

LIVING WITH LIONS:
SPATIOTEMPORAL ASPECTS OF COEXISTENCE IN SAVANNA CARNIVORES

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ABSTRACT

Top predators can suppress their smaller guild members and this can have profound consequences that cascade throughout the larger community. Suppression is mediated primarily through interference competition: (a) direct aggressive interactions, and (b) behavioral avoidance by mesopredators to minimize risks of encountering top predators. These avoidance responses can be costly, especially when they result in large-scale displacement that reduces access of the subordinate species to resources. However, fine-scale avoidance strategies may promote mesopredator persistence by minimizing risk without costly large-scale displacement. This dissertation explores the role of behavioral avoidance in driving intraguild predator dynamics. Specifically, I examine how African lions affect spotted hyenas, cheetahs, and African wild dogs in Serengeti National Park, Tanzania. Long-term lion monitoring by the Serengeti Lion Project provides a high-resolution understanding of how lions interact with each other and the landscape; I deployed a large-scale camera trapping survey to collect fine-scale spatial data on the broader carnivore community. Chapter 1 reveals that although lions displace African wild dogs from the landscape and suppress their populations, cheetahs persist with lions through space and time. Chapter 2 validates the camera trapping survey designed to study fine-scale carnivore avoidance and highlights the broad utility of citizen science for similar ecological projects. Chapter 3 applies the camera trapping survey to reveal that fine-scale avoidance does not always translate into costly spatial displacement for subordinate species. Together, these chapters identify large-scale displacement as a key driver of mesopredator suppression and fine-scale avoidance as a key mechanism for mesopredator persistence. This dissertation further establishes new methods to continue exploring community dynamics for long-lived, wide-ranging species.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS	I
ABSTRACT.....	III
TABLE OF CONTENTS	IV
LIST OF TABLES	V
LIST OF FIGURES	VI
INTRODUCTION.....	1
CHAPTER 1: CHEETAHS AND WILD DOGS SHOW CONTRASTING PATTERNS OF SUPPRESSION BY LIONS	6
INTRODUCTION	6
METHODS.....	8
RESULTS.....	11
DISCUSSION	12
TABLES AND FIGURES.....	17
CHAPTER 2: SNAPSHOT SERENGETI: A CASE STUDY IN CAMERA TRAPS AND CITIZEN SCIENCE FOR MULTI-SPECIES MONITORING	21
INTRODUCTION	21
METHODS.....	23
RESULTS.....	30
DISCUSSION	32
TABLES AND FIGURES.....	36
CHAPTER 3: LIONS, HYENAS, AND CHEETAHS: SPATIOTEMPORAL AVOIDANCE IN LANDSCAPE OF FEAR	48
INTRODUCTION	48
METHODS.....	50
RESULTS.....	52
DISCUSSION	55
TABLES AND FIGURES.....	58
CONCLUSIONS	68
REFERENCES.....	69
APPENDIX 1: ADDITIONAL TABLES AND FIGURES FOR CHAPTER 1	82
APPENDIX 2: ADDITIONAL TABLES AND FIGURES FOR CHAPTER 3	88

LIST OF TABLES

Table 1: Overview of study species	5
Table 1-1: Lion, cheetah, and wild dog ranging patterns – results from bootstrapping analysis.....	17
Table 2-1: Sample classifications	36
Table 2-2: Species identification validation results	38
Table 2-3: Species counts validation results.....	38
Table 2-4: All species captured in Snapshot Serengeti.....	39
Table 2-5: Comparison of camera trap captures to known densities	40
Figure 2-1: Study Area.....	41
Table 3-1a-c: Regression output for the best “habitat only” models for each species.	58
Table 3-2: Regression output for models of subordinate vs. dominant species.....	60
Table 3-3: Regression output for best overall models	61
Table 3-4: Regression output from temporal models	62
Table A1-1: Presence and density of lions and cheetahs across reserves.	82
Table A1-2. Model output for population analyses.	83
Table A1-3a: Cross-reserve model output – Wild Dogs vs. Lions.....	84
Table A1-3b: Cross-reserve model output – cheetahs vs. lion density.....	85
Table A1-3c: Cross-reserve model output – cheetahs vs. lion presence.....	86
Table A2-1a-c: Candidate models	88
Table A2-2: Model averaged output – “habitat only” models.....	90
Table A2-3: Model averaged output – overall models	92

LIST OF FIGURES

Figure 1-1: Study area.....	18
Figure 1-2: Predator and prey population trends	18
Figure 1-3: Comparison of wild dog ranging from a) 1985-1990 to b) 2005-2010	19
Figure 1-4: Lion, cheetah, and wild dog ranging patterns	19
Figure 1-5: Comparison of lion densities experienced by female cheetahs in different reproductive states.	20
Figure 1-6: Lion, cheetah, and wild dog densities across reserves	20
Figure 2-2: Field site examples.....	41
Figure 2-3: The <i>Snapshot Serengeti</i> interface.....	42
Figure 2-4: Example captures from Snapshot Serengeti.....	42
Figure 2-5: Monthly camera trap activity	43
Figure 2-6: Comparison of camera trap captures to known population estimates.....	44
Figure 2-7: Daily herbivore capture rates	45
Figure 2-8: Monthly distributions of herbivores vs. NDVI	46
Figure 2-9: Comparison of giraffe and lion densities to camera trap capture rates.	47
Figure 3-1: Study area.....	63
Figure 3-2: Camera trap detection curves.....	63
Figure 3-4: Mesopredator capture rates vs. dominant predator capture rates.....	64
Figure 3-5: Predictions from full spatial models	65
Figure 3-6: Temporal activity patterns	65
Figure 3-7: Short-term temporal response to prey	66
Figure 3-8: Short term temporal response to predators	67
Figure A1-1: Cross-reserve lion and wild dog densities.....	87

INTRODUCTION

In ecosystems around the world, top predators suppress populations of their smaller guild members; these dynamics can have profound consequences that cascade throughout the larger ecological community. Mesopredator suppression has been documented in over 60 systems worldwide (Ritchie & Johnson 2009, Brashares et al. 2010). Eagle owls suppress smaller owls and goshawks (Sergio *et al.* 2007). Wolves affect coyote distribution and density across North America (Mech 1966, Berger & Connor 2008, Smith *et al.* 2003). Coyotes in turn suppress many smaller carnivores such as gray foxes, red foxes, swift foxes and bobcats (Harrison, Bissonette, & Sherburne 1989, Fedriani *et al.* 2000, Kamler *et al.* 2003, Crooks & Soule 1999). Declining African lion and leopard populations have led to dramatic increases in olive baboons (Brashares et al. 2010).

The effects of top predators reach far beyond their smaller guild members. Trophic cascades have been documented for 7 of the world's 31 large predators (Terborgh & Estes 2010, Estes *et al.* 2011, Crooks and Soule 1999, Ripple *et al.* 2014), with consequences ranging from altered vegetative structure (Estes et al. 2011), heightened susceptibility to invasive species (Carlsson, Sarnelle & Strayer 2009), and altered soil fertility composition (Croll *et al.* 2005). For example, overharvesting of sharks in the Atlantic Ocean and resultant increases in cownose rays led to the collapse of bay scallop fisheries (Myers *et al.* 2007); predation by introduced foxes transformed plant communities on the Aleutian Islands by disrupting nutrient subsidies otherwise delivered by seabirds (Maron *et al.* 2006). As anthropogenic pressures increasingly push large predators towards local and global extinction, understanding the drivers of predator dynamics grows increasingly important.

Suppression by top predators is not just about food – it occurs despite minimal diet overlap and appears to be mediated primarily through *interference competition* (*sensu* Shoener 1983): (a) direct aggressive interactions (Palomares & Caro 1999; Sergio & Hiraldo 2008; Prugh *et al.* 2009), and (b) behavioral avoidance by mesopredators to minimize risks of encountering top predators (Cresswell 2008; Creel & Christianson 2008).

Top predators chase, steal food from, and kill their smaller competitors (Palomares & Caro 1999; Linnell & Strand 2000; Caro & Stoner 2003; Ritchie & Johnson 2009; Prugh *et al.* 2009). Lethal interactions can account for substantial proportions of mortality in subordinate species (Linnell & Strand 2000, Palomares & Caro 1999, Caro & Stoner 2003; Hunter & Caro 2008). For

instance, in some areas predation by lions is the leading cause of cheetah cub mortality (Laurenson 1994, but see Mills & Mills 2013) and accounts for up to 32% of African wild dog deaths (Van Heerden 1995); gray wolves can cause >50% of coyote mortality (Thurber *et al.* 1992); and coyotes up to 66% of swift fox mortality (Kamler *et al.* 2003). Strangely, in many cases, the top predator gains no immediate benefit and does not even consume the victim (unlike traditional intraguild-predation systems, *sensu* Holt & Polis 1997).

This aggression can create a “landscape of fear” (Laundré, Hernández & Altendorf 2001) in which subordinate species restrict their activity to “safe” areas or times of day (Ritchie & Johnson 2009, Creel & Christianson 2008). For instance, coyotes concentrate primarily at boundaries between wolf-pack territories (Fuller & Keith 1981), and swift and red foxes are located almost completely in gaps between coyote territories (Voigt & Earle 1983; Tannerfeldt, Elmhagen & Angerbjörn 2002; Kamler *et al.* 2003a; Kamler, Stenkewitz & Macdonald 2013).

The landscape of fear can be costly; the avoidance strategies that subordinate species employ may be greater determinants of population dynamics than actual numerical effects of killing. Experiments have suggested the primacy of these indirect “risk effects” or “fear effects” in driving community dynamics (Werner & Peacor 2003; Schmitz, Krivan & Ovadia 2004; Preisser, Bolnick & Benard 2005; Creel & Christianson 2008). Studies manipulating arachnid or insect predators to render them nonlethal (e.g. by amputating or sealing mouthparts) have demonstrated that anti-predator responses result in levels of prey mortality comparable to rates of direct killing [e.g. by switching to lower-risk, lower-quality resources (Schmitz, Beckerman & O’Brien 1997; Beckerman, Uriarte & Schmitz 1997)]. Because they act on shorter time-scales, such risk effects are likely to cascade more rapidly throughout an ecological community than numerical effects alone would predict (Preisser *et al.* 2005). However, although risk effects are well documented in invertebrate systems, their strength depends on numerous factors such as predator hunting strategy (Schmitz *et al.* 2004) and habitat productivity (Bolnick & Preisser 2005), and considerable debate exists as to the relative importance of the “landscape of fear” in driving dynamics of large mammalian predators (Kauffman, Brodie & Jules 2010).

Thus, the ultimate drivers governing patterns of suppression and coexistence in predator guilds remain unclear: coexistence outcomes can vary dramatically – across different species within the same guild, or even within a given species across different locations. For example, lynx appear to limit red fox populations, but this effect depends local ecosystem productivity (Elmhagen & Rushton 2007). African lions appear to suppress African wild dogs in all but the continent’s largest and most densely wooded protected areas (Creel & Creel 1996; Swanson *et al.*

2014). Recolonizing wolves eliminated coyotes on Isle Royale, but not the Greater Yellowstone Ecosystem (Berger & Gese 2007).

In this dissertation, I explore behavioral characteristics that drive patterns of suppression and persistence in a guild of large African carnivores. Specifically, I evaluate how hyenas, cheetahs, and African wild dogs (*Panthera pardus*, *Crocuta crocuta*, *Acinonyx jubatus*, *Lycaon pictus*) coexist with lions (*Panthera leo*). Lions dominate aggressive interactions and have been widely believed to suppress their smaller guild members through interference competition (Table 1).

I address these questions by evaluating patterns of avoidance and resultant population dynamics across spatial and temporal scales. Long-term monitoring by the Serengeti Lion Project provides the foundation for this research: lions have been continuously monitored within the Lion Project study area since 1966; all lions are individually identified by individual whisker spots and each of 23 prides is tracked regularly via radio-telemetry. The long-term data provides high-resolution data on lion ranging, density, and demographic success and are complemented by additional historical monitoring of other carnivores and prey (1970s-1990s). In 2010, I launched a new, large-scale camera trapping survey to collect fine-scale spatiotemporal data on the broader carnivore community.

I explore the mechanisms of predator-predator coexistence with the following three chapters:

Chapter 1: *Cheetahs and wild dogs show contrasting patterns of suppression by African lions.*

I use long-term demographic and radio-telemetry data to re-evaluate whether lions suppress populations of cheetahs and wild dogs, and examine possible mechanisms for coexistence. I validate the findings from Serengeti National Park against population data across a number of South African reserves. The work herein is my own, but long-term data were provided by a number of collaborators and has been published as multi-author paper in the *Journal of Animal Ecology*.

Although lions suppressed African wild dogs in Serengeti and across reserves, cheetahs were neither displaced from large areas nor suppressed. These findings demonstrated differential responses of subordinate species within the same guild and challenge a widespread perception that lions undermine cheetah conservation efforts. Paired with several recent studies that document fine-scale lion-avoidance by cheetahs, this chapter highlighted fine-scale spatial avoidance as a possible mechanism for mitigating mesopredator suppression.

Chapter 2: *Snapshot Serengeti: a case study in camera trapping and citizen science for multispecies monitoring.*

Results from Chapter 1 identified fine-scale spatiotemporal partitioning as likely key mechanism driving patterns of predator-predator dynamics. To acquire spatial data on the entire existing carnivore community, I established a large-scale camera trapping survey comprised of 225 camera traps covering 1,125km² of the long-term lion project study area. Camera traps are a rapidly growing approach for large-scale multi-species monitoring, but present a number of analytical and data-management challenges. In this chapter, I evaluate the effectiveness of (a) camera traps as a multi-species monitoring tool, and (b) citizen science to effectively process the large amounts of data produced by camera trapping surveys. Through our citizen science platform, *Snapshot Serengeti*, volunteers have processed over 1.5 million captures (>4.5 million photographs) with an average 96.6% accuracy. Furthermore, even simple data analysis of raw capture rates accurately reflects broad population sizes and seasonal trends.

Chapter 3: *Lions, hyenas, and cheetahs: spatiotemporal avoidance in a landscape of fear.*

I use the camera trapping survey from Chapter 2 to evaluate fine-scale spatial and temporal avoidance of lions by their smaller guild members, controlling for habitat preferences and localized prey distributions. I evaluate fine-scale spatial patterns aggregated through time (three years) and temporal patterns in the 72 hours following predator/prey sightings.

Although subordinate interference competitors are expected to seek out “competition refuges” by selecting marginal habitats, neither hyenas nor cheetahs avoid areas frequented by lions. In fact, hyenas and cheetahs are positively associated with lions except in areas with exceptionally high lion use. Instead, hyenas appeared to actively track lions, while cheetahs actively avoided lions on a moment-to-moment basis. These contrasting patterns suggest that hyenas and cheetahs are able to utilize alternative strategies that minimize the need for long-term spatial avoidance.

Table 1: Overview of study species

1) Schaller 1976, 2) Kruuk 1972, 3) Watts & Holekamp 2010, 4) Caro 1994, 5) Laurenson 1994, 6) Durant 1998, 7) Chauvenet 2011, 8) Creel & Creel 2002, 9) Vanak et al. 2013, 10) Creel & Creel 1996.

Species	Size (kg)	Sociality	Hunting strategies	Denning behavior	Aggression by lions	Responses
Lion	120-240 ¹	2-9 adult females	Ambush predators; require cover ¹	Hide cubs in dense vegetation ¹		
Hyena	45-90 ²	~50 m/f/cubs	Cursorial; run long distances ²	Use holes in higher ground ²	Steal food and kill. At high densities, can reduce hyena reproductive success ³	No documented avoidance; reciprocally aggressive in large groups ²
Cheetah	25-40 ⁴	Solitary ⁴	More cursorial, though benefit from moderate cover to approach prey ⁴	Hide cubs in dense vegetation ⁴	Steal food, kill >50% of cheetah cubs ⁵	Active avoidance ⁶ ; widely believed to be suppressed by lions ⁷
Wild dogs	18-28 ⁸	2-27 adults and young ⁸	Cursorial; run long distances ⁸	Use holes in thick vegetation ⁸	Steal food and kill ⁸	Active avoidance ⁹ , large-scale displacement ⁹ , pop. Suppression ⁰¹

CHAPTER 1

Cheetahs and wild dogs show contrasting patterns of suppression by lions

with Tim Caro, Harriet Davies-Mostert, Michael G. L. Mills, David W. Macdonald, Markus Borner, Emmanuel Masenga, & Craig Packer

Introduction

Top predators can dramatically affect population sizes of smaller guild members (mesopredators). Mesopredator suppression has been documented in over 60 studies worldwide, in taxa ranging from fish to birds to large mammalian carnivores, and can play a significant role in structuring the larger ecological community (Soulé *et al.* 1988; Crooks & Soulé 1999; Sergio & Hiraldo 2008; Ritchie & Johnson 2009; Prugh *et al.* 2009; Wallach *et al.* 2010; Estes *et al.* 2011). Meta-analyses indicate that top predators have disproportionate effects on their smaller guild members such that a change in top predator abundance results, on average, in a ~4-fold change in abundance of mesopredators, even in cases with minimal diet overlap (Ritchie & Johnson 2009).

Mesopredator suppression appears to be mediated primarily through *interference competition* (*sensu* Schoener 1983) which involves (a) direct aggressive interactions (Palomares & Caro 1999; Sergio & Hiraldo 2008; Prugh *et al.* 2009) and (b) behavioral avoidance by mesopredators to minimize risks of encountering top predators (Cresswell 2008; Creel & Christianson 2008). Direct aggression such as harassment and kleptoparasitism can be substantial, and top predators are often responsible for >50% of mesopredator mortality (e.g. gray wolves on coyotes, (Thurber *et al.* 1992); coyotes on swift foxes (Kamler *et al.* 2003a, Kamler *et al.* 2003b); and dingoes on red foxes (Moseby *et al.* 2012)), but unlike traditional intraguild-predation systems (*sensu* Holt & Polis 1997), top predators rarely consume their mesopredator victims.

The threat of direct aggression can further create a ‘landscape of fear’ (Laundré *et al.* 2001) that excludes mesopredators from large portions of suitable habitat. For instance, coyotes

concentrate primarily at boundaries between wolf-pack territories (Fuller & Keith 1981), and swift and red foxes are located almost completely in gaps between coyote territories (Voigt & Earle 1983; Kamler *et al.* 2003a; see also Tannerfeldt, Elmhagen & Angerbjörn 2002; Kamler, Stenkewitz & Macdonald 2013). By restricting their activity to safe areas, mesopredators may lose vital access to prey, water, or shelter, resulting in severe demographic consequences (Creel & Christianson 2008; Cresswell 2008; Sergio & Hiraldo 2008).

Anthropogenic-induced losses of top predators and associated cascading effects have highlighted an urgent need to understand the dynamics of predator-predator coexistence (Estes *et al.* 2011). While spatiotemporal partitioning (Case & Gilpin 1974; Carothers & Jaksic 1984) and active avoidance (e.g. Durant 2000; Webster, McNutt & McComb 2012) play a prominent role in reducing the frequency of direct aggression, coexistence outcomes may also depend on habitat structure (Finke & Denno 2006; Janssen *et al.* 2007) and ecosystem productivity (Elmhagen & Rushton 2007; Borer, Briggs & Holt 2007).

African lions (120-180 kg) live in fission-fusion social groups (Schaller 1972), and wild dogs (18-28 kg) forage in packs (Creel & Creel 1996), whereas cheetahs (25-40 kg) are mostly solitary (Caro 1994). Lions kill up to 32% of African wild dogs (Van Heerden *et al.* 1995; Woodroffe & Ginsberg 1999) and 57% of cheetah cubs (Laurenson 1994) and occasionally steal food from both species (Schaller 1972; Fanshawe & Fitzgibbon 1993; Caro 1994). Across reserves, wild dog and cheetah densities have both been reported to vary with lion densities (Laurenson 1995; Creel & Creel 1996; Mills & Gorman 1997), and conservationists have advocated focusing wild dog and cheetah conservation in areas with few or no lions (Creel & Creel 1996; Kelly & Durant 2000), even voicing concern that lion-inflicted mortality could drive localized cheetah populations to extinction (Chauvenet *et al.* 2011). However, despite high levels of interspecific aggression by lions and fine-scale avoidance by both wild dogs and cheetahs, it remains unclear how these interactions translate into population-level dynamics.

Spotted hyenas (48-55 kg, Kruuk 1972) also occur in most savanna ecosystems and steal food from wild dogs and cheetahs (Fanshawe & Fitzgibbon 1993; Caro 1994; Creel & Creel 2002). However, hyenas inflict less mortality than lions do: ~5% mortality in wild dogs (Woodroffe & Ginsberg 1999) and ~21% in cheetah cubs (Laurenson 1994), and playback experiments indicate that both wild dogs and cheetahs perceive hyenas as lesser threats than lions (Durant 2000; Webster *et al.* 2012).

In this study, we test whether African lions (*Panthera leo*), suppress populations of cheetahs (*Acinonyx jubatus*) and African wild dogs (*Lycaon pictus*), and we examine possible

mechanisms for coexistence between these species. To assess the possibility of competitive exclusion by African lions, we first compare joint population dynamics of lions, cheetahs, and African wild dogs using > 30 years of data on population sizes in Serengeti National Park. Because hyena data were insufficient to include in the joint population analysis; we can only address their potential effects in cheetah/wild dog suppression qualitatively. We then explore the role of spatiotemporal partitioning as a possible mechanism for lion-cheetah-wild dog coexistence in the Serengeti using concurrent radio-telemetry data. Finally, we examine population data from fenced game reserves in southern Africa to test whether patterns observed in Serengeti hold across other African ecosystems.

Methods

Data Collection

Study System: The 2,200 km² study area is located in the center of Serengeti National Park, at the intersection of open plains and savanna woodlands. Soils and rainfall follow a gradient from the wetter northwest woodlands to the drier southeast short-grass plains (Sinclair 1995). The ecosystem is dominated by the annual migration of the combined 1.6 million wildebeest and zebra that follow the seasonal rainfall onto the nutrient-rich plains (Holdo, Holt & Fryxell 2009).

Population Numbers & Ranging: Lion, cheetah, and wild dog populations and ranging patterns have been monitored by three separate long-term research projects in overlapping study areas in the southeastern Serengeti National Park (Figure 1). Population data for cheetahs are taken from Chauvenet *et al.* (2011) and reflect continuous monitoring by the Serengeti Cheetah Project from 1980 – 2011. Wild dog numbers are taken from Burrows (1995) from 1970 until their disappearance within the joint study area in 1992. Wild dogs continued to reside in the greater Serengeti ecosystem over the following decade (Maddox 2003), but formal monitoring was only resumed in 2005 (by EM). The Serengeti Lion Project has monitored lions continuously in the joint study area since 1966 (Packer *et al.* 2005), with the exception of 1969-1974. All three species are individually identifiable by natural markings (pelage patterns in cheetahs and wild dogs; “whisker spot” patterns in lions), allowing for precise measurements of population size. Prey population data are taken from aerial surveys conducted by the Tanzania Wildlife Research Institute (Serengeti GIS and Data Centre 2007).

All three species were concurrently monitored via radio-telemetry from 1985-1990. The lion project has radio-tracked 1-2 females in every pride in the joint study area since 1984,

providing the necessary coverage necessary for mapping lion densities across the region. Twenty-two female cheetahs were radio-collared by TC between 1985 and 1990. Ten wild dog packs were radio-collared by MB from 1985 to 1990. Since 2009, EM has monitored eight wild dog packs (~130 individuals); two of these packs were radio-collared from 2007 to 2009. Existing GIS data on habitat type were taken from the Serengeti Mara Data Library (Serengeti GIS and Data Center 2007).

Data Analysis

Joint Population Dynamics: We used generalized least-square models fitted by maximum-likelihood estimation (Package *nlme*, function *gls*, Pinheiro, Bates & Sarker 2012) to compare lion population sizes to 27 years of wild dog numbers and 29 years of cheetah numbers. We used square-root transformations (as per Zuur *et al.* 2009) to normalize the response variables and applied autoregressive correlation structures ($\text{corAR1}[\text{form} = \sim\text{Years}]$) to control for temporal autocorrelation. We chose an autoregressive structure to reflect the biology of the system; qualitatively similar results were produced by alternative autocorrelation structures (corARMA). We also compared the effect of lion numbers on annual percent change in wild dog and cheetah populations, running regressions (*gls*, incorporating autoregressive correlation structure as indicated by examining autocorrelation functions) with and without an intraspecific term to control for any density dependence (e.g. $\% \text{ change cheetah}_{(\text{time } t \text{ to } t+1)} \sim \text{lion}_{(\text{time } t)}$ as well as $\% \text{ change cheetah}_{(\text{time } t \text{ to } t+1)} \sim \text{lion}_{(\text{time } t)} + \text{cheetah}_{(\text{time } t)}$). We incorporated prey availability into these models based on population totals for preferred prey of cheetahs (Thomson's gazelle, Caro 1994) and wild dogs (Thomson's gazelle plus wildebeest, Schaller 1972). Because of the limited availability of joint annual predator-prey data (eight years for cheetah, four years for wild dogs), we performed separate statistical analyses with and without prey numbers. We also interpolated prey population estimates between surveys that occurred 1-4-years apart (Package *timeSeries*, Function *interpNA*, Wuertz & Chalabi 2013).

Home Range and Density Calculations: We calculated habitat-use patterns from 1985–1990, when lions, cheetahs, and wild dogs were simultaneously radio-collared ($n_{\text{lion}} = 3,328$ independent locations; $n_{\text{cheetah}} = 996$; $n_{\text{dog}} = 73$). All analyses were limited to sightings (located via radio-telemetry) within the regularly monitored study area for all three species.

Because territories shift seasonally but are relatively stable across years, we analyzed data separately for wet and dry seasons. We mapped lion core areas by first calculating pride-

specific kernel utilization distributions from daily radio-collar locations of females (fixed kernel, Program R, package *adehabitat*, Calenge 2006). We selected the 75 Percent Volume Contour (PVC) as the territory boundary (as per Mosser *et al.* 2009). To calculate long-term lion density, we divided the total number of lions per pride by the area of the territory (75PVC) to calculate lions per 1-km². We then mapped these density-values onto a raster layer of 1-km x 1-km grid cells. Densities were summed in grid cells where territories overlapped.

To evaluate cheetah and wild dog ranging with respect to the long-term risk of encountering a lion, we conducted a bootstrapping analysis comparing the mean lion density of n independent cheetah and wild dog sightings to the mean lion density of 1,000 iterations of n simulated points. Points were generated as random locations within the study using Package *splancs*, function *csr* (Rowlingson & Diggle 2013). We compared the actual mean lion density to the distribution of 1,000 simulated means and calculated significance using a 2-tailed Fisher's exact test. We further calculated the average lion density at the location of each cheetah sighting and compared these values across cheetah reproductive states (e.g., denning females (cubs 0-2 mos), females with mobile cubs (>2 mos), and females without cubs), testing for significance with a Wilcoxon rank-sum test.

Cross-Reserve Comparison: HDM, DWM, and MGM collected annual population counts of all individuals to calculate densities of reintroduced African wild dogs and lions at four fenced reserves in South Africa (6-10 years at each reserve, see Figure S1). Densities for the first year following each reintroduction were excluded to reduce artifacts of management approaches (see (Davies-Mostert 2010)). We used a linear mixed model (function *lmer*) to evaluate log-transformed wild dog densities against concurrent lion densities and reserve size, implementing an autoregressive correlation structure (`corAR1[form = ~Years]`) and random effects for *Reserve* to control for repeated measurements within each reserve.

Lion and cheetah densities were extracted from published data in 38 fenced reserves in South Africa (Table A1-1, see Lindsey *et al.* 2011 for management practices). We calculated prey biomass for eight reserves using species-specific prey densities (given in Lindsey *et al.* 2011) and average male weight per species (taken from Estes 1991). We used linear regression (function *lm*) within a backwards-stepwise selection framework to compare log-transformed cheetah densities as a function of reserve size, prey biomass, and log-transformed lion density (where lions were present). We separately evaluated the effect of lion presence/absence on cheetah density, controlling for reserve size (function *lm*). Because so few reserves had values for prey

biomass, we first compared models without considering biomass, and then ran models on only those reserves with biomass values.

Results

Population Dynamics

The Serengeti lion population increased threefold over the last 30 years (Figure 2a). African wild dogs disappeared from the Serengeti study area over the same period, despite considerable increases in wildebeest and overall prey biomass (Figs. 2a and b). In contrast, the Serengeti cheetah population remained stable, matching a relatively stable prey base of Thomson's gazelle (Figure 2b). Time series analysis shows a substantial decline in African wild dogs as lion numbers increased (Figure 2c), reflecting a decline in total number of packs as opposed to decreasing pack sizes. Mean total pack size during the years of decline (9.28 +/- 1.17, 1986-1990) did not vary significantly from pre-decline levels (9.8 individuals, 1967-1978 (Frame *et al.* 1979)) or from pack-sizes recorded after monitoring was resumed in 2005 (10.1 +/- 1.40 individuals). Wild dog numbers were lower in years of high lions ($n = 23$, $p = <0.0001$), and were lower after a one-year time lag of high lion populations ($n = 22$, $p = 0.0012$). In contrast, cheetah populations were not related to lion populations in concurrent years ($n = 29$, $p = 0.1983$) or after a one-year time lag ($n = 29$, $p = 0.6336$). Per capita population growth rates for wild dogs and cheetahs were not correlated with lion population size in univariate regressions ($p = 0.8746$ and $p = 0.3248$, respectively) or when controlling for density dependence in wild dog or cheetah numbers ($p = 0.7246$ and $p = 0.3138$, respectively). Prey density (both the subset of years with raw data and the subset of years with interpolated data) was not a significant term in any analysis of growth rate or population size, nor did including prey density change the relationship between lion and cheetah or wild dog numbers [See Table A1-2 for detailed model output]. Note that though wild dogs disappeared from the joint study area in 1992, they continued to reside elsewhere in the greater Serengeti ecosystem (Maddox 2003), and the population just outside the park boundary is known to have remained stable since at least 2005 (EM unpublished data). However, recent monitoring by EM confirms that wild dogs have failed to re-establish ranges within the joint study area (Figure 3).

Space Use

Figure 4 shows cheetah and wild dog locations overlaid on lion densities each season. Both lions and cheetahs concentrate in the northwestern woodlands in the dry season, whereas wild dogs are scattered on the fringes of high-lion density areas. During this time, wild dogs occupied areas of *lower* lion density than expected by chance ($p = 0.004$), whereas cheetahs occupied *higher* lion-density areas ($p < 0.0001$, Table 1). In the wet season, lions are more evenly distributed, whereas wild dogs and cheetahs concentrate more on the short grass plains. Wild dog and cheetah ranging was unrelated to lion density in the wet season ($p = 0.202$ wild dogs; $p = 0.942$, cheetahs). Throughout the year, denning female cheetahs experienced higher lion density than those with mobile cubs or no cubs at all, while there was no difference between females with mobile cubs or without cubs (Figure 5).

Cross-Reserve Comparison: Wild dog densities were negatively related to lion density across reserves and through time (Figure 6a, A1-3a). Model comparison (function *anova* with a likelihood ratio test) including reserve size and lion density indicates that lion density alone was the best predictor of wild dog densities. In contrast, cheetah densities were not significantly related to lion densities across South African reserves (Figure 6b, Table A1-3b-c). For the full set of reserves, regression of cheetah density on reserve size and lion presence/density indicates that reserve size alone is the best predictor of cheetah density; model comparison shows no support for models incorporating lion presence ($n = 38$ reserves; $p = 0.221$) or lion density ($n = 25$ reserves; $p = 0.445$) [See Table A1-3 for detailed model output]. In the subset of reserves for which prey biomass has been measured, the sample size was too small to capture statistically significant relationships of cheetah density for any predictors; the null model is the best fit.

Discussion

Our results demonstrate markedly different responses of two mesopredators to the same top predator. Lions appear to have contributed to the disappearance and continued absence of wild dogs from the Serengeti while having no effect on cheetah numbers. Disease also contributed to the decline of wild dogs in the early 1990s (Macdonald 1992; Creel & Creel 2002), but wild dogs never disappeared from the larger Serengeti ecosystem and persisted for the past twenty years. Today, wild dogs occasionally pass through the long-term study area without settling in the same region that they occupied in the 1960s-

1980s, when lion population density was far lower (Figure 3). These results mirror patterns seen in other reserves, where wild dogs strongly avoid areas most actively used by lions (Mills & Gorman 1997; Creel & Creel 2002; Cozzi 2012; Vanak *et al.* 2013).

It is possible that spotted hyenas also contributed to the decline of the Serengeti wild dog population: the hyena population increased from the 1960s to 1977 (Hofer & East 1995) and appears to have remained stable thereafter (Durant *et al.* 2011). Although data on hyena numbers and ranging patterns were insufficient to include in our statistical analysis, any effects of rising hyena numbers are likely to have been minor compared to those of lions: hyena-inflicted mortality is low (4-6%, Woodroffe & Ginsberg 1999), wild dogs do not demonstrate immediate (Webster 2012) or large-scale avoidance (Cozzi 2012) of hyenas, and although wild dogs are vulnerable to energetic losses incurred by scavengers (Gorman *et al.* 1998), dogs rarely relinquish kills to hyenas until they have finished eating (Fanshawe & Fitzgibbon 1993; cf. Carbone *et al.* 2005).

In contrast to the response of wild dogs, the stability of the cheetah population over the same time period indicates that neither high levels of lion-inflicted mortality (see Laurenson 1994) nor behavioral avoidance (see Durant 1998, 2000) inflict sufficient demographic consequences to translate into population-level effects. If cheetahs had been suppressed through a “landscape of fear” and/or systematic persecution by lions, their population size should have declined by as much as 9-12-fold (e.g. 3-4 times the change in lion numbers, as typically observed in the mesopredators reviewed by Ritchie & Johnson 2009). But unlike wild dogs, cheetahs are not displaced from large sections of their landscape. Cheetahs and wild dogs show similar prey preferences, thus they would be expected to show similar spatial distributions if their ranging patterns were driven solely by food-acquisition. However, wild dogs mostly occupied low lion-density areas, whereas cheetahs mostly occupied high lion-density areas in the dry season and ranged independently of lions during the wet season (Figure 4), when cheetahs follow migratory Thomson’s gazelles onto the open grass plains (Durant *et al.* 1988). Similar to results in Figure 4, Broekhuis *et al.* (2013) found that cheetahs are more likely to occur in areas with high long-term risk of encountering a lion, and Vanak *et al.* (2013) demonstrated a high degree of overlap between cheetah and lion home ranges and found that cheetahs sought out prey-rich areas regardless of long-term lion-risk or recent lion presence.

Instead of large-scale displacement, cheetahs may employ fine-scale avoidance strategies that minimize risk of encounters without reducing their access to resources. Cheetahs stay farther away from lions in open habitats than in wooded areas (Broekhuis *et al.* 2013); Vanak *et al.*

(2013) further found that although cheetahs often move towards recent lion sightings, they almost always maintain at least 110 m distance from lions. Divergent life-history strategies may further reduce the likelihood of encounter within high lion-risk areas: as ambush predators, lions prefer habitat with greater cover (Hopcraft, Sinclair & Packer 2005), whereas cheetahs select for open areas (Mills, Broomhall & du Toit 2004; Vanak *et al.* 2013; Broekhuis *et al.* 2013), where they achieve higher hunting success (Mills *et al.* 2004; Bissett & Bernard 2006). Cheetahs, which are primarily solitary, may be able to employ such fine-scale responses more effectively than dogs, which actively roam in large social groups in search of their prey. Ultimately, there is no evidence that active avoidance of lions excludes cheetahs from large areas of preferred habitat, a finding that contrasts the clear patterns of exclusion in wild dogs in several ecosystems across Africa.

Our cross-reserve analysis further supports the contrasting pattern of lion-cheetah-wild dog coexistence observed in the Serengeti. Wild dogs exist at lower densities in reserves with higher densities of lions, as well as in years with more lions. In contrast, lions have no significant effect on cheetah density across South African protected areas. Instead, cheetah population densities vary inversely with reserve size either because a relatively consistent number of re-introduced animals were subsequently confined to a small area or because the smaller reserves were established in richer habitats. Note that our results contrast with an earlier analysis by Laurenson (1995) who documented a negative relationship between lion and cheetah biomass across nine reserves in east and southern Africa but did not test for effects of reserve size.

Allaying conservation fears: The disappearance of the Serengeti wild dogs in 1992 led to considerable controversy over the role of stress, rabies and veterinary interventions (Macdonald 1992). Burrows, Hofer & East (1994) presumed that the stress from vaccinating wild dogs against rabies rendered them more susceptible to the disease. Little noted at the time, though, was the importance of interspecific interactions and the growing lion population (but see Hanby & Bygott 1979). Figs. 3 & 4 illustrate the first analysis on the spatial distribution of the Serengeti wild dogs during the years preceding their disappearance, and it is clear that the dogs were already restricted to areas that were largely unoccupied by lions. With the further growth of the lion population and the continued absence of wild dogs from the lion study area despite the successful control of rabies in Serengeti by 2005 (Hampson *et al.* 2009), the “stressful handling” hypothesis now seems highly unlikely. The long-term data from the Serengeti combined with similar patterns across the rest of Africa suggest instead that wild dogs fare poorly in areas with high lion density.

Our results also challenge a widespread perception that lions suppress cheetah populations and undermine cheetah conservation efforts (e.g. Chauvenet *et al.* 2011). Laurenson (1995) and others (e.g. Caro & Laurenson 1994; Chauvenet *et al.* 2011) attributed presumed cheetah suppression to high levels of lion-inflicted mortality on cheetah cubs (ranging from 24% actually witnessed to 57% inferred, Laurenson 1994, but see Mills & Mills 2013). Indeed, with <5% of cheetah cubs reaching independence in the Serengeti, lion-inflicted cub mortality would appear to limit cheetah population growth. Yet existing data are inconsistent; litter sizes were lower in years of higher lion density (Laurenson 1995, Kelly *et al.* 1998), but lion numbers did not affect total cub production or adult cheetah numbers (Kelly *et al.* 1998). Thus although lions may kill large numbers of cheetah cubs, lion predation may be compensatory with sources of mortality such as starvation, disease, abandonment, or predation by other smaller, less conspicuous carnivores (as described in Mills and Mills, 2013). Further, if cheetah populations are saturated, lions may only be killing cubs that would otherwise disperse from the system, as in the case of swift foxes during coyote removal experiments in southeastern Colorado (Karki, Gese & Klavetter 2007).

In addition, denning female cheetahs occupy areas of high lion density (Fig. 5), and lactating females spend more time than non-lactating females in patches of high lion density (Durant 1998), presumably because den sites are situated in areas that provide shade, water, and cover for small cubs of both species (cheetahs: Laurenson 1993; lions: Mosser *et al.* 2009). Lions occupy these high quality denning areas even at low population sizes (Mosser *et al.* 2009), thus cheetah cub mortality rates may be relatively insensitive to changes in lion numbers. Alternatively, cheetah population dynamics may not be especially sensitive to cub mortality (Crooks, Sanjayan & Doak 1998; cf. Kelly & Durant 2000), because female cheetahs quickly reproduce after losing litters (returning to estrus within ~ 2 weeks, Laurenson 1992).

Finally, immigration into the Serengeti plains may insulate cheetah dynamics against lions. The Serengeti study area is known to be an open system for both lions (Pusey & Packer 1987; Mosser *et al.* 2009) and cheetahs (Kelly & Durant 2000; Durant *et al.* 2004), which may render local interactions irrelevant in determining (cheetah) population size (e.g. Chesson 2000). Nonetheless, our analysis across the fenced South African reserves suggests that lions and cheetahs are able to coexist in the complete absence of immigration.

Conclusion: While lions have apparently contributed to the local extinction and continued absence of wild dogs, cheetahs are able to coexist with lions in the Serengeti and across South

African reserves. These findings challenge a basic tenet of cheetah conservation: that cheetahs require areas with few or no lions to survive (e.g. Kelly & Durant 2000). Such concerns about lion-cheetah coexistence may even lead to inappropriate cheetah conservation efforts, for example, by focusing too much effort on cheetah populations in lion-free ecosystems. Further investigation and longitudinal analyses in other systems might reveal additional ecological drivers that better inform cheetah conservation actions.

More generally, our study highlights a possible mechanism mitigating mesopredator suppression. Numerous studies across a wide array of vertebrates indicate that the disproportionate effect of top predators on their smaller competitors may derive not from direct killing, but by triggering costly behavioral avoidance responses (Salo *et al.* 2008; Kamler *et al.* 2013) such as large-scale displacement from large areas of preferred habitat (e.g. Kamler *et al.* 2003a; Shirley *et al.* 2009). As we find no evidence of large-scale cheetah displacement, the fine-scale avoidance found by Durant (1998), Vanak *et al.* (2013), and Broekhuis *et al.* (2013) may facilitate coexistence by minimizing large-scale displacement and associated habitat loss.

The precise mechanism of mesopredator suppression (behavioral avoidance vs. direct killing) will often have implications for wildlife management (Ritchie *et al.* 2012). For example, dingo control programs not only increased feral cat abundance in Australian rangelands, but also allowed feral cats to increase their activities in areas or at times of day that they had previously avoided (Brook, Johnson & Ritchie 2012). Similarly, in the absence of jackals, cape foxes expand their diurnal activity and select den sites that are more broadly distributed across the landscape (Kamler *et al.* 2013). These behavioral shifts can have unexpected and cascading consequences throughout the ecosystem (Wallach *et al.* 2010; Ritchie *et al.* 2012).

Experimental studies of invertebrate systems have found that habitat structure facilitates mesopredator coexistence by reducing rates of aggressive encounters between competing species (Finke & Denno 2002; Janssen *et al.* 2007). Similarly, the reduced visibility of miombo woodlands can reduce rates of lion-inflicted mortality on cheetahs (Mills & Mills 2013) and lion klepto-parasitism on wild dogs and cheetahs (Creel, Spong & Creel 2001; Bissett & Bernard 2006). Wild dogs manage to coexist with lions in many wooded ecosystems (e.g., Selous, Creel & Creel 2002; Kruger, Mills & Gorman 1997), thus, future research should focus on the interaction between habitat characteristics and multi-scale avoidance behavior to better predict patterns of mesopredator coexistence.

Tables and Figures

Table 1-1: Lion, cheetah, and wild dog ranging patterns – results from bootstrapping analysis

Results from bootstrapping analysis evaluating cheetah and wild dog ranging patterns with respect to lion densities. N reflects total number of independent radio-telemetry sightings of each species. Avg. lion density (*Actual*) reflects mean lion density (lions/km²) at the location of each sighting. Avg. lion density (*Simulated*) reflects the lion density averaged across 1,000 iterations of *n* randomly generated points. P was calculated using a two-tailed Fisher's exact test as $2 \times$ the number of simulated means above or below actual mean lion density.

Dry Season

	N	Avg. Lion Density		P
		Actual	Simulated	
Cheetahs	460	0.030	0.021	< 0.0001
Wild dogs	39	0.016	0.021	0.004

Wet Season

	N	Avg. Lion Density		P
		Actual	Simulated	
Cheetahs	536	0.021	0.020	0.942
Wild dogs	34	0.010	0.020	0.202

Figure 1-1: Study area

Joint lion, cheetah, and wild dog study area, and surrounding protected areas. Darker shading indicates areas of increased tree cover.

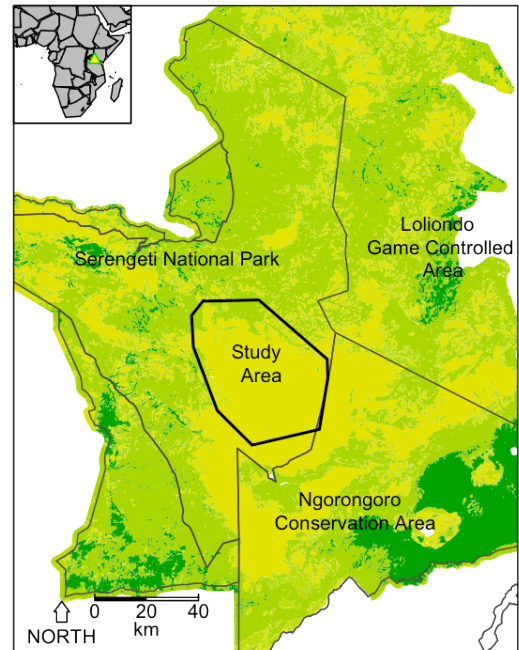


Figure 1-2: Predator and prey population trends

(A) Lion, cheetah, and wild dog numbers in the 2,200km² overlapping study area as reported by (1) Serengeti Lion Project (this study), (2) Chauvenet *et al.* (2011), and (3) Burrows (1995) and E. Masenga (this study). (B) Wildebeest and Thomson gazelle numbers in the study area (Serengeti GIS and Data Centre). (C) Cheetah and (D) wild dog populations plotted against lion populations each year. Regression lines are plotted for significant relationships from the univariate *gls* models.

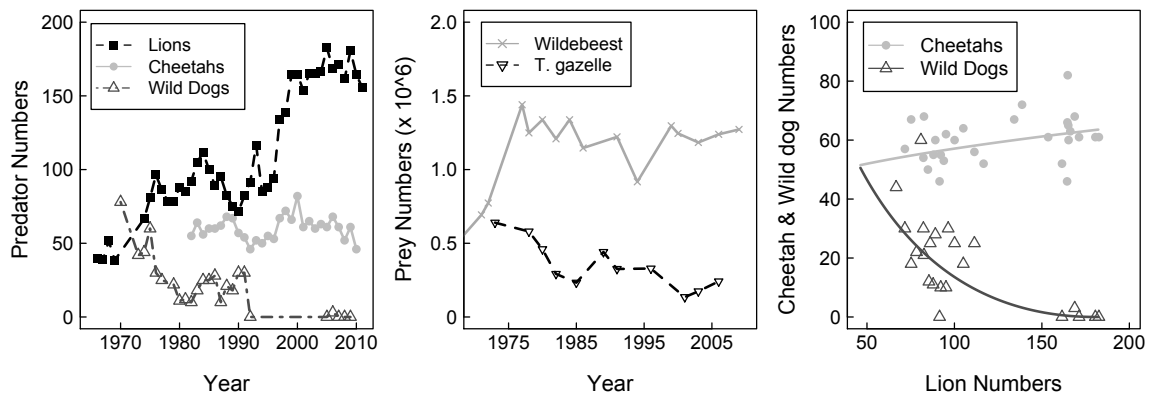


Figure 1-3: Comparison of wild dog ranging from a) 1985-1990 to b) 2005-2010

Joint lion, cheetah, and wild dog study area denoted by central polygon; black lines indicate the boundaries of Serengeti National Park and surrounding protected areas. A) Average lion densities (background shading) and all wild dog radio-telemetry locations (black triangles) collected from 1985-1990. B) Current average lion densities and all sightings (both opportunistic and radio-telemetry) of wild dogs 2005-2009, after they returned to the larger Serengeti ecosystem.

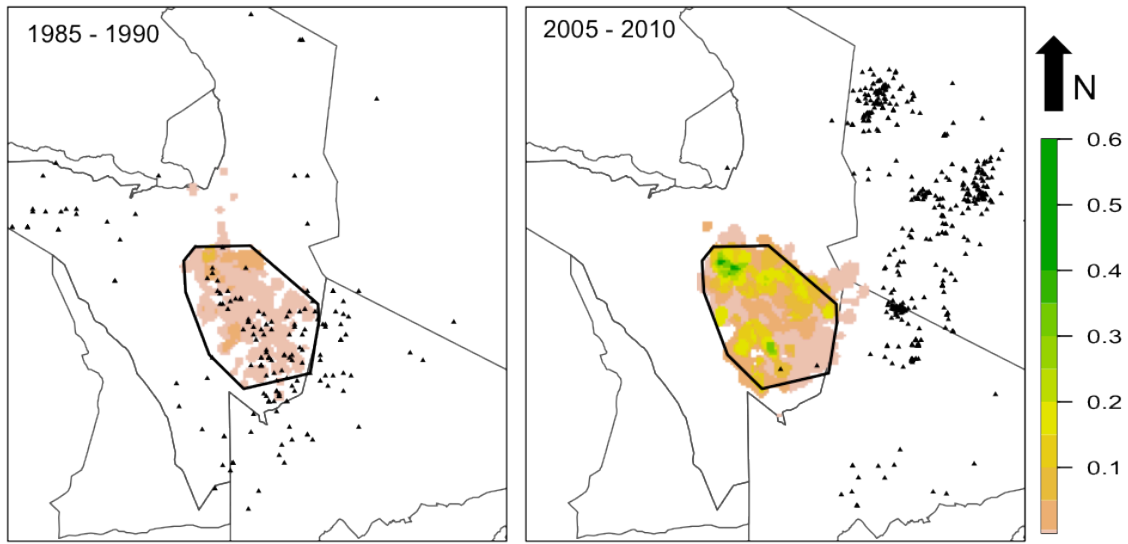


Figure 1-4: Lion, cheetah, and wild dog ranging patterns

Lion densities mapped per km² grid cell, with highest densities shown in green. Cheetah locations shown in brown circles, wild dogs in black triangles. Black line denotes limits of the shared study area.

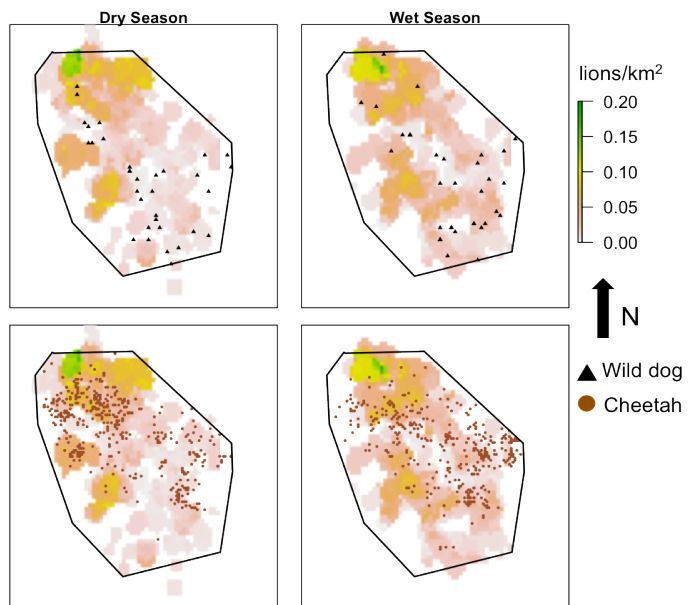


Figure 1-5: Comparison of lion densities experienced by female cheetahs in different reproductive states.

Average lion density per sighting of female cheetahs denning with young cubs (≤ 2 mos), with mobile cubs (> 2 mos), and without cubs. Wilcoxon-Rank Sum tests showed **Denning** females experienced higher lion densities than females with **Mobile cubs** (*dry* $p < 0.0001$, *wet* $p = 0.03$) and **No cubs** (*dry* $p = 0.0002$, *wet* $p = 0.03$). Females with mobile cubs were not significantly different than those without cubs in either wet or dry seasons ($p = 0.591$ and $p = 0.529$, respectively).

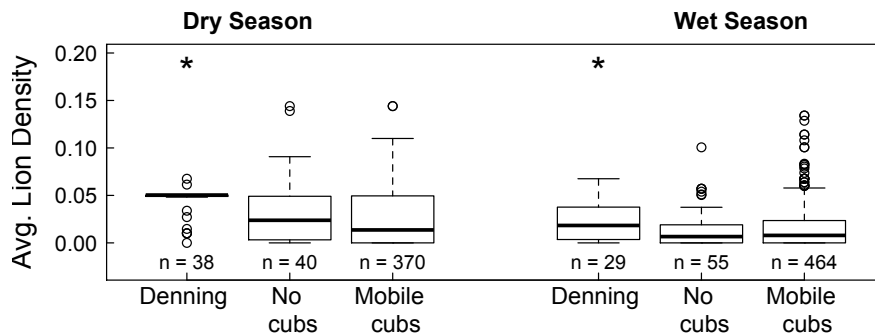
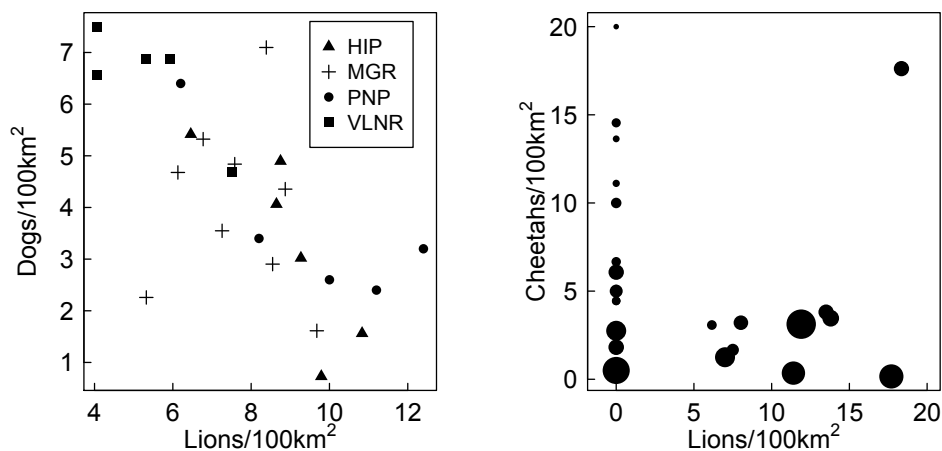


Figure 1-6: Lion, cheetah, and wild dog densities across reserves

(A) Wild dog densities vs. lion densities from Hluhluwe-iMfolozi Park (HIP), Madikwe Game Reserve (MGR), Pilanesberg National Park (PNP), and Venetia Limpopo Nature Reserve (VLNR). (B) Cheetah densities vs. lion densities in 25 reserves (see Table A1-1); circles are proportional to the size of the reserve. All statistics are presented in Table A1-3.



CHAPTER 2

Snapshot Serengeti: A case study in camera traps and citizen science for multi-species monitoring

Introduction

Exploring the dynamics of savanna ecosystems requires monitoring multiple species across large spatial scales for extended periods of time. Because large-bodied species can range over hundreds or even thousands of square kilometers, however, direct monitoring is impractical, and there is a clear need for large-scale, non-invasive, multi-species survey techniques (Zielinski & Kucera 1995; Long *et al.* 2008; O'Connell, Nichols & Karanth 2011). Over the last 20 years, camera traps have emerged as a key tool in the broader disciplines of behavioral, population, and community ecology (O'Connell *et al.* 2011). Historically, cameras have been used to document the presence of rare species in understudied protected areas (e.g. SurrIDGE *et al.* 1999; Holden, Yanuar & Martyr 2003) or to estimate densities of individually identifiable animals (e.g. Karanth 1995). But advances in digital technology have increased capacity while lowering prices, resulting in a dramatic increase in the number and diversity of camera trap studies (Rowcliffe *et al.* 2008) to the extent that they can now provide important insights into the interconnections between multiple trophic levels in complex ecosystems.

Camera traps have been used to evaluate temporal patterns of activity in elusive species (Azlan & Sharma 2006; Dillon & Kelly 2007) and temporal partitioning within guilds of carnivores (Fedriani *et al.* 2000; Wachter & Attum 2005; Bischof *et al.* 2014), herbivores (Rivero, Rumiz & Taber 2005), and between predators and their prey (Weckel, Giuliano & Silver 2006). Inventories that assess species presence and species richness across different protected areas have informed regional species distribution maps and can help track systematic declines in mammalian biodiversity (O'Brien *et al.* 2010). Traditional analytical techniques require individually identifiable animals (e.g. Karanth 1995) or complex hierarchical approaches to control for imperfect detection (Royle & Nichols 2003; MacKenzie *et al.* 2006; Kéry 2010), and increasingly complex analytical approaches are now being used to infer spatially explicit species abundances (Chandler & Royle 2013) and species movements (Pederson & Weng 2013).

However, as the number and scope of camera trapping surveys increase, so does the need for

simple, widely accessible analytical tools that allow rapid interpretation of camera trap data (Kelly 2008). For example, Rowcliffe *et al.* (2008) incorporate a simple underlying movement model to provide improved density estimates of unmarked individuals (but see Foster & Harmsen 2012). Raw capture rates (the number of photographs per unit time) have been used as a relative abundance index for different species (e.g. Carbone *et al.* 2001; O'Brien, Kinnaird & Wibisono 2003; O'Brien 2011). While these indices may be vulnerable to bias in species-specific differences in detection probability (Tobler *et al.* 2008; Foster & Harmsen 2012; Sollmann *et al.* 2013a), raw capture rates appear to correlate with actual densities (O'Brien *et al.* 2003; Kelly 2008; Rovero & Marshall 2009), although such validations are still rare (Kelly 2008).

Previous camera-trap surveys have been mostly deployed at small spatial scales or for short periods of time. Even at these scales, managing and processing the resultant images can be prohibitively labor-intensive. Larger-scale camera surveys can produce millions of images each year along with significant amounts of ancillary metadata. There are currently no repositories or data warehouses to help store, process, or disseminate camera-trapping data (O'Brien *et al.* 2010; Harris *et al.* 2010) and no standard procedures to accurately, rapidly and efficiently extract information from camera trap images (Harris *et al.* 2010).

Citizen science – the participation of volunteers in authentic scientific research – holds enormous potential to process these overwhelming numbers of images. At the same time, citizen science engages the broader public in scientific research (Newman *et al.* 2012). The integration of emerging data collection technologies and citizen science can expand the scope and scale of ecological research.

We report here on a study that has employed >200 cameras to continuously monitor 1,125 km² of the Serengeti National Park, Tanzania over three years. Operating day and night across a systematic grid, the cameras have produced hundreds of thousands of photographs of more than 47 different wildlife species. Long-term monitoring of herbivores and African lions allow calibration of camera trapping data against known densities and distributions. Our work thus provides a case study in using large-scale camera surveys for intensive, multi-species monitoring. In this paper we describe: **(1)** the design and implementation of a large-scale camera survey, **(2)** the use of citizen science to rapidly and accurately process large volumes of imagery, and **(3)** preliminary analyses of novel applications of camera trap data.

Methods

Field Survey

Study System

The 1,125 km² camera survey area covers the intersection of open plains and savanna woodlands at the center of Serengeti National Park (Figure 1a). Rainfall follows a gradient from the wetter northwest woodlands to the drier southeast short-grass plains. The ecosystem is dominated by the annual migration of the combined 1.6 million wildebeest and zebra that follow the seasonal rainfall onto the nutrient-rich plains (Holdo *et al.* 2009). Since the 1960's, the Serengeti Lion Project has monitored lion population numbers and ranging patterns (Packer *et al.* 2011), and the Serengeti Research Institute has monitored major herbivores numbers via flight counts and aerial photography (Sinclair & Norton-Griffiths 1979; Sinclair *et al.* 2008; TAWIRI 2008, 2010; Strauss & Packer 2013).

We ran an initial camera survey at 200 sites within the long-term Serengeti Lion Project study area from June to November 2010. Cameras were re-installed in February 2011 and have operated continuously thereafter. The survey was expanded from 200 to 225 traps in February 2012 and is currently ongoing. This paper includes data collected until May 2013.

Layout

The cameras were established on a grid layout with each camera at the center of a 5-km² grid cell (Figure 1b). Although designed for density estimation of elusive carnivores via mark-recapture analyses (e.g. Karanth 1995), grid layouts offer systematic coverage of the entire study area and allow simultaneous surveys of multiple species (O'Brien *et al.* 2010). The 5-km² grid design balances between the goals of maximizing the total area covered and ensuring placement of at least two cameras per home range for selected species of large carnivore and ungulate: leopards have the smallest home range of the primary species in this survey (15-30 km², Bailey 1993; Mizutani & Jewell 1998).

The actual location of each camera was selected as the nearest suitable tree to the pre-determined center point of each grid cell, and was typically within 250 m of the center. Sites were selected to minimize camera misfires by prioritizing trees that offered shade and by avoiding trees surrounded by tall grass. Where no trees were available within 1 km of the grid cell center point, cameras were placed on metal poles (Figure 2). This layout ensured at least 1 km between all cameras, minimizing the likelihood that the same individual would be captured by multiple

camera traps on a single day.

Sites

Cameras were set ~50 cm above ground level so as to capture medium to large vertebrates. Beginning in 2011, cameras were placed inside steel cases to protect against animal damage. Cases were attached to trees using 10 cm hardened-steel lag bolts. Beginning 2012, 5-cm nails were welded to the outside of each case with sharp ends outward to further discourage animal damage. Tall grass was trimmed to <30 cm using hand trimmers or string trimmers; hanging branches were trimmed to minimize risk of camera misfires and improve the view of the camera lens.

Site Metadata

After installation, every camera trap site was photographed, and landscape photos were taken in all four cardinal directions to provide a record of the local habitat. Categorical data on tree density, grass height and shade availability were estimated visually, and the average distance to the nearest 10 trees was measured with a Bushnell rangefinder to evaluate tree isolation; trees outside the estimable range of the rangefinder were assigned a value of 1,500 meters.

Hardware

We primarily used Scoutguard (SG565) incandescent cameras. We initiated the survey using DLC Covert II cameras with an infrared flash, but poor night-image quality prompted the transition to incandescent cameras. Cameras deployed in 2011 involved a mixture of the DLC Covert Reveal and SG565. Since 2012, all deployed cameras and replacements have been SG565. Approximately 15% of cameras have been lost annually to animal damage or weather and required replacement.

Camera Settings

All survey cameras used passive infrared sensors that were triggered by a combination of heat and motion. Although standard camera-trapping protocols recommend setting sensitivity to 'high' for warm climates, this produced unacceptable levels of misfires by the movements of tall grass or shadows, thus sensor sensitivity was set to 'low' to minimize misfires.

All cameras were set to take 3 photos per trigger in the daytime. At night, infrared-flash cameras were set to take 3 photos per trigger and incandescent-flash cameras were limited to 1

image per trigger. We refer to each trigger as a “capture event,” containing 1-3 images; capture events are the units of analysis in the survey, and we use the term interchangeably with “photos.” Cameras were set to ensure at least 1-minute delay between triggering events to reduce the chances of a camera being filled to capacity by a single herd of herbivores.

Maintenance

Each camera was checked once every 6-8 weeks. Except in cases of camera malfunction or damage, this schedule was sufficient to replace batteries and SD cards and ensure continuous operation. SD cards were labeled with the Site ID and the date retrieved. Images were reviewed in the field to ensure that the camera had functioned properly. New SD cards were installed, and cameras were triggered to photograph placards that indicated the Site ID, date, and time.

Field data were entered into an Access database that recorded damage to the site, camera trap, or SD card, actions taken/needed (e.g. replacement cameras), and errors in date or time.

Data Management

Photos were uploaded from SD cards to external hard drives at the Serengeti research station. Every 6 months, duplicate hard drives were transported to the University of Minnesota and transferred to the Minnesota Supercomputing Institute's servers. Directory structure reflected the season, site, and card number such that images within the S4/B03/B03_Card2/ directory were taken in season 4 at site B03 and were stored on the second SD card collected that season.

Python scripting language was used to extract date/time from the image files and season, site, and card information from the directory structure. The metadata are stored in a MySQL database.

Common errors that arise from camera malfunction (typically due to animal or weather damage) include: the recording of videos instead of still images, incorrect time-stamps for a proportion of images, and only 1-2 photos per capture event instead of three. We wrote code in Python, MySQL, and R to flag and correct these errors in the metadata.

Data Processing

Image Identification

We partnered with the Citizen Science Alliance to develop *Snapshot Serengeti* (www.snapshotserengeti.org), an online interface where the general public helps process camera trap data. The Citizen Science Alliance (www.citizensciencealliance.org) is an international collaboration of scientists, software developers, and educators who collectively develop, manage,

and utilize internet-based citizen science projects. Projects are housed on the Zooniverse platform (www.zooniverse.org) and have used crowd sourcing to produce >50 peer-reviewed publications in disciplines ranging from astronomy and climate science to ecology and archaeology (see <https://www.zooniverse.org/publications> for a full list).

Platform

Snapshot Serengeti utilizes the Zooniverse's existing Ruby on Rails application *Ouroboros*. Volunteer classifiers interact with a custom-built JavaScript front-end to classify images and results are saved in a MongoDB datastore. Each classification is recorded alongside the time of classification and the identity of the classifier in the form of either a unique identifier assigned by the Zooniverse (for logged in users) or an IP address (for users who have not logged in). *Ouroboros* also allows us to set custom rules for image retirement, as discussed below, and the system can scale rapidly to cope with the demands of a popular site. The interface and images are hosted on Amazon Web Services via Amazon's Simple Storage Service (S3).

Task Flow

Using the *Snapshot Serengeti* interface (Figure 3), volunteers identify species in each capture event, count the number of individuals (exact numbers from one to ten then binned as 11-50 and 51+), classify behavior (as many as are applicable from Standing, Resting, Moving, Eating, Interacting), and indicate the presence/absence of young. The task flow is designed to help guide people with no background knowledge through the process of identifying the animal(s) in question from 47 possible species while still providing a rapid route to classification for more knowledgeable participants. Users can filter potential species matches by morphological characteristics such as horn shape, body shape, color, pattern, and tail shape. Selection of a species from the list provides a description and a set of reference images, and these descriptions can be searched (for example, a user may look for animals whose descriptions mention 'ears'). Alternatively, users may jump straight to selecting from a list of all species. The success of this dual method of species selection acts as a teaching tool; the use of the filters declines as users become more experienced (Figure S1). A "nothing here" button allows users to classify images without any animals present, but an "I don't know" option is not provided.

Snapshot Serengeti includes an online discussion forum where volunteers can solicit help or input from scientists and one another on questions ranging from species-identification

techniques to the biology or behavior of the animals in the images. A link to a discussion page for each image is presented at the end of each classification. The discussion forum (talk.snapshotserengeti.org), blog (blog.snapshotserengeti.org), and Facebook page (www.Facebook.com/snapshotserengeti) are used to increase overall user engagement and retention, which improves individual accuracy over time (Kosmala, unpublished data).

Circulation and Retirement

Each image is circulated to multiple users. Images are retired from circulation when they have met one of the following criteria (see Table 1 & Figure 4 for examples):

- *Blank*: the first 5 classifications are “nothing here”
- *Blank_Consensus*: 10 “nothing here” classifications
- *Consensus*: 10 matching classifications of species or species combination (e.g. 10 identifications of "lion" or 10 identifications of "lion-zebra"); these classifications do not have to be consecutive.
- *Complete*: 25 total classifications (does not require consensus for any single species)

Both the task flow and retirement rules are designed to balance between comprehensiveness, accuracy, and efficiency given that nearly 70% of the photographs do not contain animals, having been triggered by shadows or grass blowing in the wind. To retain public interest, we developed the “blank” rule to remove empty images from circulation as quickly as possible. However, because beta testing indicated that some volunteers used the "nothing here" option as a way to quickly browse photos, we required 10 "nothing here" classifications if the first five were not unanimous. Therefore, if an image was classified by five users as: "nothing here", "nothing here", "nothing here", "other bird", "nothing here", "nothing here", the image would remain in circulation until reaching 10 “nothing here” classifications (the *Blank_Consensus* rule) or meeting one of the other criteria.

Data Reduction

Sending each image to multiple users increases data accuracy, but also produces a large and complex dataset with multiple identifications for each capture event. These multiple answers must be reduced to a single "correct" answer for every capture event before becoming useable for

analysis. Unreduced data include the following fields:

- *CaptureEventID*: a unique identifier for each capture event.
- *ClassificationID*: a unique identifier for each classification event (one user classifying a single capture event). If a single user identifies multiple species within a capture event, they share the same classification ID.
- *UserID*: user name for logged-in users; IP address for non-logged-in users.
- *Species*: species selected from a list of 47 options or left blank for “nothing here”
- *Count*: number of individuals, estimated as 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11-50 or >50.
- *Behavior*: users could select multiple behaviors for each species from Standing, Resting, Moving, Eating, and Interacting.
- *Babies*: binary indicator of whether young were present for each species.

We used a simple plurality algorithm to reduce the data in order to identify species. First, the number of species present in a capture event was calculated from the median number of species identified across all classifications for that capture event. For all capture events with a single species, the species with the most "votes" was assigned as the “correct” answer. For capture events with more than one species present, the two (or more) species with the most “votes” were assigned. Disagreement among answers was characterized by Pielou’s evenness index (Pielou 1966), which could be calculated for non-unanimous, single-species images; higher Pielou scores reflect more disagreement among classifications.

The number of individuals present for each species was taken from the median number reported for that image by all volunteers; binned classifications (11-50 and 51+) were assigned values of 25 and 60, respectively. Behaviors and presence of young were calculated as the percent of classifications reporting each activity or age-class.

Data Validation

Five researchers with extensive wildlife identification experience were asked to classify 4,149 randomly selected capture events containing animals using the *Snapshot Serengeti* interface; 263 images received two expert classifications and 8 images received three, for a total of 4,428 classifications. The experts noted whether any images were especially difficult and were allowed to manually classify images as "impossible," an option not available on the *Snapshot*

Serengeti interface. In cases where experts disagreed with the results of the plurality algorithm or had marked an image as particularly difficult or impossible, AS and CP made the final identification. Citizen-science classifications derived from the plurality algorithm were compared to the expert-classified dataset to assess accuracy of species identifications and counts of individuals. Validations for behavior and presence of young will be presented in a future publication.

Spatiotemporal Data Analysis

Camera trap failure led to non-constant search effort across the study area. Search effort was calculated by creating a daily "activity matrix" for each site across all dates of the survey. Sites were assigned 1 if active or 0 if inactive on that day. Search effort was calculated as the sum of active days at that site for that time period.

We evaluated raw capture rates as the total number of animals recorded across all independent capture events (defined by a 30 minute time-lag between consecutive photographs of the same species). Note that the same individual may be captured across independent capture events. Species-specific counts were calculated as the total number of animals (across all independent capture events) captured per site in a given time period, divided by the total number of camera trap days in that time period. Reduced datasets were processed in R (R Core Team 2013).

We compared capture rates to existing park-wide population estimates for major Serengeti herbivores. Resident herbivores (buffalo, bushbuck, eland, elephant, giraffe, Grant's gazelle, hartebeest, hippopotamus, impala, ostrich, reedbuck, topi, warthog and waterbuck) are monitored by routine wet-season aerial surveys (TAWIRI 2008, 2010) and occasional ground transects (Sinclair 2008, Strauss 2013), and migratory wildebeest, zebra and Thomson's gazelle by aerial photography (Sinclair & Norton-Griffiths, 1979, Sinclair 2008, Hopcraft 2013). We used simple linear regression to evaluate how well capture rates reflected actual population sizes as measured by (a) the most recent population estimates and (b) mean population estimates from all sources since 2003. We did this for all species and for non-migratory species separately.

We also compared the dry season site-specific species counts for two species with known distributions: lions and giraffes. Lions in the camera trap study area have been monitored by VHF telemetry from 1984 to present (Swanson *et al.* 2014); pride ranges are relatively stable across years (Mosser *et al.* 2009) and we used data from 2010-2013 to calculate lion distributions concurrent with the camera survey. Giraffes were monitored from 2009-2012 via regular ground

counts (Strauss 2014). We mapped the relative probability of lion or giraffe occupancy in any 100x100m grid cell (relative to the entire study area) via kernel density estimation conducted on the VHF and ground monitoring locations (package *adehabitatHR*, function *kernelUD*). To control for unequal monitoring across different lion prides, kernels were calculated separately for each pride, weighted by known pride size, and merged across the study area to produce a single probability density map. We extracted and standardized the relative probabilities at each camera location and compared these to the (square-root transformed as per Zuur *et al.* 2009) species-specific camera trap capture rates using simple linear regression. We then compared the residuals from these models to habitat characteristics: tree isolation (distance to the nearest 10 trees), shade (0-4 scale), and distance to nearest river.

To visualize temporal changes in distributions between resident and migratory herbivores, we plotted monthly wildebeest and buffalo distributions and overlaid these on maps of the Normalized Difference Vegetation Index (NDVI, taken from www.landcover.org), which reflects new vegetation growth and plant biomass. NDVI is a major predictor of wildebeest migration patterns (Boone, Thirgood & Hopcraft 2006), and NDVI and other remote sensing data that capture plant biomass, plant growth, and other measures of forage quality, hold significant predictive power for modeling herbivore distributions (Pettorelli *et al.* 2005; Boone *et al.* 2006; Anderson *et al.* 2010). To fill in the gaps left by camera trap failure, sites with at least one operational neighboring camera were assigned the average value of their four nearest neighboring traps for that time period.

Results

From June 2010 to May 2013, the camera survey accumulated 101,315 camera-trap days. Due to camera damage and loss, a random subset of sites was inactive at any period of time (Figure 5). In any given month, an average of 163 cameras were operational, producing an average of 2,063 camera-trap days per month.

Snapshot Serengeti Data Processing & Validation

Since launching in December 2012, 28,040 registered volunteers (and > 90,000 unregistered contributors identified by unique IP addresses) have contributed 10.8 million classifications and processed 1.2 million different capture events. Classifications per week are given in Figure S2. At peak classification rate, *Snapshot Serengeti* processed 98,354 classifications per hour (27 per second).

Of the 4,149 captures viewed by experts, 96.6% of algorithm-derived answers agreed with the expert species classification, though the accuracy rate varied by species (Table 2). Of the 142 images in which the algorithm did not agree with the experts, 21% (n=30) were marked as "impossible" by experts, 29.5% (n=42) reflected cases where the algorithm only identified one of two species identified by experts (for example, only zebra in a capture where both wildebeest and zebra had been present), 3.5% involved cases where the algorithm indicated two species whereas the experts only reported one, and 45.8% (n=65) reflected true errors in which the algorithm converged on the wrong species. The most common mistakes included misidentification of birds (n=11) and incorrectly identifying Grant's gazelles as Thomson's gazelles (n=11). Images for which the algorithm differed from expert IDs had higher levels of disagreement among raw classifications: the mean Pielou score (+/- standard error) was 0.451 (+/- 0.004) for correct answers vs. 0.725 (+/- 0.014) for incorrect answers.

For images where the reduction algorithm accurately captured all or a subset of species present, we compared the species-specific counts reported by the algorithm to expert classifications (n=4,269 species counts). 76.3% of algorithm-derived counts matched expert counts exactly, and 90.65% of algorithm-derived counts were within +/- 1 bin of the expert classification (Table 3). Accuracy varied by number of individuals counted: users were > 97% accurate when counting a single individual or large group (>50 individuals) and least accurate distinguishing between 5-10 individuals.

Multi-species monitoring

Snapshot Serengeti volunteers identified 47 different species, including rare and elusive animals such as aardwolf and zorilla (Table 4). Raw capture rates were significantly related to actual population densities across 17 species of large herbivores (Figure 6), regardless of how actual population densities were calculated (Table 5). Population sizes of the three migratory species (wildebeest, zebra and Thomson's gazelle) are much larger than for resident herbivores, but camera trap estimates remained significant when migratory species were excluded (Table 5).

Daily animal counts (Figure 7) show that resident herbivore abundances remain relatively stable throughout the year (with variance-to-mean ratios of 0.103 for hartebeest and 0.442 for buffalo) but document dramatic shifts in daily capture rates for migratory species (with variance-to-mean ratios of 0.836 T. gazelle, 2.107 zebra, 9.154 wildebeest). Monthly site-specific counts of the most abundant ungulates in 2011 are plotted over concurrent NDVI maps in Figure 8. The annual migration of wildebeest, zebra and gazelle is clearly revealed by the location and number

of individuals recorded at each site, and this pattern is consistent with the migration patterns reported in Boone et al. (2006). Although the resident species also move around within the grid, their distributions fluctuate less widely throughout the year.

Giraffe captures by the camera traps reflected known distributions across the giraffe study area (Figure 9a, $p=0.006$, $\text{adj-}R^2=0.138$, $n=47$ camera-trap sites). However, lion captures did not reflect fine-scale densities (Figure 9b, $p=0.259$, $R^2=0.001$, $n=222$) within this part of the long-term lion study area. Giraffes and lions were typically photographed alone or in small groups and incorporating group size did not change the results. However, habitat characteristics explained a significant portion of the deviation of camera trap captures from known distributions. Tree isolation alone explained 31.4% of the residuals for giraffes (giraffes were less likely to be found at isolated trees), and an interaction between tree isolation and shade explained 21% of the residuals of the difference for lions (lions were *more* likely to be found at isolated trees that provided shade).

Discussion

Accuracy and effectiveness of citizen science data.

Despite ongoing advances in automated image-recognition routines, classifying the highly diverse imagery collected by camera-trap projects remains a uniquely human capability, requiring a large investment of human time to inspect and classify each image. Although ecologists have previously questioned the accuracy of citizen-scientist-processed data (e.g. Gardiner *et al.* 2012), *Snapshot Serengeti* volunteers have accurately classified more than a million images in less than a year. Prior low-accuracy studies relied on only one or two volunteers whose answers were then verified by an expert (Galloway *et al.* 2006; Gardiner *et al.* 2012). In contrast, *Snapshot Serengeti* required 5-25 classifications per photo, and validation against expert IDs showed that aggregated classifications were highly accurate.

The success of *Snapshot Serengeti* likely derives from the following characteristics:

Simplified tasks that balance efficiency and accuracy: We designed *Snapshot Serengeti* carefully, identifying critical primary tasks and limiting secondary tasks so as not to overwhelm potential users. We used system-specific knowledge and beta testing to simplify tasks to meet these goals.

The primary task of *Snapshot Serengeti* is to identify and count each species of animal in every camera trap photograph. Secondary tasks were limited to identifying

broad groups of behavior and the presence of young. We simplified the counting task by asking users to bin the number of individuals counted over 10. We also limited the interface to 47 options by grouping species of lesser interest: rodents, reptiles and small birds. Unlisted species were characterized by high levels of disagreement among volunteers and were often "tagged" in the associated discussion forum, making further investigation by the science team straightforward.

Effective classification guidance: The interface structure and design guides users to the best possible answer. *Snapshot Serengeti* allows users to filter options based on physical characteristics (Figure 3). On average, individual *Snapshot Serengeti* users were 89% accurate in their answers even though they were largely non-experts without formal training and were not required to pass any qualifying tests.

The performance of *Snapshot Serengeti* volunteers suggests that the interface successfully guided non-experts to the correct answer, improving the accuracy of aggregated answers. The *Snapshot Serengeti* discussion forum, in which citizen scientists could communicate with each other and the science team, may have further increased individual accuracy over time.

Many classifications per task: Acquiring many independent classifications per image was critical to ensuring data quality. While individuals were, on average, 89% accurate in their classifications, our simple plurality algorithm combined these classifications to yield consensus classifications with 96.6% accuracy. More sophisticated data-reduction routines might further reduce the 3.4% error rate. Examining the evenness of species classifications revealed the difficulty of each image: incorrect plurality classifications had lower levels of agreement in their individual classifications. Future algorithms could target "difficult" images by incorporating information from previous or subsequent captures, incorporating information about volunteer accuracy on other images, or sending these images to experts for review.

While the inherent appeal of the Serengeti may help maintain a broad volunteer base, charismatic megafauna are not required for a successful citizen science project. Zooniverse has successfully engaged more than a million citizen scientists in a wide array of projects: Zooniverse's seminal project, Galaxy Zoo, received over 50 million classifications in its first year;

since launching in 2013, Zooniverse's Plankton Portal project has received >400,000 classifications, demonstrating that citizen science can be a broadly relevant approach to processing large quantities of ecological data, even in the absence of charismatic megafauna.

Use of camera traps for multi-species monitoring

The concurrent monitoring of several key species in Serengeti National Park provided a valuable opportunity to validate inference from a camera trapping survey against known animal densities and distributions. The results suggest that camera traps hold significant potential as a large-scale, multispecies monitoring tool but may work better for some species than for others.

There has been significant disagreement about the use of raw capture rates to assess the relative abundance of different species within a system or across multiple systems (e.g. Tobler *et al.* 2008; Kelly 2008; Sollmann *et al.* 2013b), but few attempts to validate raw capture rates against known population sizes (Kelly 2008). Our data suggest that although species-specific detection probabilities may limit the scope of inference that can be drawn about actual population numbers, raw capture rates may be a powerful tool for monitoring changes in a system through time.

We note that the camera trapping study area is not a random subsample of the larger Serengeti ecosystem for which populations are estimated. For example, topi are primarily distributed to the north and west of the camera survey, whereas ostrich primarily occupy the open plains to the southeast (TAWIRI 2008, 2010), possibly contributing to their underrepresentation in the camera photos. Similarly, the relative abundance of migratory herbivores to resident herbivores may be underestimated in overall camera trap photos because migratory species only occupy the study area for several months each year.

Nonetheless, raw capture rates strongly reflected major herbivore populations of the larger Serengeti ecosystem (Figure 6), and this relationship did not rely on the influence of superabundant migratory species. Additionally, monthly capture rates (Figs. 7 & 8) clearly reveal the massive wet season increase in migratory herbivore captures each year while resident capture rates remain largely stable, accurately reflecting the annual influx of >1.6 million wildebeest, zebra, and gazelle that sweep through the study area as they follow the rains onto the short-grass plains in the southeast (Sinclair 1995).

For giraffe, comparison of camera-trap captures to known distributions (Figure 9) suggests that camera surveys hold potential for measuring within-site species distributions, which can be integrated with other remotely-sensed data such as NDVI (Figure 8) to yield new insight into the

temporally varying drivers of herbivore distributions and movements. Existing approaches for mapping spatially explicit distributions and resource selection require high-resolution information such as individual identification (e.g. Royle *et al.* 2009; Chandler & Royle 2013) or concurrent GPS or VHF monitoring (e.g. Sollmann *et al.* 2013a p. 201), and although new techniques are being developed (Chandler & Royle 2013), our giraffe analysis provides the first validated map of spatially-explicit within-site distributions for unmarked animals.

However, for lions, comparison of camera traps to known fine-scale densities showed under-detection by cameras in the more densely wooded northwestern corner of the study area and over-detection at isolated trees on the fringes of established lion territories. Tree isolation explained a significant portion of this discrepancy. Lions are heat stressed (West & Packer 2002) and actively seek out shade. In the woodlands, each camera trap is attached to just one of hundreds of possible shade trees in a given grid cell; on the plains, cameras are often located on the only tree or clump of trees in a several km radius. Thus, although lion densities are highest in the woodlands, the probability of a lion passing by the specific tree with a camera trap is relatively low, whereas lions are attracted to the few trees on the savannas, effectively increasing the sampling area of cameras on those trees. For species with such strong biases, more complex methods may be needed to estimate distributions. For example, we have found that accounting for lion movement patterns through REM analysis produces accurate estimates of broad-scale lion densities across the entire woodlands portion of the grid (J.J. Cusack, unpublished data).

Conclusions

Camera traps are becoming an increasingly popular tool for multi species monitoring, but projects have been hindered by the intractability of processing the resultant data and the lack of validated, simple approaches for drawing multi species inference. Our study represents the largest single-site camera trap survey published to date and provides a new approach to camera trapping: the use of a large-scale survey to intensively monitor animal distributions within a broad area through time.

Our preliminary analyses suggest that camera traps may hold significant potential for baseline surveys: the cameras largely reflected known herbivore relative abundances, accurately captured the nature of the migration, and illustrated the general distribution of giraffe. Cameras may provide a less expensive, more sustainable, and higher resolution technique than other approaches, such as aerial surveys or spoor counts (Rovero & Marshall 2009). More complex analytical approaches that explicitly account for detection (e.g. hierarchical models, Royle &

Dorazio 2008; Kéry 2010) would allow more robust density measurements, but even a simple comparison of raw capture rates can provide valuable information about changes through time.

Tables and Figures

Table 2-1: Sample classifications

Sample classifications for captures retired as **A) consensus** (10 matching classifications, see Fig. 4b-c) and **B) complete** (25 total classifications, see Fig. 4d). Each row represents a classification event by a different user.

A.

(Fig. 4b) Subject retired as *Consensus* - 10 matching species identifications

ID	Species	Count	Standing	Resting	Moving	Eating	Interacting	Babies
ASG0010cz5	giraffe	1	N	N	Y	N	N	N
ASG0010cz5	giraffe	1	N	N	Y	N	N	N
ASG0010cz5	giraffe	1	N	N	Y	N	N	N
ASG0010cz5	giraffe	1	N	N	Y	N	N	N
ASG0010cz5	giraffe	1	N	N	Y	N	N	N
ASG0010cz5	giraffe	1	N	N	Y	N	N	N
ASG0010cz5	giraffe	1	N	N	Y	N	N	N
ASG0010cz5	giraffe	1	N	N	Y	N	N	N
ASG0010cz5	giraffe	1	N	N	Y	N	N	N
ASG0010cz5	giraffe	1	Y	N	N	N	N	N

(Fig. 4c) Subject retired as *Consensus* - 10 matching species identifications

ID	Species	Count	Standing	Resting	Moving	Eating	Interacting	Babies
ASG0000009	hyena	1	N	N	Y	N	N	N
ASG0000009	jackal	1	N	N	Y	N	N	N
ASG0000009	hyena	1	N	N	Y	N	N	N
ASG0000009	warthog	1	Y	N	N	N	N	N
ASG0000009	hyena	1	Y	N	N	N	N	N
ASG0000009	hyena	1	N	N	Y	N	N	N
ASG0000009	hyena	1	N	N	Y	N	N	N
ASG0000009	hyena	1	N	N	Y	N	N	N
ASG0000009	warthog	1	N	N	Y	N	N	N
ASG0000009	hyena	1	N	N	Y	N	N	N
ASG0000009	wildcat	1	N	N	Y	N	N	N
ASG0000009	hyena	1	N	N	Y	N	N	N
ASG0000009	hyena	1	N	N	Y	N	N	N
ASG0000009	hyena	1	N	N	Y	N	N	N

B.(Fig. 4d) Subject retired as *Complete* - not reaching consensus but having been viewed by 25 people

ID	Species	Count	Standing	Resting	Moving	Eating	Interacting	Babies
ASG000xzx	impala	1	Y	N	N	N	N	N
ASG000xzx	G. gazelle	1	N	N	Y	N	N	N
ASG000xzx	reedbuck	1	Y	N	N	N	N	N
ASG000xzx	reedbuck	1	Y	N	N	N	N	N
ASG000xzx	dik dik	1	Y	N	Y	N	N	N
ASG000xzx								
ASG000xzx	dik dik	1	Y	N	N	N	N	N
ASG000xzx	impala	1	Y	N	N	N	N	N
ASG000xzx								
ASG000xzx	reedbuck	1	Y	N	N	N	N	N
ASG000xzx								
ASG000xzx	impala	1	Y	N	N	N	N	N
ASG000xzx	impala	1	Y	N	N	N	N	N
ASG000xzx	dik dik	1	Y	N	N	N	N	N
ASG000xzx	T. gazelle	1	Y	N	N	N	N	N
ASG000xzx	G. gazelle	1	Y	N	N	N	N	N
ASG000xzx	G. gazelle	1	Y	N	N	N	N	N
ASG000xzx	impala	1	Y	N	N	N	N	N
ASG000xzx	T. gazelle	1	Y	N	N	N	N	N
ASG000xzx	T. gazelle	1	Y	N	N	N	N	N
ASG000xzx	dik dik	1	Y	N	N	N	N	N
ASG000xzx	w.buck	1	Y	N	N	N	N	N
ASG000xzx	G. gazelle	1	Y	N	N	N	N	N
ASG000xzx	G. gazelle	1	Y	N	N	N	N	N
ASG000xzx	dik dik	1	Y	N	N	N	N	N

Table 2-2: Species identification validation results

The top 20 most numerous species in the subset of Snapshot Serengeti images validated by experts. *Total* indicates the number of images within the validated dataset identified by experts as that species. *# Correct* indicates the number of images for which the reduction algorithm arrived at the correct answer. *Proportion Correct* is given by $\# \text{ Correct} / \text{Total}$.

Species	Total	# Correct	Proportion Correct
wildebeest	1548	1519	0.9813
zebra	685	684	0.9985
hartebeest	252	244	0.9683
buffalo	219	215	0.9817
Thomson's gazelle	200	189	0.945
impala	171	168	0.9825
warthog	114	114	1
giraffe	90	90	1
elephant	83	83	1
human	71	71	1
Grant's gazelle	60	51	0.85
guinea fowl	56	53	0.9464
Spotted hyena	55	55	1
other bird	55	55	1
hippopotamus	28	28	1
reedbuck	25	22	0.88
eland	23	22	0.9565
baboon	22	22	1
lion (female)	18	18	1
topi	14	13	0.9286

Table 2-3: Species counts validation results

Validation of species counts against expert classifications. *# Validated* is the total number of counts validated by experts. *Proportion Exactly Correct* reflects the proportion of algorithm-derived counts that matched expert classifications exactly. *Proportion within +/- 1* reflects the proportion of algorithm-derived accounts that fell within 1 bin above or below the expert classification.

Species counts	# Validated	Proportion Exactly Correct	Proportion within +/- 1
1	1744	0.931	0.978
2	654	0.797	0.928
3	411	0.706	0.920
4	309	0.612	0.851
5	232	0.466	0.789
6	171	0.462	0.737
7	132	0.417	0.720
8	99	0.283	0.636
9	72	0.375	0.625
10	58	0.172	0.793
11-50	378	0.862	0.926
51+	9	0.778	1.000

Table 2-4: All species captured in Snapshot Serengeti

Raw number of captures for each species (as identified by the plurality algorithm) in each season (defined arbitrarily as ~ 6 month periods reflecting the on-site presence of the project manager).

Species	Season 1	Season 2	Season 3	Season 4	Season 5	Season 6
aardvark	44	87	59	47	107	42
aardwolf	28	57	8	13	40	16
baboon	127	210	227	254	435	365
Bat eared fox	102	116	7	21	23	25
buffalo	477	2,362	2,052	3,173	3,794	2,292
bushbuck	12	34	39	61	68	40
caracal	19	30	7	7	4	15
cheetah	198	410	109	131	400	57
civet	8	10	4	2	6	7
dik dik	250	450	104	170	295	277
eland	38	869	319	301	607	617
elephant	604	1,246	1,319	1,396	3,816	2,278
Grant's gazelle	1,630	1,796	1,049	1,049	1,878	517
Thomson's gazelle	10,336	8,965	5,755	2,974	13,314	805
genet	10	8	4	0	6	1
giraffe	691	1,439	1,148	1,517	2,658	1,196
guinea fowl	1,094	2,319	733	914	1,591	1,387
hare	107	164	16	34	44	36
hartebeest	698	2,896	1,293	3,843	2,804	1,191
hippopotamus	122	494	383	388	687	548
honey badger	12	9	4	0	5	5
human	1,970	2,118	1,439	1,134	1,787	1,731
spotted hyena	938	1,422	614	653	1,404	353
striped hyena	36	42	8	7	18	4
impala	271	798	815	2,492	2,583	2,052
jackal	106	162	12	63	111	113
kori bustard	202	199	50	106	88	54
leopard	14	51	22	35	50	58
lion female	481	1,077	529	420	692	230
lion male	214	346	90	85	160	37
mongoose	95	41	11	30	45	29
ostrich	87	103	172	45	211	71
other bird	849	880	304	1,365	1,372	926
porcupine	44	58	47	43	47	55
reedbuck	319	674	381	399	551	616
reptiles	122	0	0	2	2	7
rhinoceros	2	17	3	2	7	1
rodents	40	5	2	1	0	0
secretary bird	65	59	28	53	162	80
serval	57	114	28	61	103	113
topi	167	673	280	217	698	326
vervet monkey	21	141	24	54	39	65
warthog	930	1,373	835	1,334	2,009	1,317
waterbuck	6	25	63	69	105	161
wildcat	13	19	0	4	11	0
wildebeest	222	21,766	17,419	25,240	30,794	7,408
zebra	1,913	17,993	11,840	12,827	22,728	5,463
zorilla	2	8	2	1	3	1

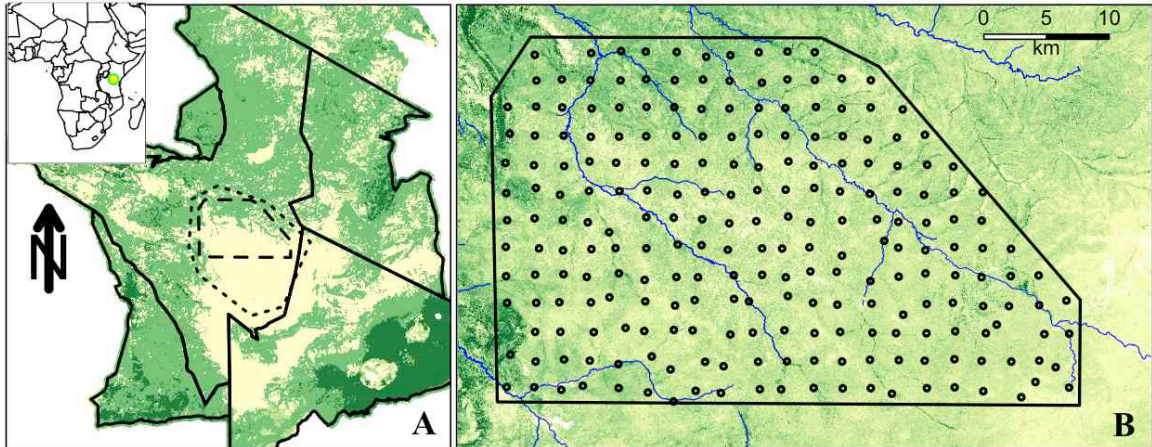
Table 2-5: Comparison of camera trap captures to known densities

Results of simple linear regression of log(camera trap captures) on log(estimated population sizes). Separate regressions were done for all species and resident species only, and for mean population estimates and the most recent population estimates for each species. Because of the strong statistical influence of bushbuck on the regression model, we excluded this point and re-ran the models.

All Species	Estimate	Std. Error	P	adj-R²
mean population estimate	0.613	0.084	< 0.0001	0.767
most recent population estimate	0.619	0.079	< 0.0001	0.790
Resident Species	Estimate	Std. Error	P	adj-R²
mean population estimate	0.489	0.107	0.000645	0.605
most recent population estimate	0.514	0.110	0.000529	0.617
All Species (bushbuck excluded)	Estimate	Std. Error	P	adj-R²
mean population estimate	0.688	0.109	< 0.0001	0.721
most recent population estimate	0.687	0.102	< 0.0001	0.748
Resident Species (bushbuck excluded)	Estimate	Std. Error	P	adj-R²
mean population estimate	0.513	0.172	0.0125	0.397
most recent population estimate	0.556	0.179	0.0100	0.419

Figure 2-1: Study Area

A) Serengeti National Park. Long-term lion project study area in center is indicated by dotted line; camera-trap study area is indicated by dashed line. **B)** Camera trap layout within the long-term Lion Project Study Area. Camera locations are plotted over tree cover (extracted from Landsat imagery), with darker green indicating increased tree cover per 30m²-grid cell.

**Figure 2-2: Field site examples**

Camera traps in steel cases were placed on trees when available (left) and steel poles when no trees were within 1,000m of the grid-cell center (right).



Figure 2-3: The *Snapshot Serengeti* interface.

A) The primary interface with all available species options. B) Filters that help narrow users' choices when classifying species.

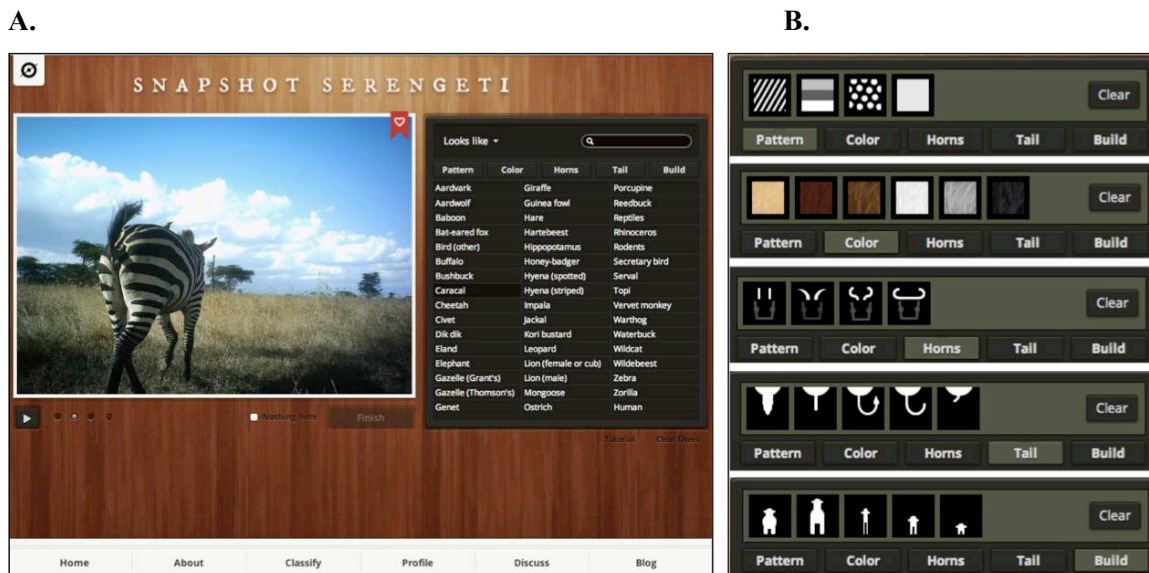


Figure 2-4: Example captures from Snapshot Serengeti

Example captures retired from Snapshot Serengeti as **A) blank**: receiving five consecutive “nothing here” classifications, **B-C) consensus**: receiving 10 matching species classifications, and **D) complete**: receiving 25 classifications regardless of agreement. Note that the data reduction algorithm correctly arrived at “giraffe,” “spotted hyena,” and “impala” for images **B-D**, respectively (See Table 1 for individual classifications).

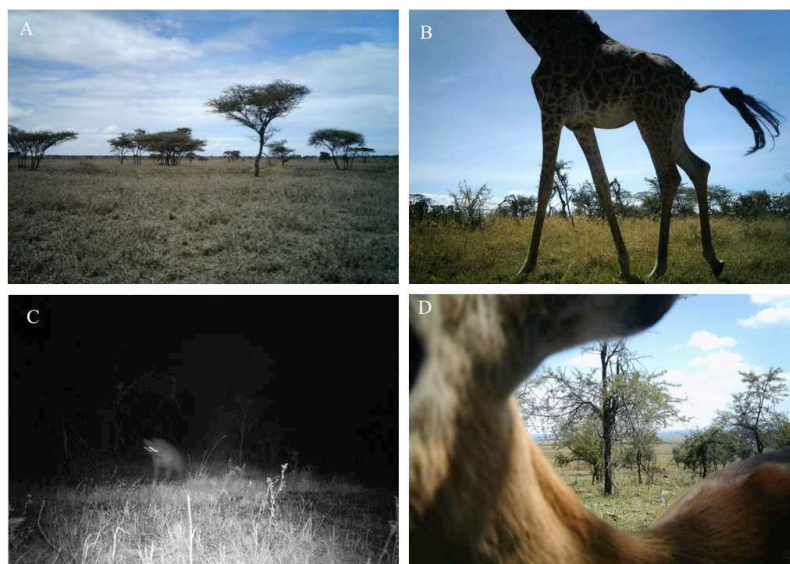


Figure 2-5: Monthly camera trap activity

Monthly camera trap activity from July 2010 through April 2013. Shaded grid cells reflect camera trap sites and are shaded blue proportional to the number of days that each camera was active each month. Gray indicates inactive sites. Note that cameras were not operational for December 2010 through January 2011, and data were sparse in August 2011 due to equipment failure.

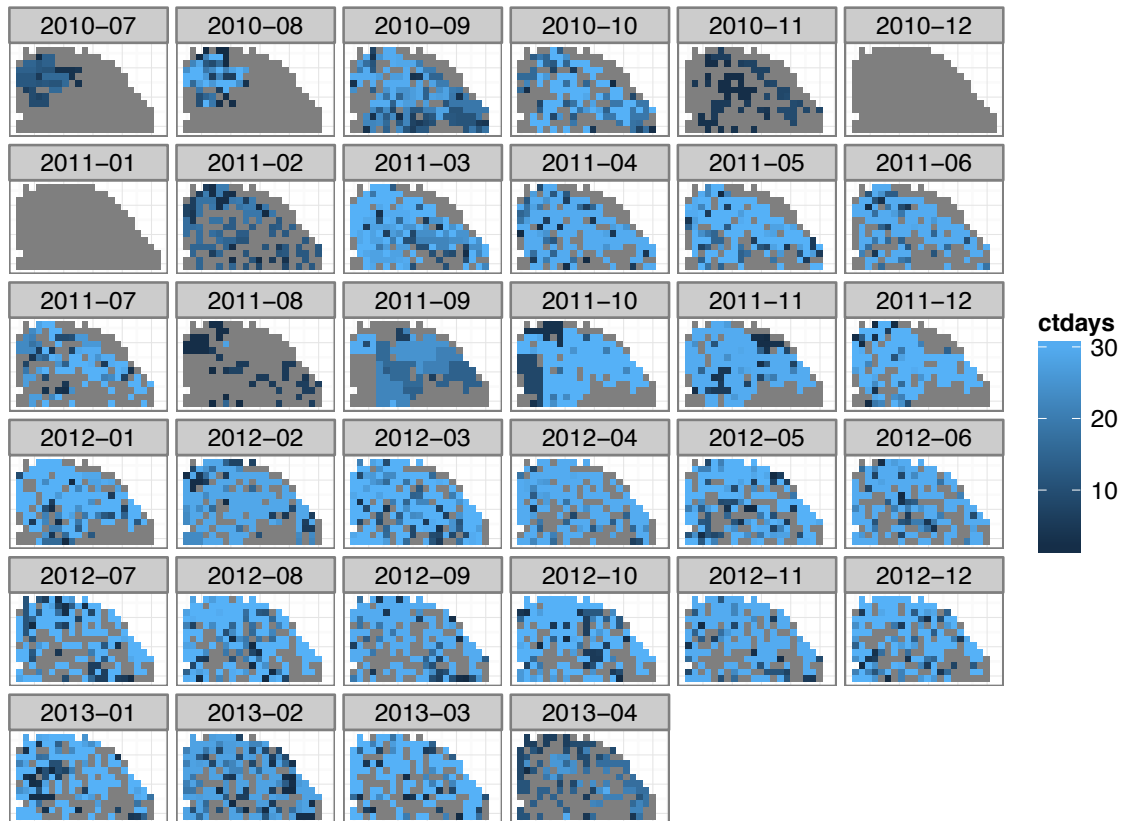


Figure 2-6: Comparison of camera trap captures to known population estimates

Comparison of photographic capture rates to all recent Serengeti-wide population estimates for major herbivore species (axes are on log scales). Migratory species are presented in gray scale, residents in color. All recent population estimates (x's) for each species are connected by horizontal lines; means are shown as solid circles. Regression of camera captures on mean population estimates indicates that the two measures are significantly related across all herbivore species (dashed line, $\text{adj-R}^2=0.767$, $p < 0.0001$) and when migratory species are excluded (solid line, $\text{adj-R}^2=0.645$, $p=0.0006$). Full regression output given in Table 5.

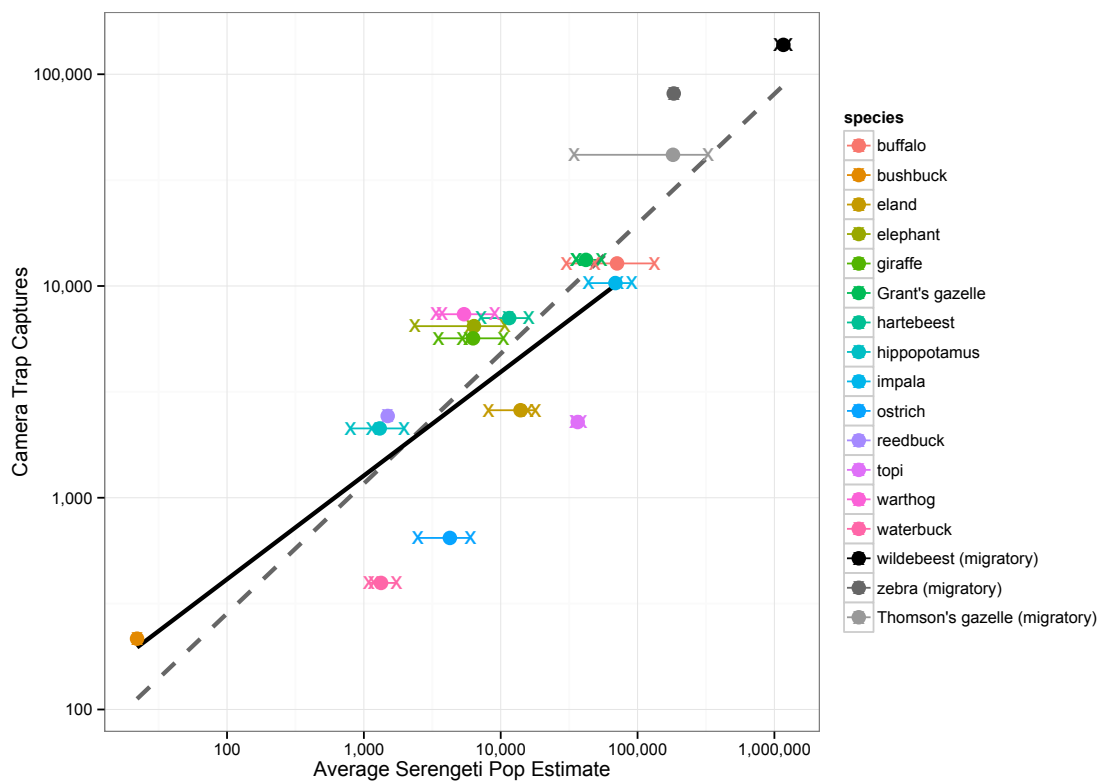


Figure 2-7: Daily herbivore capture rates

Daily capture rates for wildebeest, zebra, Thomson's gazelle, Cape buffalo and hartebeest. Rates are calculated from the number of animals captured in independent photos on a given day divided by the number of active cameras. The y-axis is plotted on a square-root scale. Note that cameras were not operational for December 2010 through January 2011, and data were sparse in August 2011 due to equipment failure. The change in average daily capture rates across the seasons reflects the influx of migratory species (wildebeest, zebra, and Thomson's gazelle).

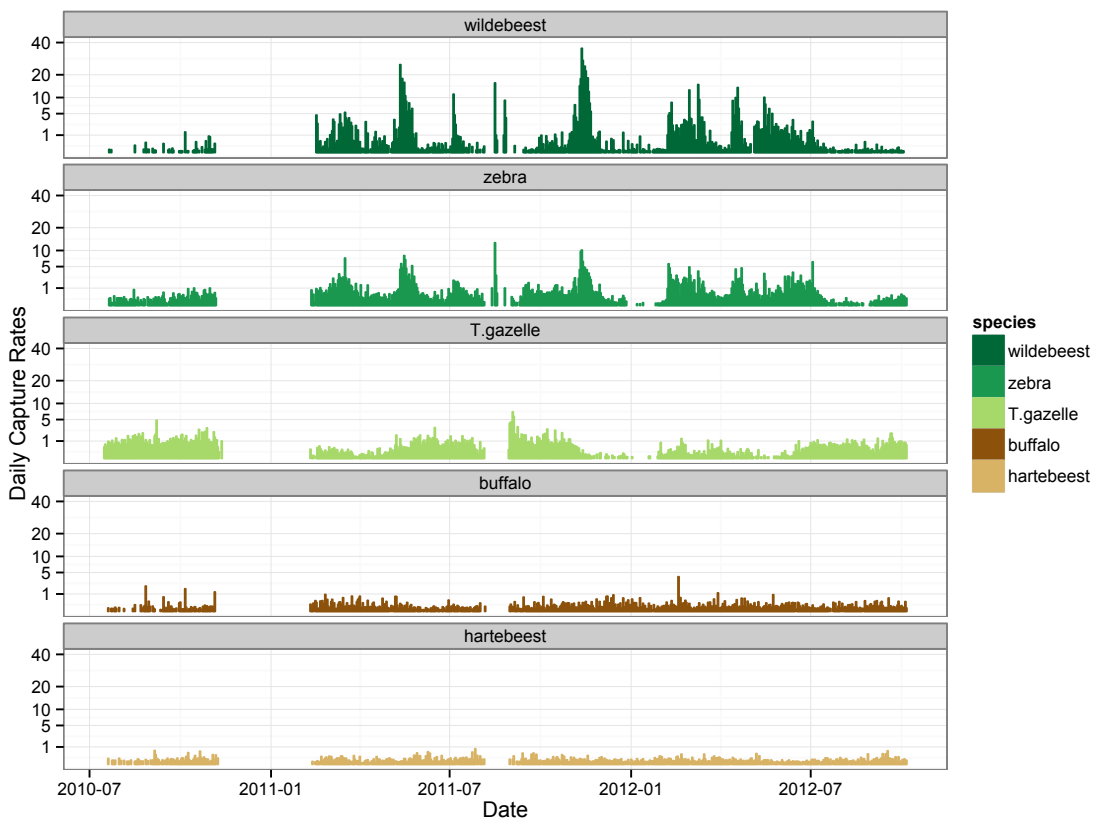


Figure 2-8: Monthly distributions of herbivores vs. NDVI

Comparison of monthly distributions of migratory wildebeest, zebra, and Thomson's gazelle and resident buffalo and hartebeest. Camera-trap captures are indicated by circles sized proportional to the number of sightings per camera trap day and are overlaid on monthly NDVI maps. The seasonal variation in number and location of wildebeest, zebra, and gazelle captures reflects the annual migration, while captures of resident species fluctuate less widely throughout the year.

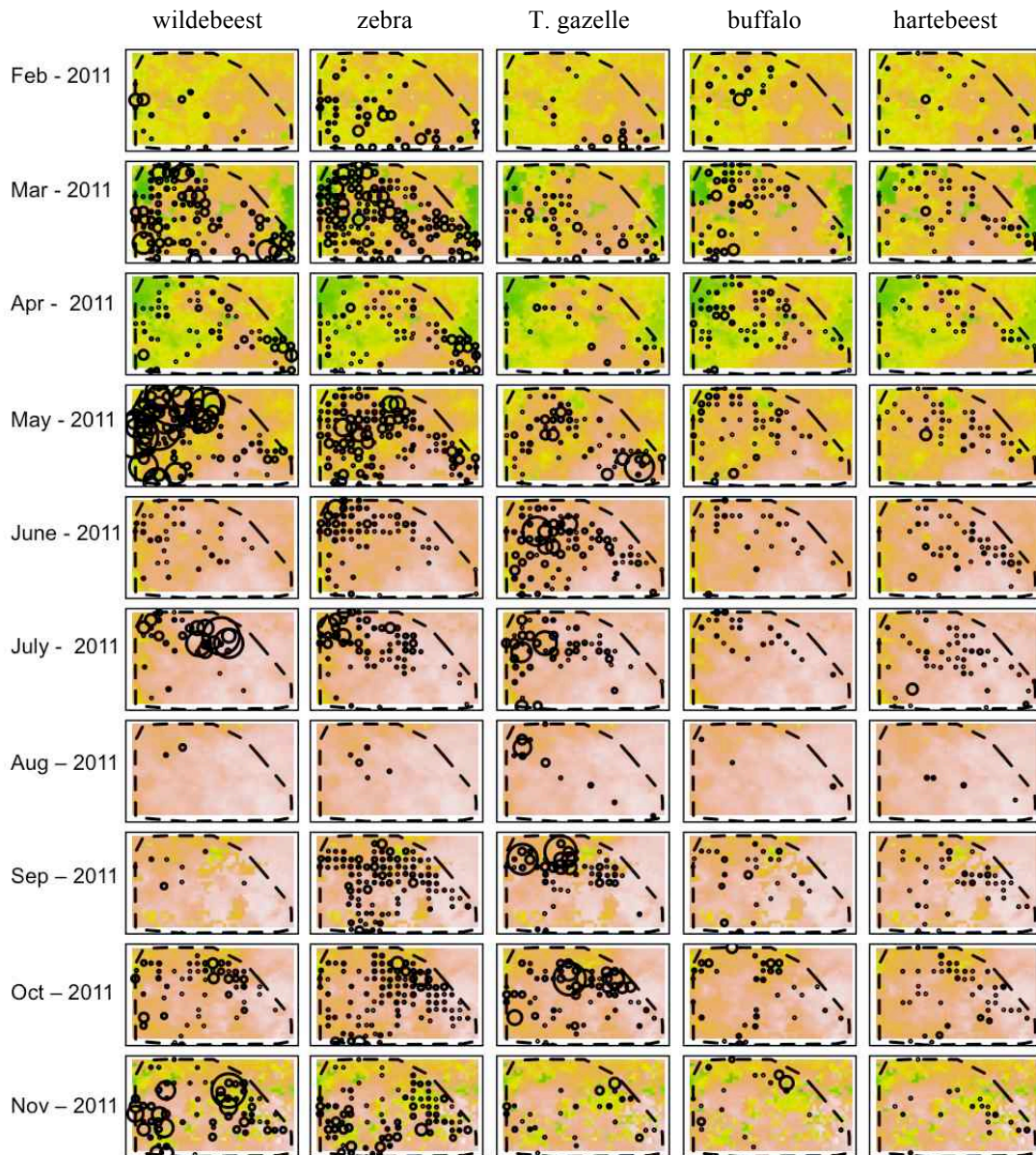
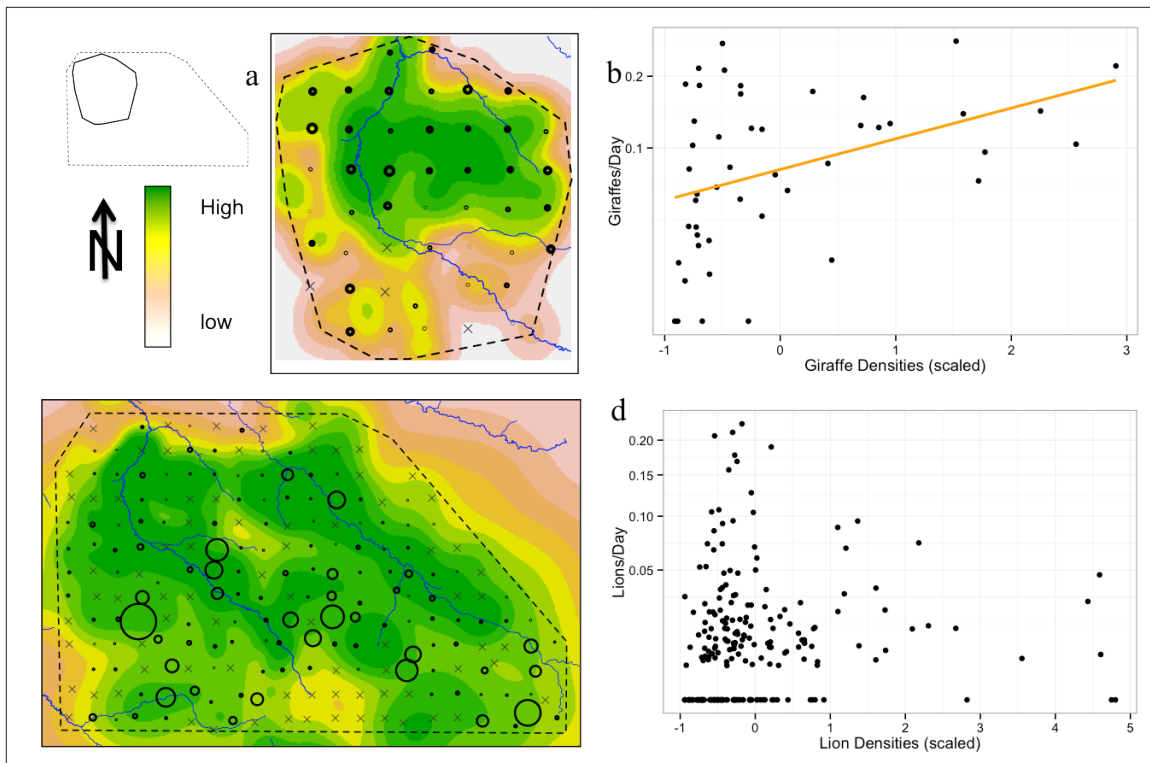


Figure 2-9: Comparison of giraffe and lion densities to camera trap capture rates.

The scale and location of the giraffe study area (solid polygon) with respect to the camera survey (dashed polygon) is given inset in the top left. Relative dry season (a) giraffe and (c) lion densities mapped from high (green) to low (tan). Dry season captures for each species are shown as circles sized proportional to the number of sightings per camera trap-day. Active cameras with no giraffe or lion captures are marked with gray X's. Camera trap capture rates plotted against scaled relative densities for (b) giraffes and (d) lions across all sites. Y-axis is on a square-root scale. Giraffe camera trap captures reflected known giraffe densities ($p=0.006$, $\text{adj-}R^2=0.138$, $n=47$) whereas lion captures did not ($p=0.259$, $R^2=0.001$, $n=222$).



CHAPTER 3

Lions, hyenas, and cheetahs: spatiotemporal avoidance in a landscape of fear

Introduction

Many species exist in a "landscape of fear" created by the risk of predation or interference competition (Brown, Laundré & Gurung 1999; Laundré *et al.* 2001). Not only do predators kill and eat prey, they also harass, steal food from, and kill their intraguild competitors (Palomares & Caro 1999; Linnell & Strand 2000; Caro & Stoner 2003; Donadio & Buskirk 2006; Ritchie & Johnson 2009). However, subordinate species can minimize the likelihood of predation or interference by restricting their activity to low-risk "refuges": they may avoid risky habitat types (Fedriani, Palomares & Delibes 1999; Fortin *et al.* 2005; Creel *et al.* 2005; Wirsing, Heithaus & Dill 2007), hours of the day (Carothers & Jaksić 1984; Hayward & Slotow 2009; Bischof *et al.* 2014), or known areas of high long-term risk (Kamler *et al.* 2003a; Valeix *et al.* 2009b; Swanson *et al.* 2014).

These responses can be costly (Schmitz *et al.* 1997; Werner & Peacor 2003; Preisser *et al.* 2005), especially if they reduce the subordinate species' long-term access to resources (Cresswell 2008; Sergio & Hiraldo 2008; Creel & Christianson 2008). In fact, large-scale displacement by top predators appears to be a primary driver of suppression in African wild dogs (Swanson *et al.* 2014) and swift foxes (Kamler *et al.* 2003a).

In contrast, fine-scale "reactive" avoidance tactics (*sensu* Broekhuis *et al.* 2013) may minimize risk and reduce landscape-level displacement. Instead of preemptively avoiding large portions of the landscape or preferred habitat types, subordinate species may alter their habitat use on a moment-to-moment basis. For example, elk shift to more densely wooded habitats when wolves are in the immediate vicinity (Creel *et al.* 2005), and many African ungulates avoid watering holes at night when lions are nearby (Valeix *et al.* 2009a).

Fine-scale avoidance behavior has primarily been evaluated via extensive use of GPS collars (e.g. Valeix *et al.* 2009b; a; Vanak *et al.* 2013; Broekhuis *et al.* 2013), but this can be prohibitively expensive. Camera traps provide an affordable alternative to simultaneously assess

fine-scale avoidance across multiple species. Camera trap surveys have so far employed hierarchical occupancy models (e.g. MacKenzie *et al.* 2006) to assess broad differences in habitat use or temporal activity patterns (spatial or temporal partitioning) or active changes in behavior to minimize contact rates (avoidance) that have been aggregated across broad scales (e.g. Waddle *et al.* 2010; Bischof *et al.* 2014; Robinson, Bustos & Roemer 2014). Here we use camera traps to assess fine-scale patterns of active spatial and temporal avoidance in a well-studied guild of large African carnivores: lions (*Panthera leo*), spotted hyenas (*Crocuta crocuta*), and cheetahs (*Acinonyx jubatus*).

Despite dissimilar hunting strategies (Kruuk 1972; Schaller 1972), lions and hyenas show considerable dietary overlap (Hayward 2006) and reciprocally harass and steal food from each other (Kruuk 1972; Höner *et al.* 2002; Kissui & Packer 2004; Watts & Holekamp 2008). Although lions can sometimes suppress hyena populations through extensive kleptoparasitism (Watts & Holekamp 2008), hyenas do not have similar effects on lions (Kissui & Packer 2004), and lions and hyena population densities are positively correlated across African reserves (Creel & Creel 1996).

In contrast, lions and hyenas have both been believed to suppress cheetah populations through high rates of direct killing (Laurenson 1994, but see Mills & Mills 2013), and cheetahs are often described as "refuge" or "fugitive" species, ranging widely and persisting in marginal areas with low lion and hyena densities (e.g. Durant 1998, Durant 2000, Caro & Stoner 2003, Saleni 2007, Chauvenet *et al.* 2011). However, recent studies show that lion-inflicted mortality is lower than previously assumed (Mills & Mills 2013) and that cheetah populations are not suppressed by high lion densities (Swanson *et al.* 2014). Although cheetahs actively avoid lions (Durant 2000), it is unclear whether this response translates into long-term spatial displacement (cf Broekhuis *et al.* 2013 and Swanson *et al.* 2014 with Durant *et al.* 1998 and Vanak *et al.* 2013).

In this paper, we use camera traps to investigate fine-scale spatial and temporal avoidance among lions, hyenas, and cheetahs in Serengeti National Park, Tanzania. After validating camera-trap captures against lion GPS collar data, we first use species-specific capture rates to measure long-term spatial attraction or avoidance (aggregated across years), while controlling for habitat preferences and localized prey abundance. We then evaluate active temporal attraction or avoidance in the hours immediately following camera-trap captures of predators and prey.

We frame our analyses according to the respective competitive abilities of each species. As the dominant competitor, lions are expected to gain access to their preferred landscape characteristics (Durant 1998, Vanak *et al.* 2013). Hyenas should be sensitive to both lions and

habitat, whereas cheetahs should distribute themselves according to lions, hyenas, and habitat. We also test the possibility that temporal avoidance strategies reduce the need for fine-scale spatial avoidance.

Methods

Study System & Field Survey

The 1,125km² study area is located at the center of Serengeti National Park, Tanzania, at the intersection of open plains and savanna woodlands (Figure 1a). Rainfall and vegetation follow a northwest-southeast gradient: wetter, denser woodlands in the northwest to drier, short-grass plains in the southeast (Sinclair 1995). The ecosystem holds some of the highest concentrations of large predators in the world (Sinclair 1995), and is dominated by the annual migration of 1.6 million wildebeest, zebra, and gazelle that follow the seasonal rains from Kenya's Masai Mara Reserve onto the nutrient-rich plains of the Ngorongoro Conservation Area and Serengeti National Park (Holdo, Holt & Fryxell 2009).

The Serengeti Lion Project has monitored lion ranging and demography since the 1960's (Packer *et al.* 2005; Swanson *et al.* 2014). The camera survey is located within the long-term lion study area, where all prides are monitored by radio telemetry of one VHF-collared female per pride.

We established 225 camera traps across a grid layout such that each camera was at the center of a 5-km² grid cell (Figure 1b). Operating continuously (aside from camera failure), the survey produced 101,315 camera-trap days between June 2010 and May 2013. Species, number of individuals, and behaviors in each image were identified by citizen scientists via the *Snapshot Serengeti* (www.snapshotserengeti.org) platform. Swanson *et al.* (*In Review*) provides details on the camera survey and data processing. Validation of citizen-scientist consensus classifications (viewed by 5-25 different people) against expert species identifications indicate >96% overall accuracy. To further improve accuracy, we restricted the analyses in this paper to photos that had received at least 85% agreement.

Analytical Approaches

Camera Validation

We validated that camera traps accurately reflected species present within the camera field of view by comparing camera trap captures to radio-telemetry locations of collared lions. Given that a lion had been located by radio-telemetry, we calculated the probability that a lion was captured

at the nearest camera trap on that day as a function of the distance between the collared lion sighting and the camera trap.

Spatial Avoidance

We evaluated patterns of fine-scale spatial avoidance among lions, hyenas and cheetahs by comparing species-specific capture rates at each site. To ensure independence across captures, we limited analyses to no more than one sighting per day for a given species at a given site.

Because the camera-trap data were zero-inflated and over-dispersed, we used hurdle models (Zuur et al. 2009) to specify two different underlying processes: a binomial process (species is present or not) and a truncated count process (how many are seen given that the species is present). Comparison via AIC indicated that hyenas were best represented by a Poisson distribution while lions and cheetahs were best represented by a negative-binomial distribution.

We evaluated patterns of partitioning aggregated across all years and controlled for site-specific search effort by specifying an offset of $\log(\# \text{ Camera-trap days})$. We first identified the best “habitat” models for the presence/absence and abundance of each species that incorporated habitat characteristics and measures of localized prey availability (wildebeest, buffalo, and Thomson’s gazelle). We incorporated a measure of *prey presence* into the binomial models and a measure of *prey abundance* into count models. We created a full “habitat” model that considered only habitat and prey variables that were significant in univariate regressions for each component process, evaluated all sub-models, and selected the sub-model with the lowest AIC values (see candidate models, Table A2-1). The habitat characteristics evaluated were: *Distance to river*, *Distance to kopje*, *Grass height*, *Percent Tree Cover (< 1 km)*, *Tree isolation (measured by the average distance to the 10 nearest trees)*, *Habitat (plains vs. woodlands)*, *Shade (scale 0-4)* and an interaction term for *Tree isolation * Shade* to reflect the “attractiveness” of an isolated tree.

We then separately evaluated the effect of *lion presence* on the presence/absence of mesopredators (binomial component) and the effect of *lion abundance* (linear and quadratic) on the number of mesopredator sightings (count component). To produce the final models, we incorporated significant predictors from the “lion” models into the best “habitat” model for each species and selected the sub-model with the lowest AIC value. We evaluated cheetah sightings with respect to the hyenas using the same approach.

We additionally evaluated patterns separately for wet and dry seasons aggregated across years as well as for each wet and dry season each year, as well as separately for day and night sightings; results were qualitatively similar to the overall aggregated analysis and are not reported

here.

Temporal Avoidance

We evaluated temporal avoidance by calculating the “time since last prey (gazelle/wildebeest/buffalo)” and “time since last predator (lion/hyena/cheetah)” for all independent predator sightings. Because many species will spend multiple hours in front of a camera, triggering the camera repeatedly, we calculated all “time since” measures using the time of the last sighting in any given visit. We truncated all “time since” calculations to those within three days of the initial sighting to explicitly test short-term responses.

We aggregated sightings into 12-hour bins (e.g. 0-12 hours since gazelle, 12-24 hours, etc.) and used Poisson regressions to evaluate whether binned counts of predator sightings showed significant linear or polynomial trends with all “time since prey” and “time since predator” sightings. We then visually examined temporal activity patterns as the percentage of species-specific sightings per hour of the day to assess whether patterns of avoidance could be due to out-of-synch diel patterns (e.g., a strictly nocturnal species followed 12 hours later by a strictly diurnal species would reflect temporal niche partitioning and not active avoidance).

Results

Camera Validation

Although raw camera trap capture rates do not reflect larger-scale lion densities (see Chapter 2), likely due to lions' attraction to isolated trees, comparison of camera trap captures to VHF-collar lion locations indicate that cameras accurately reflect localized lion presence (Figure 2). When VHF collared lions were recorded within 50 or 100m of a camera trap, that camera had a 58% probability of capturing a lion that same day, and the probability of capture declined exponentially with distance. Given that the camera field of vision covers less than 50% of the area around the camera at a 50m radius, we consider the camera traps to be point-samples of the landscape at a particular moment in time, accurately reflecting species present within the immediate field of view of the camera trap.

Spatial avoidance

Habitat models

Habitat models (Table 1) indicated lions and cheetahs were captured most often in open areas

and at isolated trees with good shade (Figure 3). In addition, cheetahs were more likely to be present at camera traps on the open plains than in the woodlands. In contrast, hyenas were more often captured in more wooded areas and at trees with less shade. These contrasting habitat patterns likely reflect different types of activity captured for each species. Camera traps on the open plains are often placed on attractants such as isolated trees or kopjes (rocky outcroppings) that provide shade, and are prime daytime resting spots for cheetahs and lions. Accordingly, whereas lions and cheetahs are primarily captured at cameras resting during the day, hyenas are mostly captured on the move and at night (see below, *Temporal Avoidance*).

Lions were positively associated with buffalo and gazelle (Table 1a) and hyenas with buffalo, gazelle, and wildebeest (Table 1b). In contrast, the best habitat model for cheetah did not include prey (Table 1c).

Candidate models and AIC values are given in table A2-1. Note that Δ AIC values between models are small; because many models performed similarly we additionally conducted model averaging on all possible sub-models (with Δ AIC < 4) from the full habitat model containing all habitat terms that had been significant in the univariate regressions, and model averaged output is given in Table A2-2. Overall results were quantitatively similar when run on daytime and nighttime sightings separately.

Model averaged output (Table A2-2) is largely similar to the “best” models (reported in Table 1). However, model averaged results indicate that while lions remain more likely to be found at sites with gazelle, both lion and cheetah numbers decline with gazelle numbers. Although these relationships are weak (relative importance = 0.4 *lions*; 0.26 *cheetahs*), they may reflect fine-scale habitat selection by resting lions and cheetahs at rest, instead of those that are actively hunting.

Avoidance

Cheetahs and hyenas were more likely to be present at sites with lions, appeared more often at sites with more lions up to a threshold, and appeared less often at sites with the most lion sightings (Table 2, Figure 4a). Cheetah presence and abundance were unrelated to hyena distributions (Table 2, Figure 4b).

Even after controlling for habitat preferences, hyenas were more likely to be present with lions, and their numbers increased quadratically with lion numbers (Table 3, Figure 5). The relationship between cheetahs and lions was driven in part by shared attraction to isolated trees

with shade: after controlling for fine-scale habitat preferences, effect sizes decreased for lion numbers and presence (Table 3, Figure 5).

Note, however, that although statistically significant, the quadratic relationship was driven almost entirely by two (of 225) sites and that confidence intervals from the resultant models overlapped significantly (Figure 5). As with the habitat models, we conducted model averaging on all possible sub-models, and results were similar to those above (Table A2-3).

Temporal avoidance

All prey species were primarily captured during the day (Figure 6). Although primarily nocturnal (lions, Cozzi et al. 2012) or crepuscular (cheetahs, Cozzi et al. 2012), lions and cheetahs were most often captured during the day, likely reflecting their use of shady trees and kopjes as daytime resting spots. In contrast, hyenas were primarily captured at night, reflecting their known diel activity patterns (Hayward & Slotow 2009; Cozzi *et al.* 2012). Hyenas were captured more often in transit than resting; although they sometimes utilized shaded trees or kopjes to rest, they were often seen resting in open areas (as described in Kruuk 1972). Thus, the camera traps appear to reflect fine-scale selection of resting spots for lions and cheetahs, but capture more general habitat use by hyenas.

Time since prey

Lions, hyenas, and cheetahs all appear to follow their primary prey, peaking in the first 12 hours after a prey sighting and then declining (Figure 7, Table 4). Although we specifically limited statistical testing to within 72 hours of the reference sighting, we have plotted counts for up to one week after each sighting, which illustrates the extent to which predator movements are influenced by recent prey movements (Figure 7).

Lion and hyena sightings peaked sharply in the first 12 hours after a wildebeest sighting then declined rapidly, suggesting that both predators actively tracked this species. Whereas hyena sightings showed a similarly dramatic decline after gazelle, lions declined more slowly, suggesting that lions do not track gazelle as closely as do hyenas. Lions are the major predator on buffalo, and lions appear to track buffalo more closely than hyenas. In contrast, the relationship between cheetahs and “time since prey” was more subtle. Cheetah sightings declined after gazelle and wildebeest, but not as rapidly as did lions and hyenas.

Time since predator

Despite both species tracking gazelle, lions do not show any tendency to appear at camera traps after cheetahs (Figure 8). In contrast, cheetahs do not appear until at least 12 hours after a lion sighting and then show an elevated rate of appearance from 12-72 hours after a lion (Figure 8). Concordant patterns of camera-trap capture across the day (Figure 6) indicate that the cheetahs' 12-hour delay is not due to divergent diel patterns. Although cheetahs do not show any patterns of attraction or avoidance to hyenas, hyenas appear at sites slightly more often in the first 12 hours after cheetah sightings.

In contrast, lions and hyenas often appear in the first hours after each other (Figure 68, and hyenas sometimes appear while lions are still at the camera (three cases, all of which involved lions making and remaining on a kill). However, whereas lion sightings remain high for the first 24 hours post-hyena, hyena sightings decline sharply 12-hours after a lion sighting, presumably reflecting the more active movement patterns of hyenas.

Discussion

Here we demonstrate that interference competition between lions, hyenas and cheetahs does not translate into long-term displacement by subordinate species, even at fine spatial scales. Although subordinate interference competitors are expected to seek out “competition refuges” by selecting marginal habitats (Durant 1998; Linnell & Strand 2000), neither hyenas nor cheetahs avoid areas frequented by lions. In fact, hyenas and cheetahs are positively associated with lions except in areas with exceptionally high lion use. Fine-scale temporal analyses further indicate that hyenas actively track lions while cheetahs actively avoid lion-occupied areas for several hours. These contrasting patterns suggest that hyenas and cheetahs are able to utilize alternative strategies that minimize the need for long-term spatial avoidance.

Hyenas

Despite dissimilar habitat preferences, lions and hyenas appear at the same camera trap sites (Figure 5) on the same days (Figure 8). These patterns of attraction could reflect active attraction between predator species: lions and hyenas actively scavenge from each other (Kruuk 1972; Kissui & Packer 2004), though interference outcomes are dependent on group size and population densities (Cooper 1991; Höner *et al.* 2002; Watts & Holekamp 2008).

Although large groups of hyenas can successfully kleptoparasitize lions (Cooper 1991), this does inflict measurable fitness costs to lions (Kissui & Packer 2004). In contrast, hyenas are sensitive to lion numbers: at low lion densities, hyenas acquire more food from lions than they

lose, but at high lion densities, hyenas suffer measurable demographic consequences (Watts & Holekamp 2008). Thus, the quadratic relationship between lions and hyenas across camera sites (Figure 5) may reflect an attraction of hyenas to lions until some threshold lion density is reached.

Alternatively, this apparent attraction may be driven by mutual attraction to shared prey. Lions and hyenas both prey upon wildebeest (Kruuk 1972; Schaller 1972; Scheel & Packer 1995; Hayward 2006) and appear to actively follow them (Figure 8). Lion and hyena peak more sharply and decline more quickly following wildebeest sightings than sightings of each other (Table 4), but further investigation is needed to determine whether lions and hyenas are actively attracted to each other or simply mutually tracking the same prey.

Cheetahs

Cheetahs are widely perceived as a ‘refuge species’, only able to persist in marginal areas with low lion, hyena, and prey densities (e.g. Laurenson 1994, Laurenson 1995, Durant 1998, Durant 2000, Caro & Stoner 2003, Saleni 2007, Chauvenet et al. 2011). However, our results indicate that active avoidance does not translate into long-term spatial displacement in which cheetahs lose access to preferred habitat patches. Lions and cheetahs are both attracted to shady trees on the open plains (Figure 2) and cheetahs continue to use these preferred habitat patches despite moderately high levels of lion use (Figure 5), though they may reduce their use of areas with exceptionally high rates of lion use.

Instead of generally avoiding areas utilized by lions, cheetahs reduce the chance of encountering a lion by avoiding habitat hotspots *when lions were present* (Figure 8). Cheetahs further appear to avoid contact with lions while retaining access to their primary prey (Figure 7).

In contrast to their temporal avoidance of lions, cheetahs show no spatial or temporal avoidance of hyenas (Figure 4) likely because hyenas are less of a threat than lions. Although hyenas also kill cheetah cubs (Laurenson 1994, 1995), they are much more conspicuous than lions and thus may be easier for cheetahs to avoid at very short distances.

By responding reactively, and only avoiding preferred habitats when lions are present, cheetahs may minimize their risk of encountering lions while still maintaining access to vital resources. Indeed, recent work by Broekhuis et al. (2013) and Vanak et al. found that cheetahs distributed themselves primarily with respect to prey and only secondarily avoided lions by maintaining a safe distance from the nearest lion. Our results confirm that this behavior does not translate into displacement at even the finest spatial scales but is instead achieved by fleeting temporal avoidance at a given location. Such fine-scale active avoidance may be key to cheetah

persistence in the face of interference competition by lions: lion density has no significant impact on cheetah numbers through time or across reserves (Mills & Mills 2013, Swanson *et al.* 2014).

Conclusions

Top predators are widely recognized to suppress their intraguild competitors through direct aggression (interference competition) and the resultant landscape of fear in which subordinate species alter their use of the landscape to minimize aggressive encounters (Ritchie & Johnson 2009). Active avoidance by subordinate species is often assumed to be costly, resulting in opportunity costs or displacement from preferred habitats (e.g. Durant 1998; 2000). However, our results suggest that active avoidance need not translate into costly displacement. Despite actively avoiding lions (Figure 8, see also Durant 2000), cheetahs are neither displaced from preferred habitat patches (Figure 4) nor larger areas across the landscape (Vanak *et al.* 2013; Broekhuis *et al.* 2013; Swanson *et al.* 2014), nor do they appear to lose access to their prey (Figure 7). In contrast, African wild dogs also actively avoid lions (Webster *et al.* 2012), but this avoidance translates into large-scale displacement that carries heavy demographic costs (Creel & Creel 1996; Swanson *et al.* 2014). Habitat complexity (Janssen *et al.* 2007) and ecosystem productivity (Elmhagen & Rushton 2007; Elmhagen *et al.* 2010) likely contribute to resultant patterns of displacement and suppression. Ultimately, the landscape of fear created by top predators is complex and species-specific; different patterns of spatial and temporal avoidance by subordinate species may help explain the diverse patterns of suppression and coexistence within predator guilds.

Tables and Figures

Table 3-1a-c: Regression output for the best “habitat only” models for each species.

Models were selected by AIC comparison of all possible sub-models from a full model that incorporated habitat characteristics that were found to be significant in univariate regressions (see Table A2-2 for candidate models and AIC scores).

A) Lions				
Count model (truncated poisson)				
	Estimate	Std. Error	Z	P
(Intercept)	-4.187	0.860	-4.867	0.0000
tree isolation	0.000	0.000	-0.344	0.7307
shade	-0.372	0.172	-2.156	0.0311
buffalo	19.418	4.327	4.487	0.0000
% cover	-0.334	0.189	-1.762	0.0780
tree isolation * shade	0.001	0.000	3.591	0.0003
Binomial model				
	Estimate	Std. Error	Z	P
(Intercept)	-2.255	0.713	-3.164	0.0016
tree isolation	0.001	0.000	1.933	0.0532
shade	0.321	0.145	2.207	0.0273
buffalo	1.416	0.391	3.619	0.0003
gazelle	1.234	0.484	2.548	0.0108
B) Hyena				
Count model (truncated poisson)				
	Estimate	Std. Error	Z	P
(Intercept)	-4.466	0.115	-38.867	< 0.0001
wildebeest	5.921	0.677	8.749	< 0.0001
gazelle	4.171	0.275	15.149	< 0.0001
buffalo	5.766	0.551	10.457	< 0.0001
shade	-0.119	0.017	-7.171	0.0000
tree cover	0.141	0.030	4.781	0.0000
Binomial model				
	Estimate	Std. Error	Z	P
(Intercept)	-1.214	0.908	-1.337	0.1811
gazelle	2.036	0.593	3.432	0.0006
wildebest	2.335	0.920	2.538	0.0112

C) Cheetah

Count model (truncated poisson)

	Estimate	Std. Error	Z	P
(Intercept)	-3.360	1.167	-2.878	0.0040
tree isolation	0.001	0.000	2.953	0.0031
shade	0.329	0.111	2.958	0.0031
% cover	-1.030	0.342	-3.010	0.0026

Binomial model

	Estimate	Std. Error	Z	P
(Intercept)	2.419	1.543	1.568	0.1169
tree isolation	0.000	0.001	-0.601	0.5477
shade	0.114	0.260	0.438	0.6612
% cover	-0.891	0.391	-2.277	0.0228
habitat	-1.494	0.431	-3.463	0.0005
tree isolation * shade	0.001	0.000	3.146	0.0017

Table 3-2: Regression output for models of subordinate vs. dominant species

Regression output for hyena and cheetah numbers against lion abundance (count model) and lion presence (binomial model), and for cheetah numbers against hyena abundance and presence.

Hyenas ~ Lions				
<i>Count model (truncated poisson)</i>				
	Estimate	Std. Error	Z	P
intercept	-3.816	0.028	-135.605	< 0.0001
lions	30.890	3.308	9.338	< 0.0001
lions ²	-253.741	50.098	-5.065	< 0.0001
<i>Binomial model</i>				
	Estimate	Std. Error	Z	P
intercept	1.609	0.330	4.873	< 0.0001
lion presence	1.629	0.531	3.066	< 0.0001
Cheetahs ~ Lions				
<i>Count model (truncated negbin)</i>				
	Estimate	Std. Error	Z	P
intercept	-5.979	0.314	-19.059	< 0.0001
lions	96.931	25.187	3.848	0.0001
lions ²	-1068.373	333.996	-3.199	0.0014
<i>Binomial model</i>				
	Estimate	Std. Error	Z	P
intercept	-1.139	0.287	-3.967	0.0001
lion presence	1.077	0.328	3.281	0.0010
Cheetahs ~ Hyenas				
<i>Count model (truncated negbin)</i>				
	Estimate	Std. Error	Z	P
intercept	-5.549	0.480	-11.573	< 0.0001
hyenas	-1.240	17.517	-0.071	0.9440
hyenas ²	64.065	134.776	0.475	0.6350
<i>Binomial model</i>				
	Estimate	Std. Error	Z	P
intercept	-1.179	0.572	-2.061	0.0393
hyena presence	0.888	0.589	1.509	0.1314

Table 3-3: Regression output for best overall models

Regression output from the best model (selected via AIC) incorporating habitat characteristics, localized prey densities, and measures of lion abundance. Because cheetahs were not significantly related to hyenas in the univariate regressions, we did not create a full model that combined habitat and hyenas.

Hyenas ~ Lions: full model				
<i>Count model (truncated poisson)</i>				
	Estimate	Std. Error	z	P
(Intercept)	-5.231	0.127	-41.350	< 0.0001
wildebeest	5.136	0.676	7.595	< 0.0001
gazelle	4.554	0.265	17.214	< 0.0001
buffalo	2.164	0.615	3.520	0.0004
shade	-0.134	0.017	-8.026	< 0.0001
% cover	0.307	0.031	10.049	< 0.0001
lions	47.143	3.624	13.009	< 0.0001
lions ²	-435.679	54.140	-8.047	< 0.0001
<i>Binomial model</i>				
	Estimate	Std. Error	z	P
(Intercept)	-1.730	0.995	-1.738	0.0822
gazelle	1.836	0.617	2.978	0.0029
wildebeest	2.245	0.978	2.297	0.0216
lion presence	1.339	0.579	2.313	0.0207
Cheetahs ~ Lions: Full model				
<i>Count model (truncated negbin)</i>				
	Estimate	Std. Error	z	P
(Intercept)	-3.882	1.112	-3.491	0.0005
tree isolation	0.000	0.000	1.866	0.0620
shade	0.288	0.108	2.663	0.0078
% cover	-0.858	0.324	-2.651	0.0080
lions	43.090	21.890	1.969	0.0490
lions ²	-461.400	306.900	-1.504	0.1327
<i>Binomial model</i>				
	Estimate	Std. Error	z	P
(Intercept)	1.571	1.617	0.972	0.3313
tree isolation	0.000	0.001	-0.414	0.6788
shade	0.121	0.269	0.451	0.6522
% cover	-0.829	0.395	-2.099	0.0358
habitat	-1.523	0.439	-3.466	0.0005
tree isolation * shade	0.001	0.000	2.794	0.0052
lion presence	0.837	0.396	2.113	0.0346

Table 3-4: Regression output from temporal models

Parameter estimates and p-values for univariate regressions of all predators on “time-since-predator” and “time-since-prey.” For example, “time-since-wildebeest” for lions reflects the number of hours since the last wildebeest was seen before each subsequent lion sighting. “Time since” values were binned into 12-hour periods, and univariate Poisson regressions run on the number of sightings in each bin for up to 3 days after the original sighting. Estimates and p-values are reported for all significant relationships.

Predator sightings since prey				
Species seen	Since	Estimate	Std. Error	P
Lion	gazelle	-0.157	0.047	0.001
	wildebeest	-0.291	0.065	<0.001
	buffalo	-0.197	0.067	0.003
Hyena	gazelle	-0.301	0.023	<2e-16
	wildebeest	-0.378	0.029	<2e-16
	buffalo	-0.198	0.034	0.000
Cheetah	gazelle	-0.175	0.088	0.047
	wildebeest	-0.265	0.116	0.022
	buffalo	<i>NS</i>	-	-
Predator sightings since other predator				
Species seen	Since	Estimate	Std. Error	P
Lion	hyena	-0.196	0.044	0.000
	cheetah	<i>NS</i>	-	-
Hyena	lion	-0.194	0.044	0.000
	cheetah	<i>NS</i>	-	-
Cheetah	lion	0.251	0.106	0.018
	hyena	<i>NS</i>	-	-

Figure 3-1: Study area

A) Serengeti National Park. Long-term lion project study area in center is indicated by dotted line; camera-trap study area is indicated by dashed line. **B)** Camera trap layout within the long-term Lion Project Study Area. Camera locations are plotted over tree cover (extracted from Landsat imagery), with darker green indicating increased tree cover per 30m²-grid cell.

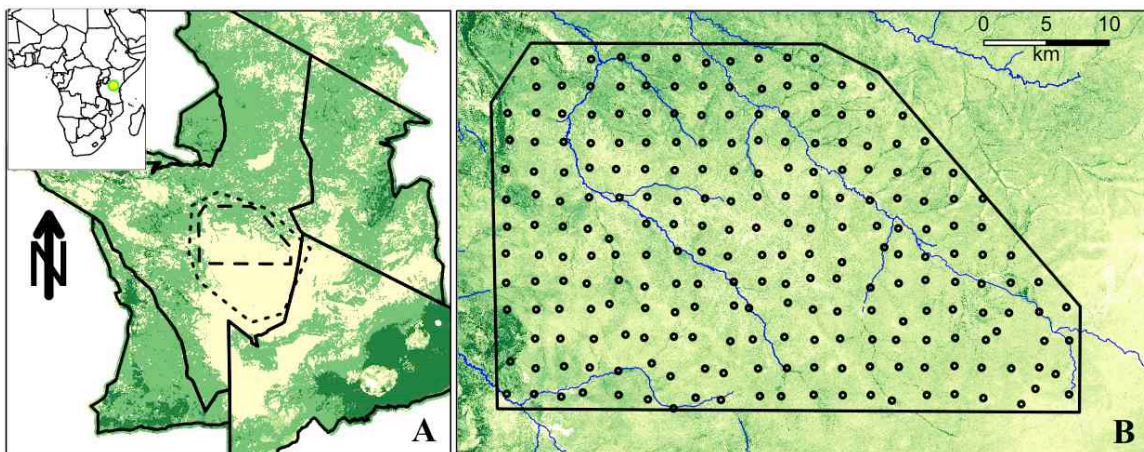


Figure 3-2: Camera trap detection curves

Probability that a collared lion was captured in a camera trap given that it was seen (via radio-telemetry) at 50, 100, 250, 500, and 1,000m away that same day. Circles are sized proportionally to the number of times a radio-collared lion was tracked within a given distance from each camera trap. Given that a lion was seen <100 m away, a camera trap had ~58% chance of photographing a lion that day, and this probability declined with distance.

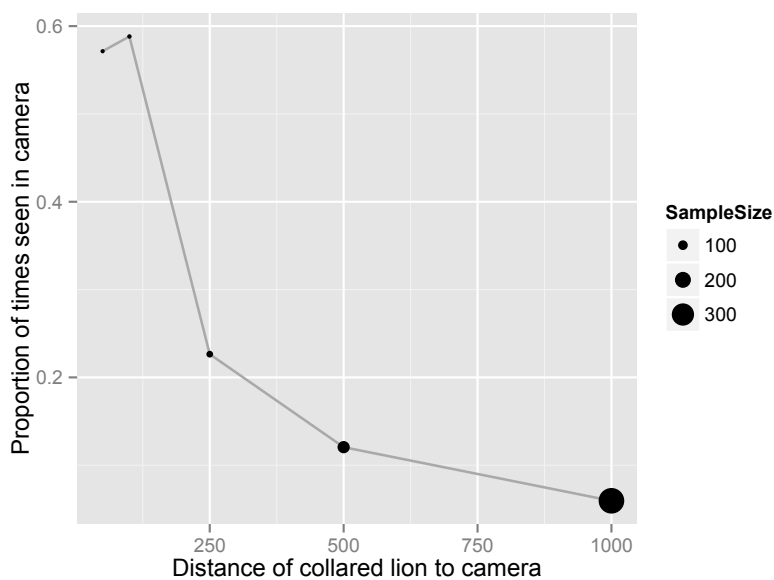


Figure 3-3: Lion and cheetah habitat relationships

Expected lion and cheetah counts at sites of varying tree isolation and shade quality, as predicted from the hurdle models (see Table 1). Both species were photographed more often at isolated trees, although lion abundance was dependent on an interaction between tree isolation and shade quality.

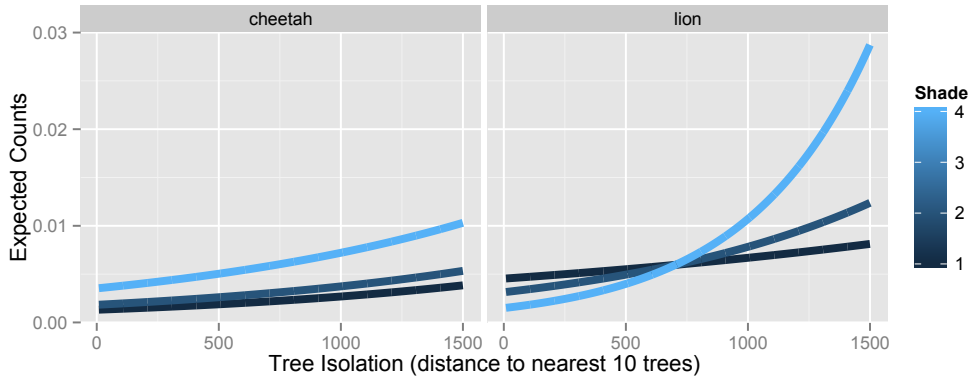


Figure 3-4: Mesopredator capture rates vs. dominant predator capture rates

A) Cheetah and hyena capture rates plotted against lion capture rates for each site. B) Cheetah capture rates plotted against hyena capture rates. Note that all axes are plotted on a square-root scale.

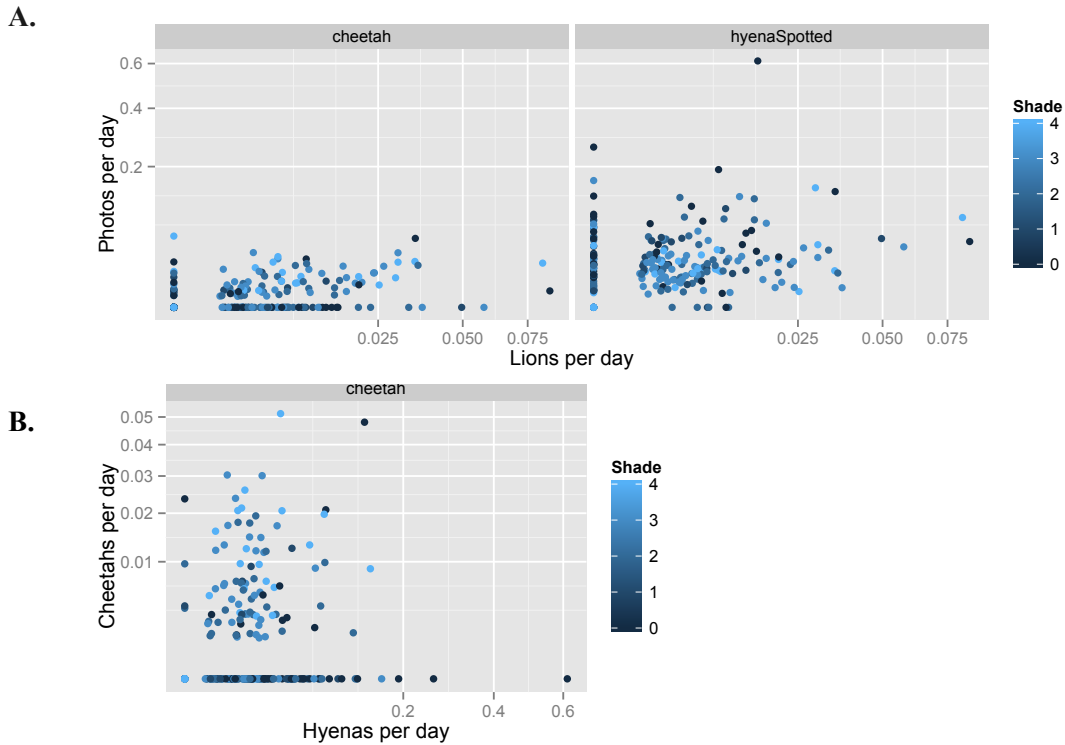


Figure 3-5: Predictions from full spatial models

Expected cheetah and hyena capture rates as specified by final regression models (hurdle models, selected via AIC, see Table 3) and plotted against lion capture rates at varying tree densities, holding all other parameters at their mean values. Cheetahs and hyenas show a significant quadratic relationship with lion numbers (see Tables 2-3), but note the high overlap in confidence intervals.

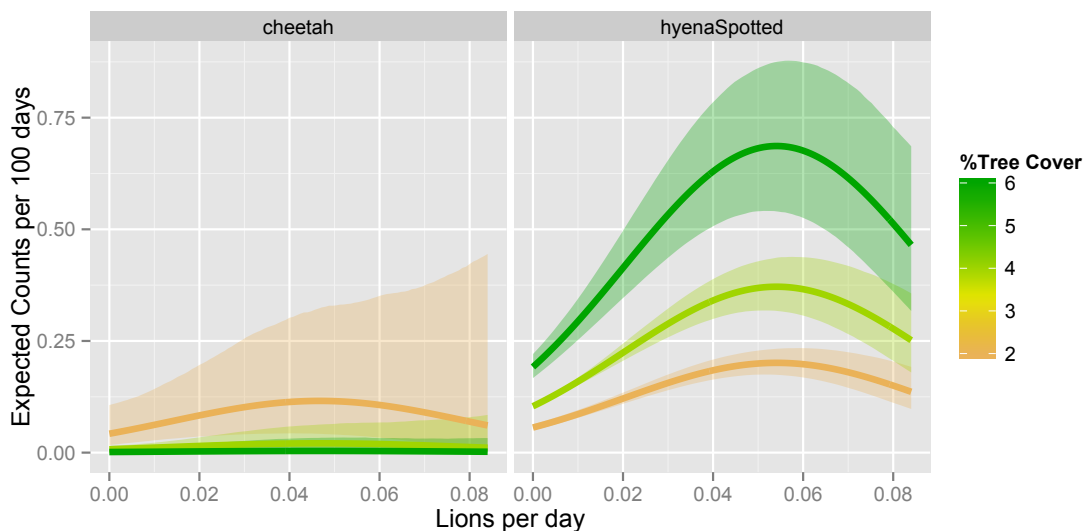


Figure 3-6: Temporal activity patterns

Temporal activity patterns calculated as the number of photographs per species per hour of the day. Daytime capture rates of lions and cheetahs reflect their use of shady trees and kopjes as daytime resting spots.

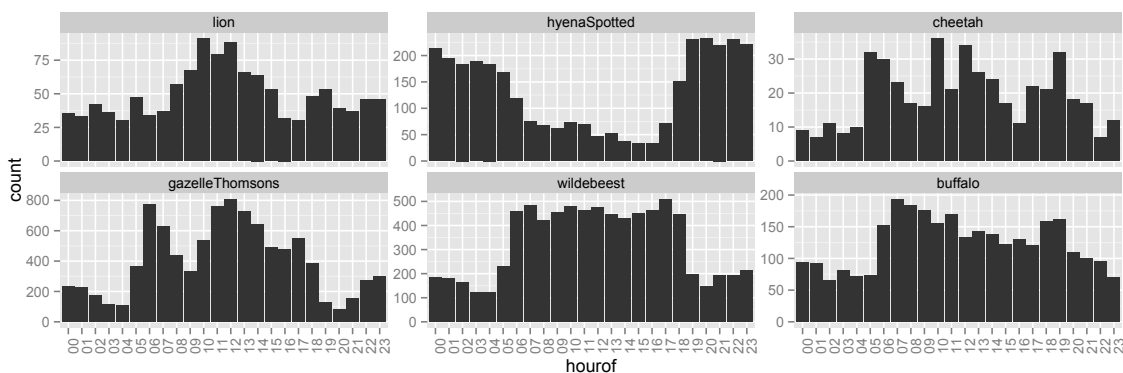


Figure 3-7: Short-term temporal response to prey

Total number of sightings lion, hyena, and cheetah sightings per 12-hour period following prey sightings, aggregated across all camera-trap sites. Histograms are faceted such that columns represent the first species seen and rows represent the species that follows. For example, the first chart in the first row shows number of lions seen per 12-hour period after a Thomson gazelle sighting.

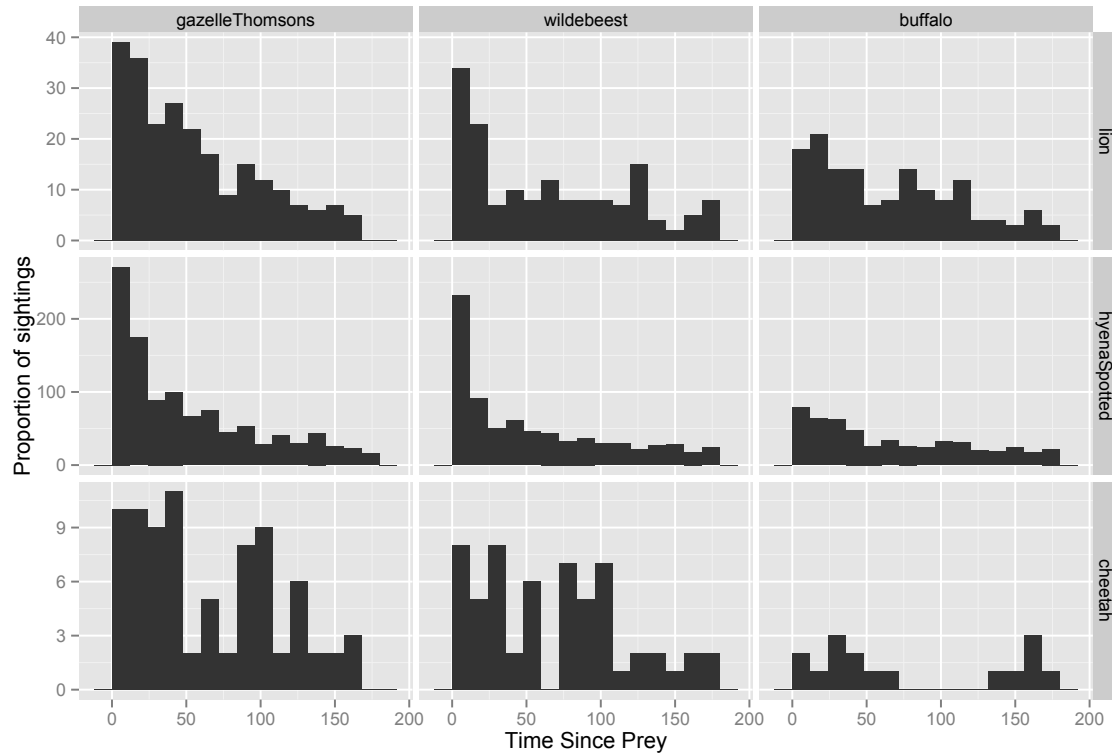
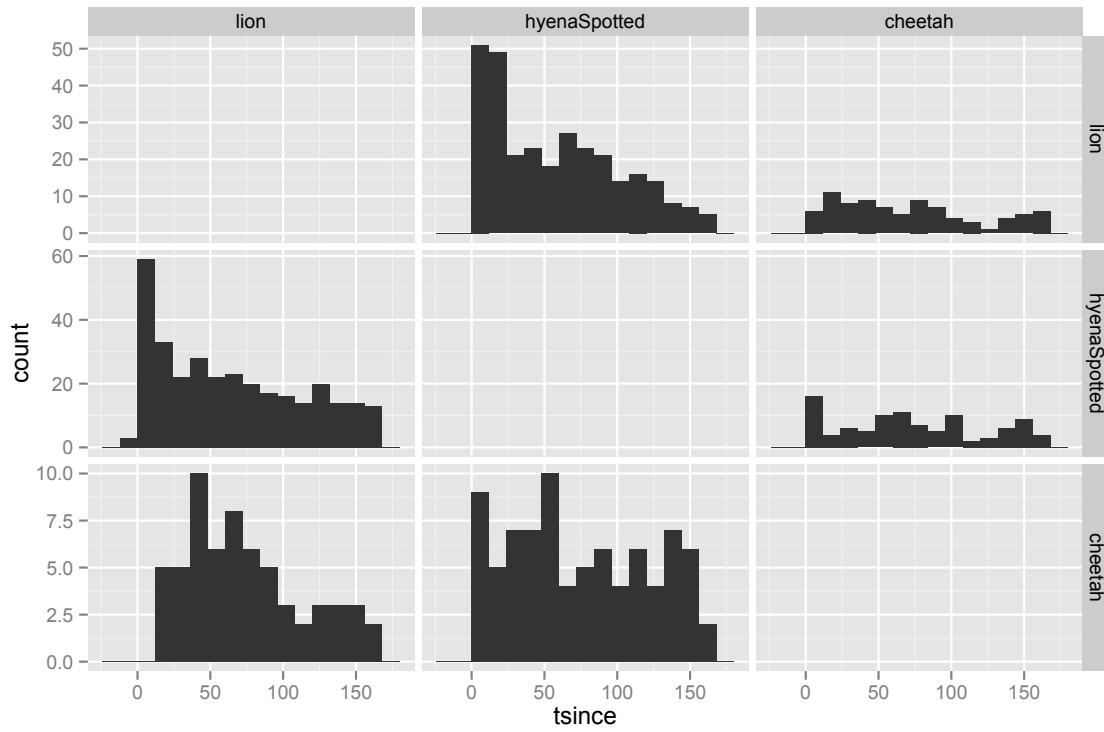


Figure 3-8: Short term temporal response to predators

Total number of sightings lion, hyena, and cheetah sightings per 12-hour period following predator sightings, aggregated across all camera-trap sites. Histograms are faceted such that columns represent the first species seen and rows represent the species that follows. For example, the middle chart in the first row shows number of lions seen per 12-hour period after a hyena sighting.



CONCLUSIONS

Together, these three chapters address the role of spatial and temporal avoidance in driving patterns of predator-predator coexistence. Chapter 1 suggests that lions suppress wild dogs primarily through non-consumptive “risk effects” by displacing them from large tracts of land. In contrast, Chapter 3 suggests that cheetahs are able to employ fine-scale temporal avoidance strategies that allow them to maintain access to prey and other necessary resources.

As expected, this dissertation raises a number of questions for future research. Theoretical and empirical studies indicate that ultimate patterns of intraguild predator coexistence should depend on habitat structure (Janssen *et al.* 2007), resource abundance (Bolnick & Preisser 2005; Elmhagen & Rushton 2007; Elmhagen *et al.* 2010), and species diversity (Creel & Christianson 2008; Brashares *et al.* 2010). To explore these scenarios, I have begun collaborations with researchers in South Africa to collate existing demographic and ranging data across a number of protected areas. This collaboration will integrate camera traps with VHF- and GPS-collar data across reserves that vary in terms of habitat structure, prey density, and even the presence and absence of lions. This collaboration will further fill a key gap from the Serengeti studies: the incorporation of leopards (*Panthera pardus*), for which data in Serengeti were too scarce.

Chapter 2 introduces and tests a powerful new approach to collecting and processing such ecological data. Camera traps are just one example of how scientists are increasingly collecting vast quantities of data through automated or remote sensing techniques. Many of these datasets contain images, videos, or sounds – types of data not easily processed by existing computer algorithms; many scientists are finding themselves overwhelmed by large volumes of data that need to be processed by people. My post-doctoral work with Zooniverse, an international citizen science organization, aims to develop generalizable tools that science teams around the world can use to build their own citizen science platform. Our first collaborations will be with the same ongoing South African research teams described above.

In this dissertation, I aimed to identify mechanisms driving patterns of intraguild predator coexistence. Not only did the studies herein identify fine-scale active avoidance as a key mechanism for mesopredator persistence, they lay a critical foundation for pursuing many more as yet unanswered questions about predator coexistence and larger ecological dynamics.

REFERENCES

- Anderson, T.M., Hopcraft, J.G.C., Eby, S., Ritchie, M., Grace, J.B. & Olf, H. (2010) Landscape-scale analyses suggest both nutrient and antipredator advantages to Serengeti herbivore hotspots. *Ecology*, **91**, 1519–1529.
- Azlan, J.M. & Sharma, D.S.K. (2006) The diversity and activity patterns of wild felids in a secondary forest in Peninsular Malaysia. *Oryx*, **40**, 36–41.
- Bailey, T.N. (1993) *The African Leopard: Ecology and Behavior of a Solitary Felid*. Blackburn Press.
- Beckerman, A.P., Uriarte, M. & Schmitz, O.J. (1997) Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. *Proceedings of the National Academy of Sciences*, **94**, 10735–10738.
- Berger, K.M. & Gese, E.M. (2007) Does Interference Competition with Wolves Limit the Distribution and Abundance of Coyotes? *Journal of Animal Ecology*, **76**, 1075–1085.
- Bischof, R., Ali, H., Kabir, M., Hameed, S. & Nawaz, M.A. (2014) Being the underdog: an elusive small carnivore uses space with prey and time without enemies. *Journal of Zoology*, n/a–n/a.
- Bissett, C. & Bernard, R.T.F. (2006) Habitat selection and feeding ecology of the cheetah (*Acinonyx jubatus*) in thicket vegetation: is the cheetah a savanna specialist? *Journal of Zoology*, **271**, 310–317.
- Bolnick, D.I. & Preisser, E.L. (2005) Resource competition modifies the strength of trait-mediated predator-prey interactions: a meta-analysis. *Ecology*, **86**, 2771–2779.
- Boone, R.B., Thirgood, S.J. & Hopcraft, J.G.C. (2006) Serengeti wildebeest migratory patterns modeled from rainfall and new vegetation growth. *Ecology*, **87**, 1987–1994.
- Borer, E.T., Briggs, C.J. & Holt, R.D. (2007) Predators, parasitoids, and pathogens: a cross-cutting examination of intraguild predation theory. *Ecology*, **88**, 2681–2688.
- Brashares, J., Prugh, L.R., Stoner, C.J. & Epps, C.W. (2010) Ecological and conservation implications of mesopredator release. *Trophic cascades: predators, prey, and the changing dynamics of nature* pp. 221–240.
- Broekhuis, F., Cozzi, G., Valeix, M., McNutt, J.W. & Macdonald, D.W. (2013) Risk avoidance in sympatric large carnivores: reactive or predictive? (ed J Fryxell). *Journal of Animal Ecology*, **82**, 1098–1105.
- Brook, L.A., Johnson, C.N. & Ritchie, E.G. (2012) Effects of predator control on behaviour of an apex predator and indirect consequences for mesopredator suppression. *Journal of Applied Ecology*, **49**, 1278–1286.

- Brown, J.S., Laundré, J.W. & Gurung, M. (1999) The ecology of fear: optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy*, **385**–399.
- Burrows, R., Hofer, H. & East, M.L. (1994) Demography, Extinction and Intervention in a Small Population: the Case of the Serengeti Wild Dogs. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **256**, 281–292.
- Calenge, C. (2006) The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, **197**, 516–519.
- Carbone, C., Christie, S., Conforti, K., Coulson, T., Franklin, N., Ginsberg, J.R., Griffiths, M., Holden, J., Kawanishi, K., Kinnaird, M., Laidlaw, R., Lynam, A., Macdonald, D.W., Martyr, D., McDougal, C., Nath, L., O’Brien, T., Seidensticker, J., Smith, D.J.L., Sunquist, M., Tilson, R. & Wan Shahrudin, W.N. (2001) The use of photographic rates to estimate densities of tigers and other cryptic mammals. *Animal Conservation*, **4**, 75–79.
- Carbone, C., Frame, L., Frame, G., Malcolm, J., Fanshawe, J., FitzGibbon, C., Schaller, G., Gordon, I.J., Rowcliffe, J.M. & Du Toit, J.T. (2005) Feeding success of African wild dogs (*Lycaon pictus*) in the Serengeti: the effects of group size and kleptoparasitism. *Journal of Zoology*, **266**, 153–161.
- Caro, T.M. (1994) *Cheetahs of the Serengeti Plains: Group Living in an Asocial Species*. University of Chicago Press, Chicago.
- Caro, T. & Laurenson, M. (1994) Ecological and genetic factors in conservation: a cautionary tale. *Science*, **263**, 485–486.
- Caro, T.M. & Stoner, C.J. (2003) The potential for interspecific competition among African carnivores. *Biological Conservation*, **110**, 67–75.
- Carothers, J.H. & Jaksić, F.M. (1984) Time as a Niche Difference: The Role of Interference Competition. *Oikos*, **42**, 403.
- Case, T.J. & Gilpin, M.E. (1974) Interference competition and niche theory. *Proceedings of the National Academy of Sciences*, **71**, 3073–3077.
- Chandler, R.B. & Royle, J.A. (2013) Spatially explicit models for inference about density in unmarked or partially marked populations. *The Annals of Applied Statistics*, **7**, 936–954.
- Chauvenet, A.L.M., Durant, S.M., Hilborn, R. & Pettorelli, N. (2011) Unintended Consequences of Conservation Actions: Managing Disease in Complex Ecosystems. *PLoS ONE*, **6**, e28671.
- Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual review of Ecology and Systematics*, **31**, 343–366.
- Cooper, S.M. (1991) Optimal hunting group size: the need for lions to defend their kills against loss to spotted hyaenas. *African Journal of Ecology*, **29**, 130–136.

- Cozzi, G. (2012) *Patterns of Habitat Use and Segregation among African Large Carnivores: A Case Study on the African Wild Dog (Lycaon Pictus), the Spotted Hyena (Crocuta Crocuta), and the Lion (Panthera Leo)*. Ph.D., University of Zurich.
- Cozzi, G., Broekhuis, F., McNutt, J.W., Turnbull, L.A., Macdonald, D.W. & Schmid, B. (2012) Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa's large carnivores. *Ecology*, **93**, 2590–2599.
- Creel, S. & Christianson, D. (2008) Relationships between direct predation and risk effects. *Trends in Ecology & Evolution*, **23**, 194–201.
- Creel, S. & Creel, N.M. (1996) Limitation of African wild dogs by competition with larger carnivores. *Conservation Biology*, **10**, 526–538.
- Creel, S. & Creel, N.M. (2002) *The African Wild Dog: Behavior, Ecology, and Conservation*. Princeton University Press, Princeton, NJ.
- Creel, S., Spong, G. & Creel, N. (2001) Interspecific competition and the population biology of extinction-prone carnivores. *Carnivore Conservation* (eds J.L. Gittleman, S.M. Funk, D.W. MacDonald & R.K. Wayne), pp. 35–60. Cambridge University Press, Cambridge.
- Creel, S., Winnie, J., Maxwell, B., Hamlin, K. & Creel, M. (2005) Elk alter habitat selection as an antipredator response to wolves. *Ecology*, **86**, 3387–3397.
- Cresswell, W. (2008) Non-lethal effects of predation in birds. *Ibis*, **150**, 3–17.
- Crooks, K.R., Sanjayan, M.A. & Doak, D.F. (1998) New insights on cheetah conservation through demographic modeling. *Conservation Biology*, **12**, 889–895.
- Crooks, K.R. & Soulé, M.E. (1999) Mesopredator release and avifaunal extinctions in a fragmented system. *Nature*, **400**, 563–566.
- Davies-Mostert, H. (2010) *The Managed Metapopulation Approach for African Wild Dog (Lycaon Pictus) Conservation in South Africa*. Ph.D., University of Oxford.
- Dillon, A. & Kelly, M.J. (2007) Ocelot *Leopardus pardalis* in Belize: the impact of trap spacing and distance moved on density estimates. *Oryx*, **41**, 469–477.
- Donadio, E. & Buskirk, S.W. (2006) Diet, morphology, and interspecific killing in Carnivora. *The American Naturalist*, **167**, 524–536.
- Durant, S.M. (1998) Competition Refuges and Coexistence: An Example from Serengeti Carnivores. *Journal of Animal Ecology*, **67**, 370–386.
- Durant, S.M. (2000) Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. *Behavioral Ecology*, **11**, 624–632.

- Durant, S.M., Caro, T.M., Collins, D.A., Alawi, R.M. & FitzGibbon, C.D. (1988) Migration patterns of Thomson's gazelles and cheetahs on the Serengeti plains. *African Journal of Ecology*, **26**, 257–268.
- Durant, S.M., Craft, M.E., Hilborn, R., Bashir, S., Hando, J. & Thomas, L. (2011) Long-term trends in carnivore abundance using distance sampling in Serengeti National Park, Tanzania. *Journal of Applied Ecology*, **48**, 1490–1500.
- Durant, S.M., Kelly, M. & Caro, T.M. (2004) Factors affecting life and death in Serengeti cheetahs: environment, age, and sociality. *Behavioral Ecology*, **15**, 11–22.
- Elmhagen, B., Ludwig, G., Rushton, S.P., Helle, P. & Lindén, H. (2010) Top predators, mesopredators and their prey: interference ecosystems along bioclimatic productivity gradients. *Journal of Animal Ecology*, **79**, 785–794.
- Elmhagen, B. & Rushton, S.P. (2007) Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? *Ecology Letters*, **10**, 197–206.
- Estes, R.D. (1991) *The Behavior Guide to African Mammals: Including Hoofed Mammals, Carnivores, Primates*. University of California Press, Berkeley.
- Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D. & Jackson, J.B. (2011) Trophic downgrading of planet earth. *science*, **333**, 301–306.
- Fanshawe, J.H. & Fitzgibbon, C.D. (1993) Factors influencing the hunting success of an African wild dog pack. *Animal Behaviour*, **45**, 479–490.
- Fedriani, J.M., Fuller, T.K., Sauvajot, R.M. & York, E.C. (2000) Competition and intraguild predation among three sympatric carnivores. *Oecologia*, **125**, 258–270.
- Fedriani, J.M., Palomares, F. & Delibes, M. (1999) Niche relations among three sympatric Mediterranean carnivores. *Oecologia*, **121**, 138–148.
- Finke, D.L. & Denno, R.F. (2002) Intraguild predation diminished in complex-structured vegetation: implications for prey suppression. *Ecology*, **83**, 643–652.
- Finke, D.L. & Denno, R.F. (2006) Spatial refuge from intraguild predation: implications for prey suppression and trophic cascades. *Oecologia*, **149**, 265–275.
- Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T. & Mao, J.S. (2005) WOLVES INFLUENCE ELK MOVEMENTS: BEHAVIOR SHAPES A TROPHIC CASCADE IN YELLOWSTONE NATIONAL PARK. *Ecology*, **86**, 1320–1330.
- Foster, R.J. & Harmsen, B.J. (2012) A critique of density estimation from camera-trap data. *The Journal of Wildlife Management*, **76**, 224–236.

- Frame, L.H., Malcolm, J.R., Frame, G.W. & Van Lawick, H. (1979) Social Organization of African Wild Dogs (*Lycaon pictus*) on the Serengeti Plains, Tanzania 1967–19781. *Zeitschrift für Tierpsychologie*, **50**, 225–249.
- Fuller, T.K. & Keith, L.B. (1981) Non-Overlapping Ranges of Coyotes and Wolves in Northeastern Alberta. *Journal of Mammalogy*, **62**, 403–405.
- Galloway, A.W.E., Tudor, M.T., Haegan, W.M.V. & West. (2006) The Reliability of Citizen Science: A Case Study of Oregon White Oak Stand Surveys. *Wildlife Society Bulletin*, **34**, 1425–1429.
- Gardiner, M.M., Allee, L.L., Brown, P.M., Losey, J.E., Roy, H.E. & Smyth, R.R. (2012) Lessons from lady beetles: accuracy of monitoring data from US and UK citizen-science programs. *Frontiers in Ecology and the Environment*, **10**, 471–476.
- Gorman, M., Mills, M., Raath, J. & Speakman, J. (1998) High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyaenas. *Nature January 29, 1998*, **391**, 479–481.
- Hampson, K., Dushoff, J., Cleaveland, S., Haydon, D.T., Kaare, M., Packer, C. & Dobson, A. (2009) Transmission Dynamics and Prospects for the Elimination of Canine Rabies. *PLoS Biol*, **7**, e1000053.
- Hanby, J.P. & Bygott, J.D. (1979) Population changes in lions and other predators. *Serengeti: Dynamics of an Ecosystem* (eds A.R.E. Sinclair & M. Norton-Griffiths), pp. 249 – 262. Chicago University Press, Chicago.
- Harris, G., Thompson, R., Childs, J.L. & Sanderson, J.G. (2010) Automatic Storage and Analysis of Camera Trap Data. *Bulletin of the Ecological Society of America*, **91**, 352–360.
- Hayward, M.W. (2006) Prey preferences of the spotted hyaena (*Crocuta crocuta*) and degree of dietary overlap with the lion (*Panthera leo*). *Journal of Zoology*, **270**, 606–614.
- Hayward, M.W. & Slotow, R. (2009) Temporal Partitioning of Activity in Large African Carnivores: Tests of Multiple Hypotheses. *South African Journal of Wildlife Research*, **39**, 109–125.
- Van Heerden, J., Mills, M.G., Van Vuuren, M.J., Kelly, P.J. & Dreyer, M.J. (1995) An investigation into the health status and diseases of wild dogs (*Lycaon pictus*) in the Kruger National Park. *Journal of South African Veterinary Association*, **66**, 18–27.
- Hofer, H. & East, M.L. (1995) Population dynamics, population size, and the commuting system of Serengeti spotted hyenas. *Serengeti II: Dynamics, Management, and Conservation of an Ecosystem* (eds A.R.E. Sinclair & P. Arcese), pp. 332–363. University of Chicago Press, Chicago.
- Holden, J., Yanuar, A. & Martyr, D.J. (2003) The Asian Tapir in Kerinci Seblat National Park, Sumatra: evidence collected through photo-trapping. *Oryx*, **37**, 34–40.

- Holdo, R.M., Holt, R.D. & Fryxell, J.M. (2009) Opposing Rainfall and Plant Nutritional Gradients Best Explain the Wildebeest Migration in the Serengeti. *The American Naturalist*, **173**, 431–445.
- Holt, R.D. & Polis, G.A. (1997) A theoretical framework for intraguild predation. *American Naturalist*, **149**, 745–764.
- Höner, O.P., Wachter, B., East, M.L. & Hofer, H. (2002) The response of spotted hyaenas to long-term changes in prey populations: functional response and interspecific kleptoparasitism. *Journal of Animal Ecology*, **71**, 236–246.
- Hopcraft, J.G.C., Sinclair, A.R.E. & Packer, C. (2005) Planning for success: Serengeti lions seek prey accessibility rather than abundance: Prey accessibility in Serengeti lions. *Journal of Animal Ecology*, **74**, 559–566.
- Janssen, A., Sabelis, M.W., Magalhães, S., Montserrat, M. & Van der Hammen, T. (2007) Habitat structure affects intraguild predation. *Ecology*, **88**, 2713–2719.
- Kamler, J.F., Ballard, W.B., Gilliland, R.L., II, P.R.L. & Mote, K. (2003a) Impacts of Coyotes on Swift Foxes in Northwestern Texas. *The Journal of Wildlife Management*, **67**, 317–323.
- Kamler, J.F., Ballard, W.B., Gilliland, R.L. & Mote, K. (2003b) Spatial relationships between swift foxes and coyotes in northwestern Texas. *Canadian Journal of Zoology*, **81**, 168–172.
- Kamler, J.F., Stenkewitz, U. & Macdonald, D.W. (2013) Lethal and sublethal effects of black-backed jackals on cape foxes and bat-eared foxes. *Journal of Mammalogy*, **94**, 295–306.
- Karanth, K.U. (1995) Estimating tiger (<i>Panthera tigris</i>) populations from camera-trap data using capture—recapture models. *Biological conservation*, **71**, 333–338.
- Karki, S.M., Gese, E.M. & Klavetter, M.L. (2007) Effects of Coyote Population Reduction on Swift Fox Demographics in Southeastern Colorado. *The Journal of Wildlife Management*, **71**, 2707–2718.
- Kauffman, M.J., Brodie, J.F. & Jules, E.S. (2010) Are wolves saving Yellowstone’s aspen? A landscape-level test of a behaviorally mediated trophic cascade. *Ecology*, **91**, 2742–2755.
- Kelly, M.J. (2008) Design, evaluate, refine: camera trap studies for elusive species. *Animal Conservation*, **11**, 182–184.
- Kelly, M.J. & Durant, S.M. (2000) Viability of the Serengeti Cheetah Population. *Conservation Biology*, **14**, 786–797.
- Kelly, M.J., Laurenson, M.K., FitzGibbon, C.D., Collins, D.A., Durant, S.M., Frame, G.W., Bertram, B.C. & Caro, T.M. (1998) Demography of the Serengeti cheetah (*Acinonyx jubatus*) population: the first 25 years. *Journal of Zoology*, **244**, 473–488.

- Kéry, M. (2010) *Introduction to WinBUGS for Ecologists – a Bayesian Approach to Regression, ANOVA, Mixed Models and Related Analyses*. Academic Press, Burlington, MA.
- Kissui, B.M. & Packer, C. (2004) Top–down population regulation of a top predator: lions in the Ngorongoro Crater. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **271**, 1867–1874.
- Kruuk, H. (1972) *The Spotted Hyena: A Study of Predation and Social Behavior*. University of Chicago Press Chicago, Chicago.
- Laundré, J.W., Hernández, L. & Altendorf, K.B. (2001) Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology*, **79**, 1401–1409.
- Laurenson, M.K. (1992) *Reproductive Strategies in Wild Female Cheetahs*. Ph.D., University of Cambridge, Cambridge.
- Laurenson, M.K. (1993) Early maternal behavior of wild cheetahs: Implications for captive husbandry. *Zoo Biology*, **12**, 31–43.
- Laurenson, M.K. (1994) High juvenile mortality in cheetahs (*Acinonyx jubatus*) and its consequences for maternal care. *Journal of Zoology*, **234**, 387–408.
- Laurenson, M.K. (1995) Implications of high offspring mortality for cheetah population dynamics. *Serengeti II: Dynamics, Management, and Conservation of an Ecosystem* (eds A.R.E. Sinclair & P. Arcese), pp. 385–399. University of Chicago Press.
- Lindsey, P., Tambling, C. j., Brummer, R., Davies-Mostert, H., Hayward, M., Marnewick, K. & Parker, D. (2011) Minimum prey and area requirements of the Vulnerable cheetah *Acinonyx jubatus*: implications for reintroduction and management of the species in South Africa. *Oryx*, **45**, 587–599.
- Linnell, J.D.C. & Strand, O. (2000) Interference Interactions, Co-Existence and Conservation of Mammalian Carnivores. *Diversity and Distributions*, **6**, 169–176.
- Long, R.A., MacKay, P., Ray, J. & Zielinski, W. (2008) *Noninvasive Survey Methods for Carnivores*. Island Press.
- Macdonald, D.W. (1992) Cause of wild dog deaths. *Nature*, **360**, 633–634.
- MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L. & Hines, J.E. (eds). (2006) *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species*. Elsevier, Amsterdam ; Boston.
- Maddox, T.M. (2003) *The Ecology of Cheetahs and Other Large Carnivores in a Pastoralist-Dominated Buffer Zone*. Ph.D., University of London.
- Maron, J.L., Estes, J.A., Croll, D.A., Danner, E.M., Elmendorf, S.C. & Buckelew, S.L. (2006) AN INTRODUCED PREDATOR ALTERS ALEUTIAN ISLAND PLANT

COMMUNITIES BY THWARTING NUTRIENT SUBSIDIES. *Ecological Monographs*, **76**, 3–24.

- Mills, M.G.L., Broomhall, L.S. & du Toit, J.T. (2004) Cheetah *Acinonyx jubatus* feeding ecology in the Kruger National Park and a comparison across African savanna habitats: is the cheetah only a successful hunter on open grassland plains? *Wildlife Biology*, **10**, 177–186.
- Mills, M.G.L. & Gorman, M.L. (1997) Factors Affecting the Density and Distribution of Wild Dogs in the Kruger National Park. *Conservation Biology*, **11**, 1397–1406.
- Mills, M.G.L. & Mills, M.E.J. (2013) Cheetah cub survival revisited: a re-evaluation of the role of predation, especially by lions, and implications for conservation. *Journal of Zoology*, n/a–n/a.
- Mizutani, F. & Jewell, P.A. (1998) Home-range and movements of leopards (*Panthera pardus*) on a livestock ranch in Kenya. *Journal of Zoology*, **244**, 269–286.
- Moseby, K.E., Neilly, H., Read, J.L. & Crisp, H.A. (2012) Interactions between a Top Order Predator and Exotic Mesopredators in the Australian Rangelands. *International Journal of Ecology*, **2012**.
- Mosser, A., Fryxell, J.M., Eberly, L. & Packer, C. (2009) Serengeti real estate: density vs. fitness-based indicators of lion habitat quality. *Ecology Letters*, **12**, 1050–1060.
- Myers, R.A., Baum, J.K., Shepherd, T.D., Powers, S.P. & Peterson, C.H. (2007) Cascading Effects of the Loss of Apex Predatory Sharks from a Coastal Ocean. *Science*, **315**, 1846–1850.
- Newman, G., Wiggins, A., Crall, A., Graham, E., Newman, S. & Crowston, K. (2012) The future of citizen science: emerging technologies and shifting paradigms. *Frontiers in Ecology and the Environment*, **10**, 298–304.
- O’Brien, T. (2011) Abundance, density and relative abundance: a conceptual framework. *Camera Traps in Animal Ecology. Methods and Analyses*. (eds A.F. O’Connell, J.D. Nichols & U.D. Karanth), pp. 71–96. Springer, New York.
- O’Brien, T.G., Baillie, J.E.M., Krueger, L. & Cuke, M. (2010) The Wildlife Picture Index: monitoring top trophic levels: The Wildlife Picture Index. *Animal Conservation*, **13**, 335–343.
- O’Brien, T.G., Kinnaird, M.F. & Wibisono, H.T. (2003) Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Animal Conservation*, **6**, 131–139.
- O’Connell, A.F., Nichols, J.D. & Karanth, K.U. (eds). (2011) *Camera Traps in Animal Ecology: Methods and Analyses*. Springer, New York.

- Packer, C., Hilborn, R., Mosser, A., Kissui, B., Borner, M., Hopcraft, G., Wilmshurst, J., Mduma, S. & Sinclair, A.R.E. (2005) Ecological Change, Group Territoriality, and Population Dynamics in Serengeti Lions. *Science*, **307**, 390–393.
- Packer, C., Swanson, A., Ikanda, D. & Kushnir, H. (2011) Fear of Darkness, the Full Moon and the Nocturnal Ecology of African Lions. *PLoS ONE*, **6**, e22285.
- Palomares, F. & Caro, T.M. (1999) Interspecific Killing among Mammalian Carnivores. *The American Naturalist*, **153**, 492–508.
- Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.-M., Tucker, C.J. & Stenseth, N.C. (2005) Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology & Evolution*, **20**, 503–510.
- Pielou, E.C. (1966) Species-diversity and pattern-diversity in the study of ecological succession. *Journal of Theoretical Biology*, **10**, 370–383.
- Pinheiro, J., Bates, D. & Sarker, D. (2012) *Nlme: Linear and Nonlinear Mixed Effects Models. R Package Version 3.1-104*.
- Preisser, E.L., Bolnick, D.I. & Benard, M.F. (2005) Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology*, **86**, 501–509.
- Prugh, L.R., Stoner, C.J., Epps, C.W., Bean, W.T., Ripple, W.J., Laliberte, A.S. & Brashares, J.S. (2009) The Rise of the Mesopredator. *BioScience*, **59**, 779–791.
- Pusey, A.E. & Packer, C. (1987) The evolution of sex-biased dispersal in lions. *Behaviour*, **101**, 275–310.
- R Core Team. (2013) *R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing*. Vienna, Austria.
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D. & Wirsing, A.J. (2014) Status and Ecological Effects of the World's Largest Carnivores. *Science*, **343**, 1241484.
- Ritchie, E.G., Elmhagen, B., Glen, A.S., Letnic, M., Ludwig, G. & McDonald, R.A. (2012) Ecosystem restoration with teeth: what role for predators? *Trends in Ecology & Evolution*, **27**, 265–271.
- Ritchie, E.G. & Johnson, C.N. (2009) Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, **12**, 982–998.
- Rivero, K., Rumiz, D.I. & Taber, A.B. (2005) Differential habitat use by two sympatric brocket deer species (*Mazama americana* and *M. gouazoubira*) in a seasonal Chiquitano forest of Bolivia. *Mammalia mamm*, **69**, 169–183.

- Robinson, Q.H., Bustos, D. & Roemer, G.W. (2014) The Application of Occupancy Modeling to Evaluate Intraguild Predation in a Model Carnivore System. *Ecology*.
- Rovero, F. & Marshall, A.R. (2009) Camera trapping photographic rate as an index of density in forest ungulates. *Journal of Applied Ecology*, **46**, 1011–1017.
- Rowcliffe, J.M., Field, J., Turvey, S.T. & Carbone, C. (2008) Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology*, **45**, 1228–1236.
- Rowlison, B. & Diggle, P. (2013) *Splancs: Spatial and Space-Time Point Pattern Analysis*.
- Royle, J.A. & Dorazio, R.M. (2008) *Hierarchical Modeling and Inference in Ecology: The Analysis of Data from Populations, Metapopulations and Communities*. Academic, Burlington, MA.
- Royle, J.A., Karanth, K.U., Gopalaswamy, A.M. & Kumar, N.S. (2009) Bayesian inference in camera trapping studies for a class of spatial capture–recapture models. *Ecology*, **90**, 3233–3244.
- Royle, J.A. & Nichols, J.D. (2003) Estimating abundance from repeated presence-absence data or point counts. *Ecology*, **84**, 777–790.
- Salo, P., Nordström, M., Thomson, R.L. & Korpimäki, E. (2008) Risk Induced by a Native Top Predator Reduces Alien Mink Movements. *Journal of Animal Ecology*, **77**, 1092–1098.
- Schaller, G.B. (1972) *The Serengeti Lion: A Study of Predator-Prey Relations*. University of Chicago Press.
- Schmitz, O.J., Beckerman, A.P. & O'Brien, K.M. (1997) BEHAVIORALLY MEDIATED TROPHIC CASCADES: EFFECTS OF PREDATION RISK ON FOOD WEB INTERACTIONS. *Ecology*, **78**, 1388–1399.
- Schmitz, O.J., Krivan, V. & Ovadia, O. (2004) Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters*, **7**, 153–163.
- Schoener, T. (1983) Field Experiments on Interspecific Competition. *American Naturalist*, **122**, 240–285.
- Sergio, F. & Hiraldo, F. (2008) Intraguild predation in raptor assemblages: a review. *Ibis*, **150**, 132–145.
- Shirley, M.D.F., Elmhagen, B., Lurz, P.W.W., Rushton, S.P. & Angerbjörn, A. (2009) Modelling the spatial population dynamics of arctic foxes: the effects of red foxes and microtine cycles. *Canadian Journal of Zoology*, **87**, 1170–1183.
- Sinclair, A.R.E. (1995) Serengeti past and present. *Serengeti II: Dynamics, Management, and Conservation of an Ecosystem* (eds A.R.E. Sinclair & P. Arcese), pp. 3–30. University of Chicago Press.

- Sinclair, A.R.E. & Norton-Griffiths, M. (1979) *Serengeti: Dynamics of an Ecosystem*. University of Chicago Press.
- Sinclair, A.R.E., Packer, C., Mduma, S.A.R. & Fryxell, J.M. (2008) *Serengeti III: Human Impacts on Ecosystem Dynamics*. University of Chicago Press.
- Sollmann, R., Gardner, B., Parsons, A.W., Stocking, J.J., McClintock, B.T., Simons, T.R., Pollock, K.H. & O'Connell, A.F. (2013a) A spatial mark–resight model augmented with telemetry data. *Ecology*, **94**, 553–559.
- Sollmann, R., Mohamed, A., Samejima, H. & Wilting, A. (2013b) Risky business or simple solution – Relative abundance indices from camera-trapping. *Biological Conservation*, **159**, 405–412.
- Soulé, M.E., Bolger, D.T., Alberts, A.C., Wrights, J., Sorice, M. & Hill, S. (1988) Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology*, **2**, 75–92.
- Strauss, M.K.L. & Packer, C. (2013) Using claw marks to study lion predation on giraffes of the Serengeti. *Journal of Zoology*, **289**, 134–142.
- SurrIDGE, A., Timmins, R., Hewitt, G. & Bell, D. (1999) Striped rabbits in Southeast Asia. *Nature August 19, 1999*, **400**.
- Swanson, A., Caro, T., Davies-Mostert, H., Mills, M.G.L., Macdonald, D.W., Borner, M., Masenga, E. & Packer, C. (2014) Cheetahs and wild dogs show contrasting patterns of suppression by lions. *Journal of Animal Ecology*, n/a–n/a.
- Tannerfeldt, M., Elmhagen, B. & Angerbjörn, A. (2002) Exclusion by interference competition? The relationship between red and arctic foxes. *Oecologia*, **132**, 213–220.
- TAWIRI. (2008) *Aerial Census in the Serengeti Ecosystem*. Tanzania Wildlife Research Institute.
- TAWIRI. (2010) *Aerial Census in the Serengeti Ecosystem*. Tanzania Wildlife Research Institute.
- Thurber, J.M., Peterson, R.O., Woolington, J.D. & Vucetich, J.A. (1992) Coyote coexistence with wolves on the Kenai Peninsula, Alaska. *Canadian Journal of Zoology*, **70**, 2494–2498.
- Tobler, M.W., Carrillo-Percegué, S.E., Leite Pitman, R., Mares, R. & Powell, G. (2008) An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. *Animal Conservation*, **11**, 169–178.
- Valeix, M., Fritz, H., Loveridge, A.J., Davidson, Z., Hunt, J.E., Murindagomo, F. & Macdonald, D.W. (2009a) Does the risk of encountering lions influence African herbivore behaviour at waterholes? *Behavioral Ecology and Sociobiology*, **63**, 1483–1494.
- Valeix, M., Loveridge, A.J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H. & Macdonald, D.W. (2009b) Behavioral adjustments of African herbivores to predation risk by lions: Spatiotemporal variations influence habitat use. *Ecology*, **90**, 23–30.

- Vanak, A.T., Fortin, D., Thaker, M., Ogden, M., Owen, C., Greatwood, S. & Slotow, R. (2013) Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. *Ecology*, **94**, 2619–2631.
- Voigt, D.R. & Earle, B.D. (1983) Avoidance of Coyotes by Red Fox Families. *The Journal of Wildlife Management*, **47**, 852–857.
- Wacher, T. & Attum, O. (2005) Preliminary investigation into the presence and distribution of small carnivores in the Empty Quarter of Saudi Arabia through the use of a camera trap. *Mammalia mamm*, **69**, 81–84.
- Waddle, J.H., Dorazio, R.M., Walls, S.C., Rice, K.G., Beauchamp, J., Schuman, M.J. & Mazzotti, F.J. (2010) A new parameterization for estimating co-occurrence of interacting species. *Ecological Applications*, **20**, 1467–1475.
- Wallach, A.D., Johnson, C.N., Ritchie, E.G. & O’Neill, A.J. (2010) Predator control promotes invasive dominated ecological states. *Ecology Letters*, **13**, 1008–1018.
- Watts, H.E. & Holekamp, K.E. (2008) Interspecific competition influences reproduction in spotted hyenas. *Journal of Zoology*, **276**, 402–410.
- Webster, H., McNutt, J.W. & McComb, K. (2012) African Wild Dogs as a Fugitive Species: Playback Experiments Investigate How Wild Dogs Respond to their Major Competitors: African Wild Dogs as a Fugitive Species. *Ethology*, **118**, 147–156.
- Weckel, M., Giuliano, W. & Silver, S. (2006) Jaguar (*Panthera onca*) feeding ecology: distribution of predator and prey through time and space. *Journal of Zoology*, **270**, 25–30.
- Werner, E.E. & Peacor, S.D. (2003) A review of trait-mediated indirect interactions in ecological communities. *Ecology*, **84**, 1083–1100.
- West, P.M. & Packer, C. (2002) Sexual Selection, Temperature, and the Lion’s Mane. *Science*, **297**, 1339–1343.
- Wirsing, A.J., Heithaus, M.R. & Dill, L.M. (2007) Living on the edge: dugongs prefer to forage in microhabitats that allow escape from rather than avoidance of predators. *Animal Behaviour*, **74**, 93–101.
- Woodroffe, R. & Ginsberg, J.R. (1999) Conserving the African wild dog *Lycaon pictus*. I. Diagnosing and treating causes of decline. *Oryx*, **33**, 132–142.
- Wuertz, D. & Chalabi, Y. (2013) *timeSeries: Rmetrics - Financial Time Series Objects*. R Package Version 3010.97.
- Zielinski, W.J. & Kucera, T.E. (1995) American marten, fisher, lynx, and wolverine: survey methods for their detection. *USDA Forest Service General Technical Report, PSW GTR-157*.

Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M. (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York.

APPENDIX 1: Additional Tables and Figures for Chapter 1

Table A1-1: Presence and density of lions and cheetahs across reserves.

Reserve size, cheetah density, and lion presence are taken from Lindsey *et al.* (2011); lion density data are from Packer *et al.* (2013), except (a) from Hayward *et al.* (2007a) and (b) from Hayward *et al.* (2007b). Densities are reported as # adults & sub-adults per 100km². Plus signs under lion density indicate lion presence but unknown density. Prey biomass (kg/km²) is calculated from species-specific densities given in Lindsey *et al.* (2011) and average male biomass (Estes 1992).

Reserve	Area	Cheetah Density	Lion Density	Prey
Amakhala	55	14.55	0.00	NA
Blaauwbosch	35	11.43	+	NA
Bushman Sands	70	2.86	0.00	NA
Entabeni	80	2.50	+	NA
Glen Lyon	100	5.00	0.00	NA
Greater	80	10.00	0.00	NA
Greater Mokolo	200	1.50	+	NA
Hlambanyati	60	6.67	0.00	NA
Hlu.iMfolozi	960	3.13	11.90	71.9
Hopewell	27	11.11	0.00	NA
Jubatus	22	13.64	0.00	32.4
Karongwe	80	6.25	+	97.5
Kuzuko/Addo	151	5.96	+	NA
Kwandwe	210	3.81	13.50	24.3
Kwekwe	10	20.00	0.00	NA
Lalibela	64	3.13	+	NA
Madikwe	620	0.16	17.70	38.7
Makalali	260	3.46	13.80	NA
Makulu Makete	45	4.44	0.00	28.7
Makutsi	39	5.13	0.00	NA
Mkhuze	400	2.75	0.00	NA
Mkuze falls	80	6.25	+	NA
Mountain Zebra	214	6.07	0.00	21.2
Nambiti	80	6.25	+	NA
Nkomazi	200	1.00	+	NA
Phinda	210	17.62	18.35	71.4
Phumba	65 ^b	3.08 ^a	6.15 ^a	NA
Pilanesberg	572	0.35	11.40	NA
Samara	140	5.00	0.00	NA
Sanbona	540	1.11	+	NA
Shambala	120	1.67	7.50	NA
Shamwari	187 ^b	3.21 ^a	8.02 ^a	27.5
Thaba Tholo	320	6.25	+	NA
Thornybush	115	6.96	+	NA
Tswalu 2	800	0.50	0.00	NA
Tswalu 1	200	2.00	+	NA
Welgevonden	400	1.25	7.00	NA
Witwater	45	4.44	0.00	NA
Zululand Rhino	220	1.82	0.00	NA

Table A1-2. Model output for population analyses.

All generalized least squares models (*gls*) were run with an auto-regressive correlation function. *Df* reflects total degrees of freedom; *Phi* reflects the autocorrelation parameter between subsequent values of the response variable. Parameter estimates are reported only for the term of interest, *Lion*.

Model	df	Phi	Est. +/- SE (lion term)	p (lion term)
Population Size				
Cheetah _t ~ Lion _t	29	0.55	0.12 +/- 0.09	0.198
Cheetah _t ~ Lion _{t-1}	29	0.51	0.04 +/- 0.09	0.634
Cheetah _t ~ Lion _t + T.gaz	8	0.00	0.25 +/- 0.06	0.011
Cheetah _t ~ Lion _t + T.gaz-interpolated _t	25	0.46	0.20 +/- 0.11	0.089
Cheetah _t ~ Lion _{t-1} + T.gaz-interpolated _{t-1}	26	0.44	0.15 +/- 0.12	0.205
Dog _t ~ Lion _t	23	0.39	-0.96 +/- 0.23	0.000
Dog _t ~ Lion _{t-1}	22	0.40	-0.95 +/- 0.25	0.001
Dog _t ~ Lion _t + (Tgaz + wildebeest)	4	0.00	-0.78 +/- 0.52	0.371
Dog _t ~ Lion _t + (Tgaz + wildebeest)- terpolated _t	20	0.44	-0.71 +/- 0.31	0.032
Dog _t ~ Lion _{t-1} + (Tgaz + wildebeest)- terpolated _{t-1}	20	0.49	-0.79 +/- 0.33	0.029
Percent Change				
%Change cheetah _{t to t+1} ~ Lion _t	28	-0.47	0.00 +/- 0.04	0.930
%Change cheetah _{t to t+1} ~ Lion _t + Cheetah _t	28	0.85	0.14 +/- 0.14	0.314
%Change cheetah _{t to t+1} ~ Lion _t + Cheetah _t + gaz-interpolated _t	24	0.85	0.13 +/- 0.17	0.435
%Change Dog _{t to t+1} ~ Lion _t	17	-0.19	-0.14 +/- 0.87	0.875
%Change Dog _{t to t+1} ~ Lion _t + Dog _t	17	0.24	0.39 +/- 1.09	0.725
%Change Dog _{t to t+1} ~ Lion _t + Dog _t + (Tgaz + ildebeest)-interpolated _t	17	0.18	0.41 +/- 1.07	0.709

Table A1-3a: Cross-reserve model output – Wild Dogs vs. Lions

Regression output and ANOVA model comparison output for Wild Dog vs. Lion Density across reserves.

All models were run using *lme()* in Package *nlme*, incorporating Reserve as a random effect and a (corAR1[form = ~Years]) autocorrelation structure.

log(Wild dog Density) ~ Lion Density + Area

Coefficients	Value	Std.Error	DF	t-value	p-value
(Intercept)	2.5865	0.4417	23	5.8562	0.0000
Lion Density	-0.1240	0.0490	23	-2.5301	0.0187
Reserve Size	-0.0006	0.0006	23	-1.0238	0.3166

N = 29

Groups (random effects): 4

Phi = 0.491

log(Wild dog density) ~ Area

Coefficients	Value	Std.Error	DF	t-value	p-value
(Intercept)	2.3310	0.3949	24	5.9030	0.0000
Reserve Size	-0.1369	0.0474	24	-2.8886	0.0081

N = 29

Groups (random effects): 4

Phi = 0.449

ANOVA comparison

Model	Residual DF	AIC	logLik	L.Ratio	P
log (Wild dog Density) ~ Reserve Size	6	37.9725	-12.9863		
log (Wild Dog Density) ~ Reserve Size + Lion Density	5	37.0915	-13.5457	1.1189	0.2902

Table A1-3b: Cross-reserve model output – cheetahs vs. lion density

Regression output (function *lm*) and ANOVA model comparison output for Cheetah vs. Lion Density across reserves.

log (Cheetah Density) ~ Reserve Size + Lion Density

Coefficients	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	2.01	0.243	8.259	< 0.0001
Lion Density	-0.014	0.032	-0.444	0.661
Reserve Size	-0.003	0.001	-3.663	0.001

$df = 23, R^2 = .46$

log (Cheetah Density) ~ Reserve Size

Coefficients	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	1.9848293	0.2325765	8.534	9.87E-09
Reserve Size	-0.0030688	0.0006903	-4.445	0.00017

$df = 24, R^2 = .45$

Table A1-3c: Cross-reserve model output – cheetahs vs. lion presence

Regression output (function *lm*) and ANOVA model comparison output for Cheetah vs. Lion Presence across reserves.

log (Cheetah Density) ~ Reserve Size + Lion Presence

Coefficients	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	2.075	0.217	9.572	< 0.0001
Lion Presence	-0.332	0.266	-1.249	0.22
Reserve Size	-0.003	0.001	-4.77	<0.0001

df = 36, *R*² = .443

log (Cheetah Density) ~ Reserve Size

Coefficients	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	1.916	0.177	10.85	< 0.0001
Reserve Size	-0.003	0.001	-5.172	< 0.0001

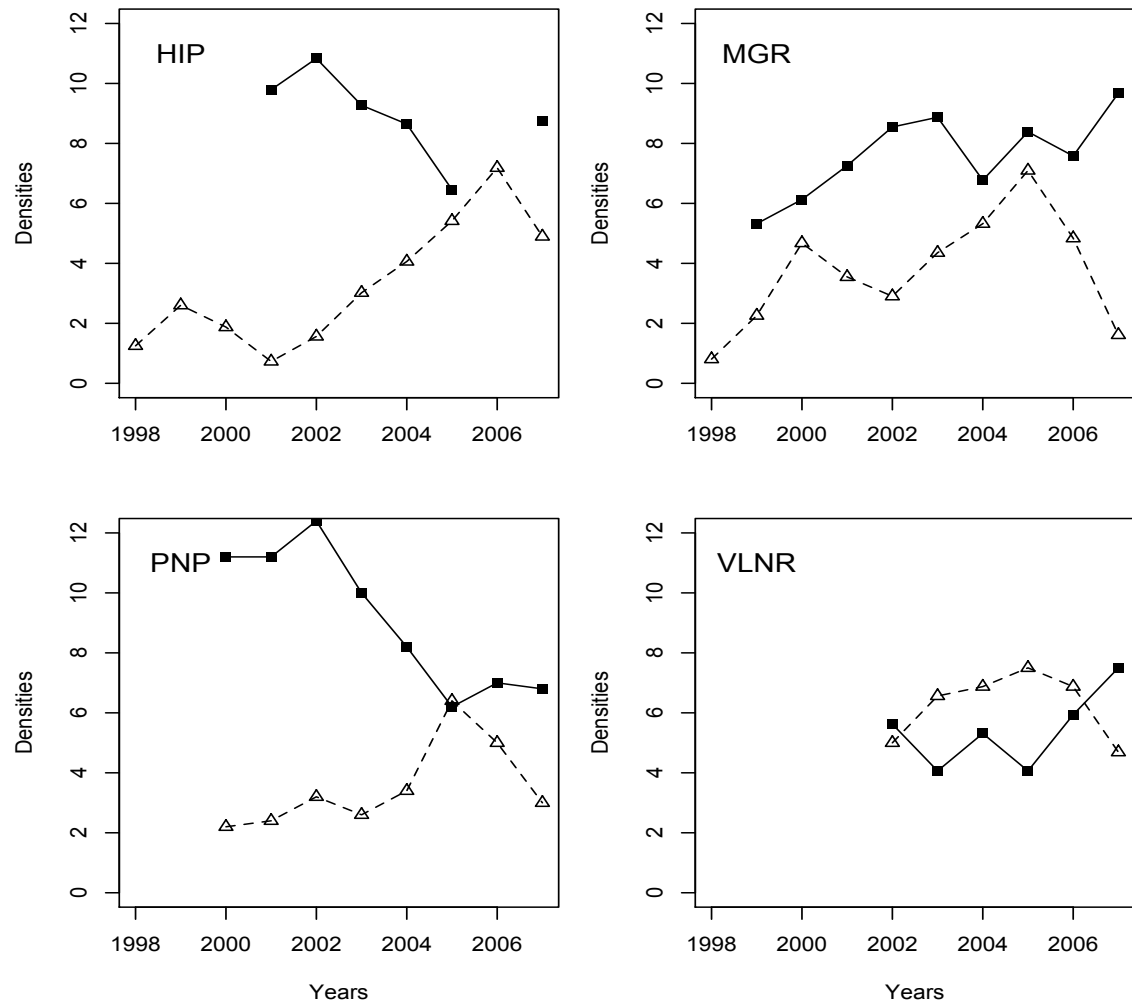
df = 37, *R*² = .419

ANOVA comparison

Model	Residual DF	RSS	SSQ	F	P
log (Cheetah Density) ~ Reserve Size	37	23.683			
log (Cheetah Density) ~ Reserve Size + Lion Presence	36	22.698	0.984	1.561	0.22

Figure A1-1: Cross-reserve lion and wild dog densities

Lion and wild dog densities collected by HDM following wild dog reintroduction programs. Lion densities are indicated by filled squares and solid lines, wild dog densities by triangles and dashed lines.



APPENDIX 2: Additional Tables and Figures for Chapter 3

Table A2-1a-c: Candidate models

Candidate models for “habitat only” models for lions, hyenas, and cheetahs. Full models included all habitat and prey characteristics that were significant in univariate regressions. All possible sub-models were evaluated and sub-models within delta AIC of 4 are reported here.

A) Lions

full model: lions ~ tree isolation + shade + tree isolation * shade + % cover + buffalo + gazelle | tree isolation + shade + tree isolation * shade + buffalo + gazelle

Candidate models	df	AIC	Delta	Weight
lions ~ tree isolation + shade + tree isolation * shade + % cover + buffalo tree isolation + shade + buffalo + gazelle	12	929.6	0.00	0.14
		5		
lions ~ tree isolation + shade + tree isolation * shade + % cover + buffalo tree isolation + shade + tree isolation * shade + buffalo + gazelle	13	929.9	0.31	0.12
		6		
lions ~ tree isolation + shade + tree isolation * shade + % cover + buffalo + gazelle tree isolation + shade + buffalo + gazelle	13	930.1	0.48	0.11
		4		
lions ~ tree isolation + shade + tree isolation * shade + % cover + buffalo + gazelle tree isolation + shade + tree isolation * shade + buffalo + gazelle	14	930.4	0.79	0.10
		4		
lions ~ tree isolation + shade + tree isolation * shade + buffalo tree isolation + shade + buffalo + gazelle	11	930.7	1.11	0.08
		7		
lions ~ tree isolation + shade + tree isolation * shade + buffalo tree isolation + shade + tree isolation * shade + buffalo + gazelle	12	931.0	1.42	0.07
		7		
lions ~ tree isolation + shade + tree isolation * shade + % cover + buffalo shade + buffalo + gazelle	11	931.6	2.04	0.05
		9		
lions ~ tree isolation + shade + tree isolation * shade + buffalo tree isolation + shade + buffalo + gazelle	12	931.7	2.09	0.05
		5		
lions ~ tree isolation + shade + tree isolation * shade + buffalo + gazelle tree isolation + shade + tree isolation * shade + buffalo + gazelle	13	932.0	2.40	0.04
		5		
lions ~ tree isolation + shade + tree isolation * shade + % cover + buffalo gazelle + buffalo + gazelle	10	932.0	2.43	0.04
		8		
lions ~ tree isolation + shade + tree isolation * shade + % cover + buffalo + gazelle shade + buffalo + gazelle	12	932.1	2.52	0.04
		7		
lions ~ tree isolation + shade + tree isolation * shade + % cover + buffalo shade + buffalo + gazelle	11	932.5	2.90	0.03
		5		
lions ~ tree isolation + shade + tree isolation * shade + % cover + buffalo + gazelle buffalo + gazelle	11	932.5	2.91	0.03
		6		
lions ~ tree isolation + shade + tree isolation * shade + buffalo shade + buffalo + gazelle	10	932.8	3.15	0.03
		0		
lions ~ tree isolation + shade + tree isolation * shade + % cover + buffalo + gazelle tree isolation + buffalo + gazelle	12	933.0	3.38	0.03
		3		
lions ~ tree isolation + shade + tree isolation * shade + buffalo buffalo + gazelle	9	933.1	3.54	0.02
		9		

B) Hyenas

Full model: hyenas ~ % cover + shade + habitat + buffalo + gazelle + wildebeest | buffalo + gazelle + wildebeest

Candidate models	df	AIC	Delta	Weight
hyenas ~ % cover + shade + buffalo + gazelle + wildebeest gazelle + wildebeest	9	2664.71	0.00	0.43
hyenas ~ % cover + shade + buffalo + gazelle + wildebeest buffalo + gazelle + wildebeest	10	2666.00	1.29	0.22
hyenas ~ % cover + shade + habitat + buffalo + gazelle + wildebeest gazelle + wildebeest	10	2666.33	1.62	0.19
hyenas ~ % cover + shade + habitat + buffalo + gazelle + wildebeest buffalo + gazelle + wildebeest	11	2667.62	2.91	0.10
hyenas ~ % cover + shade + buffalo + gazelle + wildebeest buffalo + gazelle	9	2668.53	3.83	0.06

C) Cheetahs

Full model: cheetahs ~ tree isolation + shade + % cover + gazelle | tree isolation + shade + tree isolation * shade + % cover + habitat

Candidate models	df	AIC	Delta	Weight
cheetahs ~ tree isolation + shade + tree cover tree isolation + shade + tree isolation * shade + % cover + habitat	11	624.7	0	0.64
cheetahs ~ tree isolation + shade + tree cover + gazelle tree isolation + shade + tree isolation * shade + % cover + habitat	12	626.53	1.83	0.26
cheetahs ~ tree isolation + shade + tree cover tree isolation + shade + tree isolation * shade + habitat	10	628.5	3.8	0.1

Table A2-2: Model averaged output – “habitat only” models

Model averaged output calculated on all “habitat only” models with delta AIC <4. All possible submodels were evaluated from a full model that incorporated habitat and prey, and predator variables that were marginally significant ($p < 0.1$) in univariate regressions.

A) Lions					
Model-averaged coefficients	Estimate	Std. Error	z	P	Relative importance
<i>Count model</i>					
Intercept	-4.5110	0.985	4.578	0.0000	
tree isolation	-0.0001	0.000	0.195	0.8452	1.00
buffalo	18.6900	4.248	4.399	0.0000	1.00
% cover	-0.3446	0.190	1.815	0.0695	1.00
shade	-0.3526	0.174	2.030	0.0424	1.00
tree isolation * shade	0.0005	0.000	3.386	0.0007	1.00
gazelle	-2.0310	1.769	1.148	0.2510	0.40
<i>Binomial model</i>					
Intercept	-1.7500	0.876	1.998	0.0457	
Tree Isolation	0.0003	0.001	0.627	0.5309	0.78
buffalo (presence)	1.3160	0.420	3.136	0.0017	1.00
shade	0.2061	0.221	0.933	0.3508	0.84
gazelle (presence)	1.2280	0.495	2.482	0.0131	1.00
tree isolation * shade	0.0003	0.000	1.267	0.2051	0.33
B) Hyenas					
Model averaged coefficients	Estimate	Std. Error	z	P	Relative importance
<i>Count Model</i>					
Intercept	-4.4711	0.116	38.412	< 0.0001	
buffalo	5.8126	0.574	10.134	< 0.0001	1.00
% cover	0.1439	0.031	4.682	< 0.0001	1.00
shade	-0.1192	0.017	7.177	< 0.0001	1.00
gazelle	4.1642	0.276	15.083	< 0.0001	1.00
wildebeest	5.9114	0.677	8.726	< 0.0001	1.00
habitat	-0.0316	0.051	0.616	0.5379	0.29
<i>Binomial Model</i>					
intercept	-1.1853	0.962	1.232	0.2180	
gazelle	2.0624	0.597	3.452	0.0006	1.00
wildebeest	2.2498	0.943	2.385	0.0171	0.94
buffalo	0.5912	0.622	0.950	0.3419	0.39

C) Cheetahs

Model averaged coefficients	Estimate	Std. Error	z	P	Relative importance
<i>Count Model</i>					
Intercept	-3.3305	1.176	2.833	0.0046	
tree isolation	0.0007	0.000	2.840	0.0045	1.00
% cover	-1.0303	0.342	3.015	0.0026	1.00
shade	0.3268	0.112	2.925	0.0034	1.00
gazelle	-1.0426	2.507	0.416	0.6776	0.26
<i>Binomial Model</i>					
intercept	2.1127	1.755	1.204	0.2286	
tree isolation	-0.0003	0.001	0.564	0.5729	1.00
% cover	-0.8906	0.391	2.277	0.0228	0.90
shade	0.1175	0.259	0.453	0.6506	1.00
habitat	-1.5222	0.438	3.472	0.0005	1.00
tree isolation*shade	0.0007	0.000	3.145	0.0017	1.00

Table A2-3: Model averaged output – overall models

Model averaged output for best overall cheetah and hyena models, calculated on all models with delta AIC <4. All possible submodels were evaluated from a full model that incorporated habitat and prey, and predator variables that were marginally significant ($p < 0.1$) in univariate regressions.

Hyenas ~ lions & habitat					
	Estimate	Std. Error	z	P	Relative importance
<i>Count model</i>					
intercept	-5.2308	0.1265	41.3500	< 0.0001	
buffalo	2.1639	0.6148	3.5200	0.0004	1.00
% cover	0.3071	0.0306	10.0490	< 0.0001	1.00
lions	47.1433	3.6240	13.0090	< 0.0001	1.00
lions2	-435.6794	54.1402	8.0470	< 0.0001	1.00
shade	-0.1337	0.0167	8.0260	< 0.0001	1.00
gazelle	4.5540	0.2646	17.2140	< 0.0001	1.00
wildebeest	5.1356	0.6762	7.5950	< 0.0001	1.00
<i>Binomial model</i>					
intercept	-1.3947	1.1254	1.2390	0.2153	
lion presence	1.3503	0.5762	2.3430	0.0191	0.87
gazelle	1.9094	0.6196	3.0820	0.0021	1.00
wildebeest	2.2587	0.9696	2.3300	0.0198	0.85
Cheetahs ~ lions & habitat					
	Estimate	Std. Error	z	P	Relative importance
<i>Count model</i>					
intercept	-3.5840	1.1650	3.0770	0.0021	
tree isolation	0.0005	0.0003	1.8550	0.0636	0.64
shade	0.2741	0.1138	2.4090	0.0160	1.00
% cover	-0.8986	0.3347	2.6850	0.0073	1.00
lions	51.3000	27.2100	1.8850	0.0594	0.89
lions2	-623.2000	337.7000	1.8450	0.0650	0.78
gazelle	-1.8050	2.4680	0.7320	0.4644	0.30
<i>Binomial model</i>					
intercept	2.0020	1.5820	1.2660	0.2056	
tree isolation	0.0002	0.0006	0.3490	0.7269	1.00
% cover	-1.1700	0.3686	3.1730	0.0015	1.00
shade	0.2012	0.2658	0.7570	0.4492	1.00
tree isolation*shade	0.0006	0.0002	2.6400	0.0083	0.97
lion presence	0.8254	0.3891	2.1210	0.0339	0.90