



Large carnivore menus: factors affecting hunting decisions by cheetahs in the Serengeti

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Predation plays a key role in shaping mammalian communities through prey killed and through the decisions and choices of both predators and prey. We used an extensive data set from observed hunts of a diurnal large African carnivore, the cheetah, *Acinonyx jubatus*, in combination with analysis techniques originally developed in the field of economics (discrete choice models) to examine predation decisions within the context of the immediate environment and the reproductive and hunger status of individuals. This is one of the first attempts at an integrated understanding of the suite of ecological and behavioural factors that influence hunting decisions in a large carnivore. The decision of a cheetah to hunt or not was influenced by the abundance of their main prey, the reproductive status of the cheetah and the presence of competitors and predators, but not by the hunger level of the cheetah. Given that the decision to hunt is taken, prey choice is then driven by the time of year, the sex of the predator, the abundance of prey and the presence of competitors. We believe that discrete choice models may provide a new step forward in our ability to understand the decisions that animals make in their natural environment.

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Predation plays a key role in shaping mammalian communities, not just through prey killed, but also through the decisions and choices of both predators and prey (Sih 1987; Lima & Dill 1990). The reproductive success of all consumers is influenced by what they choose to eat because each prey has particular costs and benefits to the consumer (Werner & Hall 1974). On the other hand, consumers directly influence prey population dynamics: predation can increase the amplitudes of fluctuations in prey abundance (van Baalen et al. 2001), dampen fluctuations (Fryxell & Lundberg 1994), and increase (Holt 1977)

or decrease (Krivan & Eisner 2003) the probability of prey extinctions. Furthermore, the risk of predation also affects the distribution of potential prey in an ecosystem, as well as their foraging success (Turner & Mittelbach 1990). Prey selection patterns are thus key to an understanding of prey and predator dynamics and spatiotemporal distributions. Competition adds a further layer of complexity on the organization of communities. Predators and prey compete with each other for food and resources, and may also affect their population dynamics and spatial distribution (e.g. Chesson & Rosenzweig 1991; Reseratis 1991).

The patterns of prey selection shown by various predator species therefore tend to be shaped by a suite of factors, including predator and prey behaviour, morphology and habitat requirements related to hunting, escape or predation avoidance (Bakker 1983; Kruuk 1986). Prey selection by large terrestrial carnivores can occur at several different levels, for example selectivity for prey species, for prey size and for age or sex classes, and selectivity towards physically

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substandard individuals (FitzGibbon & Fanshawe 1989; Karanth & Sunquist 1995; Radloff & du Toit 2004). This selection can be influenced by factors such as the presence of competitors (Mills & Gorman 1997), the size of the hunting pack (Creel & Creel 2002), the habitat structure (Krüger et al. 1999) and the season (Pole et al. 2004).

Despite acknowledging the complexity of predation choices, few studies have investigated prey selection decisions against the immediate ecological conditions at the time. Most studies describing large carnivore prey choices have instead focused on predator preferences based on the ratio between hunting attempts, kills or scat contents and large-scale relative abundance of potential prey, usually estimated by line transects (Karanth & Sunquist 1995; Krüger et al. 1999; Biswas & Sankar 2002; Bagchi et al. 2003; Pole et al. 2004). Some information has also been collected on correlates associated with hunting success or hunting rate (e.g. Mills 1990; Caro 1994; Creel & Creel 2002), but few data are available on the proximate factors affecting the decision to hunt. In this study we sought to close this gap, by (1) characterizing the factors that influence hunting decisions and (2), given that the predator has decided to hunt, identifying the parameters influencing the probability of hunting each potential prey.

Two of the primary techniques used to analyse foraging behaviour are dynamic optimization models (Mangel & Clark 1988) and linear programming models (Belovsky 1978, 1986; Schmitz et al. 1998). Both these models assume individuals are attempting to maximize or minimize some objective or a combination of objectives that relate to fitness (e.g. maximizing net energy intake, minimizing risk of predation). However, as the range of behaviours (or forage options) and variability in the natural environment increase, these models become computationally intensive. Previously, valid assessments of prey choice have also principally depended on choice experiments, which, owing to the restrictions of the experimental method, are never conducted in a truly natural setting, and hence may not be a true reflection of choice under the natural range of environmental variables (e.g. Sarno & Gubanich 1995; Carter et al. 1999). Logistic regression has also proven effective for analysing prey choice (Scheel 1993); however, the method cannot directly account for occasions when the set of prey items available differs over time or space.

We used a different approach by adapting discrete choice models, developed for use in economics (Ben-Akiva & Lerman 1985) and recently applied to resource selection (Cooper & Millspaugh 1999). Discrete choice models allow the calculation of the probability of a given predator choosing to hunt, and, given that it hunts, the probability of choosing a particular species of prey, as a function of the prey species present, the environmental conditions at the time, and the individual characteristics of the predator (Cooper & Millspaugh 1999). We used these models to analyse prey selection by cheetahs, *Acinonyx jubatus*, in the Serengeti National Park in Tanzania. Cheetahs represent a good model on which to explore hunting decisions and behaviour as they hunt diurnally and often in open habitat, and hence are relatively easy to observe.

Scattered information is available on factors influencing the hunting behaviour and the hunting success of cheetahs. Cheetahs hunt mainly during early mornings and late afternoons (Schaller 1968, 1972). Thomson's gazelle, *Gazella thomsoni* (in the Serengeti), springbok, *Antidorcas marsupialis* (in the Kgalagadi Transfrontier Park) and impalas, *Aepyceros melampus* (in the Kruger National Park) constitute the majority of the hunting attempts and kills (Mills 1984; Caro 1994; Broomhall et al. 2003; Mills et al. 2004). Predator sex, group size, prey sex, prey concentrations and habitat structure all influence hunting behaviour and hunting success (FitzGibbon 1990; Caro 1994; Durant 1998; Broomhall et al. 2003; Mills et al. 2004). The level of hunger is also thought to influence hunting decisions (Caro 1994). The presence of competitors such as lions, *Panthera leo*, and hyaenas, *Crocuta crocuta*, influence the cheetah's spatial distribution and hunting behaviour (Durant 1998). Finally, a cheetah with cubs needs to hunt more frequently than one without cubs, if she is to be able to provision her cubs (Laurenson 1995a). No integrated quantitative analysis of all these potential factors influencing hunting decisions and prey selection by cheetahs has been carried out. Furthermore, there has been no examination of how these factors affect the decision-making process throughout the hunt, from the first decision made to initiate a hunt through to the decision about prey selection.

We used discrete choice models to examine the decisions made by cheetahs during hunts and we tested a number of predictions about the factors influencing hunting decisions and prey selection. The discrete choices modelled in the analysis include the decision to hunt, and then, given that the decision to hunt is made, the decision of which prey to select. This method of analysis allows us to explore the different factors affecting hunting decisions as well as identifying at which point, during the decision-making process, they exert an influence. We generated the following hypotheses on the factors affecting hunting decisions from published studies of the hunting behaviour of cheetah.

(1) Cheetahs principally prefer Thomson's gazelle, then hares, *Lepus* spp., wildebeest, *Connochaetes taurinus*, and Grant's gazelles, *Gazella granti* (Caro 1994). Thus the presence of these prey species near a cheetah should influence the decision to hunt.

(2) Cheetahs are more likely to be moving and less likely to be hunting if there are lions or hyaenas in the vicinity (Durant 1998). Therefore the presence of these competitors should negatively affect the decision to hunt.

(3) A cheetah with cubs needs to hunt more frequently than one without cubs, if she is to be able to provision her cubs (Laurenson 1995a). Furthermore, the hunger level should motivate the decision to hunt (Caro 1994). Therefore the cheetah's energy needs should positively affect the decision to hunt.

(4) Cover availability should enable a stalking predator such as the cheetah to hunt more effectively (Schaller 1972; Mills et al. 2004). Therefore habitat structure and cover availability should positively affect the decision to hunt.

(5) Most of the kills occur between 0700 and 1000 hours and between 1600 and 1800 hours (Schaller 1968, 1972).

Therefore the time of the day should influence the decision to hunt.

Given that the predator has chosen to hunt, we proposed the following hypotheses about the decisions cheetahs make about their choice of prey.

(6) Wildebeest, Thomson's gazelles and Grant's gazelles are migratory species that change their spatial occupation with the season (Campbell & Borner 1995). Therefore the probability to decide to hunt each prey species should vary with the time of year.

(7) Finally, male cheetahs have been reported to hunt larger species on average than females (Caro 1994). Therefore prey selection patterns should differ between the sexes.

We used information from 845 observations of cheetahs in a variety of ecological conditions to test these predictions.

METHODS

The Model

When encountering a set of potential prey, a predator must decide both whether to hunt and what to hunt. These linked decisions, which can also be modelled under a dynamic optimization or linear programming model, may depend on many variables such as availability of prey, presence of competitors and environmental conditions, all of which will vary with time and place. Discrete choice models can explicitly account for these variables and their effect on the decision-making process in a statistically rigorous manner. These models calculate the probability of a given predator choosing to hunt, and given that it hunts, the probability of choosing a particular species of prey, as a function of the prey species present, the environmental conditions at the time and the individual characteristics of the predator. The model assumes that a predator gains some form of satisfaction (which economists call 'utility') from hunting prey, but it is not necessary to specify a priori what this satisfaction actually represents in biological terms. Satisfaction is mathematically defined by a linear combination of the attributes of the prey species, the local environmental conditions and the individual predator's attributes, but the specific attributes themselves may take on nonlinear forms (e.g. polynomial, logarithmic).

Given that a predator has chosen to hunt, the utility, u , provided by prey species i to predator j at time t (U_{ijt}), takes the form:

$$U_{ijt} = \mathbf{B}'_i \mathbf{X}_{ijt} + e_{ijt} = b_{i1}x_{1jt} + b_{i2}x_{2jt} + \dots + b_{im}x_{mjt} + e_{ijt} \quad (1)$$

where \mathbf{X}_{ijt} is a vector of length m of the environmental conditions and the attributes of species i as perceived by predator j at time t , along with the attributes of predator j at time t . \mathbf{B}_i is a vector of length m of estimable parameters, denoted by $b_{i1}, b_{i2}, \dots, b_{im}$, that determine each attribute's contribution to the utility of hunting species i , and e_{ijt} is an error term. Each prey species will then have a separate utility equation which will be a function of environmental conditions, attributes of that species and attributes of the predator. Predators are assumed to behave optimally

such that an individual will choose to hunt the species that will give the largest level of utility. Thus, in our data, the species actually chosen by the cheetah is the species that provided the maximum utility at that particular time and place. The probability of predator j choosing to hunt species A at time t given the set of i potential species, $P_{jt}(A|i)$, can therefore be written as:

$$P_{jt}(A|i) = P(U_{Ajt} > U_{ijt} \forall i) = P(\mathbf{B}'_A \mathbf{X}_{Ajt} + e_{Ajt} > \mathbf{B}'_i \mathbf{X}_{ijt} + e_{ijt} \forall i) \quad (2)$$

When the error terms are distributed as Type I extreme values, equation (2) can be rewritten as the multinomial logit discrete choice model (Domencich & McFadden 1975):

$$P_{jt}(A|i) = \frac{\exp(\mathbf{B}'_A \mathbf{X}_{Ajt})}{\sum_i \exp(\mathbf{B}'_i \mathbf{X}_{ijt})} \quad (3)$$

A predator may also choose not to hunt at all, given the prey available. To account for this, the model above was nested within a hunt versus not hunt model. In this model the probability of choosing to hunt species A is the product of the probability of choosing to hunt given the set of i species available at time t and the probability of selecting species A given both the set of i species available and that the predator chose to hunt at time t (McFadden 1978):

$$P_{jt}(A|i) = P(A|i, Y_{jt} = 1) \times P(Y_{jt} = 1|i) \quad (4)$$

where Y_{jt} equals one if predator j chooses to hunt at time t , and zero otherwise. When all predators have the same two, and only two, options at all times (such as the case of hunting versus not hunting), the discrete choice model can be simplified to the standard logistic regression model (Ben-Akiva & Lerman 1985) such that:

$$P(Y_{jt} = 1|i) = \frac{\exp(\mathbf{C}' \mathbf{X}_{jt}^* + \theta h)}{1 + \exp(\mathbf{C}' \mathbf{X}_{jt}^* + \theta h)} \quad (5)$$

where \mathbf{X}_{jt}^* is a vector of length m^* of the environmental conditions and the attributes of predator j at time t , and \mathbf{C} is a vector of length m^* of estimable parameters that determine each attribute's contribution to the utility of hunting regardless of which species is chosen. The variable h , called the inclusive value, equals the maximum expected satisfaction of selecting a species to hunt given the set of species available, and θ is an estimable parameter representing the contribution of the inclusive value to the utility derived from choosing to hunt. The inclusive value is calculated from the formula:

$$h = \sum_i (\exp(\mathbf{B}'_i \mathbf{X}_{ijt})) \quad (6)$$

The utility equation for hunting ($\mathbf{C}' \mathbf{X}_{jt}^* + \theta h$ in equation (5)) could be interpreted conceptually as the satisfaction of attempting to obtain any meat regardless of the prey species (represented by $\mathbf{C}' \mathbf{X}_{jt}^*$) which is then modified by such things as the expected ease of capture and mass of meat, which depend on what species are available and are represented by θh . The full probability

model can be described by the decision tree shown in Fig. 1, and can be written as:

$$P_{jt}(A|i) = \frac{\exp(\mathbf{B}'_i \mathbf{X}_{Ajt})}{\sum_{vi} \exp(\mathbf{B}'_i \mathbf{X}_{ijt})} \times \frac{\exp(\mathbf{C}'_A \mathbf{X}_{jt}^* + \theta h)}{1 + \exp(\mathbf{C}'_A \mathbf{X}_{jt}^* + \theta h)} \quad (7)$$

Discrete choice models are estimated using maximum likelihood procedures similar to standard linear regression models (Ben-Akiva & Lerman 1985) and these procedures are found in numerous statistical software programs (Manering 1998). The significance of all parameters was tested with $\alpha = 0.05$ using likelihood ratio tests, which are chi-square distributed. Interaction effects were tested only after the main effects were included (McCullagh & Nelder 1989; Neter et al. 1990). To estimate this model, we first calculated the parameter estimates (\mathbf{B}'_i) for the prey selection portion. This was accomplished by fitting equation (3) to the data on which species were selected when the cheetah actually chose to hunt. These parameters define the equations that describe the relative utility from selecting each prey species given that a predator has chosen to hunt (as described by equation (1)). These derived equations were then applied to every occasion when a predator was observed, to calculate the inclusive value associated with each hunting opportunity (every observation is considered a hunting opportunity). We then estimated the parameters for the equation describing the utility of choosing whether or not to hunt (\mathbf{C}' and θ) using the same technique as in the prey choice model. The preference of predators for one species over another, or to hunt versus not hunt, could then be compared using values produced by the utility equations, with higher values implying greater satisfaction and relative preference.

The Data

We applied the model to data collected on hunting behaviour of cheetahs in the Serengeti National Park in Tanzania. From 1993 to 1996, cheetahs were observed a total of 845 times out of 3000 observation periods (called scans) taken from 740 locations (Durant 1998) scattered throughout a 2200-km² region in the southeast of the Serengeti National Park (Caro 1994). During each scan, data were collected on the abundance of prey and nonprey species, date and time of the scan, bush density and the presence of kopjes (large rocky outcrops which provide a lookout point for the predator and are often the only shade on the open plains; see Caro (1994) for a complete description of the study area and Durant (1998) for more detailed

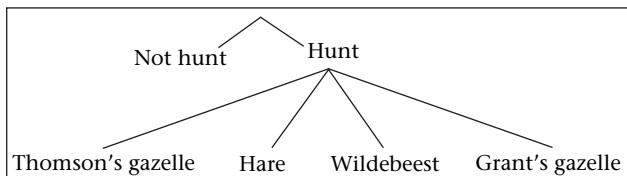


Figure 1. Decision hierarchy for cheetah prey selection. Cheetahs may choose not to hunt, or given that they choose to hunt, they may select Thomson's gazelles, hares, wildebeest or Grant's gazelles as their potential prey.

descriptions of the environmental variables). When a cheetah was observed during a scan, its age, sex, reproductive status (whether it was lactating and/or with cubs), belly size (a measure of its hunger level) and tameness index were noted (Caro 1994). Owing to the unique spotting patterns on their face, sides and tail, individuals are uniquely identifiable, and with over 20 years of cheetah research in this area, life history data are available for most individuals. Also noted were whether the cheetah engaged in hunting activities, and, if so, which species of prey was targeted.

RESULTS

Parameterizing the Model

Of the 127 times cheetahs were observed hunting, 76% targeted Thomson's gazelles, 10% targeted hares, 9% targeted Grant's gazelles and 5% targeted wildebeest. Although cheetahs may hunt other species besides those listed here (Caro 1994), they did not appear in this data set and therefore cannot be modelled. The final model consisted of six equations: utility equations for choosing to hunt and choosing not to hunt, and then four separate equations describing the utility of selecting each of the prey species listed above given that the predator decides to hunt.

The relative satisfaction derived from choosing to hunt or not hunt equals:

$$U_{\text{Hunt},j,t} = -1.91 + 0.47 \times (\text{cub}_{jt}) - 0.59 \times (\text{LA}_{jt}) + 0.008 \times (\text{TGA}_{jt}) - 0.00003 \times (\text{TGA}_{jt})^2 \quad (8)$$

$$U_{\text{Not hunt},j,t} = 0 \quad (9)$$

where cub_{jt} equals one if cheetah j had cubs present at time t and zero otherwise, LA_{jt} equals the abundance of lions for the observation of cheetah j at time t , and TGA_{jt} equals the Thomson's gazelle abundance for the observation of cheetah j at time t .

The relative satisfaction derived from choosing to target a Thomson's gazelle, Grant's gazelle, wildebeest or hare, given that the cheetah chose to hunt equals:

$$U_{\text{Thomson's gazelle},j,t} = 20 + 7.10 \cos\left(\frac{2\pi(\text{month}_{jt} - 2)}{12}\right) \quad (10)$$

$$U_{\text{Grant's gazelle},j,t} = 13.32 + 7.22 \times (\text{WS}_{jt}) - 6.91 \times (\text{CS}_{jt}) + 0.17 \times (\text{GGA}_{jt}) + 2.33 \times (\text{HA}_{jt}) \quad (11)$$

$$U_{\text{Wildebeest},j,t} = 20 + 12.16 \cos\left(\frac{2\pi(\text{month}_{jt} - 3)}{12}\right) - 6.91 \times (\text{CS}_{jt}) \quad (12)$$

$$U_{\text{Hare},j,t} = 20 \quad (13)$$

where month is the month in which the observation of cheetah j at time t occurred, and equals one for January,

two for February, three for March, etc.; WS_{jt} equals one if the observation of cheetah j at time t occurred during the long rains (February–May) and zero otherwise; CS_{jt} equals one if cheetah j observed at time t was female and zero if male; GGA_{jt} equals the Grant's gazelle abundance for the observation of cheetah j at time t ; and HA equals hyaena abundance for the observation of cheetah j at time t .

There are two items to note. First, these equations represent the relative satisfaction for the available options with $U_{Hare,j,t}$ being set as the baseline utility for choosing between species and $U_{Not\ hunt,j,t}$ being set as the baseline for choosing whether or not to hunt. Satisfaction values have order and scale, but the value for the baseline is arbitrary and was chosen to ensure all satisfaction values were positive simply for ease of interpretation. Second, the satisfaction values for choosing a species and choosing whether or not to hunt are not directly comparable because of the nested nature of the decision process and the arbitrary values set for the two baseline satisfaction values.

Factors Influencing Decision to Hunt

According to our first set of hypotheses, the presence of Thomson's gazelles, wildebeest, hares, Grant's gazelles, lions, hyaenas and cubs, the cover availability, the time of day and the hunger level were all expected to affect the decision to hunt (Table 1). Only three factors influenced the utility of hunting versus not hunting: the presence of cubs ($P < 0.05$), the abundance of Thomson's gazelles ($P < 0.01$) and the abundance of lions ($P < 0.01$). Contrary to our expectations, the presence of other possible prey, the presence of hyaenas, the hunger level of cheetahs, the cover availability and the time of day did not influence the decision to hunt.

We therefore expressed the probability of hunting, as calculated from equation (5), as a function of lion abundance Thomson's gazelle abundance and the presence of cubs (Fig. 2). According to our results, the probability of

choosing to hunt peaked at around 135 Thomson's gazelles and decreased as lion abundance increased and gazelle abundance moved away from 135 individuals. The presence of cubs shifted the probability surface, leading to higher probabilities of hunting under all scenarios (Fig. 2).

Factors Affecting Prey Selection

Significant temporal effects were found in the utility derived from selecting Thomson's gazelle ($P < 0.0001$), Grant's gazelle ($P < 0.025$) and wildebeest ($P < 0.001$), but, as expected, not for hare (Table 1, Fig. 3). The utility derived from selecting a Grant's gazelle as a potential prey increased with both Grant's gazelle abundance ($P < 0.01$) and hyaena abundance ($P < 0.025$).

The magnitude of the differences in preferences for the different species depended on the sex of the cheetah ($P < 0.001$; Table 1). Female cheetahs, which are smaller than males, showed a higher discrepancy (based on the differences in utility values) between hunting larger species (Grant's gazelles and wildebeest) compared with smaller species (Thomson's gazelles and hares) than that found in male cheetahs (Fig. 3).

DISCUSSION

Overall, the techniques developed here have proven to be powerful at extracting the motivations for hunting and prey choice in cheetahs. Results from our approach mostly conform to what was previously known about cheetahs' hunting behaviour (Caro 1994; Laurenson 1995a; Durant 1998; Broomhall et al. 2003; Mills et al. 2004), validating the use of discrete choice models to address such issues. However, the approach shows that some factors affect different stages in the decision-making process. For example, while lions affected the decision whether to hunt or not, they did not affect the decision about what prey to select, whereas hyaenas did not appear to affect the decision to

Table 1. Summary of the hypotheses and predictions tested

Hypotheses and predictions	Supported?
(1) Presence of prey should increase likelihood of deciding to hunt	
Presence of Thomson's gazelles should increase likelihood of deciding to hunt	Yes
Presence of wildebeest and Grant's gazelles should increase the likelihood of deciding to hunt	No
(2) Presence of competitors should decrease likelihood of deciding to hunt	
Presence of lions should decrease likelihood of deciding to hunt	Yes
Presence of hyaenas should decrease likelihood of deciding to hunt	No
(3) Increased energy needs should increase likelihood of deciding to hunt	
Presence of cubs should increase likelihood of deciding to hunt	Yes
Hunger level should increase likelihood of deciding to hunt	No
(4) Habitat structure should affect decision to hunt	
Cover availability should increase the likelihood of deciding to hunt	No
(5) Time of day should influence decision to hunt	
Likelihood of deciding to hunt should be highest early in morning and late in afternoon	No
(6) There should be seasonal variation in prey selection	
Prey selection should vary according to seasonal variations in spatial distribution of prey	Yes
(7) Cheetah's size should influence prey selection	
Males should select for larger prey than females	Yes

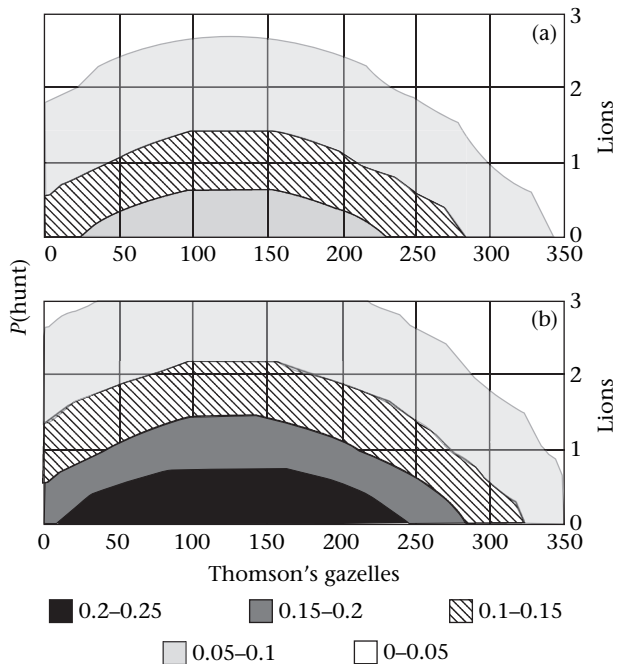


Figure 2. Surface map of the probability ($P(\text{Hunt})$) of a cheetah (a) without cubs and (b) with cubs hunting as a function of Thomson's gazelle and lion abundance.

hunt, but did affect the prey selected. Such subtleties are unlikely to be detected in a conventional analysis.

In accordance with our first prediction, Thomson's gazelle abundance was a key determinant of hunting decisions for cheetahs in the Serengeti. Thomson's gazelle and wildebeest are the most common ungulates in the Serengeti (Caro 1994), and several studies on carnivores have reported a positive correlation between abundance of prey and percentage of prey in the diet (Krüger et al. 1999; Biswas & Sankar 2002; Bagchi et al. 2003; Pole et al. 2004). Furthermore, the preference of cheetahs for medium-sized prey species has been reported elsewhere (Mills et al. 2004). However, the relation between the hunting decision and the presence of prey found in this study was not linear. The probability of choosing to hunt was related to a quadratic function of Thomson's gazelle numbers, increasing as numbers of Thomson's gazelle increased from zero up to 135 and decreasing thereafter. This final decrease contrasts, for example, with a linear increase in the probability of an encounter ending in a kill with impala herd size, observed in encounters between impala and a coursing predator, wild dogs, *Lycaon pictus*, by Creel & Creel (2002, page 140). This may be explained by two different hypotheses. First, for a stalking predator such as the cheetah, small groups of prey have lower vigilance levels than large groups and hence are less likely to detect an approaching predator (FitzGibbon 1988). This results in greater success for cheetahs when hunting small groups of prey (FitzGibbon 1990). Lions, another stalking predators, have also been reported to prefer hunting smaller herds in the Serengeti (Scheel 1993). A coursing predator, such as the wild dog, relies on selecting out slower individuals in a much longer

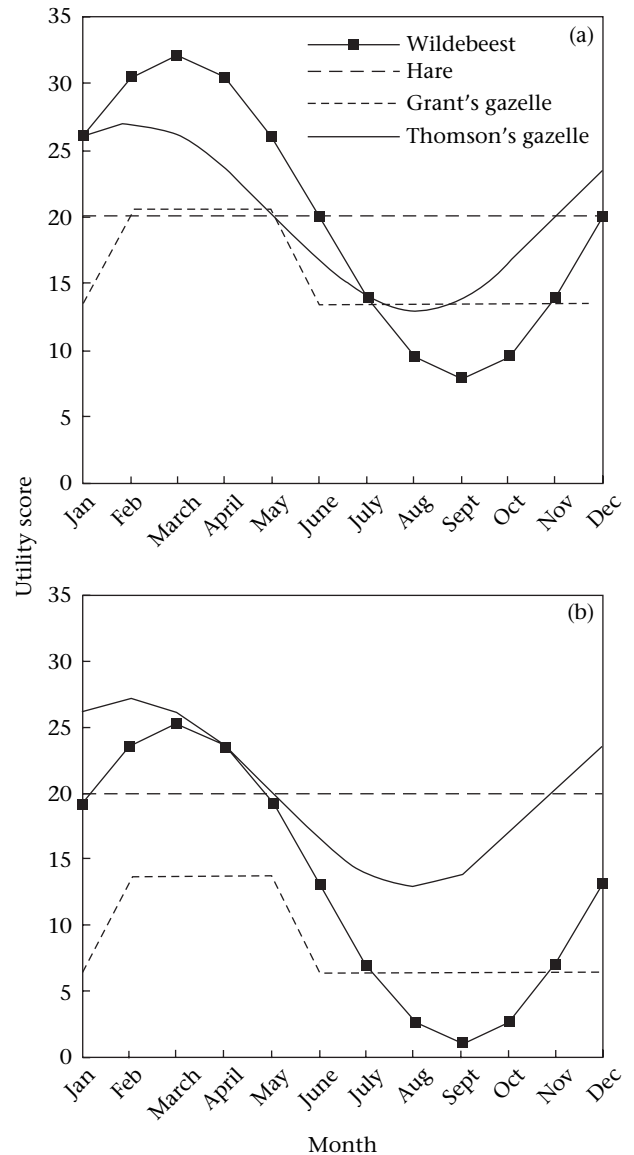


Figure 3. Temporal dynamics of prey preferences for (a) male and (b) female cheetahs. Species with higher utility scores are preferred by cheetahs over species with lower utility scores.

chase, and hence might be expected to prefer larger herds which may be more likely to contain weak individuals. The second hypothesis is that by avoiding hunting when and where Thomson's gazelles reach high densities, cheetahs are avoiding potential conflict with other predators, as gazelle abundance is correlated with hyaena and lion abundance (Durant 1998). Cheetahs may associate areas of high Thomson's gazelle abundance with a high risk of predation or kleptoparasitism, and may therefore choose not to hunt in these areas regardless of whether a competitor is present. Contrary to expectation however, the decision to hunt was not affected by the abundance of wildebeest or Grant's gazelles. This confirms the high selectivity of cheetahs for Thomson's gazelles and the opportunistic nature of wildebeest and Grant's gazelle hunts (Schaller 1968, 1972; Caro 1994).

As expected, the presence of competitors greatly influenced hunting decisions. Lions are competitors, kleptoparasites and predators of cheetahs (Caro 1994; Laurenson 1994, 1995b), and, as expected, their presence reduced hunting behaviour by cheetahs (Durant 1998). No such effect was detected in response to hyaena abundance. Durant (2000) reported differential responses by cheetahs to playbacks of hyaena and lion calls, with stronger responses to lions than to hyaenas. However, in these experiments cheetahs reduced hunting activity in equal measure as a response to both lion and hyaena playbacks, whereas in our study only lions affected the decision whether to hunt but hyaenas affected only which species to target. The difference observed between the two studies might be explained by the fact that playbacks simulated a predator 200 m from a cheetah, whereas the distance between predators and cheetahs in this study were generally much greater. Furthermore, whereas in the playbacks a cheetah was aware of the 'simulated' presence of the predator, the degree to which cheetahs in this study were aware of a predator within 1 km was unknown, and hence cheetahs might have been less aware of hyaenas than of the larger lion. None the less, this study depicts conditions as they were observed, and hence the findings are more likely to reflect behaviour more often observed in the natural environment.

Surprisingly, the decision to hunt was not based on the immediate need to acquire food, since belly size did not significantly affect either prey choice or the probability of hunting. Belly size accurately reflects the hunger level of the cheetah (Caro 1994), and so our results suggest that the decision of whether to hunt is independent of hunger. This contrasts with previous suggestions that hunger levels are associated with hunting decisions in cheetahs (Caro 1994) and lions (Elliott et al. 1977). The only exception was when females needed to provision cubs. When a cheetah was accompanied by dependent cubs, it was more likely to hunt, leading to a greater demand for prey of any kind. This is in agreement with what was expected from a previous study which showed that a cheetah with cubs needs to hunt more frequently than one without cubs (Laurenson 1995a).

Contrary to expectations, cover availability and time of day had no influence on hunting decisions. Cover availability has been shown to influence hunting success for carnivores: Schaller (1972) reported, for example, that three-quarters of lions' prey were caught near some cover. However, the height of the surrounding vegetation had no effect on the probability of wild dogs making a successful kill in the Serengeti (Fanshawe & FitzGibbon 1993). As wild dogs are coursing predators, cover may be less important for this species than for stalking predators such as lions and cheetahs. None the less, our study suggests that for cheetahs in open grassland habitat, such as on the Serengeti plains, cover, such as is found among kopjes and drainage lines, may be used more by cheetahs for resting than for hunting.

Given that a cheetah decides to hunt, prey preferences in the Serengeti were not constant over time, and factors such as the season and the sex of the cheetah all influenced the cheetah's prey selection patterns.

Seasonal variation in prey selection has been reported for other carnivores in the Serengeti, such as lions (Scheel 1993; Scheel & Packer 1995). With other variables held constant, the equations describing the utility derived from selecting Thomson's gazelle, Grant's gazelle or wildebeest each reached their maximum around the primary birth peak for each species (Fig. 3; Maddock 1979; FitzGibbon 1988; Kingdon 1989): both male and female cheetahs preferred a given species at the time of year when that species was at its birth peak, when there was a high availability of young individuals which were relatively easy to catch. However, later in the year when the newborns of each species had nearly attained their adult size, the relative utility of choosing each species ranked inversely according to their adult size, with hares, the smallest, being most preferred, followed by Thomson's gazelles, then Grant's gazelles, and finally wildebeest, the largest species considered here. This pattern was particularly marked for the smaller female cheetahs compared with larger males, as expected from the slight differences existing in the average size of the catches made by male and female cheetahs (Caro 1994). Group size also has an impact, and Scheel (1993) and Creel & Creel (2002) highlighted the importance of the number of hunting lions and wild dogs, respectively, in determining prey selection patterns. In cheetahs, males tend to form coalitions, whereas females generally hunt alone. Therefore the number of animals hunting, rather than the sex per se, might explain the difference in prey selection patterns between male and female cheetahs (Caro 1994).

Surprisingly, the utility derived from selecting a Grant's gazelle as a potential prey increased with both Grant's gazelle abundance and hyaena abundance. Hyaenas tend to be associated with high densities of migratory prey (Hofer & East 1995; Durant 1998), whereas Grant's gazelles are frequently found some distance from the main migration (Caro 1994). Therefore these results could have arisen from cheetahs choosing to hunt on the periphery of large migratory herd aggregations when hyaenas were present, thus decreasing the risk of conflict (see also Durant 1998). This finding, together with the earlier finding that the presence of lions makes cheetahs less likely to hunt, shows one of the means by which lions and hyaenas can have nonlethal impacts on cheetahs and their prey.

Several other factors have been reported to affect hunting decisions of large carnivores: Schaller (1972) noted the importance of the wind direction for lions to initiate a hunt, while Caro (1994) noted the importance of individual variability in prey selection patterns of cheetahs, and FitzGibbon & Fanshawe (1989) and then Fanshawe & FitzGibbon (1993) showed the importance of the age and condition of the prey for wild dog and cheetah hunting behaviour and success. We were unable to examine these parameters in this study.

In this paper we have demonstrated the power of the discrete choice model for analysing complex trade-off decisions within behavioural ecology, and shed light on parameters influencing hunting decisions and hunting preferences of cheetahs in the Serengeti. Our results,

although consistent with what was previously reported on hunting behaviour in that species, also clearly highlight the need to understand more clearly each chronological step of a hunt, since, for example, factors correlated with taking the decision to hunt were different from factors correlated with prey choice once the predator had decided to hunt, or even the factors correlated with a successful hunt. To ensure the general validity of our results, we also believe such an approach should be recommended in other cheetah populations, where the main prey, the habitat structure and the level of competition with other carnivores might differ (e.g. Broomhall et al. 2003; Mills et al. 2004).

Discrete choice models are designed for this type of chronological approach, since they are flexible enough to incorporate a hierarchy of decisions as well as explicitly allowing for changes in environmental conditions and prey availability across observations. The benefits of this flexibility are particularly acute when dealing with field data where controlled perturbations and designed replication are impossible, as is the case for many endangered species. Manipulating the prey base or habitat for such species may be not only difficult, but also undesirable. In cases where such control is feasible, discrete choice models will have even greater power in discerning the factors affecting behaviour.

The primary limitation for these models is the ability of the observer to gather data appropriate for their use: visibility in the great plains of the Serengeti and the habituation of cheetahs allows observers to characterize the proximate environment every time a cheetah is seen hunting. In forested areas, data on prey and competitor abundance at a scale that matters to the studied predator might be more difficult to gather, while if predators are not easily habituated, it may also be difficult to gather information on hunting behaviour. None the less, in situations where such data can be collected, this study shows that discrete choice models can provide a new step forward in our ability to understand the decisions that animals make in their natural environment, and opens promising perspectives in our ability to reach a better understanding of the factors shaping hunting decisions and prey selection in carnivores.

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