Stalk and chase: how hunt stages affect hunting success in Serengeti cheetah

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Predation is a complex behavioural process and it is only through identifying the different factors influencing each stage that is it possible to understand the evolutionary processes driving the arms race between predators and prey. Using a long-term data set from Serengeti National Park in Tanzania, we investigated the importance of demographic, environmental, and prey-based factors in influencing the success of hunt stages of a stalking predator, the cheetah, *Acinonyx jubatus*. The chase and overall hunting success were influenced by the age of the cheetah and prey size, while the effect of habitat features could only be seen in the stalk. Whether a stalk turned into a chase was dependent on prey size, and in the dry season on proximity to rivers. Contrary to expectation, the hunger level of the cheetah, the presence of cubs, and the type of habitat where the hunt took place had no effect on hunting success. Different factors thus affect the success of individual hunt stages, and the predation risk of prey is influenced not only by its size, the habitat it is in, and the age of the its predator, but also by hunt stage. This reveals an increased complexity of predation risk that has implications for predator and prey dynamics, especially in systems with multiple predator and prey species.
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The interaction between predators and their prey is one of the most important relationships between species, affecting population dynamics and the distribution and behaviour of both groups (Lima 1998; Bonsall & Hassell 2007). Predators can impact prey populations directly, through the simple removal of individuals, or indirectly, as prey respond to predation risk by changing their habitat use, feeding, activity levels and breeding efforts (Lima 1998; Creel & Christianson 2008). For a predator, predation is a complex process that depends on the success of individual behavioural stages. This complexity and the potential multiple interactions of factors within it has hampered an integrated understanding of the effects that both direct predation and predation risk have on prey populations. Breaking predation into its component parts allows investigation of the observed patterns in and between each stage, leading to a better mechanistic understanding of the whole process (Holling 1966; Hebblewhite et al. 2005). This approach can be particularly valuable when factors have opposing influences on the success of different stages of predation, which can mask the importance of such factors on the overall process (Hebblewhite et al. 2005). For example,

Hebblewhite et al. (2005) found that wolves, *Canis lupus*, are more likely to encounter but less likely to kill elk, *Cervus elaphus*, in open grasslands than in pine stands. The success of hunt stages can also be influenced by a prey's antipredator behaviour, as less vigilant gazelles are less likely to spot a predator during the stalk and are slower to react once a chase has begun (FitzGibbon 1989). These complex interactions between predator and prey can determine the survival of individuals and thus have evolutionary consequences for populations (Reznick et al. 1990).

Previous work on carnivores has highlighted several factors that can potentially shape the success of hunt stages, as well as overall hunting success. For example, success in stalking or approaching prey is related to the amount of cover (Gese et al. 1996) and prey vigilance levels (FitzGibbon 1989). Whether an attack leads to capture of prey can then be influenced by habitat (Gese et al. 1996; Hebblewhite et al. 2005) and by the age (FitzGibbon 1990a) or sex (FitzGibbon 1990b) of prey. Overall success can be shaped by the age of prey and the number of hunters (Fanshawe & FitzGibbon 1993), the age of the hunter (Holekamp et al. 1997), the habitat (Gese et al. 1996) and type of prey (Wells & Bekoff 1982; Stander & Albon 1993). While synthesis of these findings is hindered by the lack of data on multiple hunt stages from the same species, they do demonstrate that influential factors can vary by hunt stage.

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We used a long-term data set from cheetah, *Acinonyx jubatus*, in Serengeti National Park in Tanzania as a model of a stalking carnivore to examine how characteristics of the environment, the prey and the hunter impact overall hunting success through the success of stalks and chases. Cheetah have two main hunting strategies. The majority of the hunts (80% of the 295 hunts used in the analysis) 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 (17%). The remaining 3% do not follow easily classifiable behaviours. We investigated the factors affecting overall hunt success (i.e. prey capture) and the independent influences of those factors on stalk success (i.e. chase initiation) and chase success (i.e. prey capture). Based on published studies of cheetah predation, we grouped potential factors affecting the success of hunt stages in three broad categories (environmental, prey based and cheetah based) and generated the following hypotheses and predictions.

Hypothesis 1: Prey Characteristics Are Important at All Hunt Stages

The predominant prey species in the study system are gazelle. Young gazelle are less able than adults to escape cheetah, and hunting success decreases as gazelles age (FitzGibbon 1990a). Additionally, large prey are hunted less often and less successfully than small prey (Caro 1994). Therefore, we predicted that hunting success at all stages of the hunt would be higher on small and medium prey than on large prey.

Hypothesis 2: Characteristics of the Hunter Affect Hunt Stages Differently

Hunting is a learned behaviour in carnivores, and Caro (1994) found that young females have reduced stalking success compared to adults. Thus, we predicted that adults would be better than young cheetah at making a successful stalk and chase, making them more successful overall. Females with cubs need to increase their food intake to meet heightened energy demands, and they might do so by increasing their hunting success on larger prey (Laurenson 1995). Cubs can ruin their mother's stalk by being detected by prey (Caro 1986); thus, increased hunting success is more likely to come via successful chases. Therefore, compared to solitary females, we also predicted that mothers with cubs would have more successful hunts on medium and large prey due to more successful chases. Hunger level does not determine whether a cheetah starts a hunt (Cooper et al. 2007), but it may influence whether a cheetah gives up on a stalk, as a hungry cheetah may be more likely to complete a stalk and commit to the effort of a chase than a sated individual. Thus, we tested whether hungry cheetah have more successful stalks.

Hypothesis 3: Environmental Factors Affect Hunt Stages Differently

Increased hunting success has been suggested as a reason for habitat selection by predators (Gorini et al. 2012), and Serengeti cheetah preferentially use rivers and rocky outcroppings called kopjes (Pettorelli et al. 2009). The added cover and elevation of kopjes may provide an advantage to hunting cheetah, but recent evidence does not support this (Cooper et al. 2007), suggesting that cheetah select kopjes for reasons other than hunting. We tested whether distance from kopje affects stalk, chase or overall hunt success. Prey congregate near water, and rivers provide a source of vegetative cover, potentially permitting closer stalks. We therefore tested whether success of stalks and overall hunting success is higher closer to rivers. Cheetahs rely on their great speed to outrun prey and can reach speeds of up to 103 km/h over short distances (Sharp 1997). Open habitats without obstructions by dense shrubs or trees may increase a cheetah's ability to outrun prey. Thus, we predicted that the success of chases and of overall hunting success would be higher in grasslands than in woodland habitats. Ungulates are food restricted in the dry season, and carnivores kill the weaker individuals (Sinclair & Arcese 1995). Prey may be more willing to increase their predation risk when starving (McNamara & Houston 1987; Cresswell et al. 2010), making them easier to chase and kill in the dry season. Thus, we also predicted that success of chases and overall hunting success would be higher in the dry season.

METHODS

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. There are two main seasons, the wet season from November/December to May, and the dry season from June to November. The plains are divided into three rough grassland types by growth form: long grass in the north, intermediate grass in the west and south, and short grass in the east and southeast (Fig. 1). The plains are dotted with 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, *Connochaetes taurinus*, zebra, *Equus quagga,* and Thomsons's gazelles, *Eudorcas thomsonii*, move seasonally over the study area. Cheetah in the Serengeti are extremely mobile, with females and nonterritorial 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). Cheetah 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. Sinclair et al. (2008) provide a recent and detailed description of the study site and the ecosystem.

Cheetah Data

The data come from hunts observed by seven SCP staff, including S.D. and A.H., between 1993 and 2011. Staff were trained to find cheetah and record behavioural data before they collected data independently. Because the study area is mostly grasslands or open woodlands and cheetah are diurnal hunters that are fairly accustomed to vehicles, collection of good-quality observational data is relatively easy. Hunts were observed both by following focal individuals and by opportunistic observations. We defined hunts as starting when a cheetah took two or more steps towards visible prey with an alert stalking gait. A hunt ended when the cheetah brought down its prey, stopped running after failing to catch the prey, or stopped stalking or watching the prey alertly (i.e. because it had been detected by the prey or the prey had moved away). Observations were made through binoculars from a parked vehicle, and care was taken at all times not to disturb the hunt. Start and end times of hunt stages and locations of start and end of hunt were recorded on a global positioning system (GPS).

Habitat Data

We used three Geographical Information System (GIS) layers provided by Serengeti GIS and Data Centre (http://www.
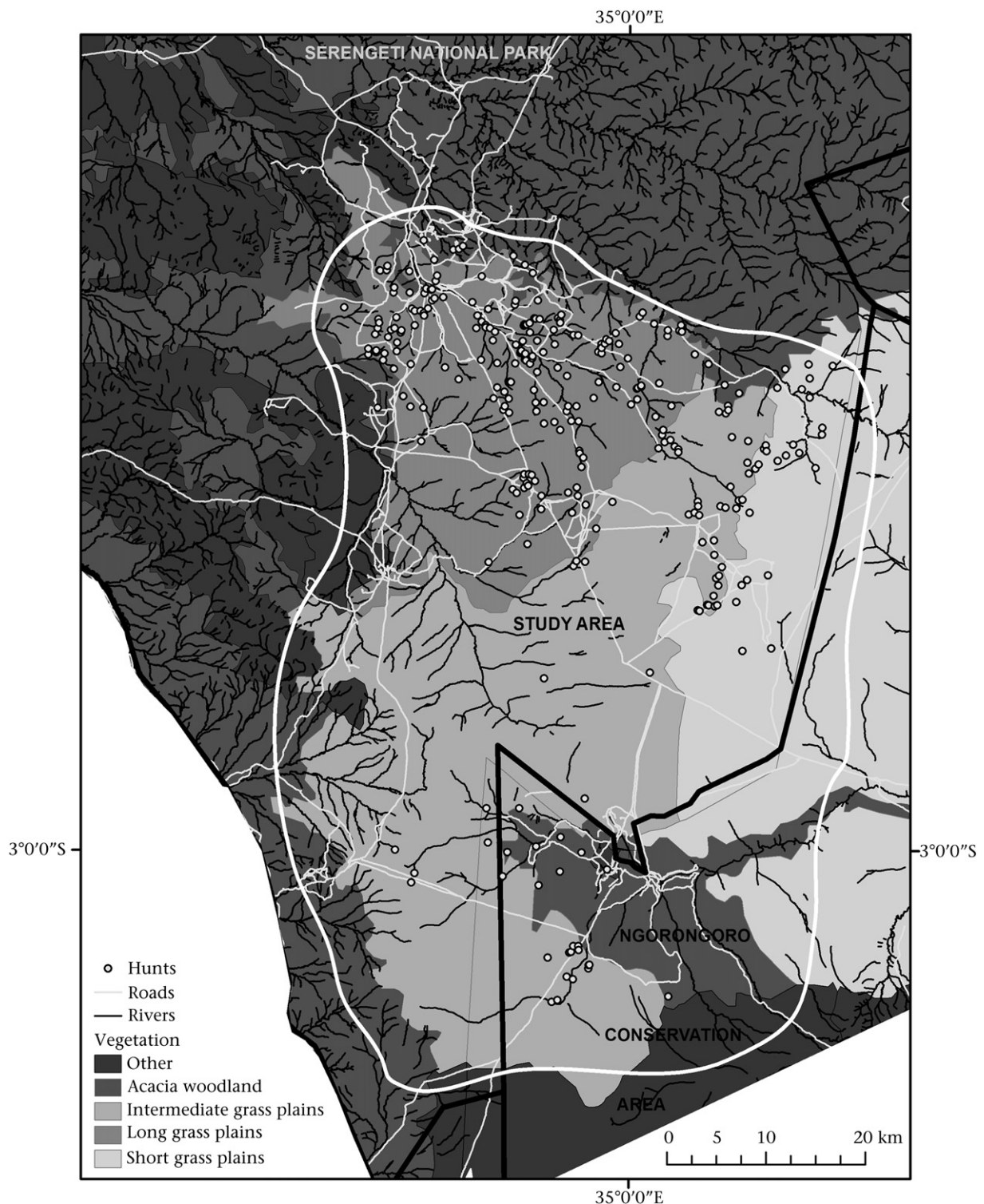
Figure 1. Map of study area with habitat features and hunts by Serengeti cheetah plotted.

serengetidata.org). The layers were (1) water courses, which included permanently flowing rivers down to ephemeral streams, (2) the location of kopjes and (3) a habitat map of grasslands and woodlands created by Sinclair et al. (2008). We plotted the locations of the 295 hunts used on the GIS map of the study area using Arc Map v.9.3.1 (Fig. 1) and calculated Euclidean distances from each hunt location to the nearest river and kopje. All GIS data were projected in metres onto UTM zone 36M using the Arc 1960 datum.

Data Analysis

We modelled the likelihood of (1) a stalk to turn into a chase (2) a chase to end in a kill and (3) an overall hunt to be successful. We limited our analysis to hunts by females as there are differences in prey choice and ranging patterns between the sexes (Caro 1994; Cooper et al. 2007) and limited hunt data were available for males. Since our response variables were binomial, and since we wished to correct for

pseudoreplication (multiple hunts by the same cheetah), we used generalized linear mixed effects models with binomial errors, including the identity of the cheetah as a random effect in all models considered. Having identity of the cheetah as a random effect takes into account the variation in success between individual cheetah. We were unable to test whether some cheetah had significantly different hunting success than others because of the generally small number of hunts observed per individual (68% of individuals had fewer than three hunts observed). Hunting success, the probability of a stalk turning into a chase and the probability of a chase ending in a kill, were then modelled as a function of the age of the hunter, belly size as a proxy for satiation, the presence of cubs, season, prey size, habitat, the distance (in metres) to the nearest kopje and the distance (in metres) to the nearest river. The age of the hunter was estimated as either adult (>44 months) or young (14–44 months) (Caro 1994). Belly size was then considered to be an ordinal variable, ranging from 1 (starving) to 14 (extremely full) (Caro 1994). The presence of cubs and season and habitat were all considered as binary factors (for cubs: presence/absence; for season: wet/dry; for habitat: acacia woodland/ grassland). Expanding on Laurenson's (1995) categories, prey size was considered as a three-level variable, distinguishing between large (>30 kg), medium (10–30 kg) and small (<10 kg) prey, based on average species body mass (Owen-Smith 1988; Estes 1991). Small prey included hares (*Lepus* spp.), fawns of Thomson's gazelle and Grant's gazelle, *Nanger granti*, dik-dik, *Madoqua kirkii*, and warthog, *Phacochoerus africanus*, piglets. Medium prey included subadult and adult Thomson's gazelle, subadult Grant's gazelle, wildebeest calves, zebra foals, kongoni, *Alcelaphus buselaphus,* calves and steenbok, *Raphicerus campestris*. Large prey included adult Grant's gazelle, juvenile wildebeest, adult kongoni, adult impala, *Aepyceros melampus,* adult warthog, and adult reedbuck, *Redunca redunca*. Distances to rivers and kopjes were log transformed. We used an Akaike's Information Criterion corrected for small sample size (AICc) approach to model selection. AICc scores of candidate models were compared and the model with the lowest score was considered the best model (Burnham & Anderson 2002; see Appendix, Table A1). As there is substantial support for models within two AICc points of the best model (Burnham & Anderson 2002), we discuss such models whose fixed effects had P values of <0.1. All analyses were performed in R 2.11 (R Core Development Team 2011) using the lmer function in the lme4 library (Bates et al. 2011).

RESULTS

We used 295 hunts in the total analysis, of which 120 successfully ended in a kill. Of the 232 hunts that started as a stalk, 144 resulted in a chase. When all chases were considered, including chases without a preliminary stalk, 114 of 196 ended in a kill. Eight hunts lacked information on whether a stalk or a chase took place, so they were included in the analysis of overall success only. The majority of prey hunted during this study were Thomson's gazelle (69%), followed by Grant's gazelle (16%), hares (6%), and wildebeest (3%).

Our best models for overall hunt success and the success of the stalk and chase stages of hunting included a relatively small subset of variables: hunter age, prey size and distance to river (Table 1). The importance of considering the success of hunt stages separately was seen in the difference between the stalk and chase. The success of stalking depended on the prey size and the distance the stalk took place from a river (Table 1). Stalks closer to a river were more likely to end in a chase (slope + SE = −0.73 + 0.35, Z = −2.08, P = 0.04), as were stalks on small (estimate + SE = 4.10v + 1.14, Z = 3.60, $P \leq 0.001$) and medium prey (estimate + SE = 1.22 +0.376, Z = 3.26, P = 0.001) compared to large prey. Interestingly, the success of stalks occurring during the wet season tended to be less

Table 1
Effect size and significance of fixed effects included in the best models for each hunt stage by Serengeti cheetah

Model	Fixed effect	Estimate	SE	Z	P
Overall success					
	Intercept	−2.623	0.625	−4.193	<0.001
	Medium prey	2.149	0.644	3.338	<0.001
	Small prey	4.661	0.722	6.459	<0.001
	Young	−0.869	0.348	−2.499	0.01
Success of stalk					
	Intercept	1.444	1.035	1.395	0.16
	Medium prey	1.225	0.376	3.261	0.001
	Small prey	4.099	1.139	3.598	<0.001
	Distance to river	−0.728	0.349	−2.084	0.04
Success of chase					
	Intercept	−1.461	0.650	−2.246	0.02
	Medium prey	1.749	0.674	2.597	0.009
	Small prey	3.499	0.744	4.701	<0.001
	Young	−0.912	0.371	−2.457	0.01

influenced by distance to river than the success of stalks occurring during the dry season (Z = 1.90, P = 0.06; see Appendix, Table A1).

Season and habitat features were excluded from the best model for success of chases, and only prey size and hunter age determined whether prey would be captured (Table 1). Chases by young cheetah were less likely to end in a kill (estimate + SE = −0.91 + 0.37, Z = −2.46, P = 0.01) than chases by older cheetah, while chases were more successful on small (estimate + SE = 3.50 + 0.74, Z = 4.70, $P \leq 0.001$) and medium (estimate + SE = 1.75 + 0.67, Z = 2.60, P = 0.009) prey compared to large prey. Similar patterns of the importance of prey size and hunter age were seen in overall hunting success, reflecting the importance of the chase stage to the final outcome (Table 1). Young cheetah were less likely to be successful (estimate + SE = −0.87 + 0.35, Z = −2.50, P = 0.01) than adults, and hunts on both small (estimate + SE = 4.66 + 0.72, Z = 6.46, $P \leq 0.001$) and medium (estimate + SE = 2.15 + 0.64, Z = 3.34, $P \leq 0.001$) prey were more successful than those on large prey.

DISCUSSION

By using cheetah as a model of a stalking predator, we examined how factors affecting different stages of a hunt combine to produce overall hunting success. Additionally, we tested whether factors affecting the success of the chase also affect the success of the stalk. Prey size and cheetah age were the most important factors determining the success of chases, and thus, overall hunting success. Factors predictive of stalks turning into chases were prey size and distance to river. There was no significant effect of distance to kopje, hunger level of the cheetah, whether the cheetah had cubs or overall habitat on the outcome of any of the hunt stages.

Prey size was consistently the most important factor in the success of hunt stages, with higher success on small and medium prey in stalks, chases and overall. Small prey are predominantly made up of gazelle fawns (66%) and hares (25%), which are vulnerable to predation as they cannot outrun a cheetah, leading to 77% of gazelle fawns that were chased being caught (FitzGibbon 1990a). Availability of vulnerable prey appears to affect cheetah hunting behaviour much more than characteristics such as hunger level, as belly size was not an important factor in hunting success and satiated cheetah were not more likely to abandon stalks or chases. Thus, hunger does not appear to influence predation greatly at any stage, from decision to hunt to probability of capture (Cooper et al. 2007). Traditionally, hunger is thought to be an influential factor in predatory behaviour, with satiation helping to limit the amount of prey killed by reducing the effort spent in searching for new prey (Mills 1982; Jeschke et al. 2002). However, some

carnivores engage in 'surplus' killing of many more prey than can be eaten due to a glut of vulnerable prey such as young animals or weakened adults (Kruuk 1972; Miller et al. 1985; French & French 1990; DelGiudice 1998). While surplus killing has not been reported in cheetah, they seem unable to resist chasing gazelle fawns regardless of their hunger level, possibly because fawns are so easy to catch and hunting is usually much more difficult. While not classic surplus killing, this sort of behaviour may help explain why belly size is not a good predictor of hunting behaviour, and suggests that, in some cases, availability of vulnerable prey may have a greater influence on carnivore predation than hunger.

The importance of characteristics of the hunting cheetah to hunting behaviour varied. Like hunger level, the presence of cubs did not appear to influence hunts. Our results indicate that contrary to Laurenson's (1995) suggestion, females with cubs do not have increased hunting success on medium and large prey. Instead, to increase their food intake, mothers may be able to hunt large prey at a greater rate (Laurenson 1995). In contrast, age of cheetah influenced some hunt stages, as adult cheetah were better at chasing and capturing their prey than were younger cheetah. Hunting is a learned behaviour, and it takes time for young predators to become capable hunters (Fox 1969; Caro 1994; Holekamp et al. 1997). For a stalking predator to capture prey, both the stalk and the chase need to be mastered, and our results highlight the different skills needed to be proficient at both. To approach vigilant prey without being detected, the hunter must learn to use available cover like that found around rivers, and behaviours like crouching and freezing when prey look up (Caro 1994). Capturing prey requires the hunter to catch up with and knock down its target. Our results are not clear-cut about which of these stages cheetah master first. It appears that because age influences the success of chases, but not stalks, that young cheetah master stalking before chasing. However, not only are young cheetah more likely to be detected in the stalk than are adults (Caro 1994), they can also start chasing from too far away, or even after being seen by the prey, leading to more chases than would be attempted by older cheetah. The two behaviours by younger cheetah (more failed stalks, more attempted chases) may confound any trend for age to be a predictor of stalks becoming chases.

Differences in hunting ability by age could impact the population dynamics of both the predator and prey. Hunting skills could be a factor in survival after independence in solitary carnivores (Caro 1994), and as young females rely more on small prey like gazelle fawns and hares than do adults (Caro 1994), the seasonal availability of small prey could affect the survival rates of newly independent cheetah. On the other hand, the difference in hunting ability between age classes of predators can lead to differential predation pressure on prey (MacNulty et al. 2009); thus, the age composition of the cheetah population could impact gazelle populations by affecting how many and which age classes of gazelle are successfully hunted.

A recent review by Gorini et al. (2012) highlights the multiple ways environmental variables can be important in carnivore hunting behaviour. Hunting success is influenced by the habitat where hunts take place (Stander & Albon 1993) and where predators make kills (Hopcraft et al. 2005; Bergman et al. 2006; Balme et al. 2007). Additionally, within a hunt itself, habitat can influence stages differently (Hebblewhite et al. 2005). Likewise, our results illustrate that the influence of habitat is better understood when hunts are looked at in stages. The broad habitat of a hunt was not a significant factor at any stage of the hunt, yet the stalk's distance from a river influenced whether a chase occurred. Like lions, *Panthera leo* (Hopcraft et al. 2005), cheetah may be able to use the vegetative cover around rivers to approach their prey more closely. However, unlike lions, the importance of proximity to rivers is seasonal for cheetah, suggesting that cheetah hunt around rivers when prey congregate there in the dry season. In the wet season, when prey are spread out on the plains, cheetah can both exploit increased grass cover beyond the rivers and use behaviours like crouching and freezing to approach prey when cover is not available (A. Hilborn & S. M. Durant, personal observations). The ability to hunt away from rivers may help cheetah avoid lions (Durant 1998), which make more kills and have higher reproductive success around rivers (Hopcraft et al. 2005; Mosser et al. 2009), and are known to steal carcasses from cheetah (Hunter et al. 2006) and kill both cubs and adults (Laurenson 1994; Durant et al. 2010). This flexibility in habitat use during hunting extends to kopjes. While lions seasonally use kopjes for hunting (Hopcraft et al. 2005), cheetah appear to select them for shade, territorial marking (Caro 1994) and denning sites (Laurenson 1994) rather than for hunting. This lack of dependence on habitat features is perhaps not surprising in highly mobile individuals whose home ranges average 800 km^2 (Caro 1994).

The complex and multistage nature of predation and the limited data available make it challenging to look at the factors that affect every stage simultaneously. Being mesopredators, the predation process may be particularly complicated for cheetah. For them, ultimate success (i.e. net energy gain; Rasmussen et al. 2008) rests on being able to master and balance several independent behaviours, from detecting prey, stalking, chasing and killing it, to moving and consuming the kill before it is stolen by other carnivores. Our work on the stalk and chase is only a part of the process, augmenting Cooper et al.'s (2007) work on the factors that determine whether a cheetah starts a hunt and Hunter et al.'s (2006) examination of kill loss to scavengers. Many aspects of cheetah predation remain to be examined fully, and once the factors that lead to the success of individual components are known, we will have a greater ability to look at overarching issues such as the relationship between prey choice, the success of hunt stages, the net energy gain and how hunting behaviour influences social organization and fitness (Caro 1994; Rasmussen et al. 2008)

Breaking predation into stages can also help illuminate its complexities for prey. In addition to direct predation, predation risk is thought to have both obvious and far-reaching effects on structuring ecosystems (Ripple & Beschta 2004). The ungulates of the Serengeti face a suite of carnivores (cheetah, lions, leopards, *Panthera pardus*, hyaenas, *Crocuta crocuta*), all of which have different hunting styles and habitat uses, creating a variety of predation risks and a very complex 'landscape of fear' (Laundré et al. 2001). Our work helps illustrate how predation risk can be more complex than previously thought, varying not only by habitat and prey species, but also by the demographics of predator populations and the stage of hunt. Thus, antipredator defences may have to evolve to be sensitive not only to predator species, but also to the specific stage of predation. Further investigation into how the demographics and habitat use of prey and predator species interact to influence vulnerability to predation could add realism to predator–prey models (Lima 2002) and contribute to a greater understanding of population dynamics and trophic interactions.

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Appendix

Table A1

Candidate models for stalk and chase, and overall success within two AICc points of the model with the lowest AICc score

Fixed effects	Deviance	AICc	Delta	Weight
Model: overall success				
Target size + age	**307.28**	**317.49**	**0**	**0.23**
Target size + age + season	305.94	318.23	0.74	0.16
Target size + age + river	306.28	318.57	1.09	0.13
Target size + age + habitat	306.71	319	1.51	0.11
Target size + age + season + river	304.79	319.18	1.69	0.1
Target size + belly + cubs	307.01	319.3	1.81	0.09
Target size + age + kopje	307.18	319.47	1.99	0.09
Target size + age + belly	307.18	319.48	1.99	0.09
Model: success of stalk				
Target size + river	**267.18**	**277.45**	**0**	**0.4**
Target size + river + season + river∗season	**263.61**	**278.11**	**0.67**	**0.29**
Target size + age + river	266.98	279.35	1.9	0.16
Target size + habitat + river	267.06	279.43	1.98	0.15
Model: success of chase				
Target size + age	**226.26**	**236.57**	**0**	**0.46**
Target size + age + habitat	224.61	237.05	0.48	0.36
Target size + age + season	225.94	238.38	1.81	0.18

AICc: Akaike's Information Criterion corrected for small sample size. Shown are differences in AICc scores between candidate models and the model with the lowest AICc score (Delta), and the relative weight of the models. Models discussed in the text are shown in bold.