The effect of individual variability and larger carnivores on the functional response of cheetahs

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ACADEMIC ABSTRACT

Functional response is the framework thorough which we can quantify how predator hunting behaviors such as rate of successful attack and time spent handling prey interact with prey density to determine the rate at which prey are killed. Cheetahs are mesopredators and their behavior can be shaped by the need to avoid larger predators while hunting relatively large bodied and mobile prey. I used data from 34 years of observed cheetah hunts in Serengeti National Park in Tanzania to investigate how reproductive condition, prey density, seasonality, and the proximity of larger predators affect cheetah kill rates, probability of successful attack, and time spent handling prey. Mothers with cubs had an asymptotic Type II functional response where kill rate increased but eventually leveled-off at high prey densities, while cheetahs without cubs had a dome shaped Type IV functional response where kill rates actually declined at high prey density. Probability of successful attack on prey was higher for mothers with cubs, and increased slightly with prey density. Mothers with cubs had different prey handling behavior than other cheetahs. Cheetah mothers spend longer at kills then other cheetahs despite the risk that the carcass can attract lions and hyenas that could steal the carcass and potentially kill her cubs. Mothers must make sure their cubs have sufficient time at the carcass to eat their fill, thus they minimize risk from larger predators by being vigilant. In contrast, cheetahs without cubs are unconcerned with cub predation and can eat quickly to minimize the risk of kleptoparasitism. My results show how the pressures of cub rearing and coexisting with larger carnivores differentially shape the hunting behavior of cheetahs, and suggest that intensity of mesopredator suppression may depend on individual variability. This is the first time the functional response for a large mesopredator, has been quantified and the first time a dome shaped response has been recorded in a mammal. My work shows the value in accounting for individual variability in functional response and how linking of carnivore hunting behavior to multiple species interactions advances our understanding of how classical ecological theory applies to wild ecosystems.

ABSTRACT PUBLIC

One of the most basic interactions between species is when one kills and eats another. Determining how many prey a predator kills is challenging, especially because it is difficult to observe hunting behavior in nature. To assess killing rates, we need information on prey density, the rate predators attack prey, and how long they spent killing and eating it. In smaller bodied predators (a.k.a. mesopredators), those behaviors are often influenced by the presence of larger, dangerous predators. I used 34 years of data on wild cheetahs in Serengeti National Park in Tanzania to examine whether their hunting behavior was influenced by having cubs, the proximity of lions and hyenas, and the season. I assessed how these factors affect the relationships between cheetah kill rates and gazelle density, the probability of a successful attack, and the time cheetahs spend handling their prey. I found that cheetah hunting behavior is largely shaped by whether or not they have cubs. Mothers' kill rates are higher than cheetahs without cubs and stay high as gazelle densities increase. In contrast, the rate cheetahs without cubs kill declines at high gazelle density, the first time this relationship has been recorded in a wild mammal. Once prey are dead, mothers spend more time at the kill in order to ensure their cubs get enough time to eat. However, being at the kill is risky because lions and hyenas can arrive and kill her cubs. To minimize risks to cubs at the kill, mothers are more vigilant for predators than other cheetahs. Cheetahs without cubs spend less time at the kill, eating quickly without being vigilant. My results show how living in a landscape with multiple larger predators and mobile prey shapes the hunting behavior of all cheetahs, while providing detail on how having cubs can drive differences in those behaviors among individuals. The patterns of behavior seen in cheetahs may be indicative of how mesopredators alter hunting behavior to cope with pressures from larger predators. This is relevant as we craft conservation and management policies that take into account relationships among multiple carnivore species and their prey.

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Chapter 2: Cheetahs' functional response depends on reproductive status and nearby lions

Karen Laurenson (Frankfurt Zoological Society) provided much needed data on hunts and prey surveys for female cheetahs from 1987-1990. Ray Hilborn (School of Aquatic and Fisheries Sciences, University of Washington) helped me extensively with R coding and thinking about functional response. Marcella Kelly (Department of Fish & Wildlife Conservation, Virginia Tech), Sarah Durant and Nathalie Pettorelli (Institute of Zoology, Zoological Society of London) provided input on the shape of the chapter and the implications of cheetah functional response. Mike Cherry (Department of Fish & Wildlife Conservation, Virginia Tech) helped me solidify ideas about predator prey interactions and prey density. Ulrike Hilborn helped with data entry. Sarah Karpanty (Department of Fish & Wildlife Conservation, Virginia Tech) and Jeff Walters (Department of Biology, Virginia Tech) provided edits to the chapter

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I used data from the Serengeti Cheetah Project, Tim Caro (department of Wildlife, Fish, and Conservation Biology, UC Davis), and Karen Laurenson (Frankfurt Zoological Society). Ray Hilborn (School of Aquatic and Fisheries Sciences, University of Washington) helped me extensively with R coding and Ulrike Hilborn with data entry. Marcella Kelly (Department of Fish & Wildlife Conservation, Virginia Tech), Sarah Durant and Nathalie Pettorelli (Institute of Zoology, Zoological Society of London) helped me with interpretation of results and the implications for cheetah behavior. Sarah Karpanty (Department of Fish & Wildlife Conservation, Virginia Tech) and Jeff Walters (Department of Biology, Virginia Tech) provided edits to the chapter.

Chapter 4: Cheetahs modify their prey handling behavior depending on risks from top predators

I used data from the Serengeti Cheetah Project, Tim Caro (department of Wildlife, Fish, and Conservation Biology, UC Davis), and Karen Laurenson (Frankfurt Zoological Society). Ray Hilborn (School of Aquatic and Fisheries Sciences, University of Washington) helped me extensively with R coding and Ulrike Hilborn with data entry. Marcella Kelly (Department of Fish & Wildlife Conservation, Virginia Tech), Sarah Durant and Nathalie Pettorelli (Institute of Zoology, Zoological Society of London) helped me with interpretation of results and the implications for cheetah behavior. Sarah Karpanty (Department of Fish & Wildlife Conservation, Virginia Tech) and Jeff Walters (Department of Biology, Virginia Tech) provided edits to the chapter

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Chapter 1

Introduction

One facet of ecology is the study of interactions among species, and one of the most basic and important of interactions is when one species consumes another. For many species predation is a major part of natural mortality (Sinclair, Mduma & Brashares 2003), and can impact population dynamics (Holling 1959a), social and foraging behavior and life history strategy (Verdolin 2006) and even morphology. The paired dynamics between predators and prey are the fundamental links that create food webs and join population dynamics to community ecology (Drossel, McKane & Quince 2004; Arditi & Ginzburg 2012). Therefore our understanding of large parts of how species interact with each other, and thus how ecosystems function, is based on our understanding of predation. One of the basic building blocks of predation theory is the functional response. Functional response models use behaviors such as the rates that predators encounter and attack prey and the time it takes to handle prey, to describe the way that the per capita prey consumption of a predator increases with prey density (Holling 1959a; b) . How predator densities are affected by prey densities is termed the numerical response (Solomon 1949) and the relationship between the two responses is central to models of population dynamics between predators and prey. Originally formulated with insects, the functional response has since been expanded to include predators and prey from zooplankton and algae (Arditi, Ginzburg & Akcakaya 1991) to lions and wildebeest (Fryxell *et al.* 2007). While there has been extensive theoretical and experimental work on invertebrates, work on vertebrates is scant and has been mostly field based. This leads to a potential mismatch between theory developed, or patterns described, in well controlled experiments verses naturally messy, wild systems (Morozov *et al.* 2008). However, examining the extent of this mismatch has been hindered by difficulties in collecting data on predation behavior in the wild and has resulted in a situation where 'ecologists know pitifully little about the nature of functional responses (Abrams & Ginzburg 2000) despite its influence on a large swath of ecological theory including: foraging theory (Sih 2011), long term evolution of food webs (Drossel *et al.* 2004), the magnitude of facilitation, competition, and predation in species assemblages (van Langevelde *et al.* 2008; McCoy, Stier & Osenberg 2012a), and species persistence under very high predation rates (Lipcius & Hines 1986). Considering the wide use of functional response models, improving their applicability to wild populations could alter our predictions of how species will interact with each other, thus impacting wildlife management decisions and also potentially our understanding of basic community ecology and food web theory (Holt & Lawton 1994).

Basic Functional Responses

In a series of papers from 1959 to 1965 (Holling 1959a; b, 1961, 1963, 1965) Holling outlined three basic functional responses of predators to their prey and the set of conditions needed for the equations to effectively describe the data. All three responses assume one species of predator and one species of prey mix evenly in a homogenous environment, and that as prey densities increase, predators become limited by the rate they can capture, eat, and digest prey rather than the rate of finding prey. Over the years, there have been variations that deal with variable habitat (Abrams 2007), and grouping by predators and/or prey (Cosner *et al.* 1999) among others, but it is only recently that there have been investigations into how easily the central assumptions are violated and the potential implications thereof (Mols *et al.* 2004; Bolnick *et al.* 2011; Okuyama 2012). Despite the drawbacks, Holling's equations or their variations (Rogers 1972; Beddington 1975; DeAngelis, Goldstein & O'Neill 1975; Hassell *et al.* 1977; Arditi & Ginzburg 1989) have been, and still are, widely used for investigations into functional response in both experimental (Eggleston 1990a; b; c; Streams 1994; Altwegg *et al.* 2006; Putra & Yasuda 2006) and wild systems (Dale, Adams & Bowyer 1994; Redpath & Thirgood 1999; Hayes & Harestad 2000; Caldow & Furness 2001; Elliott & Sawrey 2003; Gilg, Hanski & Sittler 2003; Bartel & Knowlton 2005; Miller *et al.* 2006; Fryxell *et al.* 2007; Nilsen *et al.* 2009; Vucetich, Vucetich & Peterson 2011; McPhee, Webb & Merrill 2012)

Type I

In the Type I functional response predators eat a constant proportion of prey as prey density increases. This linear increase in total consumption reaches a sharp asymptote when the predator becomes limited by digestion time (Fig. 1). It is not very biologically plausible for most organisms to consume at a constant rate and Jeschke, Kopp & Tollrian (2004) concluded that the limiting conditions mean this type of response can only be found in filter feeders. Types II and III are the responses most commonly considered because they include more realistic constrains and conditions.

Type II

The asymptotic Type II functional response described by the Disc Equation and is the most commonly reported response (Fig. 1). The number of prey consumed is a function of prey density (x), an instantaneous search rate (a), and the time it takes to handle prey (b). At low prey density the number of prey eaten is limited by the predator's ability to find prey while at high density it is limited by the ability to catch, eat, and digest prey. As originally formulated by Holling (1961, 1965), the number of prey encountered depends on the search rate, and all prey encountered are successfully attacked so that the instantaneous search rate (*a*) and the attack rate are equal. For many insect predators this is plausible but for other organisms it makes more sense to break search rate into separate encounter and attack rates. However in the Disc Equation they are combined into one parameter (a) that can be referred to as either the search rate or the attack rate. Attack rate and handling time are assumed to be constant regardless of prey density, and are considered mutually exclusive behaviors. The Disc Equation takes the general form of

$$y(x) = \frac{ax}{1 + axb}$$

y=consumption rate (number consumed/predator/time). Also known as kill rate or predation rate.
x=prey density
a= attack rate, or the rate that prey are encountered and killed over the time period the predator is in active pursuit (McPhee *et al.* 2012).
b=handling time per prey item

Type III

The Type III functional response is a sigmoid function (Fig 1.) that can be obtained by making the constant attack rate in Type II response increase with prey density either linearly (Schenk *et al.* 2002)) or in an asymptotic manner (Hassell *et al.* 1977). It can also occur if time-in-patch or handling time varies with prey density (Collins, Ward & Dixon 1981). It is thought to be caused by prey switching where predators switch away from a prey type when its density gets too low, or learning by predators where they become better at catching prey with experience or as prey density increases (i.e. prey switching) (Holling 1965). Unlike Type II, Type III is considered to be prey regulating because proportion of prey items consumed decreases at low prey densities and increases at higher prey densities. Thus it can dampen incipient oscillations of predator prey populations (Holling 1961).

Although Types II and III are the most commonly reported in the literature, other functional responses are possible. If prey of the same or similar species interfere with handling time or if prey show defense behavior that increases at higher densities (swarming, vigilance, or other group defenses) , Type II and III can become dome shaped at high prey densities (Holling 1961; Jeschke *et al.* 2004) (Fig. 2). This humped or domed shaped function is sometimes known as Holling's Type IV, and has only been recorded a few times in the wild (Treherne & Foster 1982; Burger & Gochfeld 2001; Cresswell, Lind & Quinn 2010)

By including the costs predators incur while foraging, (Abrams 1982) demonstrated a variety of differently shaped functional responses. Holling's three types include few variables, and the model assumptions are easily violated in natural systems, so it is not surprising that by accounting for some of the factors that can affect how many prey a predator consumes (anti-predator defenses, habitat heterogeneity, territoriality of predators or prey, multiple prey species, differences in predator and prey sizes by age, etc.), many other responses become possible. However, these are rarely investigated or reported in field studies due to the difficulties in data collection. Examining components of functional response separately makes it possible to use field data to assess the potential impacts of such factors and to discern whether the assumptions made about them hold in a field scenario. In my study, the major components of functional response that I examine are attack rate and handling time.

Components of the functional response

Attack rate

Attack rate can be defined as the product of encounter rate, probability of attack, and probability of an attack being successful (Jeschke, Kopp & Tollrian 2002) and results in a measure of the 'number of prey encountered and killed at a given prey density over the time period that the predator is in active pursuit' (McPhee *et al.* 2012). Attack rate differs from kill rate as kill rate is the number of prey killed over time that includes both active pursuit and handling time (McPhee *et al.* 2012). Thus kill rates (or consumption rates) are calculated using both attack rate and handling time. Attack rate can either be a constant parameter (Type II), or vary linearly with prey density (Type III). Due to difficulties in measuring attack rates in the field, they are often calculated by fitting a functional response curve to data on number of prey killed in a set amount of time. Attack rates can vary by predator size (isopods preying on amphipods, (Aljetlawi, Sparrevik & Leonardsson (2004)) and age (eagles on salmon carcasses, Restani, Harmata & Madden (2000)), the presence of alternate prey (damselflies on copepods and cladocerans, Colton 1987), prey size (cannibalistic backswimmers, Streams 1994) and by landscape features (wolves preying on ungulates, McPhee *et al.* 2012). Jeschke *et al.* (2002) argue that hunger influences attack rate by making the probability of search equal to hunger level. This may not be the case with large carnivores however, as McPhee *et al.* (2012) found that attack rates in wolves did not vary with satiation, and in cheetahs, hunger does not influence the probability that a hunt is initiated (Cooper, Pettorelli & Durant 2007).

Handling Time

Jeschke *et al.* (2002) divide handling time into an active handling time, which includes attacking and eating, and the background process of digestion that does not prevent an animal from searching for, attacking, or consuming more prey. In Holling's Type II and III equations, handling time is a constant parameter, yet when it has been observed, it has been shown to vary by prey density (oystercatchers on bivalves, Wanink & Zwarts (1985); wasps on beetles, Schenk *et al.* (2002); skuas stealing fish from auks, Caldow & Furness (2001)), and vary by the size of both the predator and the prey item it is eating (isopods preying on amphipods, Aljetlawi *et al.* (2004); anis on butterflies, Burger & Gochfeld (2001) shrimp on juvenile plaice, Gibson, Yin & Robb (1995)). In order to fit Holling's functional response curves, many studies calculate a mean handling time, but the wide variance due to confounding factors may make these values informative only over long time scales and may bias calculations of attack rates or prey killed. Handling time is assumed to cause the asymptote in Type II and III, where the more dense the prey become, the less time is spent searching for prey and the more time is spent handling prey. This has been confirmed in wading birds by Vahl (2005), but was not found in skuas (Caldow & Furness 2001).

The assumptions in, and predictions stemming from, functional response theory inform predator-prey theory, population modeling, community dynamics, and optimal foraging theory (Abrams 1990). Whether a species has a Type II or III response determines whether it regulates its prey or not, which is critical for predictions of what will happen when population numbers of either predators or prey change due to natural cycles or anthropogenic impacts. Yet there are very large gaps in our knowledge of how functional response plays out in the real world, especially in extrapolating from paired relationships to interactions among multiple species. There is a need for work that can break down functional response into its components, determine what factors influence each component, and bring them together into an integrated understanding of how disparate factors and processes combine to influence the number of prey consumed per predator (Streams 1994).

Applying a theoretical framework to wild predators

There is a long and rich history of theoretical work on functional responses but testing theories in the field with wild animals has lagged behind. Difficulty in observing predation events leads to functional response being estimated from a number a proxies such as kill rate (number of kills/animal or group/time) across yearly or monthly estimates of prey density (Dale *et al.* 1994; Eberhardt 1997; Hayes & Harestad 2000; Vucetich, Peterson & Schaefer 2002; Vucetich *et al.* 2011; Hebblewhite *et al.* 2003; Nilsen *et al.* 2009), or the combination of predator diet composition and population trends of prey (Angerbjorn 1989; Korpimaki & Norrdahl 1991; Patterson, Benjamin & Messier 1998; Mahony *et al.* 1999; Redpath & Thirgood 1999; Joly & Patterson 2003; Bartel & Knowlton 2005) The usefulness of these data to inform predation trends may be limited. As Abrams (1990) and Tully & Cassey (2005) have pointed out, even in experimental situations there can be large differences in values of attack rate, search rate, and handling time derived from fitting functional response curves to the number of prey killed, compared to values derived from direct observation. These differences may be due to violations of model assumptions, use of inappropriate data, or heterogeneity in the data caused by individual behavioral variation (Tully & Cassey 2005). For field data, proxies are used precisely because direct observation is infeasible, so it is difficult to determine how close the actual rates are to the predicted rates. Given that field situations are more complex than experimental ones, it is likely that the differences could be sufficiently large to make predicted values meaningless. Tully & Cassey (2005) tested observed vs. predicted values in an experimental situation using mites, but to my knowledge it has never been fully tested in the wild (but see Aljetlawi *et al.* (2004)), let alone in a carnivore. Steps have been made to parameterize the components of the functional response through the combination of GPS collar data with ground truthing of kill locations, which allows for better estimation of handling time, time between kills (Merrill *et al.* 2010; McPhee *et al.* 2012), and encounter rates (Hebblewhite & Pletscher 2002) for wolves. However with data from GPS collars it is still difficult to parse out time between kills into time spent searching, detection and encounters of prey, unsuccessful attacks, or to distinguish digestive pauses from active handling time (Merrill *et al.* 2010). In addition, up to now field studies have either examined functional response as a whole (Vucetich *et al.* 2002, 2011; Jost *et al.* 2005; Zimmermann *et al.* 2007) or the individual stages (Hebblewhite & Pletscher 2002; McPhee *et al.* 2012), but there have been few attempts to link the two. Functional response is the basis for most predation and optimal foraging theory (Abrams 1990) and quantifying the extent that it actually applies in real world situations could have wide reaching impacts on our ability to model predator-prey interactions and their effects on population trends.

To comprehensively parse out the major components of functional response, not only do complete predation events need to be observed from start to finish, but also unsuccessful hunts, and the time between successful hunts must be known. In the case of most wild predators this is difficult, but especially so for most large carnivores because the majority of hunting activity takes place at night, making accurate observations difficult. Cheetahs in the Serengeti National Park in Tanzania are an exception and are ideally suited for this sort of study as they occur in mostly open habitat, hunt almost exclusively during the day, and most of them are habituated to vehicles, all of which makes observing predation events feasible. The Serengeti ecosystem has been well studied since the 1960's (see Sinclair *et al.* (2008) for a description) and contains remarkably intact guilds of carnivores and ungulates. In this system there are complex interactions among multiple predators. Lions, hyenas, and cheetahs have somewhat overlapping prey bases, while lions and hyenas kill cheetah cubs and scavenge kills from cheetahs and each other (Bertram 1979; Scheel 1993; Caro 1994; Laurenson 1994; Hunter, Durant & Caro 2007b). These interactions influence predation behavior and potentially complicate investigations into the factors influencing functional response. On the other hand, results will be more widely applicable to a variety of species that live in complex systems than previous studies that have limited their examinations to a single predator with a single prey species (Jost *et al.* 2005; Nilsen *et al.* 2009; Vucetich *et al.* 2011). Previous field studies on carnivores have focused on top predators such as wolves (Dale *et al.* 1994; Hebblewhite & Pletscher 2002; Merrill *et al.* 2010;

Vucetich *et al.* 2011), European lynx (Nilsen *et al.* 2009) and lions (Fryxell *et al.* 2007). Work on mesopedators such as coyotes (Bartel & Knowlton 2005) has largely ignored the effect of dominant predators on subordinate ones. The majority of animals can be thought of as both predator and prey (especially if herbivores are thought to 'prey' on plants (Spalinger & Hobbs 1992), and the effects of a more dominant predator on functional response of mesopredators are fairly unexplored yet potentially immensely influential in predator-prey relationships and community dynamics.

Cheetah Functional Response.

I approach understanding how cheetah consumption rates interact with prey density (functional response) from three angles. First, I explore how cheetah hunting behavior is driven by the need to capture large, social, and highly mobile prey, whose local densities are highly heterogeneous across a large landscape. Second, I aim to capture how the top-down pressure of coexisting with larger carnivores like lions and hyenas shaped those same hunting behaviors. Thirdly, I want to account for the possibility that top-down and bottom-up factors do not affect individual cheetahs equally. Risks from larger predators, nutritional needs, and constraints on movements all are influenced by a cheetah's reproductive status, social grouping, and potentially seasonality. By examining cheetah behavior through the framework of functional response I can bring formal ecological theory to bear on understanding how these pressures combine to shape cheetah hunting behavior. By doing so, I can assess the usefulness of this theoretical framework, originally conceived and tested mostly on insects in rigidly controlled experimental situations, in quantifying predator behavior in wild systems with multiple interacting predator species and their prey. I can do so because of the uniquely detailed and extensive observational data collected on cheetahs in Serengeti from 1980 to today. I have the opportunity to quantify encounter and attack rates as well as handling time through direct observation and compare them to values predicted from functional response curves. These data will also allow me to quantify functional response for a terrestrial mesopredator for the first time, and in doing so, account for both prey density and top-down pressures that make their hunting behavior different from more commonly studied apex predators.

Background (Field work)

Study Area:

The study area of the Serengeti Cheetah Project (SCP) covers 2200 km^2 of mostly open plains and woodland edge of Serengeti National Park and Ngorongoro Conservation Area in northern Tanzania (Fig. 3 and 4). There are two main seasons, the wet season from November/December to May, and the dry season from June to November. The plains are dotted with rocky outcrops called kopjes and crisscrossed by dry river beds and erosion embankments, with trees restricted to river beds and around kopjes. Large herds of migratory herbivores including wildebeest, zebra, and Thomsons's gazelles, move seasonally over the study area. Cheetahs in the Serengeti are extremely mobile, with females and non-territorial males ranging over an average of 800 km^2 (Caro 1994). Although some stay in the same general area year round, many follow the seasonal migration of Thomson's gazelles, their main prey (Durant *et al.* 1988; Caro 1994). Cheetahs inhabit the woodlands and long grass plains in the dry season from June to November, but as the rains start in December, they follow the gazelle south onto the short grass plains. They return north when the plains dry out in May and June.

Study Animal:

Cheetahs have a unique social system amongst carnivores. Females are solitary except when accompanied by cubs, and are not territorial, instead they occupy large overlapping home ranges of up to 800km^2 (Caro 1994). If males have brothers they may form life-long coalitions together and can be either territorial or nomadic (Caro 1994). They prey mainly on Thomson's gazelle, but also take hares, Grant's gazelles, young wildebeest and less commonly, zebra. They have two main hunting strategies. The majority of the hunts start with a stalk, which, if successful, turns into a chase. Alternately, cheetahs sometimes chase prey without a preliminary stalk, usually when they flush small hidden prey such as hares or neonate gazelles.

Data

I used data collected on ~450 hunts by cheetahs between 1980-2014, by multiple members of the Serengeti Cheetah Project (SCP). Tim Caro (TC) and Karen Laurenson (KL) did five-day follows of Serengeti cheetahs from 1980-1983 and 1987-1990. Additionally, there are data from 700 additional hunts from the

Serengeti Cheetah Project from 1991-2014, and from my 9 months of fieldwork in 2014. For all hunts data recorded included date, time, identity, age, and hunger level (based on belly size) of cheetah(s), prey species, and outcome of hunt. Many hunts also included data on sex and age of prey species, number and species in the herd of the target prey animal, grass height at the start of the hunt, and time in seconds of stalk and chase. Also recorded was: whether the chase was successful how long the cheetah spent killing, dragging the carcass, and eating, how full they were when they left the kill, whether they lost the kill to scavengers, and how much meat was left on the carcass when the cheetah left. Unfortunately, not all predation events had all of these types of data, thus I dropped hunts from the analysis if they did not have all the relevant data. The data from TC and KL was only on female cheetahs, while the data from SCP and my fieldwork comes from cheetahs followed opportunistically, including males.

Prey density

Functional response depends on prey density, but it is rare to observe predation events in the field and the prey densities directly around the predator are usually unknown. As a proxy, many studies use a metric of density that takes place over much larger spatial and temporal scales than an actual hunt. For example, pellet counts are used to infer herbivore density on a seasonal basis over and entire study area (Patterson *et al.* 1998; Hebblewhite & Pletscher 2002; McPhee *et al.* 2012), yet if prey are both mobile and live in groups, it is likely there is a large difference between a seasonal average prey density and prey densities encountered by hunting predators in real time. Both KL and I counted herbivores within 1 km of the car at regular intervals during the daylight hours. We also recorded vigilance of cheetahs on the kill down to the second. Together we recorded 460 hunts and 135 kills of cheetahs on gazelles. Having hourly data on prey density around a hunting cheetah allowed me to link hunts to actual prey density a cheetah experiences when making hunting decisions.

Individual variability in cheetahs

Classic functional response models assume that members of a population of predators or prey are homogenous or can be accurately described by the population mean. However this assumption is unlikely to hold, and as early as Holling (1959a) it was recognized that the characteristics of both the predators and prey would affect the shape of the functional response. (Okuyama 2008) took it further, postulating that not only are differences between classes of predators and prey important, but those differences among individuals are critical. Variation among individual predators in their functional responses has been large even in laboratory experiments (Eggleston 1990a; Putra & Yasuda 2006). This may be even more pronounced in the wild where individual predators and prey differ in their size, diet, habitat use, predation risk, and hunting skill, to name just a few complicating variables (Pettorelli *et al.* 2011). Taking these sources of variability into consideration may reduce variability in parameter estimates and potentially increase our understanding of the sources of stability in natural communities

(Okuyama 2008). For example, Bolnick *et al.* (2011)) showed that the extent individuals vary from the population mean can increase or decrease predation pressure, thus affecting the severity of predator-prey oscillations. Large population oscillations are common in prey dependent models of predator-prey systems, yet are only seen in certain select species in the wild (Arditi & Ginzburg 2012). Therefore accounting for individual variability can possibly aid in explaining the disconnect between predictions derived from modeling and the patterns seen in the wild. Additionally, if individual variability is not accounted for, model assumptions such as constant handling time or increasing attack rate with prey density are easily violated, making it impossible to scale up predictions from individual behavioral to the community level (Okuyama 2008, 2012). Predictions based on functional response theory enable us to better understand species interactions at the individual, community, and foodweb levels, thus increasing the accuracy of these predictions could provide revelations in our understanding of how natural communities function.

Individual cheetah vary in a number of ways including characteristics such as sex, age, social group, and reproductive state, as well as short term conditions like hunger state. There is evidence from other taxa that all of these factors have the potential to impact functional response, and therefore should be accounted for in analyses rather than assuming that individuals can be usefully represented by the population mean.

Age, sex, and social grouping

There hasn't been much work explicitly on how predator social grouping affects functional response. Experiments usually deal with one individual at a time, and work on wild predators that can account for that level of variability is rare. However Nilsen *et al.* (2009) found that in Eurasian lynx, mothers with kittens had higher kill rates than solitary individuals. Much more experimental and theoretical work has been done on age and size variation in predators and prey and it suggests that as predators age, get bigger, or become more adept at handling their prey, they can move up the response curve (Murdoch 1973). However, the empirical evidence on the effect of age is fairly scarce. Older anis (*Crotophaga ani*) had a higher capture success on butterflies compared to younger ones (Burger & Gochfeld 2001), and the functional response itself can be different among age classes. When the functional response of scavenging eagles was examined by age, adults had Type I and subadults were unclassifiable (Restani *et al.* 2000). The limited research done on carnivores in this specific area shows that predation behaviors can change with age, for example, predatory effectiveness declines as wolves get older (MacNulty *et al.* 2009b) and adult cheetahs are better at chasing and killing prey than young cheetahs (Hilborn *et al.* 2012).

Work on the effect of sex on functional response is also limited, and differences tend to be attributable to size. For instance Eggleston (1990c) examined blue crabs preying on different sizes of oysters. At low prey density, female crabs consumed a lower proportion of large oysters compared to males, possibly because males had greater crushing strength and could open oysters more easily. This led males to have a Type II and females a Type III response, meaning males could potentially drive oysters to local extinction but the presence of female crabs reduced overall predation pressure when oysters were scarce, providing an anti-predator refuge. In wolves, males were better than females at attacking, selecting, and subduing elk (MacNulty *et al.* 2009a), probably due to their larger body size.

Male and female cheetahs differ in body size and social groupings, which can influence their prey choice. For instance, coalitions of adult males will hunt yearling wildebeest, which are rarely attempted by females, which tend to focus on smaller prey (Caro 1994). The interplay of predator and prey size affects diet choice, and differential predation pressure may create predation refuges for prey of certain sizes. The number of male cheetahs within the study area tends to remain stable over time, possibly because they are limited by the number of available territories, while female numbers fluctuate (S. Durant unpublished data). For populations with dynamic demography, taking potential social grouping, sex, and/or age based differences in functional response into account will make scaling up individual predation rates to the population level much more accurate. Additionally, it will become possible to predict possible impacts on different types of prey as the demographic makeup of the population changes.

Effect of larger predators

Most species live in complex communities where multiple species impact each other in direct and indirect ways. Interactions among predators include cooperation, competition, and intraguild predation, and multiple species can impact prey species independently, synergistically, or antagonistically (McCoy *et al.* 2012a). There has been considerable work on the effect of multiple predators on prey (see Sih, Englund & Wooster (1998) and McCoy, Stier & Osenberg (2012b) for reviews) and there is evidence that the population trends and/or behavior of mesopredators like jackals, coyotes, cheetahs, and domestic cats can be dramatically affected by presence or absence of top predators through direct predation, competition for food, or exclusion from certain habitats (Ritchie & Johnson 2009).

What is missing is the behavioral link between mesopredators avoiding their predators and how that affects predation pressure on their prey. If the landscape of fear for mesopredators is "especially steep and treacherous terrain with few patches of safety" as Ritchie & Johnson (2009) suggest, then the ways that mesopredators avoid their own predators will impact how they hunt their prey. Functional response offers ways of quantifying how mesopredators that change their foraging or activity levels (Ritchie & Johnson 2009) alter predation pressure on their prey. . If they lower their activity levels in order to avoid notice by predators, it could decrease encounter rates with prey. They may also reduce their handling time if they cannot engage in anti-predator vigilance while feeding, or they may have increased handling time because they need to interrupt feeding in order to remain vigilant. All of these responses could affect predation rate in different ways, and since a majority of predators are not apex predators, understanding these behavioral mechanisms will allow us to make functional response modeling more applicable for more species and make better predictions about how prey populations with multiple predators respond to population changes in apex or mesopredator predator species.

Cheetahs suffer high levels of both kleptoparasitism (prey stealing) (Hunter, Durant & Caro 2007a) and cub death from lions and hyenas (Laurenson 1994). As a result, it is thought that cheetahs are found in areas of lower prey density than other large carnivores, potentially to avoid the lions and hyenas that can be attracted to the prey (Durant 1998). This could directly impact the encounter and attack rates of cheetah and gazelle and even handling time could be affected by lions and hyenas stealing cheetah kills. Thus the functional response of the cheetah may be strongly directly affected by the presence and density of other carnivore species.

By approaching cheetah functional response from multiple angles, I can assess how their hunting behavior is affected by pressures from their prey, their predators, and who they are as cheetahs. My second chapter characterizes functional response for cheetahs as a whole, then investigates how it is affected by whether the cheetahs has cubs, the nearby presence of lions, and season. The third chapter looks at how these factors affect attack rate and handing time individually. These are independent behaviors and cheetahs can alter them individually depending on the pressures they face. By focusing on the individual behaviors I can assess how cheetahs alter different parts of their hunting behavior in response to changing pressures from multiple trophic levels. In the final chapter I show that different risks at the kill for mothers with cubs vs cheetahs without cubs lead to different strategies for handling prey. Overall my work paints a picture of mesopredators with flexible hunting behaviors that they modify depending on their energetic demands and risks they face from larger predators, creating functional responses hat differ among social groups.

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Figures

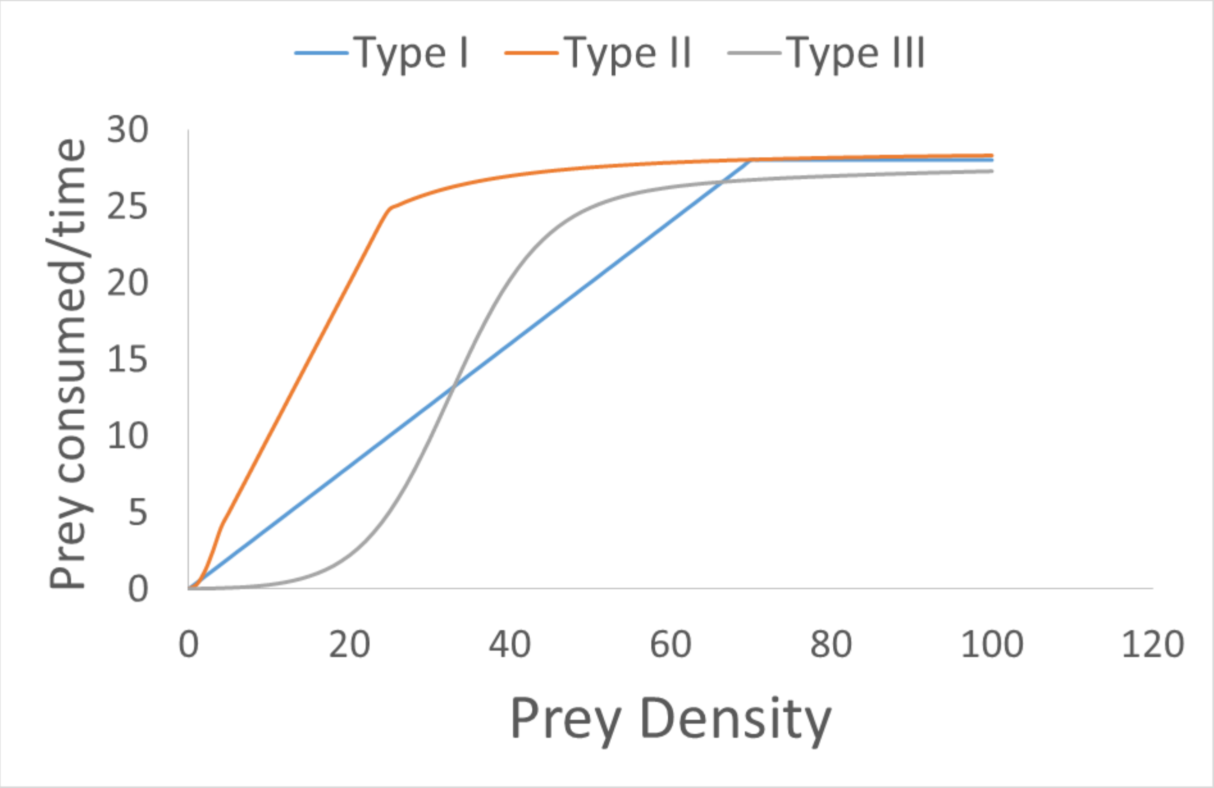


Figure 1. Holling's type I, II, III functional response curves.

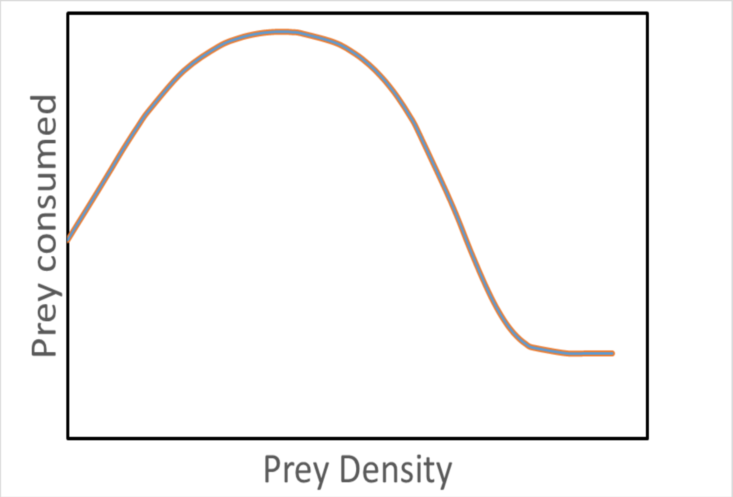
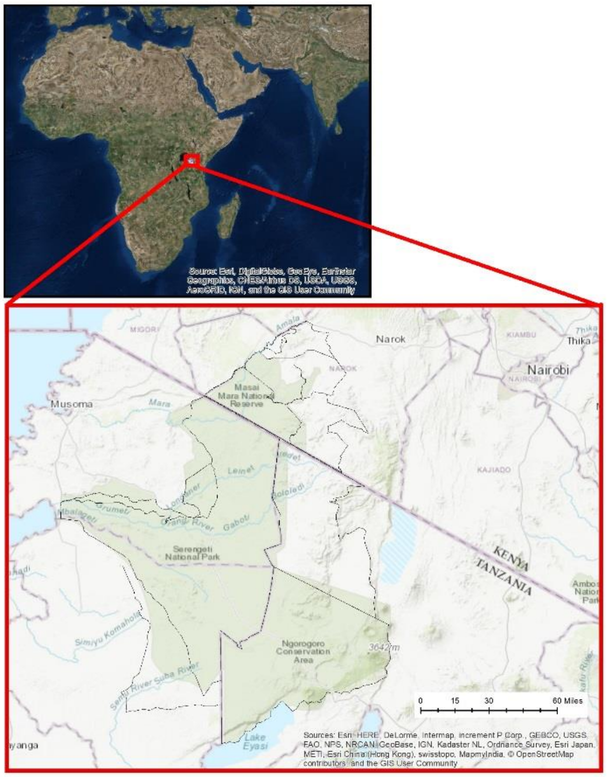


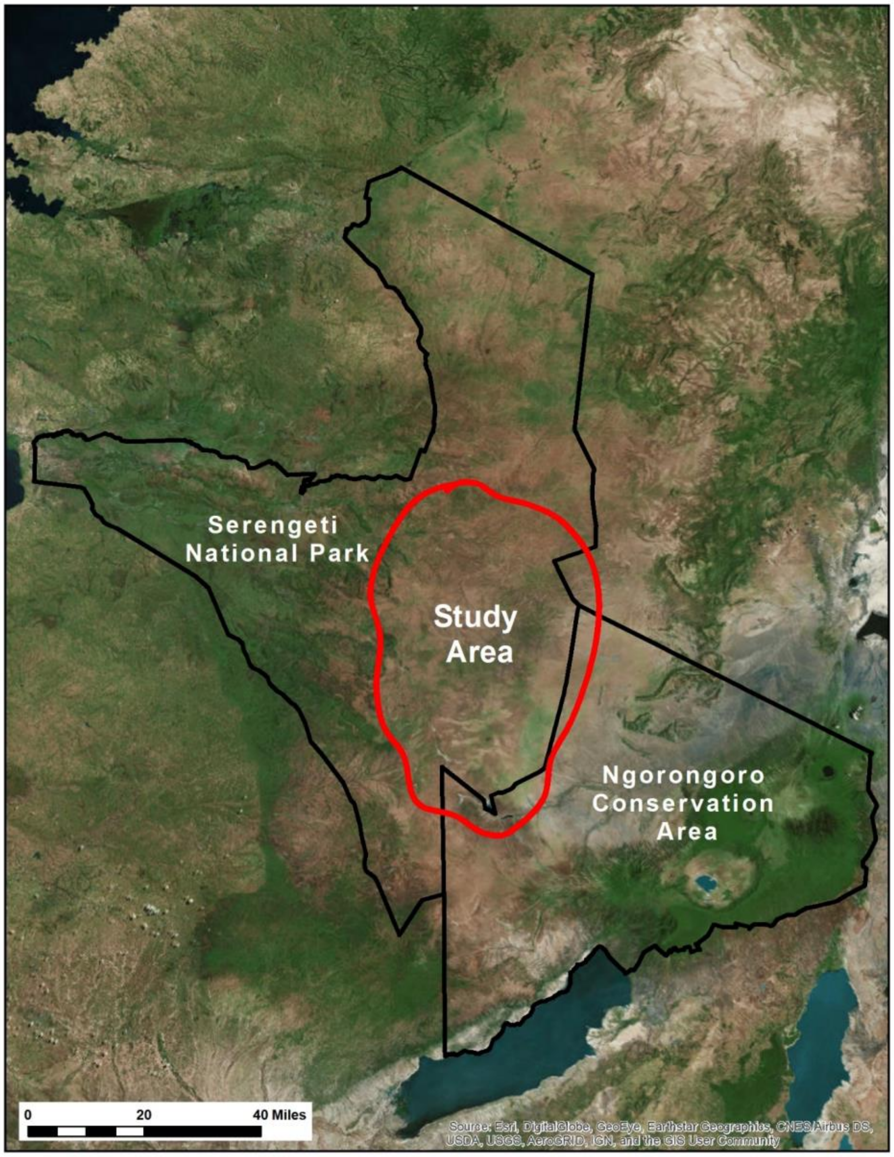
Figure 2. Type II functional response curves when prey exhibit a swarming effect, x axis is prey density, y axis is prey consumed.



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Sources: Esri, HERE, DeLorme, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, © OpenStreetMap contributors, and the GIS User Community

Figure 3. Map of Serengeti National Park and surrounding areas.



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Figure 4. Satellite map of Serengeti National Park with study area outlined

Chapter 2

Cheetahs’ functional response depends on reproductive status and nearby lions

Abstract:
Functional response quantifies how predator hunting behavior changes with prey density to determine the rate that prey are consumed, and forms the basis for much of our understanding of predator-prey relationships. However there are gaps in our understanding of how this framework applies to carnivores, specifically mesocarnivores, whose hunting behavior is affected by the presence of larger predators. With an extensive and detailed data on cheetah hunts and associated prey densities from Serengeti National Park, I used a model selection framework to evaluate whether cheetahs exhibited a Type II asymptotic functional response, or a dome shaped Type IV response. I also determined whether functional response differed by reproductive status, cub age, season, and the presence of lions nearby. As a whole population, I found that cheetahs display a Type II response. However functional response changes with reproductive status. Cheetahs with cubs use areas of relatively low prey density and increase their consumption rate with prey density (Type II), while cheetahs without cubs stop hunting and killing at high prey densities (Type IV). Lion presence within 1 km of cheetah hunts was rare, but did decrease cheetahs consumption rates across most prey densities, and resulted in unpredictable and uncharacterizable functional responses for cheetahs. This decline in the rates cheetahs consume gazelles around lions points to a quantifiable mechanism for mesopredator suppression. Cheetahs showed a Type II response in both wet and dry season. This is the first reported functional response for a mesocarnivore that quantifies the impacts of larger predators, and the first dome shaped response in a terrestrial mammal. These results illuminate the importance of including individual variability and interspecific interactions into functional response modeling as these factors are traditionally ignored, yet can be powerful forces in structuring predation behavior and predator-prey relationships.

Introduction

Animals make foraging behavior decisions based on cost-benefit analyses depending on multiple factors including prey availability and predation risk (Lima & Dill 1990). Experimental work on rodents and small birds show how prey use vigilance and giving-up densities to minimize predation risk while foraging (Brown 1999;

Sundell *et al.* 2004). Field studies of ungulates and larger carnivores have shown how predator behavior creates varying levels of predation risk and how ungulates alter their foraging behavior and/or movements to mitigate that risk (Hebblewhite, Merrill & McDonald 2005; Proffitt *et al.* 2009; Mattisson *et al.* 2011; Middleton *et al.* 2013; Creel, Schuette & Christianson 2014). However, what is still relatively unstudied is how predation risk shapes hunting behavior of predators themselves (but see Smith et al. 2015). The extensive examples of mesopredator release reviewed in Ritchie and Johnson (2009) show that the presence or absence of apex predators can radically alter mesopredator numbers and consequently predation pressure on smaller prey. Ritchie and Johnson (2009) put forward that the release is not just numeric, that the effects on prey are, in part, behaviorally mediated due to 'Fear and Loathing' of apex predators limiting where and/or when mesocarnivores hunt. Functional response provides a quantitative framework to link predator hunting behavior to the number of prey consumed. If fear of larger predators alters mesopredator hunting behaviors such as rate of successful attack and time spent handling prey, then functional response provides a mechanistic explanation of mesopredator suppression/release and a framework to quantify impacts on prey. While aspects of functional response in smaller carnivores like pole cats (Lode 2000), stoats (Jones *et al.* 2011), and coyotes (Donoghue *et al.* 1998; Bartel & Knowlton 2005), have been investigated, the studies were conducted either in systems without larger predators, or the effect of larger carnivores is not explicitly considered. Thus how larger carnivores affect the broad shape and the details of mesocarnivore functional response remains largely unexplored, despite its potential to provide a framework to link issues of ecological and conservation concern to classical ecological theory.

While there is little research yet on mesocarnivores, there are clues from other taxa for how multiple predators affect each others' functional responses. Soluk (1993) found that sculpins (*Cottus bairdi*) and stonefly larvae (*Agnetina capitate*) preying on mayflies had differing success depending on prey species. Both feed on mayflies but sculpins are also potential predators of stoneflies. One mayfly species (*Baetis tricaudatus*) can escape stonefly predation pressure by inhabiting areas with sculpins, but other mayfly species (*Ephemerella subvaria*) exhibit escape behavior around stoneflies that made them more vulnerable to sculpin predation. Facilitation and interference among predators can make predicting the effects of multiple predators on prey difficult compared to studies of a single predator feeding on a single prey species. In carnivore communities, facilitation and interference may have large impacts as multiple species often share prey species and carnivores are well adapted to harass and kill each other (Palomares & Caro 1999). Avoidance by smaller carnivores of larger ones will potentially impact the relationship between their hunting behavior and prey density.

Another relatively unexplored area of functional response in wild predators is their consumption rates (# prey killed and eaten/time) at high prey densities. In

Holling's Type II and III models, handling time limits the number of prey that can be caught and processed such that as prey density increases, the functional response eventually reaches an asymptote. However, the Type IV response curves downward at high prey density (exhibiting a dome shape) either due to a confusion effect, or the prey's anti-predator defenses like vigilance (Jeschke *et al.* 2004). The confusion effect occurs at high prey densities when predators are less able to target and isolate an individual member of a group, which lowers their hunting success (Beauchamp 2013). Lower consumption rates at high prey densities also can result when the predator is less likely to hunt at high prey density because group vigilance can make it harder for predators to approach prey unobserved (Pulliam 1973). At high prey density a predator can either chose not to hunt at all, or hunt in suboptimal conditions with lower success rates. Decreasing consumption rates with higher prey density have mostly been reported in zooplankton in lab situations (see Jeschke et al. (2004) for references), but there are a few field studies where it is also reported, though group size is used as a proxy for prey density. The rate peregrines (*Falco peregrinus*) and sparrowhawks *(Accipiter nisus*) successfully caught wading birds (redshanks, *Tringa tetanus*) in a surprise attack decreased with increasing wader group size (Cresswell & Quinn 2010). Clupid fish (*Sardinops sagax*) preying on marine insects had decreasing capture rates as group size increased (Treherne & Foster 1982). Smooth billed anis (*Crotophaga ani*) had a dome shaped functional response on purple winged butterflies (but not on yellow winged species) (Burger &

Gochfeld 2001). However, dome shaped functional responses have yet to be reported in mammalian predators.

The type of detailed observational data on carnivore hunting behavior needed for in-depth exploration of carnivore functional response is rare because such species tend to be elusive, nocturnal, and/or found in dense habitats, all of which make data collection on hunting behavior difficult or impossible. Thus most previous research on functional response in carnivores has relied on snow tracking (Hayes *et al.* 2000) and/or collar data (Smith *et al.* 2004; Sand *et al.* 2005; Nilsen *et al.* 2009) to estimate kill rates (# kills/time), and aerial surveys or pellet counts to estimate monthly or annual prey density (Merrill *et al.* 2010; McPhee *et al.* 2012). These data provide rough evaluations of predator functional response, but are missing many elements such as individual variability of predators (MacNulty *et al.* 2009b; Pettorelli *et al.* 2011), indirect effects (Creel & Christianson 2008), and seasonality (Metz *et al.* 2012), which are important in shaping predator-prey relationships. They also rely on a potentially tenuous connection between prey density and predator hunting behavior. If the density or abundance of mobile prey is measured on monthly or seasonal scales, it may give a misleading representation of the prey densities mobile predators not only encounter, but choose to hunt in. Research by Balme et al. (2007) showed that leopards prefer to hunt in areas where prey are easy to capture, not where prey are locally abundant. If carnivores are selective about the densities they spent time and hunt in, estimates of large-scale prey density may not be directly relevant to determining their hunt or kill rates.

Cheetahs provide an excellent opportunity to examine the effects of larger predators and high prey density on functional response. As mesocarnivores, cheetahs potentially have multiple factors to weigh when making decisions about where, when, and what to hunt. Not only must they consider how prey density influences likelihood of a successful hunt, but also how the presence of apex predators like lions and hyenas can affect whether or not a successful kill is stolen. Cheetahs are generally highly mobile and not restricted by territorial boundaries (Durant *et al.* 1988), thus have flexibility in choosing which densities of gazelles to hunt. Durant (1998) found that cheetahs spent more time in areas of low and medium gazelle density and avoided areas with no or high gazelle density. Cheetahs prefer to hunt gazelles that are in groups smaller than 11 individuals (Fitzgibbon 1990a), and small groups are more likely to occur in areas of lower gazelle density (Durant 1998). Vigilance behavior enables gazelles to spot approaching cheetahs, and they often signal to other members of their group and to the predator by snorting and 'inspecting' the cheetah (FitzGibbon 1993, 1994). Cheetahs are stalking predators that rely on getting close to their prey before launching a short, high-speed chase. If the cheetah is seen by gazelles, it is unlikely to either initiate or continue a hunt and often moves out of the area (FitzGibbon 1994). This suggests that cheetah consumption rates may have a different relationship with prey density than is seen in the classic Hollings Type II or Type III models. Cheetahs are likely to reach their highest consumption rates at fairly low prey density, and potentially also experience lower consumption rates at high prey densities, exhibiting a pattern more similar to a Type IV curve. I predict that overall, the cheetah population will have a dome-shaped Type IV functional response, but that whether or not the cheetahs has cubs, the local presence of lions, and the season will determine the maximum rate at which cheetahs consume their prey.

Not all cheetahs face the same costs and benefits when hunting. The presence of other predators and the shifting distribution of prey by season could influence not only the slopes and peaks of cheetah functional response, but potentially the overall shape. Mobility is important in allowing cheetahs to choose the gazelle density in which they hunt, but some cheetahs are more constrained in their movements than others. For example, mothers with young cubs are limited in how far away from their dens they can hunt as they must return to nurse their cubs (Laurenson 1995a). Durant (1998) found that mothers with cubs in the den are more likely to be found in areas of lower prey density and higher lion density as denning areas tend to be attractive to lions as well.. Lactating females with high nutritional demands, respond by increasing their food intake by both hunting more often and increasing their hunting success on larger prey like adult gazelles (Laurenson 1995a). Mothers with older cubs that can follow her have fewer restrictions on their movements but also need to keep the rate of killing elevated to provide food for cubs (Caro 1994). Due to the need to acquire more food for their cubs, I predict that all mothers with cubs will have a Type IV response but with higher consumption rates across all prey densities than cheetahs without cubs (Fig. 1). When their cubs are in the den, mothers may be limited in the densities where they can choose to hunt due to the constraints on their movements and the presence of lions. They may need to find ways to be successful in a wider range of prey densities than cheetahs without cubs and even than cheetahs with older, more mobile cubs. I predict that mothers with cubs in the den will have higher consumption rates than cheetahs without cubs, and hunt at a wider range of prey densities to take advantage of available opportunities (Fig. 1).

In Serengeti National Park, Tanzania, the seasons strongly influence local herbivore abundance and distribution. In the wet season, water and green grass are fairly homogenously distributed across the short grass plains and gazelles are abundant and widespread. Some lion prides shift their space use to take advantage of the abundant prey (some gazelles, but more commonly wildebeest and zebra) on the plains (Schaller 1972) . During the wet season, cheetahs tend to avoid the dense aggregations of zebra and wildebeest where lions and hyenas are more likely to be found and spend more time around the edges of gazelle herds (Durant 1998). When the rains stop in April or May, the gazelles move into the long grass plains and woodlands and concentrate around sources of permanent water, creating a more clumped distribution in the dry season. Durant (1998) found that during the wet season cheetahs spend more time in low and medium prey densities, possibly because the evenness of their distribution makes areas of no or very high gazelles less likely than in the dry season. In the dry season when prey are more clumped, cheetahs will spend time in, but avoid hunting in, areas of high prey density, and I predict they will have a Type IV functional response (Fig. 2). However, in the wet season I predict that the peak consumption rate will occur at low and medium gazelle densities and cheetahs will not spend time in high prey density areas, creating a Type II functional response (Fig. 2).

The presence of lions also influences cheetah hunting behavior and space use. Research by Durant (1998) and Swanson et al. (2016) shows that cheetahs facultatively avoid lions on a local scale, and are less likely to hunt if lions are nearby (Durant 2000b; Cooper *et al.* 2007). I assume that cheetahs are likely to hunt less when lions are within 1 km, and that consumption rates will be much lower across all prey densities when lions are present compared to when they are not (Fig. 3). However, the effect of lions is likely to vary by season. In the wet season when prey are spread out, it is easier to avoid lions and therefore, cheetahs may only rarely hunt and kill when they are present. In the dry season, predators and gazelles are concentrated around water sources and cheetahs spend more time within 2 km of lions (Durant 1998), probably because they are hard to consistently avoid. This may force cheetahs to hunt in the presence of lions, leading to higher consumption rates in the dry season than in the wet when there are lions present (Fig. 3).

The extensive and detailed observational data on cheetah hunting behavior and associated prey densities in Serengeti provides an opportunity to examine cheetah functional response and go beyond previous studies to quantify functional response based on direct observations of how cheetahs hunt in the prey densities they actually encounter. Overall I expect cheetah consumption rates to reflect a balance between the need to acquire resources efficiently, and avoid potentially dangerous interactions with other predators.

Methods

I used data collected by Karen Laurenson (KL) from 1987-1990 and data I collected in 2014. Both of us conducted all day, or multi-day, follows of the same cheetah and recording hunting behavior and prey numbers. I followed whichever cheetah(s) I found first while KL had radio collars on adult females and her data are mostly on single females and mothers with cubs 3 months old or younger. We recorded the start and end time of every hunt down to the second, whether the hunt was successful or not, and the target prey species and age. We counted all the herbivores and/or carnivores visible in radius of one kilometer around the vehicle every 15 minutes (AH) or hour (KL). To account for diminished views caused by topography and heat haze, I estimated the degree and distance of the viewshed in which I could see all standing animals. KL took less detailed notes on what part of the viewshed she could completely census, so I assumed it was 1000m in 360 degrees unless she indicated otherwise. If it was obvious that her view was impaired but there was no indication of what distance she could see, I removed those data from the calculation of prey density. I used the number of animals of various species and the size of the viewshed to calculate the density of visible gazelles (Thomson's gazelles, Grant's gazelle's, and animals identified simply as 'gazelle'), and lions, for every time block. A time block was calculated as the time between the prey survey and the next prey survey on the same day. Due to the exigencies of fieldwork, duration of time blocks varied from 15 minutes to six hours. I matched the density estimates of gazelles and predators that were closest in time to each hunting event. Therefore, for each prey survey, I calculated the number of total hunts, the number of gazelle hunts, and the number of successful gazelle hunts that took place during that time block. Many of the higher densities were the result of many gazelle in a small viewshed, and occasionally when no gazelles were visible there were actually gazelles present (given the number of hunts that occurred with 0 visible gazelles) so the densities may not represent wide scale prey density, but rather visible prey density, which should be similar to prey density a cheetah would experience while making hunting decisions.

Modeling

I used model selection to test whether the Type II or Type IV response best fit the data.

1. The classic Holling Type II functional response assumes a high consumption rate at low prey densities, and the asymptote at high prey densities is determined by handling time. I used kill rate (gazelles killed/hour) as a proxy for consumption

rate because the time blocks were too short to encompass consumption of the kill. Despite Type III response being the more commonly reported for larger vertebrates, especially ones who prey on multiple species like cheetahs, I did not test this model as its key assumptions is very low consumption rates at low prey densities. Since cheetahs prefer to hunt at low prey densities, it seemed unlikely to be a good fit for cheetah predation patterns.

$$\text{Gazelles killed/hour} = \frac{attack\ rate * prey\ density}{(1 + handling\ time * prey\ density)}$$

2. Type IV functional response is a Type II but with a penalty that increases with prey density, which produces a functional response that curves down at high prey density (a dome shaped functional response). The penalty is not linked to any specific behavior on the part of either cheetahs or gazelles, it merely serves to create the dome shape typical of Type IV responses. When the penalty is 0, the equation and curve are exactly the same as the Type II.

$$\text{Gazelles killed/hour} = \frac{e^{-penalty * prey\ density} * (attack\ rate * prey\ density)}{(1 + handling\ time * prey\ density)}$$

I used 5575 prey surveys to test if cheetah functional response differed depending on reproductive status, the proximity of predators, or season. For each subset of data I compared the fits of Type II and Type IV models with parameters (including the penalty) estimated using maximum likelihood with a Poisson distribution. All models within a subset were ranked by AIC and I considered models within 2 ΔAIC points of the top model to have strong support (Burnham & Anderson 2002). First I examined all data combined. Next I subset the data into cheetahs without cubs, mothers with cubs of all ages, and mothers with cubs in the den (as designated by KL). To determine the effect the presence of lions had on cheetah functional response, I examined all surveys with no visible lions within 1 km versus ones where at least 1 lion was visible. I examined functional response by Wet Season (December-April) and Dry Season (May-November). Finally, since the density of lions a cheetah encounters is likely to vary depending on season, I also examined cheetah functional response with lions versus no lions in wet and dry seasons. See Table 1 for summary of data and sample sizes for each subset

During the majority of surveys surrounding a cheetah, there were no gazelles visible. Thus, in order to plot functional response I calculated the rate of kills/hour. For prey densities where cheetahs did not spend much time, a couple of kills would result in relatively high consumption rates. To calculate the kill rates, I lumped all surveys at 0 gazelle density together, and then divided the rest of the data into 12 groups of similar observation duration. For each group of data I plotted the average gazelle density against the average rate of successful kills/hour. To test if kill rates fall in parallel with hunt rates, I used linear regression on the average hunt and kill rates for all cheetahs combined.

Results

I used data from 3248 hours of observation during which time we observed 460 hunts (both successful and unsuccessful) on gazelles by 73 (17 male, 56 female) individual cheetahs. Of those 460 hunts, 135 were successful and resulted in kills and average hunt and kill rates per hour for all cheetahs combined were 0.142 and 0.042, respectively (Table 1). Mothers with cubs hunted gazelles most often (mean=0.15 hunts/hour) while the lowest overall hunt rate was for all cheetahs during the wet season when lions were present (mean=0.066 hunts/hour). Kill rates varied from a high of 0.05 kills/hour for mothers with cubs to a low of 0.016 kills/hour during the dry season when lions were present.

Cheetahs spent time in areas with gazelle densities of 0 (i.e. no visible prey) and up to 9872 gazelles/km^2. Of that time, between 26% (dry season with lions) and 43% (has cubs in the den) was spent in areas with no visible prey (Table 2). Mothers with cubs in the den encountered the lowest maximum gazelle density (321 gazelles/km^2), while during the dry season cheetahs encountered the highest gazelle densities (9872 gazelles/km^2). All cheetahs hunted in lower gazelle densities than the maximum densities they encountered (Table 2). Mothers with cubs were able to makes kills across the entire range of prey densities they hunted in, while other cheetahs were unable to make kills in the highest gazelle densities. With the exception of the wet season when lions were present, cheetahs spent very little time in areas where gazelle densities were too high for a successful hunt (Table 2).

All Cheetahs combined

Although the kill rate fell at high prey densities (Fig. 4a), the Type IV model was not better than the Type II (Table 3) in predicting cheetah functional response (AIC <2.0). Kills rate showed a positive linear relationship with hunt rate (slope=0.31, R^2=0.65, p=0.0016, Fig. 5), indicating that hunt rates fell in unison with kill rates across the range of gazelle densities. Although cheetahs encountered very high prey densities, they spent the majority of their time in the lower prey densities where they could hunt successfully, only ~2% of their time was spent in areas with prey density higher than the densities in which they could make kills (Table 2).

Reproductive status

Mothers with cubs spent their time and hunted in much lower gazelle densities than cheetahs without cubs (Table 2). They killed across the entire range of densities in which they hunted and there was no decrease in kill rate at high prey density, thus the penalty on the Type IV model was 0, making it the same curve as the Type II model (Fig. 4b, Table 3). Females with cubs in the den only spent time in densities up to 321 gazelle/km^2 and hunted and killed in densities up to 211 gazelle/km^2 (Table 2). Similarly to all females with cubs, for mothers with cubs in the den, there was no penalty on the Type IV model making it equivalent to the Type II model (Table 3, Fig 4c). In contrast, the kill rate for cheetahs without cubs decreased at high prey densities, and there was strong support for the Type IV model being the best fit to the data (Table 3, Fig 4d). Cheetahs without cubs spent time in areas of higher prey density than cheetahs with cubs and hunted in higher densities as well (Table 2).

Lion Presence

Cheetahs spend less than 5% of their time within 1 km of a lion (Table 2). When lions are present, cheetah hunting behavior changes. They hunt and kill less frequently, and they have an unpredictable functional response relationship between kills and prey density (Table 3; Fig. 6a). Cheetahs were almost never found in relatively high prey densities when lions were around. Although the maximum density encountered when lions were present was 1528 gazelles/km^2, only 2 out of 153 hours were spent in densities more than 200 gazelle/km^2 (Table 2).

Seasonality

Cheetahs spend 40% of their time in areas with no visible prey during the wet season (Table 2). Kill rates declined at high gazelle density during the wet season (Fig. 6b), but there was no support for the Type II or Type IV model as better than the other (Table 3). There is a similar decrease in kill rates at the highest gazelle densities in the dry season, but not enough to support a Type IV model as better than a Type II (Table 3, Fig. 6c).

Seasonality x Lion Presence

Data on cheetah hunting behavior in the wet season around lions is limited. Out of ~1000 hours of observation in the wet season, only 90 of them were when the cheetah was within 1 km of a visible lion. However, in that relatively short amount of time they hunted 6 times and killed three times (Table 2). Their functional response showed no predictable pattern, and the Type IV was the same shape as the Type II (Fig. 6d, Table 3). Cheetahs spend even less time around lions in the dry season, in 2244 hours of observation, cheetahs only spent 62 hours near lions (Table 1). They only made 1 kill when lions were around, making their functional response uncharacterizable (Fig. 6e).

Discussion

The best model for cheetah functional response for all cheetahs combined was a dome shaped Type IV curve, but there was also strong support for a Type II response as a competing model. The lack of clear pattern was due to cheetahs exhibiting different functional response curves depending on their reproductive status. A dome shaped functional response was the best fit for cheetahs without cubs, while mothers with cubs had a Type II response curve with an estimated attack rate twice as high of cheetahs without cubs. The presence of lions within 1 km served to depress kill rates, and made functional response either unpredictable or difficult to characterize.

Although kill rates drop at high gazelle density, the drop was driven by cheetahs without cubs whose kill rate peaked at relatively low gazelle density and dropped to zero in areas of high prey density. Mothers with cubs displayed a different pattern. They stayed in areas of lower prey density but had attack rates twice as high as cheetahs without cubs, and in general increased their kill rates with gazelle density. Laurenson (1995) showed that mothers with cubs meet their higher metabolic needs by having higher hunting and kill rates on larger gazelles than cheetahs without cubs. I found mothers with cubs were able to keep those higher attack rates across the range of prey densities. However, compared to cheetahs without cubs, mothers with cubs were more limited in the gazelle densities they encountered and the densities in which they hunted. This was especially true for mothers with cubs in the den that spent almost all of their time in gazelle densities where they had hunting success. Staying out of areas with high gazelle density may be a strategy to maximize time in areas where hunting success is higher. The increased energetic demands of having cubs may cause mothers to be more selective in where they spend their time, and prioritize areas where they have high hunting success.

It is thought that general functional response shape is a function of predator type, i.e. filter feeder (Type I), specialized predator (Type II), and generalist predator (Type III) (Jeschke *et al.* 2004). However, my results show that individuals of the same species can differ in types of functional responses depending on their reproductive status. The increased energetic demands and spatial limitations of having cubs not only causes cheetahs to increase their kill rates, but changes what gazelle densities they encounter and kill in, precipitating a complete shift in functional response from Type IV to a Type II. Different functional responses between life stages has also reported in bald eagles scavenging on sockeye salmon (Restani *et al.* 2000). As a whole bald eagles exhibited a Type II response, but that response consisted of adults having a Type I and subadults an uncharacterizable functional response.   Given how kill rates in carnivores can vary by age (MacNulty *et al.* 2009b), social grouping, and sex (Nilsen *et al.* 2009; Mattisson *et al.* 2011), subgroups of a population with entirely different shaped functional responses than the population level response, may not be uncommon.

This is the first dome shaped functional response reported for mammals. This is likely due to two factors that make cheetahs less likely to kill at high gazelle density. The first is gazelle vigilance and group defense becoming more successful in higher densities. The parallel drop in hunting and kill rates with increasing density supports the idea that cheetahs are evaluating their likelihood of a successful hunt, and only attempt a hunt when the chances of success are good. Cheetahs are stalking predators that target less vigilant individuals, potentially because they are slower to detect cheetahs and flee, thus increasing the chance of a successful chase (Fitzgibbon 1989). However, cheetahs will abandon the hunt 74% of the time if they are seen by a gazelle in the group they are stalking (Fitzgibbon 1989). Group defense is behavioral mechanism that is thought to produce the Type IV curve (Jeschke *et al.* 2004), and it is very likely that as gazelle density increases, the chance that a cheetah remains unseen declines. Gazelle vigilance can lower the rate of successful attack either by making hunts less successful or by making it less likely a cheetah will initiate a hunt, or both. However group defense is not perfect in gazelles. While an individual gazelle will engage in behaviors like staring and predator inspecting (Walther 1969; FitzGibbon 1994) when they see a predator, this does not necessarily translate to the entire herd being alerted to the predator's presence (Fitzgibbon 1989). Individual gazelles can remain less vigilant and a worthwhile target that may explain the gradual decrease in kill rate with gazelle density seen in cheetahs without cubs. Observations of attack success in varying prey densities is not particularly common for terrestrial species, instead prey group size is often used. In the forests of Coˆ te d'Ivoire, the combined predation rates of leopards, chimpanzees, and African crowned eagles on their prey decreased with group size but increased with density of groups (Shultz *et al.* 2004). Fanshawe and Fitzgibbon (1993) found that although hunting success of wild dogs varied by gazelle group size, the differences were not significant. My results are some of the first to show hunt and kill rates of a wild carnivore change with the local prey density they encounter and provides evidence that for gazelles, density appears effective at lowering predation risk from cheetahs, both through dilution and by decreasing the overall rate of attacks and kills.

The second reason for the dome shaped functional response is avoidance of lions. Kill rates plummeted when cheetahs were within a kilometer of lions, so much so that lack of data makes it hard to characterize cheetah functional response when lions are nearby. Cheetahs do hunt when lions are present in both wet and dry seasons, but lion presence suppresses cheetah hunting behavior, or at least severely restricts the conditions in which they hunt. My data are limited to the prey densities around cheetahs, and are not ideal for determining if lions spend more time in areas of high gazelle density. Thankfully, work by Durant (1998) recorded lion presence and gazelle densities both with and without cheetahs. She found that lions were more likely to be present in scans with more than 250 Thomson's gazelle compared to scans with fewer gazelle. She also found that cheetahs were less likely to be seen in the scans with high numbers of gazelle. In later work she found that cheetahs move away and are less likely to hunt if they hear lions (Durant 2000b). Together these results provide strong support for the idea that the down turn in cheetah kill rates at high gazelle density is at least partially due to cheetahs avoiding hunting in those areas because of lions. The avoidance of high density gazelle areas for cheetahs with cubs is also likely driven by both the need to maximize hunting efficiency and the desire to keep cubs safe from predation by larger predators (Laurenson 1994). In the dry season gazelles and predators concentrate around water (Durant 1998). Although in both wet and dry season the Type II is the top model, there is also stronger support for the Type IV being a competing model in the dry season. This may be due to the both lion presence and gazelle group vigilance operating in areas of high gazelle density leading to stronger suppression of kill rates in the dry compared to wet season.

Lions suppressing cheetah hunting behavior points to a mechanism for Ritchie and Johnson's (2009) "Fear and Loathing". They suggest altered foraging behavior as a major mechanism of mesopredator suppression, and while previous research has quantified foraging/hunting behaviors of smaller carnivores under predation pressure (Mukherjee, Zelcer & Kotler 2009), it has yet to be linked to changing kill rates across a range of prey densities. Additionally, research on the functional responses of mesopredators has not considered the influence of larger predators (Bartel & Knowlton 2005; Andruskiw *et al.* 2008). By putting cheetah and lion interactions in a functional response framework, I show that the presence of lions suppresses cheetah kill rates throughout a range of gazelle densities and across seasons. However, this may not have particularly negative overall effects on cheetahs since they spend relatively little of their time in close proximity to lions (Durant 1998; Swanson *et al.* 2016) and therefore may not have to forfeit many hunting opportunities. Scantlebury et al.'s (2014) work suggests that the frequent moving required to avoid lions on very fine scales may be more costly for cheetahs than suppression of their hunting. However, changes to lion distributions or numbers, or limits on cheetah mobility caused by fencing for example, may change their ability to hunt in areas without lions, and a decreased kill rate may become problematic in such situations. Lowering hunting success in proximity of larger predators may have greater negative impacts on mesopredators like wild dogs, which are less able to avoid larger predators at fine scales or have higher energetic investments in hunting behavior (Gorman *et al.* 1998). My results point to one mechanistic explanation for mesopredator release and suggests that the absence of apex predators allows mesopredators to hunt more frequently and take advantage of a wider range of prey densities.

I found evidence that cheetahs as a population have a dome shaped Type IV functional response, the first recorded for mammals. The shape appears to be largely driven by the fact that cheetahs without cubs have this dome-shaped Type IV curve, while in contrast, mothers with cubs have a asymptotic Type II curve. If demographic groups have different kill rates that change the shape of the function response, a change in the structure of the predator population could alter the effects on prey, even if the overall predator population numbers remain similar (MacNulty *et al.* 2009b). Thus the functional response of the cheetah population is likely to be driven by the relative proportion of cheetahs with and without cubs, a state which may be dynamic through time as females shift from having cubs to being single and back again. The notion that individual variability affects vertebrate population dynamics is well established (Pettorelli *et al.* 2011), but this is the first time to my knowledge, that an individual's functional response has been found to shift between types based on reproductive status, and not just once, but potentially multiple times throughout a female's life. Unless female cheetahs are unique in this ability, it may be necessary to rethink the accepted paradigm that the type of functional response depends on feeding mode (Jeschke *et al.* 2004).

Difficulties in data collection present daunting limits to applying a primarily experimental framework to the study of wild predators and assessing how variability in prey individual predators encounter affects population level responses. By linking cheetah hunting behavior with the actual prey densities that influence those behaviors, I was able to uncover aspects of mesopredator functional response that would likely have been obscured if I had used daily, monthly, or coarse spatial estimates of prey densities. The flexibility of not just slopes and asymptotes, but also the type of functional response among individual cheetahs depending on reproductive status and the proximity of lions, point to how individual variability and interspecific interactions can be powerful forces in shaping the predation behavior that influences predator-prey relationships.

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Tables and Figures

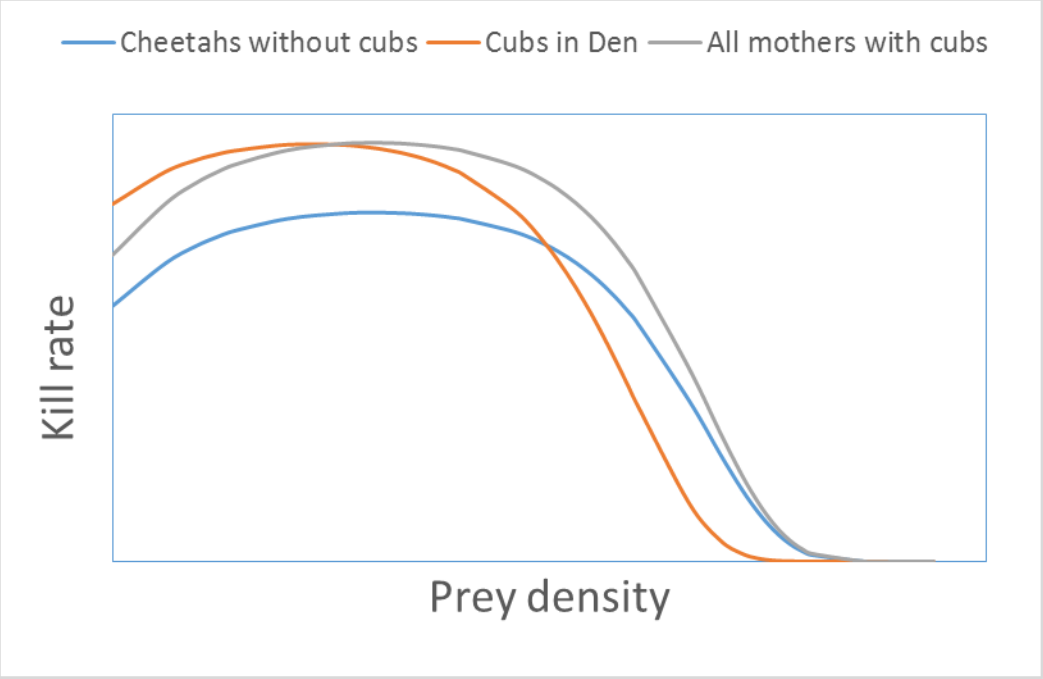


Figure 1. Predicted functional responses depending on reproductive condition. Cubs in Den refers to mothers whose cubs are in the den and do not follow her. All mothers with cubs includes mothers with cubs in the den and following cubs.

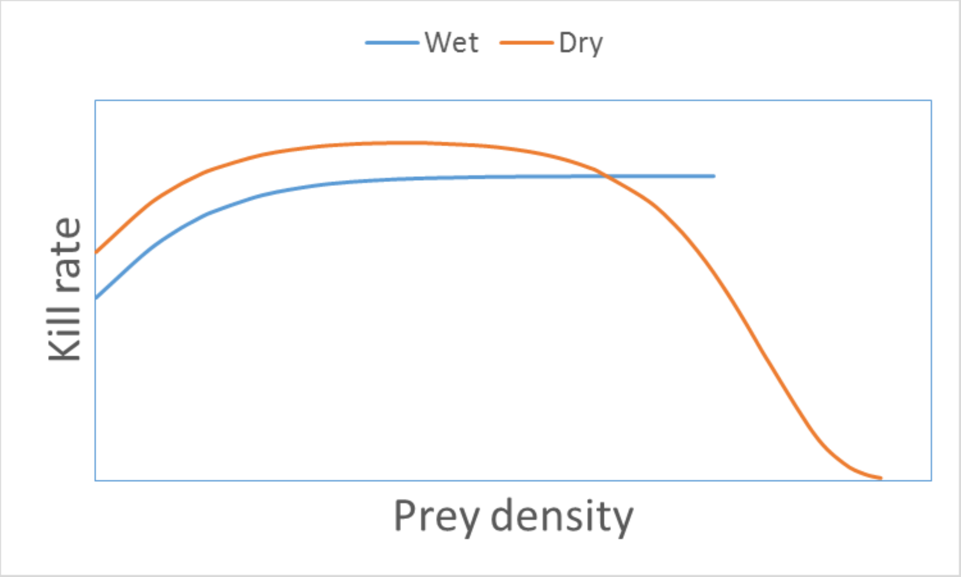


Figure 2. Predicted functional responses depending on season.

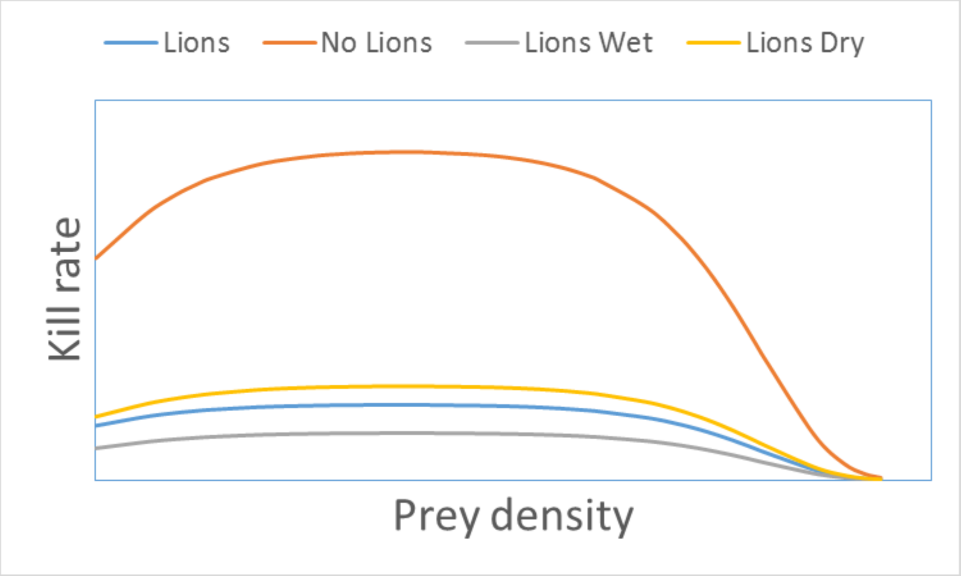


Figure 3. Predicted functional responses depending on whether lions are visible within a 1 km radius of the cheetah. Lions=when lions are visible in all seasons, No Lions =when there are no lions visible in all seasons, Lions Wet =when lions are visible in the wet season, Lions Dry= when lions are visible in the dry season.

Table 1. Summary of data sets used. All datasets are subsets of the Overall dataset (all cheetahs combined). Individual cheetah refers to the number of different cheetahs present in that dataset. Hunts/hour and kills/hour are overall averages for that dataset. Hunts and kills data only refers to gazelles.

Dataset	Total hours watched	Hunts	Kills	Individual cheetahs	Males	Females	Hunts/hour	Kills/hour
Overall	3248	460	135	73	17	56	0.14	0.04
Has Cubs	1452	217	71	24	0	24	0.15	0.05
Has Cubs in Den	924	125	41	14	0	14	0.14	0.04
Has No Cubs	1798	243	64	67	17	50	0.14	0.04
Lions present	153	12	4	26	5	21	0.08	0.03
Dry Season	2244	332	97	59	14	45	0.15	0.04
Dry Season with Lions	62.4	6	1	18	2	16	0.10	0.02
Wet Season	1003	128	38	33	5	28	0.13	0.04
Wet Season with Lions	90	6	3	12	2	10	0.07	0.03

Table 2. Descriptive data on hunting behavior and prey densities. All datasets are subsets of the Overall (all cheetahs combined) dataset. Densities are in gazelles/km^2. Hunt density= Highest prey density for hunt. Kill density= Highest prey density for a kill

Dataset	**% Time spent w no visible prey**	**Maximum Gazelle Density**	**Highest prey density for hunt**	**Highest prey density for a kill**	**% Time spent above highest hunt density**	**% Time spent above kill density**	**# of hunts above kill density**	**% of hunts above the kill density**
Overall	38	9872	2961	529	<1	2	7	2
Has Cubs	40	745	211	211	<1	1	0	0
Has Cubs in Den	43	321	211	211	<1	0	0	0
Has No Cubs	36	9872	2961	529	<1	4	7	3
Lions present	28	1528	125	86	3	8	3	25
Wet Season	41	8768	1498	529	<1	2	6	2
Wet Season with Lions	29	1528	125	71	3	15	3	50
Dry Season	32	9872	2961	208	<1	4	1	1
Dry Season with Lions	27	703	108	86	3	4	1	17

Table 3. Subsets of data investigated and parameter values from models. For each subset of data Type II and Type IV models were compared via AIC. Penalty refers to the 3rd parameter in the Type IV model that creates the downward curve. When the penalty is 0 there is no support for the Type IV model over the Type II. In all cases the Type II model has 2 parameters and the Type IV has 3. Weight= Akaike weight

Data	**Models**	**Attack rate**	**Handling time**	**Penalty**	**AIC**	**ΔAIC**	**Weight**
Overall	Type IV	0.14	2.00	0.0008	1151.33	0.00	0.60
	Type II	0.15	2.26		1152.11	0.77	0.40
Has Cubs	Type II	0.18	2.33		567.90	0.00	0.73
	Type IV	0.18	2.33	0.0000	569.90	2.00	0.37
Has Cubs in Den	Type II	0.20	2.78		332.41	0.00	0.73
	Type IV	0.20	2.78	0.0000	334.41	2.00	0.27
Has No Cubs	**Type IV**	**0.09**	**1.33**	**0.0014**	**580.95**	**0.00**	**0.74**
	Type II	0.10	1.85		582.99	2.04	0.26
Lions present	Type II	0.04	0.89		38.86	0.00	0.73
	Type IV	0.04	0.89	0.0000	40.86	2.00	0.27
Dry Season	Type II	0.15	2.11		826.88	0.00	0.55
	Type IV	0.14	1.89	0.0007	827.26	0.37	0.45
Wet Season	Type II	0.15	2.82		327.96	0.00	0.59
	Type IV	0.14	2.37	0.0011	328.69	0.73	0.41
Wet Season with Lions	Type II	0.08	1.60		29.05	0.00	0.73
	Type IV	0.08	1.60	0.0000	31.05	2.00	0.27
Dry Season with Lions	Type II	0.10	2.00		14.14	0.00	0.52
	Type IV	0.00	0.00	0.0051	14.29	0.16	0.48

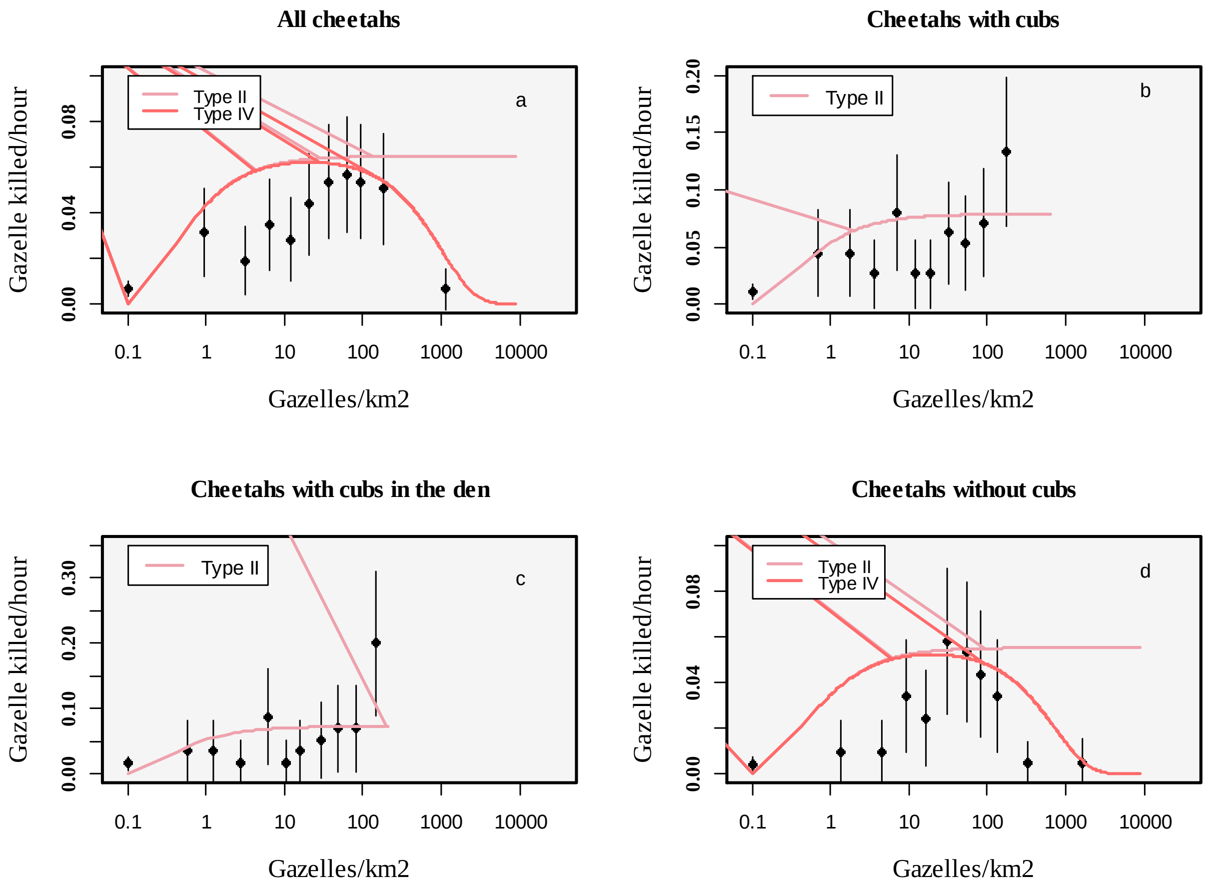


Figure 4. Functional response curves for cheetahs estimated using maximum likelihood. Points represent averaged kill rates, and bars are 95% confidence limits. Note: x axes are the same, but scale of y axis is differs by panel

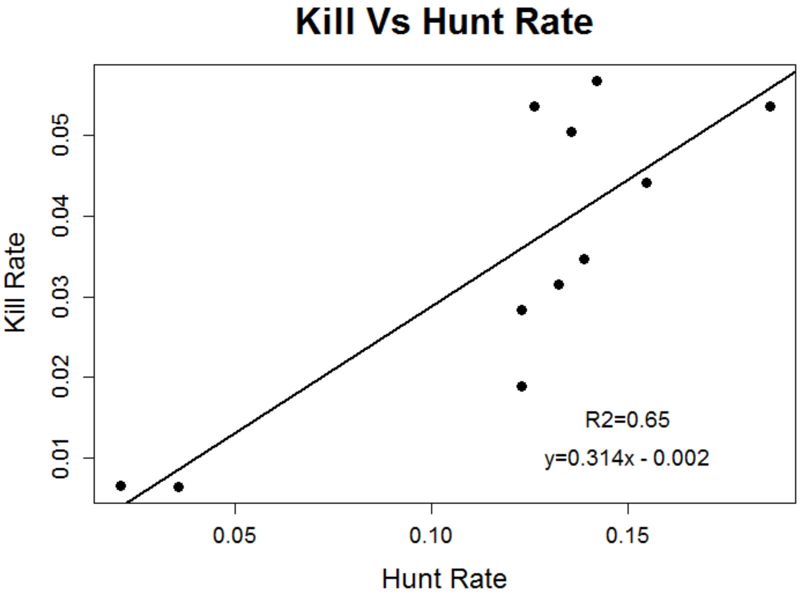
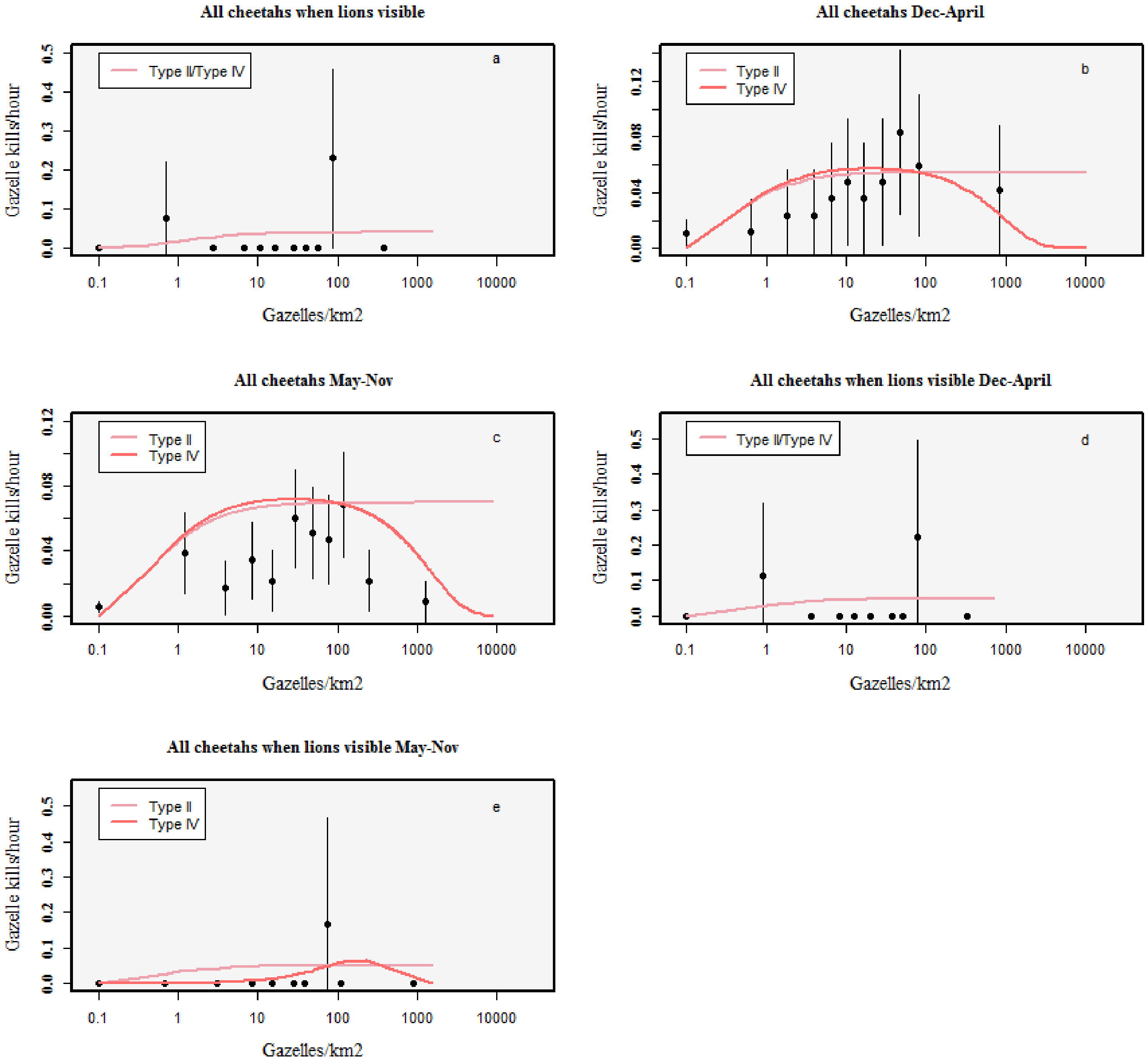


Figure 5. Linear regression of kill rate as a function of hunt rate. Slope of regression line =0.314, adjusted R^2 = 0.65.



All cheetahs when lions visible

All cheetahs Dec-April

All cheetahs May-Nov

All cheetahs when lions visible Dec-April

All cheetahs when lions visible May-Nov

Figure 6. Functional response curves for cheetahs estimated using maximum likelihood. Points represent averaged kill rates, and bars are 95% confidence limits. Note: x axes are the same, but scale of y axis is differs by panel.

Chapter 3

Balancing risk and reward: Individual variability in cheetah kill probabilities and handling time results from differing reproductive status and larger predators.

Abstract: One of the most basic interspecific interactions is when one species consumes another. Functional response models are used to relate predation rate to prey density, and are central to our understanding of predator-prey interactions. Probability of making a successful attack and time spent hunting and eating a prey item are factors that determine how many prey a predator kills per unit of time. Although usually assumed to be constant in functional response, studies of apex predators show that both behaviors can exhibit considerable variation. Additionally, mesopredators must balance hunting mobile prey with avoiding predation themselves and thus may display even more variable attack and prey-handling behaviors. I used 34 years of data on 272 hunts by a mesopredator, the cheetah, from Serengeti National Park to investigate variability in kill probability and handling time, and determine whether variability reflects tradeoffs in balancing food acquisition with risk posed by apex predators. I found that kill probability was higher for mothers with cubs than cheetahs without cubs, and lion presence did not directly affect kill probability. However, lions and hyenas did shorten cheetah handling time directly by stealing kills. The more meat available per cheetah, the longer cheetahs spent handling prey. Mothers with small, vulnerable cubs had longer handling times than cheetahs without cubs, likely due to increased vigilance in time spent scanning for incoming predators. My results show that the impact of larger predators on cheetah handling time varies by stage in the predation process and that characteristics of individual cheetahs modulate the impacts apex predators have on handling time. Quantifying the effects apex predators have on mesopredators via functional response provides a better understanding of predator community ecology. However, the likely violation of model assumptions means that caution should be exercised when using such models to predict predator-prey dynamics or when extrapolating hunting behavior to the population level.

Introduction

Functional response is a formal representation of the relationship between predator feeding behavior and prey density and is used to determine the rate of prey eaten by predators (Holling 1959a; b). There are several shapes that this relationship can take, but a Type II functional response curve is commonly used for species that take time to handle their prey (i.e. are not filter feeders) (Jeschke *et al.* 2004). At low prey densities, the number of prey eaten is determined by the attack rate. Attack rate is the number of prey items encountered, attacked, and successfully captured across the amount of time spent in active pursuit (McPhee *et al.* 2012). However, the Type II is asymptotic for predator feeding rate as prey density increases because eventually, predators become limited by the time is takes to handle prey. This handling time is defined as the amount of time a predator spends hunting, killing, and eating a prey item (Jeschke *et al.* 2002). A higher attack rate means more prey are consumed in a specified amount of time while a longer handling time results in fewer prey killed within that time. In functional response modeling, both parameters are traditionally considered to be a constant, but laboratory and field studies across a variety of taxa show that assumption commonly may be violated. For large predators attacking large prey, hunting is an energetically costly behavior (Gorman et al. 1998, but see Scantlebury et al. 2014), and before launching an attack, predators likely evaluate multiple factors including the chance of success, potential energetic output versus gain, and the risk of injury, leading to multiple factors influencing attack rate. For example in wolves, attack rate can be lower near man made features (McPhee *et al.* 2012), higher in drainages (DeCesare 2012), lower in larger packs (Thurber & Peterson 1993), and higher on larger groups of prey (Hebblewhite & Pletscher 2002).

Handling time also varies among individuals. Laboratory studies show that handling time decreases as prey get smaller and/or predators get bigger (Boulding 1984; Kaspari 1990; Verwaijen, Van Damme & Herrel 2002; Grefsrud, Strand & Haugum 2003), and that predator age (Xia, Rabbinge & Van Der Werf 2003), sex (Eggleston 1990a), and hunger level (Bindoo & Aravindan 1992) can influence handling time. Research on handling time outside of the lab is less common, but studies have found that handling time of apex predators like wolves (Messier & Crête 1985) or pumas (Anderson & Lindzey 2003; Smith *et al.* 2015) can vary widely. However, we know even less about the handling time of mesopredators that must contend with avoiding predation/harassment by apex predators, which can alter their hunting behavior substantially (Ritchie & Johnson 2009). The behavioral modifications individual mesopredators use to balance avoiding apex predators with hunting and consuming prey, likely increases the variability in their handling time, which can compromise the ability of Holling's equations to make accurate, mechanistic predictions about their predation (Okuyama 2012).

In Chapter 2, I estimated attack rate and handling time parameters by fitting Type II and Type IV functional response curves to observed number of gazelles killed across gazelle densities. In these models attack rate and handling time are assumed to be constant, yet the estimated parameter values differed depending on whether curves were fit for data on cheetahs with or without cubs, in wet versus dry season, and whether or not lions were visible within 1 km. Bolnick et al. (2011) and Okuyama (2008) show that if attack rate or handling time is variable among individuals, using the value of the population mean will result in chronic over or underestimation of predation rate respectively, which potentially affects predictions about predator-prey dynamics. Variability among individuals is not the only way to violate model assumption of constant attack rate. Kill rates declined at higher gazelle densities, and for cheetahs without cubs, the trend was pronounced enough to cause a shift in functional response from Type II to Type IV (Chapter 2). This suggests that attack rate may not only vary among individuals, but with prey density as well. Functional response is made up of the combination of behaviors related to hunting and handling prey which cheetahs can potentially alter in different ways in response to the same factor or pressure. If model assumptions are violated, then the differences in estimated attack rates and handling times depending on reproductive state or the presence of lions may not actually represent how cheetahs alter those behaviors in response to specific pressures. By understanding how reproductive status, environment, and the abundance of prey and other predator species affect the constituent behavioral components that make up part of functional response, we can improve our abilities to predict how cheetah functional response as a whole will respond to changing conditions. Due to modeling constraints I couldn’t quantify attack rate directly, so in this chapter I separate probability of a cheetah making a kill during a prey survey (probability of successful kill) and handling time to determine how reproductive status, season, lion presence, and prey density affect these distinct components of hunting behavior.

I used data from 34 years of observed cheetah hunts from the Serengeti Cheetah Project to examine the factors influencing individual variability in attacking behavior and handling time of cheetahs in Serengeti National Park. I hypothesize that cheetah attacking behavior and handling time will exhibit considerable variability that will reflect the differing needs of individuals in balancing food procurement with risks from apex predators. I expect probability of a successful attack per unit time (kill probability) to be higher for mothers with cubs than cheetahs without cubs as they need to increase their food intake to feed their cubs (Laurenson 1995a), but that their kill probability will not be affected by prey density. However following the pattern seen in Chapter 2, I expect the kill probability for cheetahs without cubs will decrease at high gazelle density. For all cheetahs I expect that the presence of lions will lower kill probability since cheetahs are less likely to start a hunt if they are aware lions are nearby (Durant 2000b). I also expect kill probability for all cheetahs to depend on season due to the increased availability of vulnerable gazelle fawns in the wet season (AH pers. obs).
Apex predators such as lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) are attracted to, and steal, about 10% of cheetah kills (Hunter *et al.* 2007b). Lions

and hyenas also cause >50% of cheetah cub mortality (Laurenson 1994), making handling prey a potentially risky activity for mothers with cubs. Thus I expect handling times to be shorter when cheetahs are more vulnerable to predation, when they are more energetically constrained, or when they are more experienced. Small cubs (<4 months old) are particularly vulnerable to predation (Laurenson 1994) and I expect mothers with small cubs to decrease their handling time in order to minimize predation risk to their cubs, resulting in the shortest handling times than other social groups. Males are unconcerned with predation risk to cubs and are occasionally able to defend their kills from kleptoparasitism, potentially leading to longer handling times. Single females also do not face predation risk, but are less able to defend their kills, thus I predict they will have intermediate handling times. Large prey will require longer handling times than small prey. Thin cheetahs are more energetically constrained than fatter ones, and hence will have a shorter handling time as they eat quickly. Older cheetahs are more experienced and better hunters (Hilborn *et al.* 2012), which could translate into spending less time at kills. Cheetahs almost never defend their kills, so if nearby lions and hyenas discover and steal the kill, handling time will be shortened. A summary of my hypotheses and expectations of factors potentially structuring variability in kill probability and handling time can be found in Table 1.

Methods

Data

I used observations of cheetah hunts by members of the Serengeti Cheetah Project collected between 1980 and 2014. Cheetahs are mainly diurnal hunters and are usually habituated to vehicles, making it possible to directly observe and record their hunting behavior. Researchers observed hunting behavior with binoculars from a distance to minimize disturbance and recorded handling time in seconds. For groups of mothers with cubs, the mother was always the focal animal and researchers recorded her handling time. For other social groups, the handling time was recorded for the cheetah that hunted when possible, otherwise it was randomized. Handling time was defined as the time from when a cheetah started hunting (took 2 or more steps in a purposeful manner towards prey), through the chase and the kill, and ended when the cheetah was finished eating. We did not consider digestion to be part of handling time as immediate hunger level does not significantly impact a cheetah's decision to initiate a hunt (Cooper *et al.* 2007). Sex and age of prey was determined at the kill site; flesh weights of the prey were estimated following the method outlined by Blumenschine & Caro (1986).

To examine how attacking behavior varied depending on reproductive condition and season, I used data collected by Karen Laurenson (KL) from 1987-1990 and data I collected in 2014. Both of us conducted all-day or multi-day follows on the same cheetah and recording hunting behavior and prey numbers around cheetahs. I followed whichever cheetah(s) I found first while KL had radio collars on adult females and her data are mostly on single females and mothers with cubs 3 months old or younger. When with a cheetah, we counted all the herbivores and carnivores visible in radius of one kilometer around the vehicle every 15 minutes (AH) or hour (KL). To account for diminished views caused by topography and heat haze, I estimated the degree and distance of the viewshed in which I could see all standing animals with a 180 degree semicircle. KL took less detailed notes on what part of the viewshed she could completely census, so I assumed it was 1000m in 360 degrees unless she indicated otherwise. If it was obvious that her view was impaired but there was no indication of what distance she could see, I removed those data from the calculation of prey density. I used the number of animals of various species and the size of the viewshed to calculate the density of visible gazelles (Thomson's gazelles, Grant's gazelle's, and animals identified simply as 'gazelle'), lions, and spotted hyenas, for every time block. A time block was calculated as the time between the prey survey and the next prey survey on the same day. Due to the exigencies of fieldwork, duration of time blocks varied from 15 minutes to six hours. Many of the higher densities were the result of a many gazelles in a small viewshed, and often when no gazelles were visible, there obviously were gazelle present (given the number of hunts at 0 gazelle density) so the densities may not represent wide scale prey density, but rather visible prey density, which should be similar to prey density a cheetah would experience while making hunting decisions. I matched the density estimates of gazelles and predators that were closest in time to each hunting event. Therefore, for each prey survey, I determined whether a successful gazelle hunt took place during that time block and could calculate prey density at that hunt. Since time between consecutive prey surveys varied between 15 minutes and several hours, I included duration of survey in the models.

Statistical Modeling

Probability of successful attack

To examine to examine factors influencing a successful attack, I used data from 5915 prey surveys, 3043 of which were from KL's data from 1987-1990, and 2872 were from my PhD fieldwork in 2014. During 3201 hours spent surveying cheetahs and their prey, KL and I observed 134 gazelle kills. Due to the distribution of the data, I used mixed effects binomial models to examine the factors influencing whether a successful attack took place during a time block (kill probability), rather than attack rate (#of successful attacks/hour of active pursuit). To investigate what factors affect the kill probability in all cheetahs, my first model included all available data. However, the different functional response shapes for mothers with cubs versus without (Chapter 2), suggest that factors influencing attack rates are likely different, therefore I ran models separately for each group based on reproductive status (i.e. cheetahs with or without cubs). Males are included in cheetahs without cubs as I did not expect there to be differences in kill probability between females without cubs and males. In all models the dependent variable was whether a successful attack occurred during that time block (yes/no), and fixed effects were duration of time block, season (Wet/Dry), logged gazelle density, and a random effect representing the identity of the cheetah. To account for the effect of lions on probability of a successful attack, I created a factor that accounted for whether lions were visible or not, and included it in models for all cheetahs and for cheetahs without cubs. However the global model for cheetahs without cubs containing lion presence as a factor did not converge. Therefore in the cheetahs without cubs model, I instead used a three level factor for predator presence that included both lions and spotted hyenas. "None" was when there were no visible predators, "Low" was if there was 1 visible predator per km^2, and "High" if there were >1 visible predator per km^2. The model for all cheetahs included cubs as a factor. In the model selection for functional responses in Chapter 2 for all cheetahs and cheetahs without cubs, the Type IV model was either the top or competitive model, thus I included a second order term for gazelle density as a fixed effect in the models for those groups. For each model set (kill probability for cheetahs overall, mothers with cubs, and cheetahs without cubs), I compared models with all possible combinations of fixed effects. All models were ranked by AIC and I considered models within 2 ΔAIC points of the top model to have strong support (Burnham & Anderson 2002). I calculated how much variability is explained by the fixed effects (marginal R squared) and by the fixed + random effects (conditional R squared) using the method outlined in Nakagawa & Schielzeth (2013).

Handling time

For the handling time analysis, I did not need to link hunts to prey densities, instead I used any gazelle hunts where handling time was observed start to finish (N=272); 86 were by females with old cubs, 73 were by females with young cubs, 92 by single females, 9 by males in groups, and 12 by single males. These hunts were carried out by 112 different individuals or groups of cheetahs. Handling time on gazelles was log transformed to achieve normality and used as the dependent variable. Since there were multiple hunts from the same cheetah, I used linear mixed models with identity of cheetah as the random effect. Doing so avoids problems of pseudoreplication and accounts for variation in hunting behavior among individual cheetahs. Fixed effects considered in my analyses align with my predictions: cheetah age, hunger state, whether the kill was stolen, the amount of meat available per cheetah, and social grouping. Age was a three level factor (Adolescent=18 months-2 years, Young=2-4 years, Adult=4+years) as per Hilborn *et al.* (2012). Short term hunger state was determined by estimating belly size by eye on a 14 point scale (Caro 1994) and treated as a continuous variable. Whether the kill was stolen was a bivariate (Yes/No) variable. I divided cheetahs into the following social groups: mothers with small cubs (≤4 months), mothers with large cubs (>4 months), single females, single males, and males in groups. To account for variable prey size and differing numbers and ages of cheetahs on a kill, I created a variable that calculated the amount of meat available per cheetah. For mothers with cubs, I calculated the number of adult cheetah equivalents present at the kill.

Data on how much cheetah cubs of various ages eat is sparse, but guided by Laurenson (1995), I assumed cubs' food intake was proportional to their body height relative to their mother (Table 2). Thus if a mother and two half sized cubs ate at a kill, I considered the two cubs as one additional cheetah, therefore the food consumed was equivalent to two adult cheetahs. I then divided the expected amount of meat from the carcass by the number of cheetah equivalents to obtain amount of meat available per cheetah. I compared models with all possible combinations of fixed effects. All models were ranked by AIC and I considered models within 2 ΔAIC points of the top model to have strong support (Burnham & Anderson 2002). I calculated how much variability is explained by the fixed effects (marginal R squared) and by the fixed + random effects (conditional R squared) using the method outlined in Nakagawa & Schielzeth (2013)

Results

Kill probability

There was no clear top model for the kill probability for all cheetahs, however all models with strong support (within 2 ΔAIC points of top model) included factors representing whether the cheetah had cubs or not, the duration of the time block, and the density of gazelles (Table 3). The top model was the most parsimonious of the strongly supported models, and had 23% of the weight. Kill probability increased if the cheetah had cubs and as the duration of the time block increased (Table 4, Fig. 1, Fig. 2). There was a slight increase in the kill probability as prey density increased (Table 4, Fig. 1). The second model included an extra parameter (gazelle density^2), however it failed to converge. The third model included season as a parameter but the ΔAIC was 2, indicating that the extra parameter did not add much explanatory power.

There was no clear top model for females with cubs (Table 5), but duration of the time block is common to all models with strong support. Logged gazelle density and season were included in three of the four models with strong support. The top model had 28% of the weight and showed that kill probability was higher when time blocks were longer (Table 6, Fig.3). Again there was a slight increase in kill probability as gazelle density increased, and kill probability increased in the dry season compared to the wet season (Table 6, Fig. 3, Fig. 4).

There were six models with strong support explaining the kill probability for cheetahs without cubs (Table 7). They all contained duration of time block as a parameter. Four of them, including the top model, included logged gazelle density. The second best model was the most parsimonious, therefore the addition of the gazelle density in the top model added explanatory power. Season and logged gazelle density^2 were only in two of the models with strong support, and I do not consider them to be important parameters. In the top model the kill probability increased slightly with logged prey density, and increased more steeply with duration of time block (Table 8, Fig. 5). The calculations of variability explained by the fixed effects and random effects did not converge for any of the models for probability of successful attack.

Handling time

Untransformed handling time of Thomson's gazelles by cheetahs ranged from 6-530 min (mean= 81.65 min, SD= 70.5 min). The majority of time handling prey was spent eating (mean time eating= 55.9 min, SD= 48.63 min), with the rest of the handling time taken up by hunting (mean time hunting= 6.73 min SD= 11.07 min), killing, and the recuperative pause after the chase and before eating. Due to differing sizes of Thomson gazelles and numbers of cheetahs at the kill, the amount of meat available per cheetah ranged from 1.16 kg to 20.43 kg.

Our best model of handling time for cheetahs in the Serengeti accounted for 94.9% of the model weight and the second best model was >4 ΔAICc from the top model (Table 9). This top model included amount of meat available per cheetah, social grouping, and whether the kill was stolen (Table 10). If a kill was stolen by apex predators, average handling time decreased by 37.2% (mean handling time for stolen kills= 52.9 min SD= 72.2 min, mean handling time for intact kills= 84.2 min SD= 38.5min). Single females and single males had the shortest handling times compared to females with young cubs, and handling times for mothers with young cubs were longer than mothers with old cubs (Table 10). Mothers with old cubs took similar times as other social groups to handle large prey, but took longer to finish smaller carcasses (Fig. 6). The more meat available per cheetah, the longer the handling time (Fig. 6).

Amount of meat available per cheetah, cheetah social grouping, and whether the kill was stolen explained 33.73% of the variation in the data while the model as a whole (fixed plus random effects) explained 47.3% of the variation (Table 9) indicating that individual cheetah influenced model results. Age of cheetah and belly size were not important predictors of handling time.

Discussion

Both kill probability and handling time exhibit variation that reflects tradeoffs made by hunting cheetahs when balancing risk and reward. In all situations, the probability that a kill took place increased slightly with gazelle density, and mothers with cubs exhibit higher kill probabilities than cheetahs without cubs. Time spent at a kill is influenced by the presence of apex predators, in addition to characteristics of cheetahs and their prey. Handling time was longer on larger prey, shortened if the kill was stolen by lions or hyenas, and influenced by the cheetah's reproductive status and vulnerability to predation.

Duration of survey period was the strongest factor influencing probability of a kill, which is intuitive since the longer the survey, the more likely a successful hunt would take place. Although I did not model attack rate directly, once duration of time block is accounted for, it is very likely that the same factors influencing kill probability also affect attack rate. In concordance with previous findings (Chapter 2), cheetahs with cubs had higher kill probability, however against expectations, kill probability of cheetahs without cubs did not decrease at high density. This suggests that the relationship between kill probability and prey density is more complex than can be captured by a second order relationship, or that some other factor drives a decrease in gazelles killed per hour that I found in Chapter 2. Although they can successfully take a wide variety of prey (Caro 1994), cheetahs selectively target individuals who are less vigilant, physically isolated (Fitzgibbon 1990a), or young (Fitzgibbon 1990b), and hunts tend to be more successful on smaller, younger gazelles (Hilborn *et al.* 2012). Therefore the kill probability may depend less on overall availability of prey than availability of vulnerable prey. The availability of prey worth hunting may not be tightly linked to prey density and instead may be more influenced by group size, individual vigilance levels, or relative abundance of young gazelle.

Unexpectedly, the presence of lions did not appear to suppress kill probability in my analysis. There are a couple of possible explanations. First, cheetahs spend so little time around lions (<5%), that even four successful attacks on gazelles when lions are nearby are enough to keep the probability of a kill from being significantly lower. However, the average rate of kills/hour for cheetahs when lions are visible is ~40% lower than the overall kill rate (Chapter 2), making it likely that lion presence suppresses cheetah hunting activity overall as Durant (2000b) found. There also may be a complex interaction with risk of hunting around lions and vulnerability of prey. All of the successful attacks around lions were by adult female cheetahs with no following cubs and on Thomson gazelle fawns, which are one of the most vulnerable of cheetah prey. It is possible that even when lions are present, it is worth attacking fawns as chance of success is high and no cubs are at risk. However, caution should be used in interpreting the probability of kill results. The failure of some of the top models to converge and the inability to calculate the amount of variability explained by any of the models suggests that the results should not be used for prediction unless corroborated by other sources of data.

As predicted (Table 1), cheetahs' variable handling time is affected by a number of factors relating to coexisting with apex predators and the individual differences in both cheetahs and their prey. When a kill is stolen, cheetahs cannot eat to completion and handling time is shortened. Handling time increased with the amount meat available per cheetah because more food takes longer to eat. Unexpectedly, social grouping affected handling time opposite to the prediction, such that females with large cubs had longer handling times than other social groups. The need for mothers to teach their cubs to hunt may account for their relatively long handling times on prey (Fig. 8). Once cubs are 6 months of age, mother cheetahs bring live gazelle fawns back for their cubs to practice their hunting and killing skills (Caro 1994). Depending on the level of cub inexperience this can be a prolonged process, adding up to 30 min (pers obs AH) to handling times. On the other hand, behavioral modifications to avoid predation, such as vigilance, may explain why mothers with young cubs had the second longest handling times (Laurenson 1994). Vigilance at the kill allows cheetahs to spot incoming predators but it increases the overall amount of time spent at the kill as they cannot be vigilant and eat at the same time.

Cheetahs do not linger at kills even if the kill is not stolen by lions or hyenas. If after eating to satiation there is meat left over, cheetahs leave to digest their meal elsewhere and do not return to feed again (Caro 1994). In contrast, we know that apex predators can eat multiple meals from the same kill. For example, Messier & Crête (1985) report that wolves (*Canis lupus)* stayed at adult moose (*Alces alces)* kills for 8-23 days, and cougars (*Puma concolor*) in Wyoming can spend up to 8 nights at a kill (Anderson & Lindzey 2003). Mesopredators do not have this luxury, lost kills and reduced handling times means they potentially have to kill more prey than if apex predators were not present. For example, Smith et al. (2015) found that as human settlement increased, female pumas in California spent less time at kills, and increased their kill rates as a way to compensate for eating less at each kill.

Due to the complex nature of pressures faced by mesopredators, a different reaction to kill loss is also possible. The 'fear and loathing' effect (Ritchie & Johnson 2009) can cause mesopredators to move out of the immediate area and/or wait a longer time to hunt again after an encounter with an apex predator. That did not appear to be the case for cheetahs, but it is possible for species where the cost of an encounter with a larger predator is higher. Overall the impact of larger predators fell unevenly across different hunting behaviors. The effects on kill probability may be more complex than could be uncovered by my analysis, while the effect on handling time differed depending on cheetah social status.

Both kill probability and handling time show variation based on social group of the cheetah, with mothers with cubs having higher kill probabilities and handling times than cheetahs without cubs. By examining the behaviors separately I confirmed results from chapter 2 that mothers with cubs have higher kill probabilities, and they take longer handling their prey. However the results of the effect of lions are less neat, and lower kill rates weren't mirrored in lower kill probabilities. In addition the shortening of handling time due to kleptoparasitism would push kill rates higher in the proximity of lions all other things being equal. The variability of both kill probabilities and handling times within subsets of cheetahs highlights the shortcomings of using Holling's functional response models on carnivores. Okuyama (2008) points out that if both attack rate and handling time are flexible (i.e. can take on non-linear relationships with prey density), then multiple combinations of parameter values can create the same functional response curve. This becomes problematic when functional response curves are fitted to data on number of prey killed, and model assumptions are then applied to predator attack or handling behavior without directly measuring those behaviors.

With wild predators it is difficult to collect the data needed to assess functional response, let alone examine variation in individual hunting behaviors. Our study is novel and the results for a mesopredator like cheetahs suggest that the assumptions of Holling's models are likely violated in the field and we should be cautious when using such models to predict predator- prey dynamics or extrapolate hunting behavior impacts to the population level (Okuyama 2008, 2012).

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Tables and Figures

Table 1. Predictions regarding factors affecting kill probabilities and handling time in cheetahs.

Factor	Predicted impact on kill probability
Mothers with cubs	Increased kill probability compared to cheetahs without cubs
Prey density	Kill probability will not be affected for mothers with cubs, will decline at high prey density for cheetahs without cubs
Lion presence	Will lower kill probability in all cases
Season	Attack rate higher in wet season
Factor	Predicted impact on handling time
Social grouping	Shorter for females with young cubs compared to other social groups
Meat available per cheetah	Longer the more meat available
Belly size	Shorter when hungry because eat quickly
Age	Shorter for older more experienced cheetahs who are better hunters
Kill stolen by scavengers	Shorter if stolen

Table 2 Estimated amount of food cheetah cubs of varying ages eat compared to adults, based on relative body size (Caro 1994)

Cub age (months)	Adult cheetah equivalents
2-2.9	0.2
3-5.9	0.33
6-7.9	0.5
8-10.0	0.75
10.1-independence	1

Table 3. Model selection table for kill probability with all cheetahs, showing all models with ΔAIC<4 and the null model. ΔAIC= difference in AIC scores between model and top model. Weight refers to AIC model weights. Cubs=whether the cheetah has cubs, Duration=duration of survey period, Gazelle Density=logged gazelle density, Gazelle Density^2= second order term of logged gazelle density, Season=wet vs. dry season, Lions= lions were visible within a radius of 1km. In all models the random effect was identity of cheetah. K= Number of parameters.

Fixed Effects	**K**	**AIC**	**ΔAIC**	**Weight**
Cubs + Duration+ Gazelle Density	6	1230.0	0	0.208
Cubs + Duration+ Gazelle Density + Gazelle Density^2	7	1230.4	0.36	0.173
Cubs + Duration+ Gazelle Density + Lions	7	1231.8	1.82	0.084
Cubs + Duration+ Gazelle Density + Season	7	1232.0	2.00	0.076
Cubs + Duration+ Gazelle Density + Gazelle Density^2+ Lions	8	1232.2	2.16	0.070
Cubs + Duration+ Gazelle Density + Gazelle Density^2 + Season	8	1232.3	2.34	0.065
Cubs + Duration+ Gazelle Density^2	6	1233.0	2.99	0.047
Cubs+ Duration	5	1233.7	3.72	0.032
Cubs + Duration+ Gazelle Density + Lions + Season	8	1233.8	3.81	0.031
Null	3	1269.3	39.33	0.000

Table 4. Effect size and significance of fixed effects in the top model of kill probability for all cheetahs. Cubs=whether the cheetah has cubs, Duration=duration of survey period, Gazelle Density=logged gazelle density.

Fixed Effect	**Estimate**	**Std. Error**	**Z**	**P**
Intercept	-4.744	0.184	-25.825	<0.001
Gazelle Density	0.053	0.022	2.389	0.0169
Duration	1.178	0.206	5.707	<0.001
Cubs	0.502	0.191	2.629	0.009

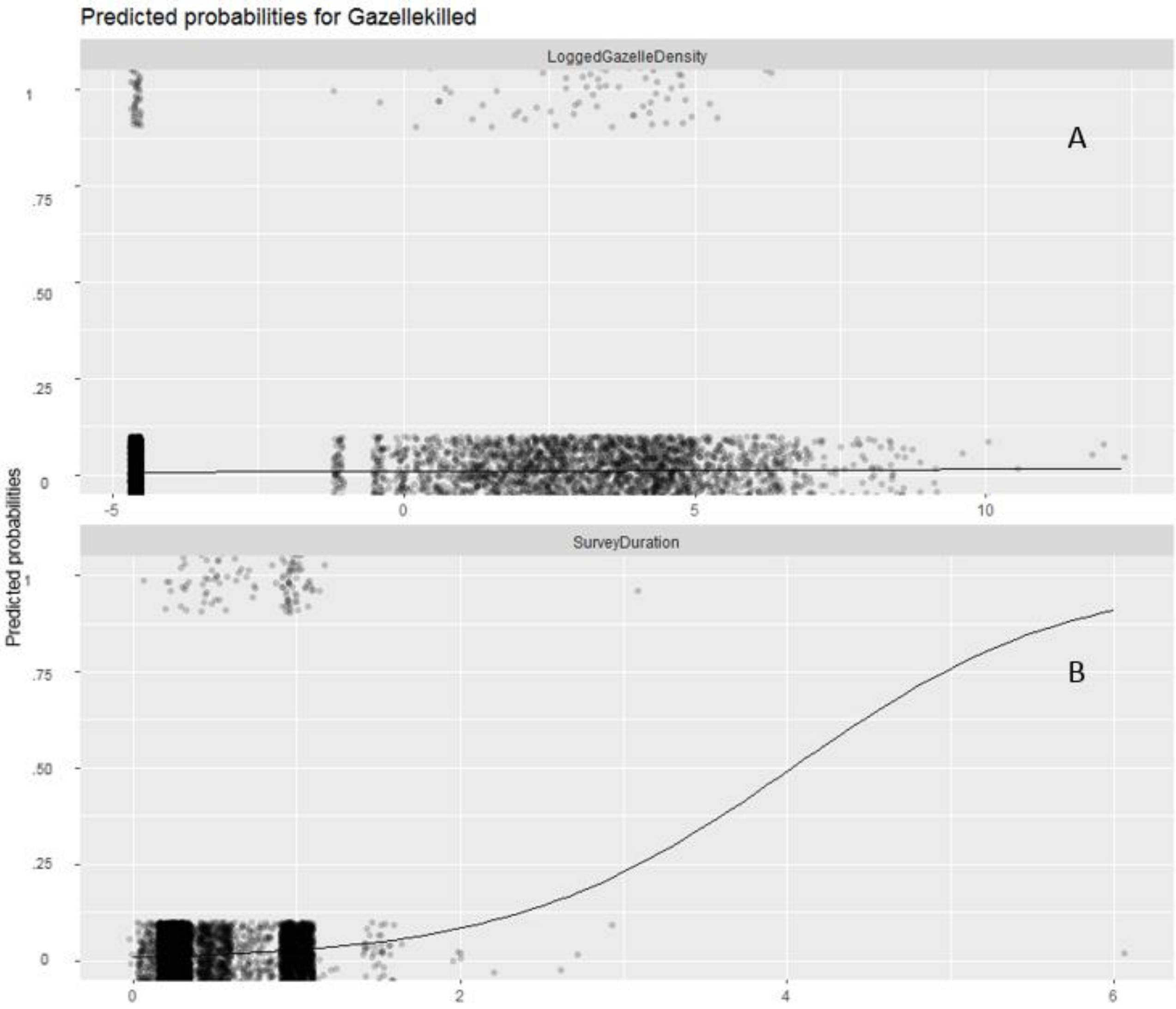

Figure 1. Effect of logged gazelle density (A) duration of survey (B) on the probability of a gazelle being killed by a cheetah. Results from the top model for attack rate for all cheetahs and the dots represent the data.

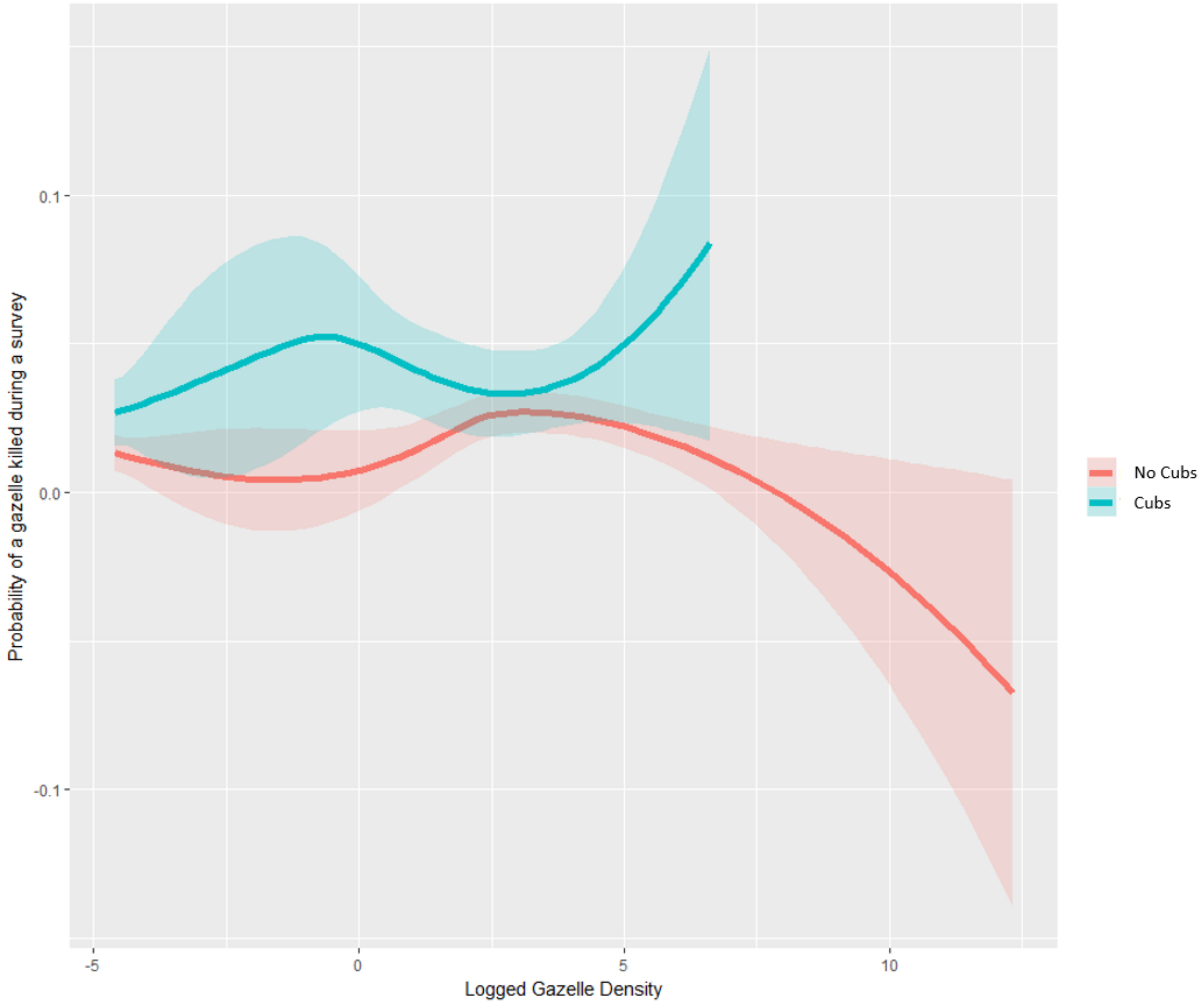

Figure 2 Loess smoother with 95% confidence intervals on the raw data, showing differences in probability of a gazelle kill when a cheetah has cubs or not.

Table 5. Model selection table for kill probability for cheetahs with cubs, showing all models with ΔAIC<4 and the null model. ΔAIC= difference in AIC scores between model and top model. Weight refers to AIC model weights. K= Number of parameters. Duration=duration of survey period, Gazelle Density=logged gazelle density, Gazelle Density^2= second order term of logged gazelle density, Season=wet versus dry season, Lions=whether lions were visible within a radius of 1km or not. In all models the random effect was identity of cheetah.

Fixed effects	K	AIC	ΔAIC	Weight
Duration+ Gazelle Density+ Season	6	599.0	0	0.28
Duration + Gazelle Density	5	600.0	1.0	0.18
Duration+ Gazelle Density+ Season + Lions	7	600.3	1.3	0.15
Duration+ Season	5	600.6	1.6	0.13
Duration + Gazelle Density + Lions	6	601.3	2.3	0.09
Duration	4	601.6	2.6	0.08
Duration+ Lions + Season	6	602.2	3.1	0.06
Null	3	613.4	14.4	0.00

Table 6. Top model for kill probability of cheetahs with cubs. Duration=duration of survey period, Gazelle Density=logged gazelle density, Wet Season is in comparison to dry season. In all models the random effect was identity of cheetah

Parameter	Value	Std. Error	Z	P
Intercept	-3.958	0.267	-14.813	<0.001
Gazelle density	0.062	0.033	1.873	0.061
Duration	0.946	0.285	3.319	<0.001
Wet Season	-0.490	0.350	-1.400	0.161

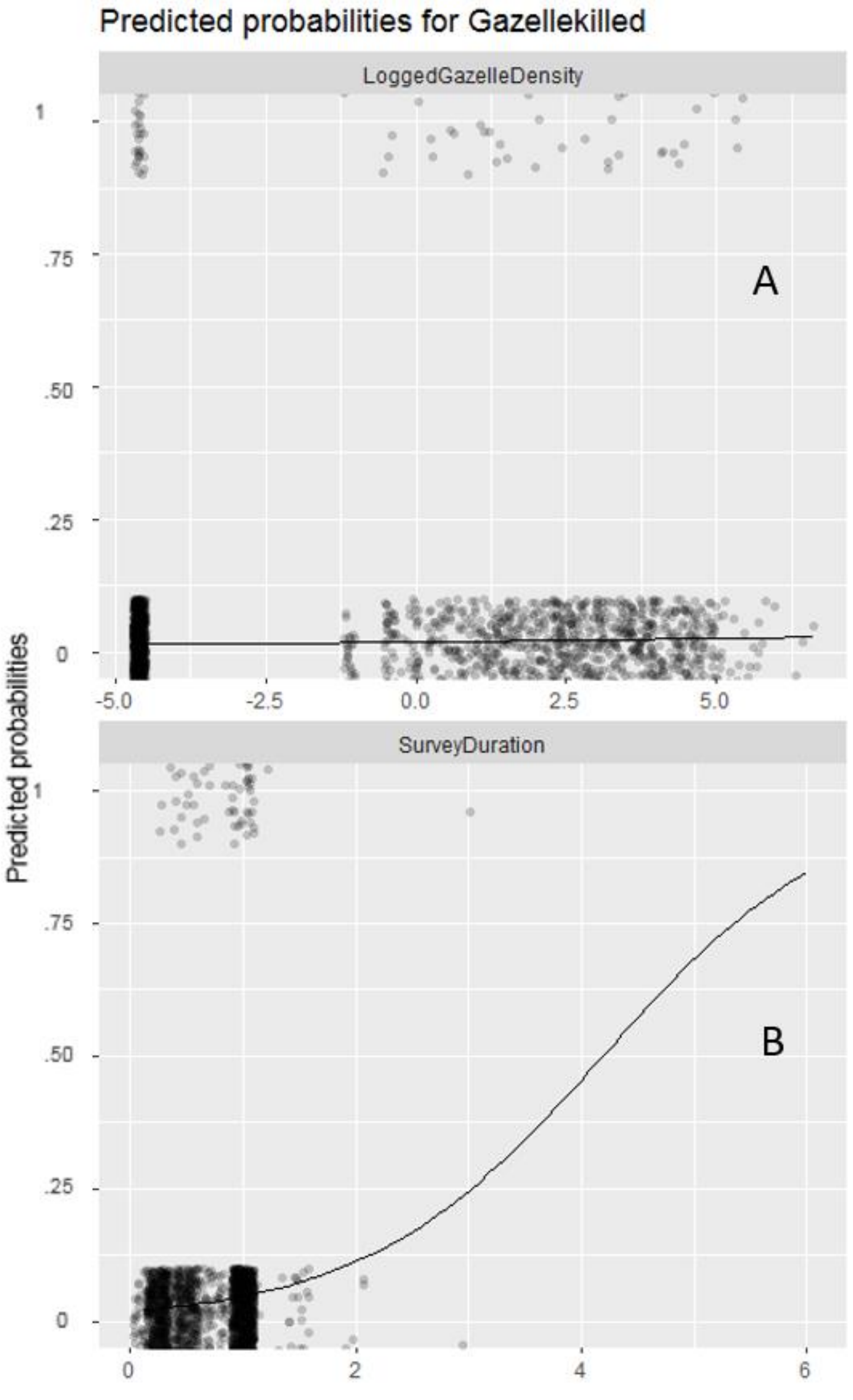

Figure 3. Effect of logged gazelle density (A) and duration of survey (B) and on the probability of a gazelle being killed by a cheetah with cubs. Dots represent the data.

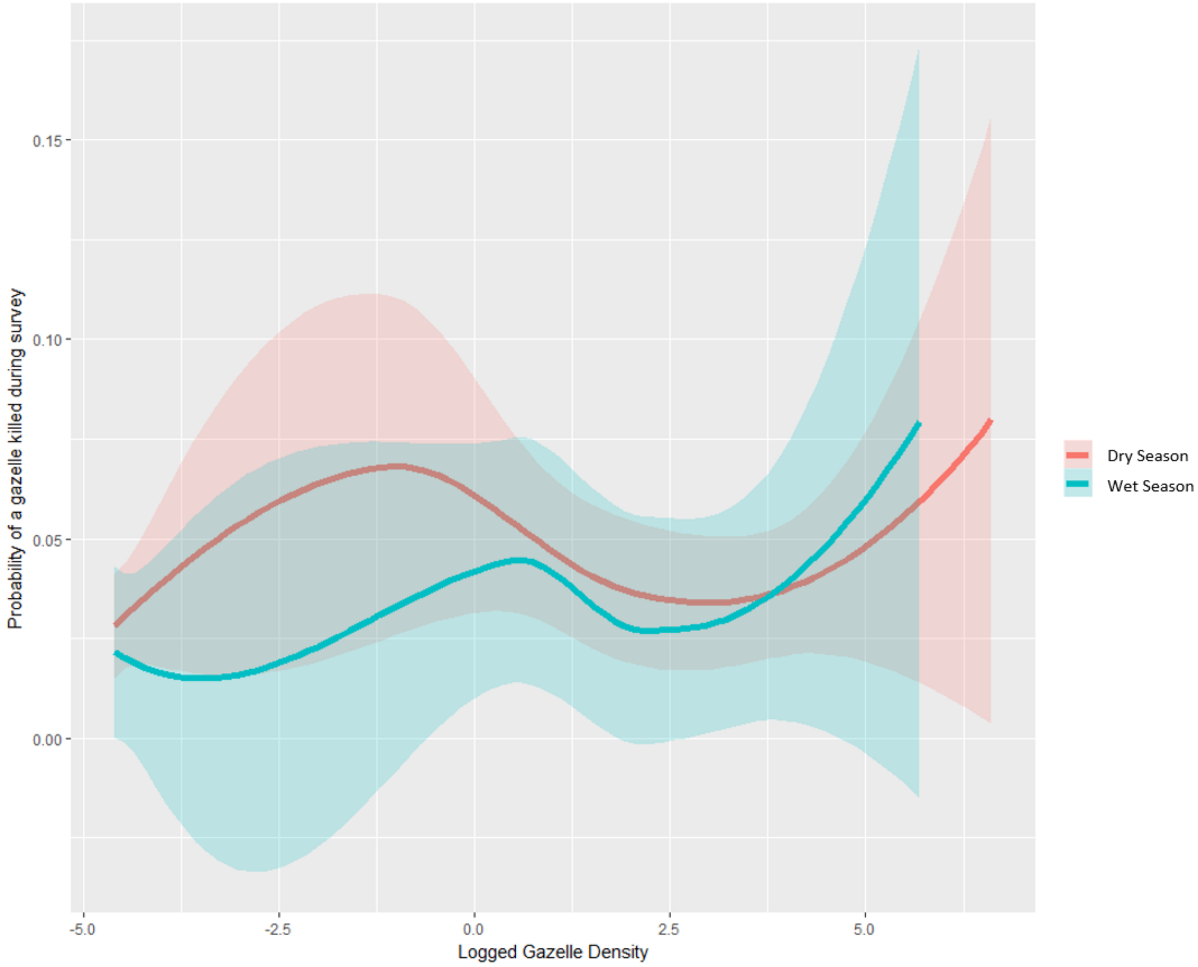

Figure 4. Loess smoother with 95% confidence intervals on the raw data for cheetahs with cubs, showing differences in probability of a gazelle kill during a survey in the wet versus dry season.

Table 7. Model selection table for kill probability for cheetahs without cubs, showing all models with ΔAIC<4 and the null model. ΔAIC= difference in AIC scores between model and top model. Weight refers to AIC model weights. Duration=duration of survey period, Gazelle Density=logged gazelle density, Gazelle Density^2= second order term of logged gazelle density, Season=wet versus dry season, Lions=whether lions were visible within a radius of 1km or not. In all models the random effect was identity of cheetah.

Fixed effects	**K**	**AIC**	**ΔAIC**	**Weight**
Duration+ Gazelle Density	5	633.6	0	0.191
Duration	4	634.0	0.43	0.154
Duration+ Gazelle Density + Gazelle Density^2	6	634.7	1.08	0.111
Duration+ Gazelle Density + Season	6	634.7	1.11	0.109
Duration + Season	5	634.9	1.27	0.101
Duration+ Gazelle Density^2	5	635.3	1.68	0.082
Duration+ Gazelle Density + Gazelle Density^2+Season	7	635.9	2.32	0.060
Duration+ Gazelle Density^2+ Season	7	636.3	2.65	0.051
Duration+ Predator	5	637.3	3.66	0.031
Null	3	646.8	13.16	0.000

Table 8. Top model for kill probability of cheetahs without cubs. Duration=duration of survey period, Gazelle Density=logged gazelle density. In all models the random effect was identity of cheetah

Fixed Effect	**Estimate**	**Std. Error**	**Z**	**P**
Intercept	-4.993	0.261	-19.161	<0.001
Gazelle Density	1.413	0.293	4.822	<0.001
Duration	0.049	0.032	1.569	0.117

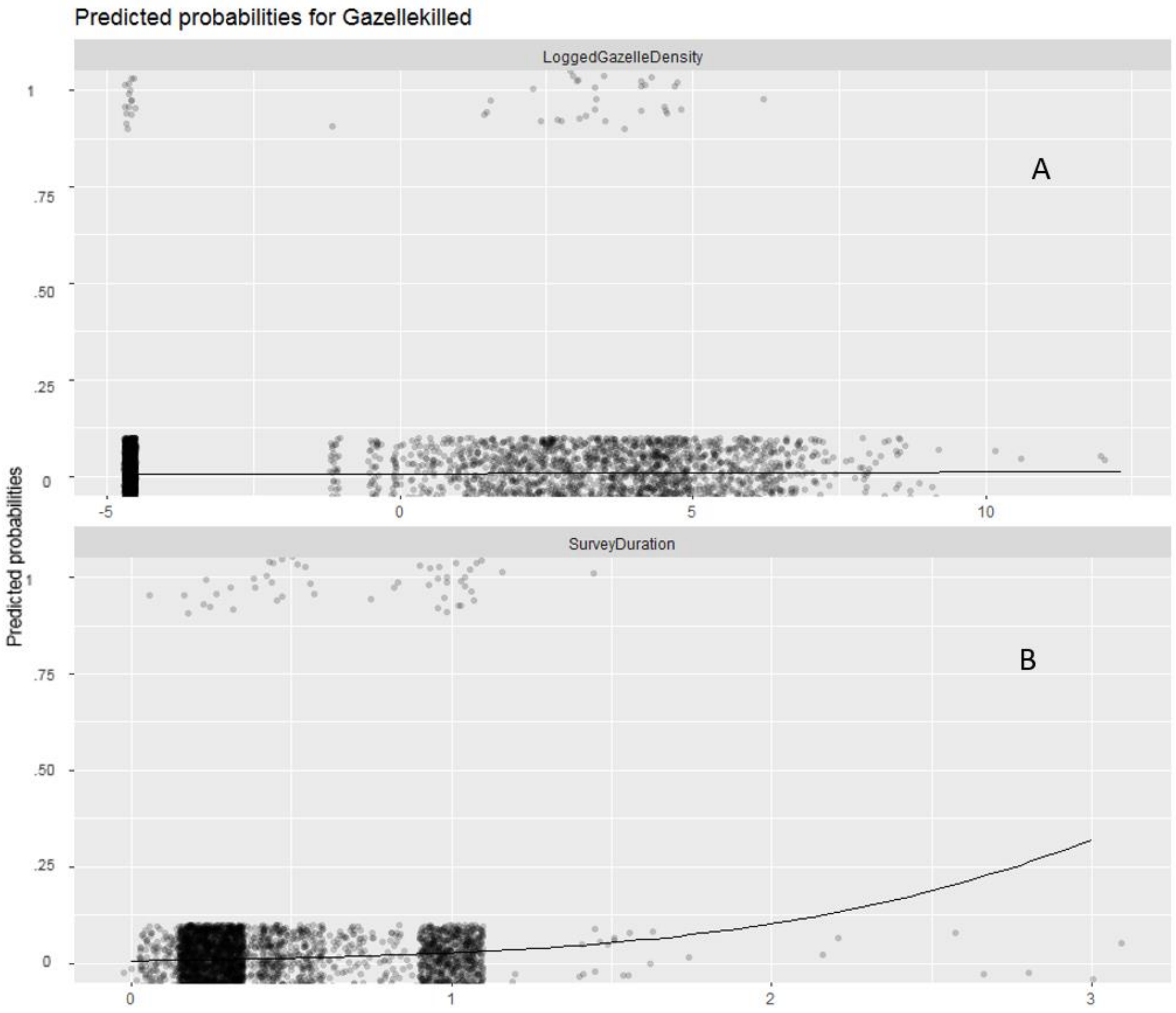

Figure 5. Effect logged gazelle density (A) and duration of survey (B) on the probability of a gazelle being killed by a cheetah without cubs. Dots represent the data.

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Table 9. Partial model selection table for cheetah handling time, showing all models with ΔAIC<10. K=number of parameters. ΔAIC= difference in AICc scores between model and top model. Weight refers to AIC model weights. R2m= marginal R squared, R2c= conditional R squared. Meat=meat available per cheetah, Social= Social grouping, Stolen= whether or not kill was stolen, and Age=Age of cheetah, Belly=Belly size of cheetah. In all models dependent variable =log transformed handling time, and random effect=ID of cheetah.

Fixed Effects	K	AIC	ΔAIC	Weight	R2m	R2c
Meat +Social +Stolen	6	529.1	0	0.949	0.337	0.487
Meat +Social +Stolen+ Age	7	536.2	7.18	0.026	0.34	0.478
Meat +Social +Stolen + Belly	7	536.4	7.36	0.024	0.337	0.487

Table 10. Effect size and significance of fixed effects in the top handling time model (lowest AICc value) for cheetahs. Note: Females with old cubs, male groups, single females, and single males are in comparison to females with young cubs. Meat per cheetah=logged kg of meat available per cheetah, and was stolen refers to kills that were stolen.

Fixed effects	Value	Std.Error	t-value	p-value
Intercept	3.773	0.117	32.030	<0.001
Meat per cheetah	0.579	0.058	9.818	<0.001
Females with old cubs	-0.368	0.101	-3.649	<0.001
Male groups	-0.464	0.222	-2.091	0.039
Single females	-0.058	0.104	-5.539	<0.001
Single males	-0.761	0.194	-3.925	0.002
Was Stolen	-0.923	0.128	-7.200	<0.001

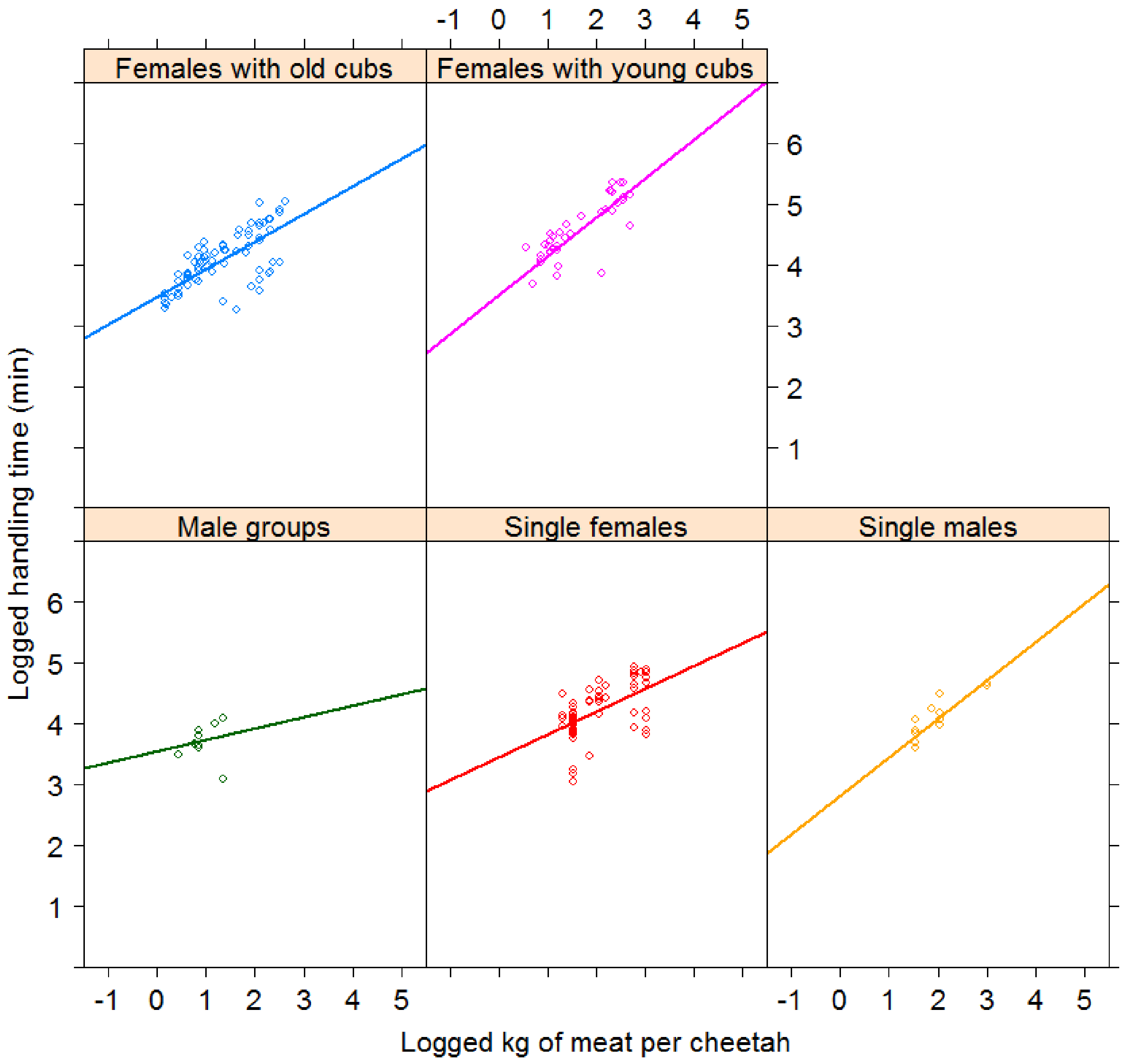

Figure 6. Top model results of the effects of cheetah social group and meat availability on cheetah handling time in Serengeti National Park. Note both axes are log transformed and are the same for all panels. Y axis: handling time of 3 = 20 minutes, 6=403 min. X axis: kg of meat 0.5=1.64 kg, 3=20.08 kg

Chapter 4

Cheetahs modify their prey handling behavior depending on risks from top predators

Abstract: While handling large kills, mesocarnivores are particularly vulnerable to kleptoparasitism and predation from larger predators. We used 35 years of observational data on cheetah (*Acinonyx jubatus*) hunts in Serengeti National Park to investigate whether cheetahs' prey handling behavior varied in response to threats from lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*). Male cheetahs and single females, whose main threat was kleptoparasitism, minimized time on the kill by being less vigilant and eating quickly, thereby shortening their handling times. Mothers with cubs showed a different strategy that prioritized vigilance over speed of eating, which increased time spent handling prey. Vigilance allowed them to minimize the risk of their cubs being killed while giving cubs the time they need to eat at the carcass. Flexible behavioral strategies that minimize individual risk while handling prey likely allow mesocarnivores to coexist with numerous and widespread apex predators.

Introduction

Predation is a key factor in shaping ecological communities (Sih 1985), and the direct impact of apex carnivores goes beyond their primary prey species, extending to mesocarnivores (i.e., carnivores that are mid ranking in a food web, Prugh et al. (2009)). Apex carnivores can negatively affect mesocarnivores through direct predation, kleptoparasitism, and harassment (Prugh *et al.* 2009; Ritchie & Johnson 2009), yet smaller carnivores do manage to coexist with numerous apex carnivores. For example, in Serengeti National Park in Tanzania where lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) live at high densities, there are eight species of mesocarnivores in the felid and canid families alone (Estes 1991).

This raises a question about carnivore coexistence: what behaviors do mesocarnivores use to minimize negative interactions with dangerous larger predators? Illuminating coexistence strategies can expand our knowledge of how diverse communities of carnivores are structured and maintained (Vanak *et al.* 2013), and potentially aid in our understanding of how top down pressures affect relationships between mesopredators and their prey (Dunphy-Daly *et al.* 2010; Suraci *et al.* 2016).

Many of the known strategies mesocarnivores use to minimize risk from apex predators rely on spatial avoidance. For example, wild dogs (*Lycaon pictus*) can coexist with lions by shifting their core areas to areas lions do not use (Darnell *et al.* 2014). In the presence of wolves (*Canis lupus*), coyote (*Canis latrans*) home ranges tend to occur in between, or on the edges of, wolf pack territories (Fuller & Keith 1981; Arjo & Pletscher 1999). However, in systems where apex predator densities are high and their habitat use is broad, avoiding them completely may not be possible, and more fine scale strategies are likely to come into play. For example in both the Okavango Delta of Botswana and Serengeti National Park in Tanzania, cheetahs (*Acinonyx jubatus)* avoid lions and spotted hyenas on short temporal and spatial scales (Durant 1998, 2000b; Broekhuis *et al.* 2013; Swanson *et al.* 2016), which allows them to coexist within the larger landscape. Fine scale avoidance requires the ability to react appropriately and rapidly to changes in current risk, which can negatively affect foraging behavior. For example the proximity of larger carnivores lowers the chances that cheetahs will hunt (Durant 1998, 2000b; Cooper *et al.* 2007). Once a hunt is initiated, moving to avoid larger carnivores may not be the optimal reaction to changes in risk as moving involves abandoning a kill or losing opportunities to hunt prey. Thus it is probable that mesocarnivores will actively modify other aspects of their foraging behavior in order to hunt and retain sufficient prey while avoiding potentially dangerous interactions with larger predators.

Foraging in the presence of predators is inherently risky and the tradeoffs between time spent foraging and safety have been extensively studied (Brown 1988; Verdolin 2006). Vigilance is a common strategy used by a wide variety of taxa to lower predation risk (Bøving and Post 1997; Toïgo 1999; Randall and Boltas King 2001; Favreau et al. 2010). Mesocarnivores are no exception, for example, captured wild stoats (*Mustela ermine*) were more vigilant while feeding in patches closer to caged ferrets (*Mustela furo*) or feral cats (*Felis catus*) (Garvey, Glen & Pech 2015); and coyotes scavenging carcasses in Yellowstone National Park became more vigilant once wolves were reintroduced (Switalski 2003). Larger mesocarnivores like cheetahs and wild dogs may face lower predation risk than smaller species like stoats and coyotes, but by hunting relatively large prey that cannot be consumed rapidly, they may increase the risk of losing their kills to apex predators (kleptoparasitism) (Gorman *et al.* 1998; Hunter *et al.* 2007b). One strategy to lessen kleptoparasitism is to spend less time with the carcass, lowering the chances of detection by predators. For example, wild dogs who pay a steep metabolic cost when kills are stolen (Gorman *et al.* 1998), eat the majority of the carcass within 15 minutes (Carbone *et al.* 2005).

This range of responses by mesocarnivores to different threats from larger predators suggests that the strategies used to minimize risk while handling prey could follow a continuum. At one end are behaviors that maximize amount of food consumed before the kill is potentially stolen. However, eating quickly usually requires spending extended periods with a lowered head, which is risky since it prevents scanning for incoming threats. A larger predator could potentially approach a feeding mesocarnivore undetected, creating the possibility of a dangerous encounter. Therefore when an encounter is potentially extremely dangerous and predation is the primary concern, we might expect to see behaviors at the other end of the continuum that prioritize vigilance and safety over speed in eating.

Vulnerability to predation can vary among individuals (Pettorelli *et al.* 2011), potentially shaping their reactions to threats from predators. To examine whether individual cheetahs use different prey handling behaviors to cope with risks from large predators, we used a long-term data set from Serengeti National Park (SNP). Predation risk varies by age for cheetahs as larger predators are the leading cause of cheetah cub death in SNP (Laurenson 1994), but adults are relatively safe from predation (Caro 1994). In SNP cheetahs lose ~11% of their kills to lions and spotted hyenas (Hunter *et al.* 2007b). Some of the behaviors cheetahs use at kills can lower the risks of predation and kleptoparasitism, for example, moving kills to longer grass and leaving immediately after finished eating can lower the chance of detection by larger carnivores who may steal the carcass and/or kill the cubs (Hunter *et al.* 2007b). However, how much time a cheetah spends on the carcass may reflect a tradeoff between avoiding kleptoparasitism and cub predation. Our study builds on Hunter et al.'s (2007a) work on the environmental and ecological factors that affect specific cheetah behaviors at the kill, to uncover whether cheetahs vary the speed at which they handle prey depending on whether cub predation or kleptoparasitism is the primary threat. In general, the more time spent handling prey, the greater chance of detection by larger carnivores. Therefore we hypothesized that cheetahs without cubs (i.e. single females, single males, and male groups), whose main threat is kleptoparasitism, would adapt their behavior to minimize time spent handling prey. Losing a kill to larger predators is a temporary nutritional setback, but losing a cub lowers fitness, so we expected that mothers with cubs would prioritize cub safety over quick nutritional gain and use prey handling behaviors at the safer end of the continuum. Mother cheetahs are vigilant at kills primarily to protect cubs rather than to scan for prey (Caro 1987). Thus we hypothesized that mothers would adjust their behavior to be more vigilant than cheetahs without cubs, primarily to minimize the risk of their cubs encountering predators.

The time cheetahs spend handling prey is made up of three major behaviors which are hunting, pausing before eating (during which cheetahs can recover breath, move the kill, and/or scan for predators), and eating. We predicted that to shorten handling time, cheetahs without cubs whose main threat is kleptoparasitism would spend less time pausing and/or eating than mothers with cubs. If cheetahs without cubs spent less time handling prey, we predicted that they would lose a lower percentage of their kills to lions and hyenas than mothers with cubs. To account for the contribution of time spent hunting to overall handling time, we also investigate whether time spent hunting differed between mothers and cheetahs without cubs.

Vigilance lengthens time spent handling prey, but increases the chance mothers will see approaching lions and spotted hyenas and be able to lead cubs to safety. Therefore, we predicted that mothers would be more vigilant while eating, leading to longer eating times when compared to cheetahs without cubs. We also expected mothers to spend longer paused to scan for predators before eating, which combined with longer eat times would lead to longer handling times.

We also test whether there was variation in prey handling strategy between mothers depending on cub age. Cubs younger than 4 months old cannot run at full speed and are especially vulnerable to predation (Caro 1987), therefore we predicted that mothers with young cubs would be more vigilant, leading to more time spent eating and handling prey than mothers with older cubs.

Methods

Study System

The Serengeti Cheetah Project (SCP) study site covers an area of 2,200 km^2 of open plains and woodland edge in the Serengeti National Park and Ngorongoro Conservation Area in Tanzania. Serengeti cheetahs are highly mobile and many follow the seasonal migration of Thomson's gazelles (*Eudorcas thomsonii)*, their main prey (Durant *et al.* 1988; Caro 1994). Detailed descriptions of the study site and ecosystem can be found in Sinclair and Arcese (1995).

Cheetah social system

Cheetahs have a unique social structure among cats, with multiple types of social groups (Caro 1994). Adult females are solitary unless they have dependent cubs. From birth until they are about 2 months old, cubs stay in the den and are not with their mother when she is hunting. Adult males can either be solitary or in lifelong coalitions with other males. We divided cheetahs into the following social groups: (i) mothers with following cubs up to four months of age, (ii) mothers with cubs older than four months, (iii) single females, (iv) single males, and (v) males in groups. Note, mothers with cubs in the den were classified as single females since cubs were not present while they handled prey.

Data collected

I used observations of cheetah hunts by members of the Serengeti Cheetah Project collected between 1980 and 2014. Serengeti cheetahs are mainly diurnal hunters and are usually habituated to vehicles, making it possible to directly observe and record their hunting behavior. Hunting behavior was observed with binoculars to minimize disturbance and recorded the amount of time spent hunting, pausing, and eating in seconds (see Caro 1994). Handling time was defined as the time from when a cheetah started hunting (took 2 or more steps in an alert stalking gait towards prey), through to the chase and the kill, and ended when the cheetah was finished eating. Protocols for data collection on hunts used a standardized checksheet, and hence were standard across observers. Hunt time began at the start of the hunt and finished when the prey was immobilized (i.e. the cheetah has applied a stranglehold). Pause time started when the prey was dead (i.e. the cheetah dropped the stranglehold) to when the cheetah started to eat. Eat time was from the first bite taken to when the last bite was taken as long as the cheetah did not start eating again within an hour. If a cheetah stopped eating for an hour or more, we considered them to be finished eating. When we observed single females or single males, they were the focal animal. For mothers with cubs, the mother was always the focal animal, and the amount of time spent hunting, pausing, and eating represents her behavior. Males in groups usually hunt and eat together, and times recorded were for how long the group took over a particular activity. Thus handling time was from when the first male initiated a hunt to when the last male finished eating. Likewise, hunt time was from when a male initiated a hunt until he or another male applied the stranglehold to prey. Pause time was from when the stranglehold was dropped to when any of the males started to eat. Eat time was from when any male started eating until the last one had finished. We were not always able to collect data on all stages of handling time at every successful hunt therefore the number of observations for each stage varies (see Table 1).

For time spent vigilant I used three years of data from Karen Laurenson (KL) and 7 months of my data from 2014. KL focused on females, while I followed cheetahs opportunistically. Thus the sample sizes for single females are larger than those for other social groups (Table 1). Time spent vigilant (looking up from the carcass either while standing, sitting, or crouching) was recorded to the second for each individual except for mothers with cubs, when vigilance was only recorded for mothers. Vigilance was then calculated as a percentage of total time spent eating. For males in groups, I randomly chose data from one individual in the group to use in the analysis.

Statistics and modeling

Handling time was log transformed to achieve normality and used as the dependent variable in the models. I included data on all prey, not just gazelles, as I expected the general risks and rewards to be the same regardless of prey species. Since there were multiple hunts by the same cheetah, I used linear mixed models with a coefficient representing the identity of cheetah as the random effect to avoid problems of pseudoreplication and to account for variation in hunting behavior among individual cheetahs. I included the following fixed effects in the models to account for the factors previously found to influence time spent handling prey in a variety of species (Croy & Hughes 1991; Bindoo & Aravindan 1992; Hilborn *et al.* 2012): social group, age of hunting cheetah (Adolescent = 18 months-2 years, Young

= 2-4 years, Adult = 4+years), hunger state, whether the kill was stolen, social and reproductive grouping, and the amount of meat available per cheetah. Short-term hunger state was determined by estimating belly size by eye on a 14 point scale (Caro 1994) and treated as a continuous variable. Whether the kill was stolen was a bivariate (Yes/No) variable. We calculated the amount of meat available per cheetah by dividing the expected amount of meat from the carcass (estimated following Blumenschine & Caro (1986)) by the number of cheetahs present, except in the case of mothers with cubs. For mothers with cubs, we calculated the number of adult cheetah equivalents present at the kill. Following Caro (1994) and Laurenson (1995) I assumed cubs' food intake was proportional to their body height relative to that of their mother (for values used, see Table 2). Thus if a mother and two half sized cubs ate at a kill, I considered the two cubs as one additional cheetah, and therefore the food consumed was equivalent to two adult cheetahs. I log transformed meat available per cheetah to achieve normality.

All handling time models were ranked by their AICc (Akaike Information Criterion corrected for small sample size) score and I considered models within 2 ΔAICc points to be competing and those from 2-4 ΔAICc points of the top model to have moderate support (Burnham & Anderson 2002). I calculated how much variability was explained by the fixed effects (marginal R squared) and by the fixed + random effects (conditional R squared) of each model using the method outlined in Nakagawa & Schielzeth (2013).

After modeling handling time as a whole, I further broke it into its consecutive components to determine if the differences in handling time among social groups could be accounted for by differences in amount of time spent on the hunt, the pause before eating, or the time spent eating. The amounts of time spent hunting and pausing were not normally distributed, therefore I used non-parametric Wilcoxon sum rank tests to check for significant differences in the median amount of time mothers with cubs spent in those activities compared to other social groups.   I pooled mothers with cubs together and compared amount of time they spent in an activity to time spent by all other cheetahs grouped together. I then separately compared mothers with cubs to single females, single males, and male groups to test if time spent in the activity varied significantly among social groups.

I normalized our data on time spent eating through a log scale conversion. To determine if mothers with cubs spent more time eating than other cheetahs, I used a mixed effects model with time spent eating as the dependent variable. I included a coefficient representing the identity of cheetah as the random effect, and our fixed effects were the factors identified as important in the handling time model, i.e. social group, meat available per cheetah, and whether or not the kill was stolen. In the model I separated mothers into those with old versus young cubs. As with the handling time models, the variability explained by the fixed effects and the model as a whole was calculated using the method outlined in Nakagawa & Schielzeth

(2013). I used a chi squared test to see if there were differences in rates of kleptoparasitism among social groups.

I normalized our data on proportion of time on a kill spent vigilant through a log scale conversion, and used it as the dependent variable in mixed effects models. To test my *a priori* expectation that mothers with young cubs are more vigilant on a kill than those with old cubs, I first examined only kills made by mothers with cubs. In the model I included a coefficient representing the identity of cheetah as the random effect, and my two fixed effects were a factor representing mothers with old versus young cubs, and prey size. Previous work shows cheetah are more vigilant on kills larger than 10 kg (Hunter *et al.* 2007b), therefore I included a two level factor for prey size (greater or less than 10 kg) according to Blumenschine and Caro (1986). I also combined all mothers with cubs together and used another mixed effects model with the same random and fixed effects, except that social group was a four level factor with mothers with cubs compared to single males, single females, and males in groups.

Results

Handling time

Total handling time for 351 successful hunts ranged from 6-530 min. The majority of handling time was spent eating prey, with the rest taken up by hunting and pausing before eating (Figure 1). My top model showed handling time depended on cheetah social group, meat available per cheetah, and whether or not the kill was stolen (Table 3; Table 4.) Age of cheetah and short term hunger state were not included in the top model therefore there is little evidence that they affect how much time cheetahs spend handling prey. The top model for handling time had 96% of the weight, and all other models were >4 ΔAICc from the top model and thus were not considered (Table 4). Cheetahs without cubs had shorter handling times than mothers. Single males had the shortest handling time followed by male groups, then single females (Table 3). Mothers with young cubs spent significantly longer handling prey than mothers with old cubs (Table 3). The larger the kill, the longer the handling time, and if the kill was stolen, handling time was necessarily shortened (Table 3; Fig. 2). The fixed effects (i.e. amount of meat available per cheetah, social group, and whether the kill was stolen) explained 41.9% of the variation in the data, while the model as a whole (fixed effects plus the random effect of identity of cheetah) explained 56.8% of the variation, indicating that identity of individual cheetahs influenced model results.

Hunting

Once I broke handling time into its constituent parts (i.e. hunting, pausing, eating), I found that the median amount of time mothers with cubs spent hunting was not significantly different than all other cheetahs combined. When I compared mothers to the different social groups separately, the only significant difference was that mothers had shorter hunts than male groups (Fig. 3a).

Pausing

Pause time ranged from -8 min to over 2.5 hours. The negative pause times were usually the result of one male in a group starting to eat before his brother had finished strangling the prey. However, some negative numbers came from single cheetahs who were ineffective at strangling and started to eat before prey were dead. Cheetahs without cubs (single females and males combined) paused for significantly less time (median=3.9 min) than mothers with cubs (median=11.4 min, p=0.004, Figure 3b). When comparing mothers with cubs to other social groups individually, mothers paused significantly longer than single males (median =3.2 min, p=0.012) and male groups (median=0 min, p=<0.001), but not single females (median=8.1 min, p=0.163).

Eating

Out of the 447 observations of time spent eating, 84% were of Thomson's gazelle, ~10% were hares (*Lepus* spp.), with reedbuck (*Redunca redunca)*, impala (*Aepyceros melampus)*, and wildebeest (*Connochaetes taurinus)* making up the remainder. Mothers with young cubs did not spent significantly longer eating than those with older cubs, however single males, male groups, and single females spent less time eating than both mothers with young and old cubs (Table 5), though the difference between mothers with old cubs and male groups was not significant. The more meat that was available per cheetah, the longer they took to eat. The three fixed effects we included in our eat time model (social group, meat available per cheetah, and whether the kill was stolen) explained 37.7% of variability in the data, while the full model including identity of cheetah explained 48.4% of the variability. There were no significant differences in rates of kleptoparasitism among social groups (χ^2 =4.15, df=4, p=0.38).

Vigilance while eating

When prey size was accounted for, there was no significant difference in amount of time on a kill spent being vigilant between mothers with young versus old cubs (Table 6). When I grouped all mothers with cubs together, they spent significantly more time being vigilant than single males and single females, but not male groups (Table 7). Cheetahs were less vigilant on small kills than large ones though the difference was only marginally significant (Table 7).

Discussion

My research reveals that aspects of cheetah prey handling behavior depend on risk from larger carnivores. Males and single females whose primary risk is kleptoparasitism have comparatively short overall handling times because they spend less time paused before eating and they eat relatively quickly. Mothers take a different approach since their primary threat is larger carnivores killing their cubs. Instead of speed, they use vigilance to minimize risk. They spend more time paused before eating and are more vigilant, increasing the amount of time they spend eating, which increases their overall handling time.

In order to reduce the chances of encountering large predators while hunting, mesopredators can avoid hunting when predators are close by (Durant 1998; Cooper *et al.* 2007), or they can preferentially forage when the predators are less active (Harrington *et al.* 2009; Mukherjee *et al.* 2009). However once prey are caught, there are other behaviors a mesopredator can use to lower the risks of predation and kleptoparasitism. When hunting large prey, maximizing nutritional gain requires spending substantial time handling the carcass, which increases the time spent in a risky situation. Moving the kill to a refuge is a strategy used by leopards (*Panthera pardus*) to lower risk of kleptoparasitism while handling large prey (Balme *et al.* 2017), while pumas (*Puma concolor*) cache large carcasses and thus kills are less likely to be detected by bears (*Ursus americanus* and *arctos*) (Murphy *et al.* 1998). Cheetahs cannot conceal their prey nor can they reliably defend their kills against larger predators and therefore they must employ different strategies. While lions and hyenas are more likely to find and steal larger kills (Hunter *et al.* 2007a), previous work by Hayward et al. (2006) shows that cheetahs do not preferentially select smaller prey to avoid kleptoparastism. Irrespective of size, to minimize the risk of their kill being stolen, they need to lower the chances of being detected by predators. Moving the kill to where it is better hidden by vegetation can extend the amount of time before it is discovered by hyenas (Hunter *et al.* 2007a), but regardless of habitat, decreasing handling time gives other predators less time to find the kill. When size of prey is taken into account, cheetahs without cubs decrease handling time by reducing time spent pausing after hunting, and reducing vigilance, which allows them to eat more quickly. Vigilance may enable a cheetah to see an approaching lion or spotted hyena, but it does not prevent the kill from being stolen. Although like Broekhuis et al. (2017), we found no significant differences in rates of kill loss by different cheetah social groups, out of 22 kills by single males in our dataset, they did not lose a single one to lions or hyenas. Habitat affects rates of kill loss (Hunter *et al.* 2007a), however it is likely that spending the lowest amount of time eating and handling prey contributed to single males' low rate of kleptoparasitism.

Since mothers with cubs on a kill face the risk of both predation and kleptoparasitism (Caro 1987), we might expect that they would also try to minimize time spent handling the carcass. A short handling time would reduce the chances of being discovered by lions and hyenas, lowering both risks. However, having cubs at the kill puts constraints on the ability of mothers to shorten their handling time. First, they have to make sure their cubs get enough to eat. Young cubs potentially slow their mothers down considerably since they have small mouths and are unfocused eaters, taking frequent breaks to rest and/or play (Caro 1994). Second, starting at ~4.5 months the cubs practice chasing and killing live gazelle fawns brought to them by their mothers (Caro 1995), which increases the time spent handling prey. However it does not increase hunt time or pause time as it occurs after the prey is captured but before the prey is dead. A short handling time might minimize the time the cubs spend being vulnerable to predators, but it could compromise the cubs’ ability to eat to completion and to practice hunting. We expected mothers with small cubs to spend more time eating than mothers with old cubs, and for them to be more vigilant since their cubs are more vulnerable to predation. However, there were no significant differences in the amount of time mothers with young versus old cubs spent eating, pausing, or being vigilant. In general mothers were more vigilant, paused for longer before eating, and spent more time eating, which led to longer handling times than for cheetahs without cubs. The longer pauses shown by mothers may allow them to simultaneously take time for breath recovery while scanning for predators before starting to eat. Cheetahs without cubs do not pause as long, likely because predation is not a major threat and starting to eat quickly reduces the chance of kleptoparasitism. This suggests that mothers favor behaviors that slow down their handling time but keep them and their cubs safer, using vigilance to lessen the primary threat to the cubs while allowing them the time they need with prey.

Group size can affect the amount of time animals spend handling and eating prey through group vigilance (Lima 1995; Roberts 1996) and intragroup competition for food (Lamprecht 1978). Theoretically, group vigilance means each individual can be less vigilant while maintaining similar levels of safety, while intragroup competition for food favors those who eat quickly. Both of these factors should push males in groups to shorten their handling time. Yet we found they eat more slowly and are more vigilant than single males, resulting in longer handling times. The explanation may lie in the multiple uses of vigilance, as Caro (1994) found that males use vigilance not as an anti-predator strategy but mainly to look out for potential mates. Thus intragroup competition for mates may cause males to favor behaviors that result in a slower and more vigilant prey handling strategy. For male cheetahs, group living does not lead to reduced individual vigilance or less time spent eating as seen in many other species (Lima & Dill 1990).

The variety of risks cheetahs face from larger predators and the tradeoffs imposed by having cubs creates two broad prey handling strategies. A short handling time is favored by those primarily facing kleptoparasitism, while mothers slow down, taking time to be vigilant in order to lessen predation risk to their cubs. How cheetahs shorten their handling times varies by social group. For example single males ate the fastest and were the least vigilant, while males in groups shorten their pauses instead of the time they spend eating. Individual identity also played a role in time in determining how long cheetahs spent eating and handling prey suggesting that cheetahs display a continuum of prey handling and vigilance behaviors that individuals adapt depending on the risks and pressures they face at the kill. Therefore, we expect that these behaviors would vary in areas where the pressures on cheetahs are different. For example in Kgalagadi (Kalahari) Transfrontier Park (KTP) in South Africa and Botswana, lion densities are three times lower and spotted hyena densities are one hundred times lower than in SNP, and cheetah cub survival is eight times higher (Mills & Mills 2014). Thus we might expect lower risks to cubs from lions and hyenas at the kill in KTP will result in different prey handling behaviors by mothers compared to those in Serengeti, though this remains to be investigated. These flexible and individual strategies to minimize risk from apex predators likely contribute to successful coexistence of cheetahs with lions and spotted hyenas across a steep gradient of large carnivore densities.

How apex predators affect mesocarnivore prey handling behavior has implications beyond coexistence. Studies of mesopredator release have provided detail on how the reduction or extirpation of apex predator populations leads to mesopredators increasing predation pressure on prey species (Ritchie & Johnson 2009). Functional response models quantify how alterations in predator foraging behaviors such as handling time change the number of prey they kill (Beddington, Hassell & Lawton 1976; Messier 1994; Murdoch, Briggs & Nisbet 2003), aiding in our understanding of how mesopredator release operates on a behavioral level. The role that apex predators play in shaping the functional response parameters of mesopredators indicates a mechanism for understanding the interactions among carnivores on multiple trophic levels together with their prey. Our work adds to the evidence that not only do other predators influence the functional response parameters of carnivores, but that the influence is not equal across individuals. Smith et al. (2015) found female pumas in California increased their kill rates to compensate for abandoning kills in areas with higher human housing density, while males did not. In this case female pumas reacted to the increased pressure from a human 'predator' by having shorter handling times, leading to an increase in prey killed. Altering prey handling strategies along a continuum based on individual risk levels may aid mesocarnivores in coexisting with multiple apex predators, and be key to mesocarnivore survival, especially when spatial avoidance of predators is not possible (Durant 2000a; b).

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Figures and Tables

Table 1 Number of observations used in the models or statistical for specific behaviors, broken down by social group. With the exception of time spent vigilant, models used either pooled all mothers with cubs or broken them out by cub age. Kills lost is the number of kills used in the analysis of time spent eating (eat time) that were taken by kleptoparasites. Number of individuals refer to how many different individuals were included in the observations for that specific behavior

	Single females	Females with young cubs	Mothers with old cubs	Mothers with cubs	Single males	Males in groups	Total sample size	Number of individuals
Handling time	119	81	110	*	18	23	351	128
Hunt time	124	*	*	246	20	23	413	159
Pause Time	50	*	*	55	16	10	131	87
Eat time	144	101	154	*	22	26	447	159
Kills lost	13	5	14	*	0	3	35	
Time spent vigilant	106	16	7	23	4	4	137	45

Table 2. Estimated amount of food cheetah cubs of varying ages eat compared to an adult. Based on relative body size (Caro 1994)

Cub age (months)	Adult cheetah equivalents
2-2.9	0.2
3-5.9	0.33
6-7.9	0.5
8-10.0	0.75
10.1-independence	1

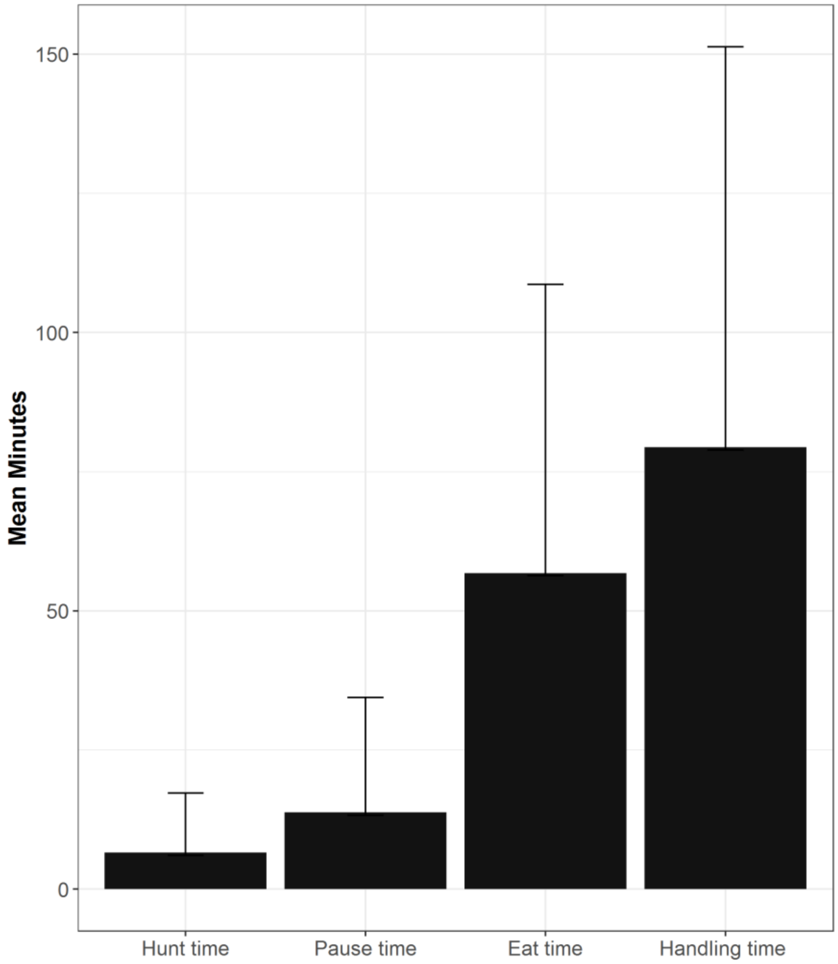

Figure 1 Mean time (untransformed) cheetahs spent on activities making up handling time, and handling time as a whole in Serengeti National Park in 1980-2014. Bars are standard deviation.

Table 3. Effect size and significance of fixed effects in the top handling time model. Logged handling time is the dependent variable, ID of hunting cheetah is the random effect. Note: Females with young cubs, Male groups, Single females, and Single males are in comparison to Females with old cubs (older than 4 months)

Parameter	Value	Std.Error	t-value	p-value
Intercept	3.553	0.076	46.866	<0.001
KG meat per cheetah	0.460	0.034	13.597	<0.001
Females with young cubs	0.427	0.096	4.472	<0.001
Male groups	-0.279	0.158	-1.770	0.0781
Single females	-0.160	0.091	-1.758	0.0801
Single males	-0.494	0.171	-2.888	0.0046
Kill Stolen	-0.756	0.106	-7.129	<0.001

Table 4. Partial model selection table for handling time models for Serengeti cheetahs. Shows all models with ΔAICc<10. ΔAICc= difference in AICc scores between model and top model. Weight refers to AICc model weights. R2m= marginal R squared, R2c= conditional R squared. Meat=meat available per cheetah, Social= Social grouping, Stolen= whether or not kill was stolen, Belly=Belly size, and Age=Age of cheetah. In all models the dependent variable was log transformed handling time, and random effect was ID of cheetah

Fixed Effects	AICc	ΔAICc	Weight	R2m	R2c
Meat+ Social+ Stolen	622.60	0.00	0.96	0.419	0.568
Meat+ Social+ Stolen+ Belly	629.70	7.07	0.03	0.419	0.570
Meat+ Social+ Stolen+ Age	631.30	8.69	0.01	0.420	0.567

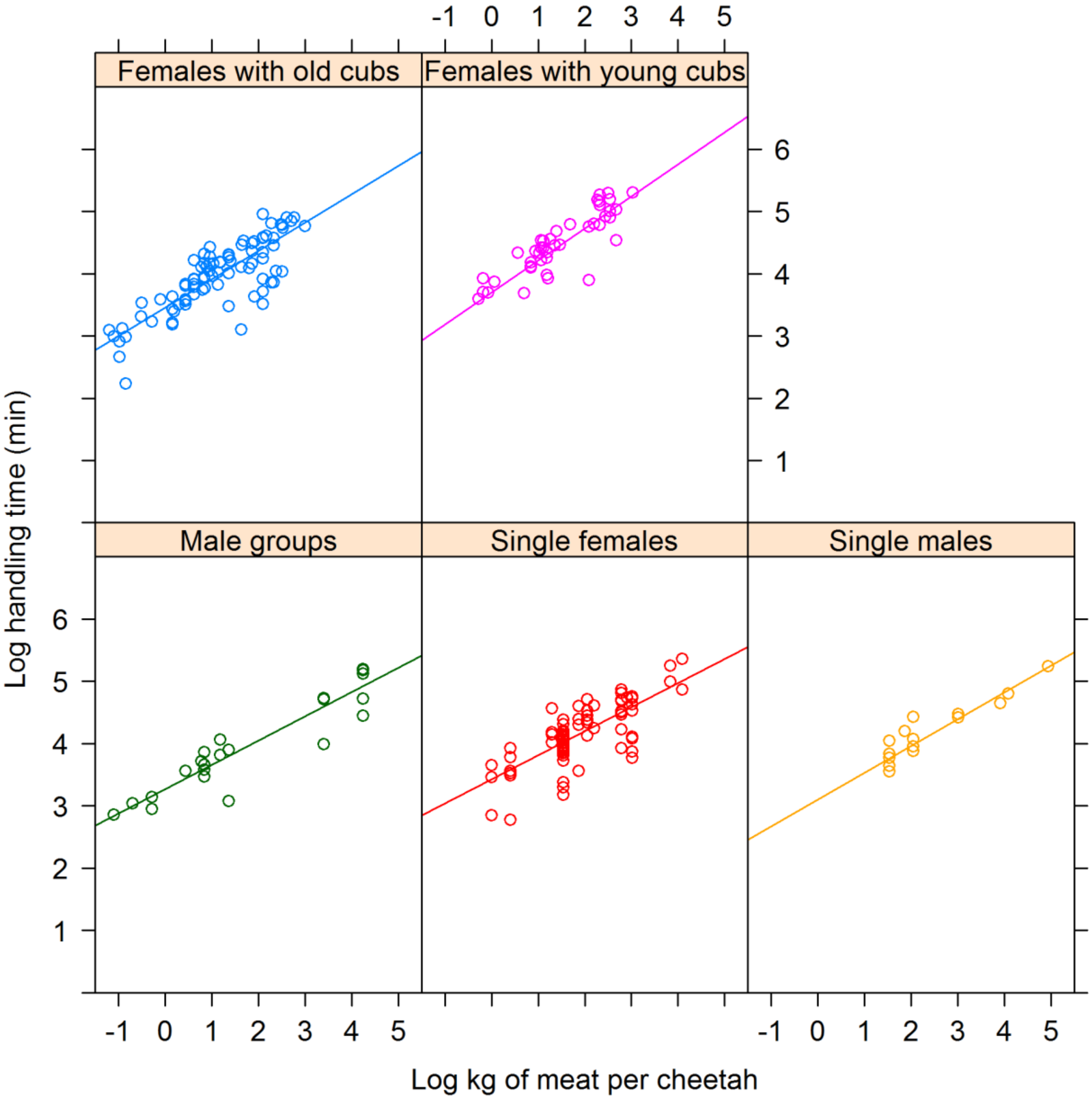

Figure 2. Model predictions of top handling time model. Shows minutes spent handling (logged) by social group and meat available per cheetah (logged). .Note both axes are log transformed and are the same for all panels. Y axis: handling time of 3 = 20 minutes, 6=403 min. X axis: kg of meat 0.5=1.64 kg, 3=20.08 kg

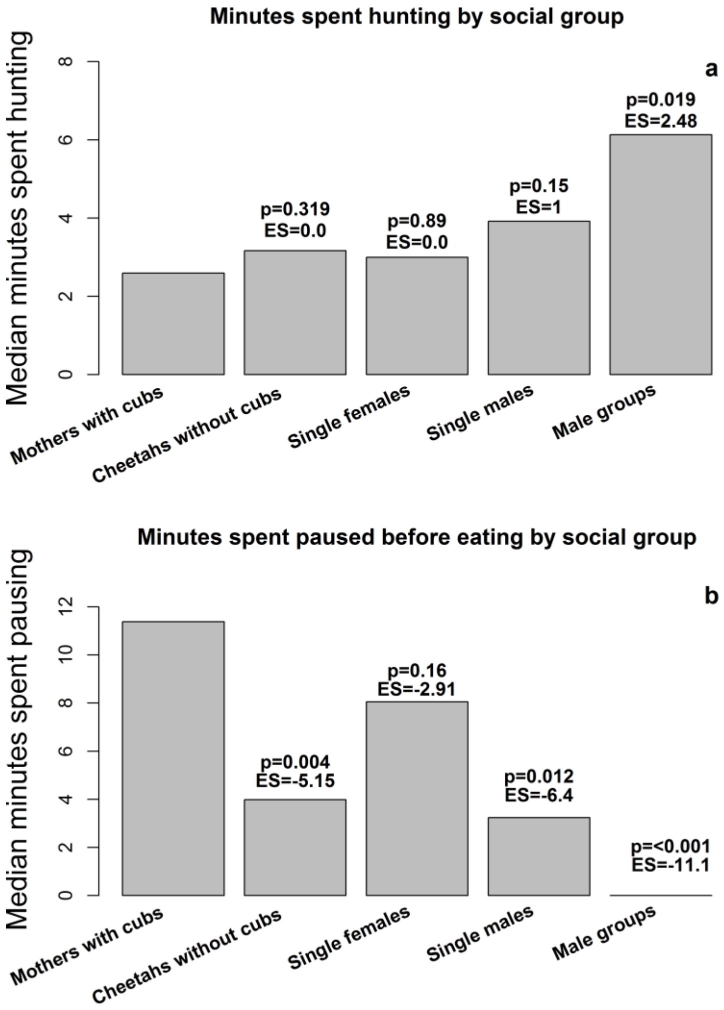

Figure 3. Median time spent hunting (a), pausing (b) between cheetah social groups. ES= Effect size and p value refer to the test of that social group against mothers with cubs. Cheetahs without cubs refers to pooling the data from single females, single males, and male groups. Values are from raw data.

Table 5. Effect size and significance of fixed effects in model of social grouping and meat available per cheetah on time spent eating (logged). Note: Females with young cubs, male groups, single males, single females are in comparison to mothers with old cubs (cubs >4 months)

Parameter	Value	Std.Error	t-value	p-value
Intercept	3.176	0.070	45.517	<0.001
KG meat per cheetah	0.469	0.033	14.298	<0.001
Females with young cubs	0.124	0.090	1.373	0.171
Male groups	-0.252	0.152	-1.656	0.099
Single females	-0.188	0.086	-2.196	0.029
Single males	-0.393	0.162	-2.432	0.016
Kill Stolen	-1.067	0.110	-9.686	<0.001

Table 6. Effect size and significance of fixed effects in model of social grouping and prey size on proportion of time on a kill spent vigilant. Note: Females with young cubs are in comparison to mothers with cubs four months of age and older. Small prey (<10 kg flesh weight) is in comparison with prey >10 kg flesh weight.

Parameter	Value	Std.Error	t-value	p-value
(Intercept)	-1.557	0.593	-2.628	0.024
Females with young cubs	0.551	0.680	0.811	0.439
Small prey	-0.719	0.229	-3.141	0.009

Table 7. Effect size and significance of fixed effects in model of social grouping and prey size on proportion of time on a kill spent vigilant. Note: male groups, single males, single females are in comparison to mothers with cubs (all ages). Small prey (<10 kg flesh weight) is in comparison with prey >10 kg flesh weight.

Parameter	Value	Std.Error	t-value	p-value
(Intercept)	-1.131	0.216	-5.242	<0.001
Male groups	-0.490	0.442	-1.109	0.276
Single females	-0.399	0.178	-2.242	0.027
Single males	-0.892	0.421	-2.118	0.042
Small prey	-0.347	0.177	-1.961	0.053

Conclusion

Functional response is the basis of our understanding and predictions of predator prey interactions, but applications to wild large bodied predators with complex hunting behavior have been complicated by lack of the type of detailed data that is available in experimental systems. By using a large and wonderfully detailed dataset on Serengeti cheetahs I could examine wild predator functional response with many fewer restrictions than past studies. I explicitly considered cheetahs as individual mesopredators in a multiple predator multiple prey ecosystem, and examined how their hunting behavior is shaped by prey density, the presence of apex predators, and their reproductive status.

My main findings were

-Cheetahs have an asymptotic Type II functional response overall, but cheetahs without cubs have a dome shaped Type IV.

-This is the first time that a Type IV has been found in a mammal and that functional response can vary between recognizable types by reproductive stage.

-The presence of lions within 1 kilometer lowers kill rates and makes cheetah functional response hard to characterize.

-The probability of a successful kill being made during a set time depended on whether the cheetah had cubs or not and prey density.

-Time spent handling time was longest for cheetahs with cubs, due to more time spent vigilant while eating, and pausing before eating.

-Cheetahs with cubs adopt a slower more vigilant strategy for handling prey that keeps their cubs safe from predation, while cheetahs without cubs go for speed, eating quickly and being less vigilant in order to lessen the risk of kleptoparasitism.

Future work

A potential avenue for future work is examining how the interactions of multiple predator species impacts prey. Predator interference has been reported in other species, work on waders shows that red knots and ruddy turnstones interfere with each other at high density, but they can adjust their behavior to minimize any decrease in prey intake (Vahl 2005). However carnivores are more directly antagonistic towards each other (Palomares & Caro 1999), and the direct and indirect effects of aggressive interactions between large bodied predators of different species on their functional response still remains mostly in the theoretical (Beddington 1975). Since cheetahs only vary in their kill rates at high gazelle density and cheetahs without cubs only rarely kill in those areas and mothers without cubs not at all, the effect on prey is likely to be minimal. Thus grouping and group vigilance by gazelles appears to be an anti-predator strategy against cheetahs. The suppression of kill rates around lions and the minimal role gazelles play in lion diet (Scheel 1993) suggests that gazelles may also be able to use lion presence as a refuge from cheetah predation. In a system like Serengeti with so many predators, habitat based refuges for gazelle may be rare. However the plethora of predators and the negative interactions between them may provide gazelles with relative respite from at least some predation pressure. The combined effects of gazelle density and lion presence on cheetah hunting behavior provide some clues into the potential impacts of changing community dynamics on cheetahs. Large scale changes in gazelle density, or density of larger apex predators due to poaching, hunting, fencing, the creation of water holes or any of a myriad of conservation challenges faced by megafauna, are likely to affect mothers with cubs differently than other cheetahs. Mothers must kill gazelles at higher rates, but are more restricted in the areas they use and the prey densities in which they hunt. Mothers face more severe pressures from larger predators whose presence alters their hunting behavior in ways not seen in single cheetahs. Given the already high rate of cub mortality on Serengeti cheetahs (Laurenson 1994), management or conservation actions that inadvertently lower the ability of females to raise cubs may have negative consequences for the population as a whole

Another direction of future work is exploring the effect of individual predators encountering different prey densities either through territoriality, differential habitat use, or as we see in cheetahs, the need to maintain high kill rates while avoiding larger predators. That cheetahs without cubs spend time in areas of higher density than mothers with cubs would have been obscured without the detailed data on prey densities experienced by individual cheetahs. Yearly, seasonal, or even monthly prey surveys of the study system would have been very unlikely to uncover those patterns. Yet even at rough spatial scales, differences in prey densities can impact our conclusions about functional response. For example, the functional response of the wolves of Isle Royale changed from the Hassell–Varley type 2 model to a ratio dependent Type II response when the moose density encountered were calculated on a pack scale vs a whole island scale (Jost *et al.* 2005).

My results also highlights the utility in breaking down hunting behavior into its component parts, as risks and rewards from bottom-up and top-down pressures affect behaviors differently. How those constituent parts come together to create the overall functional response of a population is still an area rich for investigation. For example, handling time is assumed to be constant in functional response models. My results show that it varies widely depending on cheetah social group, size of prey, and the presence of kleptoparasites, but the effect of violations of model assumptions in predator-prey relationships is understudied, especially in the field. Work by Okuyama (2008) and Bolnick *et al.* (2011) shows mathematically that variation in handling time increases predation pressure, and potentially destabilizes predator-prey interactions. However, for digestion-limited predators like cheetahs and most other large carnivores (Jeschke *et al.* 2002; Jeschke 2007), time spent actively handling prey probably does not limit the number of prey killed. Cheetahs start scanning for their next meal not when they have finished eating, but when digestion is well advanced and their belly sizes have shrunk, which can be up to a day later. Thus variation in active handling time is relatively short and may have little impact on kill rates in cheetahs or other predators that prey on relatively large bodied species. It is unclear whether patterns I uncovered regarding different functional responses by reproductive state and the effects of apex predators are general across mesocarnivores or arise from the specific risks and tradeoffs that cheetahs face in Serengeti. As data collection and analysis methods with GPS collars and accelerometers improve, we may be able to obtain the level of detailed behavioral data needed to examine individual variability in hunting behavior in more carnivore species, especially elusive ones. However linking those behaviors to the prey densities they encounter is likely to remain a major stumbling block in quantifying mesopredator functional response at anything more than a relatively coarse level. As humans cause apex predators to decline in many ecosystems (Dinerstein *et al.* 2007; Kang *et al.* 2010; Henschel *et al.* 2014) and humans reintroduce them in some others (Fritts *et al.* 1997), understanding how mesopredator behavior is impacted by both their prey and other predators is helpful to predicting potential effects of anthropogenic change or management actions on biotic communities.

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