LION PREDATION IN RELATION TO LANDSCAPE FEATURES IN TARANGIRE NATIONAL PARK

BY

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ABSTRACT

This study aimed at assessing the relationship between lion predation and landscape features to test whether existing evidence from other studies elsewhere applied for Tarangire lions given the uneven terrain in Tarangire National Park. From a four-year data set (July 2005 to October 2009) of lion sightings, predation dataset were extracted and supplemented with data collected during this study, making a total of 133 carcasses. Radio telemetry was used to track lion prides from 6.00 am to 7.00 pm daily, and the list of prey having at least one carcass for the entire period of data collection in the study area was compiled. The standardized selection ratios (B*i*) were computed to determine lion prey species preference. Also, Geographical Information System (GIS) in Arc Map 9.2 (ESRI) was used to create layers of drainage pattern, roads, vegetation cover, aspect, slope and swamps. Logistic regression analysis and Akaike Information Criteria were employed to associate lion predation and landscape features. Of 133 carcasses for both dry and wet seasons, only one hundred and twenty one (121) prey carcasses comprised of zebra, wildebeest, buffalo, giraffe and warthog were considered for species preference. Consequently, the standardized selection ratios (B*i*) suggests that in both wet and dry seasons lions selected warthogs and buffalo compared to their and other key prey species abundance. However giraffe kills were made only during wet season with none in dry season. Logistic regression analysis showed that the best model with the highest Akaike weight, (ωi=0.357) containing predictors distance to river confluences, elevation, vegetation types and road for predicting the influence of landscape features on lion predation. Subsequently, the analysis of parameter estimates for the best model indicated the effects of roads, river confluences, vegetative cover and elevation to be most significant, whereas aspect and slope had weak effect on lion predation

DECLARATION

I, DENNIS MINJA, do hereby declare to the Senate of Sokoine University of Agriculture that this dissertation is the result of my own original work and that it has neither been submitted nor being concurrently submitted for degree award in any other institution.

18th Nov. 2011

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DEDICATION

This dissertation is dedicated to my loving family Mr. Goodluck L. Minja, Mrs. Elly G. L. Minja and my siblings Giscar G. Minja, Fred G. Minja "Dr" and Kelvin G. Minja for their love, encouragement and support. My beloved wife Mary L. Msilanga and our beloved daughter Angela D. G. Minja.

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LIST OF ABBREVIATIONS

AIC	Akaike Information Criteria
AICi	The AIC for model *i*
AWF	African Wildlife Foundation
Delta AIC	(AICi - min AIC)
GIS	Geographical Information System
GPS	Global Positioning System
K	Number of estimable parameters (covariate + intercept) in approximating model
Min AIC	The minimum AIC value of all models
NP	National Park
TANAPA	Tanzania National Parks
TAWIRI	Tanzania Wildlife Research Institute
ωi	refers to Akaike weight (the probability that model *i* is the best among candidate models) Akaike Information Criterion

CHAPTER ONE

1.0 INTRODUCTION

1.1 Background Information

Large predators by virtue of their size and ecological requirements may have great influence on prey populations (Terborgh, 1990; Seidensticker and McDougal, 1993), a process which may result in marked effects on the function and structure of ecosystem (Berger *et al.*, 2001; Soule *et al.*, 2003). According to Sinclair (1985), predation can exert more influence upon resident population of herbivores (Sinclair, 1985) compared to migrating prey population (Schaller, 1972; Mills, 1990). These observations largely support the contention of Fryxell *et al.* (1988) that predators can regulate resident herbivores at low population densities, whereas such regulation is rare for migratory herds. However, recent reviews about African large predators have shown that each species has a limited range of optimal prey species available (Hayward and Kerley, 2005; Hayward, 2006; Hayward *et al.*, 2006a, 2006b, 2006c) and if the optimal preys are not available in an ecosystem, then the predator is unlikely to survive.

There is persuasive substantiation that herbivore distribution/abundance is the most important factor that influences the abundance of large carnivores on a broad scale (Ritchie & Olff 1999; Carbone & Gittleman 2002). But, at a fine scale, Hopcraft *et al.*, 2005 reported that a drastically large number of kill events took place in areas where lions can ambush their prey rather than where preys are most abundant. Subsequently, prey catchability is considered essential to models of habitat selection by ambush predators (as opposed to herbivores or, possibly, cursorial predators).

Apparently, studies of carnivore diet may be based on a list of observed kills and typically includes the analysis of the prey choices, kill frequency and daily consumption (Schaller, 1972; Mills, 1984; Ruggiero, 1991). There is evidence that the diet of lions comprise of a diverse range of foods from the size of a rat to as huge as young African elephant (Stander. 1997) but mostly feed on medium sized to large sized ungulates. Lions. *Panthera leo* are known to be opportunist stalk-and-ambush hunters, relying on a combination of good cover, acceleration, body weight and occasional cooperation with other pride members to overcome their prey, while seeking landscape features with adequate prey, cover and other resources (presumably water) (Manly *et al.*, 2002). Nevertheless, Hopcraft *et al.* (2005) demonstrated that *Panthera leo* in Serengeti preferred hunting in areas with good cover rather than high prey density, and made use of fine-scale landscape features that made hunting success easier. However, Hopcraft *et al.* (2005) concluded that either the abundance of prey or its catchability or both may be the driving factor in deciding where to hunt.

1.2 Problem Statement and Study Justification

Medium and large-sized mammal prey species differ in abundance and distribution over time and space due to diversity of habitat and vegetation type (Kissui and Packer, 2004). These factors are likely to influence lion's predation behaviour leading to prey choice in distinct features. On the other hand, habitats with good cover and camouflage are recognised by prey species as dangerous such that they tend to avoid them, and thus preferring to feed in more open habitats (Hik, 1995). Despite descriptive information on lion diet in many parts of East Africa (Honer *et al.*, 2002; Patterson *et al.*, 2004), knowledge of feeding ecology of lions of Tarangire National Park is lacking. Specifically, no information exists on Tarangire prey profile and prey selection, and how it relates to landscape features. This knowledge is essential given the complexity of the area both inside and outside the park with regard to livestock keeping which is a prime activity for the livelihood of the neighbouring local communities. This study will enhance knowledge on the key prey species preferred by Tarangire lions, landscape features which foster prey predation inside and outside the Park as well as information to local communities regarding areas where livestock predation events are likely to occur and therefore take all possible precautions. This will reduce retaliatory killings of lions that would ensue due to livestock depredation. Consequently, locals may make a better use of their landscape.

1.3 Objectives

1.3.1 Overall objective

To determine lion prey preference and the influence of landscape features on their predation.

1.3.2 Specific objectives

i. To determine lion's prey profile and preferred prey species
ii. To assess lion predation relative to landscape features

1.4 Research Questions

i. What are the important prey species for the lions in Tarangire National Park?
ii. Is there any relationship between lion predation success and landscape features?

1.4.1 Hypotheses

1. Null hypothesis: All potential prey species are preyed on equally by the lions

   Alternative hypothesis: Lions show prey preference

2. Null hypothesis: Prey abundance and landscape features have no influence on lion predation.

   Alternative hypothesis: Prey abundance and landscape features have influence on lion predation.

CHAPTER TWO

2.0 LITERATURE REVIEW

2.1 Lion's Behaviour and Ecology

Lions live in stable social groups called prides. A pride comprise of 2-30 individuals with a composition of 1-7 adult resident male coalition, 2-18 adult females, and juveniles and cubs born in the pride. The males, who are newcomers (i.e. born from other prides) win access to the pride after passing through a solitary phase as nomads, and a successful 'take over' (Pusey and Packer, 1993). Prides occupy territories of varying sizes that depend upon the availability of food, shelter, and water (Heinsohn and Packer, 1995). Females usually protect the resources within territories against other female intruders while males do the same against other males (Heinsohn, 1997). Lions possess a non seasonal reproduction pattern which takes place just about once for every two years (Van Orsdol *et al.*, 1985). Breeding generally takes place after individuals in the previous litter reach their second birthdays. Moreover, occasionally it may occur after a pride takeover by newly coming males, where cubs under a year old are killed by infanticidal males or by forced abandonment (Pusey and Packer, 1993).

Hunting activities are achieved either by group (cooperatively) or by a single individual. The prey profile of a lion includes more species than that of a small carnivore (Radloff and du Toit, 2004). Nevertheless, lions mostly feed on medium sized to large sized ungulates that range from 50 kg to 300 kg (e.g. gazelle, kudu, eland, buffalo, giraffe and infant elephant) in their suitable habitats such as protected areas (Kissui and Packer, 2004).

2.2 Prey Species Ideal to Lion's Predation

Prey attributes influencing attack by a predator include abundance and size, temporal and spatial distributions, and defences and anti-predatory tactics (Sunquist and Sunquist, 1997). Large felids can subsist on small, abundant prey, and they are morphologically specialized to take prey of their own size or slightly larger (Sunquist and Sunquist, 1997). Although grouping may actually aid predator detection, prey in a group may alternatively increase their chances of being detected and thus attacked. However, during the attack phase it has been shown that many predator species suffer a reduced capture success when attacking grouped prey due to predator's conspicuousness to prey and risks of being harmed by the prey group (Krause and Godin, 1995). For this reason, prey may be at an advantage if their grouping behaviour is highly flexible, which might help explain why group sizes are often very dynamic in the wild (Schradin, 2000). Consequently, lions do select for the most abundant prey within their preferred size classes (Sunquist and Sunquist, 1997).

Profitability of prey is another factor that has to be taken into account whereas predators tend to select for the largest possible prey that can safely be killed (Schaller, 1972). Studies from Serengeti confirm that lions prefer wildebeest and zebra during the migration, and warthog and buffalo during prey scarcity suggesting that they are risk-sensitive foragers that maximize food intake (Scheel and Packer, 1995) such that their minimal prey size is 150 kg (Packer, 1986). Differences in food habits of a species between sites reflect prey availability and vulnerability (Sunquist and Sunquist, 1997). Conversely, larger-bodied prey species are also thought to avoid predation through their larger size as lions dislike excessively large prey. Smaller prey depend less on their ability to evade predators at the subduing stage, and instead aim to evade predators during search, stalk and attack phases (Elliott *et al.*, 1977).

2.3 Hunting Landscape Features of the Lions

Risk can be a factor in foraging decisions if at the time of making forage the forager cannot specifically determine the pay-offs available from alternative options. Studies of risk-sensitive foraging rarely focus on the behaviour of the predator (Lima, 2002), and furthermore the role of landscape influencing the catchability of prey is often overlooked when examining predator–prey interactions. While most animals seek landscape features with adequate food, shelter, nest sites or other resources (Manly *et al.*, 2002), the choice of feeding habitat for a sit-and-wait predator is less clear. Most felids prefer stalking that relies on cover and stealth to approaching prey closely and then rushing and pursuing an individual over a relatively short distance (Sunquist, 1981). This form of ambush hunting has been reported for mountain lions, *Puma concolor* – Bank (Franklin, 1998; Beier *et al.*, 1995) as well as African lions (Packer and Pusey, 1997).

Some recent studies have explicitly linked predation risk to landscape attributes. Kunkel and Pletscher (2000) compared landscape features where wolves killed moose (*Alces alces*) to those at random sites, and found that moose were more likely to be killed closer to roads and trails and farther from forest cover. Thogmartin and Schaeffer (2000) however compared the influence of roads from where turkeys (*Mellagris gallapavo*) lived to the distance at which they were killed, and concluded that they were more likely to be killed farther from roads. Moreover, Cresswell and Quinn (2004) showed that distance to cover influenced the success of predation by sparrow hawk (*Accipter nisus*) predation on redshanks (*Tringa totanus*). All three studies attributed these results to habitat covariates that modified vulnerability to predation. However, ambush predators might often benefit by hunting in areas where prey are locally scarce due to the reduced probability of being recognized by prey during stalking process. Nevertheless, prey may occasionally be forced to utilize high-risk habitats in order to obtain essential resources and consequently suffer higher predation (Hik, 1995).

CHAPTER THREE

3.0 MATERIALS AND METHODS

3.1. Description of the Study Area

Tarangire National Park is located between 3°40' and 5°35' south and 35°45' and 37° east (Fig. 1) at an elevation of 1200 to 1600 m above sea level with a total area of 2800 km^2 (TANAPA, 2001). Its climatic condition is highly variable characterized by periodic droughts. The annual rainfall pattern generally consists of short rains from October to December followed by a short dry spell in January, with long rains occurring anytime from February to June.

The vegetation type is the wooded steppe in an arid Acacia savannah belt comprised by *Acacia* and *Commiphora* species with Somali-Maasai regional centre of endemism (White, 1983). The dominant vegetation types comprise of: Riparian woodland, *Acacia tortilis* parkland, Wetlands and seasonal flood plain and *Acacia-Commiphora* mosaics. Other vegetation types include Riverine grassland, Combretum species, *Darbegia melanoxylon* woodland, *Acacia drepanolobium* woodland, kopjes vegetation, deep gully vegetation, and grasslands with scattered baobab trees (TANAPA, 2001).

Tarangire National Park provides habitat for a large diversity of fauna. During the dry season when much of the game from the Maasai Steppe emigrates in search of forage and water, it harbours one of the largest concentrations of wildlife with the highest biomass totals of any National Park (TANAPA, 2001). With predictable population of 2,300 to 2,700 elephants, the park has the highest density of elephants than any National Park in northern Tanzania. There are also 18 ungulate species namely, lesser and greater kudu *Tragelaphus imberbis* and *Tragelaphus strepsiceros* respectively, plain zebra, *Equus burchellii*, wildebeest, *Connochaetes taurinus*, elands, *Taurotragus oryx*, warthog, *Phacochoerus africanus*. Others are giraffe, *Giraffa camelopardalis*, oryx, *Oryx gazelle*, buffalo, *Syncerus caffer*, hartebeest, *Alcelaphus buselaphus*, impala, *Aepyceros melampus*, waterbuck, *Kobus ellipsiprymnus*, gerenuk, *Litocranius walleri*, reedbuck, *Redunca arundinum*, bushbuck, *Tragelaphus scriptus*, Thompson's gazelle, *Gazella thomsoni*, Grant's gazelle, *Gazella granti* and mountain reedbuck, *Redunca fulvorufula*). The five major carnivores are as well present in the Park and includes:- cheetah, *Acinonyx jubatus*, leopard, *Panthera pardus*, hyena, *Crocuta crocuta*, bat eared fox, *Otocyon megalotis* and jackals, *Canis mesomelas*, and one primate species of baboon, Olive baboon, *Papio cynocephalus* (TANAPA, 2001). During the dry season (June–November), the wildlife move between Tarangire and Manyara National Parks, and the adjacent dispersal areas (Lamprey, 1964), where as to some extent the migratory routes are threatened by human encroachment, wildlife road kills and possibly pollution with an example of Kwakuchinja corridor. The sedentary species such as warthog, waterbuck and giraffe remain inside protected areas but extend their range to communal village lands for most of the wet season (November–May) (Kahurananga and Silkiluwasha, 1997).

3.2 Lion Population Trends in Tarangire NP

The long-term population monitoring records by the Tarangire Lion Project (2003-2007), suggests a general declining trend of lion population in 2004 with slight increase in 2005. This was followed by a significant decline in 2006 (Fig. 1 below). This huge drop was associated with intense drought that occurred in Maasai steppe region. From 2007 the population seems to be mending but it remains to be seen if the upward trend will be sustained to reach the 2003 levels. The age-sex structure of the Tarangire lion population seems to be of fairly equal sex ratio for both juveniles and sub-adults, but many more adult females than adult males (Kissui, 2006), signifying either higher male dispersal rates from the Tarangire ecosystem or much higher male mortality rate.

The very low number of adult males may reflect either high off-takes from tourist hunting blocks neighbouring the National Park or greater numbers of males being killed in the course of problem animal control or retaliation for cattle killing in areas outside Tarangire (human-lion conflicts) (Kissui, 2006). However, the difference in the proportions of juvenile males vs. juvenile females does not appear to be significant (and this is true for sub-adult males vs. sub-adult females).

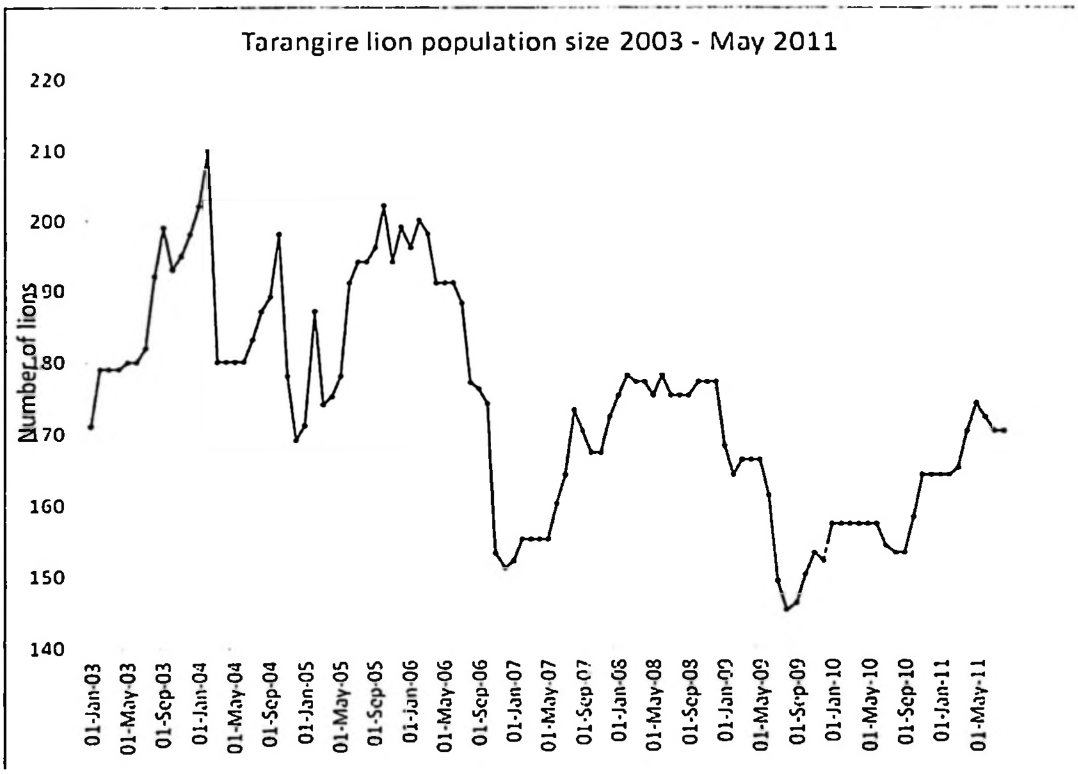

Figure 1: A graph showing Tarangire lion population size from 2003 to 2011

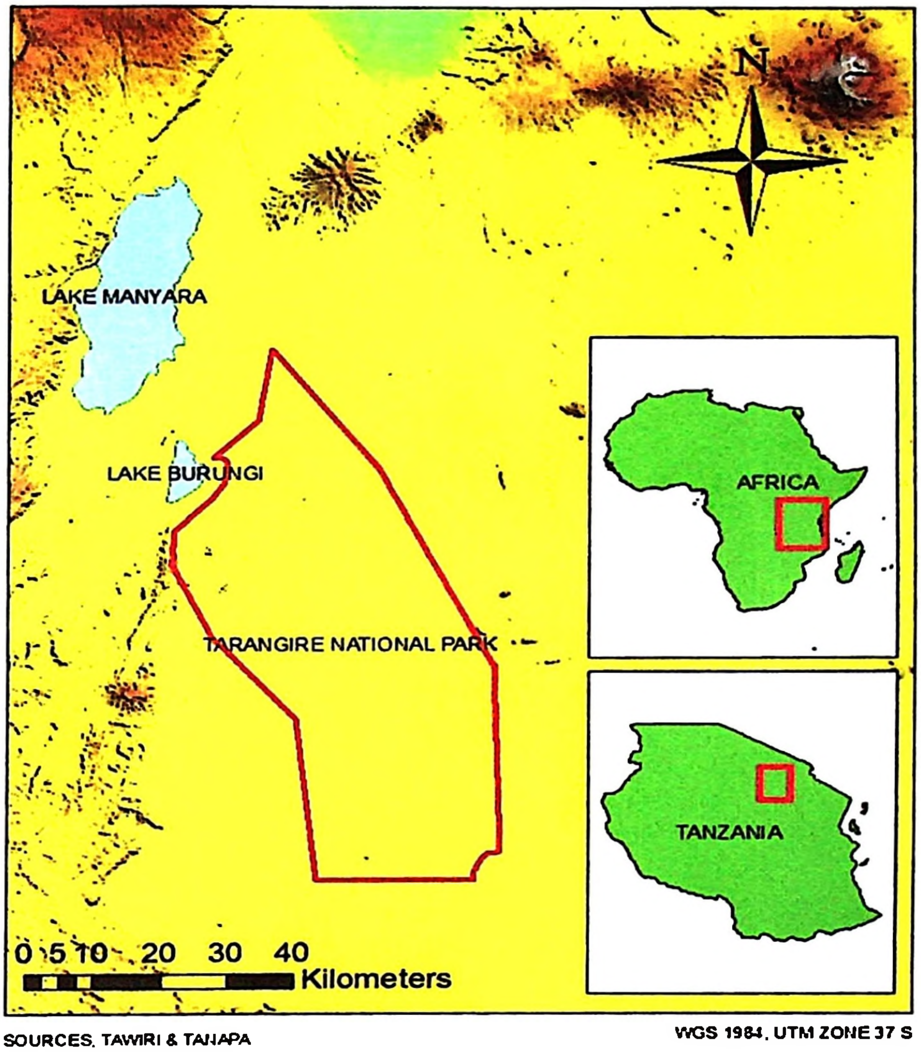

Figure 2: A map of Tarangire National Park. Inserted are the maps of Tanzania (below) and Africa (top)

3.3 Data Collection

Retrospective telemetry data from July 2005 to August 2009 acquired from the long term lion population monitoring programme gathered by the Tarangire Lion Project was used to obtain previous records of kill locations and species involved. Prospectively data collected during this study period from August 2009 to October 2009 was supplemented. Radio telemetry was used to track lion prides from 6.00 am to 7.00 pm daily. This method had an advantage of maximizing chances of encountering predation events during dawn, and late afternoon when hunting lions presumably avoid high energy loss through sweating during sunny day time. When a pride was found with a carcass, observation of the carcase was done from a vehicle at distance ranging from 2-10 metres away from an individual animal or pride, first to confirm if the prey was killed by lions. A carcass was identified as being killed or scavenged by lions with reference to where the predator consuming a carcass was seen in a previous day and the state of the carcass (fresh or old). The following variables were recorded: - prey species killed and its sex (using body size of the carcass and reproductive organs if present), date and time when the kill was found, method used by lions to acquire the prey (i.e. kill or scavenge), pride size and the name of the pride. Other information recorded were the level of carcass consumed (1=Intact carcass, 2=Internal organs seen but not removed, 3=all of internal organs removed from the carcass, 4=when ½ of the carcass remained, 5= when ¼ carcass remained and 6=when almost all carcass consumed), and position of the carcass taken using Global Positioning System (with the aid of Garmin II). Predation information was also recorded from prides without radio collared individuals found opportunistically with carcasses.

3.4 Data Analysis

3.4.1. Determination of lion prey profile and preferred species

A list of prey species killed by lions was compiled and relative predation rate/proportion (the ratio of each number of prey carcass to the total prey carcasses) computed in Microsoft Office Excel 2003. Systematic Reconnaissance Flight (SRF) data for year 2004 and 2007 collected by Tanzania Wildlife Research Institute (TAWIRI) were used to estimate the population size of each lion prey species (zebra, wildebeest, buffalo, warthog, impala, waterbuck, eland, hartebeest, ostrich, grants gazelle and giraffe) available. A list of prey having at least one carcass collected during the entire data collection period was compiled. The prey species with zero carcasses were not used. In this study, prey preference refers to the probability of a particular prey species being selected if all prey types were equally available. Therefore, preference was determined using selection ratio or sometimes called preference index which is the ratio of carcass proportion to the prey population proportion (Kissui and Packer, 2004). Only carcasses sighted at a predation frequency of at least five (Giraffe 5, Warthog 7, Wildebeest 28, Buffalo 31 and Zebra 50) were considered in testing a hypothesis whether lions killed prey species non-randomly in relation to prey abundance and Chi-square goodness of fit test was employed.

3.4.2 Assessment of lion's predation in relation to landscape features

Geographical Information System (GIS) using Arc Map 9.2 (ESRI) was used to create landscape layers of drainage pattern, roads, vegetation cover and land use of the study area, aspect, slope and swamps (Fig. 3-8).

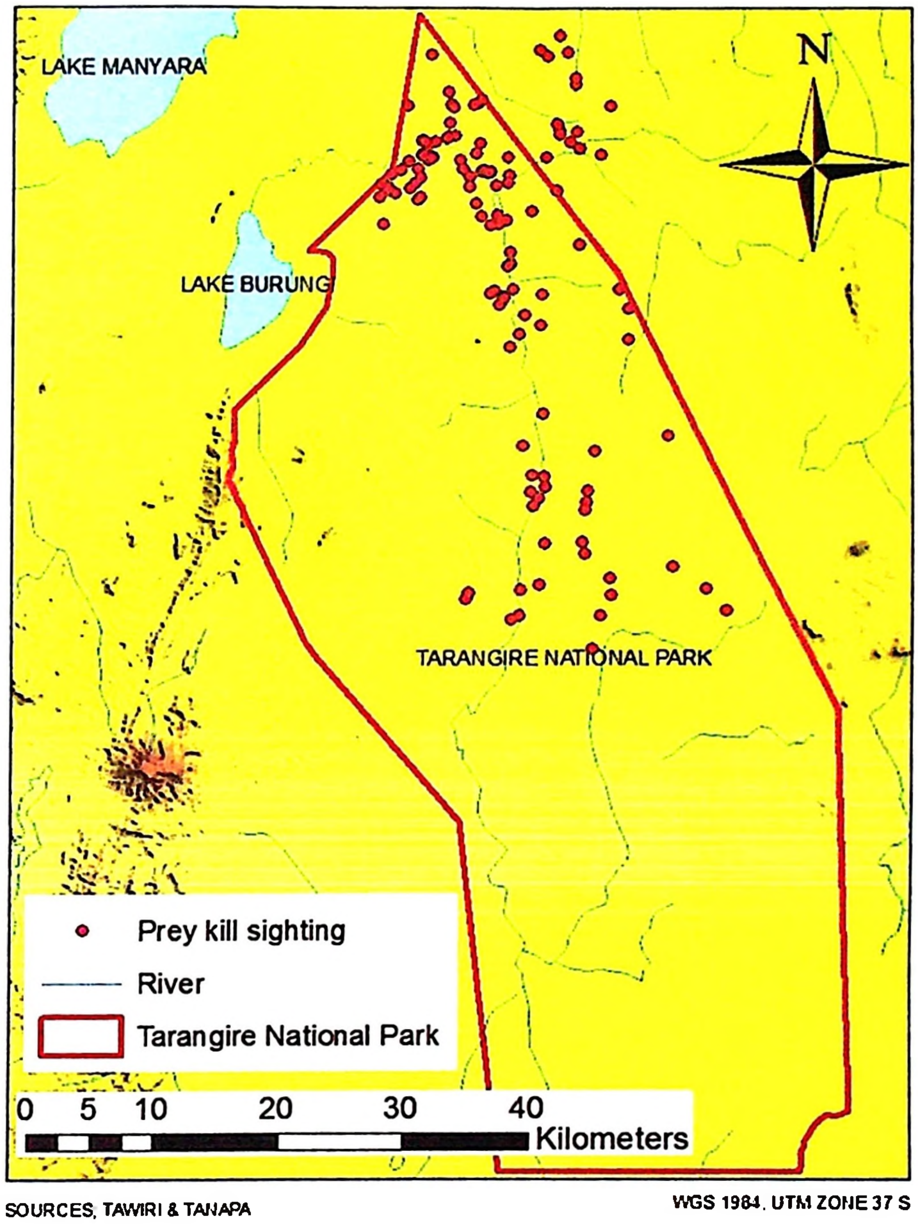

Figure 3: A map of Tarangire National Park showing drainage pattern, including prey kills along the main river

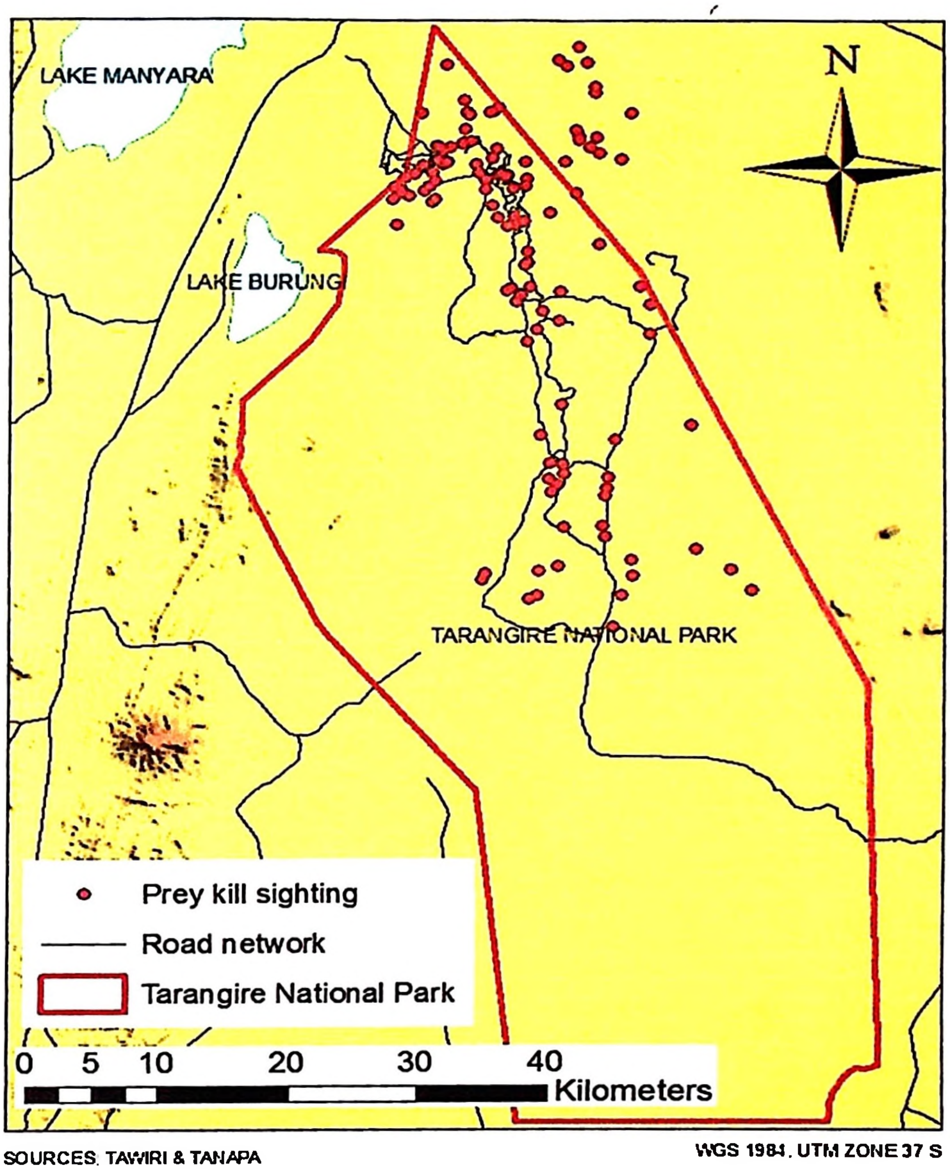

Figure 4: Map showing a relation between road network and lion predation sightings

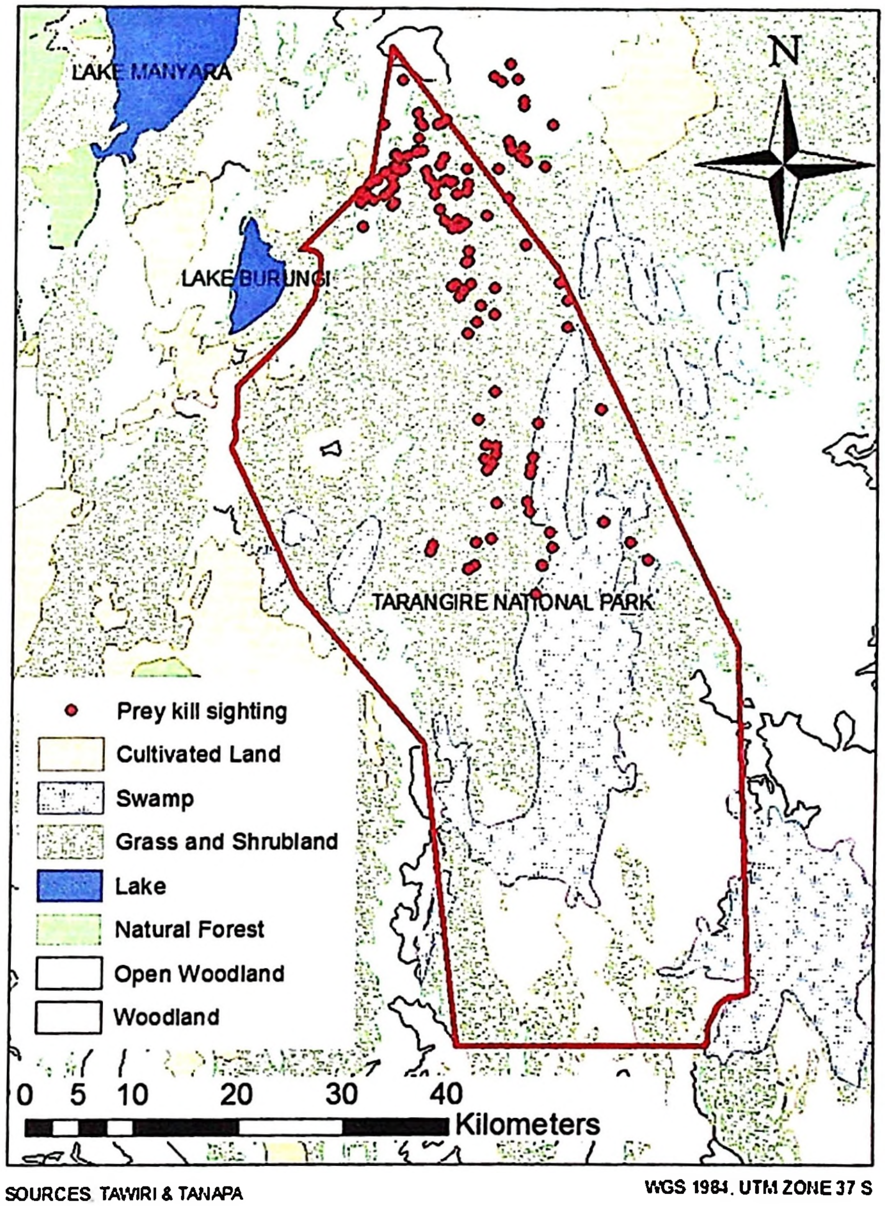

Figure 5: Map showing Tarangire vegetation types and land use in relation to prey kills

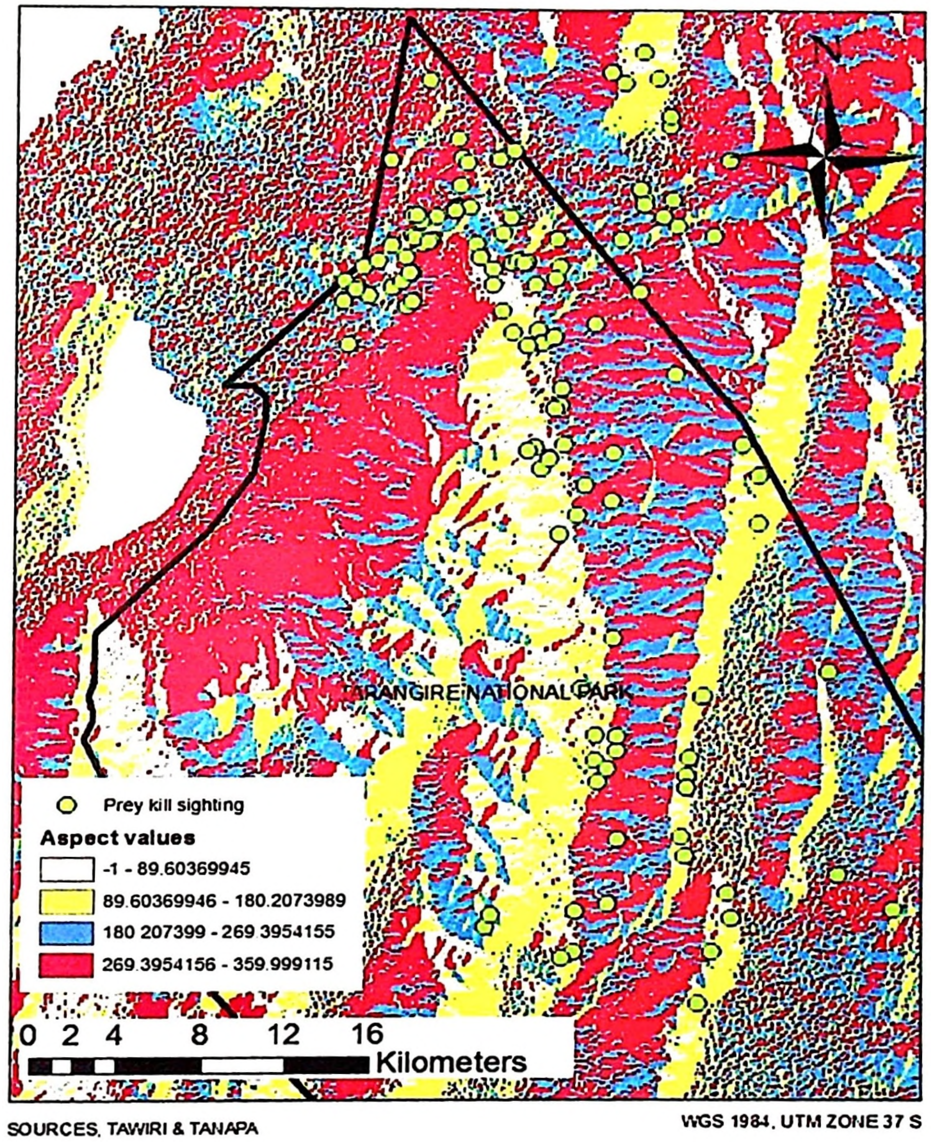

Figure 6: Map showing aspect in relation to lion predation in Tarangire National Park

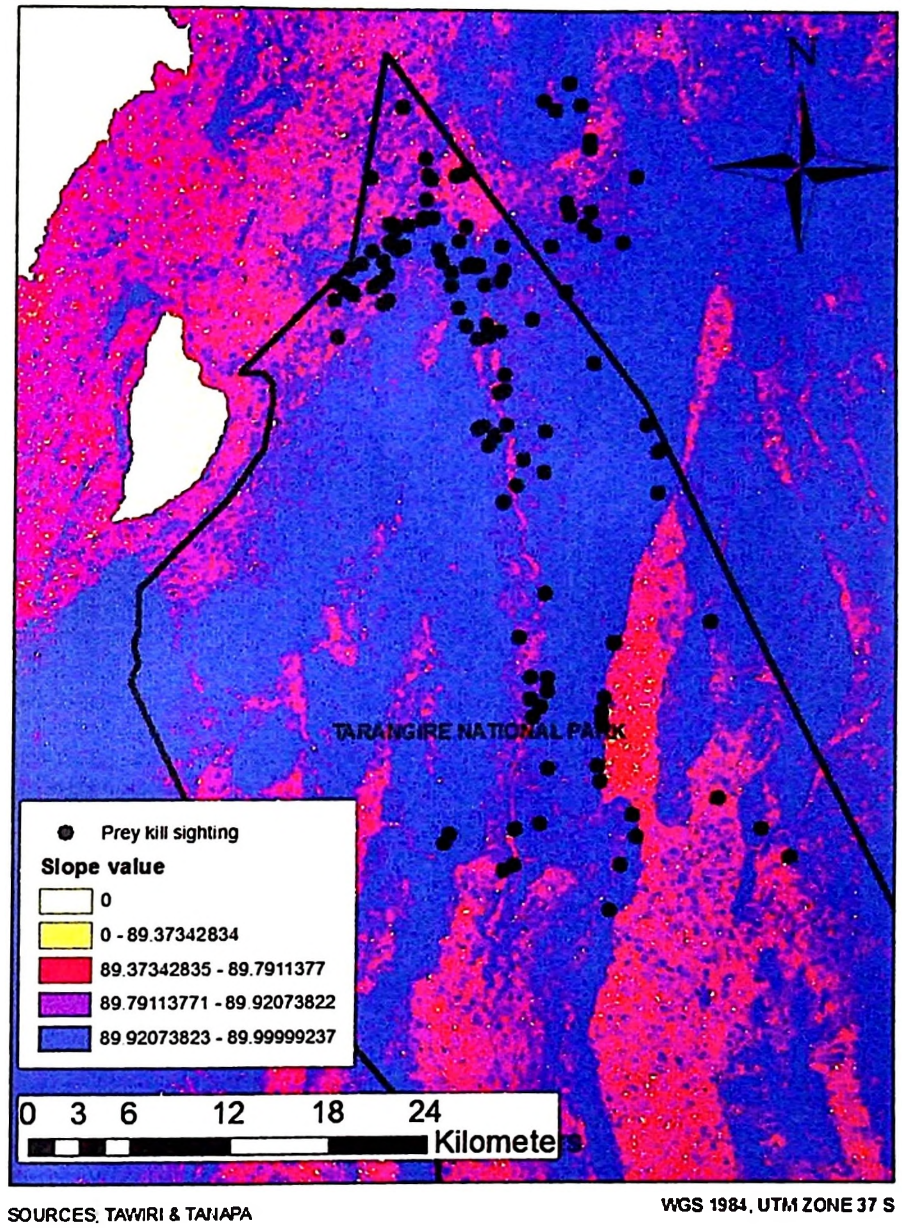

Figure 7: Map showing slope in relation to lion predation in Tarangire National Park

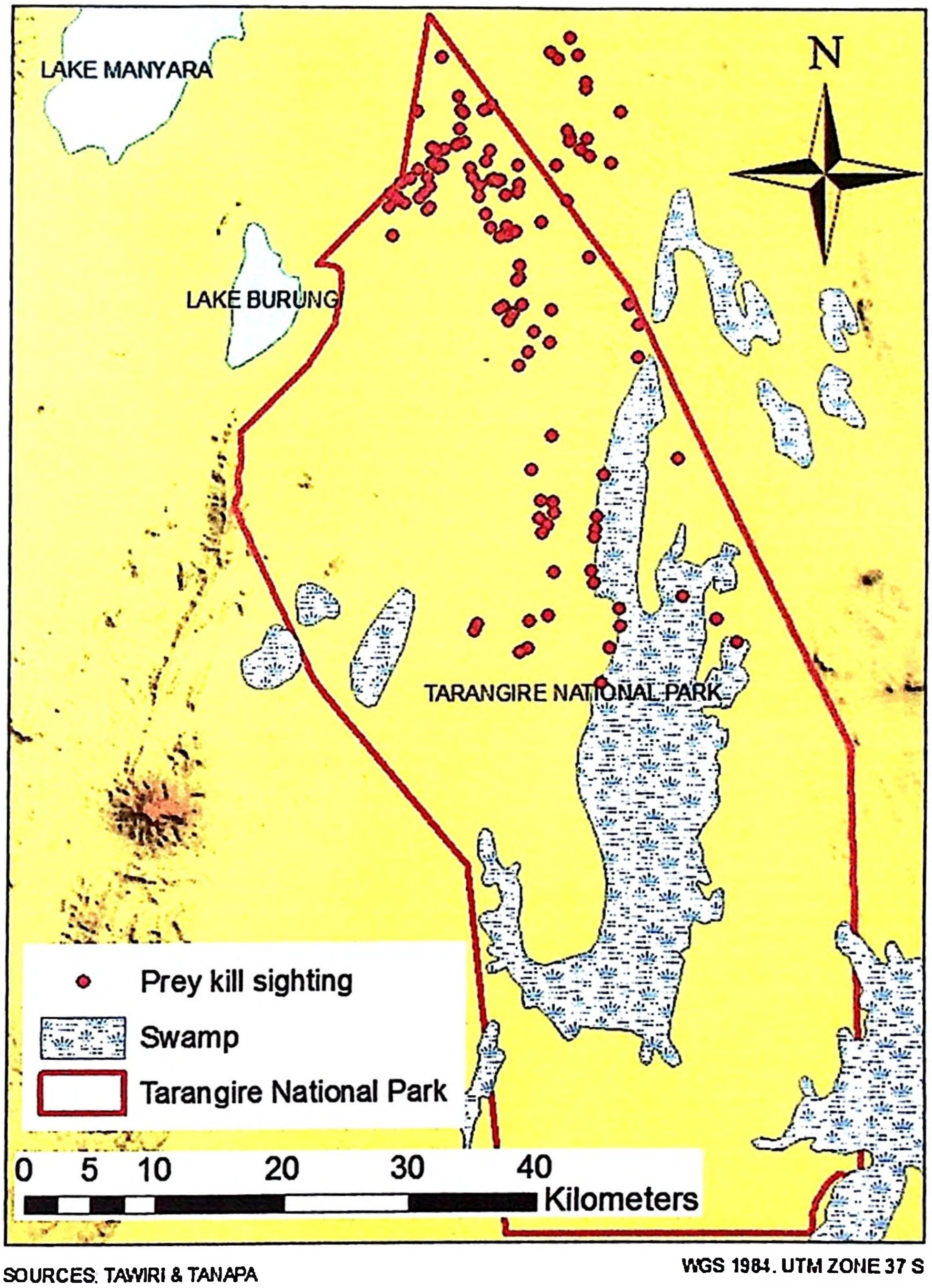

Figure 8: Map showing swamps in relation to lion predation in Tarangire National Park

The landscape layers of drainage pattern, roads, vegetation cover and land use of the study area, aspect, slope and swamps above were converted into 1 × 1 km grid and the distance between prey carcasses and the features around was calculated from the centroid of each grid cell to the nearest features such as swamp or river. Vegetation cover was categorized into 1= cultivated land/agriculture (since there were some prey killing sighted, figure 1), 2= grassland, 3= shrubs, 4= open trees/woodland, 5= forest, 6= swamps, and 7=mixed vegetation type (a grid was categorized as having a mixed vegetation type if it contained more than one vegetation type with equal proportion in an entire grid). Other vegetation types in grids were categorised based on the vegetation type that had the largest proportion in the entire grid, for example when category 2 (grassland) covered more than 50% compared to other categories the grid was characterized as grassland.

Following overlay analysis in GIS, the resulting dataset was subjected to binary logistic regression analysis to determine landscape features influencing lion predation. Presence or absence of carcass sightings in grid cells were used as a binary response variable, with grids with at least a single kill scoring as 1 and 0 for grid cells with no carcass. Landscape features were used in the binary logistic regression as predictors for lion predation. Analyses were carried out in STATA (ver. 9.2, StataCorp LP).

To determine important landscape features influencing lion predation, a set of *A Priori* candidate models were formulated representing hypothesis concerning the influence of landscape features on lion predation in Tarangire National Park. Given the available data, each candidate model was constructed based on the plausibility of *a priori* hypothesis based on the approach described by Burnham and Anderson (2002). Model selection was performed using Kullback–Leibler information theoretic approach with Akaike

Information Criteria (AIC) (Anderson and Burnham, 2002; Burnham and Anderson, 2002).

Maximized log-likelihood for each candidate model was calculated using STATA (ver. 9.2, StataCorp LP) and the values for AIC determined. Change in AIC was expressed as = (AICi - min AIC), where min AIC is the minimum AIC value of all models, and ωi = Akaike weight, which is regarded as the weight of evidence that model *i* is the best approximating model given the landscape features data and set of candidate models or probability that *i* is the best model given the data and set of candidate models using equations by Burnham and Anderson (2002). Models with delta AIC less than 2 are considered to have strong support and represent a confidence set of the best model; delta AIC values of 2–4 have weak support; delta AIC values of 4–7 have little support, and values above 7 have no support at all (Burnham and Anderson 2002). Pearson's correlation coefficients was employed to check for redundancy in predicting distance to road, distance to river, elevation, slope, aspect, vegetation type and distance to confluences to see if there was a significant correlation. This procedure allowed elimination of predictors that did not correlate with each other in a statistical analysis when r_s >0.5, with P<0.05 as threshold.

CHAPTER FOUR

4.0 RESULTS

4.1 Lion's Prey Profile and Preferred Prey Species

One hundred and thirty three carcasses comprised of eleven prey species were recorded from 9 pride sightings for both dry and wet seasons (Appendix 1). However, only one hundred and twenty one (121) prey carcasses comprised of zebra, wildebeest, buffalo, giraffe and warthog were extracted from the same prey carcasses dataset and considered for species preference (Table 1 and 2) because they met a criterion of at least five carcasses set for key prey species. Consequently, the standardized selection ratios (Bi) suggests that in both wet and dry seasons lions selected warthogs and buffalo more than other key prey species abundance. However all giraffe kills were made only during wet season (Table 1) with none in dry season (Table 2). The number of prey kills ranged from 2 to 34 animals with the Tarangire Hill pride killing the highest number of prey (Table 3). This number comprises one quarter of the total number of prey killed, contrary to New Silale and Kuro prides, which had the least number of prey, together accounting for less that 4 % of all kills (Table 3).

Table 1 : Estimated selection indices and prey preferences for the Tarangire National Park lions in wet seasons (November-May) from 2005 to 2009.

Prey species	Prey pop (n)	Pop prop (p_i)	Number of carcasses (u_i)	Carcass prop (o_i)	Sel. Ratio (w)	Stnd. Ratio (B_i)	Stnd. Error (w_i)	chi-square value	p-value	Pref.
Zebra	18 473	0.563	21	0.368	0.655	0.030	0.117	8.7306	0.0031	-
Wildebeest	8 743	0.266	14	0.246	0.922	0.042	0.220	0.1243	0.7244	0
Buffalo.	3 828	0.117	12	0.211	1.806	0.082	0.365	4.8853	0.0271	-
Warthog	170	0.005	5	0.088	16.944	0.767	1.836	75.4043	<.0001	-
Giraffe	1 623	0.049	5	0.088	1.775	0.080	0.581	1.7790	0.1823	-
Total	32 837	1.000	57	1.000	22.102	1.000				

Table 2: Estimated selection indices and prey preferences for the Tarangire National Park lions in dry seasons (June-October) from 2005 to 2009.

Prey species	Prey pop (n)	Pop Prop (p_i)	Number of carcasses (u_i)	Carcass prop (o_i)	sel. Ratio (w)	Stnd. Ratio (B_i)	Stnd. Error (w_i)	chi-square value	p-value	Pref.
Zebra	18 473	0.563	29	0.453	0.805	0.079	0.110	3.1150	0.0776	-
Wildebeest	8 743	0.266	14	0.219	0.822	0.080	0.208	0.7393	0.3899	0
Buffalo.	3 828	0.117	19	0.297	2.547	0.249	0.344	20.2018	<.0001	+
Warthog	170	0.005	2	0.031	6.036	0.591	1.733	8.4475	0.0037	+
Giraffe	1 623	0.049	0	0.000	0.000	0.000	0.548	3.3277	0.0681	-
Total	32 837	1.000	64	1.000	10.210	1.000				

NOTE: (n) - Prey population

(p_i) – Population proportion = prey species number / Total population

(u_i) – Carcass number

(o_i) – Carcass proportion = Carcass number / Total carcass

(w) – Selection ratio = Carcass proportion: population proportion

(B_i) – Standardized selection ratio = Selection ratio number / Total selection ratio

Table 3: Summary of kills made by prides in Tarangire National Park from 2005 to 2009.

Pride name (ID)	Number of carcasses of prey species	Estimated number of lions	Relative percentage of carcasses (%)
Altipiano (C*)	22	8	16.54
New Wazi	16	6	12.03
Silale Minyonyo (C*)	14	22	10.53
Old Silale (C*)	11	6	8.27
Wazi (C*)	19	4	14.29
New Silale	2	5	1.50
Tarangire Hill (C*)	34	35	25.56
Kuro (C*)	2	4	1.50
Boundary Hill (C*)	6	10	4.51
Nomads	7	15	5.26
Total	133	115	100%
Average	13	Approx. 12	9.77

Note: (C*) – Radio collared prides.

4.2 Influence of Landscape Features on Lion Predation

The best model was selected among a set of 30 *a priori* candidate models constructed to predict factors affecting lion predation in Tarangire NP. Table 4, below shows only models with delta AIC rank of less than 6 including null model (i.e. the model with only the intercept). Logistic regression analysis showed that the model containing distance to confluences, elevation, vegetation types and distance to road was the best for predicting lion predation. It constitutes the first model with the minimum delta AIC and the highest Akaike weight which is the best predicting model among a set of candidate models tested to check on each landscape feature with effect on lion predation.

Table 4: *A priori* candidate models explaining the influence of landscape and vegetation factors on lion predation

Model number	Model Set	K	Log likelihood	AIC	ΔAIC	Exp (-0.5*Δ)	ωi
1	confluence, elevation, vegetation, road	4	-321.0639	650.13	0.00	1.000	0.357
2	confluence, elevation, road	3	-322.7870	651.57	1.45	0.485	0.173
3	road, elevation, confluence, vegetation, slope	5	-320.9858	651.97	1.84	0.398	0.142
4	cunfluence, road, elevation, vegetation, river	5	-321.0633	652.13	2.00	0.368	0.132
5	road, elevation, confluence, aspect	4	-322.7718	653.54	3.42	0.181	0.065
6	vegetation, river, elevation, road	4	-323.5268	655.05	4.93	0.085	0.030
7	aspect, elevation, slope, road, confluence	5	-322.7656	655.53	5.40	0.067	0.024
8	confluence, vegetation, road	3	-324.8736	655.75	5.62	0.060	0.022
9	elevation, road	2	-325.9290	655.86	5.73	0.057	0.020
10	confluence, road, elevation, aspect, slope, river, vegetation	7	-320.9689	655.94	5.81	0.055	0.020
11	null model	0	-395.1239	790.25	140.12	0.000	0.000

Table 5: Model averaged parameter estimates and the 95% confidence intervals (CI) for the best model for the factors affecting lion predation

Parameter	Estimate	Standard error	95% CI	
			Upper	Lower
Confluence	2.054×10^{-4}	8.490×10^{-5}	3.980×10^{-5}	3.709×10^{-3}
Elevation	4.147×10^{-3}	1.549×10^{-3}	1.120×10^{-3}	7.166×10^{-3}
Vegetation	1.662×10^{-1}	1.014×10^{-1}	3.144×10^{-2}	3.639×10^{-1}
Road	2.941×10^{-4}	3.866×10^{-5}	2.200×10^{-4}	3.695×10^{-4}

Analysis of parameter estimates for the best model indicated the effects of distance to roads, distance to confluences, amount of vegetative cover (grassland and shrubs) and elevation to be most significant, but aspect and slope had weak effect on lion predation (Table 4 and 5). Parameter estimates in the best predicting model shows greater influence on lion predation with negative slopes indicating that as prey approached these landscape features they became most susceptible to predation, whereas river confluences (2.054×10^{-4}) and roads (2.941×10^{-4}) were the most predicting parameters of predation compared to elevation and vegetation (4.147×10^{-3}) and (1.662×10^{-1}) respectively (Table 5).

CHAPTER FIVE

5.0 DISCUSSION

5.1 Lion's Prey Profile and Preferred Prey Species

Of the 11 key prey species (Appendix I), only 5 formed the most key prey species for the Tarangire lions (Table 1a and 1b) and they constitute 90.97% (n = 121) of all kills. These species are: - zebra (37.59%, n = 50), wildebeest (21.05%, n = 28), buffalo (23.31%, n = 31), warthog (5.26%, n = 7) and giraffe (3.76%, n = 5). Warthog and buffalo were preferred by lions in both wet and dry seasons presumably because warthogs are none migrants and evenly distributed within the park throughout a year.

These results are close to the previously reported results for the same area by the Tarangire Lion Project in 2000, which evidenced that lion foraging in Tarangire National Park consists of 39% wildebeest, 34.1% zebra and 17.1% buffalos (Farina, 2000). Moreover, results of this study almost matches with results by Stander and Albon (1993) and Viljoen (1993) in Northern Botswana in where about five big prey species including buffalo, zebra and wildebeest were also reported to make up between 88 - 95% of all kills made by lion.

According to Radloff and Du Toit (2004) lions classically prey on proportionally much larger prey, and as a result do not contend directly with the smaller predators for most prey species. This is also publicized in Hayward and Kerley (2005) who state that lions prefer medium to large prey weighing between 190 – 550 kg and corresponds to prey such as adult wildebeest, zebra and buffalo while impala are not significantly selected for by lions. Predation on giraffe carcasses occurred specifically on wet season where dense cover appears to reduce lion detectability by giraffes at a distance compared to dry season where grasses are short. Similar predation has been observed in Selous Game Reserve where the vegetation is predominantly woodlands and lions successfully prey on giraffe (Mpanduji, D. G. personal communication, 2010).

5.2 Influence of Landscape Features on Lion Predation

Vegetation cover, river confluences, roads and elevation appeared to be the most important factors that highly affect lion predation in Tarangire. A lion must stalk and ambush a prey species in order to make a kill, hence habitat type play a significant role in predation success. While the density of vegetation may affect the detectability of prey, prey appears to avoid areas with dense cover as they may be dangerous (Sinclair 1985; Prins and Iason, 1989; FitzGibbon and Lazarus, 1995; Sinclair and Arcese, 1995). Good cover provided by shrubby and grassland habitats appear to provide sufficient stalking cover for lions during hunting. Similar to Serengeti ecosystem, the grasses of the Tarangire National Park remain short during dry season because of intense grazing by ungulates (McNaughton, 1983). The only cover available is shrubs which favour stalking. Previous research has shown grass height to significantly affect the success of the hunt (Funston *et al.*, 2001). However, the effect of cover is most likely associated with elevation during lion's stalking. On the other hand, elevation plays an important role on predation by increasing the predator's visual capacity from top-down view as far as the uneven terrain of the park is concerned. The top down view gives the lion a better opportunity to see and select prey. During the present study all kills appeared to be located between 1000 to 1300 metres above the sea level suggesting elevation to have contributed to an increase hunting success.

Since Tarangire river supplies water to wildlife throughout a year, the streams were found to have vital influence on lion predation. In addition, river confluences (the areas within a 500 m radius of the junction between two drainages (Hopcraft *et al.*, 2005) were the most critical points where more kills were located (Table 5). This trend was associated with permanent water availability at the river confluences. During dry season water flows underground and form spring on river confluences. Water availability at these sites attracts prey and predators and their interplays. Results of this study therefore matches well with Hopcraft *et al.* (2005), who reported presence of natural water sources to have influence on the location of the lion kill sites.

Outstandingly, roads appeared to have strong positive influence on lion predation events exemplified by prey kill sightings to concentrate near Tarangire road networks. Since roads are used as primary paves to locate lions, it is possible to explain this strong relationship between road network and lion kill sites. Yet, roads have been found to cause such confounding effects in previous study where Kissui and Packer (2008) found them to significantly influence pride persistence in the Ngorongoro crater. Experience shows that lions do prefer to walk along roads more often during wet seasons to avoid wet grasses. On the other hand, prey species are also attracted to near road areas where there is less cover to avoid predators, as a result incursions and successfully predation occasions are highly located near the roads (Hik, 1995).

Nevertheless, the influence of slope and aspect which demonstrated weak predation influence should not be ignored as they also contributed to some lion predation.

CHAPTER SIX

6.0 CONCLUSION AND RECOMMENDATION

6.1 Conclusion

Although, work has been done on the predation behaviour of lions in a number of protected areas, this study illustrated the lion's key prey species in Tarangire National Park. Tarangire lions preferred larger-sized ungulate species, buffalo, and small sized ungulate, warthog. Migrant species, zebra and wildebeest were not much taken relative to their abundance. This may be due to their un-even availability to lions throughout a year. Thus, long term monitoring of population trends of the most preferred prey species is emphasized given that habitats outside protected area in the Tarangire-Manyara ecosystem are currently undergoing rapid deterioration and change due to increased demand on wildlife resources driven by rapid human population growth and probably a global climate change. Such habitat destruction may affect the health of lion populations.

In Tanzania no animal should be killed without obtaining permit from the Director of Wildlife. There are five types of non natural mortality of lions in Tanzania which are poaching (illegal killings), tourist hunting, problem animal control (PAC), traffic accidents (e.g. Mikumi highway and TAZARA railways) and infrequently iatrogenic death during anesthesia for various researches. The latter two do not occur in statistically relevant numbers.

The Park's narrow width (about 40 km at its widest point) means that wildlife, including the resident lion populations, often moves in and out of the Park boundaries, thereby interacting with nearby human populations. This increases the chances of human lion conflicts. The depredation events on livestock tend to instigate retaliatory killings resulting into many lion deaths. Such acts may threaten lion populations in the near future if measures are not seriously implemented. Tarangire Lion Project encourages people living near park boundaries most of them being Maasai to build chain-link cattle bomas to avoid livestock depredation caused by lions and other carnivores. To date more than seventy five chain link fences have been reinforced in twelve project's study villages.

6.2 Recommendations

As indicated by the results and discussions of this study the following recommendations are given:

i) Since vegetation as one of the landscape features that demonstrated significant role on lion predation, Park management should seek out appropriate fire management regime in order to use fire as management tool safely to avoid animal deaths due to fire and starvation following blazing of vegetation as it happened in 2010. Information on lion predation pattern availed by this study is expected to help management in making rational decisions on fire management for improving forage quality inside the park boundaries.

ii) Local communities should be aware of the lion conservation and its importance in the course of special programs which will focus on significance of lions in the ecosystem and therefore transform local community's feelings toward these carnivores and thus minimized lion retaliatory killings outside of the park boundary since the effect of human activities is likely to result from the type of human conflicts that have been identified as an important cause of population decline in many ecosystems.

iii) Although Tarangire Lion project is doing very well on tracking and monitoring lions inside and some of the outer parts of the Tarangire National Park, much more effort is needed in order to conserve and monitor lions in the study area for accurate estimate of lions number in the Maasai Steppe ecosystem, which will be achieved by escalating the number of collared prides whereas comprehensive monitoring of each pride should be implemented in order to determine demography of each pride.

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APPENDICES

Appendix 1: Prey species, prey population, proportion of prey population, number of carcasses sighted, proportion of carcasses, selection ratio for the various prey species and prey preference as exhibited by lions in Tarangire National Park from 2005 to 2009.

Prey species	Prey Population (n)	Proportion of prey population (pi)	Number of carcasses (ui)	Proportion of carcass prop (o)	Selection. Ratio (w)	SR (Bi)	SE (w)	chi-square	p-value
Zebra	18.473	0.399	50	0.376	0.942	0.035	0.106	0.2941	0.5876
Wildebeest	8.743	0.189	28	0.211	1.115	0.042	0.180	0.4089	0.5225
Buffalo.	3.828	0.083	31	0.233	2.819	0.106	0.289	39.6733	<.0001
Warthog	170	0.004	7	0.053	14.335	0.538	1.428	87.1532	<.0001
Impala	4.636	0.100	2	0.015	0.150	0.006	0.260	10.6871	0.0011
Waterbuck	96	0.002	1	0.008	3.626	0.136	1.902	1.9061	0.1674
Eland	1.700	0.037	3	0.023	0.614	0.023	0.444	0.7539	0.3852
Hartebeest	3,120	0.067	3	0.023	0.335	0.013	0.323	4.2528	0.0392
Ostrich	452	0.010	2	0.015	1.540	0.058	0.873	0.3829	0.5361
Grants G.	3,461	0.075	1	0.008	0.101	0.004	0.305	8.6918	0.0032
Giraffe	1,623	0.035	5	0.038	1.073	0.040	0.455	0.0254	0.8734
Total	46,302	1.000	133	1.000	26.651	1.000			