including primates and carnivores (Mills and Gorman, 1987; Richardson, 1991; Sillero-Zubiri and Macdonald, 1998; Jordan *et al.*, 2007; Parker, 2010). African wild dogs also communicate with each other through scent marks and physical postures. One hypothesis of the functional purpose of scent marking is to demarcate territories (Johansson *et al.*, 1995; Johansson and Olof, 1996; Gosling and Roberts, 2001; Crooks, 2002). Territorial behaviour should thus be an energetically expensive endeavor, as it includes defence of vast geographical ranges (Ralls, 1971; Gosling, 1982). This suggests that if scent marks are used to maintain territories, the animal has to strategically distribute them spatially and temporally. Hence, many large canids should intensify scent marking rates at particular times and home range locations (Roper *et al.*, 1993; Begg *et al.*, 2003; Jordan *et al.*, 2007). For example, Maude (2010) reported that *Hyaenea brunnea* increased pasting rates during the 'lean season' when food resources were scarce and decreased pasting rates during the 'peak season', when home range sizes decreased too.

African wild dogs are territorial (Creel and Creel, 2002; Parker, 2010); however, it is not well understood how they use scent marks to maintain exclusive territories. Like many other large carnivores, African wild dogs have been observed to scent mark as they traverse their ranges (Parker, 2010; Jordan *et al.*, 2013), possibly for various other reasons that include territory demarcation. It is thus important to enhance scientific knowledge on the wild dogs' spatiotemporal distribution of scent marks across their home ranges.

Two studies attempted to understand the scent marking behavior of African wild dogs in northern Botswana. Parker (2010) attempted to experimentally describe and quantify African wild dog scent compounds by extracting, identifying, and testing for chemical compounds in their scent marks. Parker (2010) successfully tested and compared the responses of resident packs to foreign and even their own scent marks. Yet, that study did not explore spatial and temporal patterns of African wild dog scent marks. Parker (2010) and Jordan et al. (2013) did not attempt to qualify how and where wild dogs deposit their scent marks. However, many mammals are known to specifically deposit their scent marks on particular environmental substrates (Barja 2009). The present study aimed to examine those patterns more precisely by examining the spatiotemporal distribution of scent marks at home range cores, intermediate and boundaries zones and marking substrates.

3.2 General Objective

To compare the spatiotemporal distribution of scent marks and marking substrates of African wild dogs.

3.2.1 Research questions

1. How are African wild dog scent marks distributed across their home ranges zones?
2. How do African wild dog mean scent marking rates vary between the denning and non denning seasons?
3. Is there a significant difference in African wild dog mean scent marking rates during the wet and dry seasons?
4. Do African wild dogs mark on some certain substrates more than others?

3.2.2 Hypotheses

1. African wild dogs scent mark densities are significantly higher at boundaries than cores and intermediate home range zones.
2. African wild dogs mean scent marking rates are higher during the non-denning than denning seasons.
3. African wild dogs scent marking rates are higher during the dry season than during the wet seasons.
4. Since grass is spatially ubiquitous in their ranges, African wild dogs deposit more scent marks on grass than on other substrates.

3.2.3 Specific Objectives

1. To determine seasonal home ranges of African wild dogs in the Vumbura, Selinda-Linyanti parts of Northern Botswana.
2. To determine the spatial distribution of African wild dog scent marks across different home range zones.
3. To compare scent marking densities of wild dogs across different home range zones.
4. To compare mean scent marking rates of African wild dogs during the denning and non-denning seasons.
5. To compare mean scent marking rates of African wild dogs during the wet and dry seasons.
6. To investigate African wild dogs scent marking post substrates.

3.3 Materials and Methods

3.3.1 Study areas

The study was conducted in Vumbura on the northeastern Okavango Delta and the Linyanti–Selinda Area of Botswana. The study sites are described in detail in Chapter One (Figure 1.1).

3.3.2 Methods

Over the entire study period, each study pack included at least one adult wild dog fitted with a GPS collar (GPS PLUS Globalstar-3VECTRONICS) and another with a VHF telemetry collar (Africa Wildlife Tracking, Sirtrack). The VHF collar was used for tracking (by triangulation) and locating study packs for behavioural observations, while the GPS collars were programmed to record and store nine GPS coordinate fixes every day. GPS data were used to plot and map seasonal home ranges for the rest of the pack, as wild dogs are group living animals (Creel and Creel, 2002), thus it was presumed that the GPS data was representative of the pack movements . By extension the rest of the pack's home range was inferred from the GPS collar on the tagged pack member. The general home ranges of the study packs were spatially vast (Appendix 2) and temporally varied (Figure 3.1-3.6). The batteries of the GPS collars were refurbished about every 10 months.GPS collars had the capacity to also record mortality and activity data about the tagged animal; however the data was not analyzed and presented in the present study. Immobilisations of wild dogs were performed by a qualified and licensed wildlife veterinarian. Generally, drug doses were given as a set amount per unit body weight of the animal. Approximately 1.75 mg Meditomedine and ~30 mg Ketamine was used to anesthetise the animal using a high pressure dart gun (ref Chapter 2). The animal was collared and bio samples were collected during the 45 minutes of anaesthesia effect. After completing these tasks, approximately 15 mg Atipamezole, depending on the body mass of the animal, was injected to wake the animal and it took a mean of 7.3 ±1.5 SD minutes (n = 5) for the wild dog to stand on its own. The animals took an additional 9-12 minutes to appear "normal" and join the rest of the pack. A UHF receiver was used to periodically download GPS, activity and mortality data from the GPS collars from a vehicle at a range of 1m to 300 m, depending on the thickness of the vegetation.

Following Altmann (1974)'s, All Occurrences and *Ad lib* sampling methods were used to observe and record a total of 871 scent marks during observations. A set of Bushnell, 10x50 Binoculars were used to facilitate observations of the animals. A Garmin 276C model GPS unit was used to record the geographic coordinates of every observed scent marking event in the field. The habitat and substrate on which the scent mark was deposited was also recorded. The date and exact times of scent marking were automatically recorded along with the GPS coordinates in the GPS unit.

The locations of the packs were split into wet (November - April) and dry (May - October) seasons. The denning season was defined as any time in the study period when the pack was known to be denning and observed at an identified active den site, with an identified den location that constrained the pups to that site before the litter could join the pack for hunts. The non-denning season was defined as any period when the pack was nomadic, with and without the new litter. Kernel Density Estimates in Hawth's tool extension was used to determine home ranges from location data in Arc Map 9.3. The Kernel Density estimator was set at 50%, 75%, and 95% percentage volume contours to calculate utilisation distributions within home ranges. Kernels Home range estimators were chosen rather than Minimum Convex Polygon (MCP) that calculates the area of a polygon that includes all telemetry points. The MCP does not accurately provide the true outline of the home range as it treats points that were rarely visited equally with those that were considerably traversed. Fixed Kernels were more accurate in distinguishing those points. Hence Fixed Kernels Density estimates in Hawth's tool were used to accurately to map home range cores from intermediate and edge home range boundaries of the study packs(Worton, 1987).

3.4 Data analysis

Mean rates of scent marking for individuals of different socio-demographic groups were analyzed by season to avoid potential problems of pseudo-replication (i.e., the individual dog was the unit of analysis), as has compromised interpretation of results from past studies (c.f., Jordon et al. 2013).Scent marks were grouped by individual wild dogs and analyzed as densities for spatial analysis. For ease of presentation, scent mark densities are presented as number of scent marks/100 km^2 and rates as number of scent mark per hour.

The home range edge was defined as the part of the home range for a particular season that fell between the 75% and 95% probability kernel home ranges. The home range core was defined as the 50% probability kernel home range, while the area between the core and the boundary was considered to be the intermediate zone.

Home ranges, as opposed to territories, were used to negate the debate of definitions as discussed in Burt (1943). It is difficult to distinguish within a home range where the territories begin and end, especially without contiguous pack home ranges. Territories are specific areas within a home range that contain resources defended by an individual against conspecifics (Hawes, 1977; Mitani and Rodman, 1979); these areas are likely to shift, shrink and expand in space through time. Densities of seasonal scent mark distributions were calculated by each individual during each season and grouped by demographic categories. In SPSS, an Independent *t*-test with assumed equal variances was used to test for significance of differences in the scent marking rates of wild dogs. Levine's test was used to test for homogeneity of variances ($t = -1.668$, df = 41, $p < 0.05$) among the samples before performing an independent *t*-test. All data were examined for normality using the Shapiro-Wilk and Anderson-Darling tests and passed the tests. A General Linear Model was used to examine the association between socio-demographic variables and scent marking rates. Analysis of Variance was used to test for significance in the rates of scent marking within the three home range zones. Significance was set as $p < 0.05$. Results are presented as ± 1 standard error (SE).

3.5 Results

3.5.1 Distribution of scent marks across home range zones

Neither pack (GLM, t = -0.35, p = 0.73) nor wet vs. dry season (GLM, t = 0.89, p = 0.38) significantly influenced scent marking densities across home range zones; therefore the data from different packs and wet/dry seasons was combined together for further analyses. Most scent markings were recorded within the seasonal home range cores (79.43 %, n = 632 scent mark locations) compared to the middle (9.97 %, n = 632) and edges (10.60 %, n = 632) (Figures 3.1 - 3.6).

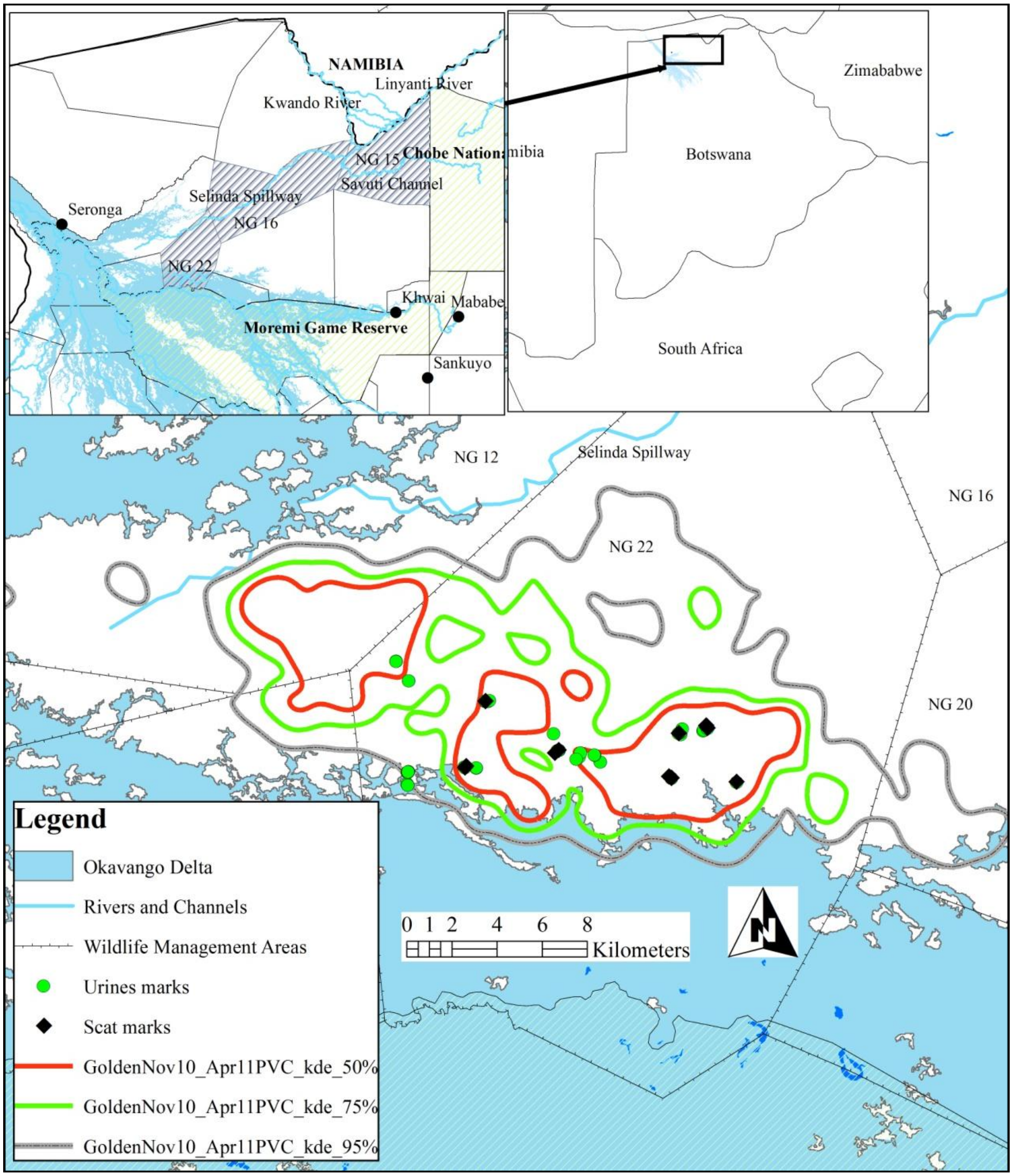

Figure 3.1: Scent mark locations from African wild dogs (*Lycaon pictus*) of the Golden pack in Vumbura Plains of the Okavango Delta in Botswana with respect to different home range zones during the wet season of November 2010 to April 2011.The area enclosed inside the 50% kernel contour is considered the core zone, 50% and 75% kernel contours is considered the intermediate zone, and the area between the 75% and 95% kernel contours is considered edge zone.

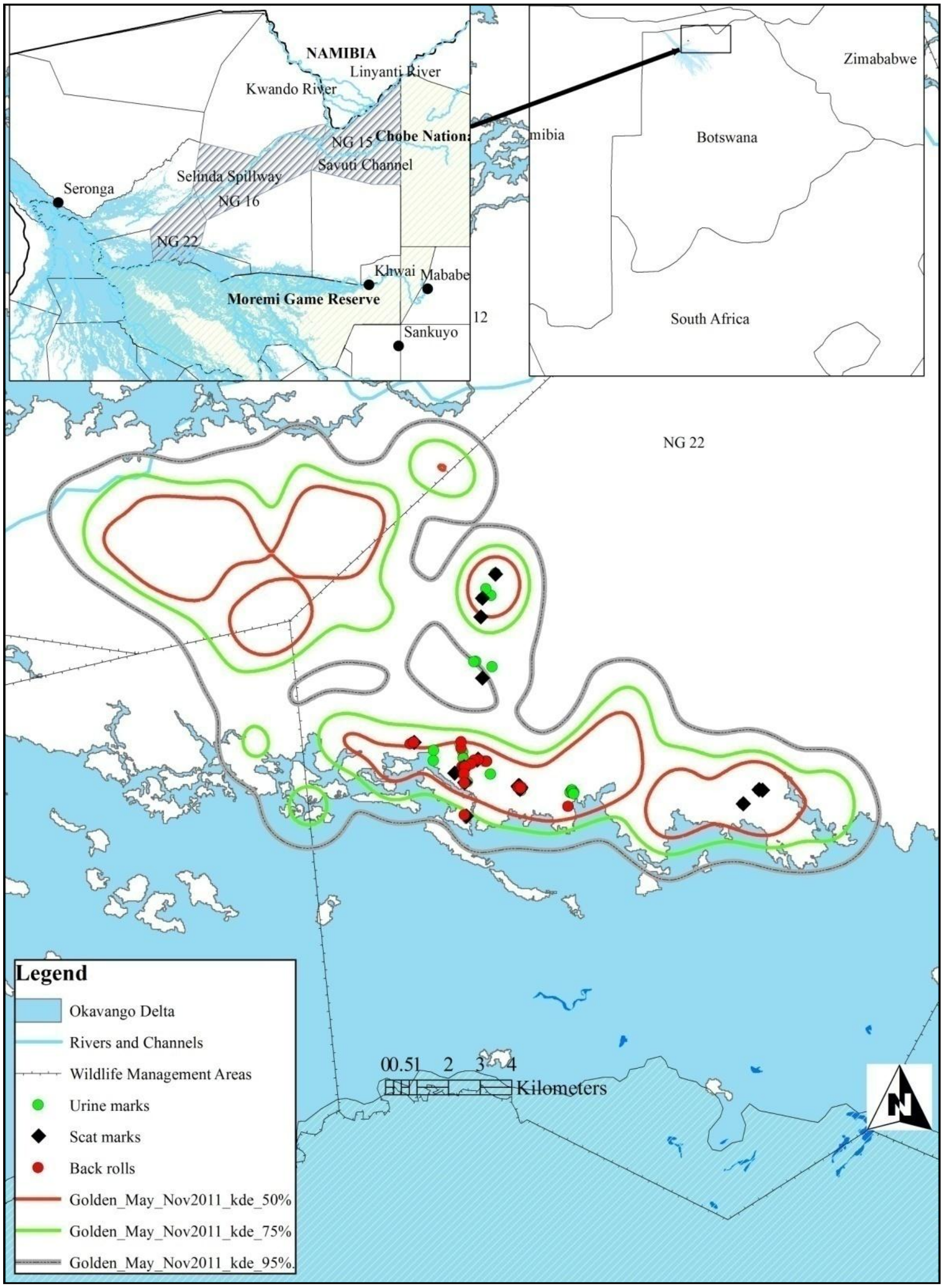

Figure 3.2: Scent mark locations from African wild dogs (*Lycaon pictus*) of the Golden pack in Vumbura Plains of the Okavango Delta in Botswana with respect to different home range zones during the dry season of May 2011 to October 2011.The area enclosed inside the 50% kernel contour is considered the core zone, 50% and 75% kernel contours is considered the intermediate zone, and the area between the 75% and 95% kernel contours is considered edge zone.

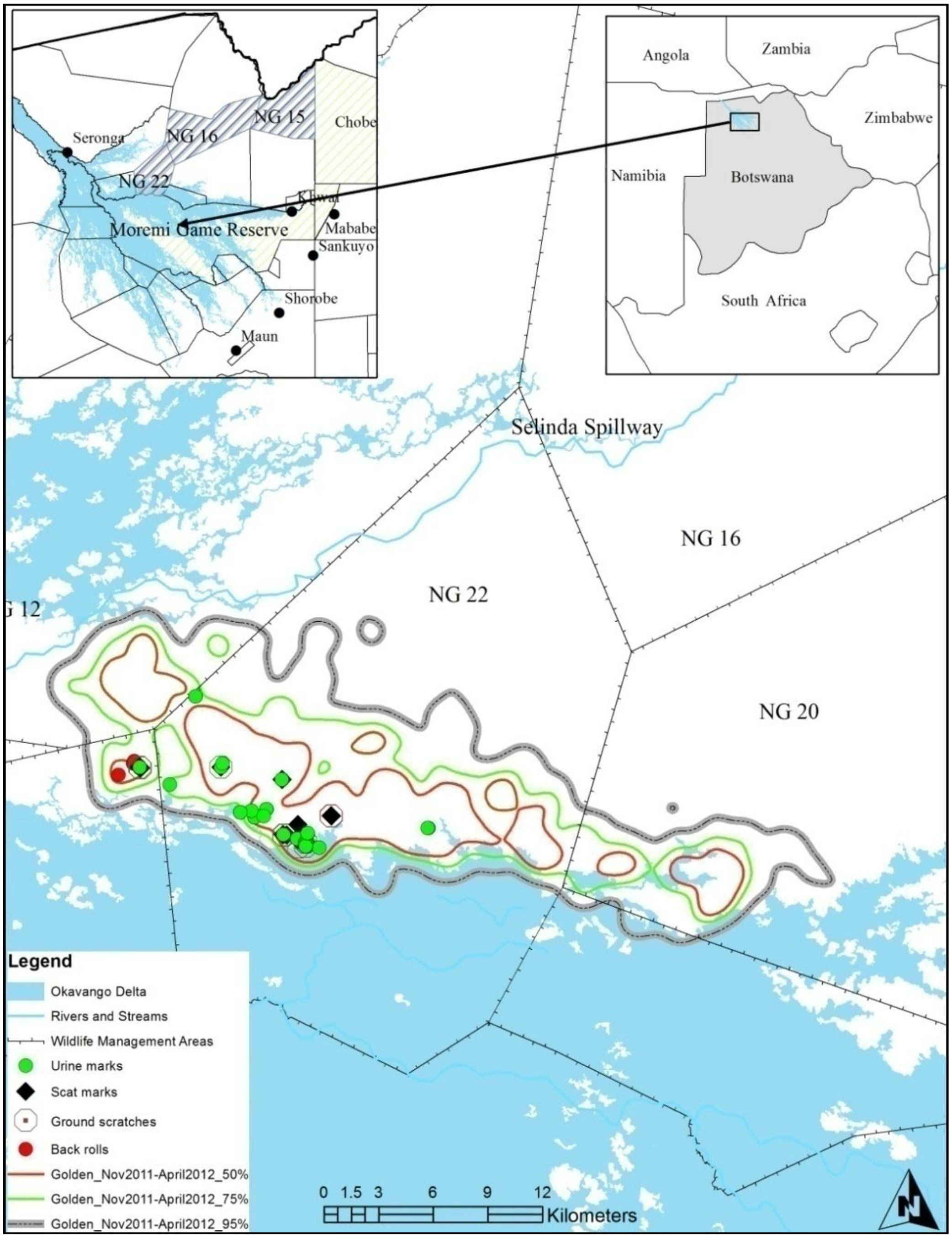

Figure 3.3: Scent mark locations from African wild dogs (*Lycaon pictus*) of the Golden pack in Vumbura Plains of the Okavango Delta in Botswana with respect to different home range zones during the wet season of November 2011 to April 2012.The area enclosed inside the 50% kernel contour is considered the core zone, 50% and 75% kernel contours is considered the intermediate zone, and the area between the 75% and 95% kernel contours is considered edge zone.

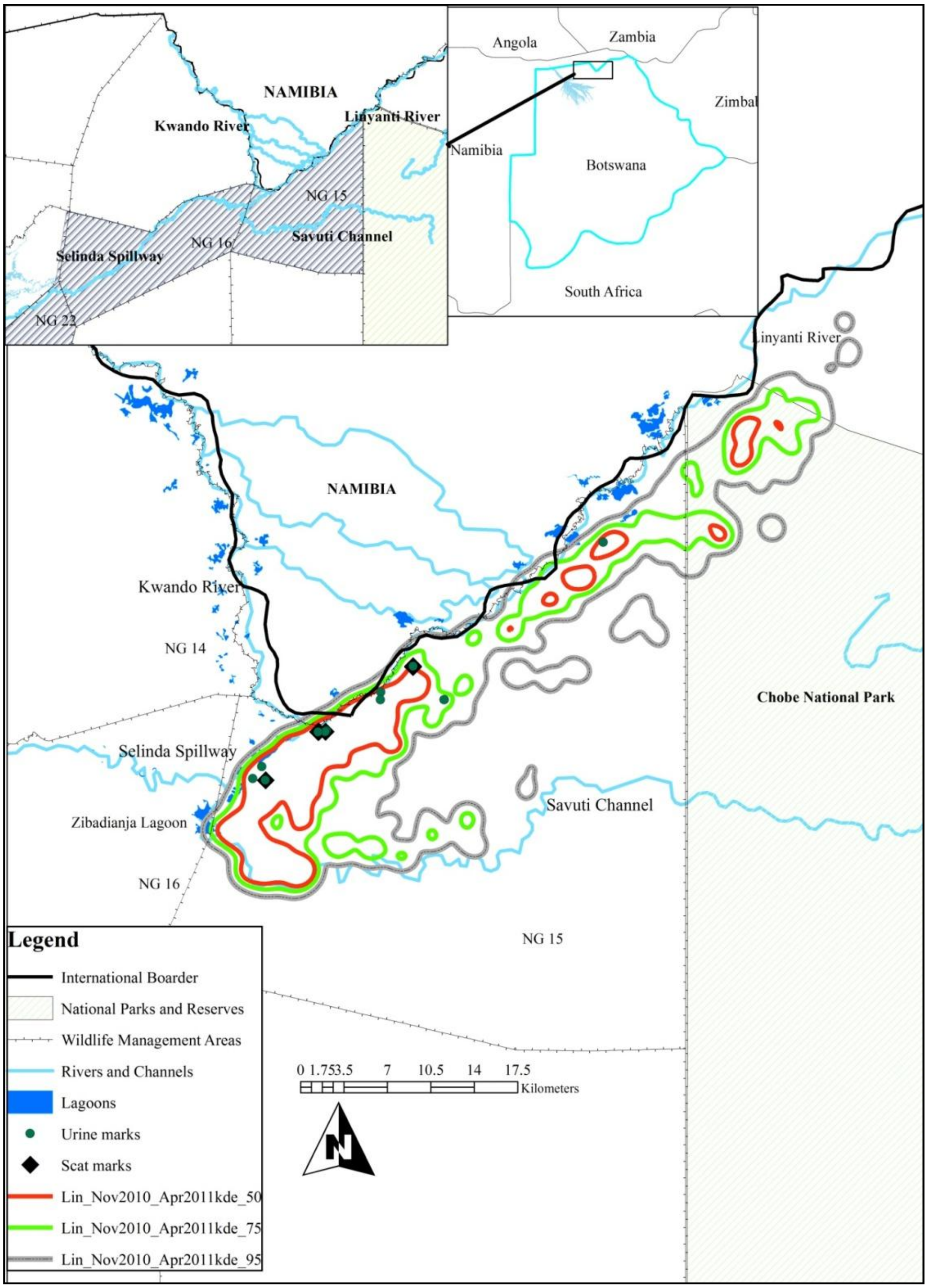

Figure 3.4: Scent mark locations from African wild dogs (*Lycaon pictus*) of the Linyanti pack in Linyanti-Selinda areas in Botswana with respect to different home range zones during the wet season of November 2010 to April 2011.The area enclosed inside the 50% kernel contour is considered the core zone, 50% and 75% kernel contours is considered the intermediate zone, and the area between the 75% and 95% kernel contours is considered edge zone.

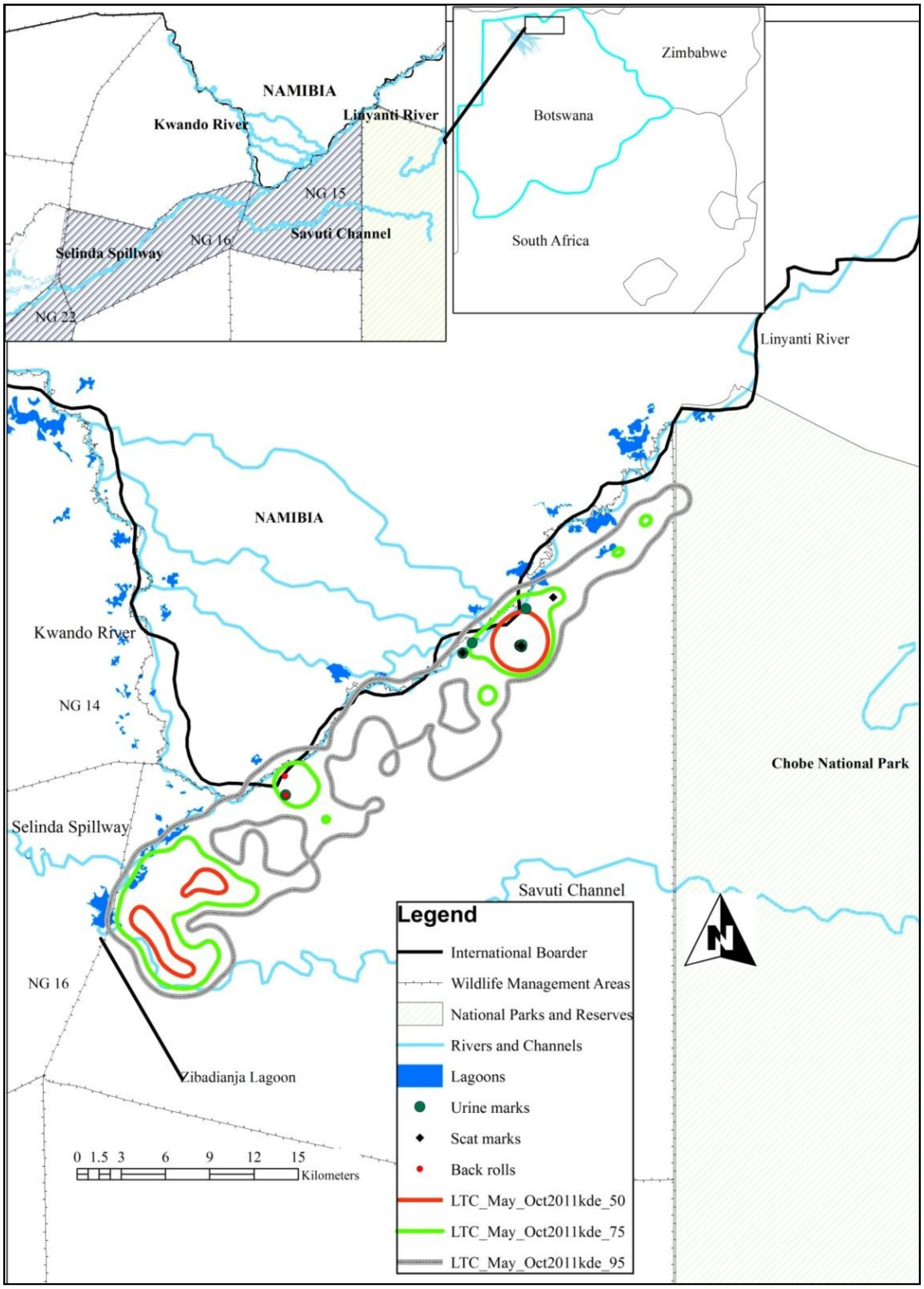

Figure 3.5: Scent mark locations from African wild dogs (*Lycaon pictus*) of the Linyanti pack in Linyanti-Selinda areas in Botswana with respect to different home range zones during the dry season of May 2011 to October 2011.The area enclosed inside the 50% kernel contour is considered the core zone, 50% and 75% kernel contours is considered the intermediate zone, and the area between the 75% and 95% kernel contours is considered edge zone.

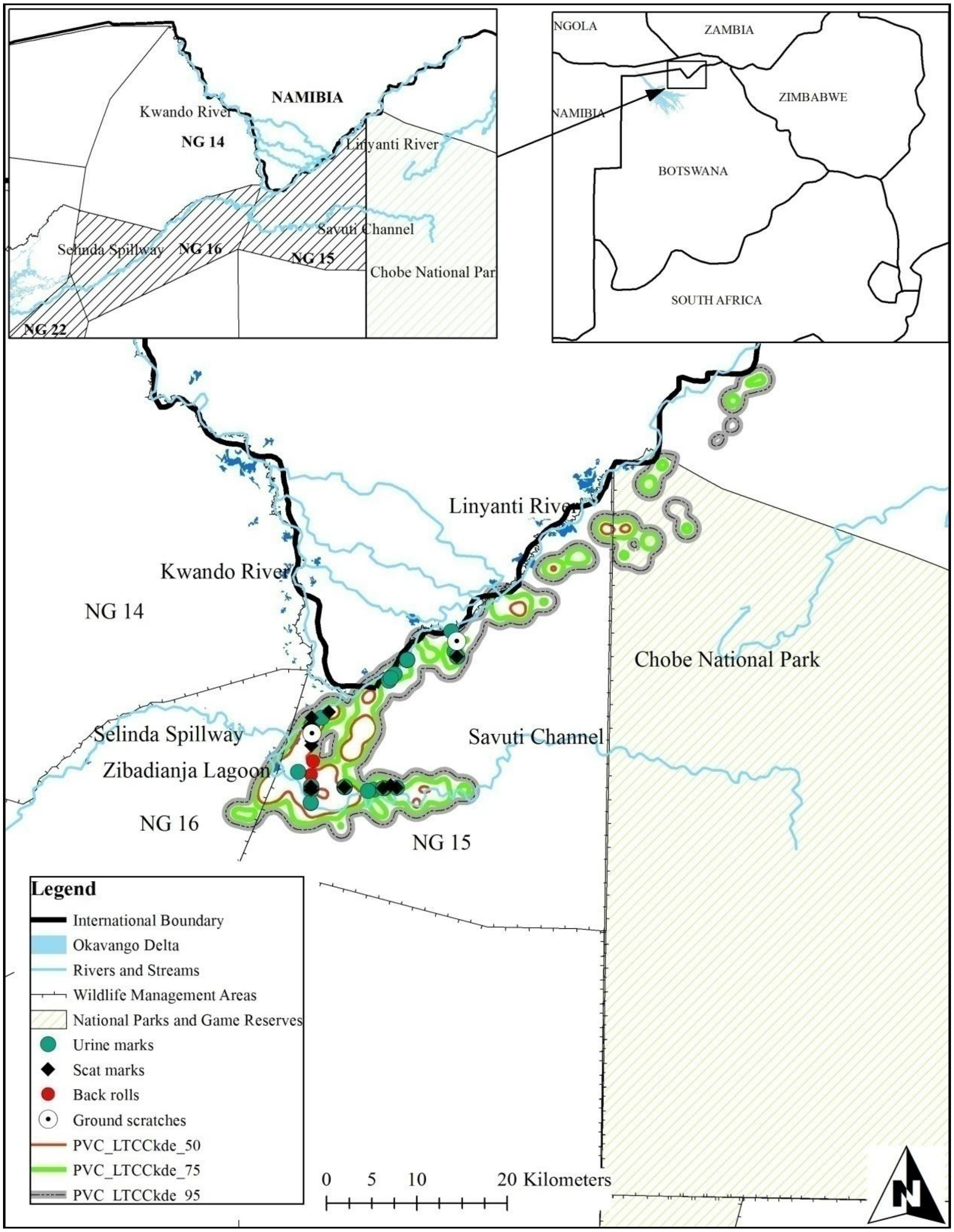

Figure 3.6: Scent mark locations from African wild dogs (*Lycaon pictus*) of the Linyanti pack in Linyanti-Selinda in Botswana with respect to home range zones during the wet season of November 2011 to April 2012.The area enclosed inside the 50% kernel contour is considered the core zone, 50% and 75% kernel contours is considered the intermediate zone, and the area between the 75% and 95% kernel contours is considered edge zone.

3.5.2 Scent mark densities by socio-demographic group

Seasonal home range zone areas (Table 3.1) were used to calculate scent mark densities of the packs. Wild dogs in all socio-demographic groups analyzed demonstrated a very similar pattern of higher scent mark densities within the core zones of their home ranges, as opposed to the intermediate and edge zones (Figure 3.7). The density of scent marks deposited by males (75.5 marks/100 km^2) was significantly ($F_{2,18}$= 6.53, $p < 0.01$) higher at home range core zones than at intermediate zones (9.4 marks/100 km^2) and the edges (3.8 marks/100 km^2) (Figure 3.7). This was also true for females, whose scent marks densities (40.8 marks/100 km^2) were significantly ($F_{2,18}$= 6.53, $p < 0.01$) higher at home range core zones than at intermediate (5.1 marks/100 km^2) and the edges zones (2.9 marks/100 km^2) (Figure 3.7). Similarly, adults' scent mark density was significantly ($F_{2,\ 18} = 13.05$, $p < 0.01$) higher at home range core zones (86.7 marks/100 km^2) than at intermediate (10.0 marks/100 km^2) and edge zones (6.7 marks/100 km^2) (Figure 3.7). Likewise, pups' scent mark densities were also significantly ($F_{2,\ 18} = 5.65$, $p = 0.01$) different when analyzed by home range zones. However, the scent mark densities of sub-adults did not significantly ($F_{2,\ 18} = 1.43$, $p = 0.27$) vary between home range zones (Figure 3.7). A comparison by social status of individuals showed that scent mark densities dominants and subordinates significantly ($p < 0.05$) differed at various home range zones (Figure 3.7).

While the same trend of wild dog scent mark densities held for each type of scent marking used, these differences were not always significant (Fig. 3.7). There was a significantly ($F_{2,\ 18} = 10.10$, $p < 0.01$) higher density of urinations at home range core zones than intermediate and edge zones

(Figure 3.7). This was also true for the density of defecations ($F_{2, 18} = 7.20$, $p < 0.01$) deposited in the home range core zones (28.3 marks/100 km^2) against the intermediate home range (3.0 marks/100 km^2) and edge zones (0.9 marks/100 km^2). However, there was no significant difference in the scent mark densities of back rolls ($F_{2, 18} = 2.86$, $p = 0.08$) and ground scratching ($F_{2, 18} = 1.00$, $p = 0.39$) among the home range zones.

Scent mark densities did not significantly ($F_{2, 36} = 1.22$, $p = 0.31$) vary between males (3.81 marks/100 km^2) and females (2.91 marks/100 km^2) within all home range zones (Fig. 3.7). Similarly, the density of scent marks at any particular home range zone did not significantly ($F_{2, 36} = 0.17$, $p = 0.85$) vary between dominants (64.39 marks/100 km^2) and subordinates (51.89 marks/100 km^2) (Fig. 3.7). Alternatively, scent marking densities of adults significantly ($F_{4, 54} = 5.31$, $p < 0.01$) varied among different home range zones as compared to those of sub-adults and pups (Fig. 3.7). Scent marking densities among home range zones varied significantly ($F_{6, 72} = 0.4.44$, $p < 0.01$) by type, with a higher density of urinations (66.52 marks/100 km^2) than other scent mark types (Figure 3.7).

Table 3.1: Seasonal home range zone areas (km^2) of the three study packs. The Zibadianja Pack GPS collar malfunctioned and the pack could not be located for the respective seasons as indicated in the table.

	Golden pack			**Linyanti pack**			**Zibadianja pack**		
Home range zone	Nov 2010-April 2011	May 2011-Oct 2011	Nov 2011-April 2012	Nov 2010-April 2011	May 2011-Oct 2011	Nov 2011-April 2012	Nov 2010-April 2011	May 2011-Oct 2011	Nov 2011-April 2012
Core	81.6	51.4	98.1	102.1	20.1	76.5	-	-	91.8
Intermediate	89.9	48.1	86.3	114.3	56.6	98.3	-	-	138.9
Boundary	151.4	91.7	143.2	236.2	169.8	202.5	-	-	256.9

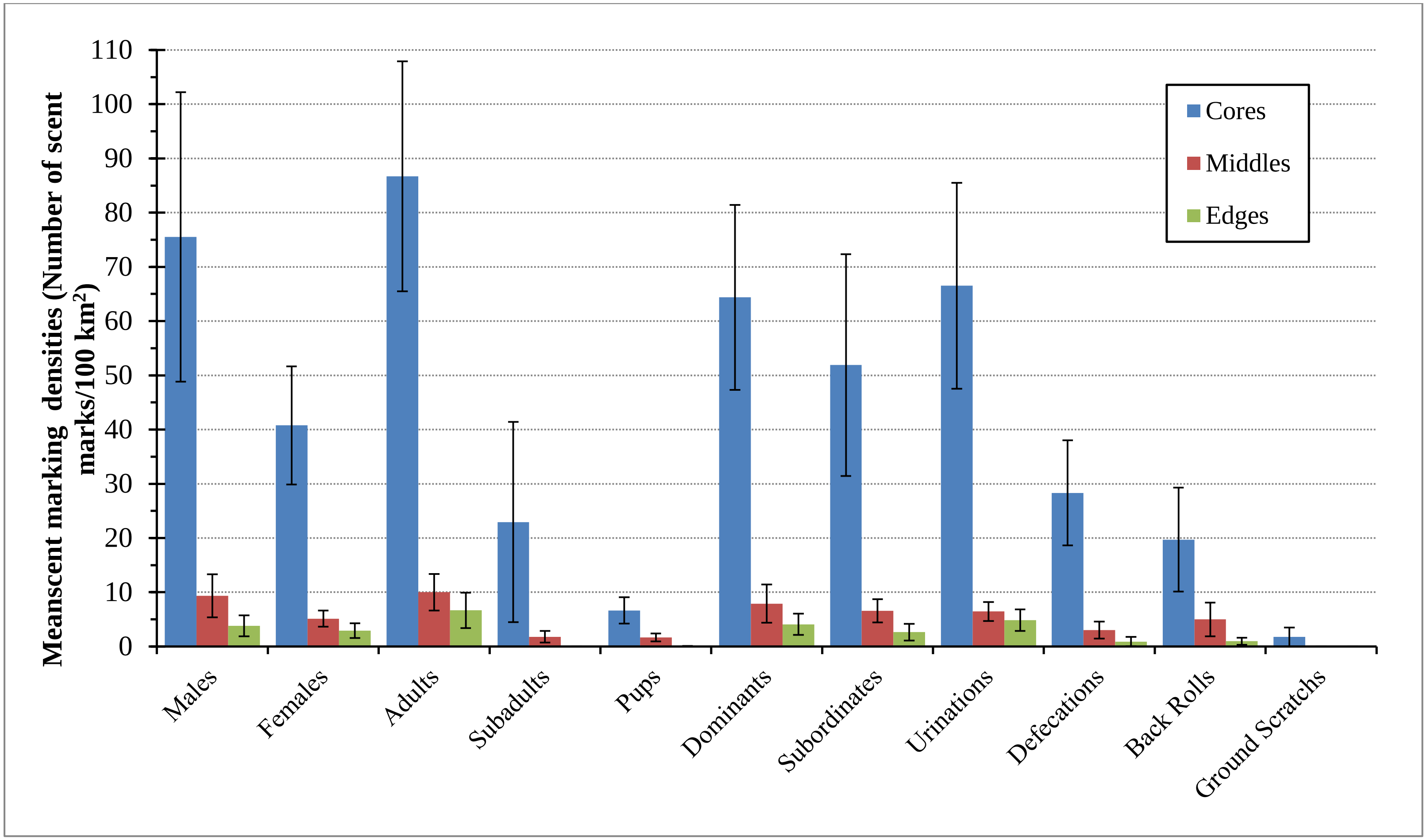

Figure 3.7: Mean scent marking densities of African wild dogs (*Lycaon pictus*) across their home ranges in Botswana. The home ranges were separated into three zone, i) core, ii) intermediate (= Middle) and iii) edge.

3.5.3 Scent marking rates during different seasons

The mean scent marking rates of wild dogs did not significantly (*t* = -1.67, df = 41, *p*> 0.05) differ between the wet (0.41 ± 0.12 marks/hour) and dry (0.23 ± 0.32 marks/hour) seasons. Seasonal scent marking rates of wild dogs were further analysed by their demographics. During the dry seasons, both males and females scent marked at rates which were not significantly (*t* = 0.03, df = 22, *p* > 0.05) different. Similarly, the mean scent marking rates of males was not significantly (*t* = 0.34, df = 23, *p* > 0.05) higher than of females in the wet season (Figure 3.8). During the denning period, the scent marking rates of males (0.18 marks/hour) and females (0.08 marks/hour) were not significantly (*t* =1.64, df = 23, *p* > 0.05) different. Similarly, the scent marking rates of males and females in the non-denning periods was also not significantly (*t* = 0.30, df = 23, *p* > 0.05) different (Figure 3.8).

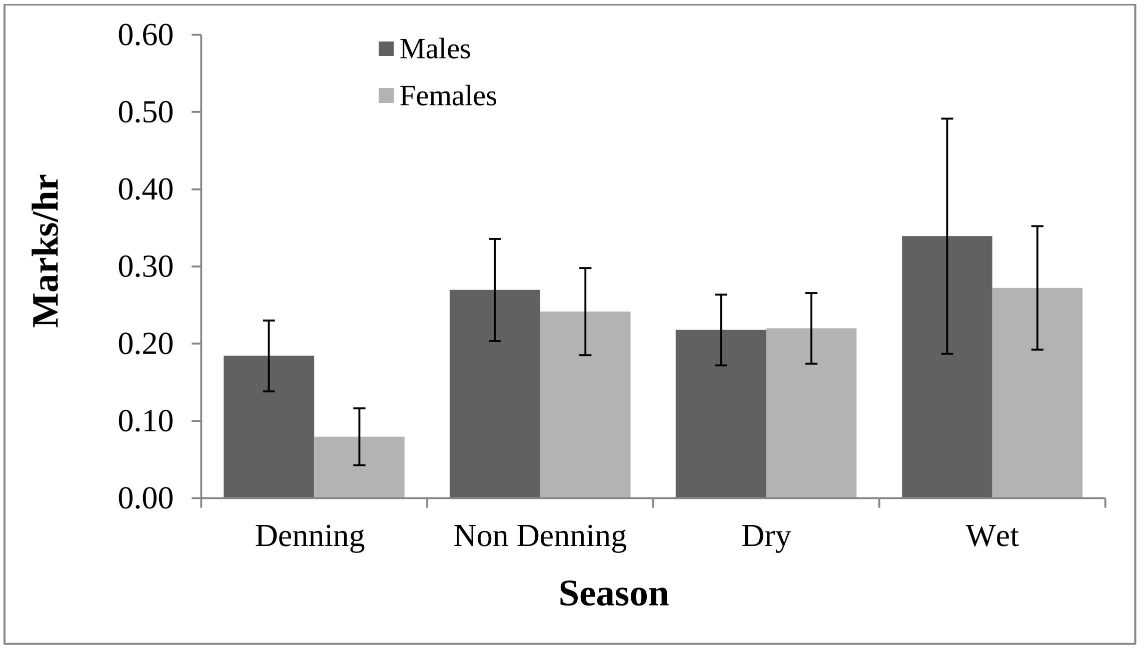

Figure 3.8: The seasonal scent marking rates of male and female African wild dogs (*Lycaon pictus*) in Vumbura and Linyanti-Selinda regions, northern Botswana.

Even though adults scent marked at higher rates than young during both wet and dry season, the difference was not significant (t =1.23, df = 23, $p > 0.05$ and t =1.24, df = 23, $p > 0.05$, respectively) (Figure 3.9). There was no significant (t = -1.66, df = 45, $p > 0.05$) difference in the mean scent marking rates of wild dogs between the denning (0.16 ± 0.03 marks/hour)and non-denning (0.26 ± 0.04 marks/hour)periods. Adults scent marked a rate not significantly (t = -0.25, df = 23, $p > 0.05$;t = -0.36, df = 23, $p > 0.05$) higher than of the young during both denning and non denning periods respectively (Figure 3.9).

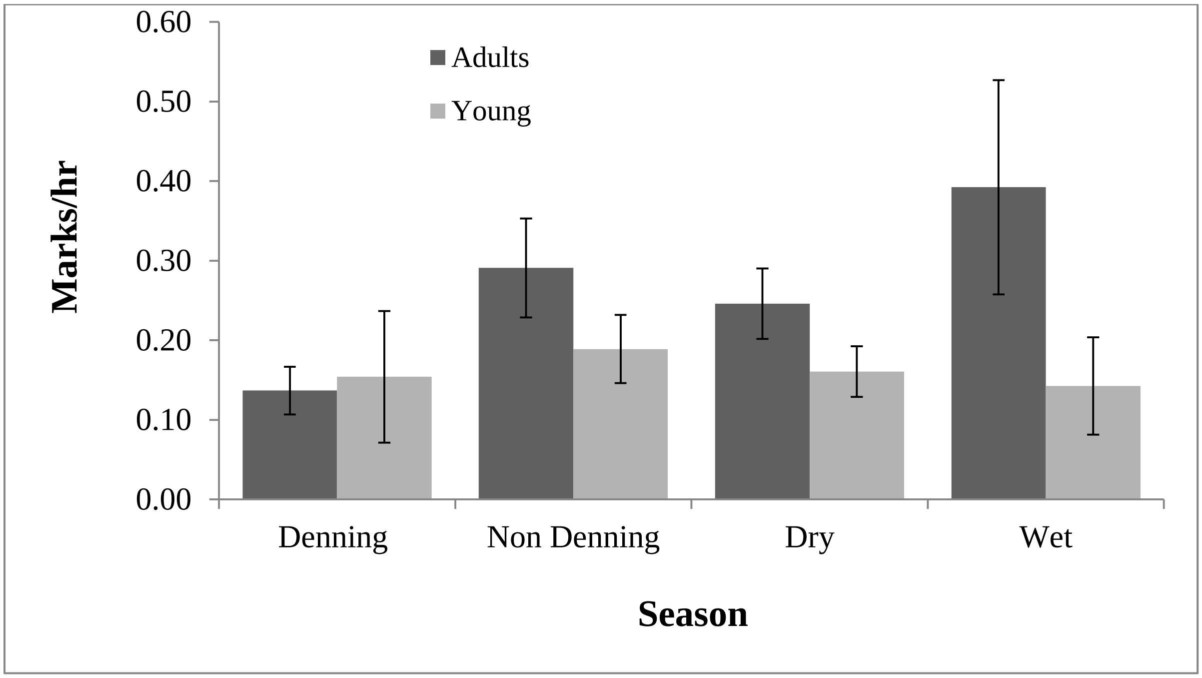

Figure 3.9: The seasonal scent marking rates of adult and young African wild dogs (*Lycaon pictus*) in Vumbura and Linyanti-Selinda regions, northern Botswana

Table 3.2: Mean scent marking rates (marks/hr) of African wild dogs (*Lycaon pictus*) during the denning and non-denning, wet and dry season for the Golden, Linyanti (Lin) and Zibadianja accordingly. Individual dogs arranged by pack of origin.

				Period		**Season**	
Dog name	**Sex**	**Age**	**Pack**	**Denning**	**Non- denning**	**Dry**	**Wet**
Gauta	F	A	Golden	0.370	0.440	0.428	0.449
Cally	M	A	Golden	0.250	0.970	0.607	2.306
Motsumi	M	A	Golden	0.060	0.080	0.083	0.098
Dennis	M	S	Golden	0.060	0.100	0.148	0.083
Browny	M	S	Golden	0.710	0.130	0.133	0.065
SM3	M	S	Golden	0.000	0.160	0.273	-
SF1	F	S	Golden	0.150	0.180	0.305	-
SF2	F	S	Golden	0.000	0.050	0.130	-
Madame	F	A	Linyanti	0.106	0.079	0.396	0.260
Margie	F	A	Linyanti	0.062	0.037	0.062	0.037
Comet	M	A	Linyanti	0.239	0.275	0.239	0.275
Mokoka	M	A	Linyanti	0.261	0.220	0.261	0.220
Vitali	M	A	Linyanti	0.120	0.180	0.120	0.181
SM1	M	S	Linyanti	0.168	0.451	0.165	0.455
Oscar	M	S	Linyanti	0.118	0.240	0.105	0.337
Zico	M	S	Linyanti	0.027	0.201	0.027	0.201
Vienna	F	A	Linyanti	-	0.527	**-**	0.527
F1	F	A	Zibadianja	0.000	0.436	0.291	0.774
F2	F	A	Zibadianja	0.108	0.214	0.189	0.329
F3	F	A	Zibadianja	-	0.324	0.299	0.164
Hearty	F	A	Zibadianja	-	0.129	0.100	0.183
M1	M	A	Zibadianja	0.375	0.720	0.636	0.865
M2	M	A	Zibadianja	0.094	0.110	0.104	-
M3	M	A	Zibadianja	0.094	0.106	0.202	-
M5	M	A	Zibadianja	0.188	0.101	0.163	-
				0.162	**0.258**	**0.228**	**0.411**

3.5.4 Scent marking substrates

African wild dogs scent marked mostly on grass (69.6%, n = 871), followed by bare ground (19.2%, n = 871), then tree branches (7.6%, n = 871), and finally water (3.6%, n = 871) (Figure 3.10). However, this finding should not be interpreted as to mean African wild dogs preferred to scent mark more on grass than other substrates, as the proportion of each available substrate was not quantified.

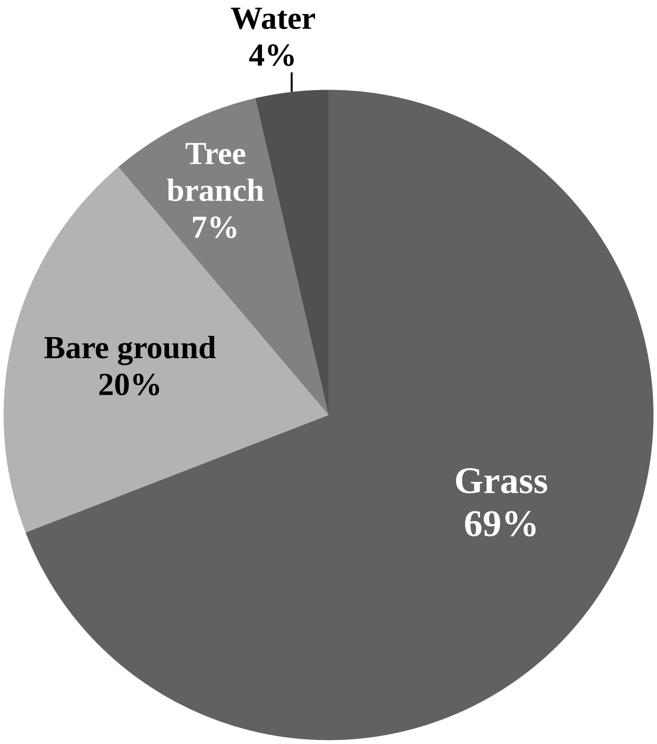

Figure 3.10: The scent marking post substrates marked by African wild dogs (*Lycaon pictus*) in Botswana. ‘Grass’ actually includes vegetation layers below~1m including herbaceous plants but not tree shrubs.

3.6 Discussion

3.6.1 Distribution of scent marks in home range zones

The results of the present study show a scent marking distribution pattern that is not consistent with the territorial fence hypothesis, as scent mark densities were higher in home range cores than in the intermediate and edges of home ranges (Figure 3.7).These results suggest that scent marks serve functions other than mere territoriality. However, the present study did not attempt to delineate wild dog territories from their broader home ranges. Possibly, home range core zones are proxies for territories. If so, a measure of territorial space can be inferred from the former (Hawes, 1977; Jonsen *et al.*, 2005).

The distribution of scent marks in the present study favours the scent cloud hypothesis as described by Parker (2010). The results also support Parker (2010)'s conclusion that the distribution of African wild dogs scent marks results from their movements, rather than is dictated by a conscious pursuit for maintaining their territories through scent marks. Unlike *Canis familiaris* (Cafazzo *et al*. 2012), wild dogs did not show evidence of creating scent fences using their scent marks as the home range core zones were more densely scent marked than peripheral zones. Habitat utilisation may explain the distribution of African wild dog scent marks. However, the present study lacked in mapping the vegetation and relating the distribution of scent marks to physiography, vegetation and hydrology. Thus the spatiotemporal distribution of scent marks could not be related to such aspects of the environment.

In several other species (Richardson, 1991; Begg *et al.*, 2003), males scent mark at higher densities at home range boundaries than their female counterparts, as they bear a greater responsibility for territorial defence (Richardson, 1991). For example, Sliwa (1996) reported that male aardwolves scent marked more at territory edges than females. However, the present study found no significant difference in scent mark densities between dogs of different sexes. The lack of such significant difference could be attributed to small sample sizes of male and female scent marks within each home range zone.

3.6.2 Seasonal scent marking rates

There was no significant seasonal variation in wild dog mean scent marking rates (Table 3.1, Figs. 3.8.and 3.9), contrary to *Meles meles* that showed seasonal variations in latrine marking (Roper *et al.*, 1993). The denning season is probably the period where dominance and subordination are reinforced through scent marking and aggression (Johnson, 1973; Creel and Creel, 2002), as yearling cohorts (referred categorically in the present study as 'young') graduate into sexually maturing sub-adults. Thus potentially opening 'dominance vacancies' that, along with other 'stochastic variables such as levels of stress hormones, health of the dominant, etc,' may help potential dominance contenders challenge the incumbents and neighbouring packs's dominants (Jordan, 2007).Post denning period is followed by escalation of aggression and intrapack tensions (*pers. observ.*) as maturing young adults, especially females, are more likely to disperse from their natal packs (McNutt, 1996b),creating social space for the next young cohort.

Similarly, there was lack of a significant difference in mean scent marking rates between wet and dry seasons which led to rejection of the hypothesis that mean scent marking rates would be higher during the dry season when scarce food resources require defence. These results suggest that African wild dogs probably do not defend food resources using scent marks, as opposed to *Hyaenea brunnea* that intensify scent marking rates during the ‘lean’ dry season (Maude, 2010), possibly to defend resource holding territories. However, the present study did not examine the relationship between scent marking and food resource defense. Such a study might help us understand why and where wild dogs scent mark in light of the Resource Dispersion Hypothesis (RDH) and or the Territory Inheritance Hypothesis (TIH) (Lindström, 1986). If the territorial defense hypothesis holds, wild dogs should variably place scent marks in certain places and not others.

3.6.3 Substrate marking

Mammals probably make conscious decisions as to when and where to deposit scent marks. (Johansson *et al.*, 1995; Pal, 2003; Barja, 2009). In the present study, African wild dogs mostly deposited their scent marks on grass despite the fact that grass as a post substrate, was prone to being degraded by flood water or burned by veldt fires (Alberts, 1992). This suggests that wild dog scent marks are probably not long leaved and not offers little support for the territorial hypothesis as articulated by (Roberts, 2012b). Other studies also found that other species seemed to consciously select where to deposit their scent marks. For example, *Canis lupus* significantly scent marked on wooden plants over herbaceous plants as marking posts (Barja, 2009), while *Oreotragus oreotragus* marked on low tree brunches and shrubs significantly more than other locations (Roberts and Lowen, 1997). In the present study, grass was ubiquitous in wild dog ranges and that could possibly explain the higher marking frequency on grass as opposed to other substrates such as shrubs and water bodies. Future studies should quantify the availability of potential wild dog marking substrates and compare scent marking frequency and substrates usage.

3.6.4 Summary

- African wild dogs' scent mark distributions did not significantly vary by season.
- The densities of African wild dogs scent marks were significantly higher in home range core zones than intermediate and edge zones.
- Mean scent marking rates of African wild dogs denning and non-denning were not significantly different between sexes and age groups.
- African wild dogs marked significantly more on grass than on other substrates.

3.5 .Link with next chapter

Scent marking behaviour and foraging habits are a spatiotemporal phenomena. When animals scent mark, they often do so to establish and or defend a particular resource(s), such as food or reproductive mates, against conspecifics. To understand if dogs defend food resources, it is necessary to first examine the dietary habits of Africa wild dogs in the study areas and relate those data to home range utilization. It is important to understand the relationship between these two aspects of African wild dog ecology. The next chapter discusses dietary characteristics of the African wild dogs in the Vumbura and Linyanti-Selinda areas study sites.

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Chapter Four

Diurnal African Wild Dog Diets and Seasonal Prey Availability in the Vumbura and Linyanti-Selinda Areas of Botswana

4.0 Introduction

Effective carnivore management requires a sound understanding of species ecology within several disciplines, including behaviour, physiology, and community ecology. The present study seeks to understand the dietary patterns of African wild dogs in northern Botswana. These data can subsequently be used to explore if and how wild dogs use scent marks to defend food resources. Diets varies considerably among large and widely distributed carnivores, such as *Panthera leo* (Elof, 1973) and *Canis lupus* (Lui and Jiang, 2003). African wild dog diets also vary across their geographic ranges (Woodroffe and Ginsberg, 1999a; Creel and Creel, 2002; van der Meer *et al.*, 2014). Variations in dietary composition result from an array of biotic and abiotic factors. The primary factor determining predator diets is availability of prey. Anti-predatory mechanisms used by prey also influence the dietary habits of carnivores (Schoener, 1971; Dawkins and Krebs, 1979).

Classic theories on predator-prey relationships and competition for food resources such as Malthus-Verhulst's *logistic theory*, Lotka-Volterra *logistic equations*, and Michaelis-Menten-Holling *modifications* (reviewed in Berryman, 1992), attempted to explain how animals forage. After some attempts to explain predator –prey relations (Berryman, 1992),the Optimal Foraging

Theory (OFT) was later proposed (MacArthur and Pianka, 1966), and has since provided the theoretical basis for many foraging studies. The (OFT)purports that a forager thrives to maximise energy intake while expending the least possible energy (MacArthur and Pianka, 1966; Perry and Pianka, 1997). OFT has been successfully supported in many predator-prey studies. However, its validity has been questioned in other studies (Pierce and Ollason, 1987; Sih and Christensen, 2001). For instance, in carnivores that must catch mobile prey, a carnivore's diet might simply depend on its killing rate (Pierce and Ollason, 1987). The hunting success of a predator depends on three critical functions: a) prey encounter rate, b) rate of prey detection by the predator, and c) probability of successful capture and killing of detected prey (Fanshawe and Fitzgibbon, 1993; Creel and Creel, 1995; Creel, 1997; Creel and Christianson, 2008). OFT does not incorporate anti-predator mechanisms evolved by prey to counter predation. Critics of OFT point to a bias that over-estimates probability of successful predation following detection (Pierce and Ollason, 1987). As such, the theory is more relevant for predators that incur little additional energy costs capturing and killing prey after detecting it. Previous studies found that wolves preyed on white tailed deer (*Odocoileus virginianus*) (Kunkel and Pletscher, 2001) and elk (*Cervus elaphus*) (Bergman *et al.*, 2006) more than expected, but preyed on moose (*Alces alces*) (Kunkel and Pletscher, 2001) less than expected relative to their abundances. These result demonstrated that carnivores do not simply pursue every potential prey encountered (Rasmussen *et al.*, 2008; van der Meer *et al.*, 2014). Most large carnivores such as African wild dog exist at low densities in natural ecosystems.

Hence determining the dietary composition of a large wild carnivores is challenging since most species occur at low densities and are elusive (Ogara *et al.*, 2010). For this reason, researchers have, over the past several decades, successfully relied on analysis of scats as a useful, non-intrusive method of studying carnivore diets (Farrell *et al.*, 2000; Trites and Joy, 2005; Wright, 2009; Ogara *et al.*, 2010). While scat analysis offers a good and relatively cheap method (Floyd, 1978), it is useful to precisely identify the prey remains in scats and to avoid data contamination with other samples.

Previous studies in east Africa (e.g. Fanshawe and Fitzgibbon, 1993) and southern Africa (Mills and Biggs, 1993; Hayward *et al.*, 2006; Hayward *et al.*, 2007) showed that African wild dogs subsist primarily on medium-sized antelopes for prey. In southern Africa's wild dog subpopulations, impala (*Aepyceros melampus*) and kudu (*Tragelaphus strepsiceros*) had been identified as key prey species (Krüger *et al.*, 1999; Hayward *et al.*, 2006). Since northern Botswana harbours a significant proportion of the world's African wild dog population, it is important to understand their diets in their northern Botswana ecosystems to enhance *in situ* conservation strategies.

Published information on the African wild dog's dietary composition and seasonal patterns remains scarce for northern Botswana. To date, wild dog studies conducted in northern Botswana by focused on the general ecology (Ginsberg *et al.*, 1995a; McNutt, 1996a), dispersal (McNutt, 1996b), and human-wildlife conflict (Gusset *et al.*, 2009). These studies paid little attention to the dietary composition of wild dogs. In an effort to fill this knowledge gap, I investigated and described African wild dog dietary composition and seasonal variation, and its relation to prey densities in the Vumbura and Linyanti-Selinda Areas of northern Botswana. The present study predicted that the African wild dog's dietary breadth was wide and changed with seasonal prey densities. The study also predicted that impala represented the primary food resource for wild dogs in these areas as it geographically ubiquitous, highly abundant, and falls within the weight range of wild dog's preferred prey species in southern Africa (Hayward, 2011).

4.2 General Objective

To determine dietary patterns of African wild dogs in Vumbura, and the Linyanti-Selinda in northern Botswana.

4.2.1 Research Questions

1. How do potential African wild dog prey ungulate densities vary seasonally?
2. Which species constitute the diet of the three study packs?
3. Do diets of the three wild dog study packs vary?
4. What prey ungulates do the three study packs prefer?
5. Is there seasonal variation in the diet of the three study packs?

4.2.2 Hypotheses

1. Large ungulate densities vary seasonally, while densities of impala and other medium-sized ungulates do not vary.
2. African wild dogs prey on impala significantly more than other ungulate species in the Vumbura and Linyanti-Selinda areas, since it is the most abundant prey species in the area.
3. African wild dog diets in the Vumbura and Linyanti-Selinda areas are narrow and overlap greatly.

4. African wild dogs in the Vumbura and Linyanti- Selinda areas significantly prefer medium-sized ungulates more than impala and large sized ungulates.
5. There is a significant seasonal variation in the dietary composition of the Vumbura and Linyanti- Selinda African wild dog subpopulations.

4.2.3 Specific Objectives

1. To determine seasonal densities of impala and other potential wild dog prey resident in the ranges of the study packs.
2. To describe dietary composition of the study packs.
3. To determine dietary breadth and overlap between the study packs.
4. To determine prey preferences, if any, of the study packs.
5. To compare seasonal dietary composition of the study packs.

4.3 Materials and Methods

4.3.1 Study sites

The study was conducted in the Vumbura Plains on the northeastern side of the Okavango Delta and near the Linyanti-Selinda reserves (Chapter one, Figure 1.1). The two study sites depict great ecological similarities both structurally and functionally. The study sites are described in detail in Chapter 1.

4.3.2 Potential wild dog ungulate prey densities

A line transect technique for distance sampling was used as described by Buckland et al. (2001)to survey and estimate populations densities of potential African wild dog prey. Distance sampling techniques are the most commonly used and trusted methods of estimating large herbivore densities and distributions patterns (Buckland *et al.*, 2001). The researcher together with two observers (whom were field assistants) surveyed a total of (18) four- kilometer long transects in each of the two study sites during both dry (April-October) and wet (November-March) seasons of 2010 and 2011. Transects locations were randomly selected along roads in both study sites. Using a habitat map of both study areas (data from Okavango Wilderness Safari, Environmental Department), transect sampling was stratified to represent each habitat strata in the study areas. Crepuscular (early morning and late afternoon) transects were surveyed to control for the effects of temperature on animal movements. Morning transects were conducted between sunrise and 10:00 hrs and afternoon transects between 16:00 hrs and sunset. It was anticipated that temperatures during this time windows were conducive to maximizing herbivore sightings as it is usually cool for herbivores to be foraging out on plains. All transects animal counts were conducted during the day, there were no nocturnal counts. A vehicle was driven at a speed of $\geq 10 \leq 20$ km/hr along transect routes with two observers sitting on raised seats (~1.80m above ground) on the back of a research vehicle. Observers independently recorded animal sightings on either side of the transect line (road) while the researcher drove, recorded data and confirmed species identification. At that speed, it was easy to drive and spot animals on either side of the road without causing the animals to flee. For each sighting, we recorded species name, number of individuals in the group, animal age group and sex, GPS coordinates, habitat type, angle from the transect line to the animal(s) cluster , and perpendicular distance to the middle of each cluster using a range finder (Nikon Riflehunter 550). Perpendicular distances ranged from 0 to 300m.Transects lines were not straight as they followed roads. All transect lengths were measured from the trip odometer using a GPS unit.

Table 4.1: Potential wild dog prey ungulate species in categorical classes according their body mass and significance in the diet of African wild dogs (*Lycaon pictus*) in the Okavango Delta and Linyanti-Selinda Regions of Botswana based on data from previous studies and sightability during transect surveys.

	Potential prey Species Category	
Impala	Medium-sized ungulates	Large ungulates
Impala(*Aepyceros melampus*)	Red Lechwe (*Kobus lechwe*)	Elephant (*Loxodonta africana*)
	Reedbuck (*Redunca arundinum*)	Giraffe (*Giraffa camelopardalis*)
		Hippopotamus (*Hippopotamus amphibius*)
	Steenbok (*Raphicerus campestris*)	
	Duiker (*Sylvicapra grimmia)*	Waterbuck (*Kobus ellipsiprymnus*)
		Zebra (*Equus burchellii*)
	Kudu*(Tragelaphus strepsiceros*)	Cape buffalo (*Syncerus caffer*)
	Warthog (*Phacochoerus africanus*)	
	Wildebeest (*Connochaetes taurinus*)	
	Sable (*Hippotragus niger variani)*	
	Roan (*Hippotragus equinus*)	
	Tsesebe (*Damaliscus lunatus*)	

4.3.3 Wild dog kill composition

Since each of the three study packs had one individual radio tagged with a Very High Frequency (VHF) collar, packs could be tracked, located and followed throughout daylight hours. Wild dog packs were followed in a 4x4 research vehicle (Landrover, 110 Defender TDi). During follows of a hunt, wild dog packs were observed as they pursued, killed, and fed upon prey. Given the difficulty of keeping up with the wild dog pack during hunts, often through thick vegetation, the actual kill was usually not observed, but instead the observers arrived when the dogs had already begun feeding. Kill sites were recorded as Global Positioning System (GPS) waypoints that encoded date, time, and location coordinates. Habitat type and prey species, sex, approximate age of were recorded.

Only fresh scats were collected while following and observing wild dog packs during hunting, feeding and resting activities to avoid misidentification of scat sources. A pair of dry sticks was used to collect each scat sample and place it into a labelled paper bag. Each scat was collected using a new pair of sticks to avoid scat contamination. The individual that produced the scat, the date, time, and GPS coordinates of collected scats were recorded on the bag. Scats were then sun dried for several days (2-7days) before storing them in a plastic box for laboratory analysis.

4.3.4 Scat analysis

Scat samples were washed with clean water in a 100% nylon stocking until only residual hairs and other undigested solid items (e.g., bones and insect parts) remained in the stocking. Ten hairs strands were randomly sampled from each scat sample using a pin-drop method as described in (Ciucci *et al.*, 1996). Each hair was mounted on a plastic cover slip between two glass slides and clipped tightly together before being oven burned for 5 minutes at 108º C. After cooling, the burnt hair samples were peeled off the plastic cover slip where the imprint of the burned hair strand remained. The plastic cover slip was placed under a microscope at 40X magnification to examine the hair imprint for morphological patterns. The imprint pattern on the plastic cover slip was compared with template pictures of known prey hair to identify the species. Hair strands templates were acquired from a local taxidermy company that trades wild animal hides.

4.4 Data analysis

4.4.1. Potential ungulate prey densities

Distance 6.0 program was used to determine potential prey densities (Buckland *et al.*, 2001). Line transect sampling is based on the following assumptions that the present study met: (1) Certainty of detection of animals on the transect line, (2) animals are detected at their initial position, (3) animals are counted properly in their clusters and distance is accurately measured and, (4) animal clusters are detected independently. This technique is based on the premise that probability of detection decreases as perpendicular distance from the transect line increases. Since detectability differed considerably among different sized ungulate species, potential wild dog prey were categorised into three groups: 1) Impala (40 - 60 kg), 2) Medium-sized ungulates, and 3) Large ungulates. Medium-sized ungulates were defined as ungulates with a body mass of 15 -250 kg. Large ungulates were defined as animals with a body mass > 250 kg. The former included *Phacochoerus africanus, Kobus lechwe, Tragelaphus strepsiceros* and *Raphicerus campestris* while the large ungulates included *Equus burchellii*, *Syncerus caffer*, *Giraffa camelopardalis* and *Loxodonta africana*. *Aepyceros melampus* was separated from the rest of medium-sized antelopes as it occurs at much higher densities and larger group sizes in the study areas than the other medium-sized species, and because previous studies demonstrated that

Aepyceros melampus represent key prey species for wild dogs in southern African ecosystems (Krüger *et al.*, 1999; Hayward *et al.*, 2006). In addition, medium-sized species other than *Aepyceros melampus* were not encountered frequently enough to meet the minimum required sightings (n = 40) for the software. Grouping all other medium-sized ungulates provided a sufficient sample size for the Distance program and, although sample sizes were very small, exploratory analyses suggested that dectabilities were similar.

Density analyses were modelled using three series expansions (Cosine, Simple and Hermite polynomials) against four key functions (Uniform, Half normal, Hazard rate and Negative exponential) provided by the program to achieve the best model fit for the data(Anderson *et al.*, 1983; Buckland *et al.*, 2001; Jathanna *et al.*, 2003; Buckland *et al.*, 2010). The program was set to automatically select the best model based on the highest *P*-value and lowest Akaike Information Criterion (AIC) for each analysis. Transect data could not be analyzed by habitat as the number of counts of each animal species per transect were insufficient (very low sample sizes). Thus, transects were grouped by study area, season, and year. We set significance at non-overlapping 95% confidence limits. The same prey count data were used for the Linyanti and Zibadianja packs, as both packs' home ranges overlapped considerably.

4.4. 2 Wild dog kill composition

EcoSim 5.0 software (EcoSim: Null models software for ecology. Version 5.0, Acquired Intelligence Inc. &Kesey-Bear, Burlington, USA) (Gotelli and Entsminger, 2000) was used to examine overlap between the diets of the study packs using Pianka’s Index. Pianka’s niches overlap formula:

$$O_{12} = O_{21} = \frac{\sum_{i=1}^{n} p_{2i} p_{1i}}{\sqrt{\sum_{i=1}^{n} \left(p_{2i}^{2}\right)\left(p_{1i}^{2}\right)}}$$

Where p_{2i}= proportion of *i*th prey species in the total number of kills from wild dog pack *j*. $O_{12}$and O_{21}arethe two populations (wild dog packs 1 and 2). The closer the index is to 1, the greater the overlap in the diets of the two packs. The closer the index is to 0, the less the overlap in the diets of the two packs. So, a 1 means complete overlap and a 0 means no overlap at all.

Each pack’s dietary breadth was examined using Levin’s Standardised Niche Breadth test (Krebs, 1999; Gotelli and Entsminger, 2000). Levin‘s Index (*B*) measured niche breadth as

$$B = \frac{1}{\sum \mathrm{Pj}^{2}}$$

Where P_j= proportion of items in the diet from food item *j*.

A standardised Levin’s niche breadth measure (B_A) is an extension of Levin’s niche breadth using the following formula.

$$B_A = \frac{\mathrm{B}-1}{\mathrm{N}-1}$$

Where B= Levin‘s Index and N = the total number of food items (species).This equation puts niche breadth on a scale of 0 to 1, where a 0 means the species (forager) is an extreme specialist and a 1 indicates that the species is an extreme generalist.

The program EcoSim 5.0 was used again to calculate whether Pianka’s and Levin’s indices differed between packs by generating 1,000 simulated matrices and examining the proportion of values that fell below the calculated mean Pianka’s and Levin’s indices (Gotelli and Entsminger, 2000). If> 95% of the simulated means fell below the observed mean, the index was considered significantly greater than what would otherwise be out of chance.

4.4. 3 Prey preferences

Jacobs index (1974; in Lechowicz, 1982) was used to determine prey preference by African wild dogs in each study area. The index has been widely used in many habitat selection studies (e.g. Lechowicz, 1982; Hayward *et al*., 2006; Balestrieri *et al*., 2009; Kauhala and Auttila, 2009). The index was calculated using potential ungulate prey densities and the actual wild dog kill composition (Table 4.1 and 4.3). The index measures the quantity of a resource used relative to the availability of that resource in the environment (Krebs, 1999; Kauhala and Auttila, 2009). In the present study, the resource was all potential ungulate prey. Jacob’s formula used was

$$\text{Jacobs's index } D = \frac{r-p}{r+p-2rp},$$

Where r is the proportion of the resource utilised/consumed and p is the proportion of the resource available. The index results range from -1 to +1, with -1 indicating that that resource was completely avoided and +1 indicating the resource was used exclusively.

4.4. 4 Seasonal diet variation

The seasonal variability in the diet of wild dogs was tested using scat analysis data. There are many methods of scat analysis and the choice of method depends on the objectives of the study, as the results of each method can have far reaching ecological implications (Marucco *et al.*, 2008; Klare *et al.*, 2011). In the present study, Frequency of Occurrence of each prey item per scat (%FOC/I) was used to quantify the presence of prey items in the diet of wild dogs. This method permits comparison of diets across seasons. Seasonal variations in pack diet were tested using independent *t*-tests. Significance was set at $p < 0.05$.All results reported as ± 1 standard error (SE).

4.5 Results

4.5.1 Potential ungulate prey densities

The most densely populated ungulate group in both study sites, by proportion, was impala (Table 4.2). In both study sites, impala occurred at higher densities during all seasons when compared with other medium-sized and large ungulates, except for large ungulates in Vumbura in the wet season of 2012(Table 4.2).In Vumbura, the mean density of medium-sized ungulates varied from a low of2.90 ± 1.39 animals/km^{2}in the wet season of 2011 to a high of 8.88 ± 2.39animals/km^2 in the dry season of 2011 (Figure 4.1). The proportion of impala kills in all seasons was higher than that of medium-sized and large ungulates, except for the wet season of 2011 in both study sites (Figure 4.1 and 4.2).

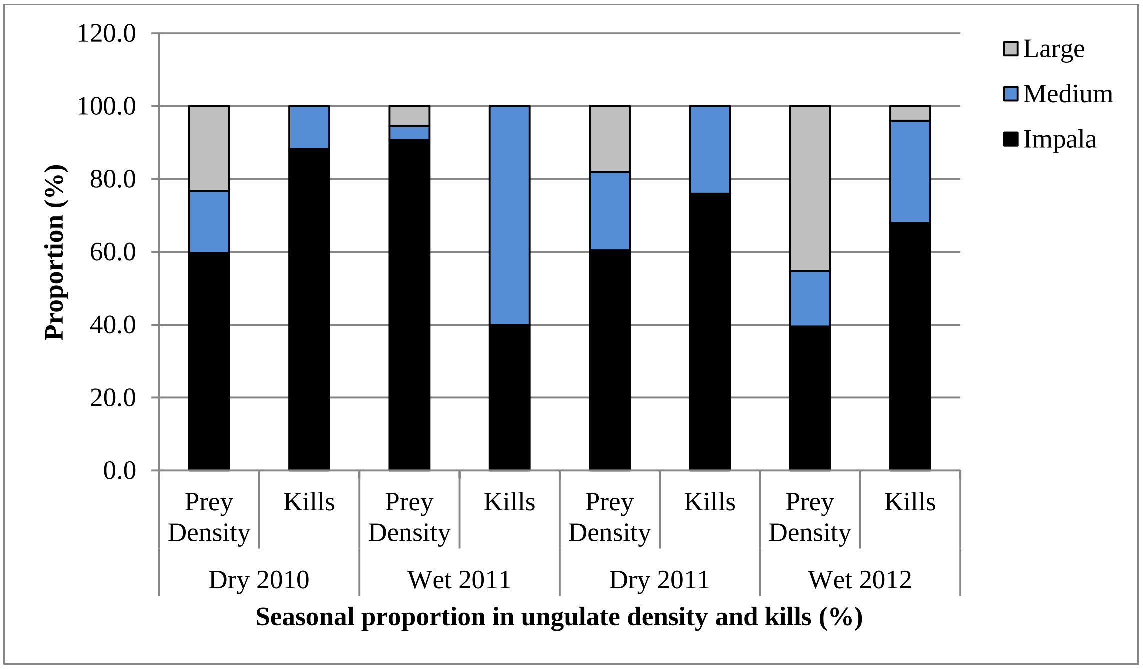

Figure 4.1: Comparison of the percent prey density with percent of prey killed by African wild dogs (*Lyacaon pictus*) in the Vumbura Plains, Okavango Region of Botswana. Medium and large refers to medium-sized (15 – 250 kg) and large ungulates (>250 kg) respectively.

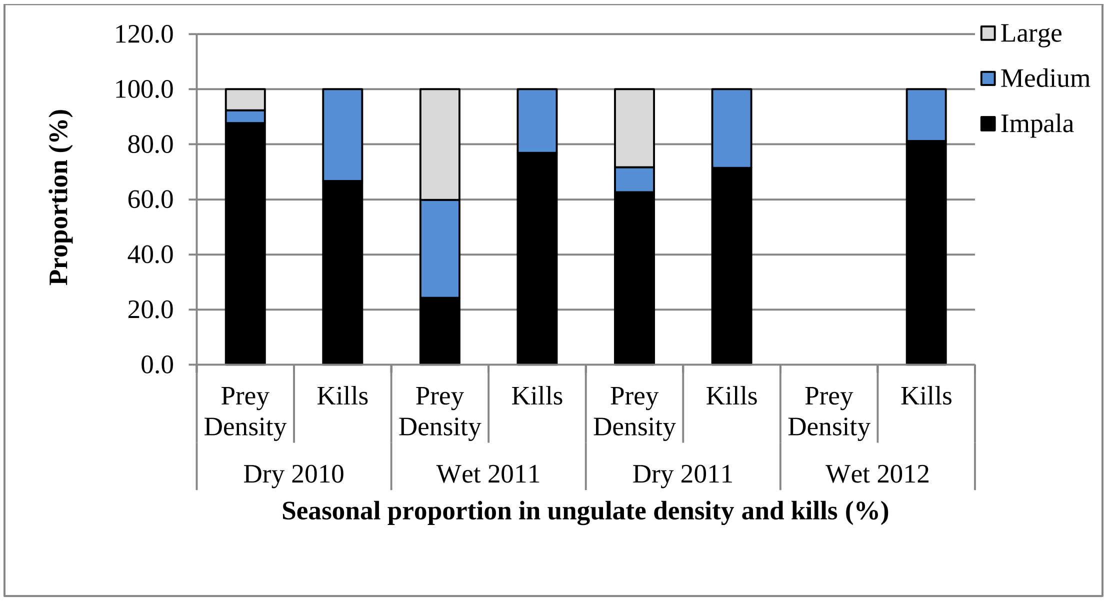

Figure 4.2: Comparison of the percent prey density with percent of prey killed by African wild dogs(*Lycaon pictus*) in the Linyanti-Selinda Region of Botswana. Medium and large refers to medium-sized (15-250 kg) and large (>250 kg) ungulates respectively.

Impala occurred at highest densities during the 2011 wet season in Vumbura and at their lowest density in Linyanti-Selinda during the same season. In most seasons, the density of impala's higher than that of other ungulates groups. However, in Linyanti-Selinda during the wet season of 2011 all prey occurred at approximately the same density and during the dry season of 2012, large ungulates occurred at their highest densities (20.79 ± 7.49 animals/km^2) of the study (but still significantly lower than impala densities). Also, in the wet season of 2012 densities of none of the prey groups differed significantly, as impala and large ungulates occurred at similar densities (Table 4.2). In Linyanti-Selinda site, impala's densities were significantly higher in the dry seasons than wet season (Table 4.2).

Table 4.2: Mean density estimates (± standard error) of potential African wild dog (*Lycaon pictus*) ungulate prey in Vumbura and Linyanti-Selinda Regions of Botswana. Calculated using the Distance program on line transects data.

		Density estimate (animals/km^2)	
Season	**Ungulate group**	**Vumbura**	**Linyanti-Selinda**
Dry 2010	Impala	13.15 ± 3.92	49.04 ± 16.59
	Medium size ungulates	3.76 ± 0.82	2.55 ± 0.96
	Large size ungulates	5.12 ± 1.94	4.28 ± 0.97
Wet 2011	Impala	69.35 ± 38.30	3.57 ± 0.78
	Medium size ungulates	2.90 ± 1.39	5.22 ± 1.4
	Large size ungulates	4.18 ± 1.88	5.91 ± 1.6
Dry 2011	Impala	24.95 ± 10.12	46.03 ± 13.41
	Medium size ungulates	8.88 ± 2.39	6.63 ± 2.38
	Large size ungulates	7.45 ± 2.70	20.79 ± 7.49
Wet 2012	Impala	11.03 ± 9.07	-
	Medium size ungulates	4.26 ± 1.64	-
	Large size ungulates	12.61 ± 8.48	-

4.5.2 Wild dog kill composition

During field data collection, observations were conducted on African wild dogs while hunting and preying on some of the many potential ungulate species mentioned earlier (Table 4.1). A total of 152 kills were observed among all three study packs. All kills were observed at crepuscular hunts and no nocturnal kill was recorded. Data of 35 kills (23%) was acquired from records of experienced safari field guides who operate full-time in the study areas. A total of nine species were identified at wild dog kill sites (Table 4.3).Overall, the three most common prey species were impala (73.0%), followed by kudu (11.2%), and lastly warthogs (7.2%) (Table 4.3). All three study packs followed this same basic trend, with impala constituting 73.0%, 69.5%, and 84.2% of daytime kills made by the Golden (n = 74 kills), Linyanti (n = 59 kills) and Zibadianja (n = 19 kills) packs, respectively (Table 4.3). The second most frequently killed prey after impala varied somewhat by pack. The Golden pack had a higher percentage of warthogs kills (9.5%) than the other packs, while the Zibadianja pack had a higher percentage of Red lechwe kills (10.5%) than other packs. Except on a single scavenging event, African wild dogs rarely preyed on large ungulates (Table 4.3).

Table 4.3: Numbers of observed ungulate prey killed by African wild dogs (*Lycaon pictus*) from three study packs in Vumbura and Linyanti regions of Botswana.

	Study pack			
Ungulate name	**Golden**	**Linyanti**	**Zibadianja**	**Total**
Impala	54 (73.0%)	41 (69.5%)	16 (84.2%)	111 (73.0%)
Kudu	6 (8.1%)	10 (16.9%)	1 (5.3%)	17 (11.2%)
Warthog	7 (9.5%)	4 (6.8%)	0 (0.0%)	11 (7.2%)
Red Lechwe	1 (1.4%)	1 (1.7%)	2 (10.5%)	4 (2.6%)
Steenbok	0 (0.0%)	2 (3.4%)	0 (0.0%)	2 (1.3%)
Duiker	0 (0.0%)	1 (1.7%)	0 (0.0%)	1 (0.7%)
Reedbuck	1 (1.4%)	0 (0.0%)	0 (0.0%)	1 (0.7%)
Tsesebe	1 (1.4%)	0 (0.0%)	0 (0.0%)	1 (0.7%)
Zebra	1 (1.4%)	0 (0.0%)	0 (0.0%)	1 (0.7%)
Unknown	3 (4.1%)	0 (0.0%)	0 (0.0%)	3 (2.0%)
Total	**74**	**59**	**19**	**152**
Medium-sized Ungulates	17 (23.0%)	18 (30.5%)	3 (15.8%)	38 (25.0%)
Large Ungulates	1 (1.4%)	0 (0.0%)	0 (0.0%)	1 (0.7%)

A comparison of the diets of three study packs showed that they overlapped substantially with each other (O = 0.97 - 0.99) (Table 4.4). There was no significant difference in the observed prey killed by all 3 study packs ($P> 0.05$ for Pianka's index simulation) (Table 4.4). The Golden and Linyanti packs demonstrated the highest dietary overlap (O = 0.99) while the Zibadianja and Linyanti packs showed the least overlap (O = 0.97), but the diets were still significantly similar ($P > 0.05$) (Table 4.4).

Table 4.4: (Pianka's Index) for observed kill data in African wild dog (*Lycaon pictus*) packs in Vumbura and Linyanti-Selinda regions of Botswana. Probability (*P*) for Pianka's Index was calculated using simulations in EcoSim 5.0 software (Gotelli and Entsminger, 2000).

Wild dog pack pair	**Pianka's Index**	***P*-value**
Golden and Linyanti	0.99	0.60
Golden and Zibadianja	0.98	0.99
Zibadianja and Linyanti	0.97	0.94

Using observed kill data and scat analyses, the present study found that niche breadth was very low for all the three packs (*B* = 1.38 – 1.93) (Table 4.5). Dietary niche breadth did not differ significantly among packs (*P* = 0.97 for simulations of Levin's indices) (Table 4.5). Similarly, standardized niche breath was low and similar among packs (B_A = 0.12 – 0.19) (Table 4.5), indicating that wild dogs are specialist hunters of impala in the study areas. These results reflect the high proportion of a single prey item, Impala, in wild dog diets.

Table 4.5: Levin's niche breadth Index and Standardized Levin's Index for the prey of African wild dog (*Lycaonpictus*) packs in the Vumbura and Linyanti-Selinda Regions of Botswana. Standardized index on a scale of 0 to 1, where a 0 indicates no niche breadth (specialist feeder) and a 1 indicates high niche breadth (generalist feeder). OKD = Observed Kill Data and PO = Proportion of Occurrence in scat samples.

	Levin's Index (*B*)		**Standardized Levin's Index (B_A)**	
Wild dog Pack	**OKD**	**PO in scats**	**OKD**	**PO in scats**
Golden	1.82	2.42	0.12	0.16
Linyanti	1.93	2.20	0.19	0.13
Zibadianja	1.38	2.80	0.19	0.20

All the three packs frequently preyed on impala during most seasons (Table 4.6).Preference for impala was particularly strong for the Golden pack in the dry season of 2010, the Linyanti pack in wet season of both 2011 and 2012, and the Zibadianja pack in the wet season of 2012 (Table 4.6). Alternatively, medium-sized ungulates were strongly preferred over impala by the Golden pack in the wet season of 2011 and the Linyanti pack in the wet seasons of 2010 and 2011 (Table 4.6). Large sized ungulates were almost completely avoided by all three packs for the entire study period (Table 4.6). During the wet season of 2011, the Golden pack almost completely avoided impala (-0.87) (Table 4.6).

Table 4.6: Seasonal prey preference by African wild dog (*Lycaon pictus*) packs during the entire study period (Oct 2010-April 2012). Preference was calculated using Jacob's (1974) index. Values close to -1 indicates high avoidance, while values those close to +1 indicate strong preference. Values close to zero indicates that a food resource was used in proportion to its availability. More than 0.60 or superscript * indicates that prey was considered strongly preferred by wild dogs, while less than -0.60 or superscript ** indicates that prey was considered strongly avoided by wild dogs, and [a] means the ungulate group was completely avoided. Underlined figures show the most optimally consumed prey. Prey preference by the Zibadianja pack could not be calculated for the 2010 dry and 2011 wet seasons as the telemetry collars failed.

Season	**Impala (*Aepyceros melampus*)**			**Medium sized ungulates**			**Large ungulates**		
	Golden	Linyanti	Zibadianja	Golden	Linyanti	Zibadianja	Golden	Linyanti	Zibadianja
Dry 2010	0.67*	-0.17	-	-0.21	0.61*	-	-1.00[a]	-1.00[a]	-
Wet 2011	-0.87**	0.82*	-	0.97*	-0.29	-	-1.00[a]	-1.00[a]	-
Dry 2011	0.35	0.01	0.59	0.07	0.71*	0.49	-1.00[a]	-1.00[a]	-1.00[a]
Wet 2012	0.50	0.77*	0.64*	0.47	0.14	0.30	-0.91	-1.00[a]	-1.00[a]

4.5.3 Seasonal dietary variation

Through scat analysis, it was detected that 96.6 % and 97.4% of all fecal samples collected during the wet (n = 50) and dry (n = 38) seasons contained impala hair samples, respectively. The next most common hair strands identified in scats were of steenbok, kudu, red lechwe, and warthog in that order for both seasons (Table 4.7). The difference between the frequency of detected impala hairs in wild dogs scats during the dry and wet seasons was not significant (t = -0.35, df= 86, p = 0.73) (Table 4.7). Similarly, for all other prey hairs except for Tsesebe, the frequency of detecting such hairs strands in scat samples did not differ significantly ($p > 0.05$) between the seasons. Thus, generally there were no significant seasonal dietary differences (Table 4.7). Steenbok and common duiker were not found in Observed kills (Table 4.3), but were found in scat analyses (Table 4.7).

Table 4.7: Frequency of occurrence of prey species in scats (N = 88 scats) of African wild dogs (*Lycaonpictus*) in Vumbura and Linyanti-Selinda Regions of Botswana

	Frequency of scats with total scats (%)				
Food item	Wet(n = 50)	Dry(n = 38)	*t*-test	df	*P*-value
Impala (*Aepyceros melampus*)	96.0%	97.4%	-0.35	86	0.73
Steenbok (*Raphicerus campestris*)	38.0%	44.7%	-0.63	86	0.53
Kudu (*Tragelaphus strepsiceros*)	30.0%	36.8%	-0.67	86	0.50
Red Lechwe (*Kobus lechwe*)	22.0%	26.3%	-0.47	86	0.64
Warthog (*Phacochoerus africanus*)	12.0%	13.2%	-0.16	86	0.87
Tsesebe (*Damaliscus lunatus*)	0.0%	7.9%	-2.05	86	0.04*
Duiker (*Sylvicapra grimmia*)	2.0%	2.6%	-0.20	86	0.85
Waterbuck (*Kobus ellipsiprymnus*)	0.0%	2.6%	-1.15	86	0.25
Vegetation	12.0%	5.3%	1.08	86	0.28
Unknown	26.0%	23.7%	0.25	86	0.81

*Significantly different

4.6 Discussion

4.6.1 Potential ungulate prey densities

Quantifying a carnivore’s diet requires a basic understanding of its prey’s availability (Mills and Shenk, 1992). The present study surveyed and seasonally quantified African wild dog potential ungulate prey to attempt to answer the question of diet preference. Generally, the proportion of impala in the diet was higher than that of medium-sized and large ungulates for both study areas and seasons. The proportion of impala in the prey base of the study packs increased considerably during the wet seasons probably due to an increase in juveniles as females gave birth to fawns. Though other ungulates also fawned at around the same periods as impala, the later probably provided more foraging opportunities for wild dogs, as *Aepyceros melampus* do not migrate like large ungulates and they were distributed in high densities throughout the study areas. The low proportion of medium-sized and large ungulates during the wet seasons could be attributed to seasonal migrations away from the Kwando-Linyanti River systems (including the Chobe River area as well) and the Okavango Delta during the wet seasons. Large herds of *Loxodonta africana* , *Syncerus caffer, Equus burchellii* and , and *Connochaetes taurinus*, in particular, are known to migrate from the Okavango Delta to Mababe, Savuti marshes and Makgadikgadi Pans as the wet season begins (Kgathi and Kalikawe, 1993; Bonyongo, 2004; Brooks and Harris, 2008; Bartlam-Brooks *et al.*, 2011). The higher density of impala in the 2011 wet than dry season in Vumbura probably resulted from dry season floods in the whole Okavango Delta which most likely restricted distribution of ungulates to certain habitats and not others. However, the inverse was true for the Linyanti-Selinda site, which was not affected by high floods. Clustering of large herds of impala had likely enhanced the probability of impala being detected during line transects campaigns.

4.6.2 Diet composition and preference

Though it is difficult to quantify the composition of large wild carnivore diets (Farrell *et al.*, 2000), the present study used observed kill data to measure dietary breadth and similarities in African wild dogs inhabiting Linyanti-Selinda and Vumbura. The present study's findings are similar to previous studies in southern Africa in that *Aepyceros melampus* and *Tragelaphus strepsiceros* were also common prey (Krüger *et al.*, 1999; Mech, 1999; Radloff and Du Toit, 2004; Hayward *et al.*, 2006). The findings of the present study confirms the hypothesis that impala is the most common prey for African wild dogs in northern Botswana. The results also show that African wild dogs have the ability to subdue prey that are larger (>45%) in body size than themselves, such as the medium-sized kudu and red lechwe. Similarly, lions prey on much larger buffalos, zebras, giraffes, and even elephants (Hayward and Kerley, 2005). The narrow niche of African wild dog diets in both study areas suggests a specialist feeding habit as opposed to generalist diet, probably due to the high proportion of a single species (impala) in their diets.

Comparatively, the diet of the three packs showed very high overlap. Though the Vumbura and Linyanti-Selinda study areas are geographically separate and independent systems, similarities in diets of wild dogs suggest that the two areas are ecologically comparable. Previous studies show that the Kwando-Linyanti and the Okavango Delta have geological and ecological linkage through the Selinda spillway(Thomas and Shaw, 1991).This continuity between study sites might influence spatial and temporal prey density availability and therefore the feeding habits of large carnivores (Creel and Creel, 2002). The narrow niche breadth of wild dogs packs rejects the hypothesis that wild dog utilize a wide dietary niche in the study areas. This finding is similar to a previous study in Hluhluwe-Umfolozi-Park, South Africa (Krüger *et al.*, 1999).

Africa's large carnivores, including African wild dogs, tend to select prey within specific body mass ranges (Hayward *et al.*, 2006; Hayward *et al.*, 2007; Hayward, 2011). In the present study, wild dogs were rarely observed hunting and successfully preying on large ungulates (e.g. wildebeest, zebra, buffalo, etc.) as reported in other studies (Creel and Creel, 2002; Hayward *et al.*, 2006). Creel and Creel (1995, 2002) found a relationship between prey selection and preference and wild dog pack size, where smaller prey, especially Thomson's gazelles, were largely preferred by smaller packs (< 11 individuals) and a wild dog pack's preference for larger ungulates increased with pack size. In the present study, the number of adult dogs in a pack never exceeded 12 for all three packs. Smaller ungulates like *Raphicerus campestris*, *Sylvicapra grimmia* and notably *Aepyceros melampus*, probably presented less capture risks than larger prey.

The present study found that, though impala was the most common ungulate species in both study areas and it was however not the most preferred prey item. Alternatively, Krüger *et al*. (1999), Creel and Creel (2002), Hayward *et al.* (2006) and Hayward (2011) observed that wild dogs preferred a wider variety of medium-sized species. The finding concurs with the optimal foraging theory, because wild dogs maximised their hunting success by focusing on the most common and therefore most frequently encountered prey, maximizing energy expended relative to energy expended and capture risks (Rasmussen *et al.*, 2008; van der Meer *et al.*, 2014). As described in Creel and Creel (2002), prey selection by a particular wild dog pack is a function of several variables, among them the size of prey species, its abundance, and distribution. Ecologically, it improves the collective fitness of individuals to expend energy on better yielding foraging activities (van der Meer *et al.*, 2014).

4.6.3 Seasonal dietary variations

Scats analysis has shown that, there were no significant differences in the frequency of occurrence of ungulate prey species in the diet of wild dogs by seasons. Lack of significant seasonal variation in the diet of the study packs confirms the present study’s hypothesis that there are no seasonal differences in the dietary composition of wild dogs in the study areas. Lack of seasonal variation in the diet of wild dogs could be attributed to the consistently high densities of impala (by proportion relative to other medium-sized and large ungulates) in both study areas throughout the year.

Some prey species (e.g. steenbok, duiker, and waterbuck) detected in scat analyses were not recorded at kill sightings. For steenbok and duiker, this could be attributed to the small size and the rapid rate at which wild dogs ingest their kills to minimize competition with larger, sympatric lions, leopards and spotted hyaenas (Carbone *et al.*, 1997; Creel and Creel, 2002) and the time lag before the researcher arrived at the kill site.

4.6.4 Summary

The present study found the following key information about African wild dog diets in Vumbura and Linyanti-Selinda:

- The density (not necessarily biomass) of impala generally exceeded the collective densities of all other medium-sized and large ungulate groups in both the wet and dry seasons.
- Dietary composition and breadth of African wild dogs was narrow and did not differ significantly among study areas.
- Impala was generally the most preyed upon and most preferred prey species by African wild dogs in the Vumbura and Linyanti–Selinda areas. In some cases, wild dogs preferred medium-sized prey, but strongly avoided large prey in all seasons.
- African wild dog dietary composition did not vary significantly between wet and dry seasons.
- Scat analyses detected some prey species remains, especially small ungulates, which were not directly observed at kill sites.

4.7. Link with the next Chapter

The next chapter summarizes the whole thesis. Major findings and limitations of the study are highlighted. Recommendations for future work are also suggested.

4.8 References

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Chapter Five

5.0 Synthesis

Little published information exists on the scent marking behaviour and dietary patterns of African wild dogs in northern Botswana and elsewhere. The aim of the study was to contribute to understanding the scent marking and dietary patterns of African wild dogs in the Vumbura and Linyanti-Selinda areas in Botswana. Firstly, a set of fundamental questions sought to describe the underlying demographic and spatiotemporal variations in the scent marking behaviour of African wild dogs. Secondly, the dietary patterns of the African wild dogs were descriptively discussed. The study sought to answer the following questions:

1. What is the relationship between demographic factors and scent marking rates of African wild dogs?
2. What are the spatiotemporal scent marking patterns of African wild dogs?
3. What is the seasonal dietary composition of African wild dogs in the Vumbura and Linyanti-Selinda areas of northern Botswana?

By attempting to answer the above questions, the study generated crucial information on:

i. Demographics of an individual wild dog associated with its scent marking behaviour.
ii. There are spatial and temporal variations in the scent marking patterns of African wild dogs.

iii. There are dietary similarities and overlaps between African wild dog packs in the Linyanti-Selinda and Vumbura Plains, Okavango Delta.

iv. Impala was the most common prey species but other medium sized ungulates were also highly preferred.

v. African wild dog diets did not change with seasons.

In Chapter 1, I presented and discussed several scent marking hypotheses relative to functionality of the scent marking behaviour. Several previous studies attempted to explain the true function of scent marking with a view that scent marking should serve a singular function (Gosling and Roberts, 2001; Lledo-Ferrer *et al.*, 2012; Roberts, 2012a; Jordan *et al.*, 2013). But evidence suggests that scent marks serve various functions across different species and individuals (Gosling and McKay, 1990a; Heymann, 2000; Lledo-Ferrer *et al.*, 2011, 2012). The most common scent marking function is the territorial hypothesis. However, another hypothesis suggested that scent marking can be used by individuals or species primarily for intragroup social dynamics. The findings in Chapter 2 provided partial support for the hypothesis that an individual African wild dog's scent marking rate is significantly associated with social status. Dominant breeding pairs (dominant male and female) had the highest scent marking rates compared to other pack members. However, an individual's sex and age were not significantly associated with its scent marking rates.

When identifying individuals to immobilise for reintroductions or translocations, a decision on how to avoid or choose the dominant or subordinate can be made based on Chapter 2's findings by observing the scent marking rates of individuals in a pack. The present study found that dominance is associated with higher scent marking rates in African wild dogs. The spatiotemporal distribution of scent marks were then discussed in light of the territorial demarcation hypothesis.

Results in Chapter 3 suggested that African wild dogs did not use scent marks as a territorial fence, but as a scent cloud as concluded by Parker (2010). In addition to territorial functions, scent marks are likely functions in synchronizing intra-pack social structures. Contrary to the hypothesis that African wild dogs scent marking will be more intense along territory edges than within the home range core zones, wild dogs loosely scent marked as they moved without a preference for the home range edges. These findings concur with Parker (2010) whose results suggested that wild dogs scent marks are distributed across their entire ranges hence supporting a scent cloud theory rather than a scent fence theory. The scent fence theory holds that the territory holder scent marks intensively at the territory boundary and less so within the territory core (Gosling, 1982). On the other hand the scent cloud hypothesis proposes that the animal scent marks randomly across its range. The hypothesis predicts that the scent marks should be distributed throughout the home range (Parker, 2010). African wild dogs scent marking behaviour is a daily phenomenon, conducted as they traverse their home ranges. To understand the relationship between scent marking and resource defence, it is necessary to understand the diet of a species, of which food is the defendable resource worth defending. Such research requires a manipulative study to control for scent marking’s role in such resource defence. Thus, the present study endeavoured to begin with a basic assessment of the dietary composition of wild dogs in the study areas.

Data presented in Chapter 4 showed little variation in dietary composition and breadth for African wild dog packs in the Linyanti-Selinda and Vumbura. Using scat analysis, it was shown that African wild dog diets in the two study sites did not change significantly between the dry and wet seasons. However, dry season prey availability (by density) increased from that in the wet season for large and medium-sized ungulate groups but not impala. This suggested that large ungulates, such as elephant, buffalo and zebra, dispersed and migrated out of the area, perhaps to the Mababe and Makgadikgadi pans as reported in a previous study (Bartlam-Brooks *et al.*, 2011). Seasonal changes in the distribution of medium-sized ungulates probably left impala as the most common available prey for wild dogs during the wet seasons. However, the diets of the wild dog packs did not substantially shift towards the non-migratory medium-sized ungulates and impala. Even when larger ungulates were available during the dry seasons, they were not preyed upon as would otherwise be expected; probably due to the high energetic costs of appropriating prey of large size (Creel and Creel, 2002)as suggested by the optimal foraging theory (Charnov, 1976; Krebs *et al.*, 1977). The current study’s finding supports the hypothesis that a predator’s prey preference and choice is an ‘economic’ decision more than a supply-demand phenomenon. The findings of the present study also support the optimum foraging theory, which holds that animals strive to forage in a way that maximises energy intake and the lowest possible energetic costs (Charnov, 1976; Krebs *et al.*, 1977; Creel *et al.*, 2008).

5.1 Management Implications and Recommendations

5.1.1 Mitigation of Edge effects

The scent marking behaviour of African wild dogs can be explored to manipulate movement patterns and territorial habits of African wild dogs. The bio-fence experiments need to appraise the fundamental demographic, spatial and temporal patterns of wild dog scent marking behaviour. Meanwhile, limited prey and intense interspecific competition in protected areas can push smaller and less competitive carnivores out into communal farmlands, where they can suffer from edge effects. Edge effects are essentially changes in population and community dynamics as a result of two or more habitat types overlapping (Harris, 1988; Woodroffe and Ginsberg, 1998). Many large carnivores in African ecosystems continue to be affected by edge effects, as a direct consequence of degraded, fragmented and even completely lost habitats due to human activities (Woodroffe and Ginsberg, 1998). As already noted in Chapter 1, African wild dog populations are reported to be declining possibly due to various factors, including loss of habitat to agricultural practices by an expanding human population. As a result, wild dogs often face persecution in areas boarding protected reserves. Loss of habitat affects successful dispersal rates negatively due to lack of new areas into which dispersing animals can establish new ranges (Woodroffe *et al.*, 1997). Fragmented habitats lead to limited interactions between populations, hence negatively affecting gene flow (Oehler and Litvaitis, 1996; Crooks, 2002). Loss of habitat inflates the rate of communicable diseases transmission, such as rabies between wild canids and *Canis familiaris* (Woodroffe *et al.*, 2012). A sound understanding of the fundamental aspects of scent marking behaviour might help facilitate the bio-boundary initiative (and ultimately management through manipulations of wild dog spatial habits), whence synthetic scent marks can be strategically distributed in critical areas to manipulate, contain and control of wild dogs movements. For example, synthetic scent marks could be distributed in pastoral areas to communicate a false home range to intruding wild dog packs as a means of keeping them out of farmlands and hopefully retain them in protected areas.

However, the discussion in Chapter 3 is not suggesting support for the territory hypothesis but rather insinuating that African wild dogs probably also use scent marking for intra-pack social purposes. As mentioned above, dispersing young adults in search of reproductive mates in new territories could be deterred from pastoral rangelands by using synthetic scents of dominant individuals to create bio-boundaries and lack thereof of potential reproductive mates in farmlands. Although dispersal fell outside the scope of the present study, dispersing individuals from study packs occasionally returned to their natal ranges.

5.1.2 Carnivore –prey relationships and ecosystem management

African wild dogs occur in ecosystems with other large carnivores provide an assemblage of a carnivore guild. Intraguild relationships and interactions among carnivores influence the distribution and availability of prey (Brown *et al.*, 1999; McIntyre and Wiens, 1999). The present study found that impala was the most abundant and most common prey species. Thus there is a need for ecosystem, rather than species management approach for African wild dogs as evidenced by impala's critical importance to their dietary requirements. In Botswana, African wild dog diets outside of protected areas remain poorly understood. African wild dogs continue to disappear from protected areas into human populated habitats(Woodroffe *et al.*, 2005). This might lead to a point in time when reintroductions are required not only for management of wild dogs but all top carnivore predators. However, reintroduced wild dogs may struggle to survive if their prey base at release sites does not meet their natural dietary requirements similar to those in natural systems. There is thus a need to periodically monitor population densities of herbivore ungulates and study predatory impacts of African wild dogs on such prey species populations.

5.2 Limitation of the Study

Direct observations in behavioural studies of large carnivores are often difficult to conduct (Creel and Creel, 2002). The heterogeneous nature and dynamism of the Okavango Delta makes such studies difficult to conduct successfully. Though the study describes the dietary patterns of African wild dogs in the Vumbura and Linyanti-Selinda, it could not relate those data to an assessment of intra-guild competition with the larger sympatric lions, hyaenas, and leopards. Broader holistic carnivore community studies are necessary to understand the factors that determine their population dynamics, spatial ecology and ultimately their inclusive fitness.

5.3 Future Work

The present study has contributed to the scientific understanding of African wild dog scent marking behaviour, with results whose implications go beyond northern Botswana. Yet, this contribution requires further research with a larger sample size of packs and, if possible, improved methods and use of constantly improving technologies. Future studies should aspire to further examine how scent marking can be used to manipulate the communication and spatial ecology of African wild dogs. This might help improve our understanding of wild dog space use, movement patterns, and ultimately help us develop methods to reduce human-wild dog's conflicts. Rigorous studies have been conducted on other aspects of African wild dogs' ecology in East and South African reserves, but in Botswana, little has been published on African wild dogs. It would be of great interest for future studies to focus on the scent marking behaviour and its relationship with prey availability dynamics with respect to the Resource Dispersion Hypothesis (RDH) (Johnson *et al.*, 2002; Valeix *et al.*, 2012) and the Territory Inheritance Hypothesis (TIH) (Lindström, 1986; Revilla, 2003). Such research would shed light into variables affecting the fitness of the species. In addition, we need more research on the linkages between scent marking, food resource availability, ecological and evolutionary benefits of group living, dispersal and territory retention. The present study began to assemble a collection of hair samples from several various species in the area. Future research work should endeavour to add to that collection to facilities future scat analysis studies. The present study only began to examine several questions that future studies could consider on the following topics:

- What are the ecological and evolutionary implications of the relationship between medium-sized prey and African wild dogs?
- What ecological impacts would a disturbance (*i.e.*, epidemic diseases) have on the relationship between African wild dog diets and medium-sized prey (herein *Aepyceros melampus* included) population dynamics?
- Does scent marking have any applied significance for the conservation and management of the African wild dog?

5.4 Conclusion

Most of the published scientific knowledge available on African wild dogs comes from studies conducted in east African and South African reserves. Nonetheless, there is scarcity of published research addressing the aspects of scent marking behaviour of African wild dogs that the present study did. As a result, published knowledge on the basic ecology of scent marking behaviour of African wild dogs has remains limited, with only inferences from other species like *Crocuta crocuta* informing this topic.

Scent marking behaviour of African wild dogs is largely associated with dominance status and less so to the sex and age of an individual. African wild dogs do not seem to engage in territorial scent marking only at home range edges, but rather they seem to merely create a ‘scent cloud’ throughout their home ranges and also possibly to instil intrapack sociological purposes. On hindsight, if indeed wild dogs scent marked for territorial purposes, then the significantly higher densities of scent marks in home range core zones indicate core zones as proxies for territories. The diet of African wild dogs in the relatively prey rich habitats in Vumbura and Linyanti-Selinda reserves did not vary seasonally in the present study. Impala was found to be the most common and most preferred prey. African wild dogs generally avoided large ungulates as prey except on rare scavenging occasions. These findings on dietary behaviour conform to predictions from optimal foraging theory. A similarity in diets of Vumbura and Linyanti-Selinda wild dog sub-populations suggests an ecological connection between the two ecosystems. Thus, it is necessary to conserve and manage wild dogs in these areas at a metapopulation approach rather than as isolated ecosystems. This draws into the Kavango-Zambezi Transfontier Conservation Area (KAZA-TFCA) ideals whence wild dogs are designated as a flagship species.

Scent marking behaviour in African wild dogs deserves further research attention as it may well provide the means to understand communication mechanisms and spatial ecology of the species. Predator-prey relationships of African wild dogs require additional study, with particular reference to interactions with other sympatric carnivores, especially in such spatially vast and dynamic systems as the Okavango Delta and the Linyanti-Kwando Rivers systems. Such ecosystem understanding is crucial for holistic ecosystem management, particularly for the continually diminishing African habitats.

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