THE EFFECTS OF HABITAT FEATURES AND PREY DENSITY ON THE HUNTING AND SCAVENGING SUCCESS OF SERENGETI LIONS (*PANTHERA LEO*).

by

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ABSTRACT

This thesis addresses the question of whether Serengeti lions choose foraging sites that facilitate the capture of prey, or whether they choose foraging sites where prey are most abundant. The alternate choices between good habitats and high prey densities have rarely been addressed in resource selection studies of predators.

The observed distributions of kills and scavenges by lions were compared to the predictions of two alternate hypotheses; (a) if lions forage in areas that facilitate the capture of prey, such as areas with cover, then more kills and scavenges should occur in these areas than expected. Conversely, (b) if lions forage in areas with high prey densities, and prey avoid risky habitats, then most of kills and scavenges should occur in areas with reduced cover.

The hypotheses were tested by comparing the use and availability to lions of 5 habitat types: viewsheds from kopjes, river confluences, erosion embankments, woody vegetation, and sites with access to free water. The amount of each habitat type available was estimated from maps created by GIS analyses and ground truthing, and were tested with univariate, goodness of fit, exact tests as well as multivariate resource selection functions. The results indicate that on the large scale lions move according to the distribution of prey. However, at a finer scale lions select areas that facilitate foraging over areas with high prey densities. Plains and woodland lions selected different habitats depending on season. However, the most important habitats that were selected by both plains and woodland lions for either hunting or scavenging were, river confluences, eroded areas, and areas with water nearby. Viewsheds from kopjes and areas with woody vegetation were also selected, but were not as important. Furthermore, areas with vegetation associated with confluences, vegetation associated with water, and eroded sites associated with water were preferred for foraging more often than predicted.

Therefore, the major finding from this study is that although lions require adequate prey for survival, the habitat features available to them for hunting and scavenging are more important than simple prey densities.
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1 INTRODUCTION

1.1 Identifying the Problem

Worldwide, the combined effects of rapid human population growth and an unprecedented rate of consumption of natural resources is resulting in the fracturing of previously continuous areas of available habitat. Many animal populations are faced with shrinking islands of habitat in a growing sea of humanity. This presents ecologists and conservationists with a serious problem (Ellis and Seal 1995, Teer 1996, Hackel 1999, Sinclair et al. 2000a, Rozdilsky et al. 2001). How can we optimize the survival of these threatened populations while meeting our own resource requirements? One way in which we have attempted to alleviate this problem is by setting aside areas for these threatened populations. How should these protected areas be prioritized? Due to social and political concerns, the areas commonly set aside for conservation are considered to be non-useable or non-productive areas (i.e. non-agricultural land, unproductive forests, mineral-poor areas, etc.) (Teer 1996). Consequently, there is a tendency for conservation areas to be in marginal or extreme habitats. Conservation, therefore, will fail in its objectives if such areas do not include the habitat requirements of threatened species (Mills 1991, Sinclair et al. 1995, Weber and Rabinowitz 1996, de Leo and Levin 1997, Rozdilsky et al. 2001). We need to identify habitats selected by animals and determine what constitutes 'good' versus 'poor' habitat.

1.2 Background of Habitat Selection Studies

Comparisons of the quantity or the quality of resources available with those that the animal actually uses provides an indication of habitat selection. Resources are defined as being used selectively when they are used disproportionately to their availability (Manly et al. 1995). Thomas and Taylor (1990) as well as Manly et al. (1995) describe 3 basic designs for resource selection studies based on increasing complexity in the measures of use and availability, from the population to the individual level. Furthermore, habitat selection by an animal often varies spatially and temporally: diurnal versus nocturnal patterns, seasons, age, sex, home range,
predator avoidance, and reproduction can complicate a seemingly straightforward process (Millspaugh et al. 1998, Mysterud et al. 1999).

Although there are a number of techniques that can be used to quantify 'use' versus 'availability' in the field (Neu et al. 1974, Johnson 1980, Marcum and Loftsgaarden 1980, Porter and Church 1987, Thomas and Taylor 1990, Manly et al. 1995, Alldredge et al. 1998, Knick and Rotenberry 1998), recent advances in computing have increased the efficiency of identifying and mapping these areas. With the advent of Geographical Information Systems (GIS), detailed multi-layered maps of available habitat can be generated using pre-existing maps, satellite imagery, aerial photography and ground truthing. Areas that are used by animals can be overlaid on these base layers, creating a map of the animals’ distributions in relation to the available habitat (Erickson et al. 1998). Furthermore, the data can be stratified, resulting in a display of habitat use by season, by life stage, or by any other parameter identified by the researcher. These techniques enable researchers to define trends in habitat selection on both spatial and temporal scales (Johnson 1990, Clark et al. 1993, Chang et al. 1995, Maehr and Cox 1995, Helle and Nikula 1996, Knick and Rotenberry 1998, Thom et al. 1998, Gros and Rejmanek 1999, Pike et al. 1999). However, the potential of GIS goes far beyond this; it can be linked with spatially explicit models to predict future patterns and distributions of animals (Johnson 1990, Akcakaya et al. 1995, Tucker et al. 1997, Boyce and McDonald 1999, Cooper and Millspaugh 1999, Akcakaya 2000, Glenz et al. 2001), thereby making it a prominent tool for management (Ellis and Seal 1995).

There are several methods available for analyzing resource selection data. A commonly used technique incorporates Bonferroni z-statistics with a $\chi^2$ goodness of fit test (Neu et al. 1974, Byers et al. 1984), although this technique has been criticized (Thomas and Taylor 1990, Jelinski 1991, Alldredge and Ratti 1992, Alldredge et al. 1998, Dasgupta and Alldredge 2000). Several techniques compare the ranks of the used versus the available habitats (Johnson 1980), or compare the difference in ranks between the used and the available habitats (Friedman 1937), or compare the ranks of the variance between the used and the available habitats (Quade 1979). However, ranking methods have also received criticism (Mysterud et al. 1999). Alldredge and Ratti (Alldredge and Ratti 1986, 1992) provide a complete overview and comparison of several univariate techniques, including Neu’s,
Johnson's, Friedman's, and Quade's. Similarly, Cherry (Cherry 1996) compares several confidence interval methods used in resource selection studies, including the Bonferroni z-statistic.

Additionally, multivariate techniques have been employed to look at patterns of resource selection. These include models using Mahalanobis distance statistic (Clark et al. 1993, Knick and Rotenberry 1998), log-linear models (Heisey 1985), discrete-choice multinomial logit models (McCracken et al. 1998, Cooper and Millspaugh 1999), compositional analysis (MANOVA/MANCOVA-type linear models) (Aebischer et al. 1993), and resource selection functions based on the logistic regressions and proportional hazards models (Manly et al. 1995, North and Reynolds 1996, Campos et al. 1997, Aldredge et al. 1998, Boyce and McDonald 1999).

The choice of design for a resource selection study and the associated analyses can be overwhelmingly complex and confusing, particularly due to the contradictory nature of the literature. However, ultimately the choice depends on the goals of the study, the hypotheses being tested, the assumptions that can be satisfied, and regrettably the cost of the project (Aldredge and Ratti 1986, Thomas and Taylor 1990, Manly et al. 1995, Aldredge et al. 1998).

Regardless of the design used or the choice of statistics, there are several assumptions implicit to any resource selection study. The most common assumptions are (Thomas and Taylor 1990, Jelinski 1991, Aldredge and Ratti 1992, Manly et al. 1995, Aldredge et al. 1998, Millspaugh et al. 1998): (1) the study involves a random sample of animals, (2) that relocations of the same animal are independent of each other (i.e. they are not spatially or temporally correlated), (3) the selection of habitat by one animal is independent of selection by any other conspecifics (i.e. the animals are not gregarious or territorial nor do they inherently depend on each other for survival), (4) all animals in the study have equal access to the available habitat, (5) available habitats are known, correctly identified, and remain constant over the period of the study, (6) used habitats are correctly identified and have equal detectability (i.e. there is an equal probability of finding animals in all habitats), and (7) if the study involves sampling of used and available resources, then the sampling was random and independent.
Although there is a profusion of habitat selection studies in the literature, there have been relatively few studies on habitat selection by carnivores in particular. The exceptions are taxonomically diverse and include everything from otter, to mountain lions, to northern spotted owls (Litvaitis et al. 1986, Crawshaw and Quigley 1991, Murray et al. 1994, Kurki et al. 1998, Meyer et al. 1998, Thom et al. 1998, Gros and Rejmanek 1999, Pike et al. 1999, Funston et al. 2001, Glenz et al. 2001, Palomares et al. 2001, Edwards et al. 2002). Typically, the areas used by carnivores are determined to a large extent by the distribution of their prey. Furthermore, prey may select habitat based not only on foraging preferences, but also on predator evasion (a subject which I will address in section 1.5.1 Affect of Predation-Sensitive Foraging). Therefore, identifying habitats selected by carnivores can become a complicated two-tier procedure. Most carnivore habitat selection studies to date avoid the issue of prey density and distributions, assuming that areas selected by the carnivores have at least some prey (the exceptions are Litvaitis et al. (1986), Murray et al. (1994), Thom et al. (1998), Palomares et al. (2001)). Therefore, the relative importance of prey density versus habitat for carnivore habitat selection remains largely unanswered.

In this thesis I use a GIS approach to identify some of the habitat parameters that may be important for the African lion (Panthera leo) population in the Serengeti National Park, Tanzania. The intention of this study is to distinguish between the roles of habitat selection versus prey distribution for this particular population.

1.3 The Data and the Primary Question

Long-term data from the Serengeti Lion Project (C. Packer, University of Minnesota) provide an opportunity to use this habitat selection approach. Distribution data of lions in the Serengeti National Park, their habitat characteristics, and the locations at which they have been observed with carcasses, can be analyzed to identify areas and features that may be important to lions in obtaining food (see Appendix 1). The primary question that I will address in this thesis is: to what extent do lions depend on terrain as opposed to prey density for foraging? I use the GIS approach outlined above plus \( \chi^2 \) goodness-of-fit exact tests (a Bayesian style approach) to investigate the preliminary effects of 5 habitat
types on selection of foraging locations by lions. I then use a multivariate approach (loglinear analyses) to further investigate the preferred habitat used by lions to obtain food, and finally develop logistic regression models to predict these locations. Ultimately, the predictive power of the results can be tested in other areas.

1.4 The Study Area

The study area, approximately 2300 km$^2$, is located in the southeastern section of the Serengeti National Park (34° to 36° E and 1° to 3° 30' S), Tanzania (Figure 1). The high elevation (about 1600 m) keeps temperatures between about 15° and 30° C. There are two rainy seasons - the long rains generally occur from late February until mid May and the short rains are typically from November to December (Figure 2). Occasionally these two periods fuse into one long rainy season or fail altogether (Norton-Griffiths et al. 1975, Sinclair 1995b). The average yearly rainfall for the southeastern section of the park (i.e. the study area) is about 700 mm (pers. obs.) and is consistently lower than the northern areas (Norton-Griffiths et al. 1975).

Figure 1. The location of the study area (shaded) within the Serengeti National Park, Tanzania.
The study area is predominantly open grassland interspersed with large rocky outcrops called ‘kopjes’. The riparian areas generally have more herbaceous and woody vegetation. There are moderately dense Acacia and Commiphora woodlands with occasional grass openings (termed ‘mbugas’) in the north. The distribution of lion pride territories along the Ngare Nanyuki River delineate the northern boundary of the study area. The eastern edge of the study area includes the prides along the boundary of the Serengeti National Park, however these prides occasionally drift into the neighbouring Ngorongoro Conservation Area. The prides living in the area of the Mbalageti River and Girtasho River to Lake Magadi mark the southern boundary of the study area, and the western boundary is marked by the Nyaraboro Mountains north to Nyaraswiga Mountain.

Figure 2. Average monthly rainfall (+/- standard errors) from 1984 to 1997 for the southeastern section of the Serengeti National Park, Tanzania.

The study area can be divided into three broad habitat types: woodlands, long grass plains and short grass plains. Within each of these broad habitat types riparian and non-riparian areas differ significantly in soils, moisture and vegetation,
resulting in a catena from valley bottom to hill tops (Ben-Shahar 1991). The study area can therefore be divided into six habitat categories: woodland riparian, woodland non-riparian, short grass riparian, short grass non-riparian, long grass riparian, and long grass non-riparian (Table 1).

**Table 1. Broad scope classification of habitat categories and their characteristics.**

<table>
<thead>
<tr>
<th>Habitat Category</th>
<th>Characteristics</th>
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</thead>
<tbody>
<tr>
<td>Woodland Non-riparian</td>
<td>open woodland, mbugas, xeric soils</td>
</tr>
<tr>
<td>Woodland Riparian</td>
<td>large trees and scrub thickets, moister soils, taller grass, waterholes, drainage banks and confluences</td>
</tr>
<tr>
<td>Short Grass Non-riparian</td>
<td>short grass with bare areas, xeric shallow soils, and erosion terraces</td>
</tr>
<tr>
<td>Short Grass Riparian</td>
<td>short grass, no trees or shrubs, moister soils, waterholes, drainage banks and confluences</td>
</tr>
<tr>
<td>Long Grass Non-riparian</td>
<td>long grass, very occasional tree or shrub, xeric soils, and occasional erosion terraces</td>
</tr>
<tr>
<td>Long Grass Riparian</td>
<td>long grass, shrubs and open woodland, moister soils, waterholes, drainage banks, and confluences</td>
</tr>
</tbody>
</table>

There are currently 14 prides in the study area with a total of approximately 240 resident lions. There are also a number of solitary females and nomadic male coalitions in the area. Each lion is individually identifiable by a unique and permanent upper lip whisker spot pattern (C. Packer, Serengeti Lion Project, pers. com.). Individuals can be recognized throughout their lives, even after periods of long absences. Identification cards and records are updated with each observation. All observations are recorded in a computer database to provide information on survival, reproduction, and population demography.
1.5 Hypotheses on Lion Foraging Strategies

1.5.1 The Affect of Predation-Sensitive Foraging

Before I address the alternate strategies of lion foraging, I will outline the way prey select their own habitats. Prey must balance the conflicting demands of acquiring sufficient resources (primarily food and water) while avoiding predators (Pienaar 1974); that is, prey should forage in a predation-sensitive manner. By avoiding predators, prey should in fact avoid habitats where predators are found. However, as resources become depleted and the competition between prey increases, the prey will be forced to forage in more dangerous areas (Hugie and Dill 1994). Most likely, the least competitive individuals will be forced into the more dangerous areas first. To avoid being killed while foraging in more dangerous areas, prey can (a) spend less time in dangerous areas, and / or (b) be more vigilant in dangerous areas, and /or (c) reduce the probability of being detected in dangerous areas (Caro and FitzGibbon 1992, Brown 1999). However, foraging in dangerous areas will only be advantageous if the prey can acquire more resources than by staying in safer areas. Therefore, the habitats selected by prey depend primarily on (a) their safety and (b) the relative amount of resources available (Mysterud et al. 1999, Bouskila 2001, Heithaus 2001).

Sinclair (1985) as well as FitzGibbon and Lazarus (1995) suggest that predation strongly influences the prey community of the Serengeti. There is evidence of predation-sensitive foraging in wildebeest (Sinclair and Arcese 1995) and Prins and Iason (Prins and Iason 1989) have shown that buffalo have a higher risk of predation near cover where lions can hide. Wilmshurst et al. (1999) have shown that wildebeest select areas with short to medium length grasses as opposed to long grass and Ben-Shahar (Ben-Shahar 1992) has shown zebra and wildebeest both select open areas over wooded. Furthermore, there is evidence that the birthing synchrony and migration of wildebeest assist in minimizing the impact of predation (Fryxell et al. 1988, Fryxell and Sinclair 1988, Fryxell 1995, Sinclair et al. 2000b). Therefore, the premise of prey avoiding risky areas in the Serengeti is not far fetched.
1.5.2 Lion Foraging Strategies

Lions are opportunist hunters and scavengers. They typically take advantage of situations where success is likely, using stealth and ambush hunting techniques (Schaller 1972b). They rely on acceleration, body weight, and in some cases cooperation with other pride members to overcome the prey (Schaller 1972b, Elliott et al. 1977, Packer et al. 1990, Scheel and Packer 1991, Stander 1992, Stander and Albon 1993, Packer and Pusey 1997). Previous studies suggest that lions require a minimum of 40cm of vertical cover to conceal themselves, rarely start stalking prey that are more than 200m away, and charge when they are closer than 20 meters (Elliott et al. 1977, van Orsdol 1984, Stander 1992, Scheel 1993a). This behaviour differs from that of other predators that rely on secrecy and camouflage (e.g. leopard, Panthera pardus), speed (e.g. cheetah, Acinonyx jubatus), or high endurance pursuits and cooperation (e.g. wild dogs Lycaon pictus and spotted hyenas Hyaena hyaena) (Kruuk and Turner 1967, Schaller 1972a, b, Bertram 1979). Given these hunting techniques a successful hunt requires a lion to be both hidden and in close proximity to prey. Therefore, certain habitat features should increase the opportunities for a successful hunt.

Lions overcome competitors for scavenging opportunities by using body mass and cooperation with other pride members (Schaller 1972). No cover is required for scavenging and, in fact, it may impede scavenging by hiding the carcass. Habitat features that help lions search for carcasses should improve scavenging opportunities.

1.5.3 The Hypotheses

Lions should maximize their time at locations where the chances of successful foraging are highest (hunting or scavenging). In contrast, prey should avoid risky habitats as a result of predation-sensitive foraging. However, as resources decline, prey are forced into high-risk areas in order to acquire sufficient food and water (Jarman 1972). The availability of these resources changes predictably with season, and prey populations adjust their distribution to optimize resource acquisition, while minimizing the risk of predation (Pennycuick 1975, Maddock 1979, FitzGibbon and Lazarus 1995, Fryxell 1995). In particular, food
and water resources used by prey generally become more abundant in the wet season, thereby allowing prey populations to avoid high-risk areas. This forces lions to change their foraging techniques between the wet and dry seasons (Elliott et al. 1977) and, as a result, the effectiveness of certain habitat characteristics for successful foraging becomes dependent on season (as suggested by Scheel (1993a)).

Given this premise, it is clear that the effects of habitat characteristics on the success of lion foraging must be clearly separated from the effects of prey distribution. With this in mind, I suggest three hypotheses:

- **H₀**: the foraging behaviours of lions and their prey cancel each other out resulting in the net appearance of a random distribution of kills and scavenges (i.e. habitat and prey distribution have no effect on the location of kills or scavenges)

- **H₁**: foraging success depends on habitat. Therefore, the distribution of lion kills and scavenges are determined by habitat characteristics that may assist by providing cover or increasing searching efficiency (i.e. given there are prey in the vicinity, areas with these habitat features will have more kills and scavenges than areas without these habitat characteristics).

- **H₂**: foraging success depends on prey availability. Therefore, the distribution of lion kills and scavenges are determined by the distribution of prey so that successful hunts and scavenges occur in areas of high prey concentration (i.e. prey distribute themselves in relation to habitat characteristics thereby forcing lions to forage in areas where the majority of the prey are most of the time).

### 1.6 The Predictions on Lion Foraging Strategies

#### 1.6.1 Randomly Distributed (No Selection)

If lion kills and scavenges occur randomly, then there should be no difference between the mean distance to the nearest neighbour (i.e. the next closest kill or scavenge) and the expected distance to the nearest neighbour. That is, the index of aggregation (mean distance to nearest neighbour / expected distance to nearest neighbour) should not differ significantly from 1. If kills and scavenges are clustered then the nearest neighbour distance should be significantly less than expected, and the index of aggregation should approach 0. If the observations have
a regular distribution, the index of aggregation approaches 2.15 (Clark and Evans 1954, Krebs 1999). Comparisons of the nearest neighbour distances are stratified by season and by woodland versus plains lions.

1.6.2 Selecting for Prey Distribution

The majority of prey move onto the short grass plains during the wet season as described by Maddock (1979) most likely (a) to take advantage of the flush of calcium rich grasses for lactation (Kreulen 1975) and (b) to relieve predation pressure while calving (Sinclair et al. 2000b). Therefore, if lions select areas of high prey density for foraging purposes, there should be more kills and scavenges than expected during the wet season on the short grass plains and, conversely, fewer than expected during the dry season (Table 2). The movement of prey through woodland areas cannot be predicted with the same accuracy, therefore predictions can be made only for the plains.

Table 2. Predictions of lion hunting and scavenging based on the seasonal movement of prey on and off the short grass plains (SGP). Observations are predicted to occur more frequently than expected by random (+) or less frequently than expected by random (-).

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<tr>
<th></th>
<th>Dry Season</th>
<th>Wet Season</th>
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<tr>
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<td>On SGP</td>
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<td>Kills</td>
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<td>Scavenges</td>
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1.6.3 Selecting for Habitat

Table 3 outlines the predictions for lion foraging based on habitat features and season according to the above hypotheses. The following sections describe in detail how each of the proposed habitat features outlined in Table 3 may assist in foraging and why their effectiveness may change with season.
1.6.3.1 Viewsheds From Kopjes

The large rocky outcrops known as kopjes may provide lions with a better view to observe potential prey or carcasses. Searching for prey can be time consuming (Elliott et al. 1977), therefore any feature that decreases the time spent should be advantageous. Kopjes are also commonly associated with large shady trees and often hold pools of water in depressions and crevasses in the rock. Thus, they could attract lions for reasons other than increasing the search area by providing a view. Kopjes are associated with passive hunting as they provide retreats from which lions can wait for prey to come into view. Generally, kopjes provide little to no cover for ambush hunting unless the prey are in the immediate vicinity. Therefore, if lions use kopjes to search for potential prey and carcasses (according to $H_{A1}$), areas in the viewsheds of kopjes will have higher than random probabilities of successful hunts and scavenges.

The effectiveness of kopjes in increasing the search area is predicted to be similar in wet and dry seasons, however kopjes in specific areas (i.e. woodland versus long grass plains versus short grass plains) may be used preferentially depending on season and the distribution of prey.

If the location of lion kills is determined by prey distribution (according to $H_{A2}$), the proportion of kills in areas surrounding kopjes will be no different from random since it is assumed prey do not distribute themselves in relation to kopjes.
Table 3. The predicted effects of habitat characteristics on the seasonal foraging success of lions if the distribution of lion kills is determined by habitat characteristics ($H_{A1}$) as opposed to prey distributions ($H_{A2}$). The symbols +, -, or 0 indicate the observed number of kills or scavenges in the area of interest are predicted to be more than, less than or no different from random, respectively. Pl = plains lions and Wd = woodland lions.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Pride</th>
<th>Season</th>
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<th>Habitat Predictions ($H_{A1}$)</th>
<th>Prey Predictions ($H_{A2}$)</th>
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1.6.3.2 River Confluences

Most prey species have a natural aversion to approaching and crossing drainages. This is probably because the risk of predation associated with the cover in these areas is greater (Schaller 1972b, Prins and Iason 1989, Ben-Shahar 1992, FitzGibbon and Lazarus 1995). As a result, confluences (where two drainage lines meet) may serve to concentrate and funnel prey into relatively enclosed areas. Lions may be able to use these areas by simply waiting for prey to be funnelled towards them, or for more active hunts where they can take advantage of the cover associated with the drainages and use the barriers formed by the drainages to increase their hunting success (Elliott et al. 1977).

Confluences are probably most effective at the beginning and the end of the dry season when the large herds of wildebeest and zebra are moving to or from the plains. They may be important areas during the dry season, partially because they are often associated with waterholes; larger, more stable pools occur at the junction of smaller, more ephemeral streams. However, during the wet season their effectiveness is probably minimal since the majority of prey are on the short grass plains and are avoiding these areas (Pennycuick 1975, Maddock 1979, FitzGibbon and Lazarus 1995, Fryxell 1995).

It is apparent that the effect of confluences is complicated by the effect of the rivers of which they are an inherent part. Therefore, if lions are selecting confluences (according to HA1), then not only should there be more kills in confluences compared to all other available areas, but there should also be more kills in confluences than at any other point along the river (Table 3). In other words, if lions are selecting confluences there should consistently be more kills in confluences than anywhere else. Furthermore, if the habitat hypothesis is true, there should be no difference between the observed and expected number of scavenges in confluences, since confluences should neither enhance nor impede the lions' ability at finding carcasses.

Prey should form unusually high concentrations in and immediately adjacent to confluence areas as they migrate through plains and woodlands based on season. Therefore, if the distribution of lion kills and scavenges are determined by the distribution of the prey herds (according to HA2), then there should be more kills
and scavenges in confluences only during times when prey are in the vicinity (i.e. the woodlands during the dry season and the plains during the wet season).

However, during the times when the majority of prey are infrequent in the vicinity (i.e. the wet season in the woodlands and the dry season on the plains), there should be fewer kills and scavenges in confluences in comparison to the total available area (since prey generally avoid rivers and furthermore they should not be moving through the area), and no difference should occur between the number of kills and scavenges in confluences in comparison to rest of the river (Table 3).

1.6.3.3 Erosion Embankments

Erosion embankments include erosion terraces, drainage banks and ditches. Erosion terraces are most likely caused by the erosion of well-worn game trails, especially during heavy rains. They are typically associated with the short grass plains, especially in the area between Gol Kopjes and Barafu Kopjes. Erosion terraces typically vary in height from a few centimeters to about 60 cm. Drainage banks differ from erosion terraces in that they are associated with riparian areas, and as a result, they often reach several meters in height. Ditches are man-made and are commonly associated with roads. They are occasionally found along firebreaks and along the national park boundary, both of which are graded by bulldozers.

Embankments may be useful for hunting lions in that they may provide cover for ambushes or assist stalking lions in concealing themselves. Therefore, if the distribution of lion kills is determined by habitat (according to H_a1), then areas with erosion embankments should have more kills than predicted by a random distribution in both wet and dry seasons since they provide cover. Furthermore, there should be no difference in the number of scavenges observed in eroded areas since embankments neither assist nor impede a lions’ ability to search for carcasses.

There is no evidence that prey distribute themselves in relation to erosion embankments. Therefore, if the distributions of lion kills and scavenges are determined by prey density (according to H_a2), then there should be no difference
from the observed distribution of kills and scavenges to a random distribution (Table 3).

1.6.3.4 Woody Vegetation

Woody vegetation such as trees, bushes and large perennials not only provide cover for stalking lions, but can also impede the prey’s escape routes during a chase (Schaller 1972b, Elliott et al. 1977). For the most part vegetation probably assists with active hunts, although lions can use vegetation to conceal themselves while waiting for ambush opportunities (Schaller 1972b, Elliott et al. 1977, Scheel 1993b, Funston et al. 2001). Therefore, if the location of kills is determined by habitat (according to H_{A1}), areas with thicker vegetation should have more kills than predicted by random. Furthermore, thick vegetation blocks the view and should impede the searching efficiency of scavenging lions. Therefore, areas with thick vegetation should have fewer scavenges than predicted by random if the habitat hypothesis is true (Table 3).

The majority of the prey in the Serengeti avoid areas with dense vegetation in favour of more open areas, presumably due to the danger of hidden predators (Schaller 1972b, Prins and Iason 1989, Ben-Shahar 1992, FitzGibbon and Lazarus 1995). Therefore, if the locations of kills and scavenges are determined by the distribution of the majority of prey (as predicted by H_{A2}), then there should be fewer kills and scavenges in areas with thicker vegetation than expected by random.

1.6.3.5 Access to Water

The study area receives an average of about 700mm of rainfall a year. This means that animals have limited access to free water (Wolanski and Gereta 2001). Although many of the prey are adapted to arid conditions, thereby reducing their water dependency (Taylor 1968), free water is still vital (Western 1975, Mills et al. 1995). Waterholes in the area are typically ephemeral. Small waterholes dry quickly with the passing of the wet season, however the larger ones become critical for resident prey herds, especially during the dry season (Jarman 1972, Western 1975, Gereta and Wolanski 1998, Wolanski and Gereta 2001). Most prey spend as little time as possible at water holes other than for brief drinking bouts, however
their arrival is virtually inevitable. Therefore, waterholes could provide lions with predictable locations for encountering prey. However, during the wet season, when access to water is not limited, waterholes probably provide less assistance in hunting since prey can avoid these high-risk areas.

Therefore, following this logic, if the location of lion kills is determined by habitat parameters (as predicted by $H_A$), then there should be more kills in the vicinity of water than predicted by random, since these areas provide predictable locations for encountering prey (albeit, brief). The effect of waterholes should be greatest during the dry season when there is the least amount of water. Waterholes should provide no assistance to lions searching for carcasses, and therefore the distribution of scavenges in relation to water should be no different from random.

However, if the distribution of prey determines the location of kills (according to $H_A$), then there should be fewer kills and scavenges near water than expected, since the majority of prey avoid water most of the time (other than for brief drinking bouts) (Table 3).

1.7 Loglinear Regression

Habitats are often not independent (i.e. they occur in combinations with each other), and these combinations may be selected for by animals (Rettie and McLoughlin 1999). For example, thick vegetation may be more commonly found near water. It is conceivable that lions may select areas with vegetation associated with water over areas with only thick vegetation or with only water. Loglinear regressions provide a method of multiway frequency analysis that can be used to investigate relationships between discrete habitat variables (Everitt 1977, Tabachnick and Fidell 1996). In the case of resource selection studies, loglinear analyses can be used to identify autocorrelated habitat variables. A loglinear analysis creates tables with one-way, two-way, three-way and higher-order associations between variables. The expected cell frequencies within this table are calculated using a linear logarithmic model. The relationships between variables are tested by systematically dropping as many as possible of the one-way, two-way, three-way and higher-order associations from the model, while maintaining a good fit between the observed and expected cell frequencies. When a one-way, two-way
or higher-order association is dropped and causes a significant deviation between the observed and the expected cell frequencies, the association between the variables involved is identified as being significant. Significance is tested using the likelihood ratio statistic ($G^2$). Therefore, a good model (i.e. one in which there is a good fit between the observed and expected cell frequencies) fails to reject the goodness of fit hypothesis (tested by $G^2$).

1.8 Resource Selection Functions & Logistic Regression

Resource selection functions (RSFs) are mathematical functions that are proportional to the probability of an animal using a particular habitat (Manly et al. 1995). Resource selection probability functions (RSPFs) differ from resource selection functions (RSFs) in that they estimate the actual probability of use, rather than being proportional to the probability of use. However, to calculate the RSPF the investigator must know the total number of habitat units used versus those that are available (Manly et al. 1995, Campos et al. 1997). This is difficult when the data are based on radiotelemetry locations (Campos et al. 1997, Boyce and McDonald 1999), since the number of possible locations are infinite. In most studies using radiotelemetry methods, resource selection is estimated using RSFs.

Typically, resource selection functions use logistic regression equations to predict habitat use, however other probability functions can be used (Manly et al. 1995, Knick and Rotenberry 1998, Boyce and McDonald 1999). A logistic regression predicts a discrete outcome, such as a kill, from a group of habitat variables. The objective of a logistic regression is to find the best combination of habitat variables ($X_p$) and associated coefficients ($\beta_p$) that maximize the likelihood of obtaining the observed frequencies (Trexler and Travis 1993, Tabachnick and Fidell 1996). Therefore, the logistic regression can account for combinations of habitats that may be selected, rather than single habitats (Boyce and McDonald 1999). Furthermore, the logistic regression assumes nothing about the distribution or variance of the variables, which contributes greatly to its versatility and robustness in resource selection studies (Trexler and Travis 1993, Manly et al. 1995, Tabachnick and Fidell 1996, Boyce and McDonald 1999). Resource selection functions using models such as logistic regressions are arguably the most comprehensive method for analyzing and interpreting resource selection data.
(Manly et al. 1995, Campos et al. 1997, Boyce and McDonald 1999) and have been used by several authors (North and Reynolds 1996, Erickson et al. 1998, Meyer et al. 1998, Gros and Rejmanek 1999, Glenz et al. 2001).

In this study the logistic regression predicts the probability of a kill \( \text{p(kill)} \) at a given point as being

\[
p(\text{kill}) = \frac{e^z}{1 + e^z}
\]

where

\[
z = \beta_0 + \beta_1 X_1 + \beta_2 X_2 \ldots + \beta_p X_p
\]

and \( \beta_1 \ldots \beta_p \) are the coefficients for each of the habitat variables \( (X_1 \ldots X_p) \) and \( \beta_0 \) is the intercept. The habitat variables \( (X_1 \ldots X_p) \) are discrete values \( (1,0) \) indicating the presence or absence of the habitat (for example, the presence or absence of water, or presence or absence of erosion). The habitat variables could be continuous instead of discrete, but were not in this study.

The probability of a kill being made can be assessed from the odds ratio which is calculated by \( e^\beta \). This predicts whether at any given point the presence of a habitat will significantly improve the chances of a kill being made. This means that if the coefficients for any habitat \( (\beta_1 \ldots \beta_p) \) are greater than 0, then \( e^\beta \) will be greater than 1 and the probability of a kill is improved. Conversely, if the coefficients \( (\beta_1 \ldots \beta_p) \) are less than 0, then \( e^\beta \) will be less than 1 and therefore the probability of a kill occurring at that point are decreased (Trexler and Travis 1993, Tabachnick and Fidell 1996).

The coefficient \( (\beta_p) \) for each of the variables can be tested for significance using the Wald test and the Lagrange Multiplier test. The Wald test is used to test the significance of the variable included in the model, while the exclusion of the variable is tested with the Lagrange Multiplier test. In either case, failure to reject the null hypothesis (i.e. the coefficient is not significantly different from zero) results in the habitat variable not being included in the logistic regression equation (Trexler and Travis 1993, Tabachnick and Fidell 1996).
The overall adequacy of the logistic regression model can be assessed using a Hosmer-Lemeshow goodness-of-fit $\chi^2$. Failure to reject this test indicates that the model being tested is not significantly different from a perfect or complete model, which is the desired outcome. Therefore, if a variable is not included in the logistic regression equation, and the equation is not significantly different from a perfect model, this variable is not considered to be a significant predictor. Conversely, if a variable is not included in the equation, and the equation is significantly different from a perfect model, this variable is considered to be a significant predictor and should be included (Trexler and Travis 1993, Tabachnick and Fidell 1996).
2 General Material and Methods

2.1 The Maps

The maps used in this study were digitized from 1:50,000 topographic maps of the Serengeti National Park (Projection: UTM, Units: meters, Datum: ARC 1960, Spheroid: Clarke 1880) by Frankfurt Zoological Society and the Tanzanian Wildlife Conservation Monitoring Program. The contours, kopjes and the hydrology (rivers and lakes) from these maps were the baseline themes for this study. The geographic analyses were conducted using ESRI's ArcView Version 3.2 with the Spatial Analyst and 3D Analyst extensions. ESRI's ArcInfo was also used initially to check and correct the maps.

2.2 Checking the Maps

The initial step in checking the maps was to import and examine the baseline themes (contours, kopjes and hydrology) in ArcView 3.2 to ensure they were consistent. The themes were overlaid with each other and a quick visual check was made to ensure the contours agreed with the river courses and lakes. Since the maps were digitized from a series of 1:50,000 UTM maps the joins between the digitized map sheets were also checked. It became evident that although the rivers theme and lakes theme agreed with the contours, some of the river systems between map sheets were not joined.

Prior to joining the rivers properly, the relevant portions of the map pertaining only to the study area were clipped out from the entire map of the Serengeti with the intent of simplifying the process. The result was river, lake, and contour themes pertaining only to the study area.

Using the build function the contours and rivers were converted into arcs and the lakes converted into polygons. This saves the attributes in the file as a given geographical data type (point, arc or polygon) and allows the themes to be edited accordingly.

A trace function was conducted to simplify the identification of the rivers systems that were not properly connected between the digitized map sheets. The
trace function highlights the path of flow through a network of arcs. Any arcs that are not properly connected to the network will not be highlighted. The first step in conducting the trace function was to establish the direction of flow using trace direction. The output files from the trace direction function (which specifies the direction of flow for each arc) were subsequently used in a trace upstream function. The trace upstream function highlights the path of flow in the river network from all areas upstream of an allocated point. In this case the allocated points were the outflow for each major river system from the study area. The output from the trace upstream function highlighted all of the areas upstream from the discharges of each river system that were connected to the network, allowing portions of the river systems that were not properly connected to be easily identified. Using the snap and move functions in ArcEdit (a component of ArcInfo) the rivers were reconnected into continuous networks. With the rivers connected the above trace functions were repeated to identify any other areas further upstream that were not connected. The process was repeated until each river system in the study area was properly connected. The updated river coverage was re-saved and again converted into a series of arcs using the build function.

The corrected themes were converted back into shape files. The shape files were then used as base line themes in ArcView 3.2 for the rest of the analyses.

2.3 Sorting the Data

Data were extracted from the original Serengeti Lion Project database (unpublished data of C. Packer). Observations where lions with a carcass had been located by radiotelemetry were extracted. This decreased the observer bias in searching for lions as well as eliminating the bias inherent in estimating location by triangulation (Nams 1989, Rettie and McLoughlin 1999), but reduced the data to those records from 1984 to 2001. Furthermore, by selecting only radio collared individuals, complications with multiple observations of other pride members were avoided (i.e. habitat selection studies are biased when selection by one individual is dependent on the selection by another individual such as in gregarious or territorial animals (Aebischer et al. 1993)). Prior to 1984 radiotelemetry was not used. Observations of the same individual on consecutive days were deleted to reduce
duplication of observations and decrease the degree of autocorrelation between observations (Harris et al. 1990, Aebischer et al. 1993, Otis and White 1999). The extracted data had the following categories: a pride identifier, the date of observation, the UTM location of observation (to the closest 100m either using 1:50,000 topographical maps or a Global Positioning System), and the species of the carcass. Each carcass was scored as either killed or scavenged if the observer actually saw the event, or unknown if the observer did not see the event (see Appendix 1). The data were not stratified by species of the carcass or by whether the prey was a resident or a migrant. Furthermore, the data were virtually entirely from diurnal observations.

To distinguish any possible seasonal shifts in resource selection (Orians and Wittenberger 1991, Aebischer et al. 1993, Schooley 1994, Boyce and McDonald 1999), each observation was classified as occurring either in the wet season or in the dry season. All the locations where lions were observed with a carcass were overlaid with the location of rain gauges using ArcView 3.2. If the average total rainfall for the 2 months prior to the kill at the rain gauge closest to the observation was greater than 50mm per month the observation was classified as being wet, if less than 50mm per month the observation was classified as being dry (Norton-Griffiths et al. 1975). Rainfall records are archived at the Serengeti Wildlife Research Centre and were corrected for missing data (A.R.E. Sinclair, pers. comm.).

Both the habitat and the prey that are available to a pride depends on the area that is within their range (McClean et al. 1998). Furthermore, the very presence of a home range implies that the pride has already made a selection (Johnson 1980), therefore assessing only habitat that is available to lions is justified. However, dividing the study area into individual pride ranges reduced the sample size of observations too much. Instead, the prides were grouped into woodland and plains prides based on the majority of the habitat in their territory. This assumes that prides in similar habitat types have equal access to all resources and that their selectivities for resources are similar, which is justified (Scheel 1993a). Note that not all of the following prides are still in existence. The prides that had the majority of their territory in woodlands since 1984 are as follows: Campsites (CS), Campsite 2's (C2), Campsite 3's (C3), Kibumbus (KB & KI), Kibumbu 2's (K2), Loliondos (LL), Mukoma Hills (MH), Sangere (NW), SRI's (SR),
Transects (TR) and the nomads (NO) that were in the vicinity. The prides that had or have the majority of their territory on the plains since 1984 are as follows: Barafu (BF), Boma (BM), Cub Valley (CV), Gol (GO), Gol East (GE), Gol West (GW), Gol United (GU), Maasai (MS), Maasai Kopjes (MK), Mukoma (MU), Naabis (NB), Naabi 3's (N3), Plains (PN), Simba (SB), Simba Numbers (S#), Simba solitary (SG), Sametu (SM), South West (SW), Sympatica solitary (SY) and the nomads (NO) that were in the vicinity.

The area available to the woodland and plains lions was determined by displaying all the locations where woodland and plains lions were seen with a carcass. Using ArcView 3.2 range polygons were drawn around the area where woodland lions and plains lions typically operate, as suggested by McClean et al. (McClean et al. 1998) and by Porter and Church (Porter and Church 1987). Areas that were inaccessible during field research (e.g. mountains) were excluded from the polygon. The areas within these two polygons represented the area that was available to the woodland and plains lions. The habitat within each area was then compared to the habitat where these lions were making kills.

Therefore, the original data set was broken down into 12 independent data sets as described in Table 4. It should be noted that the sample units in this case are the individuals, and not the observations. Using the observations as the sample unit rather than the individuals constitutes pseudoreplication (Hurlbert 1984, Aebischer et al. 1993, Otis and White 1999). Allredge and Ratti (1986) found that using 20 individuals, with 15 observations per individual, and between 4 to 7 habitat categories, the chances of a Type I error were acceptably low when using Neu's (1974) $\chi^2$ technique. Similarly, Aebischer et al. (1993) recommended using at least 10 individuals for resource selection studies. This study used data from a total of 116 radio collared lions, and therefore is adequate. There were 48 lions radio collared in the woodlands (37 females and 11 males), and 68 on the plains (51 females and 17 males) since 1984. Although males and females differ in their hunting strategies and success (females are more successful (Schaller 1972b)), by combining these data I am addressing the average foraging success of Serengeti lions in general.
Table 4. The available area (km$^2$) and the number of observations for each data set.

<table>
<thead>
<tr>
<th>Data set</th>
<th>Area (km$^2$)</th>
<th>Number of Obs.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plains kills wet season</td>
<td>2028</td>
<td>56</td>
</tr>
<tr>
<td>Plains kills dry season</td>
<td>2028</td>
<td>65</td>
</tr>
<tr>
<td>Plains scavenges wet season</td>
<td>2028</td>
<td>26</td>
</tr>
<tr>
<td>Plains scavenges dry season</td>
<td>2028</td>
<td>26</td>
</tr>
<tr>
<td>Plains unknown wet season</td>
<td>2028</td>
<td>248</td>
</tr>
<tr>
<td>Plains unknown dry season</td>
<td>2028</td>
<td>265</td>
</tr>
<tr>
<td>Woodland kills wet season</td>
<td>508</td>
<td>20</td>
</tr>
<tr>
<td>Woodland kills dry season</td>
<td>508</td>
<td>63</td>
</tr>
<tr>
<td>Woodland scavenges wet season</td>
<td>508</td>
<td>4</td>
</tr>
<tr>
<td>Woodland scavenges dry season</td>
<td>508</td>
<td>10</td>
</tr>
<tr>
<td>Woodland unknown wet season</td>
<td>508</td>
<td>231</td>
</tr>
<tr>
<td>Woodland unknown dry season</td>
<td>508</td>
<td>252</td>
</tr>
<tr>
<td>Total</td>
<td>2275</td>
<td>1266</td>
</tr>
</tbody>
</table>

### 2.4 Testing for Random Distribution (Nearest Neighbour Test)

The distribution of kills and scavenges were tested for spatial randomness using the Clark-Evans nearest neighbour test (Clark and Evans 1954) outlined by Krebs (1999). The distribution of kills and scavenges by plains and woodland lions were analyzed separately.

1) The mean distance to nearest neighbour ($r_A$) for all kills and scavenges was calculated.

2) The Clark-Evans test in Programs for Ecological Methodology (Krebs 2001) was used to calculate the expected nearest neighbour distance ($r_E$). The calculation for the expected nearest neighbour distance was based on the number of observations and the total area available to the lions.

3) The Index of Aggregation ($r_A / r_E$) was calculated. Any significant deviation from randomness (i.e. the Index of Aggregation being significantly different from 1) was tested using the z-test in Programs for Ecological Methodology. Observations are clumped if the Index of Aggregation approaches 0, whereas they are regular if the Index of Aggregation approaches 2.15 (Clark and Evans 1954, Krebs 1999).
2.5 Selection for Prey Distribution

The broad scale movement of lions with prey was analyzed in the following manner.

1) The majority of prey are on the short grass plains during the wet season (Pennycuick 1975, Maddock 1979). Prey movement in the woodlands cannot be accurately predicted, so analysis on the effect of prey distribution was limited to the plains only.

2) Habitat information was gathered at points over the entire study area on a 2km grid system (see Appendix 1). Each point was classified as being woodland, long grass, or short grass.

3) A Triangular Irregular Network (TIN) of the study area was created in ArcView 3.2 based on these broad scale habitat types. A TIN is a continuous surface model describing any continuous parameter (usually elevation, but in this case it models broad habitat categories). A TIN describes a surface as a series of adjoining, non-overlapping and not necessarily equal sized triangles. The node of each triangle has a value associated with it. Therefore any value between nodes can be interpolated (by trigonometry) based on the distance and differences between nodes, resulting in a continuous surface model.

4) A polygon defining the short grass plains was created using the habitat TIN (step 3) and the area was calculated.

5) A ratio of the short grass area to the total available area for plains lions was used to estimated the expected number of kills and scavenges on the short grass plains during dry and wet seasons.

6) Since the short grass plains are furthest away from the research base and therefore may be searched less often than the areas that are closer, the observed number of kills and scavenges were corrected for searching bias. There was an average of 412 observations per pride living on the short grass plains as opposed to an average of 536 observations per pride not living on the short grass plains during the study period (1984-2000). Therefore, the number of kills and scavenges
observed on the short grass plains were corrected for searching bias by multiplying by 536/412.

7) The expected number of kills and scavenges for dry and wet seasons (from step 5) were compared to the observed number of kills and scavenges on the short grass plains, as well as with the corrected number (from step 6).

2.6 Kopje Viewsheds Analysis

The viewsheds of kopjes and their selection by lions were analyzed in the following manner.

1) All the kopjes in the study area were visited. Their location was recorded using a Garmin Global Positioning System (GPS) Plus II. The heights of the kopjes were calculated using trigonometry. The angle from the point of observation to the highest accessible peak of the kopje was determined using the inclinometer on a Sylva compass. The distance from the point of observation to the kopje was determined using the GPS (the distance measurement of the GPS is accurate to about +/- 10 meters if the Dilution of Precision reading is kept below 10).

2) A Triangular Irregular Network (TIN) describing the elevation of the study area was created in ArcView 3.2. The TIN was created using the contour theme only (with 20m contour intervals identified as soft breaklines) as the original rivers and lakes themes did not have elevation data associated with them.

3) Kopjes were grouped based on their proximity to each other and their common habitat type (i.e. either woodland or plains).

4) The maximum distances that could be seen from kopjes were determined by climbing up several and visually estimating. Kopjes in the woodland had a much lower maximum visible distance than kopjes on the plains due to trees and shrubs blocking the view. The maximum distance that could be seen from kopjes in the woodland was estimated to be 1.5 km, whereas the maximum distance that could be seen from kopjes on the plains was estimated to be 3.5 km.

5) The maximum visible distance that could theoretically be seen from woodland and plains kopjes was outlined in ArcView 3.2 by creating 1.5 and 3.5 km radius polygons (termed buffers) around woodland and plains kopjes, respectively.
6) The viewsheds from each group of kopjes was calculated using the TIN elevation model (from step 2) and the height of the kopjes (from step 1). The viewsheds analysis determines which areas can and cannot be seen from the top of the kopjes given the contouring of the surrounding area.

7) The viewshed themes for each group of kopjes (from step 6) were clipped using the maximum distance buffer created in step 5. This identifies the areas that could and could not be seen, given the contouring of the surrounding area, within the maximum visible distance.

8) All the viewsheds from the woodland kopjes were then merged and dissolved so that areas within overlapping viewsheds (i.e. areas that could be seen from two or more kopjes) were not counted twice. The resulting output was a theme of the maximum visible distance that could be seen from any woodland kopje (1.5 km) divided into areas labeled "visible" or "not visible". The same procedure was performed for all plains kopjes.

9) The merged and dissolved viewshed themes from step 8 were then clipped again using the polygon describing the total range available to woodland and plains lions. The result was a theme of the maximum visible distance that could be seen from any woodland or plains kopjes, that was available to either the woodland or plains lions, and was divided into "visible" and "not visible" areas.

10) These final viewshed themes for the woodland and plains lions were then pixilated into a grid. The grid cell size was 0.04km² (200m X 200m) which was large enough to gain sufficient detail without losing too much resolution (lions rarely stalk prey that are further than 200m away (Scheel 1993a, Stander 1992)). Each 0.04km² grid cell was identified as being "visible" or "not visible" based on the majority of the "visible" or "not visible" area within that grid cell. The total number of "visible" grid cells was calculated.

11) A ratio of the total number of "visible" and "not visible" 0.04km² grid cells available to woodland lions to the total number of 0.04km² grid cells in their range was calculated. The same was done for plains lions.

12) The expected number of kills and scavenges occurring inside or outside the viewsheds based on season were calculated by multiplying the total number of kills or scavenges by the ratio of "visible" or "not visible" cells available (from step
Therefore, the expected number of observations inside versus outside the viewsheds, for both dry and wet season were calculated for (a) woodland kills, (b) woodland scavenges, (c) plains kills, and (d) plains scavenges.

13) Locations of (a) all woodland lion kills made in the wet season, (b) all woodland lion kills made in the dry season, (c) all woodland lion scavenges made in the wet season, and (d) all woodland lion scavenges made in the dry season were overlaid with the woodland viewsheds theme. The same was done for plains lions.

14) The total number of kills and scavenges made by woodland lions within the viewsheds as opposed to outside the viewsheds for each season were calculated and compared to the expected ratio based on the area and season as determined in step 12. The goodness of fit exact test ($\chi^2$) outlined in Appendix I was used and Bonferroni corrected ($\alpha / 5 = 0.01$) for multiple comparisons between habitats. The same procedure was followed for plains lions.

2.7 Confluence Analysis

The confluences and their selection by lions were analyzed in the following manner.

1) Woodland and plains drainages differ substantially. Plains drainages tend to be much more ephemeral (Gereta and Wolanski 1998), have less erosion and less woody vegetation associated with them, and therefore may not funnel prey as effectively as woodland confluences. With this in mind, woodland confluences were defined as being areas within a 500 meter radius of where two drainages that were each longer than 2km met. Whereas, plains confluences were defined as being areas within 500 meter radius of where two drainages that were each longer than 3km met.

2) A confluence point theme was created in ArcView 3.2 according to the above definitions for all the woodland and plains confluences. The points, which represent the center of the 500 meter radius, were placed about 300 meters upstream of the actual confluence and equidistant between the two drainages (Figure 3). Therefore, the area defined as being “confluence” contained the area between the two drainages (i.e. within the funnel effect of the two drainages), as well
as some of the area beyond the drainages. Although this method may overestimate the area within the funnel, the areas immediately adjacent to the confines of the two drainages were also considered to be important since they provide exit routes for funneled prey.

Figure 3. The center of the 500m confluence buffer was placed 300m upstream of the actual confluence of the rivers. The arrow signifies the direction of flow.

3) The areas within 500m radius of the confluence points (from step 2) were defined as being "within the confluence", and identified by a 500m radius polygon (called a buffer).

4) The confluence theme from step 3 was pixilated into a grid file format with the grid cell size being 0.04km². Each 0.04km² grid cell was identified as being "within the confluence" or "not within the confluence" based on the majority of the area that was classified as "within" or "not within" for each cell. The total area classified as being "within the confluence" was calculated.

2.7.1 Testing for Selection of Confluences Over Total Available Area

5) The total area available to woodland lions was pixilated into 0.04km² grid cells and the area was calculated. The same was done for plains lions. Plains and woodland territories were grouped for the scavenging analysis since sample sizes were small.
6) The ratio of the total area “within confluence” (from step 4) to the total area available (from step 5) was calculated.

7) The expected number of dry and wet season kills and scavenges were calculated based on the ratio of the area “within confluences” (from step 6) and the total number of kills and scavenges in the available area.

8) The expected number of kills and scavenges made within confluences (from step 7) was compared to the observed number based on season using the goodness of fit exact test ($\chi^2$) outlined in Appendix I and corrected for experiment-wise error using the Bonferroni technique ($\alpha / 5 = 0.01$).

2.7.2 Testing for Selection of Confluences Over Rivers

Since confluences are an inherent part of river systems, selection for confluences over and above any other part of the river was tested in the following manner.

9) 500m polygons around all rivers available to woodland lions were created. The same was done for plains lions. Plains and woodland territories were grouped for the scavenging analysis since sample sizes were small.

10) The buffers from step 9 were pixilated into 0.04km$^2$ grid cells. The total amount of area within 500m of a river was calculated.

11) The ratio of the total area “within confluence” (from step 4) to the total area within 500m of a river (from step 10) was calculated.

12) The expected number of dry and wet season kills and scavenges were calculated based on the ratio of the area (from step 11) and the total number of kills or scavenges within 500m of the river.

13) The expected number of kills and scavenges made within confluences (from step 12) was compared to the observed number based on season using the goodness of fit exact test ($\chi^2$) outlined in Appendix I, and Bonferroni corrected for multiple comparisons between habitats ($\alpha / 5 = 0.01$).
2.8 Erosion Embankment Analysis

The selection for erosion embankments for hunting and scavenging was analyzed by comparing the total amount of erosion embankments available to lions to the amount of embankments at locations used by lions (see Appendix 1). The availability of embankments was estimated separately for riparian and non-riparian areas since the amount of erosion differed between the two. The territories of plains and woodland lions were analyzed separately.

2.8.1 Estimating Riparian Erosion Embankments

1) The amount of erosion embankments available to lions in riparian areas (within 200m of a drainage) was estimated along 100m transects running perpendicular to the direction of flow. These transects were placed every 3 km along the drainage on one side of the river (the side was randomly allocated). Embankments were measured at two points along each transect: the first point being at 0m from the river (i.e. on the bank), and the second point at 100m from the bank (Figure 4).

2) The minimum amount of cover required by hunting lions is approximately 40cm high (Elliott et al. 1977). Furthermore, lions seldom stalk prey that are over 200m away (Scheel 1993a). Therefore, all erosion embankments over 50cm deep produced by roads, river banks and natural erosion terraces within a 100m radius from each sampling point were summed (in meters). Care was taken to ensure erosion embankments were not double counted: embankments that were equidistant from the 2 sampling points were attributed to the 0m sampling point rather than the 100m sampling point.

3) Polygons were created surrounding all available rivers at a distance of 50 meters in ArcView 3.2 (these polygons are termed buffers). A second group of buffers were created around all available rivers at 200 meters. These buffers highlight the areas that are adjacent to rivers and are used as a means of identifying riparian areas for further analyses (Figure 4).

4) The first transect points at 0m from the bank of the river (from step 1) were overlaid onto the 50m buffer areas (from step 3). A continuous surface model, called a Triangular Irregular Network (TIN), of the total amount of erosion
embankments within 50m of a river was constructed using the 0m transect points and the 50m buffer area. The TIN surface model provides an estimate of the amount of erosion available over a continuous surface from a series of point measurements, from which the total amount of area eroded can be calculated.

5) Similarly, all of the second transect points 100m from the bank of the river (from step 1) were overlaid onto the 200m buffer areas (from step 3). However, since the total amount of erosion was measured at 200m from the bank of the river on only one side, the point was duplicated and placed equidistant on the opposite side. This resulted in two identical records of total erosion embankments 100m on either side of the river. This was necessary since it increases the accuracy of the TIN surface model under the following assumptions: (a) the amount of erosion decreases equally on both sides of the river with the distance from the river bank, and (b) the amount of erosion decreases equally on both sides of the river with the distance up the drainage. The total amount of erosion embankments from the duplicate points 100m from the bank and the 200m buffer area (from step 3) were used to create a continuous TIN surface model of the total amount of erosion embankments within 200m of the river for all available rivers.

Figure 4. Riparian habitats were measured along 100m transects perpendicular to the direction of flow. Habitats were measured at 2 points along the transects (0m and +100m). The data from the +100m point was duplicated for the opposite side of the river (-100m). TIN surface models using the 0m data points were made for areas with 50m of the river, as well as for areas within 200m of the river using the +100m and -100m data points.
6) The two surface models estimating the total eroded area within 50m of the river (from step 4) and within 200m of the river (from step 5) were overlaid to give the cumulative amount of erosion embankments within 200m of the river (i.e. an estimate of cumulative riparian associated erosion). This method of creating two surface models separately and overlaying them was more accurate than creating one surface model using both the 0m and 100m sampling points combined, since it more closely approximates the real distribution of erosion (pers. obs.). Areas closer to the river generally have more erosion as well as thicker vegetation.

2.8.2 Estimating Non-Riparian Erosion Embankments

7) The total amount of erosion embankments in non-riparian areas was estimated at points on a 2km grid for woodland and plains lions separately.

8) The total amount of erosion embankments at each point was measured using the same technique as outlined in step 2.

9) The total amount of erosion embankments at each point from step 8 was used to create a TIN surface model for all non-riparian areas. The TIN surface model enables the total eroded area to be estimated for all non-riparian areas that were available to lions.

2.8.3 Estimating the Total Amount of Available Cover from Erosion Embankments

10) The total amount of erosion embankments available to lions was estimated by overlaying the non-riparian TIN surface model (from step 9) with the riparian TIN surface model (from step 6).

11) Erosion embankments were classified into 6 distinct categories: 0m, 1-75m, 75-125m, 125-175m, 175-250m, 250+m based on natural breaks in the data.

12) By the use of ArcView 3.2, the total area per category available to plains and woodland lions was calculated separately and corrected. That is, areas with multiple overlays were subtracted.
13) A ratio of the area per category to the total available area was used to calculate the expected number of kills and scavenges per category for the woodland and plains lions based on season.

2.8.4 Selection for Erosion Embankments

14) The total amount of erosion embankments for all locations that radio collared lions had been seen with a carcass was measured using the same method as previously described for riparian and non-riparian areas (step 2).

15) The data were divided into carcasses that were killed, scavenged, or acquired through unknown circumstances.

16) The number of kills and scavenges, divided by season, made in areas with 0m, 1-75m, 75-125m, 125-175m, 175-250m, 250+m of embankments were compared to the expected number (from step 13) using the goodness of fit exact test ($\chi^2$) outlined in Appendix I. A Bonferroni correction was used to correct for errors incurred from multiple comparisons between habitats ($\alpha / 5 = 0.01$).

17) Since erosion is correlated with riparian areas, the selection for erosion embankments in riparian areas was analyzed separately from the erosion in non-riparian areas. The two were also analyzed together. The intention was to distinguish selection for erosion embankments from selection for riparian areas alone. For the non-riparian analysis, the last 2 categories (175-250m and 250+m) were combined due to insufficient data.

2.8.5 Assessing the TIN Surface Models of Erosion

The accuracy of the TIN surface models in describing erosion was assessed by comparing the estimates of erosion from the maps with ground truthing estimates. Field measurements of erosion at all the locations that lions had been seen with a carcass comprised the ground truthing data set. Although these ground truthing points may not be random (i.e. there may be some form of selection involved), they provide at least some indication of erosion which the estimates from the maps can be compared to. The $\chi^2$ results suggest that the map estimates were
not independent of the field measurements for both the plains ($\chi^2 = 238.14$, $p < 0.001$) and the woodlands ($\chi^2 = 248.38$, $p < 0.001$). Tables 5 and 6 indicate that the TIN surface models generally over-estimated the amount of erosion available, which in effect would decrease the selection coefficients (i.e. the ratio of use : availability). Therefore, since the TIN maps overestimate the amount of available cover, the results of the selection analyses are conservative estimates of selection by lions.

Table 5. A cross-tabulation comparison of the TIN surface model estimates of soil erosion with field measurements for the area available to plains lions.

<table>
<thead>
<tr>
<th>TIN Estimate of Erosion</th>
<th>0-1m</th>
<th>1-75m</th>
<th>75-125m</th>
<th>125-175m</th>
<th>175-250m</th>
<th>250+ m</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-1m</td>
<td>257</td>
<td>125</td>
<td>17</td>
<td>9</td>
<td>2</td>
<td>410</td>
<td></td>
</tr>
<tr>
<td>1-75m</td>
<td>30</td>
<td>36</td>
<td>6</td>
<td>4</td>
<td>4</td>
<td>1</td>
<td>81</td>
</tr>
<tr>
<td>75-125m</td>
<td>15</td>
<td>10</td>
<td>3</td>
<td>6</td>
<td>3</td>
<td>2</td>
<td>39</td>
</tr>
<tr>
<td>125-175m</td>
<td>9</td>
<td>13</td>
<td>3</td>
<td>1</td>
<td>6</td>
<td></td>
<td>32</td>
</tr>
<tr>
<td>175-250m</td>
<td>16</td>
<td>16</td>
<td>5</td>
<td>7</td>
<td>14</td>
<td>2</td>
<td>60</td>
</tr>
<tr>
<td>250+m</td>
<td>8</td>
<td>10</td>
<td>10</td>
<td>5</td>
<td>15</td>
<td>8</td>
<td>56</td>
</tr>
<tr>
<td>Total</td>
<td>335</td>
<td>210</td>
<td>44</td>
<td>32</td>
<td>44</td>
<td>13</td>
<td>678</td>
</tr>
</tbody>
</table>
Table 6. A cross-tabulation comparison of the TIN surface model estimates of erosion with field measurements for the area available to woodlands lions.

<table>
<thead>
<tr>
<th>TIN Estimate of Erosion</th>
<th>0-1m</th>
<th>1-75m</th>
<th>75-125m</th>
<th>125-175m</th>
<th>175-250m</th>
<th>250+ m</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-1m</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>345</td>
</tr>
<tr>
<td>1-75m</td>
<td>21</td>
<td>14</td>
<td>11</td>
<td>5</td>
<td>5</td>
<td></td>
<td>56</td>
</tr>
<tr>
<td>Field Measures of Erosion</td>
<td>75-125m</td>
<td>8</td>
<td>7</td>
<td>11</td>
<td>6</td>
<td>10</td>
<td>42</td>
</tr>
<tr>
<td></td>
<td>125-175m</td>
<td>6</td>
<td>7</td>
<td>8</td>
<td>3</td>
<td>13</td>
<td>37</td>
</tr>
<tr>
<td></td>
<td>175-250m</td>
<td>14</td>
<td>10</td>
<td>11</td>
<td>6</td>
<td>36</td>
<td>78</td>
</tr>
<tr>
<td></td>
<td>250+m</td>
<td>1</td>
<td>1</td>
<td>7</td>
<td>1</td>
<td>8</td>
<td>18</td>
</tr>
<tr>
<td>Total</td>
<td>279</td>
<td>121</td>
<td>68</td>
<td>27</td>
<td>79</td>
<td>2</td>
<td>576</td>
</tr>
</tbody>
</table>

2.9 Woody Vegetation Analysis

The selection for woody vegetated cover by lions for hunting and scavenging was analyzed by comparing the percent cover of woody vegetation at locations used by lions to what was available (see Appendix 1). The territories of plains and woodland lions were also analyzed separately. The sampling design for estimating the amount of cover due to vegetation was identical to the method used for estimating cover from erosion embankments, with the following exceptions.

1) The locations of the sampling points were identical to those used to estimate erosion. The amount of woody vegetation available to lions was measured separately in riparian areas (within 200m of a river) as opposed to non-riparian areas, since the quantity of vegetation differs between the two (Ben-Shahar 1991). In brief summary, the vegetation in riparian areas was estimated at 2 points along 100m transects running perpendicular to the direction of flow, and placed every 3km as previously described (see section 2.8.1 Estimating Riparian Erosion Embankments). Similarly, the amount of woody vegetation in non-riparian areas was estimated at points on a 2km grid system as previously described (see section 2.8.2 Estimating Non-Riparian Erosion Embankments).
2) The amount of woody vegetation that was over 50cm high was estimated at each sampling point (Elliott et al. 1977). Since lions generally initiate a charge from under 10 to 20 meters (Elliott et al. 1977, van Orsdol 1984, Stander 1992), four measurements of the percent cover of woody vegetation within a 15m radius of each point were averaged. The four measurements were 90° from each other, starting with the thickest piece of vegetation.

3) The average percent cover of woody vegetation was classified into 5 distinct categories based on rounded natural breaks in the data: 0-<5%, 5-10%, 10>-20%, 20>-35%, and 35>-100% cover.

4) The total amount of vegetated cover available to lions in riparian and non-riparian areas was compared to vegetated cover at locations where lions had been seen with a carcass using the goodness of fit exact test ($\chi^2$) outlined in Appendix I, in the exact manner as previously described for erosion embankments. Likewise, a Bonferroni correction was used to correct for experiment-wise error ($\alpha / 5 = 0.01$).

2.9.1 Assessing the TIN Surface Models of Woody Vegetation

The accuracy of the TIN surface models in describing woody vegetation was assessed in the same manner as previously outlined for erosion (see section 2.8.5 Assessing the TIN Surface Models for Erosion). The $\chi^2$ results suggest that the map estimates of vegetation were not independent of the field measurements for both the plains ($\chi^2 = 226.62, p < 0.001$) and the woodlands ($\chi^2 = 182.57, p < 0.001$). Tables 7 and 8 show that the TIN surface models over-estimate the amount of erosion available, which effectively would decrease the selection coefficients (the ratio of use : availability). Therefore, since the TIN maps overestimate the amount of available cover, the results of the selection analyses are conservative estimates of selection by lions.
Table 7. A cross-tabulation comparison of the TIN surface model estimates of woody vegetation with field measurements for the area available to plains lions.

<table>
<thead>
<tr>
<th>TIN Estimate of Woody Vegetation</th>
<th>0-&lt;5%</th>
<th>5-10%</th>
<th>10&gt;-20%</th>
<th>20&gt;-35%</th>
<th>35&gt;-100%</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-&lt;5%</td>
<td>444</td>
<td>36</td>
<td>38</td>
<td>9</td>
<td>5</td>
<td>532</td>
</tr>
<tr>
<td>5-10%</td>
<td>26</td>
<td>1</td>
<td>5</td>
<td>7</td>
<td>2</td>
<td>41</td>
</tr>
<tr>
<td>10&gt;-20%</td>
<td>14</td>
<td>1</td>
<td>7</td>
<td>2</td>
<td>1</td>
<td>25</td>
</tr>
<tr>
<td>20&gt;-35%</td>
<td>15</td>
<td>6</td>
<td>16</td>
<td>14</td>
<td>5</td>
<td>56</td>
</tr>
<tr>
<td>35&gt;-100%</td>
<td>6</td>
<td>1</td>
<td>5</td>
<td>3</td>
<td>8</td>
<td>23</td>
</tr>
<tr>
<td>Total</td>
<td>505</td>
<td>45</td>
<td>71</td>
<td>35</td>
<td>21</td>
<td>677</td>
</tr>
</tbody>
</table>

Table 8. A cross-tabulation comparison of the TIN surface model estimates of woody vegetation with field measurements for the area available to woodland lions.

<table>
<thead>
<tr>
<th>TIN Estimate of Woody Vegetation</th>
<th>0-&lt;5%</th>
<th>5-10%</th>
<th>10&gt;-20%</th>
<th>20&gt;-35%</th>
<th>35&gt;-100%</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-&lt;5%</td>
<td>47</td>
<td>17</td>
<td>16</td>
<td>9</td>
<td>3</td>
<td>92</td>
</tr>
<tr>
<td>5-10%</td>
<td>8</td>
<td>6</td>
<td>19</td>
<td>14</td>
<td>3</td>
<td>50</td>
</tr>
<tr>
<td>10&gt;-20%</td>
<td>10</td>
<td>5</td>
<td>19</td>
<td>41</td>
<td>8</td>
<td>83</td>
</tr>
<tr>
<td>20&gt;-35%</td>
<td>14</td>
<td>20</td>
<td>64</td>
<td>100</td>
<td>49</td>
<td>247</td>
</tr>
<tr>
<td>35&gt;-100%</td>
<td>3</td>
<td>4</td>
<td>18</td>
<td>58</td>
<td>20</td>
<td>103</td>
</tr>
<tr>
<td>Total</td>
<td>82</td>
<td>52</td>
<td>136</td>
<td>222</td>
<td>83</td>
<td>575</td>
</tr>
</tbody>
</table>

2.10 Water Analysis

To determine whether lions select areas near water for hunting and scavenging, the observed number of kills or scavenges adjacent to water was
compared to the expected frequency. The expected frequency was calculated from the ratio of the area adjacent to water to the total area available to lions. Since access to water varies considerably with season due to the ephemeral nature of the drainages (Gereta and Wolanski 1998, Wolanski and Gereta 2001), the data for dry and wet seasons were calculated and analyzed separately. The analysis was conducted independently for plains and woodland lions. The area near water was estimated as follows:

1) The seasonal distribution of water was established by simultaneously recording (a) the cumulative monthly rainfall between September 1999 and August 2000 at 15 locations and (b) recording the location of the first pools in each drainage. Rivers that had no water during certain months were noted.

2) Records from step 1 were divided into dry season and wet season. Wet season records were defined as having either (a) 50mm or more of cumulative monthly rainfall (Norton-Griffiths et al. 1975) or (b) 75mm or more of cumulative rainfall for 2 months (thereby accounting for the delay between a pool filling and emptying (Gereta and Wolanski 1998, Wolanski and Gereta 2001)). Records with less than this amount of cumulative monthly rainfall were classified as being dry season.

3) The locations of dry season pools were plotted in ArcView 3.2.

4) The river systems from these dry season pools and downstream were identified as areas where water was available during the dry season. This assumes that pools continue to occur downstream until the river eventually starts flowing.

5) The locations of the wet season pools were much more erratic, and therefore could not be predicted as accurately as the dry season pools. They did, however, consistently occur upstream from dry season pools and typically became smaller and more ephemeral closer to the headwaters. As a result, all drainages were assumed to have water during the wet season.

6) Polygons were created surrounding all the drainages classified as having water during the dry season (from step 4) using ArcView 3.2. The buffer polygons surrounded the rivers at 200m from the bank, and were defined as being "near to water". These polygons were used to calculate the amount of area that was close to water relative to the total area, and from which the expected number of kills and
scavenges were calculated. The same was done for drainages with water during the wet season (from step 5).

7) The procedure from step 6 was repeated using a 50m buffer area (as opposed to 200m) around rivers with water during the dry season and rivers with water during wet season. These polygons were defined as being "adjacent to water". By calculating the expected number of kills or scavenges using the relative amount of area within these 50m buffer polygons, the importance of water could be refined further.

8) The number of kills and scavenges near water (i.e. within 200m) were counted for the dry season and the wet season.

9) Of these kills, the number that were adjacent to water (i.e. within 50m) were recorded for the dry season and the wet season.

10) Using ArcView 3.2, a ratio of the area within 200m of water to the total area available was used to calculate the expected number of kills and scavenges near water for both the dry and the wet season.

11) Likewise, the ratio of the area within 50m of water to the total area available was used to calculate the expected number of kills and scavenges adjacent to water for both seasons.

12) The observed number of kills and scavenges within 200m of water (from step 8) was compared to the expected number of kills and scavenges (from step 10) for both the dry and the wet season, and for plains and woodland lions separately. The goodness of fit exact test ($\chi^2$) outlined in Appendix 1 was used to test for significant differences between the observed and expected values, since the small expected values would have biased the conventional $\chi^2$ test. The test was corrected for multiple comparison between habitats using the Bonferroni technique ($\alpha / 5 = 0.01$).

13) In a similar fashion, the number of kills and scavenges observed within 50m of water (as determined from step 9) was compared to the expected number (from step 11) for both the wet and the dry season, and for plains and woodland lions.
2.11 Loglinear Analysis and Resource Selection Functions (Logistic Regression)

The relationships between the habitat variables were investigated using loglinear regression. The approach is outlined by Tabachnick and Fidell (1996) as well as by Everitt (1977). Predicting resource use through resource selection functions (RSFs) were determined by logistic regressions (Manly et al. 1995, Boyce and McDonald 1999).

1) The objective of the loglinear analysis was to identify naturally occurring relationships between the habitat variables, therefore only the availability measures were used (i.e. not the kill or scavenge data set). A total availability data set was compiled by randomly selecting one of the three samples taken at each riparian transect (+100m, 0m or -100m from the bank of the river), thereby avoiding over sampling of riparian areas, and adding it to the non-riparian data set. Plains and woodland areas were analyzed separately.

2) A loglinear regression requires at least 5 times as many cases as there are cells in the design. By dividing the data by season as well as into areas available to plains as opposed to woodland lions, it became apparent that there were too few cases. Therefore, the data used for the loglinear regression were reduced in the following manner. Of the five habitat variables measured for this study (viewsheds, confluences, erosion embankments, vegetation and access to water) the variables most likely to co-vary were the ones dependent on water (i.e. confluences, erosion embankments, and vegetation). Therefore, viewsheds were not included in the loglinear regression, thereby reducing the number of possible cells. Furthermore, of the remaining habitats, the data were reduced to binomial variables according to the following key, which further decreased the number of possible cells.

Confluence

\[
\text{out of confluence} = 0 \\
\text{in confluence} = 1
\]

Erosion embankments

\[
\text{no erosion (0m)} = 0 \\
\text{some erosion (>0m)} = 1
\]
Vegetation
little to no vegetation (<5%) = 0
some vegetation (≥5%) = 1

Water
no water within 200m = 0
water within 200m = 1

Since the data were reduced to 4 binomial habitat variables, there were a total of 16 \(2^4\) possible cells and a minimum of 80 (16 x 5) cases required per data set.

3) SPSS 11.0 was used to conduct a loglinear analysis on each of the total availability data sets (from step 2) using a hierarchical backwards elimination process. Combinations of variables did not co-vary if they failed to cause a significant change in the model \((p > 0.05)\) after they had been systematically deleted.

4) Based on the relationships between habitat variables as determined by the loglinear analysis (from step 3) the kill, scavenging, and availability data were all re-coded to account for the correlations between habitat variables (see Appendix 2 for the re-coding key).

5) New data sets were compiled in preparation for the logistic regression by combining the re-coded availability data with the re-coded kill or scavenging data (from step 4), and including the viewsheds from the kopjes. The eight new logistic regression data sets included use and availability data for (a) plains wet season kills, (b) plains dry season kills, (c) woodland wet season kills, (d) woodland dry season kills, (e) plains wet season scavenges, (f) plains dry season scavenges, (g) woodland wet season scavenges, and (h) woodland dry season scavenges.

6) Binary logistic regressions predicting kill versus non-kill, or scavenge versus non-scavenge, were calculated in SPSS 11.0 for plains and woodland lions, for both the wet and dry seasons, using the new re-coded data sets from step 5. The logistic regressions were calculated using the stepwise backward elimination based on the Wald statistic. The Wald statistic tests the hypothesis that the coefficient \((\beta)\) generated by the logistic regression is equal to 0. Variables were considered to be
significantly different from zero if the probability was less than 0.2, as opposed to the usual 0.05. A less stringent criterion for the inclusion of a variable decreases the chances of a predictor, which may be highly correlated with the outcome, getting bumped by another predictor or group of predictors (Tabachnick and Fidell 1996). The classification cut-off (i.e. the probability above which the outcome is considered a success) was set at 0.1. The adequacy of the logistic regression equation at correctly predicting kills and scavenges was tested using the Hosmer-Lemeshow test.

7) The logistic regression equations for plains and woodland lions during wet season and dry season were used to calculate the probability of a kill or scavenge at each of the available points in the riparian and non-riparian data sets. The riparian data sets were divided into points measured at 0m (i.e. on the river bank) and points measured 100m from the river bank, in preparation for creating the continuous surface models.

8) Continuous surface models called Triangular Irregular Networks (TINs) predicting the probability of kills or scavenges in the total available areas were created using ArcView 3.2 with the Spatial Analyst and 3D Analyst extensions. The TIN surface models provide an estimate of the probability of a kill or scavenge over a continuous surface from a series of point measurements (i.e. step 7). Three groups of TINs were created independently: (a) non-riparian, (b) within 200m of a river, (c) and within 50m of a river. The 200m and the 50m TINs were created using the 100m riparian points and 0m riparian points (from step 7) together with 200m and 50m polygons surrounding rivers, respectively.

9) The three groups of TINs from step 8 were overlaid resulting in a complete coverage predicting kills and scavenges for the entire available area. This method of creating 3 separate surface models and overlaying them was more accurate than combining the non-riparian, 100m riparian, and 0m riparian data sets and creating a single surface model.
3 RESULTS

In the interest of clarity, the results are in the following logical progression. I first address the issue of spatial randomness (i.e. the null hypothesis). I then present the results from broad scale selection for prey distribution, which sets the stage for the intensive univariate tests of the alternative hypotheses for each of the 5 habitat types (the $\chi^2$ goodness of fit exact tests). From this point, I further investigate the interaction of the habitats with each other using the loglinear approach. Finally, using the combined interaction of habitats, I conclude with the results of the predictive multivariate analyses of resource selection using logistic regressions.

3.1 Nearest Neighbour Test and Spatial Randomness

The distribution of kills by plains and woodland lions appears clumped (Figure 5a and b). Woodland and plains kills were typically clustered to the north and west of the available areas, especially during the dry season. The distribution of scavenges by plains and woodland lions were less clustered than the kills (Figure 5c and d). The scavenges by plains lions were more dispersed than the kills, especially towards the southeast.

The results of the nearest neighbour tests (Table 9) suggest that the distribution of kills were significantly clumped regardless of season, with the exception of the woodland lions during the wet season. Although there was evidence that woodland lion kills during the wet season were not random (Index of Aggregation = 0.82), the distribution was not significantly clustered ($Z > -1.96, \alpha = 0.05, n = 20$).

The distribution of scavenges by plains lions were significantly clumped (Table 9). However, the scavenges by woodland lions were not significantly different from a random distribution. There were few scavenges observed by woodland lions (dry season $n = 10$ and wet season $n = 4$).

Overall, the distributions of dry season kills and scavenges were consistently more clustered than the wet season distributions (Table 9).
Table 9. The observed and expected mean nearest neighbour distances (according to the Clark-Evans method) and associated Z-test. Distributions were clumped when the Index of Aggregation was less than 1 and were significant (*) when $Z < -1.96$ ($\alpha = 0.05$).

<table>
<thead>
<tr>
<th></th>
<th>Observed</th>
<th>Expected</th>
<th>Index of</th>
<th>Z-test</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>Mean</td>
<td>Aggregation</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Nearest</td>
<td>Nearest</td>
<td>($R_a/R_e$)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Neighbour</td>
<td>Neighbour</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(RA/RE)</td>
<td>(RA) (km)</td>
<td>(RE) (km)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plains Kills</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dry Season</td>
<td>64</td>
<td>1.512</td>
<td>2.814</td>
<td>0.54</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plains Kills</td>
<td>56</td>
<td>1.874</td>
<td>3.009</td>
<td>0.62</td>
</tr>
<tr>
<td>Wet Season</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Woodland Kills</td>
<td>63</td>
<td>0.877</td>
<td>1.420</td>
<td>0.62</td>
</tr>
<tr>
<td>Dry Season</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Woodland Kills</td>
<td>20</td>
<td>2.074</td>
<td>2.520</td>
<td>0.82</td>
</tr>
<tr>
<td>Wet Season</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plains Scavenges</td>
<td>26</td>
<td>2.354</td>
<td>4.416</td>
<td>0.53</td>
</tr>
<tr>
<td>Dry Season</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plains Scavenges</td>
<td>26</td>
<td>3.105</td>
<td>4.416</td>
<td>0.70</td>
</tr>
<tr>
<td>Wet Season</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Woodland Scavenges</td>
<td>10</td>
<td>3.275</td>
<td>3.564</td>
<td>0.92</td>
</tr>
<tr>
<td>Dry Season</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Woodland Scavenges</td>
<td>4</td>
<td>5.985</td>
<td>5.635</td>
<td>1.06</td>
</tr>
<tr>
<td>Wet Season</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

3.2 Selection for Prey Distribution: The Effect of the Short Grass Plains

The distribution of dry and wet season lion kills and scavenges does not appear to be similar. During the wet season, both woodland and plains lion kills and scavenges tended to disperse more to the south and east of the available areas (Figure 5). Scavenges were more dispersed to the southeast during the wet season than kills were. There were relatively fewer kills on the short grass plains (Figure 5a) than scavenges (Figure 5c), however both were uncommon.
There were fewer than expected kills ($\chi^2_{\text{obs}} = 37.91, p << 0.001$) and scavenges ($\chi^2_{\text{obs}} = 7.15, p = 0.007$) on the short grass plains during the dry season (Table 10). When the number of observations were corrected for searching bias, there were still fewer kills and scavenges than expected during the dry season ($\chi^2_{\text{Corrected}} = 37.91, p << 0.001$ and $\chi^2_{\text{Corrected}} = 5.33, p = 0.02$, respectively). Similarly, during the wet season there were also fewer kills on the short grass plains than expected regardless of the correction ($\chi^2_{\text{obs}} = 21.36, p < 0.001$ and $\chi^2_{\text{Corrected}} = 18.29, p < 0.001$). Of the 4 kills observed on the short grass plains during the wet season, 2 were juvenile animals. There were no differences between the observed and the expected number of scavenges on the short grass plains during the wet season regardless of correcting for searching bias ($\chi^2_{\text{obs}} = 0.05, p > 0.8$ and $\chi^2_{\text{Corrected}} = 0.74, p > 0.3$).

Table 10. The observed, the corrected (for searching bias), and the expected number of kills and scavenges by plains lions on and off the short grass plains (SGP) based on season.

<table>
<thead>
<tr>
<th></th>
<th>Dry Season</th>
<th>Wet Season</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>On SGP</td>
<td>Off SGP</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed Kills</td>
<td>0</td>
<td>65</td>
</tr>
<tr>
<td>Obs. Corrected</td>
<td>0</td>
<td>65</td>
</tr>
<tr>
<td>Expected</td>
<td>23.9</td>
<td>41.1</td>
</tr>
<tr>
<td>Observed Scavengers</td>
<td>3</td>
<td>23</td>
</tr>
<tr>
<td>Obs. Corrected</td>
<td>3.9</td>
<td>22.1</td>
</tr>
<tr>
<td>Expected</td>
<td>9.6</td>
<td>16.4</td>
</tr>
</tbody>
</table>
Figure 5. The short grass plains in relation to the distribution of (a) wet and dry season kills by plains lions, (b) wet and dry season kills by woodland lions, (c) wet and dry season scavenges by plains lions and (d) wet and dry season scavenges by woodland lions.
3.3 Viewsheds Analysis

3.3.1 Plains Kills

The distribution of kills by the plains prides in relation to the viewsheds from kopjes (Figure 6a) suggests a strong overlap, especially in the north and west parts of the study area. Although, there were relatively few kills made in the viewsheds on the short grass plains.

There were more kills made by plains lions in the viewsheds of kopjes than expected for both seasons, however the differences were not significant (dry season $\chi^2 = 1.39, p > 0.2$ and wet season $\chi^2 = 4.41, p = 0.04$) (Table 11). Conversely, there were consistently fewer kills out of the viewsheds.

Table 11. The observed and expected number of kills by plains lions inside and outside the viewsheds of kopjes based on season.

<table>
<thead>
<tr>
<th>Season</th>
<th>Dry</th>
<th>Wet</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>In Viewsheds</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed</td>
<td>29</td>
<td>29</td>
<td>58</td>
</tr>
<tr>
<td>Expected</td>
<td>24.4</td>
<td>21.4</td>
<td>45.8</td>
</tr>
<tr>
<td>Out of Viewsheds</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed</td>
<td>35</td>
<td>27</td>
<td>62</td>
</tr>
<tr>
<td>Expected</td>
<td>39.6</td>
<td>34.6</td>
<td>74.2</td>
</tr>
<tr>
<td>Total</td>
<td>64</td>
<td>56</td>
<td>120</td>
</tr>
</tbody>
</table>

3.3.2 Woodland Kills

Kills by woodland lions were strongly clustered outside the viewsheds, especially during the dry season, and occurred primarily towards the north and west of their available area (Figure 6b). This clustering seemed to be less well defined in the wet season when the lion kills were more dispersed.

There was a significant difference between the observed and the expected number of kills made by woodland lions in and out of the viewsheds only during the
dry season (dry season $\chi^2 = 6.77$, p < 0.01 and wet season $\chi^2 = 0.4$, p > 0.5) (Table 12). However, the total number of kills indicates an opposite trend to that of the plains lions: overall, there were fewer kills made by woodland lions in the viewsheds of kopjes than was expected (Table 12).

Table 12. The observed and expected number of kills by woodland lions inside and outside the viewsheds of kopjes based on season.

<table>
<thead>
<tr>
<th>Season</th>
<th>Dry</th>
<th>Wet</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>In Viewsheds</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed</td>
<td>14</td>
<td>9</td>
<td>23</td>
</tr>
<tr>
<td>Expected</td>
<td>24.0</td>
<td>7.7</td>
<td>31.7</td>
</tr>
<tr>
<td>Out of Viewsheds</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed</td>
<td>49</td>
<td>11</td>
<td>60</td>
</tr>
<tr>
<td>Expected</td>
<td>39.0</td>
<td>12.3</td>
<td>51.3</td>
</tr>
<tr>
<td>Total</td>
<td>63</td>
<td>20</td>
<td>83</td>
</tr>
</tbody>
</table>

3.3.3 Plains Scavenges

The distribution of scavenges by the plains lions appears clustered (Figure 6c), although there were more scavenges in the viewsheds on the short grass plains than there were kills in this area (compared to Figure 6a), especially during the wet season.

There were more scavenges made by plains prides in the viewsheds of kopjes than expected for both the dry and the wet seasons, however only the wet season was significant (dry season $\chi^2 = 2.71$, p = 0.1 and wet season $\chi^2 = 6.03$, p = 0.01) (Table 13). Conversely, there were consistently fewer scavenges out of the viewsheds for both seasons.
Table 13. The observed and expected number of scavenges by plains lions inside and outside the viewsheds of kopjes based on season.

<table>
<thead>
<tr>
<th>Season</th>
<th>Dry</th>
<th>Wet</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>In Viewsheds</td>
<td>Observed</td>
<td>14</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>Expected</td>
<td>9.9</td>
<td>9.9</td>
</tr>
<tr>
<td>Out of Viewsheds</td>
<td>Observed</td>
<td>12</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>Expected</td>
<td>16.1</td>
<td>16.1</td>
</tr>
<tr>
<td>Total</td>
<td>Observed</td>
<td>26</td>
<td>26</td>
</tr>
</tbody>
</table>

3.3.4 Woodland Scavenges

Scavenges appear to be distributed primarily in and around the viewsheds to the north and west of the area available to woodland lions (Figure 6d). This distribution was maintained during the dry season. However, woodland scavenges were slightly more spread out to the southeast during the wet season. Some of the viewsheds, especially in the north-central part of the area, were seldom used.

There were no significant differences between the observed and the expected number of scavenges by woodland lions inside or outside the viewsheds based on season (dry season $\chi^2 = 0.01$, $p > 0.9$ and wet season $\chi^2 = 0.24$, $p > 0.6$) (Table 14). The total number of observations for woodland scavenges was relatively small ($n = 14$) in comparison to the other data sets.
Table 14. The observed and expected number of scavenges by woodland lions inside and outside the viewsheds of kopjes based on season.

<table>
<thead>
<tr>
<th>Season</th>
<th>Dry</th>
<th>Wet</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>In Viewsheds</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed</td>
<td>4</td>
<td>2</td>
<td>6</td>
</tr>
<tr>
<td>Expected</td>
<td>3.8</td>
<td>1.5</td>
<td>5.3</td>
</tr>
<tr>
<td>Out of Viewsheds</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed</td>
<td>6</td>
<td>2</td>
<td>8</td>
</tr>
<tr>
<td>Expected</td>
<td>6.2</td>
<td>2.5</td>
<td>8.7</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed</td>
<td>10</td>
<td>4</td>
<td>14</td>
</tr>
</tbody>
</table>
Figure 6. The viewsheds from kopjes in relation to the distribution of (a) wet and dry season kills by plains lions, (b) wet and dry season kills by woodland lions, (c) wet and dry season scavenges by plains lions and (d) wet and dry season scavenges by woodland lions.
3.4 Confluence Analysis

3.4.1 Plains Kills

Kills by plains lions were clustered to the north and west of the available areas, which also coincides with the distribution of the majority of confluences (Figure 7a). Confluences to the northeast and southwest of the areas available to plains prides tended to be relatively unused.

There were significantly more kills in confluences than expected from a random distribution in the total area available to plains lions (dry season $\chi^2 = 13.82$, $p = 0.004$ and wet season $\chi^2 = 10.78$, $p = 0.009$) (Table 15).

Although plains lions killed more often in confluences than along any other part of the river (Table 15), the differences were not significant (dry season $\chi^2 = 1.2$, $p = 0.29$ and wet season $\chi^2 = 3.31$, $p = 0.08$).

Table 15. The observed number of kills by plains lions in confluences compared to the number of kills expected based on (i) the density of kills in the total available area, and (ii) the density of kills within 500m of rivers.

<table>
<thead>
<tr>
<th></th>
<th>Dry</th>
<th>Wet</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>In Confluence</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed</td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>Expected (in area)</td>
<td>1.5</td>
<td>1.3</td>
</tr>
<tr>
<td>Expected (along rivers)</td>
<td>3.9</td>
<td>2.3</td>
</tr>
<tr>
<td><strong>Out of Confluence</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed</td>
<td>58</td>
<td>51</td>
</tr>
<tr>
<td>Expected (in area)</td>
<td>62.5</td>
<td>54.7</td>
</tr>
<tr>
<td>Expected (along rivers)</td>
<td>60.1</td>
<td>53.7</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>64</td>
<td>56</td>
</tr>
</tbody>
</table>
3.4.2 Woodland Kills

The distribution of kills by woodland lions in relation to confluences (Figure 7b) was clustered to the northwest. There were few kills in the confluences to the south and east of the area available to woodland lions.

There was a significant difference between the observed number of kills by woodland lions in confluences and a random distribution in the total area available to woodland prides only during the dry season (dry season $\chi^2 = 21.96$, $p << 0.001$ and wet season $\chi^2 = 0.06$, $p > 0.9$) (Table 16).

Similarly, there were more kills by woodland lions in confluences than along any other part of the river only during the dry season (dry season $\chi^2 =13.95$, $p < 0.001$ and wet season $\chi^2 = 0.01$, $p < 0.9$) (Table 16).

| Table 16. The observed number of kills by woodland lions in confluences compared to the number of kills expected based on (i) the density of kills in the available area, and (ii) the density of kills within 500m of rivers. |
|---|---|---|---|
| Season | Dry | Wet |
| In Confluence | Observed | 16 | 2 |
| Expected (in area) | 5.5 | 1.7 |
| Expected (along rivers) | 6.8 | 2.1 |
| Out of Confluence | Observed | 47 | 18 |
| Expected (in area) | 57.5 | 18.3 |
| Expected (along rivers) | 56.2 | 17.9 |
| Total | 63 | 20 |

3.4.3 Plains and Woodland Scavenges Combined

The distribution of scavenges by woodland and plains lions did not coincide with the distribution of confluences (Figures 7c and 7d). The majority of the wet
season scavenges were in the south and east part of the available area where there were fewer confluences. The dry season scavenges were in the central and northwest part of the available area where confluences were more common, however they did not coincide.

There were insufficient data to discern any significant difference between the observed number of scavenges in confluences and the expected number of scavenges in the total available area ($\chi^2 = 2.31$, $p = 0.14$ and wet season $\chi^2 = 0.76$, $p = 0.63$) (Table 17). When the observed number of scavenges was compared to the density of scavenges within 500m of rivers, there was still no significant difference (dry season $\chi^2 = 1.56$, $p = 0.4$ and wet season $\chi^2 = 3.33$, $p = 0.12$). However, trends in the data suggest that there were more scavenges in confluences than expected (Table 17).

Table 17. The observed number of scavenges by woodland and plains lions in confluences compared to the number of scavenges expected based on (i) the density of scavenges in the available area, and (ii) the density of scavenges within 500m of rivers.

<table>
<thead>
<tr>
<th></th>
<th>Dry</th>
<th>Wet</th>
</tr>
</thead>
<tbody>
<tr>
<td>In Confluence</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Expected (in area)</td>
<td>1.3</td>
<td>1.1</td>
</tr>
<tr>
<td>Expected (along rivers)</td>
<td>1.5</td>
<td>0.6</td>
</tr>
<tr>
<td>Out of Confluence</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed</td>
<td>33</td>
<td>28</td>
</tr>
<tr>
<td>Expected (in area)</td>
<td>34.7</td>
<td>28.9</td>
</tr>
<tr>
<td>Expected (along rivers)</td>
<td>34.5</td>
<td>29.4</td>
</tr>
<tr>
<td>Total</td>
<td>36</td>
<td>30</td>
</tr>
</tbody>
</table>
Figure 7. Drainage confluences in relation to the distribution of (a) wet and dry season kills by plains lions, (b) wet and dry season kills by woodland lions, (c) wet and dry season scavenges by plains lions and (d) wet and dry season scavenges by woodland lions.
**Erosion Embankment Analysis**

3.4.4 Plains Kills

The distribution of kills by plains lions in relation to erosion embankments (Figure 8a) suggests there was relatively little selection for embankments which were not near rivers. Areas in the south and east of the study area remained relatively unused, regardless of the presence of embankments.

The number of kills by plains lions in areas with erosion embankments (Table 18) was significantly different from expected during both the dry and wet season ($\chi^2 = 300.5, p \ll 0.001$ and $\chi^2 = 1023.3, p \ll 0.001$, respectively). Generally there were fewer kills than expected in areas with under 125m of cumulative erosion embankments and more kills in areas with over 125m.

<table>
<thead>
<tr>
<th>Erosion Embank. (m)</th>
<th>Dry Season</th>
<th>Wet Season</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observed</td>
<td>Expected</td>
</tr>
<tr>
<td>0</td>
<td>37</td>
<td>40.0</td>
</tr>
<tr>
<td>1-75</td>
<td>6</td>
<td>18.9</td>
</tr>
<tr>
<td>75-125</td>
<td>3</td>
<td>2.7</td>
</tr>
<tr>
<td>125-175</td>
<td>7</td>
<td>1.4</td>
</tr>
<tr>
<td>175-250</td>
<td>6</td>
<td>0.9</td>
</tr>
<tr>
<td>250+</td>
<td>5</td>
<td>0.1</td>
</tr>
<tr>
<td>Total</td>
<td>64</td>
<td>64</td>
</tr>
</tbody>
</table>

There were significant differences between the observed and expected number of kills in eroded areas within 200m of a drainage during both the dry and the wet season ($\chi^2 = 298.4, p \ll 0.001$ and $\chi^2 = 177.9, p \ll 0.001$, respectively) (Table 19). There were more kills than expected in areas with over 125m of erosion.
Table 19. The observed and expected numbers of kills by plains lions in relation to the total amount of erosion embankments (m) in riparian areas only (within 200m of a drainage).

<table>
<thead>
<tr>
<th>Erosion Embank. (m)</th>
<th>Dry Season</th>
<th>Wet Season</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observed</td>
<td>Expected</td>
</tr>
<tr>
<td>0</td>
<td>10</td>
<td>18.1</td>
</tr>
<tr>
<td>1-75</td>
<td>4</td>
<td>8.6</td>
</tr>
<tr>
<td>75-125</td>
<td>2</td>
<td>1.2</td>
</tr>
<tr>
<td>125-175</td>
<td>4</td>
<td>0.6</td>
</tr>
<tr>
<td>175-250</td>
<td>4</td>
<td>0.4</td>
</tr>
<tr>
<td>250+</td>
<td>5</td>
<td>0.1</td>
</tr>
<tr>
<td>Total</td>
<td>29</td>
<td>29</td>
</tr>
</tbody>
</table>

Similarly, when areas beyond 200m of a drainage were analyzed independently, there were significant differences between the observed and expected number of kills in eroded areas (dry season $\chi^2 = 40.3$, $p = 0.001$ and wet season $\chi^2 = 197.5$, $p << 0.001$) (Table 20). Again, there were generally more kills than expected in areas with over 125m of erosion.
Table 20. The observed and expected numbers of kills by plains lions in relation to the total amount of erosion embankments (m) in non-riparian areas only (beyond 200m of a drainage).

<table>
<thead>
<tr>
<th>Erosion Embank. (m)</th>
<th>Dry Season</th>
<th>Wet Season</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observed</td>
<td>Expected</td>
</tr>
<tr>
<td>0</td>
<td>27</td>
<td>23.1</td>
</tr>
<tr>
<td>1-75</td>
<td>2</td>
<td>10.1</td>
</tr>
<tr>
<td>75-125</td>
<td>1</td>
<td>1.2</td>
</tr>
<tr>
<td>125-175</td>
<td>3</td>
<td>0.4</td>
</tr>
<tr>
<td>175+</td>
<td>2</td>
<td>0.2</td>
</tr>
<tr>
<td>Total</td>
<td>35</td>
<td>35</td>
</tr>
</tbody>
</table>

3.4.5 Woodland Kills

The distribution of woodland lion kills in relation to embankments (Figure 8b) was somewhat clustered in areas where embankments were more prevalent. However, there were areas to the east that remain relatively unused despite having erosion embankments. Many of the kills appear to be in areas with erosion close to rivers.

There were significant differences between the observed and the expected number of kills (Table 21) by woodland lions in areas with embankments during both the dry season and the wet season ($\chi^2 = 430.5, p << 0.001$ and $\chi^2 = 38.3, p = 0.003$, respectively). Areas with less than 75m of cumulative embankments had fewer kills than expected, while areas with more than 75m had more kills.

Furthermore, when woodland lion kills within 200m of a river were analyzed (Table 22), there continued to be significant differences between the observed and the expected amount of erosion (dry season $\chi^2 = 141.0, p << 0.001$ and wet season $\chi^2 = 38.8, p = 0.003$). Areas with more erosion embankments had more kills than expected. However, the sample size for the wet season was small ($n = 7$).
Table 21. The observed and expected numbers of kills by woodland lions in relation to the total amount of erosion embankments (m) in the available area.

<table>
<thead>
<tr>
<th>Erosion Embank. (m)</th>
<th>Dry Season</th>
<th>Wet Season</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observed</td>
<td>Expected</td>
</tr>
<tr>
<td>0</td>
<td>28</td>
<td>40.4</td>
</tr>
<tr>
<td>1-75</td>
<td>4</td>
<td>15.5</td>
</tr>
<tr>
<td>75-125</td>
<td>5</td>
<td>2.8</td>
</tr>
<tr>
<td>125-175</td>
<td>6</td>
<td>1.9</td>
</tr>
<tr>
<td>175-250</td>
<td>14</td>
<td>2.3</td>
</tr>
<tr>
<td>250+</td>
<td>6</td>
<td>0.1</td>
</tr>
<tr>
<td>Total</td>
<td>63</td>
<td>63</td>
</tr>
</tbody>
</table>

Table 22. The observed and expected numbers of kills by woodland lions in relation to the total amount of erosion embankments (m) in riparian areas only (within 200m of a drainage).

<table>
<thead>
<tr>
<th>Erosion Embank. (m)</th>
<th>Dry Season</th>
<th>Wet Season</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observed</td>
<td>Expected</td>
</tr>
<tr>
<td>0</td>
<td>12</td>
<td>17.9</td>
</tr>
<tr>
<td>1-75</td>
<td>2</td>
<td>11.5</td>
</tr>
<tr>
<td>75-125</td>
<td>5</td>
<td>3.7</td>
</tr>
<tr>
<td>125-175</td>
<td>4</td>
<td>3.1</td>
</tr>
<tr>
<td>175-250</td>
<td>13</td>
<td>4.6</td>
</tr>
<tr>
<td>250+</td>
<td>5</td>
<td>0.2</td>
</tr>
<tr>
<td>Total</td>
<td>41</td>
<td>41</td>
</tr>
</tbody>
</table>

Interestingly, when all areas excluding rivers were analyzed, there was a significant difference between the observed and the expected number of kills in
eroded areas only during the dry season ($\chi^2 = 54.7, p < 0.001$). Table 23 suggests there were more kills in areas with more erosion. However, this trend was not evident during the wet season when the sample size was small ($n = 13, \chi^2 = 2.19, p > 0.4$).

Table 23. The observed and expected numbers of kills by woodland lions in relation to the total amount of erosion embankments (m) in non-riparian areas only (beyond 200m of a drainage).

<table>
<thead>
<tr>
<th>Erosion Embank. (m)</th>
<th>Dry Season</th>
<th>Wet Season</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observed</td>
<td>Expected</td>
</tr>
<tr>
<td>0</td>
<td>16</td>
<td>16.1</td>
</tr>
<tr>
<td>1-75</td>
<td>2</td>
<td>5.1</td>
</tr>
<tr>
<td>75-125</td>
<td>0</td>
<td>0.5</td>
</tr>
<tr>
<td>125-175</td>
<td>2</td>
<td>0.2</td>
</tr>
<tr>
<td>175+</td>
<td>2</td>
<td>0.1</td>
</tr>
<tr>
<td>Total</td>
<td>22</td>
<td>22</td>
</tr>
</tbody>
</table>

3.4.6 Plains Scavenges

The distribution of scavenges by plains lions in relation to erosion embankments (Figure 8c) suggests there was little interaction. This was consistent regardless of the proximity to rivers.

The combined riparian and non-riparian results for the dry season indicate no significant differences between the observed and the expected number of scavenges ($\chi^2 = 10.1, p > 0.1$) in areas with erosion embankments (Table 24). However, surprisingly during the wet season there were significant differences between the number of scavenges observed in eroded areas and the expected ($\chi^2 = 42.6, p = 0.001$). Table 24 reveals there were more wet season scavenges than expected in areas with no embankments and in areas with many embankments.
(250+ meters), while areas with intermediate amounts of embankment (1-250 meters) had fewer scavenges than expected.

There were too few observations in riparian areas to draw conclusions on the affect of riparian associated erosion on scavenging (dry season n = 4 and wet season n = 1).

Table 24. The observed and expected numbers of scavenges by plains lions in relation to the total amount of erosion embankments (m) in the available area.

<table>
<thead>
<tr>
<th>Erosion Embank. (m)</th>
<th>Dry Season</th>
<th>Wet Season</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observed</td>
<td>Expected</td>
</tr>
<tr>
<td>0</td>
<td>22</td>
<td>16.2</td>
</tr>
<tr>
<td>1-75</td>
<td>1</td>
<td>7.7</td>
</tr>
<tr>
<td>75-125</td>
<td>2</td>
<td>1.1</td>
</tr>
<tr>
<td>125-175</td>
<td>0</td>
<td>0.5</td>
</tr>
<tr>
<td>175-250</td>
<td>1</td>
<td>0.4</td>
</tr>
<tr>
<td>250+</td>
<td>0</td>
<td>0.1</td>
</tr>
<tr>
<td>Total</td>
<td>26</td>
<td>26</td>
</tr>
</tbody>
</table>

However, when the areas away from rivers were analyzed independently, a similar trend was evident; there were significant differences only during the wet season (dry season $\chi^2 = 8.57$, p > 0.1 and wet season $\chi^2 = 40.9$, p = 0.001) (Table 25). And again, there were more scavenges observed during the wet season in areas with no erosion embankments as well as in areas with many embankments (175+ meters), but relatively few in areas with intermediate amounts of erosion (1-175 meters).
Table 25. The observed and expected numbers of scavenges by plains lions in relation to the total amount of erosion embankments (m) in non-riparian areas only (beyond 200m of a drainage).

<table>
<thead>
<tr>
<th>Erosion Embank. (m)</th>
<th>Dry Season</th>
<th>Wet Season</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observed</td>
<td>Expected</td>
</tr>
<tr>
<td>0</td>
<td>21</td>
<td>14.5</td>
</tr>
<tr>
<td>1-75</td>
<td>1</td>
<td>6.3</td>
</tr>
<tr>
<td>75-125</td>
<td>0</td>
<td>0.8</td>
</tr>
<tr>
<td>125-175</td>
<td>0</td>
<td>0.3</td>
</tr>
<tr>
<td>175+</td>
<td>0</td>
<td>0.1</td>
</tr>
<tr>
<td>Total</td>
<td>22</td>
<td>22</td>
</tr>
</tbody>
</table>

3.4.7 Woodland Scavenging

There was no apparent clustering in the distribution of woodland scavenges in relation to erosion embankments for either the dry or the wet season (Figure 8c). The maps provide no indication of any association between scavenges and erosion embankments in riparian areas.

There were no significant differences between the observed and the expected number of scavenges (Table 26) in eroded areas for the dry season ($\chi^2 = 2.96, p > 0.4$). There were too few observations in the wet season ($n = 4$) for an effective analysis, but the trend suggests there were no differences between the observed and expected number of scavenges.

Unfortunately, there were too few scavenging observations in riparian areas to draw conclusive results on the affects of riparian associated erosion (dry season $n = 3$ and wet season $n = 0$).

There were 7 scavenges observed in non-riparian areas by woodland lions during the dry season. Although the numbers were small, there was evidence that the observed and expected differed ($\chi^2 = 100.1, p = 0.004$). Table 27 suggests that there were more scavenges than expected in areas with no erosion, as well as in
areas with lots of erosion (over 175m). There were too few scavenges observed in non-riparian areas during the wet season for a reliable analysis (n = 4) (Table 27).

Table 26. The observed and expected numbers of scavenges by woodland lions in relation to the total amount of erosion embankments (m) in the available area.

<table>
<thead>
<tr>
<th>Erosion Embank. (m)</th>
<th>Dry Season</th>
<th>Wet Season</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observed</td>
<td>Expected</td>
</tr>
<tr>
<td>0</td>
<td>8</td>
<td>6.4</td>
</tr>
<tr>
<td>1-75</td>
<td>1</td>
<td>2.5</td>
</tr>
<tr>
<td>75-125</td>
<td>0</td>
<td>0.4</td>
</tr>
<tr>
<td>125-175</td>
<td>0</td>
<td>0.3</td>
</tr>
<tr>
<td>175-250</td>
<td>1</td>
<td>0.39</td>
</tr>
<tr>
<td>250+</td>
<td>0</td>
<td>0.01</td>
</tr>
<tr>
<td>Total</td>
<td>10</td>
<td>10</td>
</tr>
</tbody>
</table>

Table 27. The observed and expected numbers of scavenges by woodland lions in relation to the total amount of erosion embankments (m) in non-riparian areas only (beyond 200m of a drainage).

<table>
<thead>
<tr>
<th>Erosion Embank. (m)</th>
<th>Dry Season</th>
<th>Wet Season</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observed</td>
<td>Expected</td>
</tr>
<tr>
<td>0</td>
<td>6</td>
<td>5.1</td>
</tr>
<tr>
<td>1-75</td>
<td>0</td>
<td>1.6</td>
</tr>
<tr>
<td>75-125</td>
<td>0</td>
<td>0.2</td>
</tr>
<tr>
<td>125-175</td>
<td>0</td>
<td>0.09</td>
</tr>
<tr>
<td>175+</td>
<td>1</td>
<td>0.01</td>
</tr>
<tr>
<td>Total</td>
<td>7</td>
<td>7</td>
</tr>
</tbody>
</table>
Figure 8. Erosion embankments in relation to the distribution of (a) wet and dry season kills by plains lions, (b) wet and dry season kills by woodland lions, (c) wet and dry season scavenges by plains lions, and (d) wet and dry season scavenges by woodland lions.
3.5 Woody Vegetation Analysis

3.5.1 Plains Kills

The distribution of kills by plains lions in relation to cover from woody vegetation (Figure 9a) suggests the majority of kills were in areas where the vegetation was associated with rivers. Most of the kills occurring in non-riparian areas were during the wet season, and were in areas with virtually no cover from woody vegetation. Areas with thick vegetation in the north and northeast remained relatively unused.

The results from the kills by plains lions in vegetated areas (Table 28) indicates there was significant differences from the expected during the dry season only ($\chi^2 = 15.34, p = 0.01$). There were more kills in areas with thicker vegetation than expected. However, during the wet season, there was no difference between the observed and the expected number of kills in vegetated areas ($\chi^2 = 2.24, p > 0.6$) (Table 28).

Table 28. The observed and expected numbers of kills by plains lions in relation to the percent cover of woody vegetation in the total available area.

<table>
<thead>
<tr>
<th>% Veg Cover</th>
<th>Dry Season</th>
<th>Wet Season</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observed</td>
<td>Expected</td>
</tr>
<tr>
<td>0 - &lt;5</td>
<td>45</td>
<td>54.8</td>
</tr>
<tr>
<td>5 - 10</td>
<td>5</td>
<td>2.6</td>
</tr>
<tr>
<td>10&gt; - 20</td>
<td>5</td>
<td>3.4</td>
</tr>
<tr>
<td>20&gt; - 35</td>
<td>7</td>
<td>2.4</td>
</tr>
<tr>
<td>35&gt; - 100</td>
<td>2</td>
<td>0.8</td>
</tr>
<tr>
<td>Total</td>
<td>64</td>
<td>64</td>
</tr>
</tbody>
</table>

When riparian areas alone were analyzed, there were no differences between the observed and expected number of kills in vegetation for both seasons ($\chi^2 = $
3.67, p > 0.4 and $\chi^2 = 4.85$, p > 0.2 for dry and wet seasons respectively) (Table 29).

Similarly, there was no significant difference between observed and expected number of kills in vegetated areas away from rivers in either season ($\chi^2 = 3.90$, p > 0.3 and $\chi^2 = 2.30$, p > 0.7 for dry and wet seasons respectively) (Table 30).

Table 29. The observed and expected numbers of kills by plains lions in relation to the percent cover of woody vegetation in riparian areas only (within 200m of a drainage).

<table>
<thead>
<tr>
<th>% Veg Cover</th>
<th>Dry Season</th>
<th>Wet Season</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observed</td>
<td>Expected</td>
</tr>
<tr>
<td>0 - &lt;5</td>
<td>16</td>
<td>19.9</td>
</tr>
<tr>
<td>5 - 10</td>
<td>4</td>
<td>2.3</td>
</tr>
<tr>
<td>10&gt; - 20</td>
<td>3</td>
<td>3.2</td>
</tr>
<tr>
<td>20&gt; - 35</td>
<td>4</td>
<td>2.3</td>
</tr>
<tr>
<td>35&gt; - 100</td>
<td>2</td>
<td>1.3</td>
</tr>
<tr>
<td>Total</td>
<td>29</td>
<td>29</td>
</tr>
</tbody>
</table>
Table 30. The observed and expected numbers of kills by plains lions in relation to the percent cover of woody vegetation in non-riparian areas only (beyond 200m of a drainage).

<table>
<thead>
<tr>
<th>% Veg Cover</th>
<th>Dry Season</th>
<th>Wet Season</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observed</td>
<td>Expected</td>
</tr>
<tr>
<td>0 - &lt;5</td>
<td>29</td>
<td>30.9</td>
</tr>
<tr>
<td>5 - 10</td>
<td>1</td>
<td>1.2</td>
</tr>
<tr>
<td>10&gt; - 20</td>
<td>2</td>
<td>1.5</td>
</tr>
<tr>
<td>20&gt; - 35</td>
<td>3</td>
<td>1.1</td>
</tr>
<tr>
<td>35&gt; - 100</td>
<td>0</td>
<td>0.3</td>
</tr>
<tr>
<td>Total</td>
<td>35</td>
<td>35</td>
</tr>
</tbody>
</table>

3.5.2 Woodland Kills

The distribution of kills by woodland lions in relation to woody vegetation (Figure 9b) shows some grouping, especially in areas where vegetation was associated with rivers. Large areas to the north and east with relatively thick vegetation remain unused. This trend was less evident during the wet season.

The results show that woodland lions made more kills in areas with woody vegetation during both the dry season ($\chi^2 = 583.45, p << 0.001$) and the wet season ($\chi^2 = 193.80, p << 0.001$) (Table 31).

Furthermore, when areas within 200m of a river were analyzed separately, the observed number of kills by woodland lions was still greater than expected in areas with thicker vegetation, regardless of season ($\chi^2 = 41.41, p < 0.001$ and $\chi^2 = 15.67, p = 0.008$ for dry and wet season respectively) (Table 32).
Table 31. The observed and expected numbers of kills by woodland lions in relation to the percent cover of woody vegetation in the total available area.

<table>
<thead>
<tr>
<th>% Veg Cover</th>
<th>Dry Season</th>
<th>Wet Season</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observed</td>
<td>Expected</td>
</tr>
<tr>
<td>0 - &lt;5</td>
<td>10</td>
<td>54.0</td>
</tr>
<tr>
<td>5 - 10</td>
<td>1</td>
<td>2.6</td>
</tr>
<tr>
<td>10&gt; - 20</td>
<td>10</td>
<td>3.3</td>
</tr>
<tr>
<td>20&gt; - 35</td>
<td>26</td>
<td>2.3</td>
</tr>
<tr>
<td>35&gt; - 100</td>
<td>16</td>
<td>0.8</td>
</tr>
<tr>
<td>Total</td>
<td>63</td>
<td>63</td>
</tr>
</tbody>
</table>

Table 32. The observed and expected numbers of kills by woodland lions in relation to the percent cover of woody vegetation in riparian areas only (within 200m of a drainage).

<table>
<thead>
<tr>
<th>% Veg Cover</th>
<th>Dry Season</th>
<th>Wet Season</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observed</td>
<td>Expected</td>
</tr>
<tr>
<td>0 - &lt;5</td>
<td>2</td>
<td>9.0</td>
</tr>
<tr>
<td>5 - 10</td>
<td>1</td>
<td>4.9</td>
</tr>
<tr>
<td>10&gt; - 20</td>
<td>7</td>
<td>12.5</td>
</tr>
<tr>
<td>20&gt; - 35</td>
<td>19</td>
<td>11.5</td>
</tr>
<tr>
<td>35&gt; - 100</td>
<td>12</td>
<td>3.1</td>
</tr>
<tr>
<td>Total</td>
<td>41</td>
<td>41</td>
</tr>
</tbody>
</table>

However, in non-riparian areas there was no difference between the observed and expected number of kills in vegetated cover regardless of season ($\chi^2 = 5.22, p > 0.2$ and $\chi^2 = 6.92, p > 0.12$ for dry and wet season respectively) (Table 33).
Table 33. The observed and expected numbers of kills by woodland lions in relation to the percent cover of woody vegetation in non-riparian areas only (beyond 200m of a drainage).

<table>
<thead>
<tr>
<th>% Veg Cover</th>
<th>Dry Season</th>
<th>Wet Season</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observed</td>
<td>Expected</td>
</tr>
<tr>
<td>0 - &lt;5</td>
<td>8</td>
<td>7.3</td>
</tr>
<tr>
<td>5 - 10</td>
<td>0</td>
<td>2.1</td>
</tr>
<tr>
<td>10&gt; - 20</td>
<td>3</td>
<td>4.2</td>
</tr>
<tr>
<td>20&gt; - 35</td>
<td>7</td>
<td>6.6</td>
</tr>
<tr>
<td>35&gt; - 100</td>
<td>4</td>
<td>1.8</td>
</tr>
<tr>
<td>Total</td>
<td>22</td>
<td>22</td>
</tr>
</tbody>
</table>

3.5.3 Plains Scavenges

The distribution of scavenges by plains lions (Figure 9c) suggests there was a negligible amount of selection for woody vegetation regardless of season.

The results (Table 34) indicated there were no differences between the observed and expected number of scavenges by plains lions in vegetated areas during either the dry season ($\chi^2 = 2.72, p > 0.6$) or the wet season ($\chi^2 = 1.42, p > 0.9$).

There were too few observations in riparian areas to draw conclusions ($n = 5$). However, in non-riparian areas there were no differences between the observed and expected number scavenges in areas with vegetated cover, regardless of season ($\chi^2 = 1.98, p > 0.7$ and $\chi^2 = 2.69, p > 0.5$ for dry and wet season, respectively) (Table 35).
Table 34. The observed and expected numbers of scavenges by plains lions in relation to the percent cover of woody vegetation in the total available area.

<table>
<thead>
<tr>
<th>% Veg Cover</th>
<th>Dry Season</th>
<th>Wet Season</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observed</td>
<td>Expected</td>
</tr>
<tr>
<td>0 - &lt;5</td>
<td>23</td>
<td>22.3</td>
</tr>
<tr>
<td>5 - 10</td>
<td>2</td>
<td>1.0</td>
</tr>
<tr>
<td>10&gt; - 20</td>
<td>0</td>
<td>1.4</td>
</tr>
<tr>
<td>20&gt; - 35</td>
<td>1</td>
<td>1.0</td>
</tr>
<tr>
<td>35&gt; - 100</td>
<td>0</td>
<td>0.3</td>
</tr>
<tr>
<td>Total</td>
<td>26</td>
<td>26</td>
</tr>
</tbody>
</table>

Table 35. The observed and expected numbers of scavenges by plains lions in relation to the percent cover of woody vegetation in non-riparian areas only (beyond 200m of a drainage).

<table>
<thead>
<tr>
<th>% Veg Cover</th>
<th>Dry Season</th>
<th>Wet Season</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observed</td>
<td>Expected</td>
</tr>
<tr>
<td>0 - &lt;5</td>
<td>21</td>
<td>19.4</td>
</tr>
<tr>
<td>5 - 10</td>
<td>1</td>
<td>0.8</td>
</tr>
<tr>
<td>10&gt; - 20</td>
<td>0</td>
<td>0.9</td>
</tr>
<tr>
<td>20&gt; - 35</td>
<td>0</td>
<td>0.7</td>
</tr>
<tr>
<td>35&gt; - 100</td>
<td>0</td>
<td>0.2</td>
</tr>
<tr>
<td>Total</td>
<td>22</td>
<td>22</td>
</tr>
</tbody>
</table>

3.5.4 Woodland Scavenges

Woodland lion scavenges (Figure 9d) during the dry season appear to be somewhat correlated with woody vegetation. However, there appeared to be little correlation between wet season scavenges and woody vegetation.
The results for the dry season indicated there was a significant difference between the observed and expected number of scavenges by woodland lions in areas with woody vegetation ($\chi^2 = 52.46, p < 0.001$) (Table 36), however the sample size was small ($n = 10$). Surprisingly, woodland lions tended to scavenge more in areas with thicker vegetation than expected. There were too few scavenging observations by woodland lions during the wet season ($n = 4$) to infer any relationship. Likewise, there were too few observations in riparian areas ($n = 3$) for analysis. However, in non-riparian areas, there were no differences between the observed and expected number of dry season scavenges in areas with woody vegetation ($\chi^2 = 4.15, p > 0.3$) (Table 37).

Table 36. The observed and expected numbers of dry season scavenges by plains lions in relation to the percent cover of woody vegetation in the total available area. There were too few observations of wet season scavenges for analysis ($n = 4$).

<table>
<thead>
<tr>
<th>% Veg Cover</th>
<th>Observed</th>
<th>Expected</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 - &lt;5</td>
<td>2</td>
<td>8.6</td>
</tr>
<tr>
<td>5 - 10</td>
<td>2</td>
<td>0.4</td>
</tr>
<tr>
<td>10&gt; - 20</td>
<td>1</td>
<td>0.5</td>
</tr>
<tr>
<td>20&gt; - 35</td>
<td>4</td>
<td>0.4</td>
</tr>
<tr>
<td>35&gt; - 100</td>
<td>1</td>
<td>0.1</td>
</tr>
<tr>
<td>Total</td>
<td>10</td>
<td>10</td>
</tr>
</tbody>
</table>
Table 37. The observed and expected numbers of dry season scavenges by woodland lions in relation to the percent cover of woody vegetation in non-riparian areas only (beyond 200m of a drainage). There were too few wet season scavenges for analysis (n = 4).

<table>
<thead>
<tr>
<th>% Veg Cover</th>
<th>Observed</th>
<th>Expected</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 - &lt;5</td>
<td>1</td>
<td>2.3</td>
</tr>
<tr>
<td>5 - 10</td>
<td>1</td>
<td>0.7</td>
</tr>
<tr>
<td>10&gt; - 20</td>
<td>0</td>
<td>1.3</td>
</tr>
<tr>
<td>20&gt; - 35</td>
<td>4</td>
<td>2.1</td>
</tr>
<tr>
<td>35&gt; - 100</td>
<td>1</td>
<td>0.6</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>7</strong></td>
<td><strong>7</strong></td>
</tr>
</tbody>
</table>
Figure 9. Cover from woody vegetation in relation to the distribution of (a) wet and dry season kills by plains lions, (b) wet and dry season kills by woodland lions, (c) wet and dry season scavenges by plains lions and (d) wet and dry season scavenges by woodland lions.
3.6 Access to Water Analysis

3.6.1 Plains Kills

The distribution of kills by plains lions appears to be clustered in areas surrounding water (Figures 10a and 11a). Although this was more evident in the dry season (Figure 10a), there still appears to be some selection for water in the wet season (Figure 11a), especially to the north and west. There was little selection for water in the northeast despite this area having water during both the wet and dry seasons (Figures 10a and 11a).

There were significant differences between the observed and expected numbers of kills by plains lions within 200m of water for both the dry season ($\chi^2 = 185.86, p << 0.001$) as well as the wet season ($\chi^2 = 4.66, p = 0.047$) (Table 38). There were more kills by plains lions in areas near water (i.e. within 200m) than expected for both seasons. Furthermore, of these kills the majority were within 50m of water (i.e. adjacent to water), which was also more than expected for both seasons (Table 39). The greatest differences between the observed and expected number of kills within 50m of water was for the dry season (dry season $\chi^2 = 186.06, p << 0.001$ and wet season $\chi^2 = 27.46, p < 0.001$).

<table>
<thead>
<tr>
<th></th>
<th>Season</th>
<th>Dry</th>
<th>Wet</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Within 200m</td>
<td>Observed</td>
<td>18</td>
<td>13</td>
<td>31</td>
</tr>
<tr>
<td></td>
<td>Expected</td>
<td>1.5</td>
<td>7.5</td>
<td>9</td>
</tr>
<tr>
<td>Not within 200m</td>
<td>Observed</td>
<td>46</td>
<td>43</td>
<td>89</td>
</tr>
<tr>
<td></td>
<td>Expected</td>
<td>62.5</td>
<td>48.5</td>
<td>111</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>64</td>
<td>56</td>
<td>120</td>
</tr>
</tbody>
</table>

Table 38. The observed and expected number of kills by plains lions within 200m of water based on season.
Table 39. The observed and expected number of kills by plains lions within 50m of water based on season.

<table>
<thead>
<tr>
<th>Season</th>
<th>Dry</th>
<th>Wet</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Within 50m</td>
<td>Observed</td>
<td>9</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>Expected</td>
<td>0.4</td>
<td>1.9</td>
</tr>
<tr>
<td>Not within 50m</td>
<td>Observed</td>
<td>55</td>
<td>47</td>
</tr>
<tr>
<td></td>
<td>Expected</td>
<td>63.6</td>
<td>54.1</td>
</tr>
<tr>
<td>Total</td>
<td>64</td>
<td>56</td>
<td>120</td>
</tr>
</tbody>
</table>

3.6.2 Woodland Kills

There was evidence that woodland lion kills were clustered around areas with water in the dry season, especially in the western part of the available area (Figure 10b). This clustering was not as evident during the wet season (Figure 11b), when the distribution of woodland lion kills becomes more dispersed than in the dry season. There were relatively few kills observed in areas in the eastern part of the available area, despite water being available during both seasons.

Although woodland lions made more kills than expected in areas within 200m of water (Table 40), the difference was significant only during the dry season ($\chi^2 = 150.73$, $p << 0.001$ and wet season $\chi^2 = 0.11$, $p = 0.81$). Similarly, in areas adjacent to water (within 50m) the observed number of kills by woodland lions was significantly different from the expected only during the dry season ($\chi^2 = 109.93$, $p << 0.001$). During the wet season, there was no difference between the observed and expected number of kills ($\chi^2 = 0.32$, $p = 0.72$) (Table 41).
Table 40. The observed and expected number of kills by woodland lions within 200m of water based on season.

<table>
<thead>
<tr>
<th>Season</th>
<th>Dry</th>
<th>Wet</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Within 200m</td>
<td>27</td>
<td>7</td>
<td>34</td>
</tr>
<tr>
<td>Observed</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Expected</td>
<td>3.8</td>
<td>6.3</td>
<td>10.1</td>
</tr>
<tr>
<td>Not within 200m</td>
<td>36</td>
<td>13</td>
<td>49</td>
</tr>
<tr>
<td>Observed</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Expected</td>
<td>59.2</td>
<td>13.7</td>
<td>72.9</td>
</tr>
<tr>
<td>Total</td>
<td>63</td>
<td>20</td>
<td>83</td>
</tr>
</tbody>
</table>

Table 41. The observed and expected number of kills by woodland lions within 50m of water based on season.

<table>
<thead>
<tr>
<th>Season</th>
<th>Dry</th>
<th>Wet</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Within 50m</td>
<td>12</td>
<td>1</td>
<td>13</td>
</tr>
<tr>
<td>Observed</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Expected</td>
<td>1.1</td>
<td>1.7</td>
<td>2.8</td>
</tr>
<tr>
<td>Not within 50m</td>
<td>51</td>
<td>19</td>
<td>70</td>
</tr>
<tr>
<td>Observed</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Expected</td>
<td>61.9</td>
<td>18.3</td>
<td>80.2</td>
</tr>
<tr>
<td>Total</td>
<td>63</td>
<td>20</td>
<td>83</td>
</tr>
</tbody>
</table>

3.6.3 Plains Scavenges

There was no discernable clustering of scavenges by plains lions in relation to water during either the dry or the wet season (Figures 10c and 11c). The distribution of wet season scavenges was dispersed more into areas away from rivers (i.e. to the southeast of the available area) than the dry season.

Results show there were no differences between the observed and the expected number of scavenges by plains lions in areas within 200m of water for
either season (dry season $\chi^2 = 0.27, p > 0.9$ and wet season $\chi^2 = 2.06, p = 0.250$) (Table 42). Similarly, the number of scavenges within 50m of water showed no difference from the expected (dry season $\chi^2 = 3.22, p > 0.183$ and wet season $\chi^2 = 0.01, p > 0.9$) (Table 43).

Table 42. The observed and expected number of scavenges by plains lions within 200m of water based on season.

<table>
<thead>
<tr>
<th>Season</th>
<th>Dry</th>
<th>Wet</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Within 200m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Expected</td>
<td>0.6</td>
<td>3.5</td>
<td>4.1</td>
</tr>
<tr>
<td>Not within 200m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed</td>
<td>25</td>
<td>25</td>
<td>50</td>
</tr>
<tr>
<td>Expected</td>
<td>25.4</td>
<td>22.5</td>
<td>47.9</td>
</tr>
<tr>
<td>Total</td>
<td>26</td>
<td>26</td>
<td>52</td>
</tr>
</tbody>
</table>

Table 43. The observed and expected number of scavenges by plains lions within 50m of water based on season.

<table>
<thead>
<tr>
<th>Season</th>
<th>Dry</th>
<th>Wet</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Within 50m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Expected</td>
<td>0.2</td>
<td>0.9</td>
<td>1.1</td>
</tr>
<tr>
<td>Not within 50m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed</td>
<td>25</td>
<td>25</td>
<td>50</td>
</tr>
<tr>
<td>Expected</td>
<td>25.8</td>
<td>25.1</td>
<td>50.9</td>
</tr>
<tr>
<td>Total</td>
<td>26</td>
<td>26</td>
<td>52</td>
</tr>
</tbody>
</table>
3.6.4 Woodland Scavenges

The distribution of dry season and wet season scavenges by woodland lions suggests there was no clustering in the vicinity of water (Figure 10d and 11d).

The results for woodland lion scavenges show there were no differences between the observed and expected number of scavenges within 200m of water for the dry season ($\chi^2 = 0.28, p < 0.9$) (Table 44). These results were comparable to areas within 50m of water (Table 45), indicating there was no difference (dry season $\chi^2 = 0.20, p > 0.9$). Although these trends appear consistent in the wet season, there were too few observations for an effective analysis. The sample sizes for both the dry and wet season were small (n = 10 and n = 4, respectively).

Table 44. The observed and expected number of scavenges by woodland lions within 200m of water based on season.

<table>
<thead>
<tr>
<th>Season</th>
<th>Dry</th>
<th>Wet</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Within 200m</td>
<td>Observed</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Expected</td>
<td>0.6</td>
<td>1.3</td>
</tr>
<tr>
<td>Not within 200m</td>
<td>Observed</td>
<td>9</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>Expected</td>
<td>9.4</td>
<td>2.7</td>
</tr>
<tr>
<td>Total</td>
<td>10</td>
<td>4</td>
<td>14</td>
</tr>
</tbody>
</table>
Table 45. The observed and expected number of scavenges by woodland lions within 50m of water based on season.

<table>
<thead>
<tr>
<th>Season</th>
<th>Dry</th>
<th>Wet</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Within 50m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Expected</td>
<td>0.2</td>
<td>0.3</td>
<td>0.5</td>
</tr>
<tr>
<td>Not within 50m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed</td>
<td>10</td>
<td>4</td>
<td>14</td>
</tr>
<tr>
<td>Expected</td>
<td>9.8</td>
<td>3.7</td>
<td>13.5</td>
</tr>
<tr>
<td>Total</td>
<td>10</td>
<td>4</td>
<td>14</td>
</tr>
</tbody>
</table>
Figure 10. Access to water during the dry season in relation to the distribution of (a) kills by plains lions, (b) kills by woodland lions, (c) scavenges by plains lions, and (d) scavenges by woodland lions.
Figure 10. Access to water during the dry season in relation to the distribution of (a) kills by plains lions, (b) kills by woodland lions, (c) scavenges by plains lions, and (d) scavenges by woodland lions.
Figure 11. Access to water during the wet season in relation to the distribution of (a) kills by plains lions, (b) kills by woodland lions, c) scavenges by plains lions, and (d) scavenges by woodland lions.
3.7 Loglinear Analysis and Resource Selection Functions (Logistic Regression)

There were no significant three-way or higher order relationships in any of the loglinear regression results. The highest order relationships between habitat variables were two-way, and since loglinear models are hierarchical, they included all the relevant one-way components.

None of the logistic regression equations predicting kills or scavenges were significantly different from the perfect models (i.e. the Hosmer-Lemeshow tests consistently showed no difference), indicating that all the variables included in the equations were significant predictors.

Appendix 2 provides an example of a logistic regression equation (i.e. the resource selection function equation).

3.7.1 Plains Wet Season

The results of the loglinear analysis for the plains area during the wet season (Table 46) suggest that confluences and woody vegetation, confluences and access to water, erosion embankments and access to water, and woody vegetation and access to water were significantly associated with each other (p < 0.05, n = 505).

Table 46. Significant relationships occurring naturally between habitat variables available to plains lions during the wet season, as identified by a loglinear analysis (see section 2.11 for definitions).

<table>
<thead>
<tr>
<th>Combination of Habitat Variables</th>
<th>Name of New Factor</th>
<th>$G^2$</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Confluence &amp; Vegetation</td>
<td>Confluence Vegetation</td>
<td>7.09</td>
<td>0.0077</td>
</tr>
<tr>
<td>Confluence &amp; Water</td>
<td>Confluence Water</td>
<td>15.43</td>
<td>0.0001</td>
</tr>
<tr>
<td>Erosion &amp; Water</td>
<td>Riparian Erosion</td>
<td>6.31</td>
<td>0.0120</td>
</tr>
<tr>
<td>Vegetation &amp; Water</td>
<td>Riparian Vegetation</td>
<td>4.02</td>
<td>0.0450</td>
</tr>
</tbody>
</table>
3.7.1.1 Plains Wet Season Kills

The variables or combination of variables included in the logistic regression equation predicting wet season kills by plains lions were confluence vegetation, riparian erosion, riparian vegetation, and the viewsheds. Confluence water was not a significant predictor (Table 47).

Table 47. Test of significance for combinations of habitat variables used in the logistic regression equation predicting plains lion kills during the wet season. Variables were significant if p < 0.2 as suggested Tabachnick and Fidell (1995) (see section 2.11, step 6).

<table>
<thead>
<tr>
<th>Variables</th>
<th>Coefficient (β)</th>
<th>S.E.</th>
<th>Test Statistic</th>
<th>Sig. (p)</th>
<th>Odds Ratio (e^β)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Confluence Vegetation</td>
<td>0.600</td>
<td>0.306</td>
<td>3.858*</td>
<td>0.050</td>
<td>1.823</td>
</tr>
<tr>
<td>Confluence Water</td>
<td></td>
<td></td>
<td>0.614&quot;</td>
<td>0.433</td>
<td></td>
</tr>
<tr>
<td>Riparian Erosion</td>
<td>0.707</td>
<td>0.138</td>
<td>26.420*</td>
<td>&lt; 0.001</td>
<td>2.029</td>
</tr>
<tr>
<td>Riparian Vegetation</td>
<td>-0.459</td>
<td>0.265</td>
<td>3.009*</td>
<td>0.083</td>
<td>0.632</td>
</tr>
<tr>
<td>Viewsheds</td>
<td>0.492</td>
<td>0.294</td>
<td>2.808*</td>
<td>0.094</td>
<td>1.636</td>
</tr>
<tr>
<td>Constant</td>
<td>-2.929</td>
<td>0.254</td>
<td>132.767*</td>
<td>&lt; 0.001</td>
<td></td>
</tr>
</tbody>
</table>

* Wald test for inclusion of the variable
" Lagrange Multiplier test for exclusion of the variable

Of the variables included in the logistic regression the riparian erosion had the highest odds ratio, while riparian vegetation had the lowest (Table 47). Therefore, biologically speaking, since the odds ratio for riparian vegetation was significantly less than 1 (i.e. the coefficient (β) was significantly negative), riparian vegetation decreased the probabilities of plains lions making a kill during the wet season. The opposite was true for confluence vegetation, riparian erosion, and
viewsheds; these features increased the probability of plains lions making a kill during the wet season.

The probability of a kill by plains lions during the wet season increased nearer rivers (Figure 12a). There were large non-riparian areas in the southeast with medium probabilities of kills (0.15 – 0.6). The lowest probabilities occurred away from rivers, particularly in the central and southwest part of the available area.

3.7.1.2 Plains Wet Season Scavenges

The coefficients for confluence vegetation, confluence water, and viewsheds were significantly different from zero and were included in the logistic regression predicting wet season scavenges by plains lions (Table 48). Riparian erosion and riparian vegetation were not included in the equation, since the coefficients did not differ significantly from zero.

The odds ratio for confluence vegetation and viewsheds were greater than 1, while the odds ratio for confluence water was less than 1 (i.e. the coefficient (β) was significantly negative) (Table 48). In other words, the presence of either confluence vegetation or viewsheds significantly increased the probability of plains lions scavenging during the wet season, while confluence water significantly decreased the probability.
Table 48. Test of significance for combinations of habitat variables used in the logistic regression equation predicting plains lion scavenges during the wet season. Variables were significant if p < 0.2 as suggested Tabachnick and Fidell (1995) (see section 2.11, step 6).

<table>
<thead>
<tr>
<th>Variables</th>
<th>Coefficient (β)</th>
<th>S.E.</th>
<th>Test Statistic</th>
<th>Sig. (p)</th>
<th>Odds Ratio (e^β)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Confluence Vegetation</td>
<td>0.914</td>
<td>0.489</td>
<td>3.494*</td>
<td>0.062</td>
<td>2.493</td>
</tr>
<tr>
<td>Confluence Water</td>
<td>-0.962</td>
<td>0.589</td>
<td>2.669*</td>
<td>0.102</td>
<td>0.382</td>
</tr>
<tr>
<td>Riparian Erosion</td>
<td></td>
<td></td>
<td>0.469</td>
<td>0.494</td>
<td></td>
</tr>
<tr>
<td>Riparian Vegetation</td>
<td></td>
<td></td>
<td>1.335</td>
<td>0.248</td>
<td></td>
</tr>
<tr>
<td>Viewsheds</td>
<td>0.961</td>
<td>0.416</td>
<td>5.332*</td>
<td>0.021</td>
<td>2.616</td>
</tr>
<tr>
<td>Constant</td>
<td>-3.472</td>
<td>0.339</td>
<td>105.144</td>
<td>&lt; 0.001</td>
<td>0.031</td>
</tr>
</tbody>
</table>

* Wald test for inclusion of the variable

V Lagrange Multiplier test for exclusion of the variable

There were large areas with medium probabilities of scavenging by plains lions during the wet season in north, east and west of the available area (Figure 13a). Areas with highest probabilities occurred in the north and east, while the majority of the south had low probabilities of scavenges.

3.7.2 Plains Dry Season

The relationships occurring between the habitat features available to plains lions during the dry season were identical to the wet season (Table 49). According to the loglinear analysis, there were significant correlations between confluences and woody vegetation, confluences and access to water, erosion and access to water, and woody vegetation and access to water (p < 0.05, n = 505).
Table 49. Significant relationships occurring naturally between habitat variables available to plains lions during the dry season, as identified by a loglinear analysis (see section 2.11 for definitions).

<table>
<thead>
<tr>
<th>Combination of Habitat Variables</th>
<th>Name of New Factor</th>
<th>G²</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Confluence &amp; Vegetation</td>
<td>Confluence Vegetation</td>
<td>6.034</td>
<td>0.0140</td>
</tr>
<tr>
<td>Confluence &amp; Water</td>
<td>Confluence Water</td>
<td>3.952</td>
<td>0.0468</td>
</tr>
<tr>
<td>Erosion &amp; Water</td>
<td>Riparian Erosion</td>
<td>9.846</td>
<td>0.0017</td>
</tr>
<tr>
<td>Vegetation &amp; Water</td>
<td>Riparian Vegetation</td>
<td>15.743</td>
<td>0.0001</td>
</tr>
</tbody>
</table>

3.7.2.1 Plains Dry Season Kills

There were 3 combinations of variables that had coefficients that were significantly different from zero in the logistic regression predicting dry season kills by plains lions: confluence vegetation, confluence water, and riparian erosion. Viewsheds and riparian vegetation were not significant predictors of kills by plains lions during the dry season and were not included in the model (Table 50).

Of the 3 combinations of variables used in the logistic regression equation, the odds ratio for confluence vegetation was highest, followed by riparian erosion. The odds ratio for confluence water was less than 1 (i.e. the coefficient (β) was significantly negative) (Table 50). In biological terms this indicates that confluence water significantly decreased the probability of plains lions killing during the dry season, whereas both confluence vegetation and riparian erosion significantly increased the probability of a kill.

The probabilities of plains lions making a kill during the dry season were similar to those in the wet season in that they were consistently higher in riparian areas than in non-riparian areas (Figure 12b). The highest probabilities occurred to the north and west, while the southeast had lower probabilities. The lowest probabilities were in the southwest.
Table 50. Test of significance for combinations of habitat variables used in the logistic regression equation predicting kills by plains lions during the dry season. Variables were significant if \( p < 0.2 \) as suggested Tabachnick and Fidell (1995) (see section 2.11, step 6).

<table>
<thead>
<tr>
<th>Variables</th>
<th>Coefficient (( \beta ))</th>
<th>S.E.</th>
<th>Test Statistic</th>
<th>Sig. (( p ))</th>
<th>Odds Ratio (( e^\beta ))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Confluence Vegetation</td>
<td>0.956</td>
<td>0.295</td>
<td>10.529*</td>
<td>0.001</td>
<td>2.601</td>
</tr>
<tr>
<td>Confluence Water</td>
<td>-0.501</td>
<td>0.303</td>
<td>2.740*</td>
<td>0.098</td>
<td>0.606</td>
</tr>
<tr>
<td>Riparian Erosion</td>
<td>0.589</td>
<td>0.138</td>
<td>18.267*</td>
<td>&lt; 0.001</td>
<td>1.802</td>
</tr>
<tr>
<td>Riparian Vegetation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Viewsheds</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Constant</td>
<td>-2.624</td>
<td>0.189</td>
<td>192.920*</td>
<td>&lt; 0.001</td>
<td></td>
</tr>
</tbody>
</table>

* Wald test for inclusion of the variable

\( ^v \) Lagrange Multiplier test for exclusion of the variable

3.7.2.2 Plains Dry Season Scavenges

The variables included in the logistic regression predicting dry season scavenges by plains lions were confluence vegetation, confluence water, and the viewsheds since their coefficients were significantly different from zero. Riparian erosion and riparian vegetation were not significant predictors of scavenging by plains lions during the dry season (Table 51).

Confluence vegetation had the highest odds ratio, followed by viewsheds; both were greater than 1. The odds ratio for confluence water was less than 1 indicating that the coefficient (\( \beta \)) was significantly negative (Table 51). Therefore, confluence water significantly reduced the probability of plains lions scavenging during the dry season. Conversely, the coefficients (\( \beta \)) for confluence vegetation and
viewsheds were significantly positive, and therefore these features increased the probability of scavenges.

Table 51. Test of significance for combinations of habitat variables used in the logistic regression equation predicting scavenges by plains lions during the dry season. Variables were significant if $p < 0.2$ as suggested Tabachnick and Fidell (1995) (see section 2.11, step 6).

<table>
<thead>
<tr>
<th>Variables</th>
<th>Coefficient ($\beta$)</th>
<th>S.E.</th>
<th>Test Statistic</th>
<th>Sig. (p)</th>
<th>Odds Ratio ($e^{\beta}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Confluence</td>
<td>0.699</td>
<td>0.518</td>
<td>1.824*</td>
<td>0.177</td>
<td>2.012</td>
</tr>
<tr>
<td>Vegetation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Confluence</td>
<td>-0.843</td>
<td>0.600</td>
<td>1.974*</td>
<td>0.160</td>
<td>0.430</td>
</tr>
<tr>
<td>Water</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Riparian</td>
<td>0.111*</td>
<td></td>
<td></td>
<td>0.739</td>
<td></td>
</tr>
<tr>
<td>Erosion</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Riparian</td>
<td>1.816*</td>
<td></td>
<td></td>
<td>0.178Δ</td>
<td></td>
</tr>
<tr>
<td>Vegetation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Viewsheds</td>
<td>0.646</td>
<td>0.407</td>
<td>2.521*</td>
<td>0.112</td>
<td>1.908</td>
</tr>
<tr>
<td>Constant</td>
<td>-3.254</td>
<td>0.310</td>
<td>110.157*</td>
<td>&lt; 0.001</td>
<td>0.039</td>
</tr>
</tbody>
</table>

* Wald test for inclusion of the variable

* Lagrange Multiplier test for exclusion of the variable

Δ Despite this variable being significant according to the Lagrange Multiplier test, it was removed during the backwards Wald stepwise logistic regression procedure since it was marginally significant ($\alpha = 0.20$).

The areas with the highest probabilities of scavenging by plains lions during the dry season were mainly in the north and east of the available area (Figure 13b), similar to the wet season. The south and central areas had lower probabilities.
3.7.3 Woodland Wet Season

The loglinear analysis of the habitat variables available to woodland lions during the wet season (Table 52) indicated significant relationships occurred naturally between confluences and water, and between erosion and water ($p < 0.05$, $n = 129$). Interestingly, vegetation did not co-vary significantly with any other habitat during the wet season. There was some indication of a three-way relationship between confluences, woody vegetation, and access to water but it was not significant ($G^2 = 3.054$, $p = 0.0805$).

Table 52. Significant relationships occurring naturally between habitat variables available to woodland lions during the wet season, as identified by a loglinear analysis (see section 2.11 for definitions).

<table>
<thead>
<tr>
<th>Combination of Habitat Variables</th>
<th>Name of New Factor</th>
<th>$G^2$</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Confluences &amp; Water</td>
<td>Confluence Water</td>
<td>9.304</td>
<td>0.0023</td>
</tr>
<tr>
<td>Erosion &amp; Water</td>
<td>Riparian Erosion</td>
<td>9.322</td>
<td>0.0023</td>
</tr>
<tr>
<td>Vegetation</td>
<td>Vegetation</td>
<td>7.523</td>
<td>0.0061</td>
</tr>
</tbody>
</table>

3.7.3.1 Woodland Wet Season Kills

Only one variable (riparian erosion) was included in the logistic regression equation predicting kills by woodland lions during the wet season. The coefficients for confluence water, vegetation and viewsheds did not differ significantly from zero, suggesting they were not adequate predictors (Table 53). The odds ratio for riparian erosion was greater than 1 (Table 53) indicating that riparian erosion increased the probability of woodland lions killing during the wet season.

There was a higher probability of kills by woodland lions occurring in riparian areas rather than non-riparian areas during the wet season (Figure 12c). However, there were no areas that had a probability greater than 0.25. The areas
with lowest probability of kills were away from rivers, especially in the central and east part of the available area.

Table 53. Test of significance for combinations of habitat variables used in the logistic regression equation predicting kills by woodland lions during the wet season. Variables were significant if p < 0.2 as suggested Tabachnick and Fidell (1995) (see section 2.11, step 6).

<table>
<thead>
<tr>
<th>Variables</th>
<th>Coefficient (β)</th>
<th>S.E.</th>
<th>Test Statistic</th>
<th>Sig. (p)</th>
<th>Odds Ratio (e^β)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Confluence Water</td>
<td>0.554w</td>
<td>0.457</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Riparian Erosion</td>
<td>0.306</td>
<td>0.221</td>
<td>1.930</td>
<td>0.165</td>
<td>1.359</td>
</tr>
<tr>
<td>Vegetation</td>
<td>1.253w</td>
<td>0.263</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Viewsheds</td>
<td>1.430w</td>
<td>0.232</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Constant</td>
<td>-2.102</td>
<td>0.311</td>
<td>45.548</td>
<td>&lt; 0.001</td>
<td>0.122</td>
</tr>
</tbody>
</table>

* Wald test for inclusion of the variable
w Lagrange Multiplier test for exclusion of the variable

3.7.3.2 Woodland Wet Season Scavenges

The logistic regression predicting scavenging events by woodland lions during the wet season failed to include any of the habitat variables. The sample size was small; there were only 4 scavenging events observed. Even though only the constant was included in the logistic regression (Table 54), the equation was not significantly different from a perfect model (Hosmer-Lemeshow test \( \chi^2 = 0.03 \), p = 0.984, df = 2).

The probability of scavenging in the area available to woodland lions during the wet season was equally low across the entire area (Figure 13c).
Table 54. Test of significance for combinations of habitat variables used in the logistic regression equation predicting scavenges by woodland lions during the wet season. Variables were significant if p < 0.2 as suggested Tabachnick and Fidell (1995) (see section 2.11, step 6).

<table>
<thead>
<tr>
<th>Variables</th>
<th>Coefficient ((\beta))</th>
<th>S.E.</th>
<th>Test Statistic</th>
<th>Sig. (p)</th>
<th>Odds Ratio ((e^{\beta}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Confluence Water</td>
<td>0.004*</td>
<td>0.950</td>
<td>0.950</td>
<td>0.950</td>
<td></td>
</tr>
<tr>
<td>Riparian Erosion</td>
<td>0.063*</td>
<td>0.801</td>
<td>0.801</td>
<td>0.801</td>
<td></td>
</tr>
<tr>
<td>Vegetation</td>
<td>0.273*</td>
<td>0.626</td>
<td>0.626</td>
<td>0.626</td>
<td></td>
</tr>
<tr>
<td>Viewsheds</td>
<td>0.588*</td>
<td>0.443</td>
<td>0.443</td>
<td>0.443</td>
<td></td>
</tr>
<tr>
<td>Constant</td>
<td>-3.473</td>
<td>0.508</td>
<td>46.812* &lt; 0.001</td>
<td>0.031</td>
<td></td>
</tr>
</tbody>
</table>

* Wald test for inclusion of the variable
\(\checkmark\) Lagrange Multiplier test for exclusion of the variable

### 3.7.4 Woodland Dry Season

The results of the loglinear analysis for the area available to woodland lions during the dry season (Table 55) suggests there was a significant relationship between erosion embankments and access to water, and between vegetation and access to water (\(p < 0.05, n = 129\)). Confluences did not significantly co-vary with any other habitat variable. There was some indication of a relationship between erosion embankments and confluences, as well as between erosion embankments and vegetation however neither was significant (\(G^2 = 3.285, p = 0.0699\) and \(G^2 = 3.433, p = 0.0639\), respectively).
Table 55. Significant relationships occurring naturally between habitat variables available to woodland lions during the dry season, as identified by a loglinear analysis (see section 2.11. for definitions).

<table>
<thead>
<tr>
<th>Combination of Habitat Variables</th>
<th>Name of New Factor</th>
<th>G²</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Erosion &amp; Water</td>
<td>Riparian Erosion</td>
<td>11.510</td>
<td>0.0007</td>
</tr>
<tr>
<td>Vegetation &amp; Water</td>
<td>Riparian Vegetation</td>
<td>11.132</td>
<td>0.0008</td>
</tr>
<tr>
<td>Confluence</td>
<td>Confluence</td>
<td>98.987</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

3.7.4.1 Woodland Dry Season Kills

The coefficients (β) for riparian erosion and riparian vegetation differed significantly from zero and were effective predictors of kills by woodland lions during the dry season (Table 56). Confluences and viewsheds were not significant predictors.

There were few areas that had a low probability of a kill by woodland lions during the dry season (Figure 12d). The areas with the highest probabilities consistently occurred near rivers.
Table 56. Test of significance for combinations of habitat variables used in the logistic regression equation predicting kills by woodland lions during the dry season. Variables were significant if p < 0.2 as suggested Tabachnick and Fidell (1995) (see section 2.11, step 6).

<table>
<thead>
<tr>
<th>Variables</th>
<th>Coefficient (β)</th>
<th>S.E.</th>
<th>Test Statistic</th>
<th>Sig. (p)</th>
<th>Odds Ratio (e^p)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Riparian Erosion</td>
<td>0.758</td>
<td>0.161</td>
<td>22.102*</td>
<td>&lt; 0.001</td>
<td>2.134</td>
</tr>
<tr>
<td>Riparian Vegetation</td>
<td>0.375</td>
<td>0.181</td>
<td>4.301*</td>
<td>0.038</td>
<td>1.455</td>
</tr>
<tr>
<td>Confluence</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Viewsheds</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Constant</td>
<td>-2.003</td>
<td>0.348</td>
<td>33.172*</td>
<td>&lt; 0.001</td>
<td>0.135</td>
</tr>
</tbody>
</table>

* Wald test for inclusion of the variable
v Lagrange Multiplier test for exclusion of the variable

3.7.4.2 Woodland Dry Season Scavenges

The logistic regression predicting scavenging events by woodland lions during the dry season failed to include any of the habitat variables (Table 57). There were only 10 scavenging events by woodland lions observed in the dry season. Only the constant was included in the final equation, which did not differ significantly from a perfect model (Hosmer-Lemeshow test χ² = 0.20, p = 0.65, df = 1). Therefore, none of the habitat variables were adequate predictors of scavenging by woodland lions.

The probability of scavenging was equal across the entire area available to woodland lions during the dry season (Figure 13d), and was consistently higher than the wet season.
Table 57. Test of significance for combinations of habitat variables used in the logistic regression equation predicting scavenges by woodland lions during the dry season. Variables were significant if $p < 0.2$ as suggested Tabachnick and Fidell (1995) (see section 2.11, step 6).

<table>
<thead>
<tr>
<th>Variables</th>
<th>Coefficient ($\beta$)</th>
<th>S.E.</th>
<th>Test Statistic</th>
<th>Sig. ($p$)</th>
<th>Odds Ratio ($e^\beta$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Riparian Erosion</td>
<td></td>
<td></td>
<td>0.246$^w$</td>
<td>0.620</td>
<td></td>
</tr>
<tr>
<td>Riparian Vegetation</td>
<td></td>
<td></td>
<td>1.145$^w$</td>
<td>0.285</td>
<td></td>
</tr>
<tr>
<td>Confluence</td>
<td></td>
<td></td>
<td>1.172$^w$</td>
<td>0.279</td>
<td></td>
</tr>
<tr>
<td>Viewsheds</td>
<td></td>
<td></td>
<td>0.286$^w$</td>
<td>0.593</td>
<td></td>
</tr>
<tr>
<td>Constant</td>
<td>-2.557</td>
<td>0.328</td>
<td>60.690*</td>
<td>&lt; 0.001</td>
<td>0.078</td>
</tr>
</tbody>
</table>

$^w$ Wald test for inclusion of the variable

$^v$ Lagrange Multiplier test for exclusion of the variable
Figure 12. The relative probabilities of kills as predicted by the resource selection functions by plains lions during (a) the wet season and (b) the dry season, and by woodland lions during (c) the wet season and (d) the dry season.
Figure 12. The relative probabilities of kills as predicted by the resource selection functions by plains lions during (a) the wet season, (b) the dry season, and by woodland lions during (c) the wet season, and (d) the dry season.
Figure 13. The relative probabilities of scavenges as predicted by the resource selection functions by plains lions during (a) the wet season and (b) the dry season, and by woodland lions during (c) the wet season and (d) the dry season.
**4 Discussion**

The primary question that I address in this thesis is to what extent do lions depend on terrain as opposed to prey density for foraging? The discussion will follow the proceeding logical progression. Before distinguishing the roles of terrain versus prey density, I will first establish the distribution was not simply random (i.e. H_0). I will then continue with a discussion on the broad scale selection of prey density, and whether this can account for the distribution of kills and scavenges (i.e. H_A2). After establishing this point, I will focus the discussion on role of individual habitat features and how they affect selection by lions (i.e. refine the support for either prey or habitat hypotheses using the \( \chi^2 \) goodness-of-fit exact test). I will then discuss the possible correlations and interactions between habitat features (the loglinear analyses). I will conclude with a discussion on the combined role of habitat features in resource selection and their suitability in predicting the distribution of lion kills and scavenges in the Serengeti National Park (the logistic regressions). From these analyses we can establish whether lions select areas based on the amount of available cover or the density of prey.

A word of caution: the univariate analyses presented here should be interpreted with care. They represent multiple comparison between habitats using the same data set, which increases the risk of a Type I error. Although they have been Bonferroni corrected to reduce the risk, caution should still be exercised (Thomas and Taylor 1990). A second point is that the \( \chi^2 \) test uses observations rather than individuals as the sample unit and therefore the true degrees of freedom are misrepresented (Otis and White 1999). The third and final point is that the availability of habitat features in this study was estimated from sampling transects and maps, and therefore presumably there is some degree of variation around the estimate, which the \( \chi^2 \) test does not account for (Thomas and Taylor 1990, Jelinski 1991, Alldredge et al. 1998). The multivariate analyses (particularly the logistic regressions) are much more robust, and therefore more reliable (Manly et al. 1995, Campos et al. 1997, Alldredge et al. 1998, Boyce and McDonald 1999).
4.1 Nearest Neighbour Test and Spatial Randomness

If lion kills and scavenges occurred randomly, the observed mean nearest neighbour distance ($R_A$) should be equal to the expected mean nearest neighbour distance ($R_E$). In other words, the index of aggregation ($R_A / R_E$) should equal 1. If kills and scavenges are clustered then the index of aggregation should be less than 1. Furthermore, the clustering is significant when the Z-test is less than $-1.96$ ($\alpha = 0.05$) (Clark and Evans 1954, Krebs 1999).

Results show that the distribution of lion kills were significantly clustered, with the exception of woodland lion kills during the wet season (Table 9). Although the distribution of wet season kills by woodland lions indicated some clustering (index of aggregation = 0.82), this was not significant.

The distribution of scavenges by plains lions were also significantly clustered, however the distribution of scavenges by woodland lions was not clustered (Table 9). There were few observations of scavenging events by woodland lions ($n = 14$), which may partially account for a lack of significance.

The non-random distribution of kills and scavenges suggests that lions were selecting specific areas and further refutes the null hypothesis. Further analyses will address the question of whether these clusters occurred in areas with good habitat, or in areas with high prey density.

There was some indication that clustering becomes less well defined in the wet season (Figure 5), suggesting that there were some seasonal affects on selection. This broad scale seasonal dispersal maybe a partial result of the prey distribution, however lions may be selecting specific areas within these larger areas of prey abundance for hunting and scavenging.

It should be noted that the concentrations of points in the northwest portions of the available area (Figure 5) might have been a result of observer bias, rather than a result of the distribution of prey or habitat. This area was commonly searched for lions since it was close to the research station. Unfortunately, searching effort was not recorded in this study, and therefore searching bias could not be quantified. Despite this, all prides were searched for at least once a week and only the radio collared observations were included in this analysis, thereby decreasing the observer bias. The area to the northwest also has permanent water
(man-made dams) and so may be more attractive to lions than other unaltered areas.

4.2 Selecting for Prey Distribution: The Effect of the Short Grass Plains

From the preceding analysis it is apparent that the distribution of kills and scavenges was not random, which leads us to the next question. Can prey density account for the non-random distribution of kills and scavenges that we observe? In other words, were lions simply foraging in areas where there were the most prey?

If lions were selecting areas of high prey density for hunting and scavenging, then more kills and scavenges are predicted to occur on the short grass plains during the wet season than expected. This assumes that the majority of prey move onto the short grass plains during the wet season as described by Maddock (1979) to drop their calves and to take advantage of the calcium rich grasses (Kreulen 1975, Sinclair et al. 2000b). Furthermore, the reverse should be true for the dry season: there should be fewer than expected kills and scavenges on the short grass plains when the prey are not in the area.

According to the results there were fewer than expected kills and scavenges on the short grass plains during the dry season, regardless of correcting for searching bias. However, there were also fewer kills than expected during the wet season, and no difference in the number of scavenges from what was expected (Table 10). Although the dry season results concur with the predictions of the prey hypothesis, the wet season results do not (Table 58), which suggests that lions do not necessarily select areas of high prey density for hunting. Furthermore, active searching by lions for non-predated carcasses cannot be detected since there was no difference between the number of observed scavenges and the expected. If lions were actively searching for non-predated carcasses, the observed number of scavenges on the short grass plains during the wet season should be greater than expected (since the best place to find non-predated carcasses are where the prey are most plentiful (Sinclair et al. 2000b)). Areas with high prey density may be important primarily for supplementing their diet through scavenging.
Interestingly, of the 4 kills lions made on the short grass plains during the wet season, 2 of these were calves (i.e. 50%). Calves composed approximately 12% of the kills by plains lions during the wet season in the remaining area. This agrees with previous studies which found that lions tend to focus on young defenseless prey when cover is not available (Mills and Shenk 1992, Scheel 1993a, Stander and Albon 1993).

Table 58. The predictions of the prey hypothesis compared to the results of lion hunting and scavenging based on the seasonal movement of prey on and off the short grass plains (SGP). Observations occurred either more than expected by a random distribution (+), less than expected by a random distribution (-), or no differently from a random distribution (0).

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<th>Predictions of Prey Hypothesis (HA2)</th>
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</tr>
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<td></td>
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<tr>
<td>Kills</td>
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<td>Scav.</td>
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Even though there was little evidence supporting the broad scale selection for areas with high prey densities, the general seasonal distribution of kills and scavenges follows a similar pattern for both the woodland and plains areas (Figure 5). With the progression of the wet season, the kills and scavenges spread more to the southeast of the available areas. This coincides with the general seasonal pattern of prey distribution as described by Maddock (1979), and agrees with previously described changes in range size based on prey density (van Orsdol et al. 1985, Viljoen 1993).

It should be noted that these data represent primarily diurnal hunting and scavenging which limits the scope of the results (Palomares and Delibes 1992, Beyer and Haufler 1994). Nocturnal observations were difficult and rarely conducted, therefore any carcasses that were presumably acquired during the night were classified as "unknown acquisition" (see section 2.3 Sorting the Data). It is
possible that lions rely more on nocturnal hunting and scavenging on the short grass plains during the wet season since other forms of cover are limited (Schaller 1972b, Elliott et al. 1977, van Orsdol 1984, Stander 1992, Mills and Biggs 1993, Stander and Albon 1993, Funston et al. 2001).

### 4.3 The Use of Viewsheds for Foraging

If lions were selecting viewsheds for increasing foraging efficiency, then more kills and scavenges are predicted to occur in the viewsheds of kopjes than expected. Conversely, if prey distribution alone determines the location of lion foraging there should be no difference between the observed and expected values (i.e. prey do not distribute themselves in relation to kopjes).

The results suggest there was a trend towards more kills and scavenges in the viewsheds of plains kopjes than expected during the wet season (Table 11), however this was not consistently significant. Although this trend is questionable, it supports the hypothesis that habitat features determine the location of lion foraging (Table 59). During the dry season plains kopjes were less effective for hunting, however there was some indication they were useful for scavenging ($p < 0.1$) (Table 59). It is conceivable that plains lions may select areas with kopjes since they could increase the effective search area and thereby increase foraging efficiency. Furthermore, it appears that kopjes associated with other forms of cover (notably long grass) were useful for hunting, while kopjes on the short grass plains with limited cover were not as useful for hunting as they were for scavenging (Figure 6a and 6c). Previous research has shown that grass height can significantly effect the success of a hunt (Funston et al. 2001).

Results from the woodland lions show there were no differences between the observed and the expected number of kills and scavenges in the viewsheds of kopjes, with the exception of the dry season kills (Table 59). These results were partially consistent with either the null hypothesis of no selection, or that woodland lions were choosing hunting and scavenging locations based on the prey distribution. Curiously, however, during the dry season there were fewer kills in the viewsheds of woodland kopjes than expected, which does not concur with any of the predictions. Either this was because (a) woodland kopjes were consistently
avoided by all prey during the dry season and therefore no kills or scavenges could occur in their viewsheds, (b) woodland lions were avoiding kopjes, or (c) lions were selecting some other more important feature which was not within the viewsheds of woodland kopjes. It is unlikely that prey in the woodlands consistently avoid areas within a 1.5km radius of kopjes. Furthermore, locations of radio collared lions without carcasses provide no support for woodland lions avoiding kopjes. Lastly, Figure 6b shows kills were strongly clumped in specific areas outside the viewsheds, and suggests some other feature might be associated with the distribution of kills. Since vegetation obstructed the view from woodland kopjes, the maximum visible distance was 1.5km, as opposed to 3.5km from plains kopjes. Therefore, the reduced visibility form woodland kopjes may have excluded other important habitats from the viewshed, thus accounting for the fewer kills observed within woodland viewsheds.

4.4 The Use of River Confluences for Foraging

If lions were selecting confluences (according to \(H_{A1}\)), there should be (a) more kills in confluence areas than all other available areas, and (b) more kills than expected along any other part of the river (Table 59). Furthermore, confluences should neither increase nor decrease the searching efficiency of lions in finding carcasses, therefore there should be no difference between the observed number of scavenges and the expected. However, if lions were selecting areas with high prey density (according to \(H_{A2}\)), then there should be more kills and scavenges than expected in confluences only during times when the majority of prey were moving through the vicinity and getting funneled by the confluences (i.e. woodlands during the dry season and the plains during the wet season) (Pennycuick 1975, Maddock 1979). During the remainder of the time, when prey were not moving through the vicinity, there should be fewer kills and scavenges than expected in the total available area since prey should avoid riparian areas during these periods. If this was the case, then there should also be no difference between the number of kills and scavenges in confluences as compared to any other stretch of river.

The results show there were more kills observed in plains confluences than random (Table 15), which concurs with the habitat hypothesis (Table 59) and
suggests plains lions may be selecting confluences for hunting purposes. However, the selection for confluence areas over and above any other stretch of river was not as clear (Table 59). Although there were more kills than expected by plains lions in confluences than anywhere else along the rivers (Figure 7a), the differences were not significant (Table 15). Therefore, any selection for confluences was most likely complicated by selection for rivers.

Woodland lions killed more often in confluences than expected only during the dry season, which supports both the habitat and the prey hypotheses, and as such remains inconclusive (Table 59). However, during the wet season the results suggest that woodland lions may be selecting areas with high prey densities, since there were no differences between the observed and expected number of kills as partially predicted by the prey hypothesis (Table 59 and Figure 7b).

The scavenging results support the habitat hypothesis, which predicts confluences do not assist lions in searching for carcasses. The results consistently show no difference between the observed and the expected number of scavenges in confluences. These results could change if the sample size was larger, allowing plains and woodland lions to be analyzed separately. Trends in the data show more scavenges than expected in confluences (Figure 7c and 7d), which supports the prey hypothesis, however the differences were not significant (Table 17).

4.5 The Use of Erosion Embankments for Foraging

The predictions for the two alternate hypotheses state if (a) lions were using erosion embankments for hunting opportunities (according to Hₐ₁) then there should be more kills observed in areas with more embankments than expected regardless of season. Furthermore, there should be no difference in the number of scavenges since erosion embankments should neither assist nor impede scavenging opportunities for lions. However, if (b) lions were foraging in areas where the majority of the available prey were most of the time (according to Hₐ₂), then there should be no difference between the observed and expected number of kills, regardless of either the amount of embankments or season. Likewise, there should be no difference between the observed and expected number of scavenges,
regardless of season. This assumes that prey do not distribute themselves in relation to erosion embankments.

There were consistently more kills by plains lions in areas with embankments than expected for all seasons (Table 18 and Figure 8a). The results from the riparian areas (Table 19) as well as non-riparian areas (Table 20) concur with these findings. These results consistently support the habitat hypothesis suggesting that embankments were an important feature to the plains lions for hunting purposes, where as the distribution of prey was less important (Table 59).

Likewise, there were generally more kills than expected by woodland lions in areas with embankments regardless of season (Table 21 and Figure 8b). These results were consistent in areas within 200m of a river (Table 22) even though the sample size was precariously small. However, in areas further than 200m from a river there were more kills in eroded areas only during the dry season. During the wet season there were no differences (Table 23). The results almost entirely concur with the habitat hypothesis (Table 59), which predicts that woodland lions select areas with erosion embankments for hunting. However, erosion embankments may be less important to woodland lions during the wet season than during the dry season.

There were no differences between the observed and expected number of scavenges by plains lions in areas with embankments during the dry season (Tables 24 and 25, and Figure 8c). Since both the habitat and the prey hypotheses predict this outcome, it provides little insight (Table 59). However, during the wet season there were more scavenges than expected in areas with no embankments as well as in areas with over 250m of embankments (Table 24 and 25) which seems peculiar since erosion should not assist lions in finding carcasses. However, assuming the sample size was large enough, these results suggest that either (a) lions were scavenging from other predators that use erosion embankments for hunting, or (b) prey were dying from non-predation causes in these areas disproportionately to the habitat's availability, or (c) some combination of these factors. There were large areas on the short grass plains that had erosion terraces that were not associated with rivers (Figure 8c). These areas also correspond to the highest density of prey during the wet season (Pennycuick 1975, Maddock 1979). Therefore, if prey were dying in proportion to their density, and the eroded short grass plains have a high
concentration of prey during the wet season, then these areas may provide more scavenging opportunities than expected. There were insufficient observations of scavenges by plains lions in riparian areas to draw conclusions.

The observed number of dry season scavenges by woodland lions in areas with embankments was no different from the expected number (Table 26 and 27, and Figure 8d), supporting both the habitat hypothesis and the prey hypothesis. As such, the results remain inconclusive (Table 59). There were insufficient observations of scavenges in the wet season for an effective analysis, however the trend suggested there was no difference. Stratifying the data into riparian and non-riparian areas made the sample size too small to be conclusive. However, with this considered, the results hint there may be more scavenges in non-riparian areas with lots of erosion and with no erosion during the dry season (n = 7) (Table 27), which was similar to the results of the plains lions in non-riparian areas during the wet season (Table 59). Although this is speculative at best, this result suggests that prey may be dying in non-riparian eroded areas more than expected (perhaps due to other predators) during the dry season when prey densities in the woodlands are generally higher than on the plains (Pennycuick 1975, Maddock 1979).

4.6 The Use of Woody Vegetation for Foraging

If lions were selecting woody vegetation to conceal themselves while hunting (according to H_{A1}), then more kills are predicted to occur in thicker vegetation than expected. However, if lions were selecting areas with high prey density for hunting (according to H_{A2}), then there should be fewer than expected kills observed in areas with thicker vegetation, assuming the majority of prey avoid thick vegetation (Jarman and Sinclair 1979, Ben-Shahar 1992, FitzGibbon and Lazarus 1995). Since thick vegetation obstructs the view and makes searching difficult, there should be fewer scavenges than expected in thicker vegetation.

The results for the plains lions show that there were consistently no differences between the observed and the expected number of kills in vegetated areas (Table 28). The only exception was during the dry season when there were more kills observed in thicker vegetation than expected, however this selection appeared to be confounded by the affect of riparian associated vegetation (Figure
In riparian areas plains lions did not appear to select thicker vegetation over any other part of the river (Table 29), nor did they select areas with thicker vegetation in non-riparian areas (Table 30). These results neither support nor refute the predictions of the either habitat or the prey hypotheses (Table 59), suggesting that vegetation has a negligible affect on the distribution of kills by plains lions.

Woodland lions killed more often than expected in thicker vegetation (Tables 31 and 32) which supports the habitat hypothesis (Table 59). However, areas with thick vegetation away from the rivers were not selected (Table 33 and Figure 9b), suggesting selection for habitat was influenced by proximity to rivers. The nature of the affect of rivers on selection could simply be that (a) lions were selecting some other factor, such as water, that was associated with riparian areas, or (b) there was a synergistic affect of some other attribute associated with riparian areas (such as water) and vegetation. The possibility of a synergistic effect between vegetation and water is investigated in section 4.8 Correlations Between Habitats.

There was no difference between the observed and expected number of scavenges for plains lions (Table 34 and Figure 9c), suggesting vegetation did not significantly influence the distribution of scavenges (Table 59). There was insufficient data in riparian areas to draw conclusions, however the results from non-riparian areas (Table 35) support this conclusion.

There was evidence that woodland lions scavenge more than expected in vegetated areas during the dry season (Table 36), which does not support any of the hypotheses (Table 59). However, there was no difference between the observed number of scavenges and the expected number in non-riparian areas (Table 37), suggesting that selection for thicker vegetation may be a result of selection for riparian areas alone (small sample sizes made this impossible to test) (Figure 9d). If woodland lions were selecting vegetation alone (i.e. not necessarily riparian areas) for scavenging, then either (a) woodland lions were more effective at finding carcasses in thick vegetation (which is unlikely), or (b) prey were more likely to die by other means in areas with thicker vegetation (i.e. non-lion predation, disease, greater proportion of older or infirm animals, etc.). If prey were more likely to die by other means in areas with thicker vegetation, and thicker vegetation was correlated with riparian areas, then it is conceivable that these vegetated riparian areas may
attract infirm animals, especially since access to water is likely. Equally, vegetated riparian areas may also be locations where other predators (such as leopard) may be more successful at hunting (Bertram 1982, Mills and Biggs 1993), thereby increasing the probability of woodland lions finding a carcass. Regardless, there were only 10 observations of woodland scavenges, therefore these results remain speculative at best.

4.7 Use of Water for Foraging

If lions were selecting areas near water for hunting according to the habitat hypothesis (H_{A1}), then more kills should be observed in these areas than expected. Furthermore, since access to water should neither increase nor decrease the probability of lions finding carcasses, the observed number of scavenges in areas surrounding water should be no different from the expected number if the habitat hypothesis (H_{A1}) is true. However, if lions were hunting and scavenging in areas where the majority of the prey were most of the time, as predicted by the prey hypothesis (H_{A2}), then fewer kills and scavenges should be observed near water. This assumes prey avoid these areas most of the time, other than for brief drinking bouts.

The results from the plains lions show that not only were there more kills in proximity to water than expected (within 200m), but there were also more kills immediately adjacent to water (within 50m) for both seasons (Tables 38 and 39, and Figures 10a and 11a). This supports the predictions of the habitat hypothesis (Table 59), suggesting plains lions do not necessarily go to areas where the majority of prey are, but stay in areas where prey may be easier to catch. The differences between the observed and expected number of kills were greatest during the dry season when water was scarce. During the wet season when water was abundant and prey have unrestricted access to it, plains lions may not be able to use access to water to the same extent as they do during the dry season.

Woodland lions killed more often than expected in areas surrounding water during the dry season, however during the wet season this trend was not as clear (Tables 40 and 41, Figures 10b and 11b). The dry season results support the habitat hypothesis (Table 59), suggesting that woodland lions use water to increase
their hunting success when access to water is restricted. However, during the wet season, when the prey are less dependent on access to water, woodland lions did not select areas with water for hunting. The wet season results support neither the habitat nor the prey hypotheses, suggesting that water had only a minor influence on the location of wet season kills by woodland lions.

There were no differences between the observed and expected number of scavenges by plains or woodland lions in the areas surrounding water (Tables 42 to 45). These results suggest that lions may not scavenge in areas with high prey density, since fewer scavenges would be expected if this was the case (assuming the majority of prey avoid rivers most of the time). Therefore, the scavenging results support the habitat hypothesis, rather than the prey hypothesis (Table 59). It is possible that these results may be an artifact of small sample size, especially for woodland lions during the wet season when there were too few observations for an effective analysis.

The distribution of scavenges for both plains and woodland lions moved more to the southeast during the wet season (Figures 10c, 10d, 10c, and 10d). This movement is away from the watercourses and conforms with the general seasonal prey distribution (Pennycuick 1975, Maddock 1979). Therefore, the seasonal correlation between the location of lion scavenges and prey distribution supports the prey hypothesis on the larger scale, however on a smaller scale the scavenging results support habitat selection hypothesis.
Table 59. The predictions of the seasonal foraging success of plains (Pl) and woodland (Wd) lions if the distribution of lion kills is determined by habitat characteristics (H\textsubscript{A1}) as opposed to prey distributions (H\textsubscript{A2}), and the observed distribution of kills and scavenges. The symbols +, -, or 0 indicate the observed number of kills or scavenges were significantly (p < 0.01) higher, lower or no different from expected, respectively. Symbols in brackets indicate marginally significant trends in the data (p < 0.1).

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<th>Predictions (H\textsubscript{A2})</th>
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| Non-Rip    | +     | -   | -     | -        | 0   | 0     |
| Wet Total  | +     | -   | -     | -        | +   | +     |

| Riparian   | +     | -   | -     | -        | +   | +     |
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</table>
4.8 Correlations Between Habitats Features

Many of the habitats identified by this study were not independent of each other. In other words, as can be imagined, the presence of one habitat (e.g. vegetation) could be dependent on the presence of another habitat (e.g. water). The results of the loglinear analysis indicated that confluences and woody vegetation, confluences and access to water, erosion and access to water, and woody vegetation and access to water all naturally occurred together on the plains regardless of season, and could not be considered separately. In the woodlands only confluences and access to water, and erosion and access to water were correlated during the wet season. Interestingly, woody vegetation was not correlated with any other habitat during the wet season. Similarly, during the dry season only erosion and access to water, and woody vegetation and access to water were correlated in the woodlands, while confluences remained independent. These habitat combinations (or factors) were re-termed confluence vegetation, confluence water, riparian erosion, and riparian vegetation, accordingly.

4.9 Resource Selection Functions: Combined Habitats versus Prey Density

If lions were selecting areas with specific habitat features for foraging purposes (as proposed by H_{A1}), then the odds ratio \(e^0\) for the habitat factors included in the logistic regression should be greater than 1 (i.e. there should be a greater chance of an area being classified as good for hunting or scavenging if those features were present). However, if lions were selecting areas with high prey density (according to H_{A2}), then areas that provide cover for predators should be avoided by prey, making the odds ratio less than 1 (i.e. there should be a lower chance of an area being classified as good for hunting or scavenging if those features were present). Finally, if the distribution of kills and scavenges occurs randomly (according to H_0), then none of the habitat factors should be significant.

It should be emphasized that the probabilities generated by the logistic regression should be viewed as relative values rather than absolute. In other words, certain areas have a higher or lower probability of a kill relative to other
areas. The values are only proportional to the real probabilities (Manly et al. 1995, Boyce and McDonald 1999). Furthermore, it is assumed that the values are at least partially indicative of lions' ability to predict the suitability of a habitat for hunting or scavenging.

4.9.1 Plains Lions

4.9.1.1 Plains Wet Season Kills

The factors significant in predicting kills by plains lions during the wet season were confluence vegetation, riparian erosion, riparian vegetation and the viewsheds from kopjes (Tables 60), indicating that the distribution of kills was not random. Furthermore, of these factors, confluence vegetation, riparian erosion, and viewsheds had odds ratios greater than 1 (Table 47), and therefore support the habitat hypothesis (Table 60). Only riparian vegetation had an odds ratio less than 1, thereby supporting the prey hypothesis.

4.9.1.2 Plains Wet Season Scavenges

Wet season scavenges by plains lions were not random. Confluence vegetation, confluence water, and viewsheds were significant factors in predicting scavenges by plains lions during the wet season (Table 60). Both confluence vegetation and viewsheds had odds ratios greater than 1 (Table 48), indicating there was a higher chance of success as the amount of cover (or viewsheds) increased, and thereby support the predictions of the habitat hypothesis. Only confluence water had an odds ratio less than 1, and therefore supported the prey hypothesis (Table 60).

4.9.1.3 Plains Dry Season Kills

The factors significant in predicting the location of kills by plains lions during the dry season were confluence vegetation, confluence water and riparian erosion (Table 60). This suggests that the distribution of kills did not occur randomly. Furthermore, of these factors, confluence vegetation and riparian erosion had odds ratios greater than 1 (Table 50), and thereby support the habitat hypothesis. In
fact, kills were on average twice as likely to occur in these areas. Only confluence water had an odds ratio less than 1, which supports the prey hypothesis (Table 60).

4.9.1.4 Plains Dry Season Scavenges

The habitat factors that were significant in predicting the dry season scavenges by plains lions were the same as the wet season: confluence vegetation, confluence water, and viewsheds (Table 51). Since the distribution of scavenges can be predicted with reasonable accuracy using these variables, this suggests the scavenges were not randomly distributed. Scavenges were twice as likely to occur in confluence vegetation and viewsheds (as indicated by their odds ratios, Table 51), which supports the habitat hypothesis. Conversely, confluence water had an odds ratio less than 1 and supports the prey hypothesis (Table 60).

Table 60. A summary of the habitat factors that were significant in predicting plains lion kills and scavenges based on season. (+ indicates the habitat factor was significant and had an odds ratio greater than 1, - indicates the habitat factor was significant and had an odds ratio less than 1, 0 indicates the habitat factor was not significant).

<table>
<thead>
<tr>
<th>Habitat factor</th>
<th>Predictions</th>
<th>Kills</th>
<th>Scavenges</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$H_{A1}$</td>
<td>$H_{A2}$</td>
<td>Dry</td>
</tr>
<tr>
<td>Confluence Vegetation</td>
<td>+</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Confluence Water</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Riparian Erosion</td>
<td>+</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Riparian Vegetation</td>
<td>+</td>
<td>-</td>
<td>0</td>
</tr>
<tr>
<td>Viewsheds</td>
<td>+</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
4.9.1.5 Summarizing the Probability of Plains Kills

The areas with the highest probability of kills by plains lions during the wet season were consistently near rivers (Figure 12a), which was not surprising given the results of the logistic regression. The non-riparian areas with highest probabilities of kills generally occurred in areas with vegetation, and/or erosion terraces, and/or were in the viewsheds of kopjes. It is conceivable that any of these features could increase the chances of a kill by either increasing the searching efficiency or providing cover for a stalk and ambush style hunt.

Similarly, during the dry season the areas adjacent to rivers consistently had the highest probabilities of a kill (Figure 12b). However, the non-riparian areas that had high probabilities of a kill were due to vegetation and/or erosion terraces only, and not viewsheds.

4.9.1.6 Summarizing the Probability of Plains Scavenges

Although the overall probabilities of scavenging were much lower than killing, the areas with the highest chances of scavenging by plains lions during both the wet and the dry season were within the view of kopjes and/or had vegetation (Figures 13a and 13b). It is unlikely that vegetation would increase the searching efficiency of lions for carcasses (as kopjes would), therefore either lions were scavenging from other predators that select vegetation for hunting (such as leopard), or more prey die from non-predator causes in vegetated areas. Scavenging does not seem to be influenced by riparian areas.

4.9.2 Woodland Lions

4.9.2.1 Woodland Wet Season Kills

The distribution of kills by woodland lions could be successfully predicted by riparian erosion alone (Table 61), providing evidence that the distribution was not random. The odds ratio suggested that there was an increased likelihood of woodland lions killing closer to water and with more erosion embankments (Table 53), which supports the habitat hypothesis. Interestingly, confluence water,
vegetation and viewsheds did not significantly influence the success of kills by woodland lions during the wet season and were not significant predictors.

4.9.2.2 Woodland Wet Season Scavenges

The logistic regression predicting scavenges by woodland lions during the wet season failed to include any habitat factors (Table 54 and 61). This could indicate that the distribution of scavenges was not related to any of the habitat parameters (i.e. it was random), however it was more likely due to a small sample size (n = 4).

4.9.2.3 Woodland Dry Season Kills

Kills by woodland lions during the dry season could be successfully predicted by riparian erosion and by riparian vegetation (Table 56), thereby providing no support for the hypothesis that kills were randomly distributed. Furthermore, kills were more likely to occur in areas with riparian erosion and with riparian vegetation, since the odds ratios were greater than 1 (Table 56). This supports the habitat hypothesis (Table 61).

4.9.2.4 Woodland Dry Season Scavenges

None of the habitat factors successfully predicted the location of scavenges by woodland lions during the dry season. Although this may indicate that the distribution of scavenges was random, it was most likely a result of small sample size (n = 10).
Table 61. A summary of the habitat factors that were significant in predicting woodland lion kills and scavenges based on season. (+ indicates the habitat factor was significant and had an odds ratio greater than 1, - indicates the habitat factor was significant and had an odds ratio less than 1, 0 indicates the habitat factor was not significant, and N/A indicates the habitat combination does not occur during that season).

<table>
<thead>
<tr>
<th>Habitat factor</th>
<th>Predictions</th>
<th>Kills</th>
<th>Scavenges</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$H_{A1}$</td>
<td>$H_{A2}$</td>
<td>Dry</td>
</tr>
<tr>
<td>Confluence</td>
<td>+</td>
<td>-</td>
<td>N/A</td>
</tr>
<tr>
<td>Riparian</td>
<td>+</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Vegetation</td>
<td>+</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Vegetation</td>
<td>+</td>
<td>-</td>
<td>N/A</td>
</tr>
<tr>
<td>Confluence</td>
<td>+</td>
<td>-</td>
<td>0</td>
</tr>
<tr>
<td>Viewsheds</td>
<td>+</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

4.9.2.5 Summarizing the Probability of Woodland Kills

The probabilities of woodland lions making a kill during the wet season were consistently greater in riparian areas than in non-riparian areas (Figure 12c). The regions with the highest probabilities in non-riparian areas were associated with erosion terraces.

The probabilities of woodland lions making a kill were generally greater during the dry season (Figure 12d) than during the wet season. Riparian areas associated with erosion embankments or vegetation had the highest probabilities of dry season kills by woodland lions. Conversely, areas identified as having the lowest probability of a kill were not associated with erosion embankments or vegetation and were away from rivers. Therefore, erosion embankments and vegetation probably assist stalking lions by providing cover, thereby increasing their
chances of a successful hunt. Furthermore, the cover provided by erosion embankments and vegetation seems particularly important in areas associated with water, possibly because water could provide a predictable location where prey are encountered.

Interestingly, viewsheds did not significantly influence the probability of woodland lions making a kill. It is possible that trees may block the view from kopjes in the woodlands, thereby providing no benefit for searching lions.

4.9.2.6 Summarizing the Probability of Woodland Scavenges

None of the identified habitat features were significant predictors of woodland scavenges, therefore the probabilities of scavenges were constant across the entire area available to woodland lions for both seasons (Figures 13c and 13d). It is possible that this may have been the result of a small sample sizes (wet season \( n = 4 \), and dry season \( n = 10 \)), rather than a random distribution.

4.10 Limitations of the TIN Surface Models

The accuracy of the TIN surface models in estimating the availability of habitats such as erosion embankments and vegetation was done by comparing map estimates with ground truthing records as described in the methods (see section 2.8.5 Assessing the TIN Surface Models of Erosion and section 2.9.1 Assessing the TIN Surface Models of Woody Vegetation). It was found that the TIN surface models generally over-estimate the amount of cover available. The effect of the bias was to decrease the selection coefficient (i.e. the ratio of use : availability) for areas with more cover, and therefore the results presented in this thesis are probably conservative estimates of selection. Many of the selection coefficients are already highly significant, and therefore will be unaffected by this bias. But several others are not significant (e.g. selection for vegetation by plains lions), and so a corrected estimate of availability could result in a larger selection coefficient. This would suggest that lions could be selecting cover more than was previously estimated.
5 Conclusions

To what extent do Serengeti lions depend on habitat as opposed to prey density for foraging? Do lions hunt (or scavenge) in areas where there are many prey ($H_{A2}$), or do they forage in areas with much cover where there are fewer but easier-to-catch prey ($H_{A1}$)? The two hypotheses lead to mutually exclusive testable predictions since prey avoid high risk areas. Previous studies of habitat use by predators have rarely taken the potential affect of prey densities into account, thus making this study unique.

The distribution of kills by plains and woodland lions was not random. Although the general distribution of kills coincided with the seasonal movement of prey, there was little statistical evidence for the broad scale selection of areas with high prey densities (Table 58). Plains lions tended to hunt more often than expected in the viewsheds from kopjes (primarily during the wet season, as suggested by the logistic regression), in river confluences (although not conclusively), in areas with erosion embankments, and in areas with water nearby (Table 59). Vegetation alone was of little consequence for plains lions, however a multivariate resource selection function suggested that vegetation combined with confluences were important. Likewise, erosion embankments associated with riparian areas were also important features for hunting by plains lions (Table 60). Woodland lions were more likely to kill their prey in river confluences (only during the dry season), in areas with erosion embankments, in areas with woody vegetation (although this was not conclusive), and in areas with access to free water (only during the dry season) (Table 59). Furthermore, a resource selection function revealed that woodland lions were more likely to kill prey in riparian areas with erosion and also in areas with vegetation associated with rivers (Table 61). Therefore, although the results were not always conclusive, and somewhat reflect the opportunistic nature of lions, they do suggest that lions tend to forage in areas where prey are easier to catch, rather than where there are high numbers of prey (Tables 59, 60, and 61). These results concur with previous studies on lions and other felids that found a general selection for areas with more cover (Schaller 1972b, van Orsdol 1984, Prins and Iason 1989, Sunquist and Sunquist 1989, Crawshaw and Quigley 1991, Ruggiero 1991, Scheel and Packer 1991, Mills and
Biggs 1993, Stander and Albon 1993, Maehr and Cox 1995, Gros and Rejmanek 1999, Funston et al. 2000, Palomares et al. 2001, Edwards et al. 2002) and for riparian areas (Schaller 1972b, Litvaitis et al. 1986, Crawshaw and Quigley 1991, Ruggiero 1991, Palomares et al. 2001). This study, however, goes one step further and shows lions not only select habitats based on cover, but that lions will often select cover over high prey densities. Although this has been suggested by several authors (Litvaitis et al. 1986, Mills et al. 1995, Pike et al. 1999), it has rarely been shown in any felid (the exceptions are Murray et al. (1994), Palomares et al. (2001)). Given the lions' stalk and ambush hunting technique, these results intuitively makes sense since cover should increase a lion's foraging success.

The results from the scavenging analyses were not as conclusive as the kills, partially due to small sample sizes. Generally, the results concurred with the predictions of the habitat hypothesis (Table 59). The distribution of scavenges by plains lions were not random. A multivariate resource selection function investigating scavenging by plains lions identified viewsheds and vegetation associated with confluences as important features (Table 60). There were insufficient observations of scavenges by woodland lions to discern a non-random distribution. Furthermore, a resource selection function failed to predict the distribution of scavenges by woodland lions (Table 61), concluding the distribution was no different from random. Incidentally, there are other reports of low scavenging rates by woodlands lions (Makacha and Schaller 1969) which, assuming this was not a searching effort bias or an observer bias associated with thicker vegetation, could indicate woodland lions are less reliant on scavenging as a source of food. In summary, although it is likely that lions supplement their diet by opportunistically scavenging in areas with high prey density, there was little statistical evidence that lions actively select areas with high prey density for scavenging (Table 58).

The major conclusion from this study is that although lions require adequate prey for survival, the habitat features available to them for hunting and scavenging purposes are more important than simply prey densities.
5.1 Relation to Functional Response

The relationship between an organism's rate of consumption and the density of its food source is known as its functional response (Solomon 1949). Holling (1959) classified functional responses into three broad types.

Type II functional responses, where the rate of consumption increases with prey density then gradually decreases at higher prey densities and finally plateaus at some density, are most common. Generally, organisms with a Type II functional response are limited by the handling time of their prey. Initially, as prey density increases, finding prey becomes easier. However, above a certain density the prey are so easy to find that the consumer is limited only by the rate at which it can catch, consume, and digest its prey, therefore the relationship reaches its maximum and plateaus (Begon et al. 1996).

In a Type I functional response, the consumption rate of the predator increases linearly with the prey density. Above a certain prey density the rate of consumption reaches its maximum and plateaus: that is, the predator is satiated and is physically limited by the number of prey it can eat per unit time. The feeding rate below the plateau is limited only by the rate at which prey are found, which depends on the density of prey. There is no slowing of the feeding rate due to handling time as the density increases, unlike a Type II response (Begon et al. 1996).

In a Type III functional response, the predator's feeding rate is low at low prey densities and accelerates as the density increases, until it asymptotes at the maximum consumption rate. The maximum consumption rate is determined, as in Type II, by the predator's handling and processing time of the prey. However, unlike Type II, at low prey densities the predator either switches to an alternate prey source, or has a decreased searching efficiency and therefore a lower consumption rate than would otherwise be expected based on prey densities (Begon et al. 1996).

If lions were selecting areas with high prey density for hunting and scavenging (according to $H_{A_3}$), this would support a Type III functional response. In other words, lions would not go into areas with low prey densities, even though the
prey may be easier to catch. However, the results indicate that lions are more likely to select areas with good cover, and therefore fewer prey (assuming prey avoid these dangerous areas), which supports a Type II functional response. Furthermore, since prey densities change drastically with season (Pennycuick 1975, Maddock 1979), and lions continue to catch at least some prey regardless of season, this suggests that the rate of consumption was not entirely dependent on high prey densities. This agrees with the predictions of a Type II response. Elliott et al. (1977) also suggested that lions will search more during periods of low prey density to obtain sufficient food, which further supports a Type II functional response.

It is important to note that while this study sheds some light on the functional response between lions and their prey, the type of functional response may well change if the analyses were repeated based on individual prey species. It is entirely likely that lions switch between prey species based on season (Scheel 1993a, Mills et al. 1995, Scheel and Packer 1995), particularly since they seldom leave their territories and the majority of prey are migratory. Furthermore, not all prey are equally vigilant and lions may select less vigilant prey (Scheel 1993b). Therefore, if lions switch between prey species, this would concur with the predictions of the Type III response curve, rather than the Type II as suggested here.

5.2 Implications for Source – Sink Populations

There are some implications of this study for source and sink metapopulation dynamics of lions. It is known that male lions seldom hunt (Scheel and Packer 1991). Their large body size makes them conspicuous and slow. For the most part, males scavenge kills from their pride females, and even steal the carcass from the females and cubs (Schaller 1972b). In times of shortage, it is generally the cubs that die of starvation first (Bertram 1973, Eloff 1984, van Orsdol et al. 1985). However, in woodland habitats males are more capable of hunting for themselves, especially large prey such as buffalo (Funston et al. 1998, Funston et al. 2001). Furthermore, since cooperation between pride mates is required to hunt buffalo (Packer et al. 1990, Scheel and Packer 1991, Packer and Pusey 1997), males may be able to contribute more to a hunt due to their large body mass. It has also
been shown that males spend less time with their pride females in woodland habitats than plains habitats, and therefore scavenge less (Funston et al. 1998). This has 2 results; (a) when a pride kills a buffalo there is plenty of food (Scheel 1993a), meaning that the cubs do not go hungry, and (b) if males can feed themselves more, then they scavenge less from their pride females which results in more food for the cubs. If males hunt more in the woodlands then cub survival in the woodland environments should be greater than that in the plains environment. Therefore, woodland populations could act as a source population for the plains (Hanby et al. 1995). There is evidence that lions living in woodland habitats may be buffered against seasonal changes in prey density primarily by hunting buffalo (Scheel and Packer 1995). To speculate one step further, it is possible that if the woodland areas are more productive for lions, they could be driving the lion population dynamics on the less productive plains (Oksanen 1990, Oksanen et al. 1992). In other words, the spill over of excess lions from the woodlands (especially males which may have extremely low chances of taking over a pride), may improve their chances of survival in less competitive areas, and therefore could continually disrupt the resident plains prides through inter-pride aggression or male takeovers.

5.3 Implications for Management

The major finding from this study, which has obvious repercussions on management, is that although lions require adequate prey for survival, the habitat features available to them for hunting and scavenging are more important than simply prey densities. The results show that generally areas that provide cover for stalking lions have more kills than expected, despite having fewer prey. This seems intuitively correct, considering lions' opportunistic stalk and ambush hunting tactics (Elliott et al. 1977). The habitat features that were identified as being important for hunting at some point during the season by either plains or woodland lions are summarized in Table 59. (1) The viewsheds from kopjes provide a vantagepoint from which lions can easily search for prey. Kopjes were used for hunting primarily by lions on the plains during the wet season, and not in the woodlands, probably because thick vegetation obscured the view from woodland kopjes. (2) River confluences may serve to funnel prey into confined spaces,
however evidence that lions use confluences for hunting was weak. (3) Both plains and woodland lions selected erosion embankments (including riverbanks, ditches, and natural erosion terraces) for hunting. Presumably, erosion embankments provide cover for lions during a hunt. (4) Likewise, woody vegetation provides cover for stalking lions, however mainly woodland lions selected it. (5) Finally, access to free water was strongly selected for by both plains and woodland lions. Presumably, access to water provides a predictable location to encounter prey since prey are forced into these areas to drink, especially during the dry season. Features that were important for scavenging (Table 59) were (1) the viewsheds from kopjes (primarily by lions on the plains), and (2) erosion embankments (although this was questionable).

As one would expect, some of these habitat features occur together naturally. The combinations of habitat features that were important for either the plains or woodland lions at some point in the season were (1) confluences in conjunction with vegetation, (2) erosion embankments next to rivers with water, and (3) vegetation next to rivers with water (primarily by woodland lions) (Tables 60 and 61).

From these results it is clear that there are implications of man-made features for conservation. For example, man-made waterholes could increase the success of lions hunting in the vicinity, since they provide predictable locations to encounter prey. Road ditches increase the amount of cover available for stalking lions, and could increase the hunting efficiency, especially where the roads follow rivers. If fire suppression results in increased vegetative cover this could further increase lions’ success at capturing prey. Therefore, the impact of man-made features (such as waterholes and ditches) as well as management techniques (such as fire suppression) could impact the hunting success of lions, and conversely, the conservation of their prey.

There was little evidence that lions chose areas with high densities of prey over areas where prey may be easier to catch. However, areas with lots of prey are nevertheless still important, especially for scavenging opportunities. The short grass plains are especially noteworthy. During the wet season this area supports high densities of prey (primarily wildebeest and zebra) (Pennycuick 1975, Maddock 1979), but lions were seldom seen hunting there. Instead, when the prey were on the short grass plains, many hunts were observed in, or on the verge of, the
adjacent long grass plains. It was more common for lions to scavenge from other predators, such as hyena and cheetah, than to hunt on the short grass plains. The high predation pressure in areas surrounding the short grass plains may encourage the herds to stay in the relative safety of the short grass plains for longer than would otherwise be expected (Abrams 2000), thereby increasing the grazing pressure and helping to keep the short grass plains short (McNaughton 1983, 1984). The effect of grass height on hunting success in lions has been noted by other researchers (Funston et al. 2001). It is possible that lions focus more on young, defenseless prey which may be easier to catch on the short grass plains where the cover is limited (2 out of 4 kills observed on the short grass plains were calves, where as calves comprise about 12% of kills off the short grass plains). Furthermore, the short grass areas are probably important for nocturnal hunting; a factor that this study did not address.

Although this study indicates that lions are capable of catching prey, even when prey densities in their territories are low, there is little evidence that lions are capable of controlling the densities of large populations of prey. Their affect on smaller populations of prey may be greater. This is supported by several authors (Schaller 1972b, Bertram 1979, Eloff 1984, Sinclair et al. 1985, Fryxell et al. 1988, Caro and FitzGibbon 1992, Mills and Shenk 1992, Viljoen 1993, Sinclair 1995a, Mduma et al. 1999).
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7 APPENDICES

7.1 Appendix 1: Distribution of sampled locations (used and available)

Figure 14. The distribution of used and available locations. Used points include locations where prey were killed, scavenged, or acquired through unknown circumstances. Available points include riparian and non-riparian locations.
7.2 Appendix 2: The Goodness of Fit Exact Test

7.2.1 Notes on the Goodness of Fit Exact Test ($\chi^2$)

The use of traditional $\chi^2$ goodness of fit tests in resource selection studies has been criticized. The probability of committing a Type I error increases, especially when availability has been estimated from a small sample with large error margins (Thomas and Taylor 1990).

The premise behind this test is that observations are compared to a distribution of $\chi^2$ values that are created based on the expected probabilities from the study, rather than to the standard $\chi^2$ distribution (i.e. a Bayesian style approach (Ellison 1996)). The advantage is that the test is tailored to the data, and therefore small expected values do not bias the outcome to the same extent as the traditional $\chi^2$ test does. This decreases the chance of a Type I error. The code was written by Dolph Schluter (pers.com.). It can be run as a function (called gofsim) in S-plus.

7.2.2 Steps of the code:

1) obs = the numbers of observations in each category (in this example there were 6 categories, category 1 has 37 observations, etc.)

   expf = the expected number of observations for each category (in this example category 1 was expected to have 40 observations, etc.)

2) The code calculates the observed $\chi^2$ statistic (chisq) from obs and expf.

3) The code then generates a new set of observations (newobs) using the probabilities calculated from the expected values (expf). This is a random sample based on the expected frequency and should sum up to the total number of observations (nobs).

4) The code then calculates a new $\chi^2$ value (newchisq) from the new set of observations (newobs) and the expected values (expf).
5) It then repeats steps 3 and 4 a specified number of times (nsim). The number of simulations (nsim) should equal at least 10,000 to ensure a good estimation.

6) A distribution of the 10,000 new \( \chi^2 \) (newchisq) values (referred to as \( \chi_{E}^2 \)) is generated. The observed \( \chi^2 \) value from the data is compared to this is the new \( \chi_{E}^2 \) distribution which is tailored to the data.

7) Using this new \( \chi_{E}^2 \) distribution, the code calculates the fraction of simulated 10,000 \( \chi_{E}^2 \) that exceed the observed \( \chi^2 \). This is the p-value.

8) Reject \( H_0 \) if \( p \leq 0.05 \), although in my thesis I compare the effects of 5 habitats. Therefore, \( H_0 \) was rejected if \( p \leq 0.05/5 = 0.01 \) (i.e. a Bonferroni correction for multiple comparisons).

7.2.3 The Code

gofsim<-function (obs=c(37,6,3,7,6,5), expf=c(40,18.9,2.7,1.4,0.9,0.1), nsim=10000){
  nobs<-sum(obs)
  nexp<-sum(expf)
  if(nobs!=nexp) stop(message="number of obs and exp must be equal")
  result<-list()
  dist<-numeric(nsim)
  chisq<-sum(((obs-expf)^2)/expf)
  expfrac<-expf/nobs
  for(i in 1:nsim){
    z<-runif(nobs)
    newobs<-hist(z,breaks=c(0,cumsum(expfrac)),plot=F)$counts
    newchisq<- sum(((newobs-expf)^2)/expf)
    dist[i]<-newchisq }
}
result$chisq<-chisq
result$Pvalue<-length(dist[dist>chisq])/nsim
return(result)
7.3 Appendix 3: An Example of Resource Selection Functions Using Logistic Regressions

7.3.1 Background

Habitats often do not occur independently of each other. In other words, the presence of one habitat may predispose the area to the presence of another (for example, more vegetation may occur near areas with water). Therefore, prior to conducting the logistic regression, correlations between all the habitat variables (except the viewsheds) were investigated using loglinear analysis. Independent loglinear analyses were conducted for plains wet season, plains dry season, woodland wet season, and woodland dry season, thereby identifying all correlations between habitats based on season. The following key accounts for all possible combinations of habitats identified by the 4 loglinear analyses.

All the used and available data points were re-coded according to the loglinear regression and were then used to calculate the logistic regressions equations.

7.3.2 The Key

Confluence vegetation (CV)

- not in confluence and no vegetation (<5%) 0
- not in confluence but has vegetation (≥5%) 1
- in confluence but no vegetation (<5%) 2
- in confluence and has vegetation (≥5%) 3

Confluence water (CW)

- not in confluence and no water within 200m 0
- not in confluence but has water within 200m 1
- in confluence but no water within 200m 2
- in confluence and has water within 200m 3
Riparian erosion (RE)
- no erosion (0m) and no water within 200m: 0
- no erosion (0m) but has water within 200m: 1
- erosion (>0m) but no water within 200m: 2
- erosion (>0m) and water within 200m: 3

Riparian vegetation (RV)
- no vegetation (<5%) and no water within 200m: 0
- no vegetation (<5%) but has water within 200m: 1
- vegetation (≥5%) but no water within 200m: 2
- vegetation (≥5%) and water within 200m: 3

Viewsheds (VSh)
- not in the viewsheds of kopjes: 0
- in the viewsheds of kopjes: 1

7.3.3 An Example

The following is an example of a resource selection function using logistic regressions to predict the probability of wet season kills by plains lions.

The loglinear analysis for the area available to plains lions during the wet season identified confluences and woody vegetation, confluences and access to water, erosion embankments and access to water, and woody vegetation and access to water as being significantly correlated (Table 46). Therefore, it was clear that these habitats were more likely to be found together on the plains during the wet season, and therefore should be considered jointly rather than independently. The data points (i.e. all the locations where plains lions actually killed an animal during the wet season as well as all the sites available to plains lions during the wet season) were re-coded based on the results of the loglinear analysis to account for these correlations, according to the key outlined above. For example, if a point occurred outside a confluence and had no vegetation (<5%), the confluence vegetation (CV) value for this point was 0. Similarly, if a point occurred within a confluence and with vegetation (≥5%), the point was re-coded with a confluence vegetation value of 3.
The logistic regression predicting the probability of a kill by plains lions during the wet season was derived by comparing the re-coded data points describing the habitat at used and available locations. The logistic regression predicting the kills by plains lions during the wet season identified confluence vegetation, riparian erosion, riparian vegetation, and viewsheds as being significant factors predicting the probability of a kill (Table 47). Confluence water was the only factor that was considered not to be a significant predictor (Table 47).

Table 47 outlines the combined habitat factors, their associated coefficients, and their tests of significance. Therefore, the equation predicting the probability of a kill by plains lions during the wet season is:

\[
P(\text{kill}) = \frac{e^z}{1 + e^z}
\]

where

\[
z = -2.929 + 0.6(CV) + 0.707(RE) - 0.459(RV) + 0.492(VSh)
\]

For example, let us assume we are interested in the probability of plains lions making a kill at a specific location during the wet season. Let's pretend this hypothetical location has the following habitat characteristics: it is in a confluence between two rivers, there is no cover from woody vegetation, it is 150m from a waterhole, there is no erosion present, and it is in the viewshed of a kopje. From the loglinear regression we know that confluences and woody vegetation (CV), confluences and access to water (CW), erosion embankments and access to water (RE), and woody vegetation and access to water (RV) are significantly correlated. Therefore, according to the key, the location can be described as having the following values; confluence vegetation (CV) = 2 (i.e. it is in a confluence but it has no vegetation), confluence water (CW) = 3, riparian erosion (RE) = 1, riparian vegetation (RV) = 1, the viewshed (VSh) = 1. The logistic regression analysis identified confluence vegetation, riparian erosion, riparian vegetation, and viewsheds as being important predictors of a kill by plains lions during the wet season. Therefore, to estimate the probability of a kill occurring at this location we substitute the values describing the habitat into the logistic regression equation.
Therefore,

\[ P(\text{kill}) = \frac{e^z}{1 + e^z} \]

where

\[ z = -2.929 + 0.6(\text{CV}) + 0.707(\text{RE}) - 0.459(\text{RV}) + 0.492(\text{VSh}) \]
\[ z = -2.929 + 0.6(2) + 0.707(1) - 0.459(1) + 0.492(1) \]
\[ z = -2.929 + 1.2 + 0.707 - 0.459 + 0.492 \]
\[ z = -0.989 \]

\[ P(\text{kill}) = \frac{e^{-0.989}}{1 + e^{-0.989}} \]

\[ P(\text{kill}) = \frac{0.372}{1 + 0.372} \]

\[ P(\text{kill}) = 0.271 \]

The logistic regression provides an estimate of the probability of a kill (in this case it is 0.27). By comparing several locations we could determine which areas lions were more or less likely to make a kill.