Chapter 1: Summary

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Large predators are known to exert significant selective forces on prey assemblages. These forces manifest themselves as the direct result of predation (Owen-Smith & Mills 2008) and through in-direct non lethal risk affects (Creel & Christianson 2008). Lions (*Panthera leo*) consume the majority of prey biomass across African ecosystems (Owen-Smith & Mills 2008) and have the ability to shape not only prey behaviour, but also the behaviour of other large carnivores (Mills & Gorman 1997, Durant 2000, van Dyk & Slotow 2003). Lion diets have been assessed through numerous approaches since George Schaller's pioneering work in the Serengeti (Schaller 1972). The most common and arguably the best approach to determining lion diets is the direct observation of all prey encounters, thus alleviating the bias of missing small kills (Funston et al. 1998, Mills & Funston 2003). Alternate approaches include opportunistic observations of carcass' (Pienaar 1969, Radloff & du Toit 2004, Owen-Smith et al. 2005), analysis of stomach contents (Smuts 1979) and the analysis of scats (Purchase 2004, Breuer 2005). Hayward and colleagues (2005) reviewed lion diet selection and summarized the potential factors driving predation factors as well as the preferred weight range for lions. However, as useful as this review was, several authors still caution on the use of broad scale patterns to infer fine scale predator prey interactions (Hopcraft et al. 2005, Rapson & Bernard 2007).

GPS collars are becoming increasingly available to assess space use and other aspects of large carnivore ecology. Despite initial problems, such as unit failure (Hemson 2002) and time to data acquisition (Anderson & Lindzey 2003), GPS collars are still in use and most problems have been alleviated or reduced. GPS collars have been used to assess livestock raiding in lions (Hemson 2003), monitoring movement patterns of rare and elusive species (Bandeira de Melo et al. 2007), monitoring human disturbances (Merrill & Erickson 2003), monitor predator social activities (Merrill & Mech 2003) and determining kill rates of predators (Sand et al. 2005, Franke et al. 2006). The use of GPS collars to locate kill sites and determine kill rates has been limited to the northern temperate regions of North America and Europe. This approach still needs to be assessed and evaluated on carnivores in a complex multi prey environment in Africa. The application of GPS collars and the methods employed to locate kill sites could prove useful in African environments, potentially increasing the resolution of carcass return data and thus alleviating the bias of finding large prey items.

This dissertation forms a part of a larger research group that investigated Bovine tuberculosis (*Mycobacterium bovis*) in buffalo (*Syncerus caffer*) in the south central Kruger National Park (KNP), South Africa. I incorporate buffalo dynamics and their relationship with lions in chapter six; however the methods and approaches to obtaining the buffalo, and other species, kill data are reviewed and tested in the preceding chapters. In chapter two I investigate the potential of developing generalized linear models (GLMs) and classification trees (CTs) to locate and predict lioness kill sites from GPS data, using a combination of movement, environment and lunar variables based on factors known to influence lion hunting success. Such models have previously been used to predict kill sites and kill rates in other species such as wolves (*Canis lupus*) and mountain lions (*Puma concolor*). By developing these models I aim to develop an approach that allows the acquisition of lion kill data from many groups of lions simultaneously. Using area under the curve values as a measure of model performance, I compare the applicability of the GLM and CT approaches to predicting the state (kill or resting) of the clusters investigated. Based on GLMs and CTs constructed using 234 kills located from 1447 clusters (59% of the total clusters created) from five lioness, GLMs outperformed the CTs in their ability to predict the state of a cluster (i.e. to classify a cluster as a kill or resting site) for all subsets of the data investigated. The dominant variable in the GLMs, as well as in the CTs, was a ratio of the distance moved prior to the beginning of the cluster against the distance moved following the termination of the cluster. Clusters with greater ratios had a higher probability of being associated with kills. In addition the total length of time spent at a cluster and the available light at the start of the cluster increased the accuracy of the cluster predictions. Finally, using the GLMs constructed sequentially from remotely accessed data, I propose an adaptive approach to locate and identify lion kills. I feel that this approach has application for other large carnivores in Africa and that future work will increase the applicability of these methods in predator prey interaction studies.

In chapter three, I expand on the approach developed in chapter two to locate lioness kill sites and explore the potential addition of within group association scores to increase the predictive ability of kill site detection models. Once a kill has been made, lions tend to cluster around the carcass and feed until the carcass is eventually broken up into smaller pieces. Using this as my expectation, I compare the inter-lion distance at the start of known kill events against the inter-lion distances at the start of known resting events based on the cluster approach developed in chapter two. Inter-lion distance is calculated using proximity tags and remotely accessed GPS data. With this data I show that at the start of kill events lions tend to cluster more than at the start of resting events. This pattern remains the same for all size prey items and provides an approach that may be implemented to improve kill site determination models in social carnivores. In addition the accuracy for kill site prediction models for small prey items can be improved, as the location of small prey items remains a challenge for all kill site determination models. Although the pattern is clear for one lioness, the pattern is more obscure for a second lioness, raising questions concerning the variable behaviour of individual animals at kill sites.

Due to the small sample size of lions to infer inter-lion distance, as well as the small sample of kills associated with the second tag, these results are viewed with caution. Using this as a feasibility study, this study can be a launch pad for further research on how the spatial association of social carnivores can be used to increase the predictive ability of kill site models.

In chapter four, I assess the potential bias that arises through the use of the methods outlined in chapter two, where larger kills are expected to be located more frequently than smaller kills. The bias towards larger kills is well documented and has been observed in other studies using GPS data to locate kill sites. I employ a combination of carcass observations based on GPS cluster investigation and scats identified at GPS clusters to construct a time series of predation events for each group of monitored lions. Using this combined approach I show that the GPS cluster approach located 50% or less small prey items, namely impala (*Aepyceros melampus*) and warthog (*Phoecoceros africanus*). However, if the biomass of prey consumed is important, the impact of missing these smaller species is minimal, because most large prey items located contribute to the majority of the consumed biomass. If the relative number of prey species consumed is important for management purposes, however, the bias that is introduced through finding large prey items needs to be addressed.

In chapter five I calculate the prey selection and preference patterns of the lions in the Satara region of the KNP using the diet calculated in chapters two and four. In the majority of cases, selection patterns of large predators are calculated using aerial census data as the prey availability. However, using aerial census data for selection calculations implies that prey species are randomly distributed across the landscape. Evidence suggests that predator prey stability in models is obtained by using group availability, rather than individual availability of prey species. Using both individual and group availability I assess the diet selection patterns of lions across our study area as a whole, as well as within each pride area. The data presented suggests that large changes in the selection values, as well as order of species selected, occur when calculating selection indices from both individual and group availability. In addition fine scale variation in prey abundance influences selection patterns between prides. When assessing selection patterns of large carnivores I advocate that increased effort be made in the determination of what prey is available as well as the definition of available prey.

In chapter six I examine the fine scale habitat, temporal and spatial factors that influence buffalo vulnerability to lion predation in the study area. Buffalo are an important prey species for lions. This component of the thesis spans a seven year period from 2001 to 2007. Both male and female buffalo were prone to predation in areas with longer grass and thicker bush (i.e. areas with decreased visibility) throughout the duration of the project. However, the habitats where buffalo of each sex are vulnerable exist at different locations across the landscape. My results show that buffalo are more vulnerable to predation following extended periods of low rainfall, resulting in declines in body condition of buffalo of both sexes. The decline in body condition of buffalo and concomitant predation occurs more often at the end of the dry season for males and at the beginning of the wet season for females. This implies that buffalo are nutrient limited by quality at the end of the dry season and quantity at the beginning of the wet season. Female buffalo are predated on at a time when they are nutritionally stressed, most likely during late pregnancy, offsetting the advantages that herd dwelling may offer them. We found no indication that the available surface water was an important factor in buffalo mortality. These results support existing published patterns but do allow a finer scale investigation on the influence of rainfall and hence grass growth to sex biased survival.

In the final chapter I assess the use of the GPS cluster approach for estimating lion diets, including the application of using scats to correct for the under-estimation of small prey species. In doing so, I identify future research that may improve on the approach, especially following further observational and experimental studies. I finish the thesis by providing a framework that can be used to implement the GPS cluster technique.

Each chapter is written in the format of an intended submission to an appropriate journal. Although I am the primary author on all chapters and all work is my own, I acknowledge important co-authors at the start of each chapter.

Chapter 2: Methods for Locating African Lion Kills using Global Positioning System Movement Data

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(Published: Tambling, C.J., Cameron, E.Z., du Toit, J.T. & Getz, W.M. 2010. A Comparison of Methods for Locating African Lion Kills Using Global Positioning System Movement Data. *Journal of Wildlife Management* **74**: 549-556)

Abstract

Knowledge of the range, behavior, and feeding habits of large carnivores is fundamental to their successful conservation. Traditionally, the best method to obtain feeding data is through continuous observation but this is not always feasible. Reliable automated methods are needed to obtain sample sizes sufficient for statistical inference. The identification of large carnivore kill sites using GPS (Global Positioning System) data is gaining popularity. Here we apply statistically rigorous methods to assess the performance of generalized linear regression models (GLM) versus classification trees (CT) in a multi-predator, multi-prey African savanna ecosystem. We applied GLMs and CTs to various combinations of distance travelled data, cluster durations, and environmental factors to predict the occurrence of 234 female African lion (*Panthera leo*) kill sites from 1477 investigated GPS clusters. The ratio of distance moved 24 hours before versus 24 hours after a cluster was the most important predictor variable in both GLM and CT analysis. In all cases, GLMs outperformed our cost-complexity-pruned CTs in their discriminative ability to separate kill from non-kill sites. GLMs provided a good framework for kill site identification that incorporates a hierarchal ordering of cluster investigation and measures to assess trade-offs between classification accuracy and time constraints. The implementation of GLMs within an adaptive sampling framework can considerably increase the efficiency of locating kill sites, providing a cost-effective method for increasing sample sizes of kill data.

Introduction

Understanding prey-predator interactions is essential for managing African wildlife to mitigate human-wildlife conflict and to conserve prey populations (Hemson 2003, Sinclair et al. 2003, Owen-Smith & Mason 2005, Grange & Duncan 2006). It is well understood that carnivore abundance is dependent upon prey availability (Smuts 1978, Gasaway et al. 1992, Mills & Funston 2003, Packer et al. 2005), which is strongly linked to climate (Ogutu & Owen-Smith 2003, Ogutu & Owen-Smith 2005, Ogutu et al. 2008), and predators can regulate prey populations (Tambling & du Toit 2005, Grange & Duncan 2006, Owen-Smith & Mills 2008). However, determining relative importance of predation in regulating prey populations is challenging because predator-prey datasets commonly lack the depth and detail required for statistically rigorous analyses (Franke et al. 2006).

Hunting habits, prey selection, and range use of large African carnivores is best studied through continuous observation (Henschel & Skinner 1990, Mills 1992, Funston et al. 2001, Broomhall et al. 2003, Bissett & Bernard 2007). In African lions (*Panthera leo*, hereafter lions), continuous observation data have been used to assess factors that influence both hunting behaviour (Stander 1992, Stander 1992, Stander & Albon 1993) and success (van Orsdol 1984, Stander & Albon 1993, Funston et al. 2001), but such methods are time-consuming, labour intensive, or logistically unrealistic. Alternative techniques include opportunistic carcass location (Pienaar 1969, Schaller 1972, Mills et al. 1995, Radloff & du Toit 2004), stomach content analysis (Smuts 1979), spoor tracking (Eloff 1984), and scat analysis (Purchase 2004). All of these approaches bias the dietary results in some manner, usually by the increased detection of larger prey items (Mills 1992). Nonetheless, long term datasets have proved useful in investigating trends in lion diets in the Serengeti National Park, SNP (Hopcraft et al. 2005), Kruger National Park, KNP

(Pienaar 1969, Mills et al. 1995), and in private reserves surrounding KNP (Radloff & du Toit 2004), and methods have been suggested to correct biases (Owen-Smith & Mills 2008).

Global Positioning System (GPS) technology enables collection of high resolution spatio-temporal movement data that then can be used to locate kill sites, identify prey species, and thereby determine species-specific kill rates (Anderson & Lindzey 2003, Sand et al. 2005, Franke et al. 2006). However, this application of GPS technology is still not well developed and we know of published examples on only 2 species: pumas, *Puma concolor* (Anderson & Lindzey 2003, Knopff et al. 2009) and wolves, *Canis lupus* (Sand et al. 2005, Franke et al. 2006, Webb et al. 2008). The primary analytic focus of these studies has been on GPS cluster aggregations in time, although an alternative could be the rate or occurrence of multiple trips to a specific location (Stotyn 2005). Technical failures of collars and time lags between event recording and data downloading have hampered utility of GPS data in locating kills (Hemson 2002, Anderson & Lindzey 2003), although with remotely accessible data the approach is showing considerable promise in northern temperate regions (Franke et al. 2006, Webb et al. 2008).

In African savannas, where multiple predator species co-exist with multiple prey species (Hayward & Kerley 2005), complexity is added to the data and analysis because, for a given predator, residence time at a kill varies considerably with size and type of prey as well as intraguild aggression. Here we aim to develop and test models that increase the efficiency of locating lion kills from remotely accessed GPS data. These models can then be incorporated as research tools in an adaptive resource management framework (Kendall & Gould 2002).

Methods and Materials

Study area

We conducted our study in a 1,000-km^2 area in the central region of the KNP, South Africa, centred on Satara rest camp (31.77° E, 24.39° S). The study area was mainly open-tree savanna with a moderate to sparse shrub layer and a dense grass layer. Dominant tree species were marula (*Sclerocarya birrea*) and knobthorn (*Acacia nigrescens*) with red grass (*Themeda triandra*) and stinking grass (*Bothriocloa radicans*) dominating the grass layer (Gertenbach 1983, Venter et al. 2003). The area comprised the northern component of wildebeest (*Connochaetes taurinus*) and zebra (*Equus quagga*) migrations, resulting in high densities of these species in the wet months (Gertenbach 1983). Buffalo (*Syncerus caffer*), kudu (*Tragelaphus strepsiceros*), giraffe (*Giraffa camelopardalis*), and waterbuck (*Kobus ellipsiprymnus*) occurred in large numbers, providing a high prey density and consequently a high lion density (Gertenbach 1983, Mills & Funston 2003).

GPS collars and cluster investigation

We collared 5 female lions with GPS/global system for mobile communications (GSM) units (i.e., GPS/GSM, GPS units with mobile phone capabilities; Hawk105 units, African Wildlife Tracking ^{cc}, Pretoria, South Africa) between May 2005 and April 2007. Lions were captured using standard techniques by South African National Parks (SANParks) veterinarians (Smuts et al. 1977). Collars recorded GPS locations on 2 schedules: a) once per hour every night between 1800−0600 hours and during the day at 0900 hours, 1200 hours, and 1500 hours (16 fixes attempted) and b) once per hour over the full 24-hour period (24 fixes attempted). Collar schedules were therefore identical at night (1800−0600 hr) but differed during the day. Due to the high rate of GPS location recordings, collars had a reduced battery life and we replaced some during the study. We deployed 9 collars during the study, 4 of which attempted fixes 24 hours/day and 5 of which attempted fixes 16 hours/day. Lions in the KNP are active predominantly at night so most kills are nocturnal, with daylight hours spent resting (Mills & Biggs 1993). The combination of datasets using both collar schedules incorporated balanced sets of hourly readings at night (when lions are most active) across the entire dataset, but missed some data points during the day. The unbalanced daytime schedules should not have created any significant error due to inactivity of lions during daytime. We nevertheless performed all analyses with both schedules separately as well as with the entire pooled dataset. We downloaded data remotely via the GSM network when each collared individual entered an area of GSM coverage. We calculated distances between successive locations using the Animal Movements Extension (Hooge et al. 1999) in ArcView® 3.2 and treated missed GPS locations as stationary locations. We defined a GPS aggregation cluster (hereafter a cluster) as ≥2 consecutive recorded fixes with each consecutive pair of fixes <100 m apart (Including both day and night data; See Appendix 1). If a GPS location was not recorded and distance to the following location was >100 m, a GPS cluster was not created (even though measurement of the intervening missing points may have resulted in definition of a cluster being met).

We uploaded cluster coordinates onto a hand held GPS unit and investigated clusters on foot. We investigated an area of approximately 25-m radius around GPS points (See Appendix 1) that encompassed all GPS points for that cluster. Therefore, we included any GPS point outside the 25-m radius of the first GPS point as the centre of a new search radius so that we investigated all GPS points at the cluster (See Appendix 1). We attempted to investigate as many clusters as possible, however to maximize number of clusters investigated, we investigated clusters occurring near each other first. By conducting investigations based on proximity of many clusters, we may have biased cluster investigation to areas readily accessible by roads. We assessed this possible bias by comparing distance that clusters with or without a kill occurred from a road, as well as distance that checked and unchecked clusters occurred from a road using Wilcoxon rank sum tests. We identified predation events at clusters from presence of prey stomach contents, teeth, bones, horns, or hair and determined prey species, age, and sex when possible (age – horns and teeth development; sex – horns and canine presence in zebra). The GSM coverage in the study area was not uniform and areas existed without coverage; therefore, collared females re-entered areas of coverage sporadically, resulting in an irregular pattern of cluster investigation over time (i.e., time between cluster occurrence and investigation depended on when the female moved into GSM coverage).

We separated field observations into 2 investigative periods; initially (Jun 2005 – Feb 2006) we only noted number of days between cluster occurrence and cluster investigation for kills, but subsequently (Mar 2006 – Apr 2007) we recorded number of days between cluster occurrence and cluster investigation for clusters with and without kills. During this second period, we investigated clusters between 0−671 days ($\bar{x}$ = 54.2 days, median = 6 days) after cluster occurrence. Using Wilcoxon rank sum tests, we investigated our ability to identify species, age, and sex of the kill as time between cluster occurrence and investigation increased.

Statistical Methods

We measured 8 predictor variables for each GPS cluster. 1) Hours: length of time (hr) lions spent at a cluster from the first point of the cluster until they left the cluster for the last time. Hours was an indication of total time spent at on a carcass. 2) Return*:* a categorical variable describing a return visit to a cluster within 12 movement steps of leaving that cluster indicating the possibility that lions returned to carcass sites following initial movements away from the carcass site. 3) Ratio_24: ratio of distance moved during the 24 hours prior to the cluster beginning against distance moved during the 24 hours following termination of the cluster, where cluster duration included all return events. We based the variable ratio_24 on the premise that lions predominantly search for prey when hungry and rest following a kill, therefore resulting in higher ratios for successful hunts. 4) Dist_1: distance moved by lions during the first GPS interval of a cluster (i.e., between the first and second recorded GPS coordinate); a short dist_1 indicates that the female remained close to the carcass at the beginning of a cluster and did not move around the cluster site. 5) Dist_2: distance moved by lions during the second GPS interval of a cluster (i.e., between the second and third recorded GPS coordinate); a short dist_2 indicates that the female remained at the carcass, as apposed to moving away from the carcass while remaining at the cluster. 6) Drain: distance from the cluster to the nearest drainage line (classes 1-4, S.MacFadyen, KNP Scientific Services GIS department), which we calculated using ArcMap 9.0 and treated as a continuous variable, giving a measure of distance to available cover for hunting lions. 7) Road: distance from the cluster to the nearest road (S. MacFadyen, KNP Scientific Services GIS department), which we calculated as for *drain*, giving a measure of bias of investigating clusters near roads. 8) Dark: a 5-valued categorical variable that accounted for the combined effect of the sun and moon at the start of the cluster. The 5 categories were: 1 = daytime clusters, 2 = twilight clusters, 3 = night-time clusters with the moon up and full, 4 = night-time clusters with the moon up and in the first or third quarter, and 5 = night-time clusters with the moon up in the new moon phase or night-time clusters when the moon was down, as lions have been shown to have a greater kill success on dark nights

We used generalized linear models (GLMs) to investigate variables related to probability of a binary response (kill = 1, no kill = 0) occurring at a GPS cluster (Hosmer & Lemeshow 2000). We identified 2 possible time delays between cluster occurrence and cluster investigation that suggested declines in our ability to identify kills at cluster sights (see results). Therefore, we developed models based on data from clusters investigated during the first 4 weeks and first 16 weeks following a cluster occurrence. We used a forward stepwise α-to-enter approach (Quinn & Keough 2002) with a cut-off of $\alpha = 0.05$ as the criteria for entering parameters into the model. We tested parameters for collinearity and found that *hours* and *return* were correlated ($c = 0.52$), and subsequent investigation revealed that *return* was not an important variable if *hours* was already included in the model. We assessed model discrimination using the area under the curve (AUC) based on the receiver operator characteristic (ROC) curve, which is a plot of the proportion of true positives (i.e., sensitivity of discrimination) as a function of the proportion of false positives (i.e., one minus the specificity of discrimination). With this definition the AUC score represents the percentage of time that a true positive will have a higher probability of being a kill than a true negative when both are drawn at random (Zweig & Campbell 1993, Fielding & Bell 1997). We assessed the relative individual predictors' influence on the response variable using hierarchal partitioning analysis (MacNally 2000).

Classification trees (CTs) use a hierarchal splitting criterion that separates binary responses to predictor variables based on sets of rules (Breiman et al. 1984, Ripley 2007). Threshold criteria for each variable divide responses into homogenous groups based on prior probabilities of the input data, a splitting criterion (the Gini index), and a loss matrix (Breiman et al. 1984, Ripley 2007). Although large complex trees fit the data better than small trees, large trees are not always better at predicting new data because they often over fit the data. Consequently, the construction of a best tree involves development of large trees, followed by cost-complexity pruning (Breiman et al. 1984, Ripley 2007) of branches based on honest estimates of misclassification error obtained by cross-validation (see De'ath & Fabricius 2000). As recommended by De'ath and Fabricious (2000), we ran 50 10-fold cross-validations for each tree and selected the tree that corresponded to a) the minimum relative misclassification error and b) the 1-standard error rule. Due to the unbalanced nature of our data (84% of cases were negative) we implemented a loss matrix to increase costs of a false negative error (Breiman et al. 1984). We assessed tree discrimination using AUC values for both minimum error and 1-standard error trees.

We assessed GLM and CT validation by randomly partitioning the complete dataset into independent training and testing sets and calculating their associated AUC values (Fielding & Bell 1997, Manel et al. 1999). We developed 5 model validation sets based on the *k*-fold partitioning with $k = 2$ (Fielding & Bell 1997) and re-developed new GLMs and CTs (as described above) for each training set. We then tested these re-developed GLMs and CTs on the independent testing dataset. We restricted data partitioning to a 2-fold *k* partitioning to adhere to the suggested $M/10$ number of predictors, where M is the fewest number of cases in the binomial response (Harrell et al. 1996).

Implementation of a GLM or CT approach will be dependent on field time available for cluster investigation (i.e., more field time will enable investigation of more clusters, whereas less field time will require investigation of clusters with a higher kill probability). Therefore, we investigated the percent correct classification (PCC, all positive and negative clusters correctly identified), sensitivity (probability that a kill is correctly classified), and the specificity (probability that a non-kill is correctly classified) across a range of threshold values that enabled number of clusters investigated to vary (Fielding & Bell 1997). The threshold value converted the probability output from the model to a binary value for each cluster. Additionally, to assess how they influenced prediction success, we investigated 2 types of threshold values: 1) a default of 0.5 as the threshold and 2) the prevalence in the data as the threshold.

As part of an adaptive framework for kill-site prediction we developed GLMs and CTs using cumulative monthly cluster data between March 2006 and April 2007 (adaptive training datasets), and then predicted the location of kill sites for clusters investigated during the following month (adaptive testing datasets). For example, we used GLMs and CTs constructed using cluster data between March 2006 and September 2006 to predict the state of clusters investigated during October 2006. We then calculated AUC values for the testing sets. Finally, we used GLMs developed on the 5 training sets to assess effectiveness of using the resulting probability of finding a kill in the testing sets as a hierarchal means to order cluster investigation in the field. We compared the cumulative number of kills located with each additional cluster investigated to the cumulative number of kills found by searching clusters at random and averaged it across the 5 data sets. We conducted all presence-absence and AUC analyses using the ‘PresenceAbsence’ package and all classification tree implementations in ‘rpart’ using R2.7.0 (R Development Core Team 2008).

Results

Fix rate for GPS collars ranged from 65% to 88% ($\bar{x} = 77\%$). We investigated 59.5% (1,447 out of 2,433) of clusters and found 234 kills. Collared lions moved away and then returned to a cluster at 8.5% of checked clusters. Investigated clusters tended to occur closer to roads than unchecked clusters (checked clusters: 661 m, unchecked clusters: 756 m, Wilcoxon W = 747,710, $p < 0.05$), potentially reducing the chance of locating kills, especially because kills occurred on average farther from roads than did non kills (kills: 737 m, non-kills 647 m, Wilcoxon W = 125,383, $p < 0.005$). We investigated more clusters and found more kills during the first 4 weeks following cluster occurrence (673 clusters, 171 kills). Rate of clusters checked per kill remained constant during the subsequent 12 weeks. Following a 16-week interval between cluster occurrence and investigation, kills located per checked cluster declined even though sampling intensity remained the same (Fig. 1). During the 16-week subset, we found 222 kills by investigating 1,070 clusters. We found that number of days that elapsed between kills and cluster investigation did not influence our ability to confirm identification of the killed species (species confirmed: $n = 228$, species unconfirmed: $n = 6$, Wilcoxon $W = 495$, $p = 0.25$) or age classification of the prey item (confirmed: $n = 190$, unconfirmed: $n = 38$, Wilcoxon W = 3,247.5, $p = 0.33$). However, we did find that checking clusters sooner after cluster occurrence increased our ability to classify sex of the kill, excluding juvenile kills (confirmed: $n = 50$, unconfirmed: $n = 104$, Wilcoxon W = 2,026, $p < 0.05$).

Preliminary model development revealed that there was no substantial improvement in model fit when the individual females were included as a random variable in a mixed-effect GLM, so we used standard GLMs for the development of predictive models. For both the 4- and 16-week datasets, 4 predictor variables were included in the final model, the most important being *Ratio_24*, explaining 51% and 48%, respectively, of the response outcome. Variables *hours* and *dark* explained 30-31% and 10-17%, respectively, of the response variable depending on dataset used, and the 3 variables collectively explained 94-95% of variation in the model attributed to whether a kill occurred at a cluster. The final variable contributing to the explanation of kill sites was distance moved in the first GPS interval (*dist_1* = 5-6%). When we developed GLMs using the 2 different recording schedules the same 4 variables were selected by the α-to-enter approach and each response variable still explained a similar percentage of the response outcome.

We present CT results for the 16-week dataset only because trees developed for the 4-week dataset were similar in structure and composition. Both the 1-standard error and minimum error trees were composed of 2 splits. *Ratio_24* was the variable responsible for the main split in both CTs with kills separated from resting with a ratio >1.5. Using the variable *Ratio_24* alone resulted in location of 64% (142/222) of kills while investigating 36% (384/1,070) of clusters, therefore locating a kill every 3 clusters checked (142 kills from 384 checked clusters). By adding the second split (min. length of a cluster >21 hr) when *Ratio_24* was <1.5, we would have located 75% (166/222) of kills while investigating 40% (426/1,070) of clusters. Addition of a third split, which suggests investigating clusters with *Ratio_24* >0.99 when length of the cluster is <21 hours in addition to the criteria for the 2 previous splits, results in 88% (196/222) of kills located while investigating 58% (624/1,070) of clusters. As we increased number of branches our ability to locate future kills' increased, but total number of clusters checked and therefore kills found declined, increasing the risk of overfitting when predicting kill sites with novel data.

The GLMs showed good discrimination with AUC values between 0.81 and 0.83 (Table 1). When we ran GLMs on the data from the 2 recording schedules AUC values remained around 0.8. Area under the curve results for the cost-complexity-pruned CTs were lower than those for the GLMs for both minimum error and 1-standard error trees, respectively (Table 1). Fitting the GLM of the 16-week dataset, the PCC closely followed the specificity curve in approaching the respective asymptotes above a threshold of 0.3 (Fig. 2). The PCC for a threshold value of 0.5

was 83% compared with 73% for a threshold value of 0.21 (equal to prevalence in the data). The sensitivity, however, increased from 34% to 77% when we reduced the threshold value from 0.5 to 0.21 (Fig. 2). Results for models constructed using the 4-week dataset were again similar to the 16-week dataset and we do not present them here.

Area under the curve values for testing partitions of the GLM was similar to those for the complete dataset, outperforming the cost-complexity-pruned CTs (Table 1). Similarly, from an adaptive perspective the GLM had better discriminatory ability for the following month's cluster predictions, although there was month-to-month variation (Fig. 3). Use of a hierarchal probability-based search pattern was considerably more efficient than a random search pattern for locating kill sites, locating twice as many kills after the first 200 investigated clusters (Fig. 4).

Discussion

Although continual observation is the best method to investigate predator-prey relationships for large carnivores in open habitats such as African savannas (Mills 1992), it is often impossible in most other habitats (e.g., mountainous terrain, dense forests) and researchers need to use alternative methods. We found that GLMs and CTs predicted occurrence of kills at GPS clusters for female lions better than investigating clusters at random. It remains unavoidable however, that some small kills (prey items <100 kg) are missed (impala [*Aepyceros melampus*] and warthog [*Phacochoerus africanus*] by 50%, C.J. Tambling, unpublished thesis; Chapter 5), which is in accordance with previous studies investigating kill site detection using GPS collars (Franke et al. 2006, Webb et al. 2008).

During cluster investigation, time constraints may limit investigation to areas near roads, which could reduce number of kills located, especially in cases where predators and prey respond negatively to disturbances caused by roads (Spellerberg 1998, Kerley et al. 2002). Despite the distance to roads being non-important during model development, we did find a significant difference between distance of checked and unchecked clusters to roads. In addition, we found that clusters with kills were farther from roads than clusters without kills, therefore potentially reducing number of kills we located. We suggest that, even if time is limited, equal effort be given to investigating clusters with a high probability of being a kill at all distances from roads or access points. We expect that with increased time between cluster occurrence and investigation, false negative clusters (i.e. no kill where a kill occurred) will increase, influencing the model's predictive abilities (Vaughan & Ormerod 2005). Increasing availability of real time GPS data will assist in rapid investigation of clusters. We found no difference however, in model results based on clusters investigated within 4 weeks and 16 weeks following cluster occurrence. One observer investigated >95% of all checked clusters and experience gained by this investigator enabled detection of kills that may have been missed by observers with less experience. We therefore advocate that clusters be investigated as soon as possible after they occur, as kills will be easier to locate. Because investigating clusters at random is time consuming, our results support use of a statistical model to search sites more likely to contain kills, thereby reducing field time and increasing efficiency.

Previous research suggests that hidden Markov models could be used to uncover hidden states (kill sites, bedding sites, and transit modes) from basic movement parameters (step length and turning angle) in telemetry data (Franke et al. 2006). In contrast, our analysis based on ratio of distance moved 24 hours before and 24 hours after a cluster of points proved to be the largest contributor to reliable discrimination between kill and non-kill sites. Use of this ratio as the only predictor variable however, may result in non-detection of opportunistic kills or kills made by lions employing an ambush hunting strategy (see Hopcraft et al. 2005).

Logistic regression models have been used to predict presence or absence of kills in North American carnivores, with minimum length of time at a cluster an important predictor variable (Anderson & Lindzey 2003, Sand et al. 2005, Stotyn 2005, Webb et al. 2008). Our analysis revealed that, although important, length of time at a cluster alone was not enough to predict presence or absence of a kill. Handling time will undoubtedly vary between study sites (Sand et al. 2005, Webb et al. 2008) and this should be noted when developing models for new areas. Time spent at a kill site will be dependent on size of the prey item, as well as size of the group monitored. Previous investigations also suggest that occurrence of a return event to a cluster indicates presence of a kill. A low frequency of returns (8%) led to the variable *return* playing a minor role in our study, although its collinearity with overall length of time lions spent at a carcass was important, especially for large kills like adult giraffe.

Lions in KNP hunt and kill predominantly at night and hunting success tends to increase in absence of moonlight (van Orsdol 1984, Mills & Biggs 1993, Stander & Albon 1993, Funston et al. 2001). The significant influence of the darkest period in our regression models, as well as its individual importance in the hierarchal partitioning analysis, indicates its usefulness in kill site determination. However, we anticipate that incorporation of cloud cover, if known, on moonlight nights could lead to some improvement in our model.

The low importance of the GPS interval movement distances (*dist_1* and *dist_2*) might be due to the definition of the variables. Our use of the distance between the first and second, and the second and third, recorded fix of a cluster may stretch these distances on some occasions as the second and third recorded fix are not always one hour after the previous recorded GPS fix as a result of missed fixes. A stricter definition of a 1-hour movement distance at the start of the cluster, with clusters that have a missed GPS fix at the end of the first hour deleted from the dataset, may have a stronger affect on the model but will also reduce the sample size of usable clusters. How missing data are handled needs to be carefully considered when deciding on variable use.

We used ROC curves to assess model discrimination because they are independent of threshold determination and data prevalence and provide a way of comparing among diagnostic systems (Hanley & McNeil 1982, Swets 1988, Zweig & Campbell 1993, Fielding & Bell 1997, Manel et al. 2001). The AUC values from the GLM indicated a good discriminative ability, whereas the cost-complexity-pruned CTs did not perform as well, indicating superiority of the GLM approach over CTs for predicting states associated with clusters.

The PCC of 83%, associated with a threshold of 0.5, corresponded to specificity (i.e. correct negative classification) of 96%. However, at this threshold we only investigated 10% of clusters with an expectation of finding only 34% of kills. Similarly, previous studies concerning species distribution modelling have shown an omission of known presence sites with low prevalence associated with a threshold of 0.5 (Liu et al. 2005, Jimenez-Valverde & Lobo 2007). To find more kills requires use of a lower threshold even though the resulting PCC declines. For example, when we used prevalence of the data (0.21) as a threshold, although overall PCC declined to 73%, we found an estimated 77% of all possible kills even though we only investigated 38% of clusters. Thus, in contrast to general practice (Manel et al. 2001, table 2), our study reiterates that maximizing PCC is not necessarily a good strategy. Rather, an analysis of the trade off between sensitivity and effort is needed to meet the conflicting goals of obtaining as many kills as possible within certain logistical constraints.

Management implications

For the above approach to be properly implemented, both absence data and confirmed kills are needed for GLMs to be developed for kill site detection. To obtain absence data, we suggest investigation of low probability clusters near high probability clusters coupled with an initial period of high intensity random searching (Sand et al. 2005). From this initial data collection, models can be developed, which can improve as new data are collected from investigated clusters (Webb et al. 2008). The resulting GLM, with a sliding scale in investigative ability of researchers and a hierarchal order of cluster investigation, proved useful and therefore has merit as part of an adaptive research framework. Any combination of this approach with continual observation methods or scat collection, where possible, would refine model parameters and increase sample sizes of kills located, resulting in increased statistical power. With advances in technology related to the study of large mammals, researchers have increasing opportunities to update traditional techniques and thus enhance efficiency of field research, thereby refining investigations of predator-prey interactions in particular.

Tables

Table 1: Discriminative ability (area under the curve [AUC] of the receiver operating characteristic curve) of the generalized linear regression models (GLMs) and classification trees (CTs: including the 1-standerd error tree and min. error tree [Min]) to predict location of female lion kill sites in Kruger National Park, South Africa, between May 2005 and April 2007. Results show the discriminative ability for the full dataset against itself and the average of randomly drawn testing datasets against their associated training dataset from which we developed the models.

		GLM	SD	CT: Min	SD	CT: 1-SE	SD
4-week dataset	Complete	0.83		0.73		0.73	
	Testing	0.82	0.01	0.68	0.02	0.69	0.02
16-week dataset	Complete	0.81		0.72		0.72	
	Testing	0.80	0.02	0.67	0.04	0.66	0.03

Figures

Figure 1: Number of Global Positioning System (GPS) clusters investigated, number of kills found, and associated relative percentage of clusters investigated per kill during 4-week periods following occurrence of GPS clusters for female lions between May 2005 and April 2007 in Kruger National Park, South Africa.

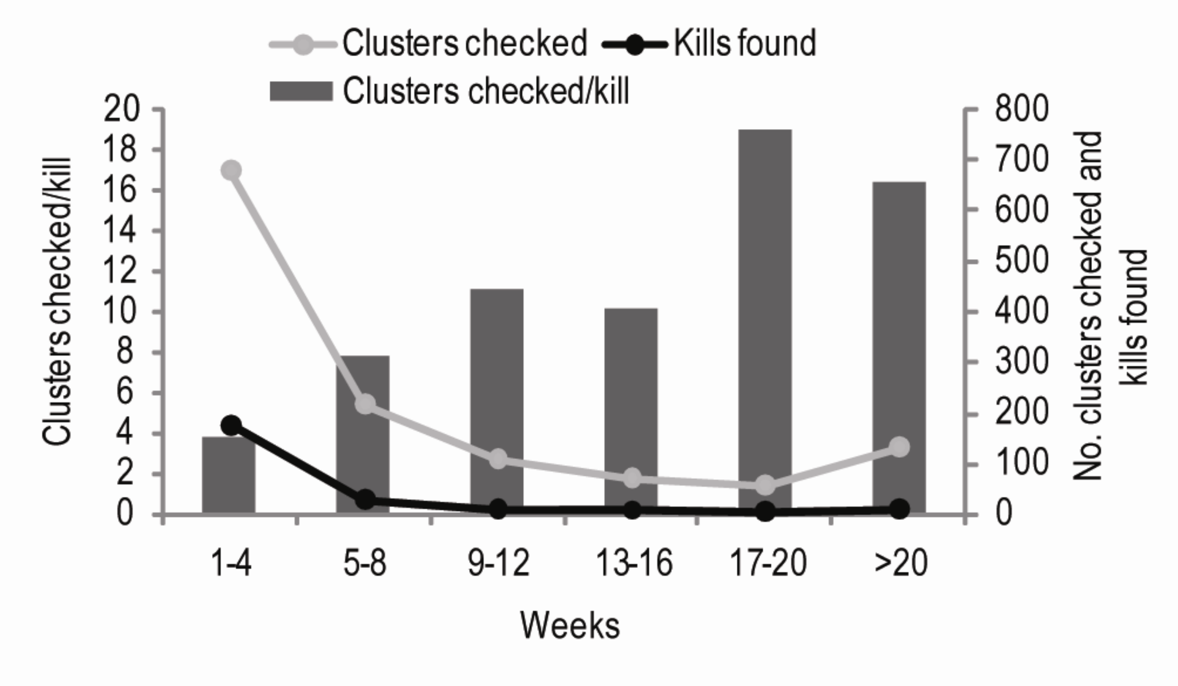


Figure 2: Sensitivity (i.e., finding a kill when a kill occurred), specificity (i.e., not finding a kill when a kill did not occur), percent correctly classified (PCC), and number of Global Positioning System (GPS) clusters we investigated for female lions between May 2005 and April 2007 in Kruger National Park, South Africa, along a range of threshold values that could be used to convert probabilities from generalized linear regression models (GLMs) to presence absence values. Two commonly used threshold points are shown by dashed lines (threshold = prevalence, 0.21: black dotted line; threshold = 0.5: grey dotted line).

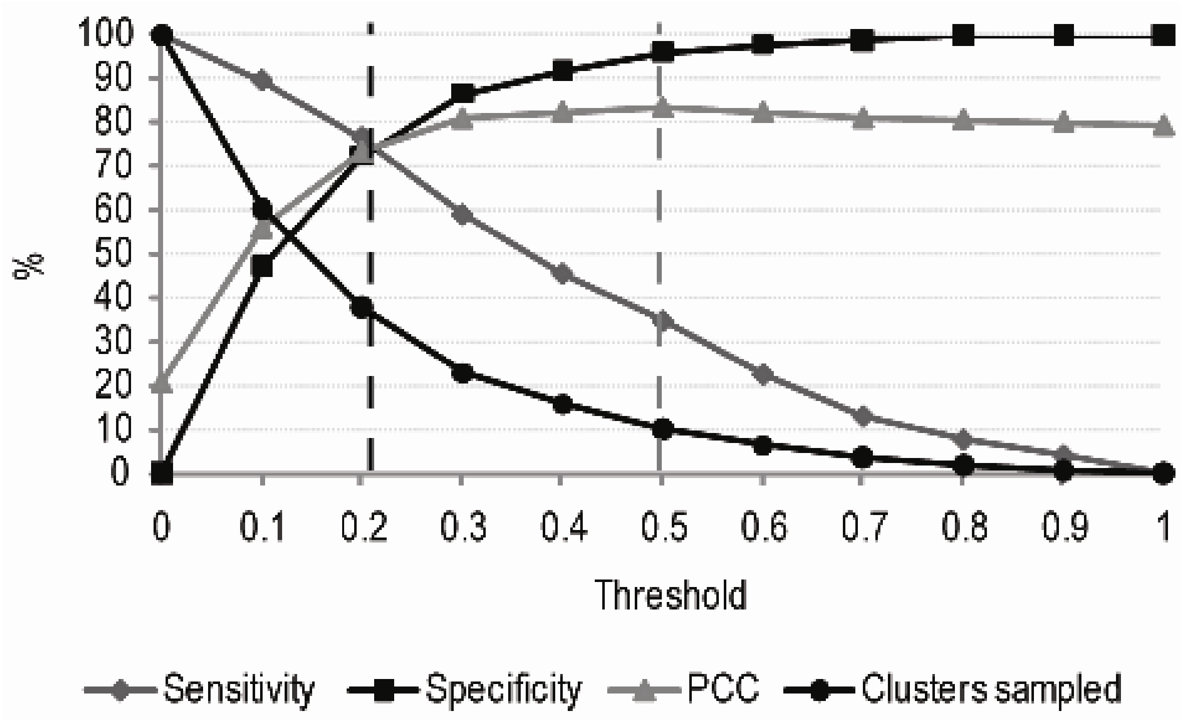


Figure 3: Discriminative (area under the curve [AUC] of the receiver operating characteristic [ROC] curve) ability of the generalized linear regression model (GLM) and minimum cost-complexity classification trees (CT) to predict the following months kill sites for female lions from March 2006 until April 2007 in Kruger National Park, South Africa.

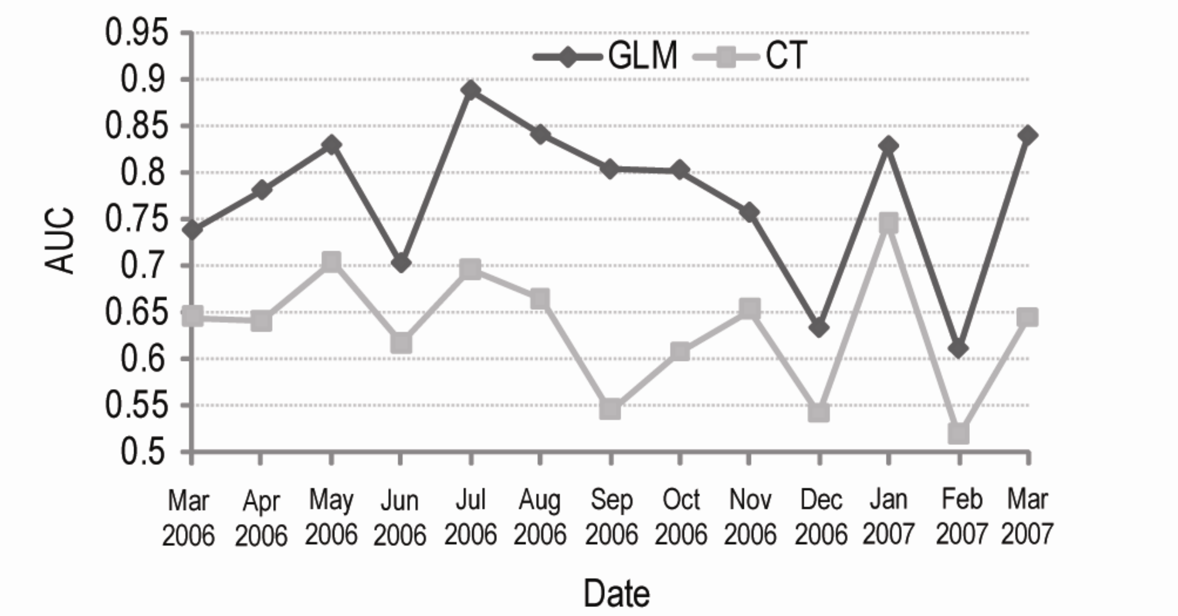
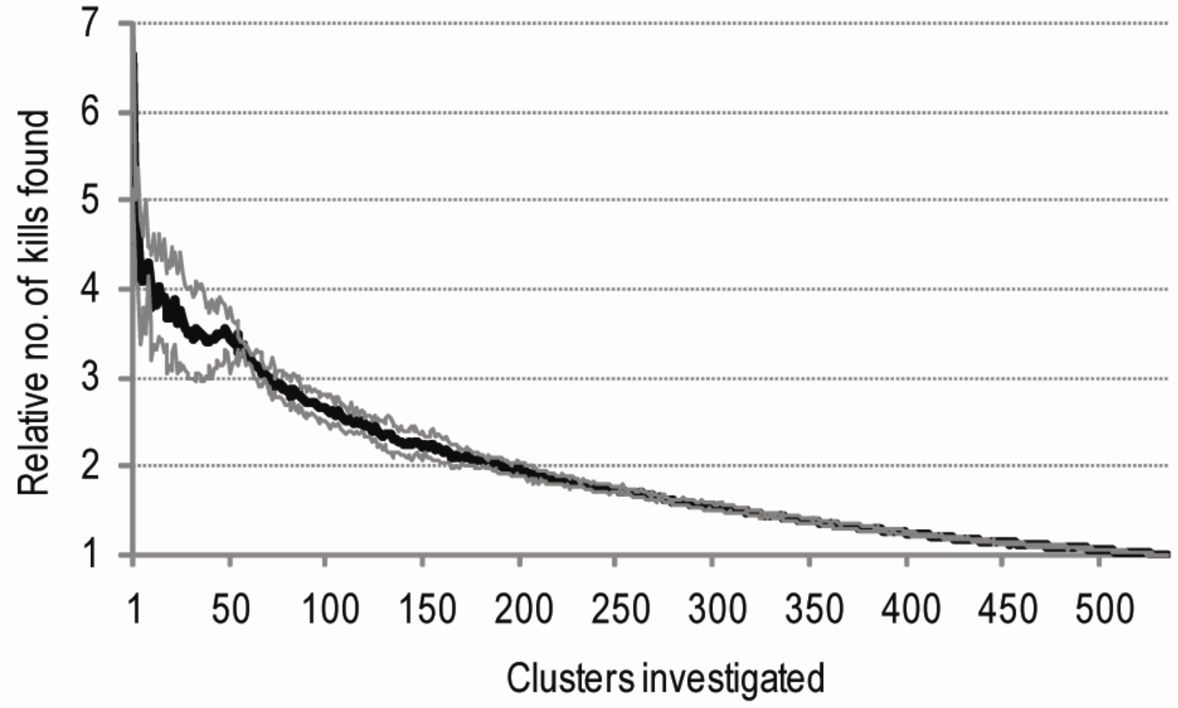


Figure 4: Cumulative number of kills located if we searched Global Positioning System (GPS) clusters based on probability output of the fitted GLM for all *k*-partitioned test datasets (grey lines represent the standard deviation for each cluster checked) relative to cumulative number of kills located if we used a random search pattern to investigate clusters for female lions in Kruger National Park, South Africa, between May 2005 and April 2007.



Chapter 3: Feasibility of using proximity tags to locate female lion (*Panthera leo*) kills

C.J. Tambling and L. Belton

(Published: Tambling, C.J. & Belton, L. 2009. Feasibility of using proximity tags to locate female lion *Panthera leo* kills. *Wildlife Biology* **15**: 435-441)

Abstract

Global Positioning System (GPS) based telemetry studies are becoming more popular in large carnivore research. Recent advancements include the detection and prediction of kill sites from GPS collar data. Thus far, the majority of models to detect kill sites focus on the patterns generated by a single focal individual. The prediction of kill sites helps increase sample sizes for diet studies of carnivores, especially when continuous observation methods cannot be employed. We propose and report on the feasibility of using the spatial association of multiple individuals from a social carnivore group to locate kill sites, using female lions (*Panthera leo*) in the Kruger National Park, South Africa as an example. Our feasibility study suggests that lionesses cluster in space while at a GPS cluster with a kill. Clustering appeared most strongly in the first two hours of a kill, where after a more random association between individuals in space is observed. Additionally we found no difference in the initial spatial clustering pattern for kills of different sizes. When clusters are not associated with a kill (i.e. resting), female lion’s exhibit the random spatial association similar to the later hours found at kill sites. We feel that based on the initial results, association of social carnivores in space in combination with current spatio-temporal patterns of focal individuals can be used to improve kill site models, but further research and larger sample sizes are required to validate our findings.

Introduction

Predation kill rates of carnivores on their principal prey provide insight into predator-prey dynamics and are important for the management of predator-prey communities (Franke et al. 2006). However, the determination of predator kill rates are often an elusive goal for researchers and managers alike (Laundre 2008). The adequate quantification of kill rates requires the location of all kill events made during a continuous time interval (Webb et al. 2008), best undertaken using continuous observation methods (Mills 1992). Methods employed for the continuous observation of carnivores, i.e. snow tracking (Marucco et al. 2008) and continuous direct observations (Mills 1992), often result in small sample sizes of kills across different individuals or groups (Webb et al. 2008). Small sample sizes in predator-prey studies are often a leading criticism aimed at studies investigating observed kill rates (Franke et al. 2006). In light of limitations in collecting large quantities of kill data from direct observations, novel methods to assess and estimate kill rates are being developed and tested. These approaches are evolving as new technology is developed.

Advances in telemetry technology are providing an increasing quantity of fine scale spatio and temporal data (Clark et al. 2006) which can be combined with statistical techniques to increase the probability of locating kill sites (Webb et al. 2008). This approach has been employed to estimate kill rates for wolves *Canis lupus* and mountain lions *Puma concolor* in North America and Europe (Anderson & Lindzey 2003, Sand et al. 2005, Franke et al. 2006, Webb et al. 2008) and lions *Panthera leo* and leopard *Panthera pardus* in South Africa (C.J. Tambling unpublished data, L.H. Swanepoel unpublished data). A common drawback in all the above mentioned studies is the failure to detect kill sites of small prey items that are characterised by short handling times (Sand et al. 2005, Webb et al. 2008). The lack of methods to identify kill sites of small prey items currently limit these approaches to detecting kill sites associated with large prey items (Franke et al. 2006). Wolves and lions coexist and hunt in social groups (Stander 1992, Adams et al. 2008), potentially allowing the incorporation of spatial interactions between members of the social group in models that could improve the current approaches in the identification of kill sites.

Proximity tags that record the association and distance between individual animals have been used and tested to detect contact rates (distances of < 40 cm) between brushtail possums *Trichosurus vulpecula* (Ji et al. 2005, Douglas et al. 2006) and contact distance and duration in racoons *Procyon lotor* (Prange et al. 2006). The main application of this technology has been the assessment of mating systems and associated close contact distances that could influence the spread of infectious diseases (Ji et al. 2005, Prange et al. 2006). Although these tags represent a valuable source of contact data which are hard to gather in the field other than by long-term observation, their wholesale and widespread use is often dependent on the saturation of detectors within a population, potentially limiting their use to readily captured and trapped species (Prange et al. 2006).

Female lions hunt and feed as part of a cohesive group (Packer & Ruttan 1988, Stander 1992). Consequently, proximity between individuals is a prospective variable that could be used to increase the predictive power of kill-site models developed using GPS collar data. The identification and monitoring of multiple lions within a single pride can be conducted using proximity tags, providing firstly presence or absence of individuals within the pride over time, and secondly, a measure of the distance between individuals based on the strength of the signal between the tags. In this study, we investigate the relationship between proximity tags and a receiver built into a GPS collar, and the feasibility of using proximity tags to increase the ability to predict the state (kill or resting) of lions during stationary bouts from GPS movement data. We hypothesise that if lions make a kill, pride members will initially associate closely with each other at the carcass, followed by a loose random association of individuals as feeding declines. Additionally, periods with no kill will be characterized by the loose random association of lions whereby lions are spaced further apart than when feeding on a kill.

Materials and methods

We conducted trial investigations on the relationship between proximity tags (hereafter referred to as tags) and the receiver in the Skukuza rest camp (31°59’ E, 25°00’ S) of the Kruger National Park (KNP), South Africa. As part of a larger investigation into the diet of lions in the central region of the KNP, we deployed a GPS collar and proximity tags on a pride of lions near the Satara rest camp of the KNP (31.77 E, 24.39 S). Our pilot study was conducted in open terrain with no vegetation between the receiver and the proximity tag.

For our study, we used GPS/GSM collars (African Wildlife Tracking) and associated proximity tags (African Wildlife Tracking), all built into collars. Proximity tags emitted a signal at a frequency of 866MHz before being converted into a signal strength score depending on the strength of the signal when it reached the receiver. In order to assess the relationship between tag distance from the GPS receiver and the relative signal strength we placed the tags at a set of fixed points along a linear transect (400 m, 200 m, 150 m, 100 m, 50 m, 20 m and 5 m) away from a stationary receiver and recorded the relative signal strength at each distance. We converted the signal strength into a relative percentage based on the maximum signal strength obtained when the tag rests against the receiver. This allows an assessment of the general relationship between the signal strength and the active tag with the possibility of expanding this relationship to field observations.

On 19 May 2005, three female lions were immobilised using standard South African National Park veterinary procedures (Smuts et al. 1977) and collared, one with a GPS collar and two with tags (Tag 21 and Tag 22). The tags remained on the lionesses for 182 (Tag 21) and 47 (Tag 22) days, respectively. The GPS collar was set to record a fix at every hour and we accessed the data remotely via the GSM service around the Satara rest camp. The GPS collar recorded the presence or absence of a signal from a tag as well as the relative signal strength. The GSM coverage around the Satara rest camp was limited, so lions often move out of GSM coverage for a period before returning and allowing data to be accessed. Using the remotely accessed data, GPS clusters (a cluster is defined as two or more consecutive GPS fixes that are < 100 m from the previous fix – see Appendix 1 for details on the calculation of 100m) were investigated for any possible indication that a kill was made at that cluster. Due to the limited GSM coverage and access to data, clusters were checked on average 7.5 (±1.2) days following the cluster occurrence. We searched an area of ~ 50 m in diameter around the GPS cluster as trials on the collars showed an average location error of <25 m depending on the structure of the vegetation (See Appendix 1). We identified kills by the presence of stomach contents, teeth, bones, horns or hair at the GPS cluster, identifying the killed species to age and sex if possible (age – horns and teeth development; sex – horns and canine presence in zebra).

For each cluster, we extracted the signal strength for seven hours following the start of the cluster. We used seven hours as this represents the average cluster duration for a kill while the tags were deployed. We used a factorial ANOVA to investigate the difference in signal strength between 1) clusters with kills and without kills, 2) the different hours following the start of the cluster, and 3) an interaction between the hour at the cluster and the state of the cluster (kill or no kill) for each individual tag. Factorial ANOVAs are generally robust and able to withstand non-normal data and departures from homogeneity of variance (Zar 1999). Additionally, for each hour we compared the size of the kill to the signal strength to ascertain if clustering was more prevalent with different size kills. All weights were obtained from Bothma et al. (2002) and any kill that had no age and sex was assigned an adult female weight. We categorised weights into the following three categories: a) small prey items of < 100 kg, b) medium-sized prey items between 100 and 500 kg and c) large prey items > 500 kg. All statistical analyses were conducted using the statistical platform R (R Development Core Team 2008).

Results

The relationship between signal strength and distance, independent of animals, can be represented by an inverse logistic curve ($R^2 = 0.9$). The observed signal strength (expressed as a percentage of the maximum signal strength) declined rapidly close to the receiver and followed a shallower decline further from the receiver (Fig. 1).

The lioness fitted with tag 21 was associated with the GPS collared lioness on 3,063 out of 3,504 (87%) recorded GPS locations. The lioness fitted with tag 22 was associated with the GPS collared lioness on 832 out of 887 (94%) recorded GPS locations prior to tag loss. During the time that tag 21 and tag 22 were deployed, we located 37 kills from 185 clusters and 10 kills from 57 clusters respectively.

For tag 21, clusters with kills had significantly higher mean signal strength ($F_{1,2974} = 18.4$, $P << 0.001$) than clusters without (Fig. 2). We found significant variation in the signal strength observed across all hours following the start of a cluster ($F_{6,2593} = 2.67$, $P < 0.05$) with elevated signal strength observed during the first two hours of clusters (Fig. 3). We also witnessed a significant interaction between cluster state (kill, no kill) and hour of cluster for tag 21 ($F_{2,4409} = 4.45$, $P << 0.05$). Tukey's post hoc tests indicate that this difference was driven by elevated signal strength at the first and second hours of kill sites (see Fig. 3).

For tag 22, we similarly found a significantly higher signal strength at clusters with kills than at clusters without ($F_{1,971} = 5.27$, $P < 0.05$, see Fig. 2) although no differences in signal strength existed across the hours or between hours and cluster state (see Fig 3).

For clusters in which a kill was confirmed, we found no difference in the signal strength associated with different sized prey categories for neither tag 21 nor tag 22. This result remained the same after investigating possible interactions between the size of prey and hour from the start of the cluster.

Discussion

Our results, although preliminary, show evidence that the use of the spatial association between members of a carnivore social group could potentially increase the predictive powers of models used to locate kill sites. Our study represents a first effort at the use of proximity tags to locate kill sites in social carnivores and the results need to be viewed with caution due to the small sample size employed. Our signal strength results need to be validated with larger data sets before the application can be included in kill-site models. Additionally, due to the short time span that tag 22 was deployed, the sample size of kills located with that tag is small, and differences in the signal strength at each hour between tag 21 and tag 22 may either reflect this small sample size or natural variation between animals. Future studies employing a greater number of tags will be needed to separate these two potential drivers of signal strength patterns across time at clusters.

Our initial testing of the relationship between distance and signal strength indicates a rapid decline in relative signal strength close to the receiver. With adequate calibration following the deployment of the tags on the animals, the estimated distance between individuals will be possible. The high sensitivity of signal strength close to the receiver could indicate small changes in mean distance between individuals. Multiple tags associated with a single collar would offer the greatest resolution of fine-scale spatial association between individuals (Prange et al. 2006), although the trade-off between applicability and logistical constraints will limit the deployment of multiple tags. In social carnivores of high tourism value (e.g. lions, wild dogs *Lycaon pictus* and spotted hyaena *Crocuta crocuta*), the trade-offs between research goals and tourism need to be considered, and this approach may only be applicable where tourism is low.

The spatial patterns observed among the females of the pride around the Satara rest camp are similar to previously studied lion prides in the KNP. Our proximity tags estimate an association with the GPS collar of 94 and 87% of time, respectively. Funston et al. (1998) showed that lionesses in the southern region of KNP spent 94% of the time with their full pride compliment or pride subgroup which they usually associate with. In Hwange National Park (HNP), Zimbabwe, pride females lions spent on average 89% of the time within the pride (Valeix et al. 2009). These levels of association for southern African lions are somewhat higher than the fission fusion driven systems of the Serengeti where pride females spend as little as 20-30% of the time together (Schaller 1972, Packer 1986). In cases such as KNP and HNP where pride fidelity is high, proximity tags will provide a valuable addition to any GPS based kill site prediction model.

However, when pride fidelity is lower, such as in the Serengeti, a modification of the above approach will be needed if sequential commencement of feeding exists. Schaller (1972) noticed that on most occasions lions would begin feeding as soon as they arrived at a kill. In this situation, instead of using the proximity tag association at the beginning of a cluster, using the proximity association between two individuals at the first hour that they are associated with each other may indicate the clustering effect of a carcass. This would, however, only be applicable for large kills, as smaller kills may be completely consumed prior to splinter groups of a pride arriving at a carcass.

The majority of kill-site models have identified the length of time that a cluster is occupied as a primary predictor of a kill (Anderson & Lindzey 2003, Sand et al. 2005, Franke et al. 2006, Laundre 2008). The use of the minimum length of time at a cluster has been shown to work well for larger kills; however, most authors still suggest limitations to predicting the location of small kills. In wolves, low success in locating small kills was assumed to be an artefact of the variation in time spent on small carcasses (Webb et al. 2008), thus limiting the applicability of cluster length to predict all kill sites. Our preliminary results suggest that in the absence of long cluster bouts (i.e. for small kills), a high degree of association of individuals at the start of a cluster could still indicate a kill. We found no difference in the association patterns between individuals at small and large kills suggesting that a similar initial feeding pattern may exist for all size kills. Although our preliminary results do suggest that the identification of clusters with small kills could be possible, we caution that further investigation may be needed to validate our initial observations.

Although not investigated in our study, the influence of the orientation of the collar, potential barriers (e.g. vegetation, other lions and carcasses) and topography will result in changes in the signal strength. The influence of these factors affecting GPS signal acquisition has been well documented in GPS collar studies (D'Eon et al. 2002, Di Orio et al. 2003, D'Eon & Delparte 2005, Lewis et al. 2007). Due to the nature of the UHF (ultra high frequency) signals used in the proximity tag, this impact will be unavoidable (Prange et al. 2006). However, even with this potential bias, the goal of kill-site prediction using GPS collars is to locate kills for wide-ranging and difficult-to-observe species where continuous observation approaches are not feasible. Unless continuous observation is done concurrently, the presence of potential barriers between proximity tags and receivers will not be known. However, calibration of the signal strength-distance relationship for different habitat types could allow adjustments of distance association relationships for each habitat type.

Apart from group fidelity and spatial association studies, further use of proximity tags exist for carnivore ecology. Proximity tags on individuals of solitary species can indicate contact periods and could be useful for the assessment of mating bouts and mating timing (see Ji et al. 2005). However, as pointed out by Prange et al. (2006), a saturation of proximity tags on all individuals in the study area will be needed for adequate mating system studies. Therefore, this approach will not be feasible for large carnivores in open systems where transitory individuals can associate with study individuals. During the course of our study, we obtained a single proximity reading for each hour at the same time as the GPS position was recorded. The increased storage capacity of collars (Clark et al. 2006) now allows for increased data capture, and proximity readings could be collected at a shorter frequency depending on the research-management question that is being addressed (Prange et al. 2006). A greater frequency of proximity readings could show potential contact networks within groups that could infer possible disease transmission routes (Ramsey et al. 2002, Ji et al. 2005, Bohm et al. 2008). Additionally, transmitter used in proximity tags vary in the frequency on which they operate (Our study: 866 MHz, Ji et al. 2005: 160 Mhz, , Prange et al. 2006: 916.5 MHz) which then has implications for the distance that the proximity tag can be effective. Lower frequencies travel further than higher frequencies because they reflect less when travelling through dense vegetation or varying terrain (Mech 1983, Mech & Barber 2002). Therefore, if greater effective distances are required (detecting possible between-pride contacts), a tag with a lower frequency might be used, whereas a tag with a higher frequency would be best for detection of close-range distance variation (activity around a carcass). In some collars, the power (determining the UHF signal strength) can be adjusted allowing the detection distance of the proximity tags to be set by the user (Prange et al. 2006).

The amalgamation of GPS technology, which is becoming more popular for carnivore research, with additional technology will increase the data that can be collected, with the possibility of increasing sample sizes for research on elusive species. However, we do caution, along with many other GPS studies, that adequate calibration is needed and the biases inherent in GPS associated data need to be assessed and corrected if possible when planning a GPS telemetry study.

Figures

Figure 1: Relationship between the relative proximity tag signal strength and the distance between proximity tags and receivers (following a negative logistic curve) during a trial period in the Kruger National Park, South Africa.

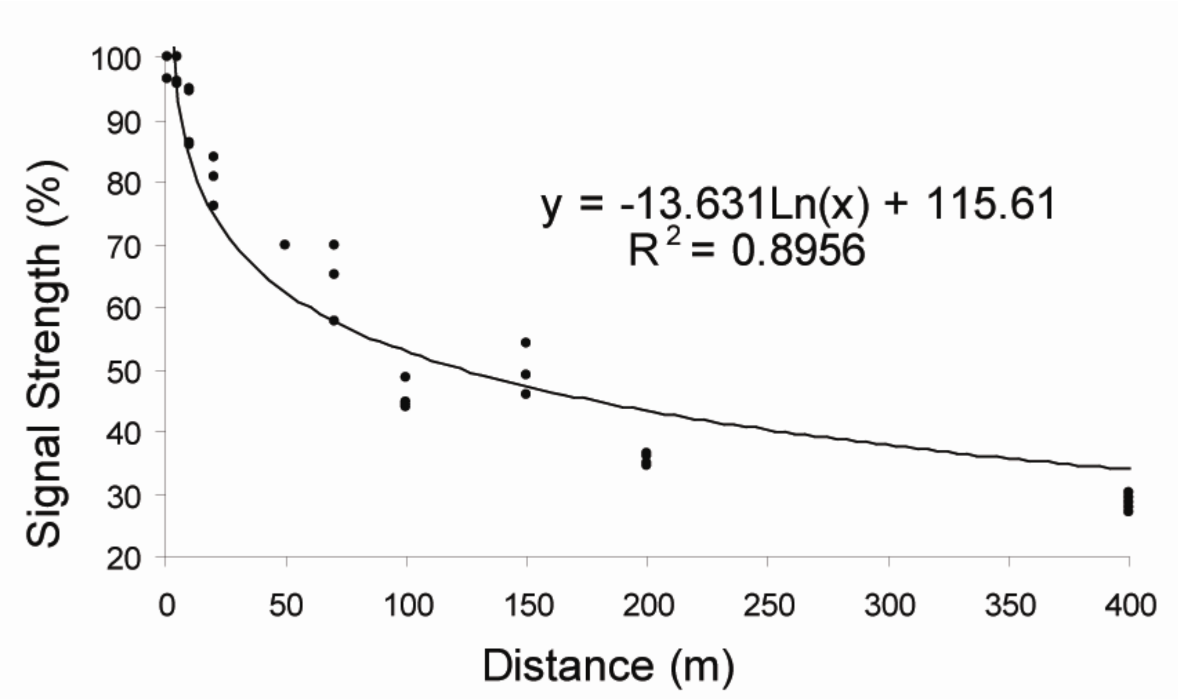


Figure 2: Mean signal strength (all hours combined) between the proximity tags of two female lions in relation to a global positioning system (GPS) collar (with proximity tag reader) fitted on the focal female lion at clusters with and without kills, from the Kruger National Park, South Africa. The asterisk signifies significant differences at a significance level of 0.05, and the maximum signal strength recorded for both tags was 72.

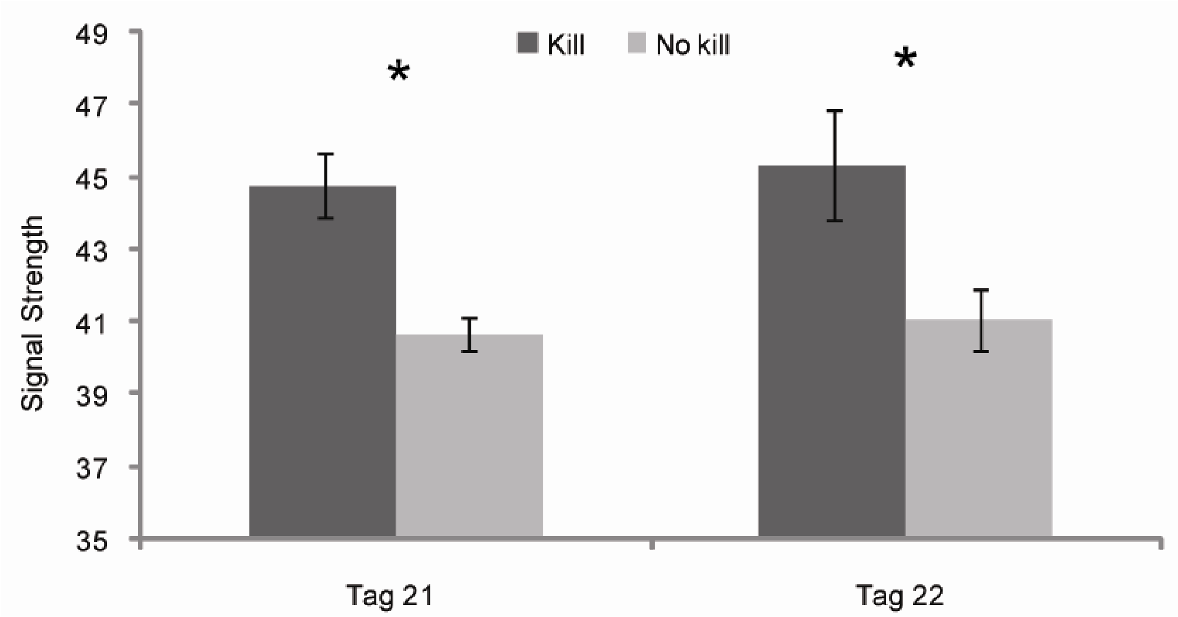
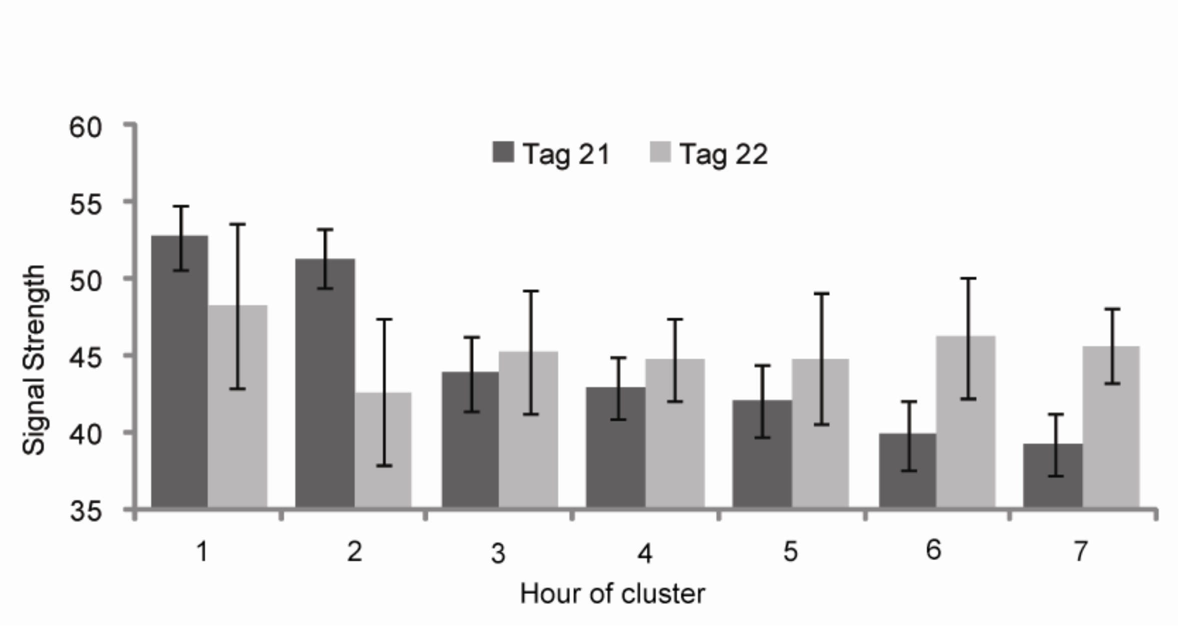


Figure 3: Mean signal strength of two female lion proximity collars (Tag 21 and Tag 22) in relation to a GPS collar (fitted with a proximity tag reader) fitted on a focal female lion indicating the interaction between the cluster state (kill or no kill) and the hour of the cluster, in the Kruger National Park, South Africa.



Chapter 4: Combining GPS locations and scat analysis to estimate the diet of a large carnivore

C.J. Tambling, S.E. Bellan, S.D. Laurence, E.Z. Cameron, J.T. du Toit & W.M. Getz

(In Preparation: Journal of Mammalogy)

Abstract

Understanding the diets of large carnivores is fundamental to their management. Numerous methods exist for estimating diets of large carnivores. Faecal analysis is commonly used to assess diets of carnivores, and GPS cluster approaches are increasingly used to locate kill sites of larger carnivores. Both approaches however have inherent biases. Recently, an additive approach has been proposed that employs a combination of direct carcass observations and scats to addresses bias inherent in carcass observation techniques and scat analysis. In this study we correct diet estimates of African lions (*Panthera leo*) in the Kruger National Park, South Africa, assessed using a GPS cluster approach, by incorporating data obtained from scats at the same clusters. We also compared the diet estimate obtained using the additive approach to a diet estimate obtained from randomly collected scats. The GPS cluster analysis (with carcass identification only) under-estimated small kills but the overall diet estimate was not significantly different to that obtained with the additive approach. The diet estimated from independently located scats differed significantly from the additive approach, clearly over-representing smaller species and under-representing larger species. We estimate that at least 50% of small prey species (impala [*Aepyceros melampus*] and warthog [*Phacochoerus africanus*]) are missed during the carcass investigation at GPS clusters. The additive approach provides a more biologically accurate estimate of the diet of large carnivores, taking into account potential pseudo-replication of clustered scats and identifying small kills missed by the GPS cluster approach. We suggest that where continuous observation is not possible, the additive approach be used to estimate the diets of larger carnivores.

Introduction

Quantifying carnivore diets is an essential step in investigating carnivore ecology (Mills 1992), and are a helpful step in beginning to understand the population level impacts that carnivores may have on prey populations (Owen-Smith & Mason 2005, Owen-Smith 2008). Numerous techniques are available for the assessment of carnivore diets (Mills 1992), including highly invasive stomach content analysis (Smuts 1979), moderately invasive continuous direct observations (Mills & Shenk 1992) and non-invasive faecal analysis (Andheria et al. 2007).

Faecal analysis is widely used where carnivores are elusive, endangered, or difficult to observe through continuous observation (Marker et al. 2003). Additionally, scat sampling enables large datasets to be collected non-invasively, which is especially helpful when handling carnivores increases stress levels and vulnerability to mortality and disease (de Villiers et al. 1995, Creel et al. 1997). Although the analysis of faeces yields a basic understanding of carnivore diets, it is widely recognized that this method over-estimates the biomass, and under-estimates the numbers, of small species eaten (Karanth & Sunquist 1995, Marker et al. 2003). The application of correction factors can reduce some of the bias when feeding trial data allow the volume of food ingested to be related to the volume of faeces produced (see Ackerman et al. 1984, Weaver 1993, Marker et al. 2003). Carnivores that consume larger prey items in relation to their body size (e.g. wild dogs *Lycaon pictus*, lions *Panthera leo*, wolves *Canis lupus*) can produce correlated clusters of scats emanating from larger prey items (Marucco et al. 2008), further biasing results based on faecal analysis.

Recent advancements in Global Positioning System (GPS) technology permit the collection of animal location data at a scale that is sufficiently fine to provide a good approximation to the continuous movement path of individuals (Getz & Saltz 2008). Despite this a trade-off between the frequency of points collected and the total length of the movement path still exists due to the limited battery life of most collars (Sand et al. 2005). Obtaining GPS fixes at an hourly interval for female lions in the Kruger National Park allowed the development of models that increased the probability of locating kills at GPS clusters in time (Tambling et al. 2010). However, it is suspected that small prey items may be entirely consumed (see Power 2002) and that scavengers may eliminate signs of feeding sites. Similarly, the use of the GPS approach for mountain lions *Puma concolor* (Anderson & Lindzey 2003) and wolves (Sand et al. 2005, Franke et al. 2006) show the approaches usefulness, but also highlight that bias towards large prey exists.

Marucco and colleagues (2008) used a combination of carcasses and scats along a known movement path to describe the diet of wolves in Europe, and suggest that the combination of these two datasets provides the most accurate assessment of the diet. This additive approach combines kills and scats originating from the same kill into a single sample unit. In doing so, the resulting diet is more biologically meaningful, as the unit of sample is a kill and not the scat, therefore reducing pseudo-replication caused by numerous scats being linked to a few large kills. Additionally, the additive approach decreases the proportion of kills missed when conducting systematic searches for carcasses (Marucco et al. 2008).

Although the most common method of investigating lion diet is through continuous observation where all predation activity is directly observed (Mills & Shenk 1992, Funston et al. 1998), this approach is not always logistically feasible. Alternate methods including scats and GPS approaches have not been comprehensively tested and hence the bias inherent in results obtained through these methods is uncertain. Due to their social nature, lions generally consume prey items the same size and larger than themselves (Radloff & du Toit 2004, Hayward & Kerley

2005) resulting in the possibility of correlated clusters of scats from a single kill. Alternatively, opportunistic observations or GPS follow-up methods are expected to bias the results in favour of large prey items. In this study we investigated a combination of scats and kills identified from GPS clusters to improve the estimation of lion diets using an additive approach (Marucco et al. 2008). Then we compared the diet estimated by the additive method with an independent sample of scats not collected at GPS clusters to assess the accuracy of scat analysis for lions.

Materials and Methods

Study area

We conducted the study between March 2005 and April 2007, in the Kruger National Park (KNP), in a 1000km^2 area around the Satara rest camp (31.77º E, 24.39º S) in the central region of the park (Fig. 1). Rainfall in the area is highly seasonal, with the majority falling between October and March, and this period is also associated with an increase in average temperature (Venter et al. 2003). As a consequence of the increased rainfall and temperature, faecal collection becomes considerably harder during the rainy season as dung beetles (Coleoptera; Scarabaeinae) and rain reduce the number of collectable samples.

Open tree savanna with a moderate to sparse shrub layer and dense grass layer dominate the study area, with *Sclerocarya birrea* and *Acacia nigrescens* the dominant tree species and *Themeda triandra* and *Bothriocloa radicans* the dominant grass species (Venter et al. 2003). Our study area comprises the northern component of the wildebeest (*Connochaetes taurinus*) and zebra (*Equus quagga*) migrations, causing high densities of these species to occur in the wet months (Gertenbach 1983). Resident buffalo (*Syncerus caffer*), kudu (*Tragelaphus* *strepsiceros*), giraffe (*Giraffa camelopardalis*) and waterbuck (*Kobus ellipsiprymnus*) occur in large numbers, all combining as a prey base for a high lion density (Ferriera and Funston, unpublished data). Across the park impala (*Aepyceros melampus*) are the most abundant prey species and provide the bulk of food for lions and the other large predators (Owen-Smith & Mills 2008).

Data acquisition and datasets

We collared seven lions (five females from four prides and two males) with GPS/GSM units (i.e. GPS with mobile phone capabilities; African Wildlife Tracking) between May 2005 and April 2007. Lions were captured and collared by SANParks (South African National Parks) veterinarians using standard SANParks protocols (Smuts et al. 1977). Spatio-temporal data from the collars were used to investigate GPS clusters (hereafter referred to as clusters) in time and space. A GPS cluster is defined as consecutive GPS co-ordinates within 100m of the previous GPS co-ordinate, until the lions move more than 100m during a recording interval (See Appendix 1). We searched an area with a diameter of ~50m around each cluster and the duration of the search time was dependent on the vegetation cover of the area (See Appendix 1). At each cluster we attempted to locate all kills and scats present.

The fix schedule of the collars (one fix per hour at night when the lions are most active, and three fixes during the day when lions tend to rest) provides a set of locations used to construct a movement path over time for each of the collared lions. Kills and scats found at clusters therefore occur at known times and dates along this movement path, and these data are used to create a history of kills related to either a) a kill alone, b) a scat alone or c) a combination of a kill and a scat from the same predation event. We assume a maximum through-gut period of five days, based on cheetah data (48 - 111 hours: Marker et al. 2003), since there is little available data on lion through-gut times (Breuer 2005, van Kesteren 2006). Thus, we assume that prey remains from a known kill will no longer be found in a scat from a group of lions associated with a kill five days after these lions left the kill site. Therefore, any scat that did not a) correspond to a previous kill/scat or b) occur >5 days after a kill/ scat was assumed to represent a different kill event. The new dataset of kills for each lion was then constructed from the time-series data of observed kills and missed kills. We investigated two datasets, the first constituting all the corrected kills (including both males and females) and the second constituting only the corrected female dataset.

We investigated the temporal relationship between the species killed and the species found in scats over a five day period following the kill event by calculating the percentage of scats that belong to the same species as the previous kill. However, consecutive kills of the same species, where the second kill was missed in the GPS cluster data, may bias these results by underestimating the proportion of different species found in the five days following a kill. To take this into account we calculate the proportion of same species kills that occur consecutively for the entire dataset and then only all observed five day intervals. While traversing the study area between GPS clusters, we opportunistically collected a second sample of scats, not associated with GPS clusters.

Scat analysis procedure

We washed the faeces under running water using a metal sieve to isolate all undigested distinguishable prey items (hairs, bones, hooves and horn remains). Hair was examined macroscopically (length, colour and texture) and microscopically (cross-section characteristics and cuticle scale patterns) to identify prey species. Cross sections of hairs were made using the method outlined in Douglas (1989) where hairs are placed in plastic tubes and set in paraffin wax, before cross sections are cut. We investigated hair cross sections under a dissecting microscope, using the medulla and cortex as a means to identify the different species (Keogh 1983, Buys & Keogh 1984). We obtained cuticle scale imprints by laying hairs on wood glue, and investigating the dried imprint under a light microscope (van Kesteren 2006). If multiple scats were found at a GPS cluster, we checked to determine if the same species occurred in more than one scat, and used the collection of scats of one species as a single sample unit as recommended by Marucco *et al.* (2008), avoiding over-representation of prey items from multiple faeces.

Data analysis

Using the first dataset (both male and female collar data) we used a chi-square test to compare the frequency of occurrence of each prey species at the investigated clusters (i.e. carcasses found) with the corrected frequency of occurrence of each prey species derived by the additive approach. In keeping with standard practices for the chi-squared statistical test (Zar 1999), we combine all prey items with a frequency below five to form a seldom eaten category. From these two kill datasets we assessed, for each prey species, the number and percent of individuals and the percent biomass that were missed in the initial investigation using the GPS-based follow-ups alone. For the biomass calculation we do not know the age of the consumed prey item when the prey item is identified from scat remains, so we define all missed kills as adult females (weights taken from Bothma et al. 2002), accounting for smaller juveniles and larger males. In the GPS cluster approach, we expect that kills of smaller species will be missed more often than kills of larger species (Anderson & Lindzey 2003, Sand et al. 2005). We tested this assumption by taking the percentage of kills missed as a function of prey body size (adult female), where we log transform the prey body size to accommodate the wide range of observed prey species.

For the independently collected scats, we estimated the lion diet as the percentage occurrence of prey species from all prey items found. In this way, the proportion of each species based on our corrected diet and the independent scats is relative to the total number of prey items identified across all methods. For each of the diets calculated using the three methods (GPS follow-up, additive approach and independent scats) 95% confidence intervals were generated by 1000 bootstrap simulations (see Andheria et al. 2007). To assess our sampling adequacy for the independent random scat collection we calculate a cumulative Brillouin index $H = \left(\ln(N!) - \sum \ln(n_i!)\right) / N$, where N is the total number of scats and n_i are the prey species found in the n^{th} scat (Brillouin 1956, Glen & Dickman 2006). We randomised the order in which we collected our scats 50 times to calculate the mean (± standard deviation) cumulative Brillouin index and plot this against the number of scats analysed (k), to determine when we have sampled enough scats to incorporate all prey items. We test the difference between our corrected kill sample and the kill sample obtained from scats using a chi-square test and, again combining categories of fewer than five individuals into a seldom eaten category.

By using the uncorrected and corrected female diets we assess the ability of the corrected diet sample to remove the bias of not locating small kills in the GPS follow-up method. Average female group size for the central and central region of the KNP ranges from 3.8 (Funston et al. 1998) to 5.1 (Smuts 1976). Including cubs prides in the region range from 10-12 lions (Smuts 1976). If we rescale cubs to female equivalents (Bertram 1973), average group size is ~7 - 10 female equivalents. We calculate the daily meat consumption per female equivalent by dividing the biomass of food consumed by the upper and lower limits of female equivalents and compare the resulting food consumption against the minimum daily requirement of lions in the KNP (5.3kg/lion/day, Funston et al. 1998). We conduct this calculation for both the uncorrected and corrected female diets to assess how much better we represent overall diets by including the scats in the GPS cluster approach.

Results

We found 293 kills using the GPS follow up method comprising 12 prey species between May 2005 and April 2007 (Table 1). We were unable to identify five of the kills to a species level. Additionally, we found 341 scats at 231 different clusters, with a further 120 scats found independently within the study area. The dominant prey items from the GPS cluster method were zebra (~26%), wildebeest (~18%) and buffalo (~15%) while impala, numerically the most abundant prey species, only accounted for ~10% of the initial observed diet based on carcasses found at GPS clusters (Table 1).

Approximately half (48%) of the scats found at a kill site (n=47) contained the prey species of that kill, so at least 52% of all scats found at kill sites are expected to have originated from a previous kill (Fig. 2). For the first two days following a kill, between 62% and 65% of scats at clusters contained the killed species (Fig. 2). This percentage declined from day three onwards until day five, when only 22% of the scats contained the killed species (Fig. 2). For all 293 observed kills sites (found by GPS cluster investigation), the same species was killed consecutively (e.g. two impalas killed in a row) on 58 occasions (20%). However, when only the five days following a kill were taken into account, the same species was killed consecutively in 47 out of 135 (35%) possible consecutive kill occurrences.

Using a combination of kills and scats, we identified a minimum of 114 missed kills, yielding a final total sample of 407 kills between May 2005 and April 2007. There was, however no significant difference between the kill sample collected at GPS clusters and the kill sample derived from our corrected sample based on scats and kills ($\chi^2 = 8.71$, df = 8, $p = 0.3674$). However, despite this non-significant difference we only located 30 out of 65 (47%) and 8 out of 17 (47%) impala and warthog (*Phacochoerus africanus*) kills respectively, whereas we located between 70% and 90% of the medium and large prey species (Fig. 3). Although we missed 53% of both impala and warthog, numerically we missed considerably more impala (35 kills) than warthog (9 kills). There was a significant negative relationship between the log weight of an adult female of each prey item and the percentage of missed kills ($F = 53.24$, $R^2 = 0.87$, $p < 0.005$, Fig 4). The large proportion of impala kills missed meant that the relative percent impala in the diet increased from 10% to 16%, with warthog almost doubling from 2.7% to 4.2% (Table 1). However, the substantial numerical change in impala in the diet calculated using the additive approach was not evident when we calculated the increased biomass of impala that the lions would have consumed, with the biomass percentage of impala in the diet calculated by the additive approach increasing by ~1% (Fig. 5). Our data suggest that only four buffalo predation events were missed using the cluster approach; resulting in a decline in the buffalo occurrence and biomass of ~4% respectively when the additive approach is used to calculate the diet (Fig. 5).

The cumulative Brillouin index asymptotes at ~ 75 scats collected (Fig. 6) indicating that the sample of scats available would be adequate to estimate the diet of the lions in the area. Impala (27.7%) was the dominant prey item in the scat analysis, followed by zebra (13.8%) and waterbuck (12.4%). We found a significant difference in the diet when investigating scats alone against our corrected diets ($\chi^2 = 31.4$, df = 8, $p < 0.001$), with impala over represented and buffalo (5.8%), giraffe (6.6%) and zebra (13.8%) under-represented in the scats (Table 1).

The daily food consumption of female lions based on the corrected diets from observed kills and scats located at GPS clusters accounts for on average between 68 and 97% (individual pride range: 55%-114%) of the minimum daily requirement, depending on the average pride size (Table 2). Thus the additive approach accounted for increases of 15% to 22% of observed consumed biomass for the females, depending on the size of the prides (Table 2).

Discussion

In order to develop a sound theory of predator-prey interactions, an accurate estimate of the predators' diet is required. Barring direct continuous observations, most approaches to estimating carnivore diets have inherent biases that need consideration (Mills 1992). Carcass observations over-estimate large prey species consumption whereas the use of scats is confounded by psuedoreplication, especially for large carnivores that hunt in groups or kill prey species larger than themselves. By combining prey carcasses and lion scats found at lion GPS clusters generates a dataset that addresses and quantifies the bias of under-estimating small prey items and reduces the impact of psuedoreplication in scat sampling.

The additive approach

Our results substantiate previous findings that only investigating kills at GPS clusters severely under-estimates the number of small kills in the diet of large carnivores (Franke et al. 2006) and that intensive field effort will be required to locate these small kills (Webb et al. 2008). The extent to which the under-representation of small species affects the biomass of prey consumed by large carnivores is still unknown (Sand et al. 2005). Several suggestions exist to attempt to counter the bias against small kills, including reducing the time between GPS fixes (Sand et al. 2005, Webb et al. 2008), using alternate movement metrics for model development (Webb et al. 2008) or by increasing the number of clusters investigated in the field (Sand et al. 2005, Knopff et al. 2009). By combining prey consumption estimates, with and without scat corrections, associated with carnivore group size data we can estimate how much GPS cluster investigation under-estimates the diet of monitored carnivores. In our study under-representation of smaller prey items (mainly impala [45-50kg] and warthog [45-100kg] by 50%) accounted for between 15% and 22% of the diet of female lions depending on group size. In a comparison of scats and carcasses found at GPS clusters in Hwange National Park (HNP), small species (common duiker *Sylvicapra grimmia* [15-20kg] and reedbuck *Redunca arundinum* [30-70kg]) were similarly under-represented in carcass observations (van Kesteren 2006). As a consequence, the bias against small prey species could have serious implications for the management of these smaller species and will alter kill rate estimates for carnivores, stressing the importance of combining sampling approaches, especially as the proportion of missed kills increased with decreasing body size.

Adequate knowledge of the movement path of the predators by GPS tracking (current study) or spoor tracking (Melville et al. 2004, Marucco et al. 2008) provides a movement path whereby scats and carcasses can be combined chronologically to identify kill events. The additive approach provides a powerful tool in dietary studies as it deals with the independence of data, an essential component of selection studies (Marucco et al. 2008). Despite having movement path for lions, other factors combine to reduce the certainty of finding independent kill events. Unlike many other species, data on the through gut period for lions is unknown, and a surrogate taken from cheetah had to be used. However, Ruhu and colleagues (2008) caution against using estimates of scat characteristics from one species to infer results on another species. Despite their cautions aimed at correction factors, we feel that these cautions are warranted for through gut rates as well. The through gut period plays a significant role in determining the independence of each kill event and if possible should be quantified for the species being studied with the prey items being consumed. During the course of our study (using a five day through gut period) we witnessed that from days four and five as little as 20% of all scats still contained the same species previously killed. Considering that both male (3.2 days/kill) and female (1.8 days/kill) lions in southern KNP kill more frequently than once every five days (Funston et al. 1998), our estimates of time to independence are no doubt overly conservative. A further complication is that same species will be killed consecutively; further confounding estimates of time to independence between kills. The uncertainty regarding through gut times, manifesting in confounded estimates of time to independence in the GPS follow up approach, emphasizes the need for accurate digestion studies in all carnivores. Through gut times and how consecutive kills are accounted for are important future issues that need attention for the generation of accurate, unbiased, diet estimates for large carnivores using combinations of scats and carcasses.

Diet estimates from scats

Within our study area, the use of lion scats alone, from the independently collected scat samples, did not result in the same diet composition to that obtained through the more rigorous additive approach using both scats and carcasses. Large prey items (buffalo, giraffe and zebra) were under-represented, whereas impala was over-represented. Three possible reasons and sources of bias may be leading to the differences observed in the two datasets. Firstly, the extended length of time that lions spend feeding on giraffe (up to five days) and buffalo kills (up to three days; Tambling, unpublished data), potentially dilutes the chance that scats will be located independently from kills or GPS clusters. Secondly, large species, with a lower body surface to volume ratio, produce less hair than smaller species (Marker et al. 2003), possibly contributing to the lower frequency of large prey species in the scats. Thirdly, male and female lions tend to hunt independently in the KNP, with different success rates on different prey species (Funston et al. 1998). The majority of the GPS cluster data were generated from female lions, whereas the majority of the independent scats were collected along roads and prominent paths more often used by males (C.J. Tambling unpublished data). Sex based differences in predation patterns, represented by sexual dimorphism in movement patterns may drive the differences in the diet estimate from scats collected randomly.

Conclusions

Our finding show that the implementation of a GPS-based approach to diet detection in lions in an African system results in the same bias (small kills missed) as previous GPS-based approaches in the northern hemisphere on mountain lions (Anderson & Lindzey 2003, Knopff et al. 2009) and wolves (Sand et al. 2005, Franke et al. 2006, Webb et al. 2008). The additive approach implemented, showed that impala and warthog are the source of the under-representation of small prey species in the diets when only GPS-based follow carcasses are used to assess the diet. Where direct continuous observation of lions is not possible, the use of the additive approach, through a combination of GPS point investigation and serial collection of scats, results in a robust estimate of lion diets. If conducted with adequate knowledge of the group size, associated with minimum daily consumption requirements, the minimum biomass missed can be estimated for monitored carnivores. The approach presented should be applicable to a wide variety of ecosystems and carnivore species (Marucco et al. 2008). In the case of social carnivores with fission-fusion societies, genetic identification of individuals producing each scat can improve efforts to obtain a fine scale representation of diets. We suggest that, as ecological methods become more diverse, it becomes important to assess the best way to combine and analyse data collected using several different techniques to yield the least biased and most accurate results possible to address the questions at hand.

Tables

Table 1. Consumption (percent ± 95% confidence limits) of prey species by lions in the central region of Kruger National Park, South Africa, between April 2005 and May 2007 utilising three methods of diet estimation. The additive approach combines scats and kills observed at GPS clusters along a known movement trajectory for each collared lion as the kill sample, observed kills are based on only carcasses located at GPS clusters and independent scats are scats collected randomly and not associated with lion GPS clusters or movement paths.

	Additive method (%)	95% CI	Observed carcasses (%)	95% CI	Independent scats (%)	95% CI
Buffalo	12.1	9.1 - 15.2	15.2	11.2 - 19.7	5.8	2.2 - 9.8
Bushbuck	0		0		1.4	0 – 3.7
Duiker	0		0		0.7	0 - 2.3
Elephant	0.2	0 - 0.7	0.3	0 - 1	0	
Giraffe	7.9	5.7 - 10.6	9.1	6.1 - 12.5	6.6	2.9 – 10.4
Impala	16.0	12.5 - 19.7	10.1	6.8 - 13.9	27.7	20.3 – 34.8
Kudu	8.0	5.7 - 10.6	8.1	5.1 - 11.5	11.0	5.8 – 16.5
Ostrich	0.5	0 - 1.2	0.3	0 - 1	0	
Porcupine	1.0	0.2 – 2	0.3	0 - 1	3.0	0.7 – 6.0

Tortoise	0.2	0 - 0.7	0.3	0 - 1	0.7	0 - 2.3
Unknown	1.2	0.2 - 2.2	1.7	0.3 - 3.4	0	
Warthog	4.2	2.5 - 6.1	2.7	1 - 4.4	4.4	1.4 – 8.1
Waterbuck	7.9	5.4 - 10.6	7.2	4.4 - 10.5	12.4	7.3 – 18
Wildebeest	17.5	13.8 - 21.1	18.0	13.9 - 22.7	11.7	7.0 - 17.3
Zebra	23.2	19.2 - 27.5	26.4	21.7 - 31.5	13.8	8.3 - 19.7

Table 2. Percent of the minimum daily requirements for each female lion in the central region of the Kruger National Park, South Africa, between April 2005 and May 2007 assuming two different group sizes. Diet estimates used in the calculations are obtained using the additive approach where scats and carcasses found along a known movement trajectory are combined to form independent kill samples.

	Pride Size estimated at 7		Pride size estimated at 10	
	GPS follow-up	Additive approach	GPS follow-up	Additive approach
Female 1	62.5	77.9	43.8	54.5
Female 2	80.1	109.8	56.1	76.9
Female 3	106.7	113.8	74.7	79.7
Female 4	65.7	93.7	46.0	65.6
Female 5	59.8	88.5	41.9	62.0
Average	75.0	96.8	52.5	67.7

Figures

Figure 1. Study area in the central region of the Kruger National Park, South Africa, showing independent field scats, scats located at GPS clusters, and kills located at GPS clusters

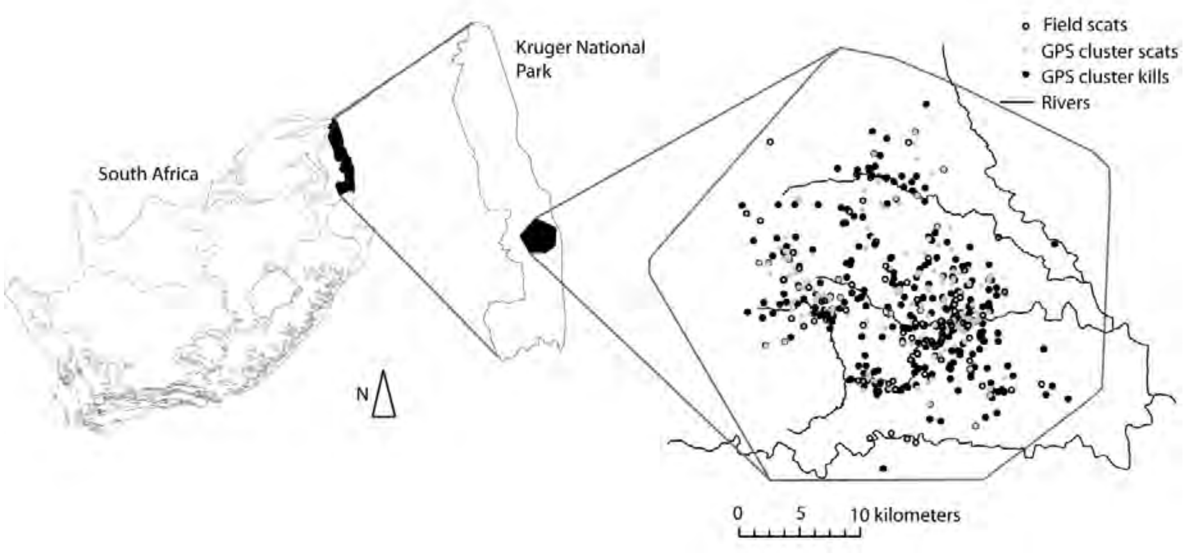


Figure 2. Percent of scats that are the same species (grey) or a different species (black) as the preceding kill (at the kill site [KS] and each day thereafter) based on the investigation of GPS clusters in the central region of the Kruger National Park, South Africa, between April 2005 and May 2007.

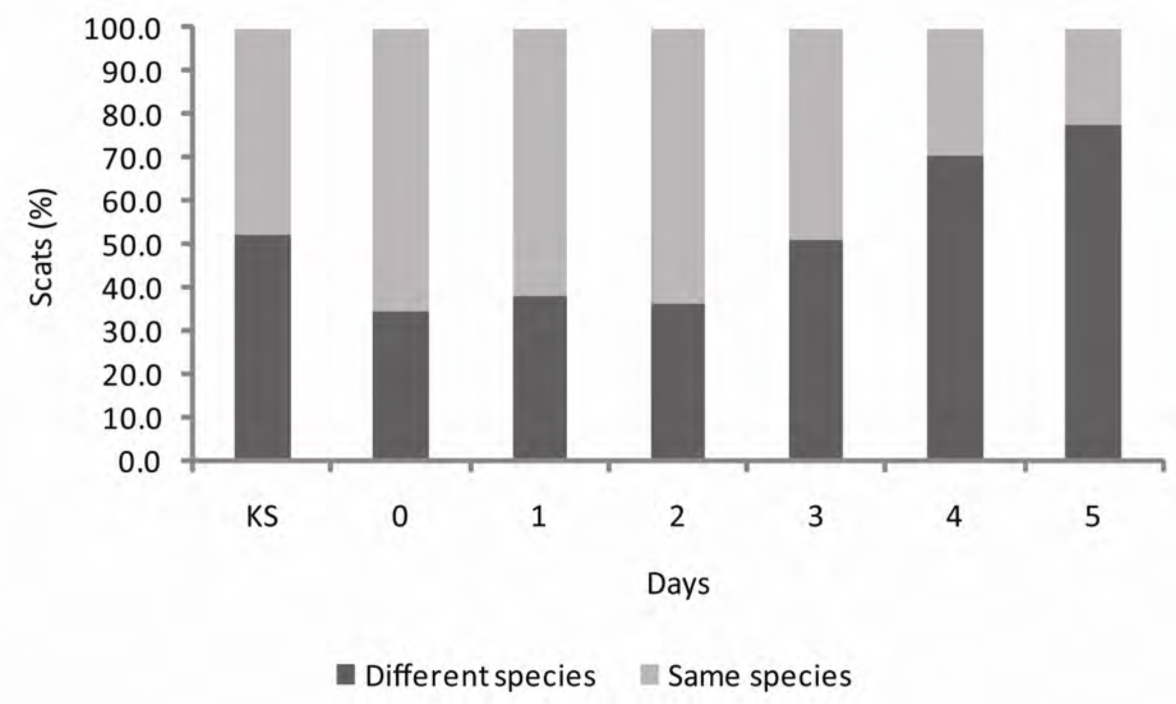


Figure 3. The percentage of kills of each prey species that were not located using the GPS point follow-up technique in the Kruger National Park, South Africa (the possible numbers of kills of each prey species that were missed are presented above the bars; i.e. for elephant (*Loxodonta africana*) and unidentified tortoise species no mortality events were missed based on the investigation of scats found at clusters whereas for ostrich (*Struthio camelus*) and porcupine (*Hystrix africaeaustralis*) one and three possible mortality events were missed respectively)

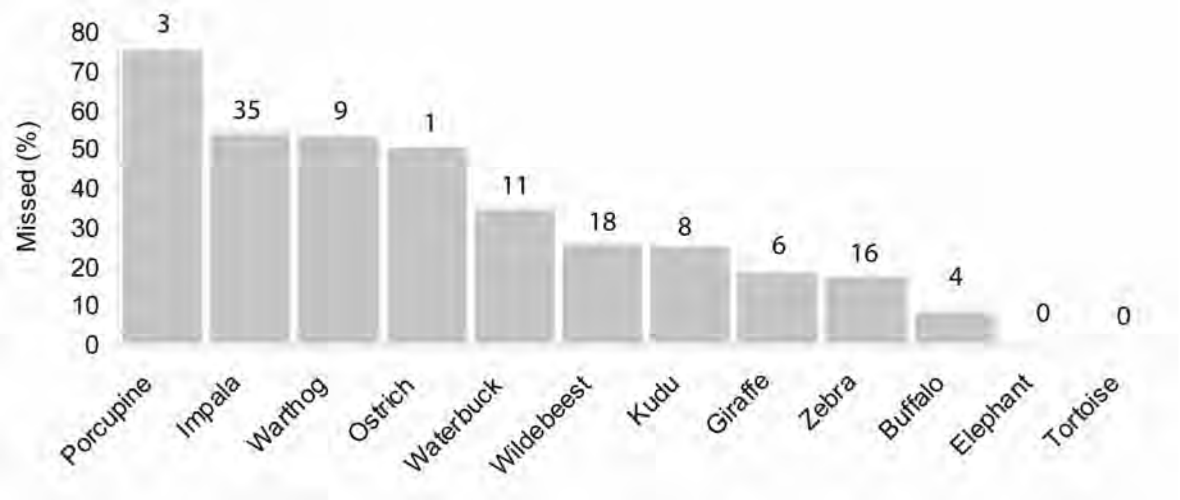


Figure 4. Relationship between the log weight of adult female prey items and the percentage of missed kills located using the additive approach in the central region of the Kruger National Park, South Africa.

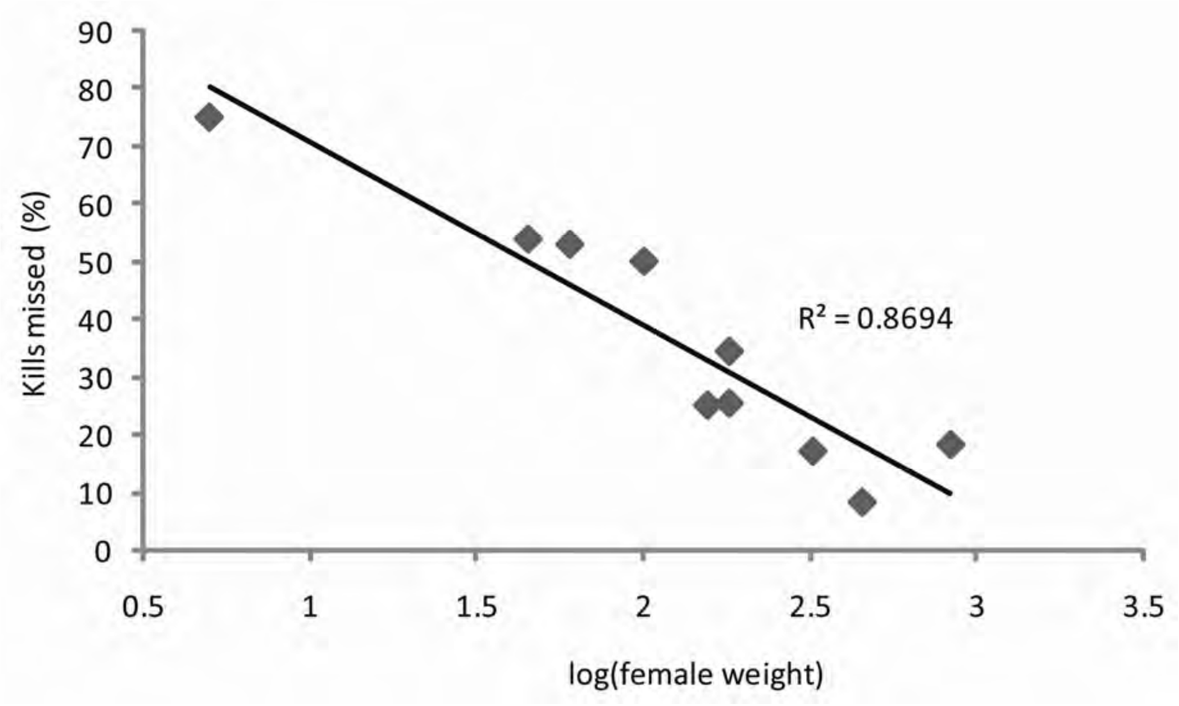


Figure 5. Percent change in consumption of the 'more often consumed' (i.e. with greater than four occurrences in the additive approach) species following the implementation of the additive approach for the total biomass consumed (black) and the total number of each prey item consumed (grey) in the central region of the Kruger National Park, South Africa.

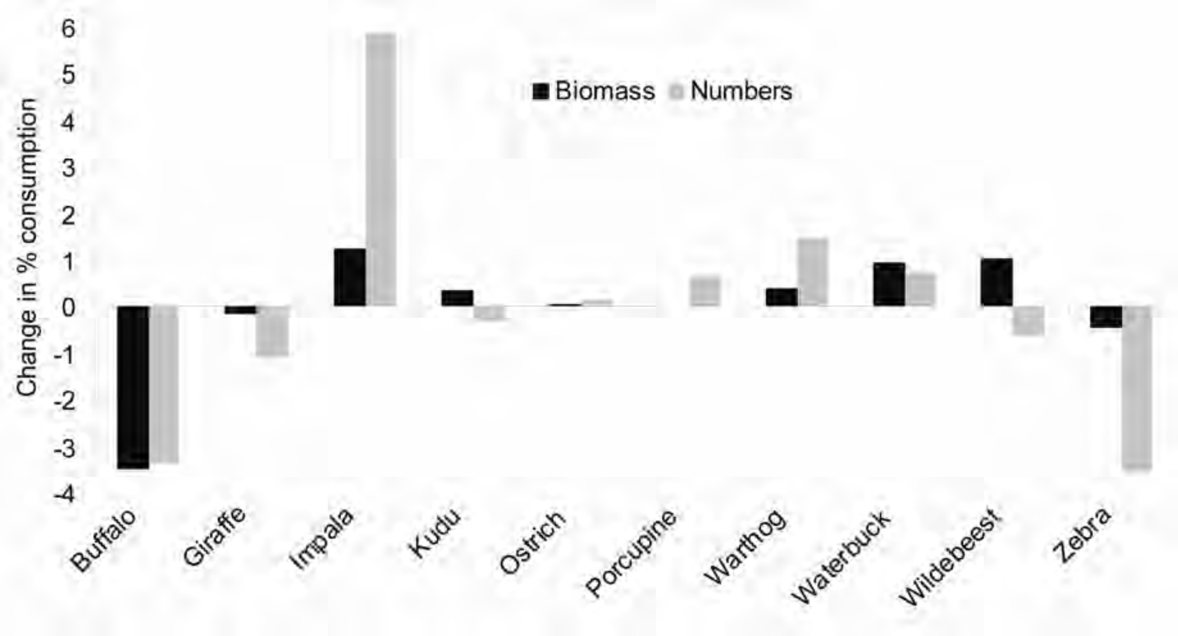
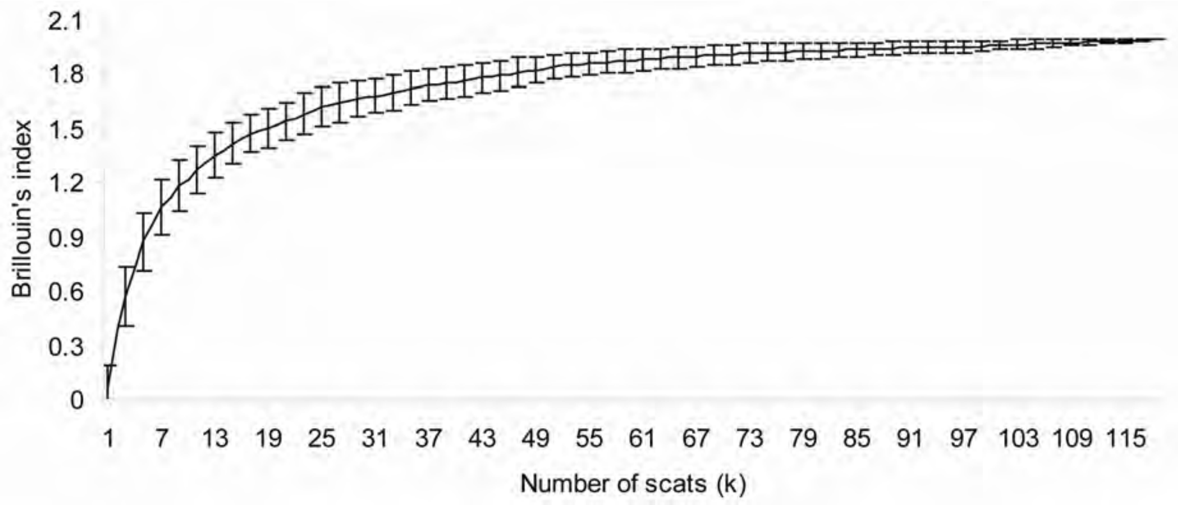


Figure 6. Cumulative Brillioun Index of diversity plotted against the number of scats (k) for the randomly collected scats in the central region of the Kruger National Park, South Africa, following 50 randomisations of the order in which scats are collected



Chapter 5: The influence of scale and count method on prey selection of a large carnivore

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(In Preparation: Journal of Zoology)

Abstract

Scale is an integral part of ecological studies, and multiscale studies are now being advocated to ensure that conservation and ecological questions are answered at the appropriate scale. In prey selection studies the accuracy and applicability of both variables: consumed prey and prey availability, need to be considered if the results are to be used for conservation and management practices. We use an investigation into the prey usage and selection of lions (*Panthera leo*) in the central region of the Kruger National Park (KNP) to investigate factors that influence changes in selection. Our results suggest that a more unified and biologically sound definition of prey availability is needed, as changes from absolute numbers of prey available to predators to available groups of prey result in large changes in selection of species. Our current results using both groups and individuals represent two extremes of selection indices with reality on a sliding scale between them. Depending on the management related questions proposed, the scale at which to conduct selection studies will generate different results. Broad scale selection patterns in the central region are in line with published lion selection patterns, but differences are detectable at finer scales. As conservation areas decline in size, this multiscale approach will allow broad and fine scale patterns of predator-prey interactions to emerge.

Introduction

All ecological processes play out on specific spatial and temporal scales and therefore all ecological patterns and process are scale dependent (Wiens 1989). As a consequence, scale is an important variable that requires consideration and should be included in all ecological studies (Sandel & Smith 2009). Multiscale experimental and observational studies have been proposed to increase the awareness of the role of scale in ecological studies, and therefore create a paradigm shift whereby scale becomes an integral component in all ecological studies (Sandel & Smith 2009, du Toit 2010). All interactions between organism and the environments in which they occur are spatially limited (Sandel & Smith 2009), however choosing the correct scale at which to investigate the impacts is often not simple. Consideration of the influence that organisms have on their environment as well as on other organisms should be investigated at multiple scales. For example, the impact that carnivores may have on prey populations will vary from local impacts measured at the home range level to broad scale impacts incorporating population and meta-population effects (Johnson 1980).

Prey selection by large African carnivores has received considerable attention in recent years (Hayward & Kerley 2005, Hayward 2006, Hayward et al. 2006, Hayward et al. 2006) and is heavily influenced by carnivore prey preference, which is often biased towards large prey items as a result of the methods employed to locate kills (Mills 1992). Additionally, discrepancies in selection indices can occur through the incorrect assessment of prey availability (Owen-Smith & Mills 2008). The accuracy and availability of data on large carnivore diets is increasing through the advancements of novel techniques used in conjunction with traditional field methods (see Sand et al. 2005, Marucco et al. 2008), however the effort to obtain relevant data on the availability of prey items has not received the same degree of attention. Whether or not prey species are used in proportion, above or below the level of availability are critically dependent on the species that researchers deem are available to the predators (Johnson 1980)

In most cases the availability of prey is estimated from aerial census data resulting in a value that represents the absolute availability of prey items. However, prey social groups rather than prey individuals should be the basic building blocks around which predator prey interactions should be modelled and assessed (Fryxell et al. 2007). Ideally, predator selection of prey should incorporate encounter rates for different prey species (see Funston et al. 1998). Encounter rates of prey species in the Serengeti National Park (SNP), Tanzania, follow power curves such that at higher density of prey, encounter rates do not increase linearly but do so at a more modest rate (Fryxell et al. 2007). This relationship between prey density and encounter rate suggests that the use of absolute numbers of prey individuals may over estimate the access that carnivores have to certain prey items. Additionally simulated data suggests that encounter rates of predators may be very sensitive to the prey aggregation and predator search strategy (Travis & Palmer 2005). However, when searching, predators should be able to locate large groups easier than small groups either visually or through their smell (Krause & Godin 1995), further confounding the assessment of prey availability.

On a fine scale, lions (*Panthera leo*) in the SNP utilise habitats that offer a greater chance of making kills rather than areas with the highest prey densities (Hopcraft et al. 2005). Additionally, pride level variation in predation patterns was observed in Queen Elizabeth National Park, Uganda, where different prides showed different hunting and predation patterns (van Orsdol 1984). In both cases, investigating selection patterns based on aerial census figures across each respective park may not capture the pride level selection that occurs at a fine scale.

Therefore, predator prey interactions should be analysed with the inclusion of precise details of the habitats that may vary between prides (Hopcraft et al. 2005).

In this paper we follow the definitions of prey selection and prey usage used by Johnson (1980) where prey selection implies disproportionate use and requires the quantification of prey availability, and prey usage refers to the absolute use of each prey consumed in a fixed period of time. We aim to describe and investigate the selection and usage of the eight most important prey types of lions encompassing four prides and two groups of male lions in our study area. We investigate how the method of counting and defining prey availability as either groups or absolute numbers affects the assessment of selection for lions. Secondly, we investigate how the spatial scale of interest (from a broad park-wide scale down to the scale of each individual lioness moving with her pride) affects the perceived prey selection.

Methods

Study area

The study was conducted in a 1000km^2 section of the central region of the Kruger National Park (KNP), South Africa (24º14’-24 º33’S, 31º39’-31º54’E). Three main vegetation types dominate the study area and the area comprises the northern component of the wildebeest *Connochaetes taurinus* (Burchell, 1823) and zebra *Equus quagga* (Boddaert, 1785) migrations, resulting in large densities in the wet months (Gertenbach 1983). Large number of resident impala *Aepyceros melampus* (Lichtenstein, 1812), buffalo *Syncerus caffer* (Sparrman, 1779), kudu *Tragelaphus strepsiceros* (Pallas, 1766), giraffe *Giraffa camelopardalis* (Linnaeus, 1758) and waterbuck *Kobus ellipsiprymnus* (Ogilby, 1833) occupy the area as well (Venter et al. 2003).

The large prey base supports a high density of lions (Mills & Funston 2003, Ferriera unpublished data). The vegetation is heavily influenced by the underlying substrate (Venter 1990) causing two alternative vegetation structures to exist within the study area and resulting in open areas dominated by grasses in the east and wooded bushveld areas towards the west (Gertenbach 1983, Winnie et al. 2008).

Estimating prey availability

We estimated potential prey availability using two approaches. Firstly, the KNP management conducted yearly aerial census counts (Viljoen & Retief 1994) on certain of the large ungulate species in the park (SANParks unpublished data). The relative availability of the eight prey species making up the bulk of the lion diets are extracted and result in relative proportions of available prey based on the number of individual animals counted. Our study spanned from 2005 until 2007 so we averaged the aerial counts over the three years to estimate an average availability during the study period. Secondly, we conducted ground counts between April 2006 and May 2007 where all groups of prey were counted while traversing all roads throughout the study area. During ground counts, GPS co-ordinates were recorded on the road approximately perpendicular to the animal group observed to give the ground counts a spatial reference. We use the ground observations (of groups, not individuals) to calculate the relative abundance of all groups of prey animals (hereafter referred to as groups of available prey) each spatially referenced across the study region and linked to the total study area and each lion group range (see below for study area and range area calculations). Since we are interested in the relative availability (and not a measure of density of abundance), the lack of clearly defined transects will not influence the resulting proportions of prey available for lions. Both, the aerial census and ground, counts were corrected with correction factors in Owen-Smith & Mills (2008) to minimize the bias of undercounts and over counts of different species (Mills & Biggs 1993, Redfern et al. 2002, Owen-Smith & Mills 2008).

Estimating lion diets and range

Between May 2005 and April 2007, we monitored five female and two male lions using GPS/GSM collars (i.e. GPS with mobile phone capabilities; African Wildlife Tracking). Lions were collared using standard techniques of South African National Parks (SANParks) veterinarians (Smuts et al. 1977). GPS collars recorded GPS positions on an hourly schedule during the night and at 09:00, 12:00 and 15:00 during the day. Lion kills were located by investigating GPS clusters (Tambling et al. 2010), with kills identified from distinguishable remains (jaw bones, horns, stomach contents and hair). Additionally, faeces were collected at GPS clusters and when combined with kills allowed the diet to be estimated based on the temporal pattern of carcass remains and faecal depositions found at the clusters (Tambling, Unpublished Thesis: Chapter 4). The five female lions collared were in four distinct prides and the diet was estimated for each of the four prides. The two collared male lions were territorial males that associated with the four prides during the course of the study period. Independent diets for each of the lion groups were calculated as well as averaged male and female diets for study region. Female and male lions in the KNP killed 98% and 60%-80% of their own food respectively, and where scavenging does occur, it is normally from other lions (Funston et al. 2001). Based on this we were confident that we located lion and not scavenged kills from other carnivores. Additionally, as a result of the territorial nature of lions within KNP (Funston et al. 2001) and the close association between GPS collars and observations of scats and carcasses, we assume that lion kills are from the GPS collared individual and not non-territorial transient individuals.

We compare two scales of lion spatial use in the study. Home ranges of each lion pride and male lion coalition were constructed using Minimum Convex Polygons (MCP's) to demarcate the overall area used by the lion group during its monitored period. The overall study area was constructed by combining all the MCP's of each lion group to create an area that encompassed all observed lions for the entire duration of the project. For each individual lion's home range as well as the overall study area, the pool of available prey was assessed by extracting the spatially referenced prey groups for each respective range calculated. Therefore, for each range estimate (full study area and each lion) the relative number of groups of each prey species can be used as the pool of prey available to the lion groups.

Prey selection

We investigated prey selection for the lions using two criteria of prey availability collected across two scales. Three measures of prey availability are used for the selection calculations; (P1) the relative number of prey individuals of each species in the study area, (P2) the relative number of prey groups of each species in the study area, and (P3) the relative number of prey groups of each species in each lions groups occupied range. We contrast these availability measures against two measures of lion diet; (D1) all lion diet data pooled for the entire study area and (D2) the lion diet for each lion group. To investigate how the method of counting prey species influences prey selection metrics, selection indices were calculated using combinations P1:D1 compared against P2:D1. To determine how the scale of counting (total study area compared with lion group range) influences prey selection metrics, selection indices were calculated using combinations P3:D2 compared against P2:D2. Prey selection for all comparisons was calculated using the Jacobs index:

$$J = \frac{r - p}{r + p - 2rp}$$

where r is the proportion of the total kills made by the female lions and p is the proportional availability of the prey species (Jacobs 1974, Hayward & Kerley 2005). The Jacobs index allows the assessment of prey selection when different relative abundances of prey are compared (Jacobs 1974). The resulting value falls between +1 and -1 with zero indicating no selection, +1 indicating maximum preference and -1 indicating maximum avoidance and alleviates many problems inherent in other selection ratios (Krebs 1989).

Fisher exact tests for goodness of fit were used to test if lions were killing prey species in relation to their abundance when abundance was assessed as individual prey or groups of prey, with sequential Bonferroni tests used to account for multiple tests (Quinn & Keough 2002). The degree of selection or lack thereof for each individual prey species was assessed by calculating the 95% confidence intervals surrounding the proportions of kills for each of the prey items (Neu et al. 1974) and comparing this range to the prey availability for each spatial extent of analysis. The degree of overlap, or lack thereof, can be considered as a test for the significance of the selection or avoidance. If there is no overlap between the availability and the 95% confidence intervals the prey item is considered significantly selected for or avoided (Landman et al. 2008).

Since groups of available prey were used for some selection calculations, we also considered all multiple kills of the same species as a single predation event on the encountered group. Implementing this reasoning, we re-conducted the analysis using multiple kills as a single predation event, but found that the low percentage of multiple kills (5% of all GPS cluster located kills, translating into 4% of all kills) did not alter the results.

To asses the magnitude of the change in selection as a result of changing the scale of availability, we calculated the sum of the absolute change in J for all species for each individual lion group between P3:D2 and P2:D2 comparisons. We expect that larger changes in absolute values of J for each individual lion will be associated with larger differences in prey availability between P2 and P3. Scale dependent availability differences for each lion group (P2 vs. P3) are assessed by calculating chi-square statistics for the prey availability for each lion group (P2) against the prey availability for the entire study region (P3). We then plot the absolute change in J against the changes in our chi-square assessment of changing availability to see if increasing heterogeneity at a fine scale results in larger shifts in average J values.

Results

Prey availability

We found no differences in the total aerial census of the entire KNP and the central region of the KNP (Fishers exact test, $p = 0.72$) with impala contributing to more than half the counted population. There was a significant difference between both the full park-wide aerial census and the central region aerial census when compared with the relative number of groups of prey assessed by ground counts (Full aerial count: $p < 0.005$, Central aerial count: $p < 0.05$, Fisher's exact test, Table 1).

Diet estimates

A total of thirteen species contributed to 293 lion kills located at 279 GPS clusters. At 14 kill sites (5%) we found more than one kill of the same species, predominantly zebra (n=8) and buffalo (n=4). On a single occasion, we found three buffalo at a single kill site. Combining scats and kills into kill events resulted in the identification of an additional 114 kill events that could have been missed by investigating GPS clusters alone. Of the resultant 407 kill events, the eight most abundant species contributed 97% of all kill events and 98% of all known kill events with zebra (23%), wildebeest (17%), impala (16%) and buffalo (12%) the dominant prey items. We found male lion collars associated with 95 kill events, and female collars associated with 335 kill events (Table 2) with male and female collars associated together at 23 (5.9%) kill events. Of the multiple sex observations, nine (39%) were kills of larger species (giraffe and buffalo), more than the corresponding percentage of large prey items in the overall estimated diet (19%, n=81). Male lions were associated with buffalo kills considerably more often than female lions (19.9% vs. 8.6%) whereas females were associated with medium sized prey species (wildebeest, kudu, zebra and waterbuck) slightly more often than male lions (54.7% vs. 47.6%, Table 2).

Prey selection

The eight most important prey species in the study area were not consumed in proportion to their availability, if availability was estimated by P1 (Fisher Exact Test, $n = 8$, $p << 0.005$) or P2 (Fisher Exact Test, $n = 8$, $p < 0.05$). The observed non-proportional predation patterns can be attributed to the high availability of impala (58% of all prey individuals and 34% of all groups of prey) that were considered to have been avoided ($J_{impala(individuals)} = -0.74$ and $J_{impala(groups)} = -0.45$, Fig. 1) by the lions. Removing impala from both the available pool of prey and from lion kills results in lion consuming prey in relation to the availability (Individuals: Fishers Exact Test, $n = 7$, $p = 0.055$, Groups: Fishers Exact Test, $n = 7$, $p = 0.144$). Buffalo were significantly selected when availability was assessed using P2 ($J_{buffalo(groups)} = 0.64$, Figure 1) due to the low number of buffalo groups seen in the study area (3% of all prey groups). Zebra remained significantly selected for both (P1 and P2) methods of counting prey ($J_{zebra(individuals)} = 0.37$ and $J_{zebra(groups)} = 0.27$, Fig. 1).

Both coalitions (Camp Coalition: Fisher Exact Test, n = 8, $p << 0.005$, Nsenami Coalition: Fisher Exact Test, n = 8, $p << 0.005$) and three of the prides (Camp Pride: Fisher Exact Test, n = 8, $p < 0.005$, Boma Pride: Fisher Exact Test, n = 8, $p << 0.005$, Nsenami Pride: Fisher Exact Test, n = 8, $p < 0.05$), except for the Thompsons pride (Fisher Exact Test, n = 8, p = 0.4171), did not consume prey in relation to the availability of prey groups within their total area used. Both male coalitions avoided impala and selected zebra, with the Nsenami coalition also having a strong preference for buffalo (Fig. 2). All prides selected zebra, significantly so for the Camp and Boma Pride, whereas all prides avoided impala. However, the avoidance of impala was not significant for the Nsenami and Thompsons Prides (Fig. 3). On average both sexes selected buffalo and females showed a considerably greater selection for kudu (Fig. 4).

The average absolute change in J increased linearly with an increasing difference in chi-square statistic between P2 and P3. The Boma Pride, closely followed by both coalitions of males had a prey base similar to P2 and accordingly had the lowest changes in absolute J. The Nsenami pride inhabited an area that was considerably different in prey makeup (see Table 1) to P2 and this resulted in the largest average change in J (~11%, Fig. 5).

Discussion

The lion diet in the central region of the KNP between 2005 and 2007 was similar to estimates based on long term data sets (Smuts 1979, Mills & Shenk 1992, Mills et al. 1995, Funston et al.

1998, Owen-Smith & Mills 2008), dominated by zebra, wildebeest, impala and buffalo. Impala, although the third most killed species during the study, is not an important prey item for lions in the central region in terms of biomass consumed and this observation is consistent with Owen-Smith and Mills (2008) assessment for the entire KNP over a 46 year period. In the central region male lions were associated with buffalo kill events more often than female lions, a finding that is consistent in many other study areas (Funston et al. 1998, Radloff & du Toit 2004, Hayward & Kerley 2005). We observed large differences in selection indices based on both comparisons of count type and scale of availability assessment. These differences will have profound influences on how we perceive large carnivore impacts on prey assemblages.

The estimation of large carnivore diets has received considerable attention over the past 40 years, initially with the work by George Schaller (Schaller 1972) and more recently with the amalgamation of techniques (Marucco et al. 2008) and technological improvements in monitoring tools (Knopff et al. 2009). Diet estimation, or usage, of large carnivores alone is only descriptive and without availability data it's relevance to studying predator-prey systems is limited. Despite the advancements in diet estimation, many selection studies still define prey availability in an arbitrary manner (Johnson 1980) without considering sources of error.

Prey selection: How do we count prey animals?

Three errors can be incorporated into how we assess the availability of prey species. Firstly, bias in under-counting certain species when using aerial census data need to be addressed. Aerial census data is routinely used for assessing availability for selection studies (see studies in Hayward & Kerley 2005). This source of bias has been recognized and studies have now been undertaken to assess the undercount bias and correction factors for certain species for certain environments now exits (Owen-Smith & Mills 2008) and should be used where appropriate.

Secondly, sources of error may be incorporated into selection studies when there is a mismatch in the temporal overlap of diet estimate and prey availability (Hayward & Kerley 2005). Although in many cases this cannot be rectified, resulting selection patterns should be viewed with caution. The third possible source of error is the manner in which researchers define availability, and whether or not group structure is incorporated into selection studies.

The calculation of most selection indices in open environments use aerial count data, as this is often readily available. The resulting prey availability represents the absolute numbers of each prey species over the entire study area and assumes that all prey individuals are randomly scattered across the landscape with an equal probability of detection. This assumption is erroneous, because different species occur in different group sizes that will influence the prey species sphere of detectability. In SNP, the relationship between absolute numbers and group numbers is represented by a power curve (Fryxell et al. 2007). This implies that a doubling of prey density will lead to a more modest increase in encounter frequency with groups, thus lowering the availability for species with larger groups. Our results show a marked change in selection patterns for species occurring in large groups (buffalo in particular), with selection indices increasing considerably for group dwelling species. Based on the SNP assessment as well as the results obtained in KNP, a more realistic measure of availability is the use of the relative number of groups as the unit of prey availability.

However, little information exists on the affect that group size has on the probability that a predator will encounter different prey types (Creel & Winnie 2005) and although a group level approach is preferred, it may not truly represent prey encounters either. Larger herds are comparably easier to detect and are more likely to be attacked on detection (Creel & Winnie 2005, Ioannou & Krause 2008). The group size may not be the only variable that influences the chance of detection by predators, and the orientation and shape of the groups, mediated by forage and movement behaviour, can similarly influence detectability (Jackson et al. 2005). Wolves *Canis lupus* have been shown to encounter and attack larger elk (*Cervus Canadensis*) herds, and elk have been witnessed to avoid predation by splitting into smaller herds (Hebblewhite & Pletscher 2002). Consequently, within African systems, buffalo exist in large herds that are easy for lions to detect through smell and hearing (Hayward & Kerley 2005). Additionally, different lion social groups travel at different speeds through different environments, resulting in different encounter rates for different prey species (Funston et al. 1998). Therefore, it may be possible that larger groups may be encountered more often by predators, increasing their representation when measuring prey availability at a group level. Our results, using both individual and group availability, could well represent the two extremes of selection, with the true value occurring between these extremes. However, further research on how detectability, encounter rate and group formation interact in the field are needed.

Prey selection: The influence of scale on determining selection indices

The issue of spatial scale has become more prominent in ecology, and many authors now advocate multi-scale approaches to ecological studies (Sandel & Smith 2009). Resource selection studies are no different, and many studies show scale dependent resource selection (Boyce 2006). In open systems, as many biological systems are, the dynamics of patterns at a given scale are likely influenced by those at a higher scale (Wiens 1989) thus stressing the importance of comparisons at more than a single scale. Conducting selection studies at multiple scales allows researchers to address patterns observed across a range of scales. In many cases the population level impacts of predators are the desired outcome, and broad scale studies assessing selection patterns generalized across a range of habitats will suffice. In these cases, broad scale availability data often drives the resolution of the scale investigated, as most fine scale (pride, or habitat level) data are not available (Boyce 2006). So for the central region of KNP, lions avoid impala and warthog and select zebra and buffalo, a result that fits into expected prey selection ranges (Radloff & du Toit 2004, Hayward & Kerley 2005). Assessing carnivores at this level may assume a homogenous landscape and that all groups of predators respond to prey species in a similar way. However, investigations at a broad scale alone may miss fine scale spatial and temporal variation of importance.

It is often fine scale landscape and habitat features that drive predation patterns (Hopcraft et al. 2005), thereby having implications for predator-prey interactions on a local scale. In heterogeneous environments, such as that found in the KNP (Venter et al. 2003), fine scale habitat and landscape features vary between prides, and as a result different species are selected by different prides, and these selection patterns are generally linked to the prey assemblages in the pride range. These fine scale variations will become more important as the size of conservation areas decline, and consequently prey species will be unable to escape predation pressure (Fryxell & Sinclair 1988, Tambling & du Toit 2005). In South Africa, over recent years there has been an increase in the development of small enclosed reserves (Bothma et al. 2008) where the diversity of species is managed for tourism (Lehmann et al. 2008). Within these small reserves, populations of species require active management (Power 2003) and the fine scale knowledge of the interaction between prey and predator, including the selection of prey species by carnivores will be essential to drive management actions.

Conclusion

As methods and approaches to determine the preference of carnivore diets improve, increased effort is needed in the assessment of prey availability. The merger of high quality diet and availability datasets will allow the greatest insight into observed patterns, providing the best platform from which to make informed management decisions. We show that the way in which the prey population is described (i.e. as absolute numbers or groups), has an influence on selection indices that may be used for management purposes. Although measuring the group availability is a more biologically sound method (Fryxell et al. 2007), we still feel that there is room for improvement in correctly estimating what is available to carnivores at the relevant scale, that takes into account encounter rates (Funston et al. 1998). As conservation areas decline in size, mismatches in ‘decision’ and ‘sampling’ scales could lead to specious conclusions regarding the ecology of the animal (Schonewald-Cox et al. 1991, Bowyer & Kie 2006) and in the case of predation, each particular situation needs to be analysed separately as the patterns may vary not only spatially but temporally as well.

Tables

Table 1. Percent availability of each of the eight major prey species for each of the methods of counting (aerial [i.e. individual availability] vs. ground [i.e. group availability]) and scales (park vs. central region vs. pride regions) of counts for the central region of the Kruger National Park, South Africa, between April 2005 and May 2007.

	Aerial (park)	Aerial (central)	Ground (central)	Ground (Camp)	Ground (Boma)	Ground (Nsenami)	Ground (Thompsons)
Impala	58.1	58.1	34.5	36.6	35.1	46.9	29.7
Warthog	3.0	3.8	7.4	5.1	6.8	14.3	5.9
Buffalo	11.4	5.5	2.8	3.1	3.3	1.0	3.0
Wildebeest	4.3	6.3	18.8	19.5	19.7	9.3	17.9
Zebra	11.5	12.6	15.3	14.5	14.2	12.6	14.1
Kudu	6.2	5.8	5.6	5.4	5.2	4.3	7.5
Giraffe	3.3	4.6	8.2	8.9	8.3	7.1	8.2
Waterbuck	2.2	3.3	7.4	6.8	7.4	4.6	13.7

Table 2: Male and female lion kill events (for the eight most killed prey species and remainder placed into an "others" category) per pride and coalition in the central region of the Kruger National Park, South Africa, between May 2005 and April 2007

	Prides					Coalitions		
	Camp (n=145)	Nsenami (n=64)	Thompsons (n=34)	Boma (n=92)	Average	Nsenami (n=68)	Camp (n=27)	Average
Buffalo	6.9	6.3	2.9	18.5	8.6	32.4	7.4	19.9
Giraffe	8.3	17.2	2.9	5.4	8.5	4.4	7.4	5.9
Impala	11.0	34.4	20.6	12.0	19.5	16.2	11.1	13.6
Kudu	11.7	7.8	8.8	4.3	8.2	4.4	3.7	4.1
Warthog	4.1	6.3	2.9	4.3	4.4	2.9	0.0	1.5
Waterbuck	9.0	3.1	14.7	6.5	8.3	5.9	7.4	6.6
Wildebeest	20.7	4.7	26.5	17.4	17.3	11.8	25.9	18.8
Zebra	26.2	17.2	11.8	28.3	20.9	19.1	37.0	28.1
Unknown	0.7	0.0	5.9	0.0	1.6	2.9	0.0	1.5
Others	1.4	3.1	2.9	3.3	2.7	0.0	0.0	0.0

Figures

Figure 1. The relative estimate of diet and prey availability for lions in the central region of the Kruger National Park, South Africa. The Jacobs Index gives a measure of the selection for each dietary item where open symbols (circles associated to group availability and triangles associated with individual availability) denote non significant selection or avoidance and closed symbols denotes significant selection or avoidance

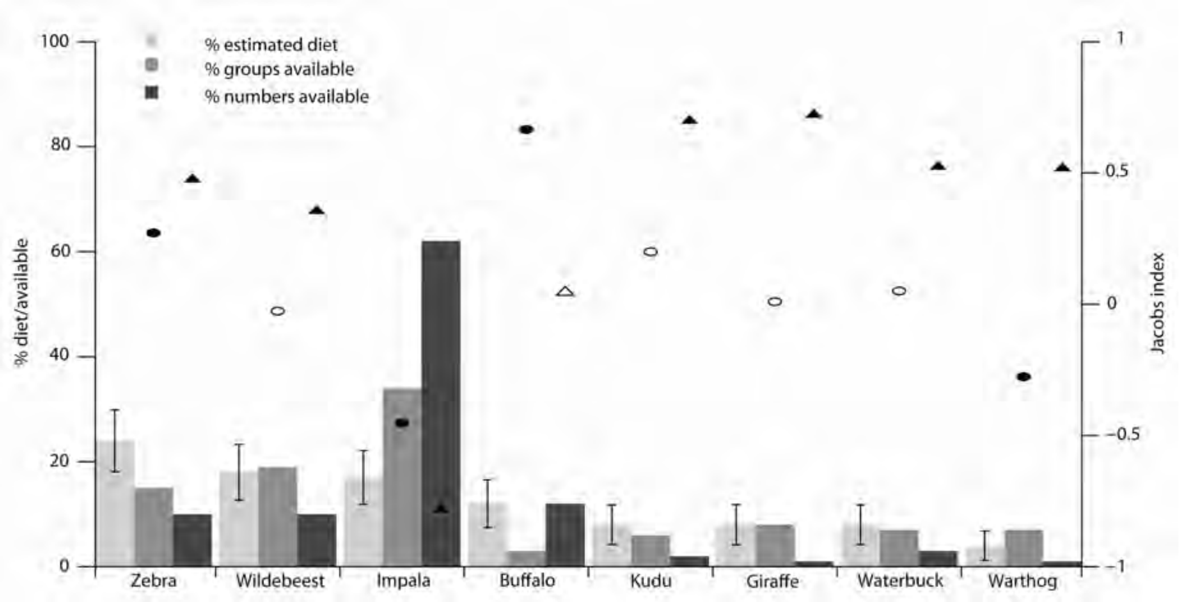


Figure 2. The differences in predation patterns and Jacobs' index of selection for each of the male coalitions in the Satara region of the Kruger National Park between May 2005 and April 2007, solid circles imply significant selection or avoidance (closed symbols denote significant selection of avoidance)

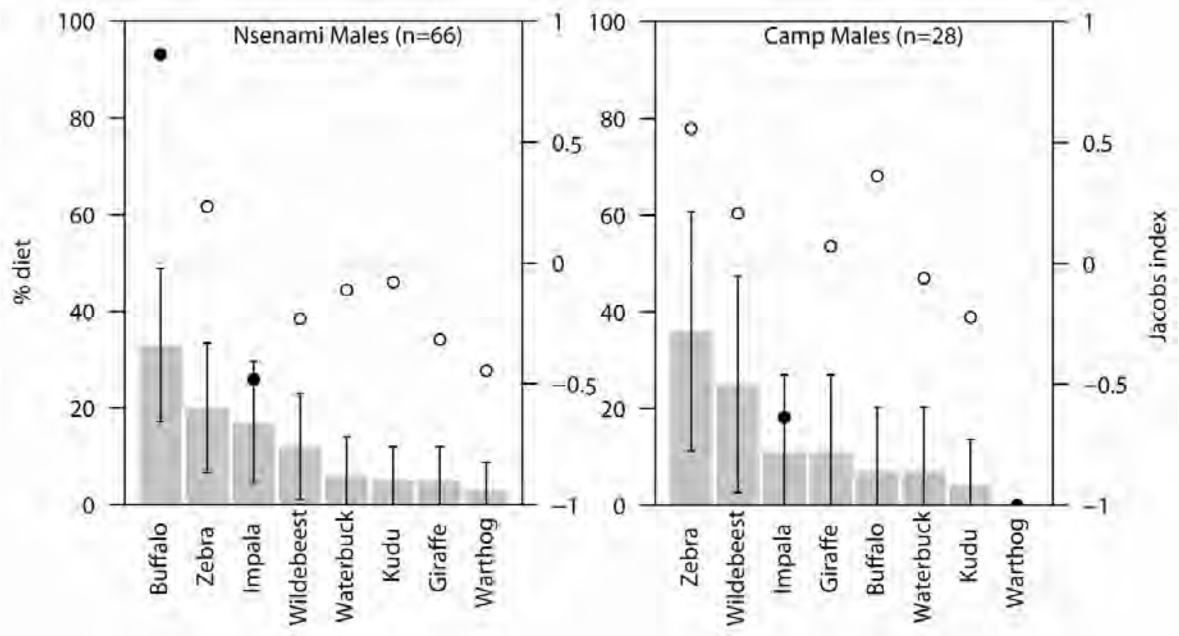


Figure 3. The differences in predation patterns and Jacobs' index of selection for each of the four prides in the Satara region of the Kruger National Park, South Africa between May 2005 and June 2007. Solid circles imply significant selection or avoidance (closed symbols denote significant selection or avoidance)

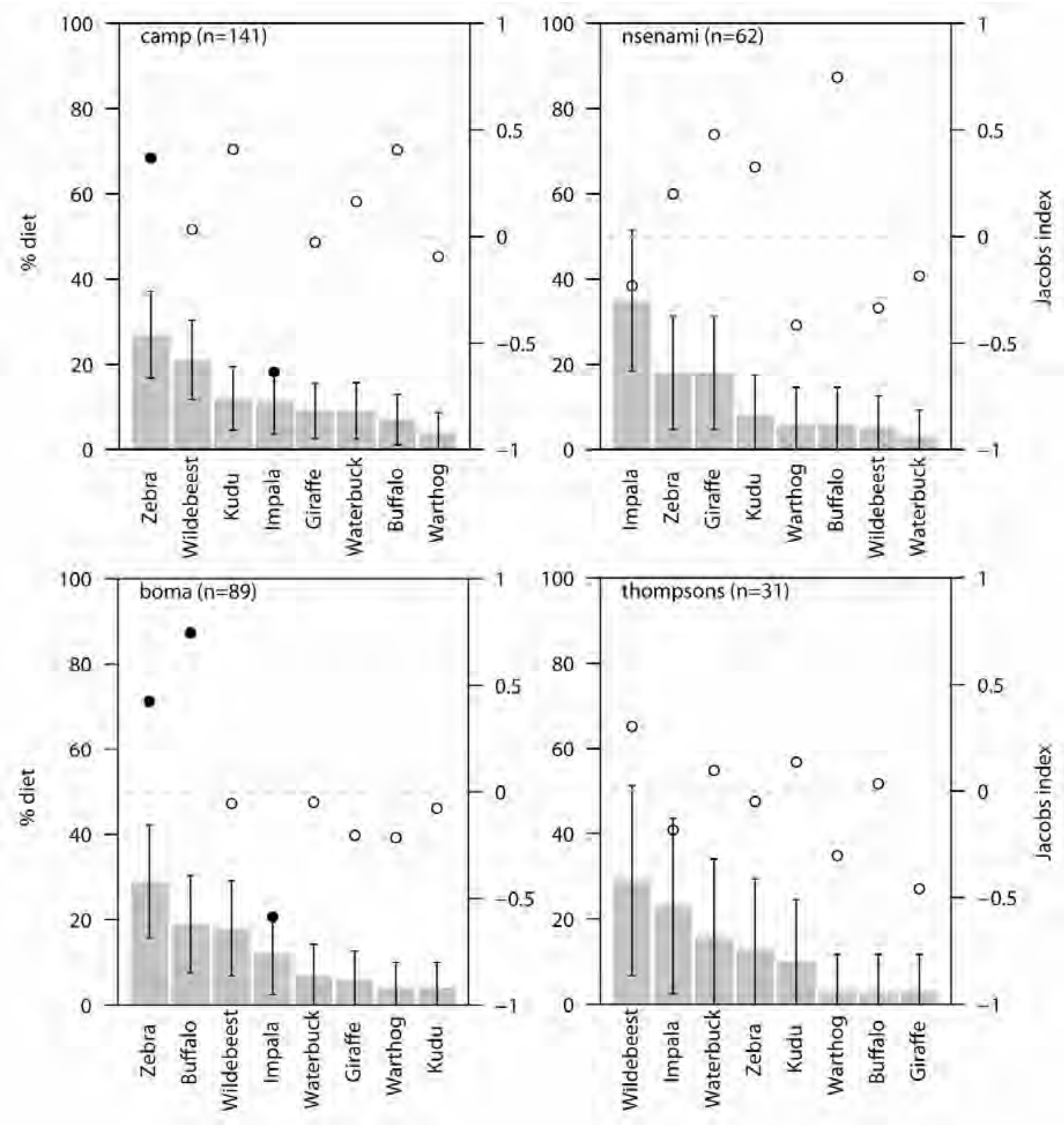


Figure 4. Average male and female Jacobs index of selection for the central region of the Kruger National Park, South Africa, between May 2005 and April 2007.

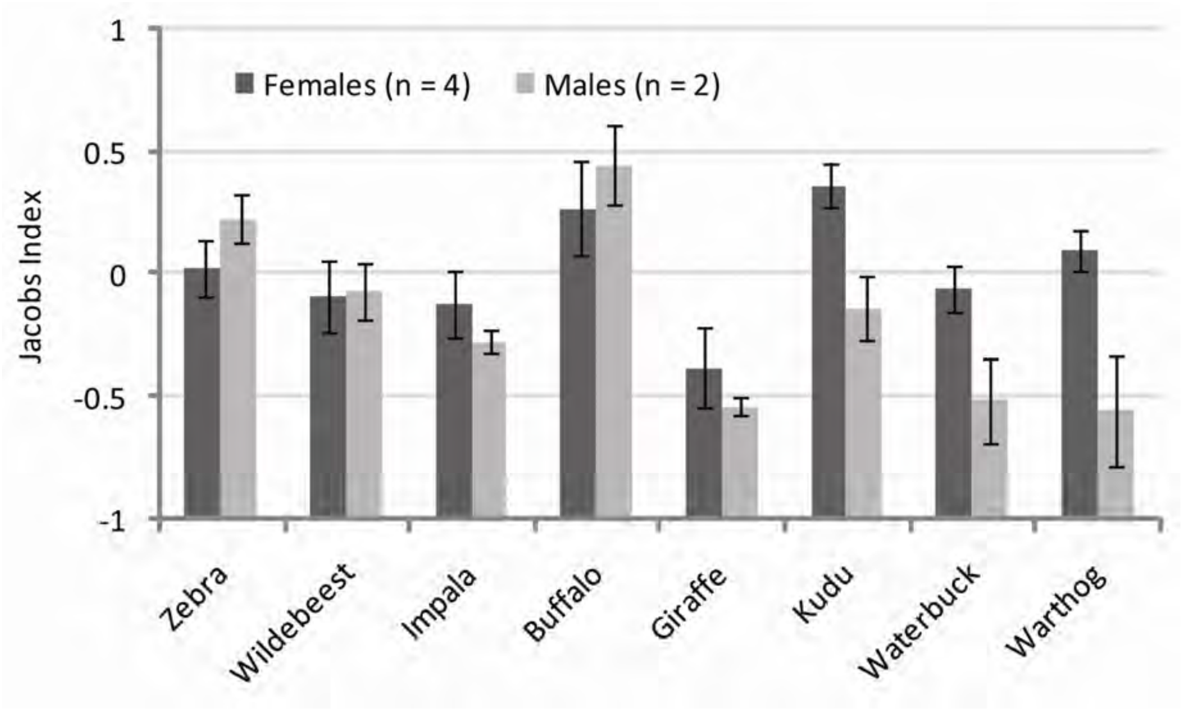
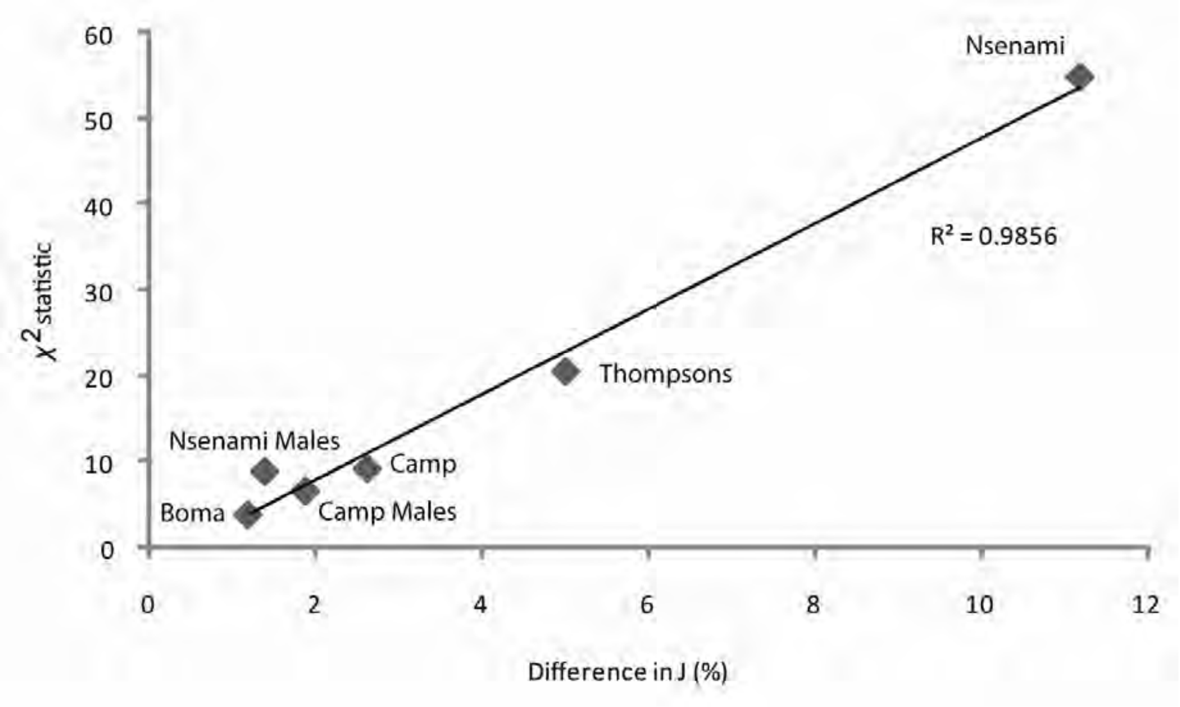


Figure 5. Relationship between the magnitude of the χ^2 statistic explaining the difference between the overall number of groups and the number of groups in each pride area and the average percent absolute change in the Jacobs index (*J*)



Chapter 6: Fine scale determinants of lion predation on buffalo

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(In Preparation: African Journal of Ecology)

Abstract

Large African herbivores are prone to both bottom-up and top-down regulatory forces that modify their behaviour, space use and population dynamics. Most of these factors have been investigated at broad scales. We investigated the fine scale temporal, spatial and demographic patterns of lion (*Panthera leo*) predation on buffalo (*Syncerus caffer*) between 2001 and 2007, spanning two projects in the Kruger National Park, to investigate how lion predation may impact the behaviour and fine scale space use of buffalo. Both male and female buffalo are prone to predation in areas with longer grass and thicker bush (i.e. areas with decreased visibility). However, these areas of decreased visibility seem to occur at different locations across the landscape, and male and female buffalo tend to enter these predation prone areas for different reasons. In accordance with previously observed patterns, buffalo are more vulnerable to predation after prolonged dry periods that result in a decline in body condition. Reduced rainfall over as short a period as six months can be long enough to significantly reduce buffalo body condition and result in a concomitant increase in predation by lions. No indications exist that surface water influenced the buffalo within the study area. We show that fine scale variation in habitat structure and rainfall variability can influence buffalo and suggest that predator prey interaction studies use a multiscale approach whereby both large and small scale interactions are measured.

Introduction

Large African herbivore behaviour, distribution and population dynamics are simultaneously acted on by both bottom-up (Sinclair 1977, Sinclair et al. 2007) and top-down selective forces (Funston & Mills 2006, Owen-Smith & Mills 2008). These two contrasting viewpoints have been widely studied and a recent review sheds light on the inter-relationship between both process across a gradient of habitats and climates in Africa (Hopcroft et al. 2010). At a broad scale, predators undoubtedly exert significant selective pressures on prey populations and this comes in the form of both direct predation (Owen-Smith 2008) and risk effects influencing prey behavioural responses (Creel & Christianson 2008). Large climatic fluctuations evident across African environments (Ogutu et al. 2008) add an extra dimension that influence predators and prey (see Mills et al. 1995, Owen-Smith 2008). A combination of all the above factors results in changing vulnerability to predation for different species through time and space. However, areas for conservation are being reduced in size with many fragmented landscapes resulting in small conservation areas (Lindsey et al. 2006). Therefore, the manner in which predators influence prey species on a fine spatio-temporal scale will become important for conservation actions.

In response to predation risk, foragers balance food and safety (Lima & Dill 1990). Broadly speaking, foraging animals will select landscapes that reduce the chances of predation while increasing the quality of resources procured (McCloughlin et al. 2005). As a result, observed ranging behaviour can be interpreted as an adaptive response to the perceived risk of predation by some predators traded against the spatial availability of resources (Willems & Hill 2009). Predators are shown to alter herbivores foraging patterns, especially where large carnivores have been repatriated into conservation areas (Creel et al. 2005, Fortin et al. 2005, Mao et al. 2005), so it can be expected that in areas with extant predators and prey, herbivore landscape use is an evolutionary result of the long term presence of predators played against resource availability driven by climatic fluctuations. Just as herbivores minimize the chances of being killed, predators use habitats that increase their chances of successful predation events rather than selecting habitats with higher prey density (Hopcraft et al. 2005, Balme et al. 2007). How these predator prey interactions play out in small conservation regions will depend on the fine scale movement of both predators and prey, tempered by the magnified impacts of climatic variability.

In small fragmented conservation areas, climatic variability may become more important, increasing the severity of oscillations between productive and dry periods, especially as prey species are unable to move away from adverse conditions (Tambling & du Toit 2005). Under these conditions, fine scale habitat selection will be driven by local limiting factors (Dussault et al. 2005), that may over-ride the necessity for safety. These fluctuating environmental conditions can result in dramatic prey switching as some species are better adapted to survival in wet or dry conditions respectively (Mills et al. 1995, Owen-Smith & Mills 2008). These prey switching patterns have emerged over long temporal scales, however, how do small changes in precipitation influence prey species and ultimately the prey base of resident predators? These questions are all the more important in the reduced modern conservation arena.

Studies of buffalo (*Syncerus caffer*) show different responses to predation pressure and forage quality depending on which social group they occur in (Hay et al. 2008). Bachelor groups forage in risky areas and are hence prone to increased predation pressure (Hay et al. 2008) whereas breeding groups are influenced by forage quality and quantity and as a consequence modify their home range and group size (Winnie et al. 2008). However, these studies did not incorporate lion (*Panthera leo*) movement in time and space as a co-variant in their analysis, although they do allude to this factor being a potential co-driver of the observed buffalo patterns. Buffalo are bulk grazers that often occur in large breeding herds (Halley et al. 2002) and have the ability to shape landscapes in which they exist. Buffalo are also one of the preferred prey species for lions (Hayward & Kerley 2005). Lion predation on buffalo in the Kruger National Park (KNP), South Africa, has been closely linked to the rainfall patterns, and predation on buffalo increases in times of severe drought (Mills et al. 1995, Funston & Mills 2006). However, the impact that lions have on the fine scale movement of buffalo, and how small changes in rainfall across small scales (months) contribute to lion predation of buffalo within the KNP is not known.

The paper combines two study periods over seven years and investigates the spatial, temporal and demographic patterns of buffalo predation in the KNP. We investigate four questions concerning the fine scale (temporal and spatial) predation patterns of lions on buffalo. 1) Are buffalo in KNP being killed in areas that offer lions an advantage, 2) are buffalo avoiding areas that may be dangerous in relation to topography and water, forcing lions to actively search for buffalo, 3) are buffalo in a worse condition after a prolonged dry periods and more susceptible to lion predation, and 4) are male buffalo more susceptible to predation than female buffalo?

Methods and materials

Study area

We conducted the study in ~1000km^2 area of the central region of the KNP, South Africa (31.77 E, 24.39 S) and included data from two study periods. Between 2001 and 2006 buffalo were tracked as part of an ongoing investigation into BTB in buffalo (Caron et al. 2003, Cross 2005, Cross et al. 2005, Winnie et al. 2008) and between 2005 and 2007 we investigated lion predation patterns within the same area (Tambling, Unpublished Thesis: Chapters 4,5). The underlying granitic soils to the west and basaltic soil to the east of the park influence the structure and composition of the vegetation in the KNP and have been shown to influence the behaviour and distribution of buffalo (Hay et al. 2008, Winnie et al. 2008). Buffalo behaviour and distribution may additionally be influenced by predation pressure acting in concert with the underlying substrate (Winnie et al. 2008). The subsequent analysis into lion predation patterns between 2005 and 2007 was limited to the basaltic region and therefore we only assess potential combined factors on the basaltic soils. The Satara region contained between four and 12 buffalo herds, and ~3000-4000 buffalo (Hay et al. 2008). Rainfall, and hence vegetation productivity has been implicated as an important factor influencing buffalo susceptibility to lion predation (Funston & Mills 2006) and rainfall within the study area is seasonal, with the majority falling during the wet season between November and April (Fig. 1). In comparison to long-term rainfall trends, dry seasons during the course of the study were considerably drier (~45.3mm) than the long-term average (1933-2000: ~85mm), although the current wet seasons (~427.9mm) are comparable to the long-term average (1933-2000: ~436mm).

Datasets

During the first study period, buffalo were collared with VHF collars (Telonics Corp, Mesa, Arizona) and attempts were made to relocate radio collared animals on a weekly basis during daylight hours (see Hay et al. 2008, Winnie et al. 2008 for detailed methods). Additionally four adult female buffalo were fitted with GPS collars (African Wildlife Tracking) between 2005 and 2006, with a one-hour relocation schedule. While conducting buffalo re-sights, all confirmed lion killed buffalo were recorded. For collared buffalo, a lion kill was confirmed if the collar belting was still intact (as it was impossible that the collar would come off a buffalo unless the belting was torn), as well as the presence of carcass remains and other evidence such as blood, rumen contents and lion spoor (Hay et al. 2008).

Between 2005 and 2007, lions were fitted with GPS/GSM collars (African Wildlife Tracking) programmed to record a fix every hour at night and three times daily (Tambling et al. 2010). We used GPS fixes to identify clusters where lions could possibly have made kills. Clusters were investigated on foot and buffalo kills that occurred at any clusters were recorded. For all buffalo kills, during both periods, the age and sex was determined if possible from horn and teeth remains (Pienaar 1969, Grimsdell 1973). Buffalo herd structure was assessed using video recordings of buffalo herds crossing roads (Winnie et al. 2008) as well as from the long term buffalo census records for the park (Whyte 2004).

Predation risk

We assessed predation risk associated with surrounding vegetation (tree density and grass height) at buffalo kill sites (May 2005 – April 2007) and compared that to vegetation at male and female lion resting sites (March 2006 – May 2007). We assumed lion resting status from GPS clusters longer than one hour with no associated kill. Due to the temporal variability in cluster investigation, only clusters checked within two weeks of occurrence were included in the analysis to prevent grass growth or grazing to change grass height. We used a five point scale to assess the grass height: 1) ~10cm tall, 2) ~30cm tall, 3) ~50cm tall, 4) ~70cm tall and 5) ~1m tall, and tree density: 1) no trees, 2) low tree density, 3) moderate tree density, 4) high tree density and 5) impenetrable tree cover. We used a Kruskal-Wallis ANOVA to assess if buffalo of different age and sex classes (juveniles, sub-adults, adult males, and adult females) were killed in areas that differed in tree density and grass height. Subsequently we used a Mann-Whitney test to investigate the grass height and tree density for male and female lion resting points. There was no significant difference for either the buffalo kills of different age and sex classes or resting sights of each of the different lion sexes with respect to grass height or tree density, so we pooled the datasets for each species, and compared the difference in grass height and tree density between buffalo kill sites and lion resting sites using a Mann-Whitney test.

Spatial analysis

For each buffalo kill, where the exact spot could be identified (i.e. rumen content), GPS co-ordinates were imported into ArcView GIS (ESRI 2004) and the distance to the nearest water source (closest tertiary, primary, or secondary river, borehole or waterhole, SANParks unpublished data), drainage line (all river classes, SANParks unpublished data) and road (tourist and management, SANParks unpublished data) was calculated. Re-sightings of each individual known buffalo enabled the separation of breeding and bachelor herds (Hay et al. 2008). The buffalo in the study area undergo fission and fusion events, with each fission event described as the formation of a new sub-herd (Cross et al. 2005). We used the average distance for each herd as a sample point and calculated the distance to drainage lines, water and roads. Each individual lions GPS co-ordinates were averaged to achieve an individual lion distance, in this way we reduce the over representation of some individuals (lions and buffalo) in the dataset. However, sequential lion locations at an hourly interval will introduce temporal autocorrelation, so we used autoregression on distance values for each lion location to identify and handle the autocorrelation. We sorted the data by date and hour and offset the data to a varying number of lags, and did regressions between the original data and the lagged data. We decided on the cut-off number of lags that removed the autocorrelation when the r^2 value between the original data and the offset data declined by less than one percent (Winnie et al. 2008). We then re-sample the male and female lion locations at the number of the lagged neighbour and calculated the respective distance to each of variable (water, drainage line and road). Due to the small number of lion collar's (5 females and 4 males), we pooled male and female collar data. Male and female buffalo locations were from weekly re-sights and we removed incidental sightings of individuals from the dataset to reduce the dependence on roads.

We used buffalo kills located by two methods, firstly those found from investigated lion GPS clusters (Tambling et al. 2010) and secondly those killed while being monitored with VHF collars (Hay et al. 2008) to reduce the bias of locating kills near roads. We investigated the distance between (1) adult male buffalo kills against all lions and adult male buffalo re-sights, (2) adult female buffalo kills against all lions and adult female buffalo re-sights, (3) sub adult and yearling buffalo kills (1-4 years old) against all lions and adult female buffalo as they would be expected to be occurring in herds, and (4) juvenile buffalo kills against all lions and adult female buffalo re-sights in relation to water, drainage lines and roads using non-parametric Kruskal-Wallis ANOVA's (normality in the data could not be achieved). Sequential Bonferroni corrections were used to correct for Type 1 errors resulting from multiple tests (Quinn & Keough 2002) and multiple Steel-tests were used as non-parametric multiple comparison tests to assess where the variation in distances occurred (Zar 1999).

Temporal analysis

We investigated the temporal association between lions and buffalo on two scales, 1) a short-term hourly scale and 2) a long-term monthly and seasonal scale. For short-term hourly relocations for buffalo, we were restricted to the analysis of herds, as only females had GPS collars. We estimated the activity patterns of lions and buffalo by investigating the distance moved between GPS co-ordinates of GPS collars at each hour. The animal was assumed to be moving if the distance between consecutive GPS locations was greater than 100m (Hayward &

Hayward 2007). In the event where GPS co-ordinates were not recorded we divided the distance moved since the previous GPS recording by the number of missed locations and used the average distance as the step length for all missing points. We used the log-likelihood-ratio (G) test (Zar 1996) to compare pairwise activity patterns between male and female lion (Hayward & Hayward 2006), witnessing no significant deviation in activity patterns. We pooled the male and female lion data and tested pairwise differences in lion and buffalo herd movement patterns throughout the day using the log-likelihood-ratio (G) test (Hayward & Hayward 2006).

We investigated long-term trends in buffalo mortality in relation to the rainfall in the previous month (30 days) and in the previous season (180 days) as we feel that it represents a better indication of the seasonal rainfall due to the variability observed in the start of the wet season. We obtained daily rainfall data from the Satara weather station (SANParks Scientific services, unpublished data) and calculated the total cumulative rainfall that fell during a 30 and 180-day period prior to buffalo kills. All buffalo kills included in the analysis were located within seven days of occurrence for buffalo observation data or had known kill dates for the lion observation period in order for us to be sure of the date of mortality. We selected 150 days at random from all possible days during the study period, and bootstrapped the random sample 150 times to insure the representativeness of our selection. However, by bootstrapping the data, we no longer maintained homogeneity of variance within our data. A Welch two sample t tests can handle homogeneity of variance (Quinn & Keough 2002) and are generally robust against assumptions of normality, below a kurtosis of two (Lix et al. 1996). We log transformed both datasets to achieve a kurtosis of below two and conducted the Welch two sampled t-test to investigate differences in the cumulative rainfall 30 and 180 days prior to kills and the random bootstrapped sample.

Body condition scores (between one and five) were assessed for known individuals during weekly re-sighting (Caron et al. 2003, Hay et al. 2008). We averaged the body condition for male and female buffalo for each day's condition scores, and regressed the cumulative 30 and 180 days rainfall values against this dataset to determine if buffalo were in worse condition following less rainfall over the long and short term.

Buffalo demographic parameters

The two datasets for buffalo demographics allowed, firstly a breakdown of the population into bachelor groups and breeding groups (Whyte 2004), followed by a fine scale separation of bachelor groups and herds into seven age classes (juveniles [0 – 1 years old], yearlings [1-3 years old], sub-adults [3-5 years old], adult males and females [5+ years old]). We multiplied the proportion of available age and sex categories by the estimated population in the study area (~3000, Cross et al. 2005) to estimate buffalo availability to the lions. Data for killed buffalo included all kills that could be aged and sexed from the GPS cluster investigation and from buffalo observations. We compared the two methods of data collection using Fisher exact tests, to account for frequencies of occurrence below five (Zar 1999). We found no significant difference in the age and sex breakdown between the two methods so we combined the two kill datasets. We assessed possible selection for an age or sex class by comparing the age and sex of buffalo kills against the availability in the buffalo population using a χ^2 tests, and show where the level of selection occurs using a Jacobs test (Jacobs 1974).

Results

Predation risk

We found no difference in the height of the grass (Kruskal-Wallis $\chi^2 = 0.8$, df = 3, $p = 0.85$) or density of the trees (Kruskal-Wallis $\chi^2 = 4.2$, df = 3, $p = 0.24$) associated with juvenile, sub-adult, adult male and adult female buffalo kills. Male and female lions rested in similar grass height (Mann Whitney U = 8850, $p = 0.65$) and tree density (Mann Whitney U = 10100.5, $p = 0.16$). Buffalo (n = 56) were killed in areas that had significantly longer grass (lion resting [n = 332]: Mann Whitney U = 10527.5, $p < 0.0005$) and greater tree density (lion resting [n = 332]: Mann Whitney U = 11409.5, $p < 0.0005$) than were found at lion resting points (Fig. 2). We found no difference in grass height or tree density for male and female lion associated buffalo kills.

Spatial distribution of kills

Buffalo of different age and sex classes were killed at different distances to the nearest available water (Kruskal Wallis $\chi^2 = 17.649$, df = 3, $p < 0.001$), with the post hoc tests indicating the main differences were between the sub-adults (2083.3 ± 520.3m) and adult females (796.7 ± 394.7m, Multiple steel test: $p < 0.005$) and between the sub-adults and adult males (816.5 ± 369m, Multiple steel test: $p < 0.005$). There was however no difference in where buffalo of different age and sex categories were killed in relation to drainage lines (Kruskal Wallis $\chi^2 = 7.4304$, df = 3, $p = 0.059$) and roads (Kruskal Wallis $\chi^2 = 3.339$ df = 3, $p = 0.3422$). We found no difference in the distance that breeding and bachelor groups of buffalo were from water, drainage or roads.

Sub-adult buffalo were killed significantly further from water sources when compared to average distances of lions and herd buffalo groups (Kruskal Wallis $\chi^2 = 11.5626$, df = 2, $p < 0.005$). Lions groups (996.3 ± 101.1) were all significantly closer to water than sub-adult buffalo kill sites. We found no differences between the kills of adult male buffalo, adult female buffalo and juvenile buffalo and their assumed group of origin's distance to water or the average distance of lions to water. Buffalo VHF and GPS collars occurred at equal distances from water sources across the course of the day, with female buffalo kills occurring slightly closer to water during the day when compared to night GPS fixes (Fig. 3a).

Male buffalo were killed closer to drainage lines (155 ± 76.5m) when compared to the average distance of lions from drainage lines (273.2 ± 24.2m), however at a similar distance to where bachelor groups normally occurred (182.6 ± 50.1). Although initially significant, this relationship was not evident following Bonferroni corrections. Similarly, we detected no differences in the distance to drainage lines between any kills of the other age and sex classes and the associated buffalo and lion groups. Buffalo herds, as indexed by the female GPS collars, moved further from drainage lines during the night when compared to daily VHF re-sighting events, corresponding with the average distance from the drainage that adult female kills occurred (Fig. 3b). We found a significant difference in the distance between roads for all comparisons of different age and sex kills, associated originating group and lions ($\chi^2 = 6.724 - 17.179$, df = 2, all $p < 0.05$), with all buffalo re-sightings occurring significantly closer to roads than kills and lions based on multiple steel tests (Table 1).

Temporal impact

We found no significant difference in the activity patterns of male and female lions (G = 11.0194, χ^2 df = 23, $p = 0.98$) over a 24 hour period with both sexes showing increased activity during the night with resting occurring during the day. After combining both male and female lions, there was a significant difference in the activity patterns of lions and female buffalo (G = 191.71, χ^2 df = 23, $p < 0.001$) over the 24 hour period, with buffalo having a pronounced peak in activity at dawn and dusk and remaining more active during the day, but equally as active as the lions at night (Fig. 4).

We found little difference in rainfall falling 30 days prior to buffalo kills (31.48 ± 7.8mm) and 150 random days (38.6 ± 0.75mm) throughout the course of the study. However, due to the non-homogeneity of variance we log transformed the data to reduce the kurtosis and subsequently found that kills were associated with a significantly lower rainfall 30 days prior to kills occurring (Welch two sampled t-test: t = 9.35, df = 144.298, $p < 0.005$). We found a considerable difference in the cumulative rainfall falling 180 days prior to kills (168 ± 24.3) and random days (226 ± 2.34mm). Following log transformation, kills occurred when significantly less rain had fallen over the previous 180 days (Welch two sampled t-test: t = 8.58, df = 144.107, $p < 0.005$). Buffalo of both sexes were in significantly worse body condition when long-term prior rainfall (180 days) was lower (females: $R^2 = 0.18$, F = 67.89, $p < 0.005$, males: $R^2 = 0.21$, F = 102.8, $p < 0.005$) but showed less difference in body condition with less rainfall over a short term (30 days, females: $R^2 = -0.003$, F = 0.0003, $p = 0.99$, males: $R^2 = 0.03$, F = 9.656, $p = 0.002$, Fig. 5).

Demographic selection

We found no difference in the breakdown of the kills between both data collection period and methods (Fishers Exact Test: $p = 0.56$) so we pooled both datasets for further analysis. There was a significant difference in what lions were killing and what was available ($\chi^2 = 34.7941$, df = 4, $p < 0.001$) stemming from the high kill rate on adult males as apposed to availability (Table 2).

Discussion

Previous studies on the buffalo in the KNP and surrounding Associated Private Nature Reserves (APNR) have addressed buffalo distributions, behaviour and habitat selection in the absence of predation (Macandza et al. 2004, Ryan et al. 2006, Winnie et al. 2008) or mediated by lion predation on different social groups (Hay et al. 2008). We extend these analyses and incorporate the influence of lions across the landscape. Our results, at a fine scale, suggest possible sexual dimorphism in spatial patterns as a result of the presence of lions, with predation patterns driven by predation vulnerability within structurally dangerous areas and predation vulnerability mediated through climatic driven forage availability. We limit our results to the basaltic geology of the park, with alternative patterns possibly occurring on the granitic soils where buffalo are shown to forage and alter behaviour (Hay et al. 2008, Winnie et al. 2008).

Fine scale habitat mediated spatial vulnerability to predation

Hopcraft and colleagues (2005) stress the importance of incorporating fine scale habitat variables into predator prey theory in conservation. At a very fine scale (<100m) lions in the SNP used areas of increased ‘catchability’ rather than areas of higher density of prey species (Hopcraft et al. 2005). Similarly, in the central region of the KNP buffalo ‘catchability’ drives the fine scale spatial location of buffalo kills. Buffalo are formidable prey species for lions to hunt, and when approached by lions if they do not initially flee will virtually preclude predation (Schaller 1972, Funston et al. 2001). This interaction between prey vulnerability and habitat structure is important as managers of protected areas can readily manipulate vegetation structure through fire, herbivory by elephants and other controls (Asner et al. 2009, Levick et al. 2009), therefore potentially influencing the interaction between predators and prey.

Males and female ungulates are often exposed to different levels of predation risk, where males tend to maximise resource gains offset against predation risks in productive habitats (Hay et al. 2008). Female on the other hand try maximise juvenile survival and will avoid areas that provide increased predation advantages (Kie & Bowyer 1999). As a result it is expected that males and females of sexually dimorphic species should be prone to predation at different spatial locations across the landscape. We found no difference in the fine scale vegetation structure where male and female buffalo were predated on, and this is consistent with a previous assessment of buffalo predation patterns in space for the region (Hay et al. 2008). The mechanisms that lead different social groups to enter areas that increase predation success for lions is different (see Hay et al. 2008), as is the location of these dangerous areas for each sex.

Within the study area, bachelor buffalo groups tend to occupy riverine habitats where the grass is greener (Macandza et al. 2004), and hence they move less in order to achieve a net energy gain compared to females (Hay et al. 2008). Similarly, we show a closer association of bachelor groups to dense drainage lines. Breeding groups, as indexed by the both GPS collars and ground observations were found further than bachelor males from drainage lines, and the distance to drainage lines increased at night. In Manyara National Park, Tanzania, no difference exists in feeding patterns for buffalo during the day or night (Beekman & Prins 1989). Assuming that the same applies to buffalo in the KNP, shifts away from drainage lines during the night may reflect movement away from dangerous habitats rather than a resource selection response and are consistent with female spatial behaviour aimed at avoiding predation in other sexually dimorphic ungulates (Kie & Bowyer 1999).

The spatial distribution of grazers in Hwange National Park, Zimbabwe, were not affected by the long term threat of lion predation (Valeix et al. 2009) suggesting limited spatial avoidance of lions by buffalo. However, at a smaller scale our study suggests that herds are characterised by short movements away from dangerous environments during the most dangerous periods (i.e. nights). Whether or not buffalo herds are in actual fact acting at scales below those measured in other studies, or if the lack of a response to lion threat from other studies is warranted, requires fine scale monitoring (i.e. one hour sampling throughout the 24 hour period in our case) to untangle. Sub-sampling GPS studies have shown that course scale sampling may propagate flawed spatial interpretations (Johnson & Ganskopp 2008), thus suggesting fine scale responses to lions may exist but are not detected in other regions. Whether or not bachelor groups have the same short term fine scaled movements is unknown, and future studies with GPS collars would be required to detect these patterns. Predation levels of adult male buffalo, generally within the drainage lines which are risky environments suggest that male bachelor groups do not respond as breeding herds do. As a consequence, movement away from dangerous regions by breeding herds may reduce predation levels when forage availability is not limited.

Climatic influence of predation and the impact of water availability

In the KNP, buffalo numbers are closely linked to rainfall driven vegetation availability which regulates body condition and hence vulnerability to predation (Owen-Smith 2008), with population crashes observed during periods of drought (Mills et al. 1995, Whyte 2004, Funston & Mills 2006, Owen-Smith & Mills 2008). Our results indicate that at a shorter temporal scale, dry periods of up to six months are sufficient to cause a loss in body condition with a corresponding increase in predation. Therefore, not only do buffalo show large scale population fluctuations in response to long temporal periods of low rainfall, but they are also susceptible to short term dry periods that could result in smaller population fluctuations. For large populations these fine scale population impacts are not important, but in smaller populations, fine scale population changes may interact with demographic factors (Legendre et al. 1999), population density (Wittmer et al. 2010) and predator-driven allee affects (Gregory & Courchamp 2010) and cause dramatic population fluctuations. In small populations managers need to aware of contributing factors that lead to population declines.

Not only are many African ungulates sensitive to rainfall driven vegetation patterns, but the direct access to water is important for many species, especially elephant (*Loxadonta africana*), waterbuck (*Kobus ellipsiprymnus*) and buffalo (Redfern et al. 2003, Skinner & Chimimba 2005, Smit et al. 2007). Since Artificial water points and rivers in semiarid African environments act as central foraging points around which many ungulate species base their activity patterns (Smit et al. 2007), predators are also known to focus predation effort on these central points, especially during dry periods (Mills & Funston 2003). Observations of previous buffalo predation in KNP indicated that the majority of buffalo predation was directly associated with waterholes (Pienaar 1969). Our results did not show a waterhole interaction with predation incidences, and indeed no interaction with water was noted for any interaction. The lack of water dependence is consistent with observations of buffalo spatial organisation in the KNP (Smit et al. 2007) and zebra and wildebeest in a water limited environment in Kenya (Groom & Harris 2010).

Conclusion

Here we have explored the fine scale temporal, spatial and demographic predation patterns associated with buffalo mortality that includes possible influences of lions in time and space. It has been shown that sexual segregation leads to an increase in predation vulnerability in male buffalo associated in bachelor herds (Hay et al. 2008), and we propose that herd dwelling buffalo may respond to predation vulnerability at night by moving away from areas that offer lions an advantage. The structural make up of the landscape seems to be equally dangerous for males and females; but the manner in which the different sexes and groups partition their time and resources leads to the seemingly same fate. The primary driver of buffalo predation by lions seems to be short term forage limitation leading to subtle changes in levels of malnutrition, with water availability playing little or no role. Our results suggest that even at fine scales, rainfall and habitat heterogeneity can influence large African ungulates and that future studies do need to incorporate fine scale components to isolate these impacts.

Tables

Table 1: The mean (± 95% confidence intervals) distance (m) of buffalo kills, buffalo VHF relocations for bachelor groups and breeding herds and GPS collared lions from the nearest water, drainage line and road.

		Water		Drainage lines		Roads	
	N	Mean	95% CI	Mean	95% CI	Mean	95% CI
Buffalo kills							
Adult Male	24	816.5	369.0	155.0	76.5	551.3	223.9
Adult Female	15	796.7	394.7	356.4	202.5	346.4	125.5
Sub-adult	10	2083.3	520.3	274.2	109.7	855.0	614.4
Juvenile	14	1568.5	518.2	173.1	89.1	726.2	366.6
Buffalo re-sights							
Bachelors	27	805.0	247.0	182.6	50.1	443.0	136.3
Herds	84	1026.2	170.1	258.0	41.2	355.8	105.8
Lion GPS locations							
Male and female (GPS)	9	996.3	101.1	273.2	24.2	662.3	36.6

Table 2. Comparison between the number and percent buffalo killed in each age class against the number and percent available in a hypothetical buffalo population of 3000 in the Satara region of the Kruger National Park. The Jacobs index provides a measure of the selection pressures on each of the age and sex classes by the lions within the study area.

	Kills (%)	Count (%)	Jacobs Index
Juveniles (0-1)	11 (7.6)	438 (14.6)	-0.34
Yearlings (1-3)	29 (20.1)	558 (18.6)	0.05
Sub-adults (3-5)	16 (11.1)	411 (13.7)	-0.12
Adult females (5+)	34 (23.6)	1030 (34.3)	-0.26
Adult males (5+)	54 (37.5)	563 (18.8)	0.44

Figures

Figure 1. Wet and dry season rainfall over the duration of the study, dotted line gives the average wet season rainfall (427.9 mm) and the dashed line gives the average dry season rainfall (45.3 mm) during the study period.

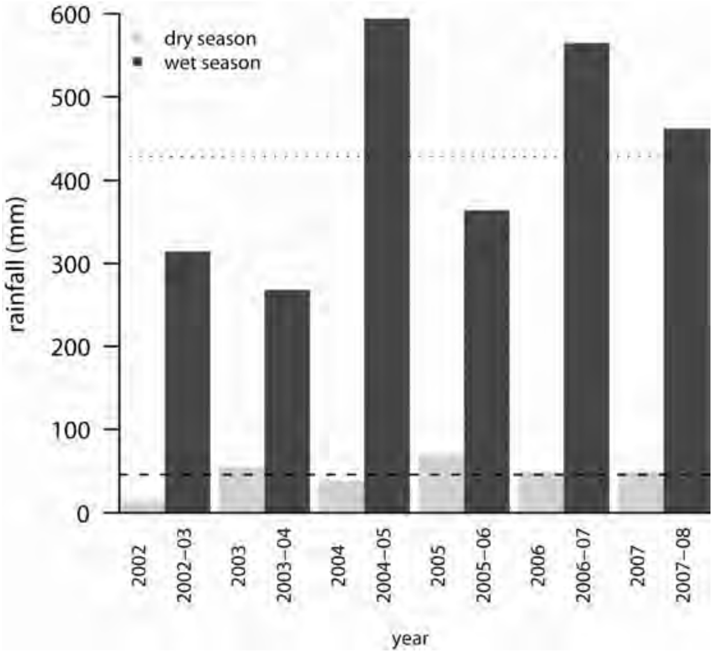


Figure 2. Average (± 95% confidence interval) tree density and grass height for lion (n = 322) resting points investigated within two weeks of occurrence compared with the average (± 95% confidence interval) tree density and grass height for buffalo kill sites (n = 56).

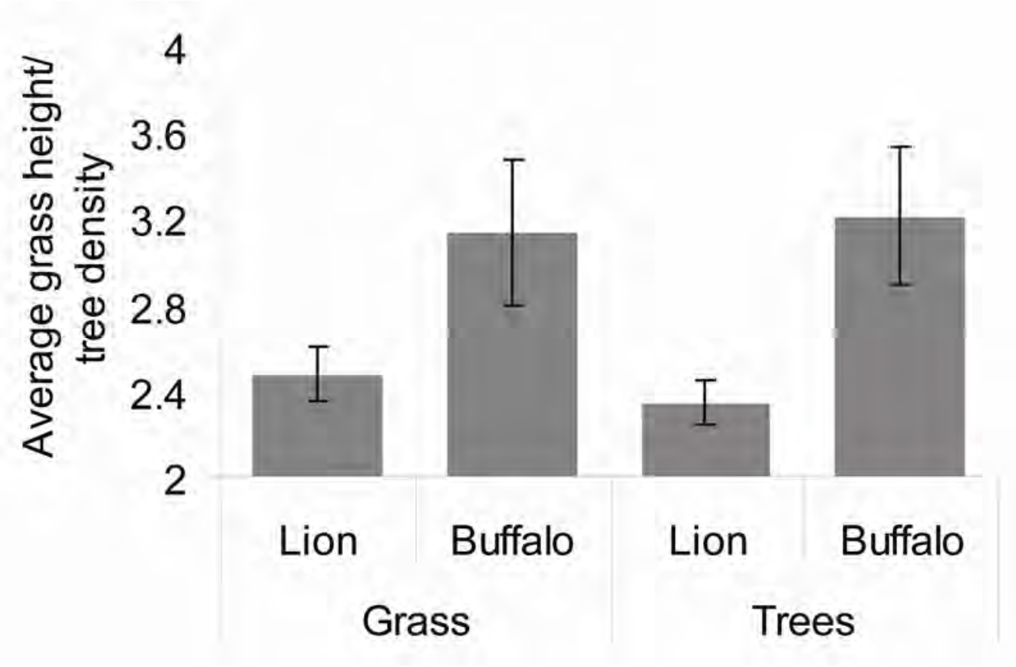


Figure 3. Average (± 95% confidence intervals) activity pattern over 24 hours for lions (n = 8) and female buffalo (n = 4)

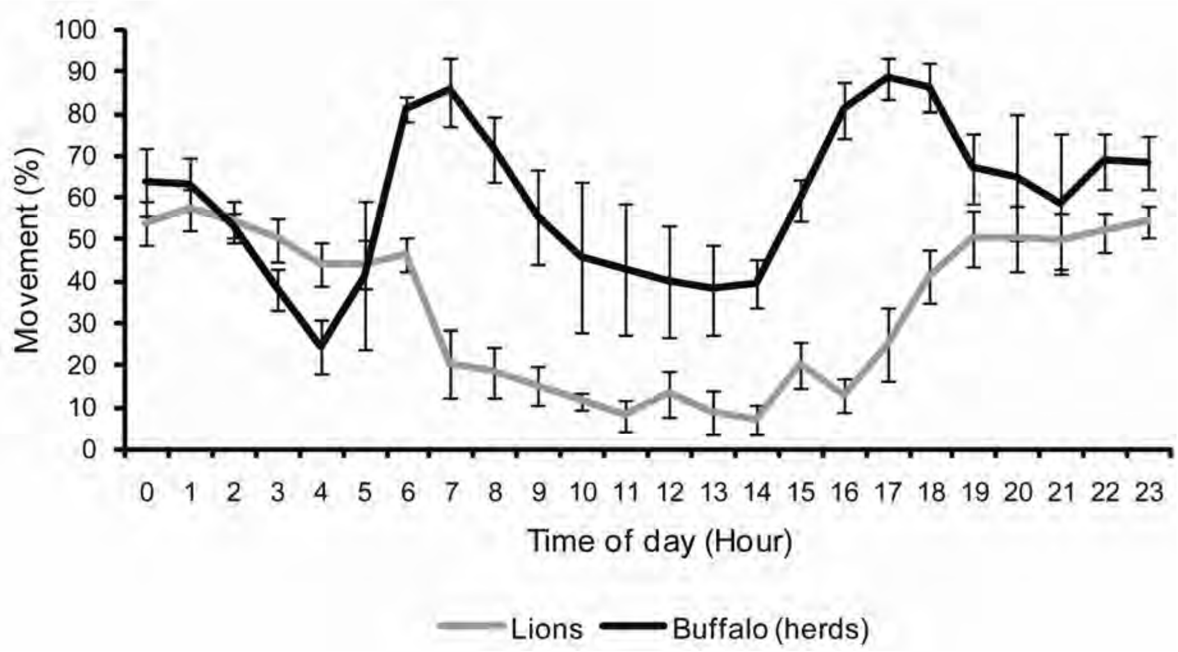


Figure 4. Average daily body condition scores for buffalo compared against the current cumulative rainfall (30 days) and the cumulative seasonal rainfall (180 days). The trend lines for males and females for the body condition scores for the cumulative seasonal rainfall are the same.

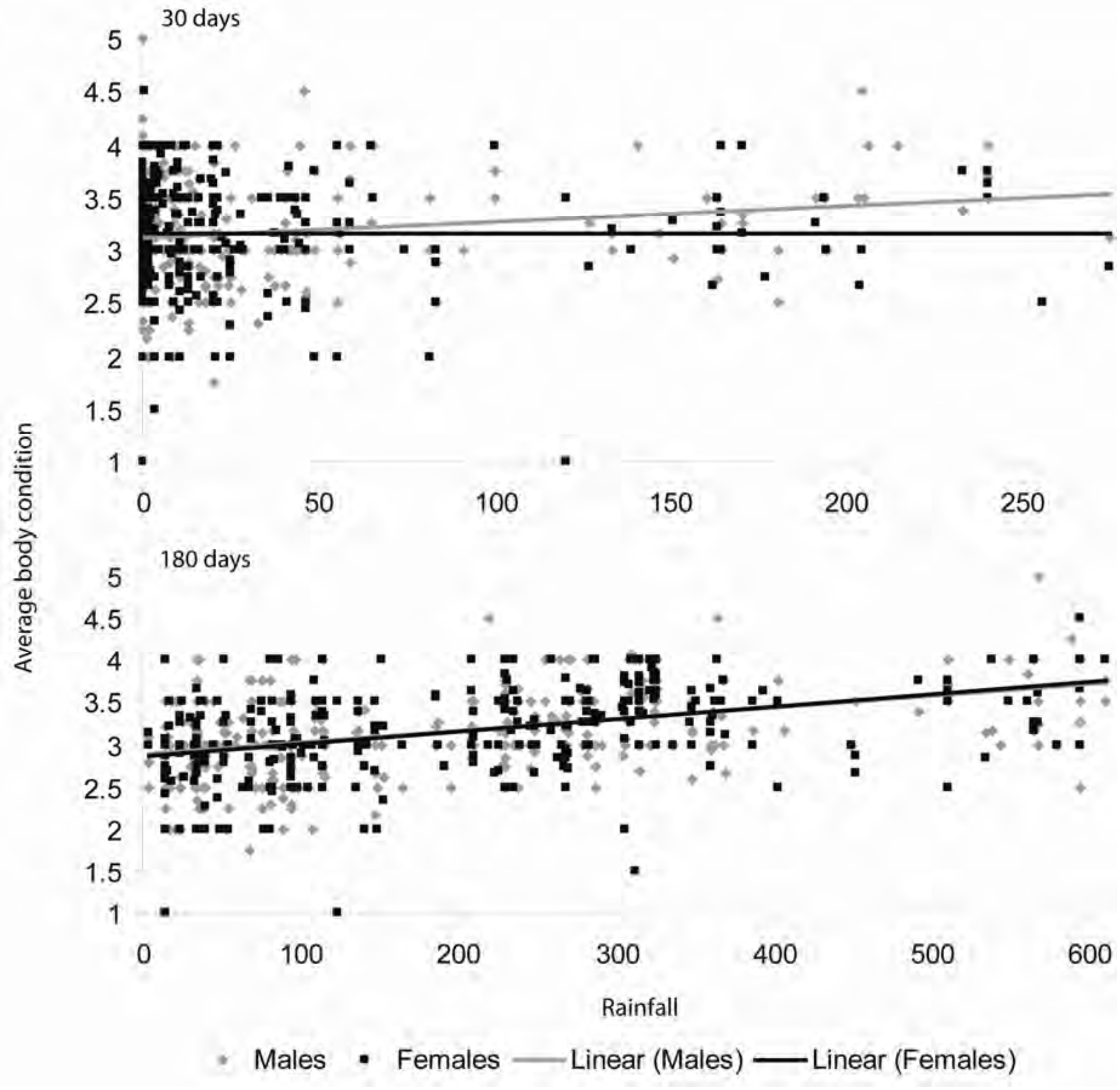
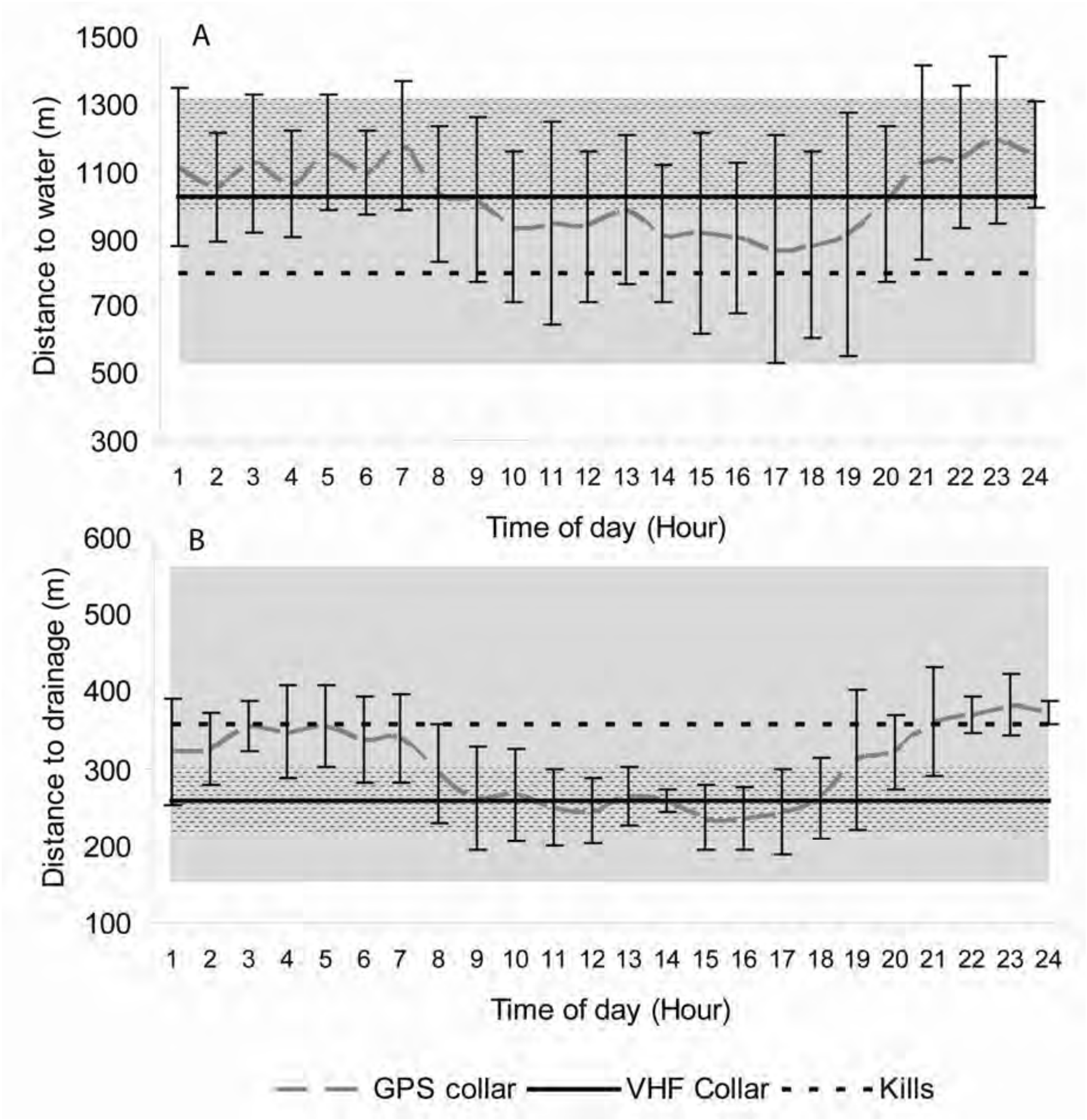


Figure 5. Hourly average distance (± 95% confidence interval) of GPS collared buffalo females from a) water and b) drainage lines compared against the average distance for breeding herds (stippled area = 95% confidence intervals) based on weekly daytime herd re-sightings and female buffalo kills (grey area = 95% confidence intervals).



Chapter 7: Quantification of predator diets for conservation

Craig J. Tambling

The quantification of large predator diets is a topic that invokes both a thrill in researchers tackling the task as well as the criticism of peer scientists for a lack of rigor and large robust datasets (Franke et al. 2006). In this thesis I tackle the estimation of large carnivore diets and attempt to combine and introduce techniques that will hopefully alleviate some of the criticisms in future studies. The quantification of large carnivore diets is undoubtedly a prominent ecological assessment that ties closely with the management of large mammals within conservation areas. With large mammals increasingly confined to protected areas (Ceballos et al. 2005), and many of these areas reduced in size from historical wilderness regions, the ecological interactions that occur within the confines of the reserves will often require greater management and monitoring to ensure that ecological patterns and processes are maintained. Indeed, sustainable large predator-prey communities are often difficult to maintain within these enclosed regions (Tambling & du Toit 2005, Slotow & Hunter 2009). In addition, there is an increasing awareness that in many environments, top down effects play a prominent role in shaping the community structure and composition (Owen-Smith & Mills 2008, Hopcroft et al. 2010), and for managers, knowing what these top carnivores are consuming plays an important role in the management of the protected areas.

As I mention throughout the thesis, continuous observation of large predators, whereby all predation events and prey encounters are observed, is still widely accepted as the best approach to determining large predator diets (Mills 1992). However, intuitively this approach is not possible for all species and in all environments. The approach outlined in the thesis presents a viable alternative to estimating predation rates where continuous observations are not possible. In addition, this research raises some important questions that need some consideration in the future. In the remainder of this chapter I introduce some of the concerns, and possible solutions, that have emerged from the research. Finally, I summarize an approach that can be used to generate diet estimates for numerous individuals simultaneously in an attempt to generate large robust datasets that will assist in monitoring large predator-prey processes.

The GPS cluster approach to quantifying predator diets

With the advancement of technology (GPS telemetry being just one) in science and the continued use thereof in ecological studies, the quantification of predator diets by investigating GPS clusters is a very realistic technique that can be implemented to generate diet estimates on multiple groups of carnivores simultaneously. In this manner large datasets of predation events can be generated that will result in robust results often limited to long term studies or datasets (see Hopcraft et al. 2005, Owen-Smith & Mills 2008). These longer term datasets (more often than not collected by numerous researchers and managers in a less than rigorous manner) are however fraught with bias and often require many assumptions to account for the bias (see Owen-Smith & Mason 2005). Despite this, these long term datasets are extremely valuable and allow the exploration of patterns longer than most conventional studies, with important conservation benefits. However, as mentioned, with the continued contraction of protected areas, many predator–prey interactions will occur on time scales far shorter than those witnessed using these previously generated datasets, and without adequate data these vital short term interactions that may shape current species assemblages may not be identified. Through the advancement of the GPS approach, it is my hope that the void of good quality short term studies may be filled. However, despite the numerous advantages that researchers employing the GPS cluster approach advocate (see Anderson & Lindzey 2003, Franke et al. 2006, Webb et al. 2008, Knopff et al. 2009, Tambling et al. 2010), bias still exists and methods to alleviate this bias needs to be developed.

The results presented here show that in the Kruger National Park (KNP), a Southern African multi-predator multi-prey ecosystem, small prey species are still missed and under-represented and replicates the sentiments expressed in previous GPS cluster studies (Franke et al. 2006, Webb et al. 2008). This is a common flaw in all carcass observation studies (Mills 1992), including those implementing GPS collar follow up techniques, and very few suggestions have thus far been raised as to how this bias can be alleviated. I present a framework of a workable approach that can be implemented to try reducing the existing bias of finding small kills. The results presented here, aligned with Marucco and colleagues (2008) investigations into wolf (*Canis lupus*) diets in Europe, show that an approach combining a movement path of predators with scats and carcasses temporally allayed along that movement path can produce biologically meaningful diet estimates that reduces the bias of missing small prey species.

Despite the perceived advantages of the GPS cluster approach with scat correction, aspects integral to the overall method still require research and calibration, both in the field and in controlled environments. An important component of lion (*Panthera leo*) predation biology that is currently unknown is the through gut retention rate of different prey species (van Kesteren 2006), and the lack of this data makes the time to independence of kill events hard to determine when correcting carcass data with scats. Use of the cheetah (*Acinonyx jubatus*) through gut rate was more than likely overly conservative and the five day window used was probably an exaggerated period of time between kills. Kill rates from the southern region of KNP suggests that females made kills every 1.8 nights and males made kills every 3.2 nights (Funston et al. 1998), considerably less than the five days that was used in the scat correction assessment. The results presented in chapter four showing a marked drop off of the killed species in the scats from three days after the kill and onwards may indicate that a similar kill pattern exists in the central region of KNP as well. Increased knowledge of the minimum and maximum through gut periods will facilitate the formulation of a better model for determining what prey items have been missed, potentially reducing the biomass consumed that is unaccounted for when using the GPS cluster approach.

The use of GPS collars in large carnivore research is undoubtedly on the increase. These will more than likely lead to more studies on large carnivores implementing the GPS cluster approach to predict kill sites of carnivores. In the Northern temperate regions the approach has advanced to the point where kill rates based purely on movement signatures of individuals are being developed (Laundre 2008). In this study mule deer (*Odocoileus hemionus*) were the only prominent prey item. Following wolf reintroductions into Yellowstone National Park, USA, elk (*Cervus elaphus*) comprised as much as 93% of their diet (Smith et al. 2003). Therefore, the majority of northern temperate regions have between one and four major prey items predated by their suit of large carnivores, often with considerable difference in prey size and GPS cluster signature. This relatively simple predator-prey system facilitates the development of these kill rate models. Unfortunately, for most African systems the wide range of prey species (eight main prey species in our study with the most important comprising only a quarter of all kills) consumed by the myriad of carnivores reduces the current ability to generate similar kill rate models and estimates. Lions, killing a large range of prey species (Radloff & du Toit 2004, Hayward & Kerley 2005), makes the generalization of cluster patterns to species very difficult. Further research is needed to untangle the relationship between GPS cluster patterns and individual species carcass detection prior to African GPS cluster investigations going beyond simple kill site detection.

The use of robust large carnivore datasets in a shrinking world

Chapters two through four introduced and explored ways in which rigorously determined diet estimates can be generated for carnivores. In chapters five and six I explored some applications for these datasets and how these applications again raise questions of interest in the changing world of conservation amidst a human dominated landscape. In the past decade there has been considerable attention given to the estimation of resource selection by herbivores (Boyce 2006, McLoughlin et al. 2010), fuelled by the increasing use of GPS collars (Swain et al. 2008) coupled with satellite imagery (Buermann et al. 2008) and advancing statistical techniques (Long et al. 2009, Duchesne et al. 2010). The current blossoming use of technology in deriving carnivore diet estimates could possibly open the door for some innovative approaches to be developed for the selection patterns of prey species by predators. However, despite the advancement of diet estimation, the majority of carnivore selection studies still use simple metrics of prey availability (but see Valeix et al. 2009), often obtained at scales beyond their direct study area to assess just what carnivores are eating and why.

As conservation areas are reduced and large predators re-introduced into areas from which they were previously extirpated (Hayward & Somers 2009) the impact of individual groups on potentially valuable prey are often required. Following the introduction of lions into 37 protected areas (often small and fenced with hard boundary) in Southern Africa numerous extinctions (Slotow & Hunter 2009) and population crashes (Tambling & du Toit 2005) of prey species have occurred. This aspect is not only limited to lions, and wild dogs (*Lycaon pictus*) have been removed from some protected areas they were having largely detrimental impacts on the existing wildlife populations (P. Lindsey, Pers. Comm. 2009). Following the re-introduction of large carnivores, effort to determine spatial movement on reserves is in many cases attempted and provides an ideal time to monitor ungulate responses, both numerical and behaviourally. During this important phase following re-introductions, the impact that predators have on prey species, which are inherently clumped in their distribution across the landscape, needs to be assessed especially as many prey populations may be naïve to reintroduced large predators (Berger 2007, Frair et al. 2007). The use of large scale aerial census data to estimate prey availability may dampen the spatially heterogeneous impact that territorial predators may have within conservation areas.

In a similar manner to the question of where to count and at what resolution, the question of how to count prey species emerged from the thesis. Recently Fryxell and colleagues (2007) show and advocate that constructing predator-prey models with groups rather than individuals stabilizes predator prey interactions. The results presented in chapter five suggest that large differences emerge in what carnivores deem to be important prey species when contrasting available prey as groups or individuals. The general theory is that attack rates will increase with increasing group size (Jackson et al. 2005) and this has been noted for wolves preying on elk (Hebblewhite & Pletscher 2002). However, in the Serengeti the relationship between prey density and encounter frequency is best modelled with power curves such that as population densities increase the encounter rate of groups does not increase at the same pace, suggesting that high density prey will be encountered less when in groups than would occur if spaced randomly across the landscape. I believe that the determination of how to count prey animals when considering predator selection patterns is key to understanding prey selection. Arising from the issue of groups versus individuals is the question of how detection and encounter rates are expressed for different species in different environments. To complicate matters different social groups may have different encounter rates for different species (Funston et al. 1998). For future selection studies the relative role that grouping has in prey species and how this impacts predator encounter rates needs to be assessed and links between modelled scenarios (e.g. Cosner et al. 1999) and field studies (e.g. Krause & Godin 1995) need to be bridged.

Use of the GPS cluster technique

Throughout this thesis I have proposed the use of the GPS cluster approach and below is a framework for the development of a study employing the technique.

1. Pre-test the GPS collars to determine the minimum errors associated with different habitat types, allowing an assessment of the definition of a cluster and the area that will be searched around GPS points for different habitat types
2. Initial tradeoffs exist between battery life and the fix rate of GPS collars. Knowing the biology of the species studied will help in this aspect so that the sampling can be designed to obtain readings when the animal is active, and allows a fix rate that will detect changes in state (i.e. activity, resting, kill and consumption). In addition this process of understanding your study species will allow the determination of a set of *a-priori* predictor variables that can be used in the model. As the approach becomes more universal so the explanatory variables for each large carnivore will emerge and this will assist in the variable selection procedure.

3. Following the deployment of the GPS clusters, an intensive period of initial follow-up field work is needed (Webb et al. 2008) in order to generate baseline data (variables associated with and without kills) for initial models. Ideally, rapid follow-up period are warranted to reduce the chances that kill remains will be lost over time. In this manner scats can also be detected before environmental and biological components degrade the scats.
4. Once the initial model (Generalized Linear Model in our case) has been developed generate a probability cut-off for clusters that will be investigated based on the time that is available for field observations. Focus attention on those clusters with the highest probability of being a kill, but also visit all low probability clusters within the immediate vicinity of the expected kill cluster so as to increase the number of clusters (with and without kills) investigated.
5. Reassess the model that was developed with the new data that has been collected in an adaptive manner, streamlining model formulation.
6. If genetic analysis is available, screen the scats collected to ensure; a) that the correct species has been collected (may be important for species that produce scats similar to other species present in the area), and b) to determine if the scat originated from the collared group or not (see Marucco et al. 2008).
7. Compile the scats collected and carcasses observed at GPS clusters (belonging to the collared group) into a time series of kill events, rather than a time series of potentially pseudo-replicated scats and carcasses. The knowledge of the maximum and minimum through-gut retention times can be used to set upper and lower bounds for kills that are missed. If the group size of the carnivore group is known, use expected consumption

rates to estimate the possible biomass that has been missed during the field observation period.

The generation of diet estimates based on the above procedure should result in rigorous biologically meaningful results that can then be used for the sound management and conservation of carnivores.