LET US PREY! PREY SELECTION AND DIETARY OVERLAP AMONGST LARGE PREDATORS IN A SEMI-ARID LANDSCAPE, HWANGE NATIONAL PARK, ZIMBABWE.

By

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CERTIFICATION OF THESIS

We, the cosignatories certify that we have read and therefore recommend for submission to the Department of Animal and Wildlife Sciences, in partial fulfilment of the requirements for the degree of Bachelor of Science Natural Resource Management and Agriculture Honors in Animal and Wildlife Sciences, a thesis by Simbarashe Pride Chatikobo.

***Let us prey*! Prey selection and dietary overlap amongst large predators in a semi-arid landscape, Hwange National Park, Zimbabwe.**

This thesis is acceptable in form and content. The candidate demonstrated the necessary knowledge through an oral examination held on the 5th of May, 2017.

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DECLARATION OF THESIS

I do hereby sincerely declare that this thesis was a result of my own effort. All sources have been acknowledged by means of reference.

Date: ____/____/_______.

Signed: ___________________________

Simbarashe. P. Chatikobo R0825188P

DEDICATION

This thesis is dedicated to:

Dr. Paul Chatikobo; for never ceasing to believe.

My late parents and brother, as a promise to continue the legacy you left.

And, it's for you too Marther, for the journey that we have begun.

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ABSTRACT

Comprehensive knowledge on the distribution and densities of large carnivores and their prey is necessary in order to understand conservation of carnivores and to mitigate human-wildlife conflict. In order to understand large carnivore ecologies, their diet, dietary overlap, niche breadth and seasonal variation was determined. Fecal analysis method was used in the determination of the diet of lions, leopards, cheetahs, wild dogs and hyenas was studied in a semi-arid savannah ecosystem of Hwange National Park, Zimbabwe. Fecal analysis revealed 20 Mammalian, 1 Rodentia and 1 Avian species ranging from small birds and rodents to large mammals. No domestic livestock prey item was found in the feces. The diet of the five large carnivores overlapped significantly. Large and medium-sized ungulates were the most frequent, with buffalo and impala being the most important prey species. Buffalo was the primary and secondary prey species for lions and hyenas respectively, and impala was the primary prey species for leopards, cheetahs, wild dogs and hyenas, and secondary prey species for lions. Diets of the carnivores significantly varied in the utilization of different prey-size categories ($p < 0.05$), large prey (>100 kg) contributed mostly to the diet of lions and hyenas, medium-sized prey (25-100 kg) contributed mostly to the diet of leopards and wild dogs, and small prey (5-25 kg) to the diet of cheetahs. Seasonal variation was not significant ($p = 0.29$) in the utilization of different prey size categories. For the diet of lions significant variation ($p < 0.05$) was detected in the large and medium-sized categories and no significant variation ($p = 0.11$) in the small sized category. Continuous annual investigations into the seasonal variations of diet selection by the large carnivores in Hwange National Park are recommended.

Key words: Zimbabwe, carnivores, diet choice, overlap, fecal analysis.

ABBREVIATIONS

CITES:	Convention on International Trade in Endangered Species.
CV:	Coefficient of Variation of Annual Precipitation.
GPS:	Global Positioning System.
HNP:	Hwange National Park.
IUCN:	International Union for Conservation of Nature and Natural Resources.
MSU:	Midlands State University.
Spp.:	Species.
WildCRU:	Wildlife and Conservation Research Unit.

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CHAPTER 1

1.1INTRODUCTION

1.1.1Background information

Information on the feeding ecology of large carnivores contributes towards a greater understanding of their behavioural ecology (Breuer, 2005), their crucial roles in the ecosystem and economically, by being major attractions in tourism (Williams, 2011). In some cases information on feeding ecology of large carnivores may be important in understanding and mitigating human-wildlife conflict (Ogara *et al*., 2010; Thorn *et al*., 2012; Bauer, 2015). Although large predators are considered as indicators of ecosystem health (Cozzi *et al*., 2013) having flagship and umbrella roles (Sergio *et al*., 2006) in the ecosystem, their numbers are declining rapidly globally (Williams, 2011; Ripple *et al*., 2014).

Factors such as prey depletion, habitat fragmentation, retaliatory killing over livestock predation, snaring and diseases have contributed to the decline of large carnivores (Thorn *et al*., 2012; Bauer, *et al*., 2015a; Chattha *et al*., 2015). Of the five large carnivores in Hwange National Park (HNP), Zimbabwe, four are threatened with extinction of with one species being endangered, the wild dog (*Lycaon pictus*) and the other three vulnerable, the lion (*Panthera leo*), leopard (*Panthera pardus*) and cheetah (*Acinonyx jubatus*). Only one is not threatened with extinction and is listed in the category, least concern-the spotted hyena (*Crocuta crocuta*) (IUCN, 2016). Successful implementation of any effective conservation programs and/or strategies relies firmly on the availability of accurate scientific data (Cozzi *et al*., 2013; Yirga *et al*., 2014).

Predator-prey interactions are key indicators of ecosystem functioning and structure (Cozzi *et al*., 2013; Chattha *et al*., 2015). Furthermore dietary analyses of predators provide a valuable insight into the key environmental resources required for the conservation of any species. Dietary analysis affords valuable data on the ecology of predators and the effects of predation on the prey species. These results act as baselines to supplement conservation efforts (Lehmann *et al*., 2008; Chattha *et al*., 2015). Dietary studies have immensely contributed towards the realization of interference and exploitation competition as pivotal forces in the shaping of ecological relationships amongst predators (Ogara *et al*., 2010; Mbizah *et al*., 2012).

Various methods have been used to study the diet of carnivores including fecal analysis (Breuer, 2005; Andheria *et al*., 2007; Ogara *et al*., 2010; Mbizah *et al*., 2012); tracking spoor, radio telemetry (Grant *et al*., 2005); opportunistic and direct observation of carcasses (Rapson & Bernard, 2007); and combinations of two or more of these methods for example, radio telemetry and scat analysis (Farrell *et al*., 2000) and carcass observation, faecal analysis and telemetry (Davidson *et al*., 2013). Scat analysis has proved to be useful in dietary studies (Breuer, 2005; Ogara *et al*., 2010) and has been largely utilized because it is non-invasive, allows for continuous determination of diet choice and scats are relatively easy to collect (Mukherjee *et al*., 1994). Scat analysis method was used in this study to determine the diet, seasonal variation and dietary overlap in lion *P.leo*, leopard *P.pardus*, spotted hyena *C.crocuta*, cheetah *A.jubatus* and wild dog *L.pictus* in a semi-arid ecosystem. It is envisaged that this study will contribute to the understanding of apex carnivores through the documentation of prey species utilizations, seasonal variations in diet selection and overlap amongst the study species in Hwange National Park (HNP).

1.1.2 Problem Statement

A number of studies have described the diet of large carnivores such as lion, leopard and hyena in other parts of Africa and across their range (Breuer, 2005; Hayward & Kerley, 2005; Hayward *et al*., 2006a). There is insufficient data on the diet composition, seasonal variation and overlap in the diets of large carnivores in HNP. Data for the extent of livestock depredation is also necessary to understand human-wildlife conflict. Human-wildlife conflict begins with the locals claiming that carnivores attack and kill their livestock and documenting the diet constituents of large predators in Hwange National Park has the potential of demonstrating the extent of utilization of domesticated animals by carnivores (Breuer, 2005), which can be used to manage and mitigate conflict.

1.1.3 Justification

Factors like predator hunting strategies, prey abundance and seasonal changes are known to affect the diet selection of large carnivores, but it is also important to understand these effects *in-situ* rather than to assume basing on the results of other studies outside the predators locality (Purchase, 2007). Diet selection also overlaps amongst large carnivores, but the extent of dietary overlap between HNP's large predator guild is still fairly unknown. Overlap is a direct indicator of competition and the potential of predators limiting each other in their ranges; without sufficient literature it is difficult to understand this in HNP.

Scientific data on large carnivore diets, overlaps and resource partitioning are vital for scientific understanding as well as for appropriate setting of conservation actions (Breuer, 2005; Andheria *et al*., 2007). Consequently, the results from this study will assist Parks and Wildlife managers in Hwange National Park (HN) in making scientifically backed inference in conservation planning.

1.1.4 Main Objective

The aim of this study was to investigate the diets of Lions *Panthera leo*, Leopards *Panthera pardus*, Spotted hyenas *Crocuta crocuta*, Cheetahs *Acinonyx jubatus* and African wild dogs *Lycaon pictus* in Hwange National Park, Zimbabwe.

1.1.5 Specific Objectives

- ❖ To investigate the diet selection of lions, leopards, spotted hyenas, cheetahs and African wild dogs.
- ❖ To investigate dietary overlap in the diets of lions, leopards, spotted hyenas, cheetahs and African wild dogs.
- ❖ To investigate seasonal variation in the diet selection of lions, leopards, spotted hyenas, cheetahs and African wild dogs.

1.1.6 Research Questions

In order to understand dietary selection, seasonal variation in diet and extent of diet overlap amongst lions, leopards, spotted hyenas, cheetahs and wild dogs answers the following research questions will be determined:

1. What is the diet composition of each of the aforementioned carnivores?
2. What is the degree of diet overlap amongst these five carnivores?
3. How does the diet composition compare between dry season (April-October) and wet season (November-March)?

1.1.7 Hypotheses

1. (H_0) There is no significant difference in the diet compositions of the lion, leopard, spotted hyena, cheetah and wild dog.
2. (H_0) There is no significant overlap in the diets of the lion, leopard, spotted hyena, cheetah and wild dog.
3. (H_0) There is no significant seasonal difference (wet and dry) in the diets of lion, leopard, spotted hyena, cheetah and wild dog.

CHAPTER 2

2.1 LITERATURE REVIEW

2.1.1 Conservation Status of Large Carnivores

Globally large carnivore populations are in sharp decline and as a result an imbalance now exists between the carnivores and their prey populations (Chattha *et al*., 2015) resulting in changes in the faces of landscapes in ecosystems around the world (Woodroffe, 2000). According to Purchase (2007), more than 75 percent of the 31 large-carnivore species populations are reported as declining and/or endangered, with 17 species now occupying less than 50 percent of their former ranges and some already locally extinct in much of the developed world, including Western Europe and the eastern United States. Southeast Asia, the Amazon and parts of Africa still have multiple large carnivore species, though their numbers are declining sharply(Purchase, 2007).

Traditionally, the African lion ranged across most of Africa but is now limited to only 34 African countries having disappeared from at least 7 others and over 80 percent of its prior range (IUCN, 2016). This is because most populations in West and Central Africa are without protected areas (Cozzi, *et al*., 2013). Currently the lion is listed as vulnerable due to a rapid decline in its populations of between 30-50 percent over the past two decades (three lion generations) (Bauer, *et al*., 2015b, IUCN, 2016).

The cheetah is currently Africa's most endangered large cat (Williams, 2011). With a huge decline in their numbers and range (Purchase, 2007). In 1990, there were 100,000 cheetahs left in the world but today, there is only an estimated 10,000 remaining in 23% of the range they once occupied (Hayward *et al*., 2006b). Cheetahs are listed as "Vulnerable" on the IUCN's (2016) Red List of Threatened Species.

The leopard is widely distributed in sub-Saharan Africa giving it more tolerance to disturbance and a broader prey base (Hayward & Kerley, 2008), feeding habits, highly adaptable hunting and hermit like nature (Chattha *et al*., 2015). Nonetheless it also suffers population declines. The leopard was first listed on the CITES Appendix I in 1973 (Bauer *et al*., 2015a). Due to inconclusive data it is currently listed as vulnerable, though it deserves a more robust listing as it is subject to local depletion (Chattha *et al*., 2015).

The African wild dog on the other hand once known to exist abundantly in most parts of sub-Saharan Africa is currently one of Africa's most endangered carnivores (Hayward, *et al*., 2006c) and is listed as such by the IUCN (Woodroffe, 2000, IUCN, 2016). Spotted hyenas like the African wild dogs used to be widespread throughout sub-Saharan Africa, though their range has shrunk considerably (Hayward & Kerley, 2008). The current distribution of spotted hyena is patchy in many places, with populations concentrated in protected areas and surrounding land (Hayward, 2006). Spotted hyenas are listed as "Least concern" by the IUCN (2016) Red List of Threatened Species.

2.1.2 Threats facing large carnivores

Due to their large range requirements large carnivores are faced with many threats including: habitat loss and fragmentation (Purchase, 2007, IUCN, 2016) and due to proximity to human settlement: human conflict being the major threat (Woodroffe, 2000). Ecological pressures such as loss of prey base and deforestation also threaten them as well (Chattha *et al*., 2015). Prey base depletion can be attributed to habitat loss, but is fundamentally due to poaching (Breuer, 2015). Killing of large predators due to problem animal control, revenge killing by locals and snaring by poachers have adverse effects on large predator populations, as it reduces recruitment and disrupts carnivore social systems (Woodroffe, 2000). A new threat is coming from trade in bones and other body parts for traditional medicine (Yirga, *et al*., 2013).

Human activities like trophy hunting, although having positive contributions to conservation efforts need proper regulation, as it can become a threat to large carnivore populations, especially lions (Bauer, *et al*., 2015a, Bauer, 2015). Bauer (2015) argues that due to increased human pressure (largely because of population expansion and the land reform program in Zimbabwe, for example) large predators have virtually disappeared from outside protected areas. This has also led to an increase in the contact between humans and large predators resulting in adverse effects on both populations as people suffer livestock losses and face risk of injury or death and large predators suffer from high levels of retaliatory killings (Bauer, 2015). This has serious negative ecological and economic implications.

2.1.3 Importance of large predators

Large carnivores are important elements of faunal biodiversity, belonging to the order *Carnivora* which is the fourth largest group in the kingdom *Animalia* and class Mammalia with diverse species varying in biological characteristics (Purchase, 2007). Large carnivores for example, lions and leopards are umbrella species (Andheria *et al*., 2007); indicators of ecosystem health (Cozzi *et al*., 2013), and their effective conservation programs enhance survival prospects of other forms of biodiversity and shape prey communities (Andheria *et al*., 2007). Large predators also play pivotal roles in the structuring of ecosystems by the regulation of their prey and/or competitors, or both (Cupples *et al*., 2011). Large predators are often unjustifiably blamed in cases of human-predator conflict (Purchase, 2007)resulting in huge economic losses and negative ecological impacts. Sustainability of all economic and ecological roles require detailed information on the large carnivores diets to ensure effective utilization and conservation efforts (Ripple *et al*., 2014).

2.1.4 Factors influencing dietary selection in large predators

Patterns in dietary selection by large terrestrial carnivores are shaped by factors such as energetic costs and benefits, mechanisms of selection including search images, prey vulnerability and habitat characteristics related to hunting or escape (Hunter, 2008; Owen-Smith & Mills, 2008; Loveridge, *et al*., 2010). Different optimal foraging strategies affect diet selection in different carnivores.

Leopards and lions are highly opportunistic predators and utilize food according to local availability (Stander, 1992; Davidson *et al*., 2013; Chattha *et al*., 2015), spotted hyenas are unselective opportunistic predators, scavengers (Hayward, 2006) and kleptoparasites (Graf, *et al*., 2009); whilst wild dogs are gregarious, social cursorial hunters (Fanshawe *et al*., 1991; Hayward *et al*., 2006c). Spotted hyenas and lions are known to exhibit seasonal variation in their optimal foraging strategies for example, prey switching in lions (Davidson *et al*., 2013) and switching between hunting or scavenging for hyenas (Cooper *et al*., 1999; Yirga *et al*., 2013), unlike cheetahs which rarely scavenge (Hayward *et al*., 2006b).

Physiological conformation and behavior also affects the diet choice of carnivores (Breuer, 2005). Spotted hyenas have a wider selection because of strong jaws and teeth; efficient digestive systems and matriarchal grouping behavior (Hayward, 2006). Larger size, diet plasticity (Pitman *et al*., 2013) and adaptability to diverse habitats in leopards widens their prey selection range (Chattha *et al*., 2015).

Social behavior (grouping or solitary) in large carnivores influences prey size selection for example, lions kill prey as large as adult giraffe *Giraffa Camelopardalis*, hyenas killing large buffalo *Syncerus caffer* (Cooper *et al*., 1999) and wild dog packs also being able to kill large buffalo (Hayward, *et al*., 2006c). This is because grouping widens the size range of species that can be subdued, lowers the energy costs and increases the chances of success.

Leopards on the other hand are almost entirely solitary, with the territories of females being overlapped by larger territories of similarly solitary males (Hayward *et al*., 2006b). Normally cheetahs hunt as solitary individuals, though grouping behavior can be observed between a mother and cubs, or male coalitions (Hayward *et al*., 2006b). As a result both leopards and cheetahs are known to avoid larger prey to minimize the risk of injury and kleptoparasitism (Owen-Smith & Mills, 2008). Adaptations to different hunting strategies for example, running by wild dogs and/or stalking by spotted hyenas affects their diet choice relating to the availability and distribution of the preferred ungulate species i.e., open habitats or thicker vegetation (Owen-Smith & Mills, 2008).

Ungulate prey species affect diet choice of carnivore due to their body sizes, physiological adaptations (grouping, defense and escape), spatial and temporal distributions. Prey availability, distribution and activity patterns influences both the dietary selection, hunting success (Breuer, 2005) and facilitate sympatry among the five predators (Andheria *et al*., 2007). Though it has been argued in other studies that for some carnivores, for example, the lion it is much more about accessibility than abundance (Grant *et al*., 2005). Specific size ranges of prey accounts for the differences in diet selection (Owen-Smith & Mills, 2008) and carnivores have been reported to selectively favor prey species approximately half to twice their mass, choosing prey classes from below (driven by encounter rates) to above (driven by foraging strategy) their own body weights (Owen-Smith & Mills, 2008). It is argued that dietary ranges for larger carnivores for example, lions is likely to be broader than that of comparatively smaller carnivores for example, cheetahs (Hayward & Kerley, 2005; Owen-Smith & Mills, 2008) due to their ability to utilize prey species from wider size ranges. Diet selection is also affected by body size and physical adaptations of the carnivore. Selection has been observed to vary between the same predator species due to sexual dimorphism, for example large females in hyenas (Périquet *et al*., 2015) and large males in lions (Davidson *et al*., 2013) tending to capture somewhat larger prey than their counterparts of the same species (Owen-Smith & Mills, 2008).

The cheetah is a highly specialized, cursorial felid that has evolved various physical adaptations that make it a rapid pursuit specialist which is necessary for them to catch their prey (Hayward *et al*., 2006b). The cheetah also hunts during the day whereas the leopard hunts solitary at night, making use of their camouflage to stalk prey and then capture after short sprints (Hayward, *et al*., 2006b).

2.1.5 Sympatric carnivore interactions

Large carnivores are important as both exploitative (indirect) and interference (direct) competitors (range and diet overlap, intraguild predation and kleptoparasitism) of each other in any ecosystem guild that they occupy in sympatry (Hayward & Kerley, 2008). Competition has been reported in other studies, for example, between the cheetah and hyena (Graf *et al*., 2009), the lion and hyena (Périquet *et al*., 2015) with hyenas losing at least 5% of their kills to lions (Hayward, 2006) and leopard and wild dog (Mbizah *et al*., 2012). Cheetahs and wild dogs are frequent victims of kleptoparasitism, up to 50% and both are sometimes killed (both adults and cubs) by larger predators that come to steal from their kills (Hayward *et al*., 2006b).

Competition is influenced not only by each species' physical ability to obtain and keep food but also by variation in the spatial and temporal availability of food (Merwe *et al*., 2009) and is mediated by inter-specific morphological, physiological and behavioral differences (Loveridge *et al*., 2010). Small body size (in cheetahs and wild dogs) and solitary physiological adaptation (in leopards and cheetahs) exacerbates the competition pressure in other species of carnivores, for example, cheetah and wild dogs are frequently forced away from their kills by larger predators such as leopards, hyenas or lions (Farrell *et al*., 2000; Andheria *et al*., 2007; Cupples *et al*., 2011; Mbizah *et al*., 2012). This competitive nature has been put forward as the supporting argument for the negative correlation between the densities of spotted hyenas and wild dogs across several ecosystems (Graf *et al*., 2009).In order to persist carnivores have developed strategies that reduce competition pressure. Strategies employed by carnivores include physiological adaptations and/or niche partitioning (Merwe *et al*., 2009; Périquet *et al*., 2015) and different activity patterns(Hayward, *et al*., 2006a). For example, cheetahs hunt during the day whereas lions and hyenas hunt from dusk to dawn during periods of low temperatures (Périquet *et al*., 2015) and leopards at night (Hayward *et al*., 2006a; Chattha *et al*., 2015). Cheetahs and wild dogs attempt to minimize competition effects by hauling the carcass up a tree for cheetahs and speed in feeding for wild dogs (Hayward *et al*., 2006b).

Carnivore families also mediate competition and predation risk through the use of alternative habitat types, strata (terrestrial, arboreal, fossorial or aquatic), and diet, i.e., niche partitioning (Hayward & Kerley, 2008; Hunter, 2008; Silva-Pereira *et al*., 2011). The extent of niche differentiation and resource partitioning determines the degree to which different species can either coexist or competitively exclude each other (Merwe *et al*., 2009). An important mode of resource partitioning is the selection of different classes of prey in order to minimize the degree of dietary overlap between sympatric species (Hayward & Kerley, 2008) and dietary studies help us understand these relationships.

2.1.6 Methods used in large carnivore dietary analysis

There are several different methods that can be used to study the diet of large carnivores including scat (Breuer, 2005; Andheria *et al*., 2007; Mbizah *et al*., 2012); field observation and stable isotope, tracking spoor, radio telemetry (Grant *et al*., 2005); opportunistic and direct observation of carcasses (Rapson & Bernard, 2007); stomach content observations; and/or combinations of two or more of these methods, for example, radio telemetry and scat analysis (Farrell *et al*., 2000) and carcass observation, faecal analysis and telemetry (Davidson *et al*., 2013).

Scat analysis is an extensively used field technique for the study of predator diets through the identification of distinguishable parts of prey that have passed through their gastrointestinal tract in comparison with reference collections of potential food items (Breuer, 2005; Andheria *et al*., 2007). Scat analysis is applicable when dealing with terrestrial carnivores and individual prey items (Cozzi *et al*., 2013), because with studies involving endangered species, for example, lions and wild dogs, analysing stomach contents becomes impractical.

Cost and handling are major technicalities that also determine the method of choice, for example, the elusive solitary nature of leopards makes field observation unreliable and extremely difficult and the use of DNA-analysis is very costly. Scat analysis presents a viable option in the study of predators diets as it is non-invasive (Reviewed, 1999; Marnewick, 2006), cheap, allows for continuous determination of diet choice and scats are relatively easy to collect (Mukherjee *et al*., 1994).

Scat analysis has been largely used for the study species and shown to be reliable in the determination of the diets for lions, leopards, spotted hyenas and African wild dogs (Breuer, 2005; Davies-Mostert *et al*., 2010; Mbizah *et al*., 2012).

2.1.7 SCAT analysis method

Scat analysis is an indirect method for the determination of prey species, that involves macroscopic and microscopic analysis of undigested constituents of prey for example, hair, feathers and bones in the predator scat (Mukherjee *et al*., 1994; Marnewick, 2006). It is a lengthy method that involves the picking of carnivore scats; accurate documentation (i.e. predator name; site and date picked; coding and storage); washing; macroscopic and microscopic analysis (scale patterns and cross sections), and finally identification (Marnewick, 2006). The microscopic analyses of scale patterns were seen not to be conclusive in the identification of prey species, but the addition of cross sections was demonstrated to greatly improve the accuracy of identification (Marnewick, 2006).

Accuracy can also be increased by the reduction of sources of bias, since scat analysis is an indirect method; several factors have been shown to present sources of bias if not properly addressed. For example, the influence of scat collection, laboratory procedures, misidentification of food remains and interpretation of raw data (Davies-Mostert *et al*., 2010) affecting the quality of the results. Most studies have looked at the frequency of occurrence of food items, either related to the number of scats analyzed or to the number of prey items found (Breuer, 2005). As a result, prey items occurring in trace amounts can be discarded from the analysis (Davies-Mostert *et al*., 2010). Other studies have reported on the volume or mass of the food items found in the scats (Andheria *et al*., 2007; Davies-Mostert *et al*., 2010). To improve on accuracy, for the interpretation of our scat-analysis data we will use frequency of occurrence method (Andheria *et al*., 2007; Davies-Mostert *et al*., 2010; Mbizah *et al*., 2012).

CHAPTER 3

3.1 MATERIALS AND METHODS

3.1.1 Study area

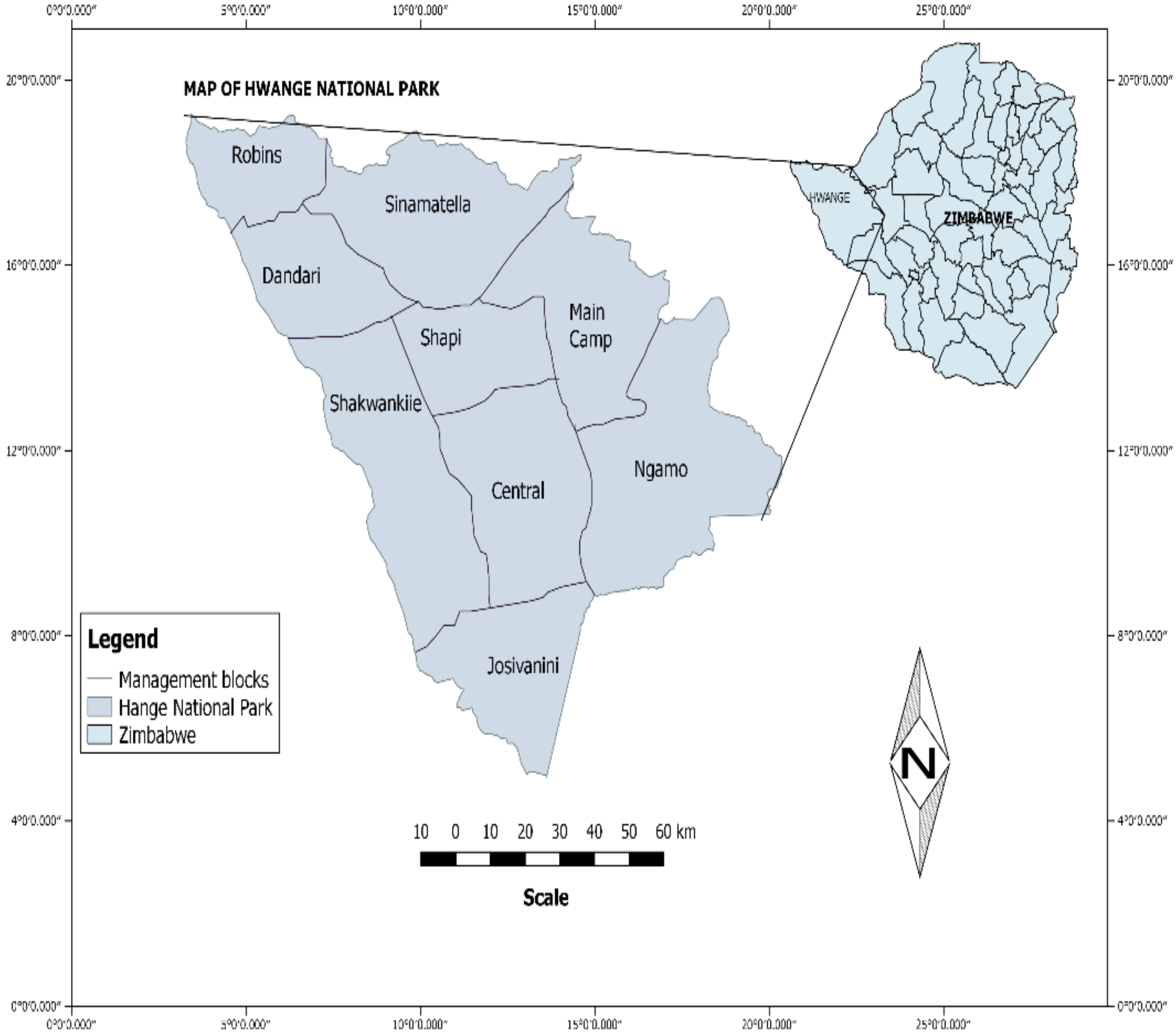

Figure 1: Hwange National Park, Zimbabwe (study area), showing the management blocks.

The study was carried out in Zimbabwe's Hwange National Park covering an area of 14,651km^2, located (19ºS, 26ºE) (Muboko *et al*., 2016) .HNP is characterized by semi-arid conditions with deciduous woodland(mostly *Baikiaea plurijuga*)and scrubland (>60% of the landscape; mostly *Combretum* spp., *Acacia* spp. and *Terminalia sericea*) (Courbin *et al*., 2015) with edaphic patches of savanna grasslands typical of southern African dystrophic soils (Kalahari sands).The area experiences low and erratic precipitation with a mean annual rainfall of 600mm and an inter-annual CV of 25%(Périquet *et al*., 2010; Kuiper *et al*., 2015). The region primarily receives rainfall between November and March with natural water rarely lasting up to July and during the dry season, natural water becomes scarce, surface water is primarily made available to animals from artificial pans, developed by pumping ground water (Périquet *et al*., 2015).

The potential prey species in HNP are diverse including: Elephant *Loxodonta africana*, Giraffe *Giraffa camelopardalis*, Buffalo *Syncerus caffer*, Zebra *Equus quagga*, Roan antelope *Hippotragus equinus*, Blue wildebeest *Connochaetes taurinus*, Waterbuck *Kobus ellipsiprymnus*, Kudu *Tragelaphus strepsiceros*, Impala *Aepyceros melampus*, Steenbok *Raphicerus campestris*, Common duiker *Sylvicapra grimmia*, Eland *Taurotragus oryx*, Warthog *Phacochoerus africanus*, Sable antelope *Hippotragus niger* and others.

3.1.2 Scat collection

Fecal samples were randomly collected during game survey's; at kill sites; and opportunistically along roads and trails that predators favor for fecal deposit (Andheria *et al*., 2007)in 2013. Details of the sample location; area and Global Positioning System (GPS) loc state, and date were recorded. Samples were placed in paper bags with unique identification codes and then stored in a cool and dry place. Experienced field personnel undertook the identification of fecal samples basing on physical characteristics: shape, color, diameter, odor and the presence of associated field signs such as den sites and tracks (Breuer, 2005) for example, spotted hyena feces are white when they are dry as a result of the high bone content constituting their meals, African wild dog feces have a strong smell, lion feces are segmented with a diameter of at least 40 mm whilst leopard feces are smaller than that of adult lion with a diameter of 20–30 mm (Mbizah *et al*., 2012). Fecal samples of uncertain origin were discarded from the analysis.

3.1.3 Processing and analysis of fecal samples

Fecal samples were soaked overnight in water containing 10ml disinfectant. Samples were then placed in a metal sieve and washed using cold running water to separate hairs, bones, hoof fragments, teeth and other prey components from the organic material. The hairs were sun-dried and placed into clearly labeled plastic sample bags. Hair samples were then extracted from the plastic sample bags placed in metal petri-dishes, washed in absolute alcohol and left to dry. Samples were analyzed macroscopically (hair form, length and color; presence of prey remains e.g. bones, claws and hooves) and microscopically based on scale patterns and cross sections observations through a light microscope at x10 magnification. Scale patterns were examined by using hair imprints made in wood glue and cross sections of hair strands were made by adapting the pustular pipette tubing method (Marnewick, 2006; Mbizah *et al*., 2012).

A reference collection was built using hairs of known prey species collected from all parts of the pelage (the fur, hair, or wool of a mammal) of available prey items. These hairs were collected from prey remains during kill site investigation and from quota kills by the Parks and Wildlife Management Authority (PWMA) staff (Marnewick, 2006).

3.1.4 Prey species population estimation

Secondary data from an aerial survey was utilized for the determination of the relative abundances of the prey species available in HNP.

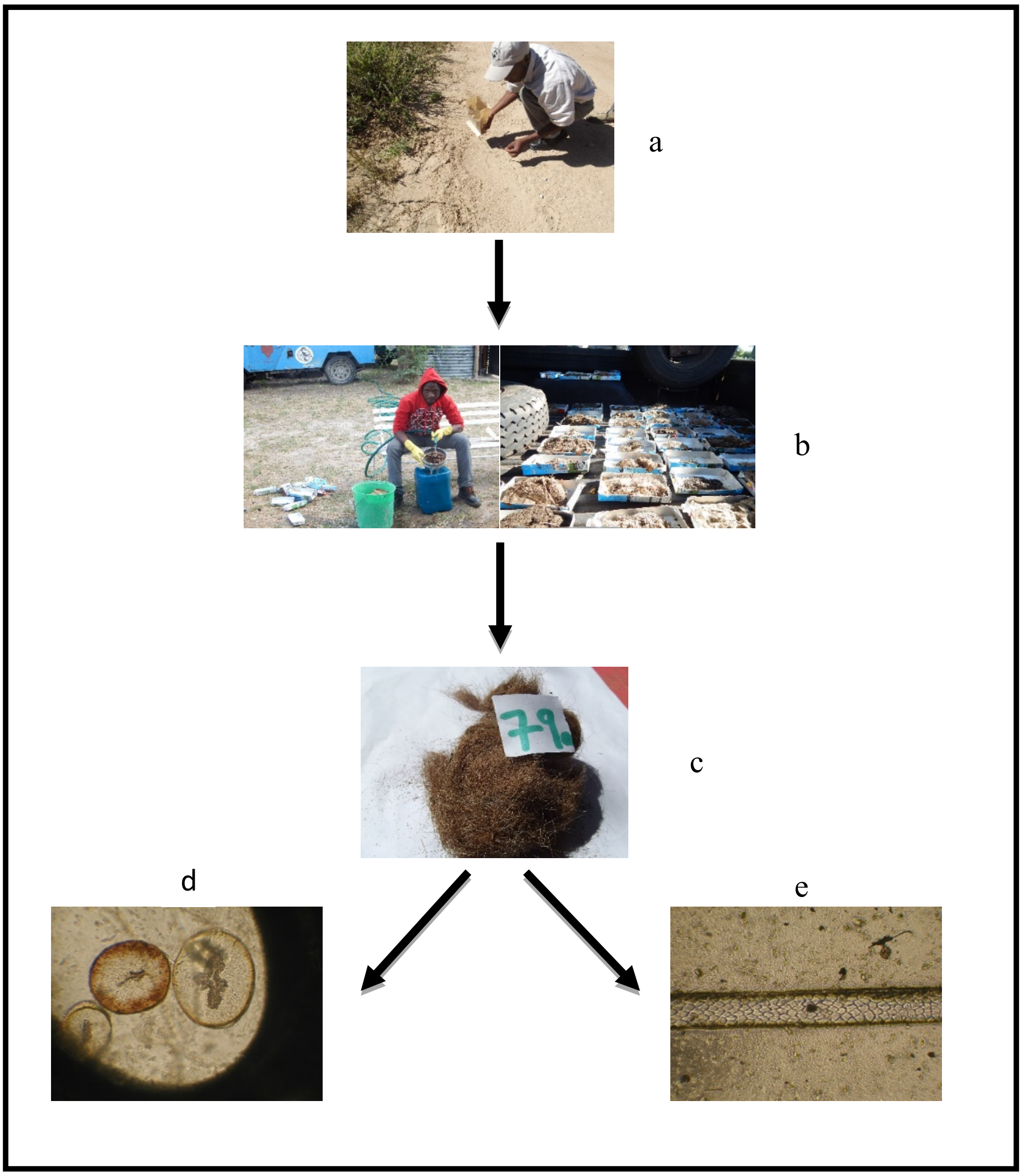

Figure 2: Scat analysis flowchart (a) collection; (b) washing and drying; (c) description of fecal samples; (d) hyena cross section and, (e) steenbok scale pattern.

3.2 DATA ANALYSIS

3.2.1 Diet composition

Diet composition was calculated using frequency of occurrence expressed as a percentage.

Absolute Prey Frequency = (n/N).

This is the number of prey items of a species (n) in relation to the total fecal samples analyzed (N). Relative frequency of occurrence was used to interpret dietary composition in terms of the importance of each prey item to the overall diet. This was calculated as;

Relative Frequency of Occurrence = (r/R).

This is the number of times the prey item was encountered in the whole sample (r) as a percentage of the total occurrence of all prey species (R). Contingency tables and Chi-square tests were applied in order to compare the composition of the different diets for the different carnivores and analyses was conducted using R-statistical package (Breuer, 2005; Mbizah *et al*., 2012).

3.2.2 Dietary overlap

Diet overlap was calculated using Pianka's index;

$$O_{ab} = (\sum n P_{ia} P_{ib}) / (\sum n P_{ia}^2 \sum n P_{ib}^2)^{1/2}$$

Where: O_{ab} is diet overlap between species *a* and *b*;

P_{ia} is the relative frequency of the item *i* found in the diet of species *a*;

P_{ib} is the relative frequency of *i* found in the diet of species *b*; and

n is the total number of prey species in the carnivore's diet.

The index ranges from 0 to 1 (no overlap to complete overlap) and becomes biologically significant when O_{ab}>0.60 (Breuer, 2005; Mbizah *et al*., 2012; Périquet *et al*., 2015).

3.2.3 Seasonal dietary variation

Seasonal dietary variation was calculated for (wet and dry seasons) using the standardized form of Levin's index niche breadth;

$$B_i = 1/(\sum P_i^2) \text{ and } BA = (B - 1)/(n - 1)$$

Where: B_i = the Levin's' measure of niche breath;

P_i= proportion of occurrence of each prey species in the carnivores diet;

BA = Levin's' standardized niche breath and

n = number of prey species in the carnivores diet.

Levin's' index of niche breadth (Bi) ranges from 1 to n, whereas Levin's' standardized niche breadth (BA) ranges from 0 to 1. Low values indicate diets dominated by few prey items (specialist predators) while higher values indicate catholic diets (Begg *et al*., 2003; Breuer, 2005; Mbizah *et al*., 2012; Périquet *et al*., 2015). A students "Welch two sample T-test" was computed for the wet and dry seasons to compare seasonal variation and "one sample T-tests" to compare seasonal variations in prey size category utilization. To reduce the potential bias brought about by small sample sizes, unequal sample sizes and unequal variances, "fisher's exact tests" were utilized for small samples and "Welch two sample T-tests" to adjust for unequal sample sizes and variance.

3.2.4 Prey species population estimation

Available aerial population estimates for the potential prey species for the year 2001 and 2014 will be presented in a table, showing the estimated numbers for the different years and the observed trend for that potential prey item.

CHAPTER 4

4.1 RESULTS

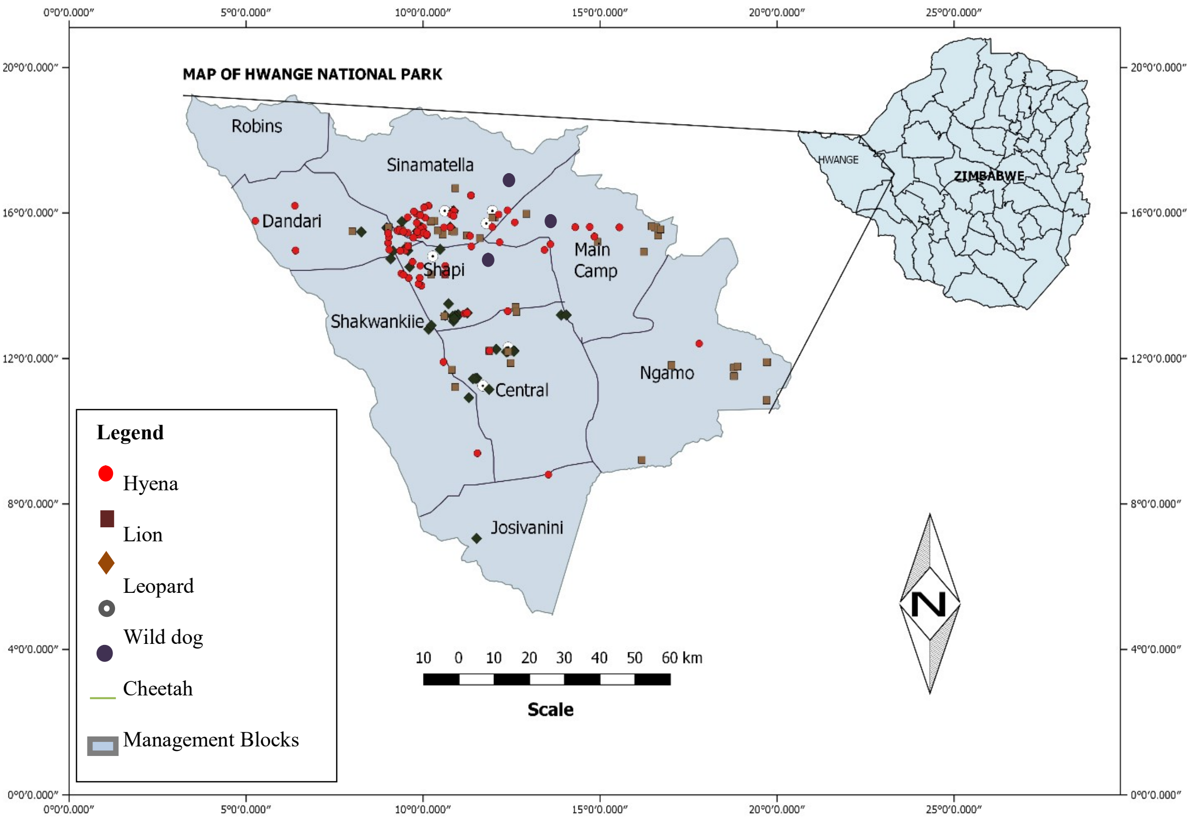

Figure 3:Study area in Hwange National Park, Zimbabwe. Showing the management blocks and sampling effort.

4.1.1 Diet composition

A total of 574 fecal samples were collected: 81 from lions; 50 from leopards; 412 from hyenas; 22 from cheetahs and 9 from wild dogs. Of these, 407 samples were analyzed and processed: 78 from lion; 50from leopards; 249 from hyenas; 21 from cheetah and 9 from wild dog (Table 1). Analysis of fecal samples revealed 20 mammalian, rodentia and avian species (spp.). Lions had the highest number of identified prey species 20 (19 mammalian and 1 rodentia spp.), hyenas had 19 (18 mammalian and 1 avian spp.), leopard had 12 (10 mammalian, 1 rodentia and 1 avian spp.), cheetah had 8 (6 mammalian, 1 rodentia and 1 avian spp.) and the wild dog had the least 6 mammalian spp. None of the identified prey species were domestic species.40 samples had two prey species: 21 in hyenas, 10 in leopards, 7 in lions and 2 in wild dogs and 1 sample in cheetahs had three prey species, as a combination of different size species.

Table 1: Scat analysis breakdown for samples collected in HNP.

	Samples Collected	Samples Analyzed	Wet Season	Dry Season
Lion	81	78	13	65
Leopard	50	50	8	42
Hyena	412	249	75	174
Cheetah	22	21	14	7
Wild Dog	9	9	0	9
Total	574	407	110	297

Buffalo was the primary (†) prey species in the diet of the lion and secondary prey species (‡) in the diet of the hyena (Table 2). Impala was the prey species most frequently recorded in the feces of all the five carnivores, being the primary prey species in the diet of four of the carnivore species: leopards, cheetah, wild dogs and hyenas (Table 2), and its frequency of occurrence was highest in the wild dog diet. The larger prey items present in the samples were elephant, buffalo, zebra, kudu, giraffe, wildebeest, eland, tsessebe, roan and sable antelope; these constituted a greater part of the lion and hyena diet (Table 2).

The contribution of prey species based on their frequency of occurrence (Table 2), was significantly different (χ^2= 866.9, d.f. = 448, p-value <0.05) among the diets of the five carnivores. Significant differences were detected in the contribution of zebra, warthog, giraffe, eland, elephant, wildebeest, avian spp., rodentia spp., baboon, aardvark, klipspringer, tsessebe, roan and sable antelopes. The frequency of occurrence of impala was significantly different between the lions and two other carnivore species: (χ^2= 68.409, d.f. = 1, p-value <0.05) with hyenas and (χ^2= 7.8365, d.f. = 1, p-value <0.05) with leopards, but not significantly different between the lion and two remaining carnivore spp.: (χ^2= 1.0012, d.f. = 1, p-value = 0.21) with cheetah and (χ^2= 2.4911, d.f. = 1, p-value = 0.06) with wild dog. Buffalo was an important prey species in the diet of lions and hyenas (Table 2) and its frequency of occurrence was not significantly different (χ^2= 0.56291, d.f. = 1, p-value = 0.45). Common duiker was important in the diet of leopards and cheetahs (Table 2) and its frequency of occurrence was not significantly different (χ^2= 1.5471, d.f. = 1, p-value = 0.13). Steenbok was an important prey item in the diet of leopards and wild dogs (Table 2) and its frequency of occurrence was not significantly different (χ^2= 0.28116, d.f. = 1, p-value = 0.27).

Table 2: Percentage (%) relative frequency of occurrence of prey species in the five carnivores' diets in HNP.

Animal	Lion(n=78)	Leopard(n=50)	Cheetah(n=21)	Wild Dog(n=9)	Hyena(n=249)
Buffalo	23.17†	5.17	0	10.00	18.38‡
Impala	13.41‡	36.21†	26.09†	40.00†	27.21†
Burchell's Zebra	7.32	3.45	0	0	5.88
Sable Antelope	7.32	0	0	0	1.10
Warthog	6.10	0	0	0	1.84
Giraffe	4.88	0	0	0	2.21
Eland	4.88	0	0	0	2.21
Waterbuck	3.66	6.90	0	10.00	8.82
Greater Kudu	3.66	6.90	0	10.00	8.82
Roan Antelope	3.66	0	0	0	1.47
Common Duiker	3.66	8.62‡	21.74‡	10.00	4.04
Bushbuck	3.66	6.90	17.39	0	6.62
Elephant	2.44	0	0	0	0.37
Blue Wildebeest	2.44	0	0	0	4.78
Steenbok	2.44	8.62‡	17.39	20.00‡	6.62
Sharpe's Grysbok	1.22	1.72	4.35	0	0
Avian spp.	1.22	8.62‡	4.35	0	0.37
Baboon	1.22	0	0	0	0
Aardvark	1.22	0	0	0	0
Reedbuck	0	5.17	4.35	0	3.31
Rodentia spp.	1.22	5.17	4.35	0	0
Klipspringer	0	0	0	0	0.74
Tsessebe	0	0	0	0	1.10

†: Primary prey specie is the prey item with the highest frequency of utilization.

‡: Secondary prey specie is the prey item with the second highest frequency of utilization.

Table 3: Percentage (%) relative frequency of prey size categories in the diets of the five carnivores in HNP.

	Very Small Prey (<5kg)	Small Prey (5-25kg)	Medium-sized Prey (25-100kg)	Large Prey (>100kg)
Lion (n=78)	2.41	8.43	25.30‡	63.86†
Leopard (n=50)	13.79	18.97‡	48.28†	18.97‡
Cheetah (n=21)	8.70	43.48‡	47.83†	0
Hyena (n=249)	0.37	11.52	39.41‡	48.70†
Wild Dog (n=9)	0	30.00‡	40.00†	30.00‡

†: Primary prey size category is the prey size category with the highest frequency of utilization.

‡: Secondary prey size category is the prey size category with the second highest frequency of utilization.

There was a significant variation in the consumption of prey of different size category by the five carnivores (χ^2= 151.03, d.f. = 12, p-value <0.05). Large sized prey (>100 kg) for example buffalo, zebra and kudu was the most frequent in the diets of the lion and hyena (Table 3) and its frequency of occurrence was significantly different (χ^2= 5.2487, d.f. = 1, p-value < 0.05). The frequency of medium sized prey (25-100 kg) for example impala, bushbuck and warthog was proportionally high across all the five carnivores ranging between 25.3% in lions and 48.3% in leopards (Table 3), it's frequency of occurrence was significantly different between the lion and two other carnivore species: (χ^2= 6.9667, d.f. = 1, p-value < 0.05) with leopard and (χ^2= 4.8766, d.f. = 1, p-value < 0.05) with hyena. But was not significantly different between the lion and the two remaining carnivore species: (χ^2= 3.3327, d.f. = 1, p-value = 0.06) with cheetah and (χ^2= 7.9556e^{-31}, d.f. = 1, p-value = 0.75) with wild dog.

Medium sized prey was also the most frequent in the diets of leopards, cheetahs and wild dogs (Table 3) and its frequency of occurrence in their diets was not significantly different across: (χ^2= 0.019947, d.f. = 1, p-value = 0.73) in leopard and wild dog; (χ^2= 5.4953e^{-31}, d.f. = 1, p-value = 1) in leopard and cheetah; and (χ^2= 0.0011957, d.f. = 1, p-value = 0.72) in cheetah and wild dog.

The high frequency of occurrence of impala across the five carnivore's diet (between 13.41% and 40%) (Table 2) contributed to the high frequency of utilization in the medium sized prey category. Small prey (5-25 kg) for example common duiker, steenbok and grysbok with high frequency in cheetah and wild dog diets (Table 3). Very small prey (<5 kg) for example avian and rodentia spp., was seen in the diet of three of the carnivore species i.e., lions, leopards and cheetahs (Table 3) with the highest frequency observed in the leopard diet (Table 2).

4.1.2 Dietary overlap

The diets of the five carnivores overlapped significantly (O_{ab}>0.60) (Table 4). Overlap was very high between the diets of hyena and cheetah (0.87); hyena and leopard (0.87); hyena and lion (0.85) and wild dogs and leopards (0.84). There was an almost complete overlap (0.91) between the diets of leopards and cheetahs. Overlap was not significant between the diets of lions and leopards (0.58) and lions and wild dogs (0.40).

Table 4: Diet overlap and niche breadth of the five carnivores in HNP.

	Diet Overlap					Niche Breadth	Standardized Niche Breadth
	Lion	Leopard	Hyena	Cheetah	Wild Dog		
Lion	_					9.89 (n=20)	0.47
Leopard	0.58	_				5.76 (n=12)	0.43
Hyena	0.85	0.87	_			7.38 (n=19)	0.35
Cheetah	0.60	0.91	0.87	_		4.17 (n=6)	0.64
Wild Dog	0.40	0.84	0.66	0.77	_	5.45 (n=8)	0.64

4.1.3 Seasonal dietary variation

Table 5: Percentage (%) seasonal relative frequency of prey size categories in the diets of the five carnivores in HNP.

	Very Small Prey (<5kg)		Small Prey (5-25kg)		Medium-sized Prey (25-100kg)		Large Prey (>100kg)	
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
Lion	6.25	1.32	18.75	5.26	43.75	27.63	31.25	65.79
Leopard	33.33	12.50	0	22.92	50	45.83	16.67	18.75
Cheetah	0	22.22	42.86	44.44	57.14	33.33	0	0
Wild Dog*	0	0	0	36.36	0	36.36	0	27.27
Hyena	1.09	3.21	8.70	12.30	47.83	33.16	42.39	51.34

*There were no samples for the determination of the wet season diet of the wild dogs.

There was no significant variation between the wet and dry season diets of the four carnivore species in HNP ($t = -1.051$, d.f. = 203.09, p-value = 0.29). No samples were analyzed for determination of the wet season diet in wild dogs. Apparent differences were noted in the remaining four carnivore species in the different prey size categories: small, medium-sized and large prey species in the lion; very small and small prey species in the leopard; very small and medium sized prey species in the cheetah, and medium-sized and large prey species in the hyena (Table 5).

One sample T-tests computed for these apparent differences to examine statistical significance. In the diet of lions significant seasonal variations were detected in the medium-sized ($t = 4.9963$, d.f. = 3, p-value < 0.05) and large size ($t = 5.273$, d.f. = 3, p-value < 0.05) prey categories, but no significant variation in the small sized category ($t = 2.2442$, d.f. = 3, p-value = 0.11).

No significant seasonal variations were detected in leopard diets in the very small sized (t = 2.9847, d.f. = 3, p-value = 0.06) and small sized (t = 2.1539, d.f. = 3, p-value = 0.12) categories. Significant seasonal variation was detected in the medium-sized category (t = 6.757, d.f. = 3, p-value < 0.05) but the variation was not significant in the very small sized category (t = 2.1412, d.f. = 3, p-value = 0.12) for the diet of cheetahs. Seasonal variation was significant in both the medium-sized (t = 7.2898, d.f. = 3, p-value < 0.05) and large size (t = 15.745, d.f. = 3, p-value < 0.05) prey species in the diet of hyenas.

Table 6: Seasonal niche breadth for the five carnivores in HNP.

	Niche Breadth		**Standardized Niche Breadth**	
	Wet	Dry	Wet	Dry
Lion	8.00 (n=10)	10.13 (n=19)	0.78	0.51
Leopard	3.60 (n=5)	6.47 (n=11)	0.65	0.55
Hyena	6.54 (n=17)	7.92 (n=17)	0.35	0.38
Wild dog*	0 (n=0)	4.17 (n=6)	0	0.63
Cheetah	4.90 (n=6)	4.50 (n=4)	0.78	0.88

*There were no samples for the determination of the wet season dietary niche breadth for the wild dogs.

There were marginal changes in the standardized niche breadth of the four carnivores, a decrease (shift towards specialization) was observed for the lions (from 0.78 to 0.51) and leopards (from 0.65 to 0.55). Which was in stark contrast to the increase (shift towards catholism) observed for hyenas (from 0.35 to 0.38) and cheetah (from 0.78 to 0.88) (Table 6).

4.1.4 Prey species population estimate

Secondary data from the results of an aerial survey by Dunham *et al*.,(2015) indicate that prey population sizes are declining at an alarming rate, for example up to (-57%) in kudu and (-54%) in giraffe. Declines have also been observed in buffalo, sable and warthog, though an increase was reported for elephant, waterbuck and wildebeest (Dunham *et al*., 2015).

Table 7: Prey population estimates for the year 2001 and 2014 from an aerial survey.

	Population Estimate		
Prey species	**2001**	**2014**	**Trend**
Elephant	49’310	53’991	Increasing
Buffalo	13’703	5’146	Decreasing
Impala	5’207	4’533	Decreasing
Wildebeest	599	818	Increasing
Roan	-	214	-
Sable	5’854	2’586	Decreasing
Warthog	1’230	546	Decreasing
Giraffe	3’437	1’568	Decreasing
Eland	725	1’115	Increasing
Waterbuck	821	1’728	Increasing
Kudu	2’735	1’182	Decreasing
Tsessebe	-	0	-
Zebra	6’566	4’154	Decreasing

CHAPTER 5

5.1 DISCUSSION

5.1.1 Introduction

Different prey species numbers have been reported for HNP and other ranges, 16 prey species (Stander & Albon, 1993) and 20 prey species in HNP (Davidson *et al*., 2013); 21 prey species including aardvark (Lehmann *et al*., 2008) and up to 38 prey species (Rapson & Bernard, 2007) for others. The 20 prey species identified in this study is therefore comparable. The number of samples for each carnivore was also different which is consistent with other scat analysis studies, due to the elusive nature of large predators and because they exist at low densities, therefore large sample sizes are rare (Davis *et al*., 2012). Sample sizes as low as n =2 (Ogara *et al*., 2010) and n =13 (Breuer, 2005) for wild dogs have been reported. The recommendation of n = between 30 and 70 for the analysis of lion and hyena diets through scat (Breuer, 2005), was met.

5.1.2 Diet composition

Diet selection by large carnivores in Hwange National Park was significantly different both in terms of prey selection and prey size category utilization. Lions and hyenas selected large sized prey (>100 kg) and in this category buffalo was the most utilized by both carnivores, a situation that was also reported from various ecosystems (Cooper *et al*., 1999; Hayward & Kerley, 2005) and in HNP (Davidson *et al*., 2013). This could be because of their high abundance in HNP as shown by a high population estimate of 5’146 (Table 7). Buffalo was also found in the diets of leopards and wild dogs, and not in that of the cheetah. Most likely because of ecological adaptations of stealth and hunting at night in leopards and large pack sizes in wild dogs enabling them to utilize larger prey, unlike the solitary nature of cheetahs which forces them to avoid buffalo due to associated energy costs (Breuer, 2005). Lions and hyenas also sparingly utilized very small (<5 kg) up to medium (25-100 kg), their frequencies of selection were proportionally lower to that of large prey species. Impala was an important prey item in the medium-sized category with high frequencies of utilization by all carnivores due to their high abundance in HNP. This trend in the high selection of impala is similar to the observations made by Mbizah *et al*., (2012) for large carnivores in Save Valley Conservancy.

Waterbuck, eland, roan and sable antelopes though within the preferred large weight class for both lions and hyenas are not frequently selected (relative frequencies of selection from 0 – 8.83%) (Table 2) by carnivores in HNP because they exist in low densities as evidenced by their low population estimates. It has also been established that they have features that reduce depredation either morphologically (e.g. sable horns), ecologically (e.g. roan and sable occurring at low density), adaptively (e.g. taste aversion in waterbuck) or behaviorally(e.g. the large herd size and increased vigilance of eland (Hayward & Kerley, 2005).A similar trend was observed for the lions by Hayward & Kerley (2005) and for the hyenas by Périquet *et al*., (2015).

Other prey species are less frequently utilized though taken in accordance with their availability due to their sympatry with the carnivore species, relatively slow evasion speed and/or lower level of vigilance (Hayward & Kerley, 2005) for example, the warthog in lions and hyenas; bushbuck in leopards. This is similar to what has been reported by Hayward& Kerley (2005) for warthogs in lions and hyenas, and by Hayward *et al*., (2006c) for reedbuck and common duiker in wild dogs.

Prey size tended to increase with predator size, though the small and medium-sized categories were also utilized by large predators, implying that large populations of lions, leopards and hyenas will result in depletion in the prey base for the smaller bodied carnivores (cheetahs and wild dogs). Evidently very small prey species (<5 kg) were found in the diets of four of the study species (lions, leopards, cheetahs and hyenas) and absent from the diet of wild dogs. This is due to social behavior and energy returns as it is unprofitable to hunt very small species in groups, therefore very small to small (<5 to <25kg) is a viable option for solitary predators e.g. cheetah, leopards; and unprofitable for social predators e.g. lions, hyenas and wild dogs (Wegge *et al*., 2009). However, very small prey species were present in the diets of lions and hyenas because they sometimes hunt as individuals and absent from the diet of wild dogs because they always hunt in groups (Hayward & Kerley, 2005).

Up to three prey items were found in a few samples supporting the opportunistic tendencies in predators for any available prey, kleptoparasitism and/or scavenging while foraging for the optimal prey specie(s) (Cooper *et al*., 1999; Hayward *et al*., 2006c; Merwe *et al*., 2009). This was also reported by Breuer, (2005) and by Muboko *et al*., (2016).

5.1.3 Dietary overlap and niche breadth

Overlap was significant between most of the study carnivores but not biologically significant between lions and wild dogs, and lions and leopards. Perhaps due to the selection of medium sized prey e.g. impala in almost all of the study carnivores. Overlap which is not biological significant between lions and wild dogs was also reported by Mbizah *et al*., (2012) due to niche differentiation as lions frequently selected large size prey and wild dogs selected medium-sized category (Table 3). Overlap was highest between the cheetahs and leopards because they frequently selected the same prey species, i.e., bushbuck, reedbuck, sharpe's grysbok and both had impala and common duiker as their first and second most frequently utilized. They also both selected prey species in the medium sized category (25-100 kg), a situation also reported by Hayward *et al*., (2006a). The frequently selected prey species and medium sized category offer minimal risk of injury (Breuer, 2005) and minimal losses due to klepoparasitism (Hayward & Kerley, 2005). They can be consumed hastily for example by wild dogs or hauled up a tree by cheetah (Hayward & Kerley, 2005).

The diet of the hyena overlapped significantly with all the study species. Most likely because hyenas are effective hunters with the ability to thrive successfully and compete with other carnivores. Due to their catholic and opportunistic nature they exert pressure to all other carnivores in all prey size niches, this was also reported by Périquet *et al*., (2015). The non-specific nature of spotted hyena predation undoubtedly contributes to its relatively secure conservation status (Hayward, 2006b). High dietary overlap between the hyena and the other classes of carnivores was also reported by Graf *et al*., (2009).This means that they can limit other carnivores where they exist in sympatry. A situation that is also true between the hyenas and lions, they select the same prey species (buffalo and impala) and both prefer the large sized category. This also supports the fact that lions and hyenas are stiff competitors against and exclusively limit each other as shown by Hayward (2006) reporting comparable findings.

Lion diet on the other hand had significant overlap with hyenas only, and though its diet did overlap with the other three carnivores the overlap was not significant with wild dog, leopard and cheetah diets (Table 4). As reported by Mbizah *et al*., (2012). This is because lions in HNP prefer the large sized prey species which is a dietary niche only closely preferred by the hyena and actively avoided by the cheetah (Table 3).

The niche breadth was highest for lions and hyenas showing a catholic dietary selection principle and it was low for cheetahs and wild dog showing a specialist tendency. A catholic niche breadth has been previously reported for hyenas in Périquet *et al*., (2015). There was a complete reversal for the standardized niche breadth, with hyenas and lions having low values whereas cheetah and wild dogs had high values. It was observed that although the lions and hyenas were catholic in their utilization of the available prey they were in fact specialist in their frequencies of selection for particular prey species (buffalo and impala) and prey size categories (large size). The opposite was true for cheetahs and wild dogs although they were specialist in prey size categories (small to medium sized) they were catholic in their frequencies of selection.

The niche breadth and standardized niche breadth was low for the leopards because they selected different prey species generally selecting prey in the small size category and large size category and particularly selected prey in the medium sized category (Table 3). In the large size they utilized buffalo, waterbuck, kudu and zebra similar to findings by Hayward*et al*., (2006a) who reported that although leopards are catholic in nature, they generally prey on medium-sized prey ungulates.

Interference competition has been sighted as one of the leading causes of carnivore species population decline, especially for the comparatively smaller bodied (wild dogs, cheetahs and leopards) (Hayward *et al*., 2006c). This study has successfully documented this, evidenced by the high overlap between the large carnivores in HNP; this could potentially be another reason for population declines.

5.1.4 Seasonal dietary variation

There was no significant seasonal variation in the diet selection for the four carnivore species i.e., lions, leopards, cheetahs and hyenas. Hayward & Kerley (2005) reported that lions consistently utilize large prey irrespective of their abundance hence dietary changes due to seasonality are minimal. More so for HNP which has pumped waterholes, giving prey items sources of water which minimizes the effect of season (Périquet *et al*., 2015). Though variation was observed in the prey size utilizations in the diet of lions, cheetahs and hyenas. An increase in the standardized niche breadth for hyenas and cheetahs seems to suggest that their diets move towards specialization during the wet season and catholism in the dry season, the opposite was observed for lions and leopards.

Marginal changes were observed in the standardized niche breadth for hyena and leopard diets (Table 6). Seasonal change in the diet of lions was visible in the utilization of large sized prey and is comparable to Davidson *et al*., (2013) who reported that primary prey preference and according to prey size had slight seasonal variation for lions. In the diet of leopards the utilization of the very small and small sized prey species showed a reduction between the wet and dry, to complete avoidance in the wet for the small sized category. An almost similar trend was observed in the diet of cheetahs, were complete avoidance for the very small sized category was observed (Table 5). Probably because the smaller prey species have lower requirements for water, therefore during the wet season they are evenly distributed, whereas during the dry they become patchy. Changes in the utilization of prey size categories were only marginal for the hyena between the wet and dry seasons in the medium-sized and large size categories but statistically significant (Table 5). Which is similar to what was reported by Cooper *et al*., (1999) that hyenas have been seen to exhibit marginal prey switching in response to seasonal changes in prey abundances. Seasonal changes in the spatial and temporary distributions of prey species are only marginal in HNP due to artificial waterholes. During the dry season, water acts as a major limiting factor that leads to changes in distribution patterns of ungulate populations. Due to the availability of pumped water sources, the limiting effects of water are marginalized. This could possibly be the explanation for the largely marginal seasonal changes observed in the diet of the study species.

CHAPTER 6

6.1 CONCLUSION AND RECOMMENDATIONS

6.1.1 Conclusion

From the study, it can be concluded that impala and buffalo are important prey items for large carnivores in Hwange National Park. It can also be concluded that competition is a strong limiting factor for carnivores and seasonality in prey selection is very marginal in HNP. The potential for carnivore scat analysis studies in Zimbabwe is recognized for the determination of carnivore diet ecologies the accuracy of which can be improved further by using it in tandem with other methods for dietary analysis such as, kill-site analysis.

6.1.2 Recommendations

The following is recommended:

1. The conservation of key prey species, like buffalo and impala to ensure the sustenance of carnivore populations.

2. Periodic examination of lion and hyena densities in for HNP to maintain them at a density threshold that is not detrimental to other carnivores like leopards, cheetah & wild dog.

3. Robust prey density evaluations during the dry and wet season to understand how it changes and how those changes are likely affecting prey selection in HNP

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APPENDICES

Appendix A: Scat analysis R-worksheet

Contribution of prey species, based on their frequency of occurrence

```
> setwd("C:/Users/Simbarashe Chatikobo/Desktop/R Analysis")
> ScatData<-read.csv("Raw.csv")
> countdf <- as.data.frame(table(ScatData))#count the frequency of
occurence
> xtabs(Freq ~ Carnivore+Prey, data=countdf)#contigency table stored in A
         Prey
Carnivore  1  2  3  4  5  6  7  8  9 10 11 12 13 14 15 16 17 18 19 20 21
22 23
        1 12  6  4  3 20  2  4  3  3  6  4  1  3  3  0  2  1  1  1  5  0
1  0
        2 21  2  2  4  3  0  0  0  0  0  0  1  5  4  3  5  5  5  0  0  0
0  0
        3 74 16  8 24 50  1  6 13  4  3  6  0 11 18  1 18  7  0  0  5  2
0  3
        4  4  0  1  1  1  0  0  0  0  0  0  0  1  0  0  3  0  0  0  0  0
0  0
        5  6  0  0  0  0  0  0  0  0  0  0  1  5  4  1  4  1  1  0  0  0
0  0
> chisq.test(ScatData, correct=T)

        Pearson's Chi-squared test

data:  ScatData
X-squared = 866.9, df = 448, p-value < 2.2e-16

Warning message:
In chisq.test(ScatData, correct = T) :
  Chi-squared approximation may be incorrect


> ScatData<-read.csv("PreySizeCategoriesRelativeFrequency.csv")
> ScatData
  Very.Small.Prey...5kg. Small.Prey..5.25kg. Medium.sized.Prey..25.100kg.
1             2.4096386            8.433735                     25.30120
2            13.7931035           18.965517                     48.27586
3             8.6956522           43.478261                     47.82609
4             0.0000000           30.000000                     40.00000
5             0.3717472           11.524164                     39.40520
  Large.Prey...100kg.
1           63.85542
2           18.96552
3            0.00000
4           30.00000
5           48.69888
> chisq.test(ScatData, correct=T)

        Pearson's Chi-squared test

data:  ScatData
X-squared = 151.03, df = 12, p-value < 2.2e-16
```

Frequency of occurrence of impala between lions and other four carnivore species:

LionLeopardImpala

```
> ScatData<-read.csv("LionLeopardImpala.csv")
> ScatData
  Lion Leopard
1   12      21
2   71      37
> chisq.test(ScatData, correct=T)

        Pearson's Chi-squared test with Yates' continuity correction

data:  ScatData
X-squared = 7.8365, df = 1, p-value = 0.00512
```

LionHyenaImpala

```
> ScatData<-read.csv("LionHyenaImpala.csv")
> ScatData
  Lion Hyena
1   12    74
2   71   198
> chisq.test(ScatData, correct=T)

        Pearson's Chi-squared test with Yates' continuity correction

data:  ScatData
X-squared = 4.957, df = 1, p-value = 0.02599
```

LionCheetahImpala

```
> ScatData<-read.csv("LionCheetahImpala.csv")
> ScatData
  Lion Cheetah
1   12       6
2   71      17
> chisq.test(ScatData, correct=T)

        Pearson's Chi-squared test with Yates' continuity correction

data:  ScatData
X-squared = 1.0012, df = 1, p-value = 0.317

Warning message:
In chisq.test(ScatData, correct = T) :
  Chi-squared approximation may be incorrect
> fisher.exact(ScatData)

        Two-sided Fisher's Exact Test (usual method using minimum
likelihood)

data:  ScatData
p-value = 0.2142
alternative hypothesis: true odds ratio is not equal to 1
95 percent confidence interval:
 0.1506 1.5351
sample estimates:
odds ratio
 0.4826767
```

LionWildDogImpala

```
> ScatData<-read.csv("LionWildDogImpala.csv")

> ScatData
  Lion Wild.Dog
1   12        4
2   71        6
> chisq.test(ScatData, correct=T)

        Pearson's Chi-squared test with Yates' continuity correction

data:  ScatData
X-squared = 2.4911, df = 1, p-value = 0.1145

Warning message:
In chisq.test(ScatData, correct = T) :
  Chi-squared approximation may be incorrect
> fisher.exact(ScatData)

        Two-sided Fisher's Exact Test (usual method using minimum
likelihood)

data:  ScatData
p-value = 0.06554
alternative hypothesis: true odds ratio is not equal to 1
95 percent confidence interval:
 0.0574 1.1122
sample estimates:
odds ratio
 0.2586908
```

Frequency of occurrence of buffalo between lions and hyenas:

```
> ScatData<-read.csv("LionHyenaBuffalo.csv")
> ScatData
  Lion Hyena
1   19    50
2   64   222
> chisq.test(ScatData, correct=T)

        Pearson's Chi-squared test with Yates' continuity correction

data:  ScatData
X-squared = 0.56291, df = 1, p-value = 0.4531
```

Frequency of occurrence of Common Duiker between leopards and cheetahs:

```
> ScatData<-read.csv("LeopardCheetahDuiker.csv")
> ScatData
  Leopard Cheetah
1       5       5
2      53      18
> chisq.test(ScatData, correct=T)

        Pearson's Chi-squared test with Yates' continuity correction

data:  ScatData
X-squared = 1.5471, df = 1, p-value = 0.2136

Warning message:
In chisq.test(ScatData, correct = T) :
```

```
  Chi-squared approximation may be incorrect
> fisher.exact(ScatData)

        Two-sided Fisher's Exact Test (usual method using minimum
likelihood)

data:  ScatData
p-value = 0.1371
alternative hypothesis: true odds ratio is not equal to 1
95 percent confidence interval:
 0.0884 1.3406
sample estimates:
odds ratio
 0.3449246
```

Frequency of occurrence of Steenbok between leopards and Wild Dogs:

```
> ScatData<-read.csv("LeopardWildDogSteenbok.csv")
> ScatData
  Leopard Wild..Dog
1       5         2
2      53         8
> chisq.test(ScatData, correct=T)

        Pearson's Chi-squared test with Yates' continuity correction

data:  ScatData
X-squared = 0.28116, df = 1, p-value = 0.5959

Warning message:
In chisq.test(ScatData, correct = T) :
  Chi-squared approximation may be incorrect
> fisher.exact(ScatData)

        Two-sided Fisher's Exact Test (usual method using minimum
likelihood)

data:  ScatData
p-value = 0.2723
alternative hypothesis: true odds ratio is not equal to 1
95 percent confidence interval:
 0.0566 3.1413
sample estimates:
odds ratio
 0.3843763
```

Frequency of occurrence of large prey species between lions and hyenas:

```
> ScatData<-read.csv("LionHyenaLarge.csv")
> ScatData
  Lion Hyena
1   53   131
2   30   138
> chisq.test(ScatData, correct=T)

        Pearson's Chi-squared test with Yates' continuity correction

data:  ScatData
X-squared = 5.2487, df = 1, p-value = 0.02196
```

Frequency of occurrence of medium prey species between lions and other carnivore species:

LionLeopardMed

```
> ScatData<-read.csv("LionLeopardMed.csv")
> ScatData
  Lion Leopard
1   21      28
2   62      30
> chisq.test(ScatData, correct=T)

        Pearson's Chi-squared test with Yates' continuity correction

data:  ScatData
X-squared = 6.9667, df = 1, p-value = 0.008304
```

LionCheetahMed

```
> ScatData<-read.csv("LionCheetahMed.csv")

> ScatData

  Lion Cheetah
1   21      11
2   62      12
> chisq.test(ScatData, correct=T)

        Pearson's Chi-squared test with Yates' continuity correction

data:  ScatData
X-squared = 3.3327, df = 1, p-value = 0.06791
```

LionWildDogMed

```
> ScatData<-read.csv("LionWildDogMed.csv")
> ScatData
  Lion Wild.Dog
1   21        4
2   62       10
> chisq.test(ScatData, correct=T)

        Pearson's Chi-squared test with Yates' continuity correction

data:  ScatData
X-squared = 7.9556e-31, df = 1, p-value = 1

Warning message:
In chisq.test(ScatData, correct = T) :
  Chi-squared approximation may be incorrect
> fisher.exact(ScatData)

        Two-sided Fisher's Exact Test (usual method using minimum
likelihood)

data:  ScatData
p-value = 0.7514
alternative hypothesis: true odds ratio is not equal to 1
95 percent confidence interval:
 0.2347 3.2088
sample estimates:
```

```
odds ratio
 0.8482886
```

LionHyenaMed

```
> ScatData<-read.csv("LionHyenaMed.csv")
> ScatData
  Lion Hyena
1   21   106
2   62   163
> chisq.test(ScatData, correct=T)

        Pearson's Chi-squared test with Yates' continuity correction

data:  ScatData
X-squared = 4.8766, df = 1, p-value = 0.02722
```

Frequency of occurrence of medium sized prey species:

LeopardWildDogMed

```
> ScatData<-read.csv("LeopardWildDogMed.csv")
> ScatData
  Leopard Wild.Dog
1      28        4
2      30        6
> chisq.test(ScatData, correct=T)

        Pearson's Chi-squared test with Yates' continuity correction

data:  ScatData
X-squared = 0.019947, df = 1, p-value = 0.8877

Warning message:
In chisq.test(ScatData, correct = T) :
  Chi-squared approximation may be incorrect
> fisher.exact(ScatData)

        Two-sided Fisher's Exact Test (usual method using minimum
likelihood)

data:  ScatData
p-value = 0.7389
alternative hypothesis: true odds ratio is not equal to 1
95 percent confidence interval:
 0.3119 5.7891
sample estimates:
odds ratio
  1.393149
```

LeopardCheetahMed

```
> ScatData<-read.csv("LeopardCheetahMed.csv")
> ScatData
  Leopard Cheetah
1      28      11
2      30      12
> chisq.test(ScatData, correct=T)

        Pearson's Chi-squared test with Yates' continuity correction
```

```
data:  ScatData
X-squared = 5.4953e-31, df = 1, p-value = 1
```

CheetahWildDogMed

```
> ScatData<-read.csv("CheetahWildDogMed.csv")
> ScatData
  Cheetah Wild.Dog
1      11        4
2      12        6
> chisq.test(ScatData, correct=T)

        Pearson's Chi-squared test with Yates' continuity correction

data:  ScatData
X-squared = 0.0011957, df = 1, p-value = 0.9724

Warning message:
In chisq.test(ScatData, correct = T) :
  Chi-squared approximation may be incorrect
> fisher.exact(ScatData)

        Two-sided Fisher's Exact Test (usual method using minimum
likelihood)

data:  ScatData
p-value = 0.722
alternative hypothesis: true odds ratio is not equal to 1
95 percent confidence interval:
 0.2909 6.4881
sample estimates:
odds ratio
  1.361836
```

Seasonal variation in diet selection:

```
> setwd("C:/Users/Simbarashe Chatikobo/Desktop/R Analysis")
> ScatData<-read.csv("Season.csv")
> countdf <- as.data.frame(table(ScatData))#count the frequency of
occurence
> xtabs(Freq ~ Season+Carnivore+Prey, data=countdf)#contigency table
stored in A
> attach(ScatData)
> names(ScatData)
[1] "Season"    "Carnivore" "Prey"
> class(Carnivore)
[1] "integer"
> class(Season)
[1] "integer"
> t.test(Prey~Season, nu=0, alt="two.sided", conf=0.95, var.eq=F,
paired=F)

        Welch Two Sample t-test

data:  Prey by Season
t = -1.051, df = 203.09, p-value = 0.2945
alternative hypothesis: true difference in means is not equal to 0
95 percent confidence interval:
 -2.0489887  0.6240998
sample estimates:
mean in group 1 mean in group 2
       7.055556        7.768000
```

Seasonal variation:

Lion

```
> setwd("C:/Users/Simbarashe Chatikobo/Desktop/R Analysis")
> ScatData<-read.csv("LionSeasonalLarge.csv")
> ScatData
    Wet   Dry
1 31.25 65.79
2 68.75 34.21
> t.test(ScatData)

        One Sample t-test

data:  ScatData
t = 4.9963, df = 3, p-value = 0.01542
alternative hypothesis: true mean is not equal to 0
95 percent confidence interval:
 18.15203 81.84797
sample estimates:
mean of x
       50

> ScatData<-read.csv("LionSeasonalMedium.csv")
> ScatData
    Wet   Dry
1 43.75 27.63
2 56.25 72.37
> t.test(ScatData)

        One Sample t-test

data:  ScatData
t = 5.273, df = 3, p-value = 0.0133
alternative hypothesis: true mean is not equal to 0
95 percent confidence interval:
 19.82322 80.17678
sample estimates:
mean of x
       50

> ScatData<-read.csv("LionSeasonalSmall.csv")
> ScatData
    Wet   Dry
1 18.75  5.26
2 81.25 94.74
> t.test(ScatData)

        One Sample t-test

data:  ScatData
t = 2.2442, df = 3, p-value = 0.1105
alternative hypothesis: true mean is not equal to 0
95 percent confidence interval:
 -20.903 120.903
sample estimates:
mean of x
       50
```

Leopard

```
> setwd("C:/Users/Simbarashe Chatikobo/Desktop/R Analysis")
>ScatData<-read.csv("LeopardSeasonalSmall.csv")
>ScatData
  Wet   Dry
1   0 22.92
2 100 77.08
>t.test(ScatData)

        One Sample t-test

data:  ScatData
t = 2.1539, df = 3, p-value = 0.1203
alternative hypothesis: true mean is not equal to 0
95 percent confidence interval:
 -23.87717 123.87717
sample estimates:
mean of x
       50

>ScatData<-read.csv("LeopardSeasonalVery.csv")
>ScatData
    Wet  Dry
1 33.34 12.5
2 66.66 87.5
>t.test(ScatData)

        One Sample t-test

data:  ScatData
t = 2.9847, df = 3, p-value = 0.05838
alternative hypothesis: true mean is not equal to 0
95 percent confidence interval:
  -3.312793 103.312793
sample estimates:
mean of x
       50
```

Cheetah

```
> setwd("C:/Users/Simbarashe Chatikobo/Desktop/R Analysis")
>ScatData<-read.csv("CheetahSeasonalVery.csv")
>ScatData
  Wet   Dry
1   0 22.22
2 100 77.78
>t.test(ScatData)

        One Sample t-test

data:  ScatData
t = 2.1412, df = 3, p-value = 0.1217
alternative hypothesis: true mean is not equal to 0
95 percent confidence interval:
 -24.31459 124.31459
sample estimates:
mean of x
       50
```

```
>ScatData<-read.csv("CheetahSeasonalMedium.csv")
>ScatData
    Wet   Dry
1 57.14 33.34
2 42.86 66.66
>t.test(ScatData)

        One Sample t-test

data:  ScatData
t = 6.757, df = 3, p-value = 0.006622
alternative hypothesis: true mean is not equal to 0
95 percent confidence interval:
 26.45079 73.54921
sample estimates:
mean of x
       50
```

Hyena

```
> setwd("C:/Users/Simbarashe Chatikobo/Desktop/R Analysis")
>ScatData<-read.csv("HyenaSeasonalLarge.csv")
>ScatData
    Wet   Dry
1 42.39 51.61
2 57.61 48.39
>t.test(ScatData)

        One Sample t-test

data:  ScatData
t = 15.745, df = 3, p-value = 0.0005569
alternative hypothesis: true mean is not equal to 0
95 percent confidence interval:
 39.89402 60.10598
sample estimates:
mean of x
       50

>ScatData<-read.csv("HyenaSeasonalMedium.csv")
>ScatData
    Wet   Dry
1 47.83 33.34
2 52.17 66.66
>t.test(ScatData)

        One Sample t-test

data:  ScatData
t = 7.2898, df = 3, p-value = 0.005329
alternative hypothesis: true mean is not equal to 0
95 percent confidence interval:
 28.17202 71.82798
sample estimates:
mean of x
       50
```