

Movement analysis for monitoring predation by large carnivores: lions in Kruger National Park

by

Craig John Tambling

Submitted in partial fulfilment of the requirements for the degree

Doctor of Philosophy

In the Faculty of Natural & Agricultural Sciences

University of Pretoria

Pretoria

June 2010



Summary

In this study I investigated how movement data acquired from Global Positioning System (GPS) data could be used to assist in the estimation of the diet and prey selection of a large African carnivore, the African lion (Panthera leo), in the central region of the Kruger National Park (KNP), South Africa. I show that Generalized Linear Models (GLMs) can be used to increase the probability of locating lion kills at GPS clusters, where a cluster is defined as two or more consecutive GPS locations within 100 m of each other. In addition, considering the social structure of lion prides, I show that using a metric of distance between individuals in a pride at the beginning of clusters associated with kills can further increase the predictive ability of models employed to locate kills from GPS data. However, similar to other GPS cluster based approaches there is an underestimate of smaller prey items in the prey profile. I collected scats at GPS clusters and used this additional dataset to show that the GPS cluster approach employed in the KNP underestimated the presence of smaller ungulates, namely impala (Aepyceros melampus) and warthog (Phacochoerus africanus) in the diet by at least 50%. I found that a negative relationship existed between prey items missed at GPS clusters and the size of the species, with more prey items missed as the size of the species declined. Therefore, investigating carcass remains at GPS clusters underestimated the numerical importance of the smaller prey species. However, this underestimation of small prey was not important when the biomass of prey consumed by lions was assessed, as the larger prey item not missed form the bulk of the In the central region of the KNP zebra (Equus quagga) were the most consumed prey item, followed by wildebeest (Connochaetes taurinus), impala and buffalo



(Syncerus caffer). I assessed two measures of prey selection for the lions in the study area, with each considering a different approach to prey availability. Prey selection varied considerably when availability was assessed as prey individuals or prey groups. In addition, generalisation of prey selection based on a broad assessment of prey availability in the region differed to prey selection patterns assessed on a fine scale in the pride range for each pride. Finally, I found that buffalo showed fine scale vulnerability to predation by lions based on climate and vegetation structure. Six months of below average rainfall appeared to be sufficient to reduce buffalo body condition and increase vulnerability to predation. Buffalo were more vulnerable to predation by lions in areas with longer grass and denser bush. Ultimately the use of GPS cluster data combined with scat corrections gives a good representation of the diet of a large African carnivore, and approaches the accuracy that is obtained through continuous observation data. Good quality diet estimates are needed for the accurate assessment of prey selection by carnivores as well as the fine scale investigation of habitat and climate mediated predation risk for ungulates.



I, Craig Tambling declare that the thesis/dissertation, which I hereby submit for the degree

Doctor of Philosophy at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

SIGNATURE:

DATE: 20 July 2010



Movement analysis for monitoring predation by large carnivores: lions in Kruger National Park

©2010

By

Craig John Tambling



Abstract

Movement analysis for monitoring predation by large carnivores: lions in Kruger National Park

By

Craig John Tambling

Doctor of Philosophy in

Department of Zoology and Entomology

University of Pretoria

Methods used to estimate the prey consumption by large carnivores include direct continuous observation, stomach content analysis, carcass observations and scat analysis. Continual observations are widely considered the best approach to estimate large carnivore diets, with lions (*Panthera leo*) being no exception. Continual observation allows the recording of all prey encounters and biases inherent in the other approaches are minimised. However, continuous observations are not always feasible, and in situations where animals cannot be observed at all times, diets are often estimated from observed carcasses. This often leads to an over-estimation of large kills in the estimated diet. Alternative methods that are free of the constraints placed on continuous observations are needed to provide data of a similar quality to that obtained using these continuous observation bouts. I employed a cluster follow up technique to locate lion kills



from remotely accessed Global Positioning System (GPS) data from lions in the Kruger National Park (KNP). I develop Generalized Linear Models (GLMs) that increase the probability of locating kills at GPS cluster events. By increasing the predictive ability of detecting kills I show that this technique can be used to locate kills in a more efficient manner than random searching of GPS clusters, with further advantages in that multiple groups of lions can be monitored simultaneously. By incorporating this technique into an adaptive research framework, the diet of lions (and that of other large carnivores) can be estimated. In addition, I show that the spatial association between lions at kill sites, while feeding on carcasses, provides a further increase in the predictive ability of kill site models. Lionesses were found to be considerably closer together at the start of clusters associated with kills in comparison to clusters where no kill was found. This pattern remained consistent for both small and large kills. This proximity approach could therefore be incorporated into the GLMs that are developed to predict kill sites of large social carnivores. To further reduce the bias (where small kills are often missed) inherent in carcass observations, I combined scats and carcasses collected from known times, locations and lion groups to construct a temporal kill record for each group of lions. By combining scats and carcasses I estimate that at least 50% of the small prey items, namely impala (Aepyceros melampus) and warthog (Phacochoerus africanus) were missed when GPS clusters were investigated for carcasses. Ultimately, I show that a combination of GPS cluster investigations based on models developed using GPS movement data in combination with lion proximity data, augmented with scats collected at GPS clusters, could provide estimates of large carnivore diets that begin to approach estimated diets obtained through continuous monitoring.

The resulting diet, estimated from the GPS cluster approach in combination with scat collection, indicated that the dominant prey item in the region was zebra (*Equus quagga*) followed by



wildebeest (Connochaetes taurinus), impala and buffalo (Syncerus caffer). Selection indices for the eight dominant prey items were calculated using prey availability measures obtained from the aerial census data and ground counts of groups. It has been suggested that group level selection is a better approach to calculating predator-prey interactions, and that stability in predator-prey systems is improved if group metrics of prey are used as apposed to individual measures of availability. I show that there is a considerable shift in selection indices, as well as in the order that prey is selected, when using different measures of prey availability. In selection studies, more effort needs to be paid to the assessment and definition of prey availability to ensure results accurately reflect selection patterns in the field, especially when data are used for the development of management practices. Combining buffalo predation data collected from GPS cluster investigations with buffalo mortality data collected over five years prior to the commencement of the GPS cluster investigations, allowed an investigation into patterns of lion predation on buffalo between 2000 and 2007. Buffalo of both sexes were more vulnerable to predation in habitats that gave lions an ambush advantage (i.e. increased grass height and tree density). Despite this similarity in landscape risk, different processes lead to similar fates in dangerous habitats for buffalo of both sexes. Predation pressure by lions on buffalo increased following periods of reduced rainfall; with more buffalo predated on following drier six month periods. Predation on males constituted a significant proportion of all predation and was focused predominantly into the late dry season.

The resulting method of locating kills by using GPS clusters and correcting carcass data with scats collected along the movement path represents a robust technique to estimate large carnivore diets. In the concluding chapter I present avenues where future research can build on the current



thesis and present a framework that can be employed when attempting to estimate large carnivore diets.



Note on the text

Each chapter is set out in the style of the journal to which it has or will be submitted. Consequently there is some repetition and stylistic differences in each of the chapters. In addition, other authors are included in the paper reference. However, for each chapter, my input was greatest. I planned the research, undertook the field work, analyzed the data and wrote the manuscripts. I was helped by my co-authors. Wayne Getz, Johan du Toit and Elissa Cameron were my supervisors and Lydia Belton, Samuel Laurence, Steve Bellan and Paul Cross were fellow students.



Acknowledgements

First and foremost I would like to thank my family, in particular my parents John and Sally. Without their continued support this thesis would not have been completed. I would like to thank everyone that contributed to my time spent as a doctoral student at the University of Pretoria and especially to the Department of Zoology and Entomology. The time spent in the department has helped mould me to who I am now, and I value every moment, all 10 years! To all my friends in Pretoria, you were always there for me even when I was stressed or worried or just in need of some company. A special thanks to Samuel Laurence, Nick Ball, James Roxburgh, Tim O'Shea and Luke Verburgt for taking my mind off the work and allowing me to relax and enjoy myself over the years. Thanks are extended to everyone in the Getz lab at the University of California, Berkeley. The time spent in Berkeley was awesome and helped tremendously with the completion of many aspects of the modelling and statistical parts of the project. Special thanks to Leo Polanskey, Richard Starfield and Steve Bellan for your continued patience with my never ending stream of question regarding R. To George Wittemyer, Niclas Norstrom and in particular Wendy Turner for many fun days in the lab, and let's not forget the inspirational Gin and Tonic sessions. Many thanks must go to the Kruger National Park game capture team and in particular Peter Buss, Danny Govender, Marius Kruger and Markus Hofmyer. Without your continued support and willingness to come out to Satara and catch lions, as much as you hated the evenings out, the project would not have been able to gather momentum and I would not have been able to achieve the results that I did. Thanks to the Bovine tuberculosis group for welcoming me into the Satara framework and for making me feel



welcome. To Paul Cross, Craig Hay, Julie Wolhuter and Justin Bowers for making me feel at home and helping me out with whatever queries I had concerning the buffalo project and the Satara region in general. Special thanks to Augusta, Kutani Bulunga, Marius Renke and Richard Fynn for walking GPS points and helping with the lion tracking, and most importantly for keeping all the dangerous beasts away from me while I blindly followed GPS co-ordinates. A very special thanks to Robert Dugtig, your friendship, support and help was invaluable in Satara. To Darren Burkipile and the grassland guys, thanks for keeping me entertained and for the numerous outings to Matikitiki to relax after long days. For everyone that came out to Satara, to either keep me company or help me out, I value the time and effort you put into visiting Satara. As with most predator studies, there comes a time where faeces need to be cleaned, which is not the most enjoyable job. To the many volunteers that helped out with the cleaning of the scats and for putting up with the wonderful aroma of old, new, fresh and wet lion dung. Thanks also to Steve Bellan and Samuel Laurence for helping with some of the hair identification, it made the many hours late into the night and on weekends worthwhile. I don't think the MRI will ever be the same again. A special thanks to Luke Verburgt for being the statistician I needed when I ran head on into the brick wall called stats. To all the people at the MRI, without you the project would have been a shambles. Martin Haupt, thanks for all the help with the collars and for all the support and many many discussions around the MRI coffee table. To Elmarie Cronje, Liz Drew, Elisabe Els and Daleen Funston for all the logistical support from the secretarial desk at the MRI, you managed to keep things rolling smoothly throughout the long process. For all those that made morning tea time at the MRI such an institution, thanks and I hope that the tradition lives on. The project would not have been possible without National Research Foundation Doctoral funding to Craig Tambling, a James S. McDonell Foundation 21st



Century Science Innovation Award to Wayne Getz and an NIH Grant (GM83863) to Wayne Getz. I would like to extend a special word of thanks to my three supervisors; Wayne Getz, Johan du Toit and Elissa Cameron who guided me through the PhD process. Although I did not spend great lengths of time in the same location as all three of you, I am grateful for the emailing correspondence as well as the open door policy that you employed, enabling me to come and ask questions whenever I needed to. Wayne, thanks for all the statistical and modelling help and for funding my trip over to Berkeley. Johan, thanks for being there to bounce ideas off and for giving my direction when needed. Elissa, thanks for stepping in and being someone I could speak to in Pretoria. Finally, I have to thank all the cooperative animals that made my stay in the Kruger National Park a pleasure and a period in my life that will not be forgotten.



Table of Contents

Chapter 1: Summary	5
Chapter 2: Methods for Locating African Lion Kills using Global Positioning Sy	ystem
Movement Data	12
Abstract	13
Introduction	14
Methods and Materials	16
Study area	16
GPS collars and cluster investigation	16
Statistical Methods	18
Results	22
Discussion	25
Management implications	29
Tables	30
Figures	31
Chapter 3: Feasibility of using proximity tags to locate female lion (Panthera leo) kills	35
Abstract	36
Introduction	37
Materials and methods	39
Results	41
Discussion	42.



Figures	47
Chapter 4: Combining GPS locations and scat analys	is to estimate the diet of a large
carnivore	50
Abstract	51
Introduction	52
Materials and Methods	54
Study area	54
Data acquisition and datasets	55
Scat analysis procedure	56
Data analysis	57
Results	59
Discussion	61
The additive approach	61
Diet estimates from scats	63
Conclusions	64
Tables	66
Figures	69
Chapter 5: The influence of scale and count method on	prey selection of a large carnivore
	75
Abstract	76
Introduction	77
Methods	79



Study area	79
Estimating prey availability	80
Estimating lion diets and range	81
Prey selection	82
Results	84
Prey availability	84
Diet estimates	84
Prey selection	85
Discussion	86
Prey selection: How do we count prey animals?	87
Prey selection: The influence of scale on determining selection indices	89
Conclusion	91
Tables	92
Figures	94
er 6: Fine scale determinants of lion predation on buffalo	99
Abstract	100
Introduction	101
Methods and materials	103
Study area	103
Datasets	104
Predation risk	105
Spatial analysis	106



Temporal analysis	107
Buffalo demographic parameters	109
Results	110
Predation risk	110
Spatial distribution of kills	110
Temporal impact	111
Demographic selection	112
Discussion	113
Fine scale habitat mediated spatial vulnerability to predation	113
Climatic influence of predation and the impact of water availability	115
Conclusion	116
Tables	118
Figures	120
Chapter 7: Quantification of predator diets for conservation	125
The GPS cluster approach to quantifying predator diets	127
The use of robust large carnivore datasets in a shrinking world	130
Use of the GPS cluster technique	132
References	135