CHAPTER 7

HUNTING BEHAVIOUR OF THE CARACAL IN THE KGALAGADI TRANSFRONTIER PARK

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ABSTRACT

Caracals were spoor-tracked in the Kgalagadi Transfrontier Park with the assistance of a Kalahari San tracker to investigate their general ecology and behaviour. Observations relating to caracal hunting behaviour were made based on large and small prey categories. Caracals use a flexible hunting technique and their hunting methods are adapted to specific circumstances. They hunt larger prey more with a higher degree of success than smaller ones. There is a logical sequence of hunting behaviour that is likely to result in a kill.

Keywords: caracal, *Caracal caracal*, spoor-tracking, hunting, Kalahari

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INTRODUCTION

There is a paucity of data relating to the hunting behaviour of nocturnal, solitary felids in general (Bothma & Le Riche 1989) and caracals *Caracal caracal* in particular. The ability to hunt and kill prey is central to the survival of any predator. Felids are among the most highly specialised carnivores (Kruuk 1986), and are killers *par excellence* (Ewer 1973). The evolutionary fitness of any animal is dependent on the quality and quantity of its diet (Griffiths 1975). Predatory strategies are designed to optimise nutrient intake within an environment that is governed by a complex system of ecological factors (Sunquist & Sunquist 1989). In the semi-arid Kgalagadi Transfrontier Park, stringent ecological constraints necessitate the refinement of hunting tactics by predators to increase their chances of survival (Bothma *et al.* 1997). Factors such as the availability, abundance, size, vulnerability and behavioural response to predation of prey animals all influence a predator's prey selection and hunting success (Bothma *et al.* 1997). Of the carnivore families, the Felidae is the family that is most specialised for the capture of vertebrate prey. However, felids prey selectively on prey animals whose size is commensurate with their own body size (Kruuk 1986).

Due to the sandy nature of the substrate in the Kgalagadi Transfrontier Park it was possible to use the spoor-tracking methods as described by Eloff (1984), Bothma & Le Riche (1984) and Stander *et al.* (1997) to study the hunting behaviour of the caracal in the Kgalagadi Transfrontier Park, and to investigate the hunting success achieved by caracals in this semi-arid environment. Different authors have variously described how a hunt consists of several component behaviours. Kruuk (1972) suggests that all predator hunts are comprised of a search and an approach, followed by the immobilisation and eating of the prey animal. Mills (1990) suggests that a hunt is any interaction between a predator and a potential prey, where the predator moves towards the prey at an increased speed, in the absence of any carrion. Schaller (1972) and Bothma & Le Riche (1984) suggest that hunts by large felids consist of at least a combination of any of three primary hunting behaviours: a stalk, a chase and a kill. Caro (1994) extended this list of behaviours to include, trotting, crouching and rushing. According to Estes (1995) all cats have the same basic hunting motivation, namely to capture, kill and eat its prey.

To investigate the hunting behaviour of caracals in the Kgalagadi Transfrontier Park the following three hypotheses were tested here:

1. Caracals display a variable hunting technique.
2. Larger prey items are hunted more vigorously than smaller ones.
3. There is an ideal sequence of behaviours that is most likely to result in a successful hunt.

STUDY AREA

This study was done in an area along the Namibian border near Mata-Mata in the southwestern portion of the Kgalagadi Transfrontier Park. For logistic reasons it was decided to confine the research to an area that extended 60 km north from the Mata-Mata rest camp along the Namibian border (20° 00' E longitude) to approximately 20 km into the interior of the Kgalagadi Transfrontier Park.

The Kalahari Gemsbok National Park was proclaimed in 1931, but it only became a reality in 1935 when a number of farms along the southern bank of the Aoub River were acquired. Today, the Park exists in much the same ecological state as it was then (Van Wyk & Le Riche 1984). An agreement to formally combine the Kalahari Gemsbok National Park (South Africa) with the bordering Gemsbok National Park (Botswana) to form the Kgalagadi Transfrontier Park was signed by representatives of the governments of South Africa and Botswana in 1999. This agreement was ratified at an amalgamation ceremony that was held on the 12 May 2000 (Donaldson 2000).

The Mata-Mata area lies in the Shrubby Kalahari Dune Bushveld of the Savanna Biome (Low & Rebelo 1996). This area is an arid savanna with temperatures varying from –10° C to 45° C in the shade with an annual mean rainfall of 153.47 mm occurring mainly in the hot season. The landscape is one of undulating dunes with sparse vegetation at altitudes varying from 1000 to 1100 m above sea level (Low & Rebelo 1996).

The vegetation is characterised by the trees *Acacia erioloba*, *Acacia haematoxylon* and *Boscia albitrunca*, a shrub layer of *Grewia retinervis* and *Rhus tenuinervis,* and a well-developed grass layer consisting mainly of *Stipagrostis amabilis*, *Eragrostis lehmanniana, Aristida meridionalis, Schmidtia kalihariensis* and *Centropodia glauca* (Low & Rebelo 1996). There is little variation in the soil forms because the area is predominantly covered by aeolian sand overlying calcrete (Low & Rebelo 1996).

The Kgalagadi Transfrontier Park forms the southern part of the greater Kalahari ecosystem. Because of the arid nature of the area, many of the plants there are ephemeral. After sufficient rain, these plants germinate quickly to complete their life cycle in a short time (Eloff 1984).

Because of the harshness of the environment, the southern Kalahari is an area that is only sparsely inhabited by humans. This above any other factor contributes to the uniqueness of the area, and it enhances the value of the area for field research in wildlife management and conservation.

METHODS

Field data collection

The spoor-tracking method as described by Eloff (1984), Bothma & Le Riche (1984) and Stander *et al.* (1997) was used. An experienced Kalahari San tracker was employed to identify and interpret the caracal spoor on a step-by-step basis. All behavioural patterns observed were recorded, and from these observations the data relating to hunting behaviour were extracted. Due to the variation in the compaction of the sand, the small size of a caracal and, hence, the variable clarity of the spoor, caracals could seldom be tracked for an entire 24-hour activity period. The data presented here are therefore random observations of the behaviour of several caracals that were tracked for variable distances and intervals from June 2000 to August 2002.

A division of hunts simply into the components of a stalk, chase and kill (Schaller 1972) was too coarse to describe the hunting behaviour of caracals fully. Therefore, it was decided to expand these behavioural components to include a crouch, a take-off, and a pounce. A hunt was therefore recorded when the tracker indicated any one of the following behaviours: a stalk, a crouch, a take-off, a chase, a pounce and a kill. Hunting success was indicated by clear evidence that the prey animal had been killed. This evidence was usually in the form of a carcass, visceral remains, hair, feathers or blood. In the absence of such evidence, a hunt was considered to have been unsuccessful. However, this might underestimate the hunting success of caracals because in some cases caracals are known to consume small prey entirely without leaving any visible evidence of a kill (Stuart & Hickman 1991). This is also known to happen in other small cats like the serval *Leptailurus serval* (Geertsema 1985).

Schaller (1972) defined minimum distances for each of the components of hunting behaviour. However, he determined these distances for lions *Panthera leo* and consequently they are too long to be directly applicable to the caracal. The following definition of a stalk and a chase was therefore used in the present study: a chase was any determined rush of 1 m or more towards a potential prey animal, while a stalk was any approach towards a potential prey item in a stalking posture for a distance ≥ 1 m. A take-off happens when a caracal begins to chase a potential prey item, and it is the transitional stage between a stationary or slow-moving activity to a full chase. This behaviour could be initiated from a crouched position, or from a stationary (standing) one, or whilst walking. However, it involves a discernible rapid acceleration towards a potential prey item. A pounce is a leap towards a prey animal. It occurs either from a stationary or a crouched position while walking about normally or when chasing prey. A hunt is defined as any response of a caracal to a potential prey animal (Bothma & Le Riche 1984). The distances covered whilst performing any of these behaviours, and the intended prey involved in any of these behavioural components were also recorded. The distance of a hunt as used here is the total distance over which a hunt takes place, including all the component distances involving stalking, chasing and pouncing that make up the behavioural sequence of a hunt.

The data were interpreted on a year-round and a seasonal basis. The seasonal analysis was based on a hot season from October to March, and a cold season from April to September.

Data analysis

For the purposes of analysis the prey animals of the caracals were separated into two distinct size classes, with large prey having a mean adult body mass of > 1 kg, and small prey weighing ≤ 1 kg (Table 1). In addition, those prey that left a visually faint or undetectable spoor were assumed to be small prey because the spoor of larger prey would be clearly visible and identifiable.

: The mean body mass (kg) of the prey of caracals in the Kgalagadi Transfrontier Park from June 2000 to August 2002. Source: Skinner and Smithers (1990)

Prey	Scientific name	Body mass	
		Males	Females
African wild cat	*Felis sylvestris*	4.90	3.70
Bat-eared fox	*Otocyon megalotis*	4.03	4.11
Black-backed jackal	*Canis mesomelas*	7.89	6.60
Brant's whistling rat	*Parotomys brantsii*	0.14	0.12
Cape fox	*Vulpes chama*	3.00	2.90
Ground squirrel	*Xerus inauris*	0.65	0.60
Kori bustard	*Ardeotis kori*	13.5 to 19.0	13.5 to 19.0
Scrub hare	*Lepus saxatilis*	2.20	2.60
Springhare	*Pedetes capensis*	3.13	2.83
Steenbok	*Raphicerus campestris*	10.90	11.30
Striped polecat	*Ictonyx striatus*	0.97	0.71
Yellow mongoose	*Cynictis penicillata*	0.59	0.55
Unidentifiable	~	~	~

~ no data relevant

Correspondence Analysis (SAS 1999) was used to model the sequence of hunting behaviours that was most likely to result in a kill. The behavioural components were weighted according to their ordered sequence leading up to an ultimate successful or unsuccessful hunt. For example, a hunting sequence for a successful hunt could be as follows: crouch-chase-pounce-kill. The weighting for the above sequence would then be: 16.6, 33.3 and 50.0 % for the crouch, chase and pounce components respectively. That behavioural component in this sequence that is theoretically furthest away spatially from a kill is the crouch, hence it receives the lowest weighting. Each hunting attempt was weighted independently. A kill would receive a weight of 1 and lack of success a weight of 0. Observations were weighted to represent an equal contribution of the successful and failed hunts because the successful hunts only contributed 10.1 % to the total number of hunts. Each behavioural component received its weighting independently for each hunt. The weighting was applied irrespective of whether the hunt was successful or unsuccessful.

By applying the Correspondence Analysis technique it is possible to plot the orientation of the data points relative to one another in a multi-dimensional space in an area with a restricted number of dimensions. The first three dimensions that were identified according to the Correspondence Analysis (SAS 1999) in this study, accounted for 78.0 % of the variation in the multi-dimensional space of the data (39.3, 21.2 and 17.5 % respectively), and were therefore used as an adequate representation of the data (Grimbeek pers.comm.)[1].

The weighted distances in a three-dimensional space were calculated according to the above dimensional weights between the points representing success and failure and the hunting behavioural components. These distances were then ordered, and

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the associated components of behaviour were interpreted as sequences leading up to a successful or unsuccessful hunt. The weightings positioned the behavioural components along a gradient relative to their likelihood of leading to a kill. Those components that were most likely to result in a successful hunt were positioned closest to the plotted success point, and those that were less likely to result in a success were oriented closer to the plotted unsuccessful hunting point.

RESULTS

Hunts

During the study 154 different sets of caracal tracks were followed for a total distance of 537.9 km. In all, 327 hunts were recorded at a rate of one hunt per 1.6 km. Seasonally, the hunting rate in the hot season was one hunt per 1.4 km, and one hunt per 1.9 km in the cold season. The hunting success rate was one kill per 16.3 km moved for the entire year. Seasonally it was 14.9 km per kill in the hot season and 17.7 km per kill in the cold season.

Of the 327 observed hunts, 166 and 161 hunts were recorded in the hot and cold seasons respectively. On 33 occasions the caracals killed the prey that they were hunting, giving an overall hunting success rate of 10.1 %. During the hot season the caracals killed 16 prey at a success rate of 9.6 % and in the cold season 17 prey at a success rate of 10.6 %. There is no significant difference in the frequency with which caracals hunt large or small prey between the hot and cold seasons (χ^2: 1.73, df: 1, $P > 0.05$).

The hunting success rates shows that caracals are more successful when hunting large than small prey. There is a significantly higher success rate for large than for small prey ($\chi^2 = 8.99$, df = 1, $P < 0.05$). When calculated for the entire year, 18.0 %

of the hunted large prey were killed, but only 7.5 % of the small prey. On a seasonal basis, 26.5 and 17.1 % of the large prey hunted were killed in the cold and hot seasons respectively. Of the small prey 7.5 and 7.4 % of the hunts were successful in the hot and cold seasons respectively.

The mean year-round distance over which all hunts took place was 18.0 m (SE = 2.2 m; range = 1 – 379 m). There is no significant difference between the mean distances over which caracals hunted in the hot and cold seasons (t = 0.9, df = 332, *P* > 0.05). On a seasonal basis the mean distance over which hunts took place was 22.5 m (SE = 3.1 m; range = 1.5 – 318 m) in the cold season, and 18.7 m (SE = 1.4 m; range = 1 – 379 m) in the hot season. There was no difference in the mean distances for successful and unsuccessful hunts on a year-round basis or in the cold season. However, in the hot season there was a significant difference between the distances of successful and unsuccessful hunts. In the hot season, there was a significant difference between the distances of caracals' successful and unsuccessful hunts. There is not a significant linear relationship between the success of a hunt and the distance over which a hunt took place (logistic regression, df = 1, *P* = 0.87) (Table 2).

On a year-round basis there is a significant difference between the hunting distances for large and small prey (t = 4.92, df = 71, *P* < 0.05). The mean hunting distance for large prey was 54.2 m (SE = 8.6 m; range = 1 – 379 m), while that for small prey was 11.6 m (SE = 0.8 m; range = 1 – 71 m). This is also true on a seasonal basis: hot season: t = 2.99, df = 30, *P* ≤ 0.05 and cold season: t = 3.91, df = 40, *P* < 0.05. The mean hunting distances for large and small prey in the cold season was 54.1 m (SE = 10.7 m; range = 8 – 318 m) and 12.1 m (SE = 1.2 m, range = 1 – 54 m) respectively. In the hot season it was 54.3 m (SE = 14.3 m; range = 1 – 379 m) and 11.2 m (SE = 1.1 m; range = 1 – 71 m) respectively.

Table 2: *The mean hunting distances (m) of caracals for various components of hunting behaviour during successful and unsuccessful hunts in the Kgalagadi Transfrontier Park from June 2000 to August 2003*

Prey	Component	Period	Mean distance		Standard error of the mean		t-value	*P*-value	Degrees of freedom
			Successful	Unsuccessful	Successful	Unsuccessful			
All	Chase	Year-round	14.70	22.50	5.1	2.50	1.63	0.11	46
Large			25.00	62.50	7.8	10.70	2.83	0.0070 *	52
Small			5.80	12.70	1.2	0.80	4.96	<0.0001 *	26
All		Hot season	5.70	21.10	1.1	3.50	4.50	<0.0001 *	158
Large			6.60	63.00	1.8	16.40	3.42	0.0020 *	25
Small			5.30	12.50	1.3	1.10	4.28	0.0002 *	25
All		Cold season	25.20	24.00	16.1	3.70	0.14	0.89	16
Large			34.30	62.00	10.6	14.00	1.58	0.12	30
Small			7.10	12.90	2.6	1.10	-2.00	0.11	4
All	Pounce	Year-round	1.60	1.80	0.2	0.10	0.75	0.45	54
Large			2.30	1.80	0.2	0.50	1.23	0.27	5
Small			1.50	1.70	0.2	0.10	1.04	0.31	32
All		Hot season	1.70	1.80	0.2	0.10	0.58	0.57	28
Large			2.50	1.80	0.4	0.40	1.05	0.4	2
Small			1.60	1.70	0.2	0.10	0.55	0.59	17
All		Cold season	1.60	1.50	0.3	0.30	0.21	0.83	15
Large			~	~	~	~	~	~	~
Small			1.30	1.60	0.3	0.40	0.66	0.52	11
All	Stalk	Year-round	17.90	5.20	8.8	1.60	-1.43	0.2	6
Large			20.00	7.45	3.9	8.30	-0.90	0.43	3
Small			15.00	4.16	12.2	1.90	-0.89	0.47	2
All		Hot season	4.30	3.00	0	1.10	1.40	0.27	25
Large			~	~	~	~	~	~	~
Small			3.00	2.26	0	0.30	-2.72	0.0100 *	18
All		Cold season	23.80	7.50	11.5	5.40	1.33	0.24	5
Large			20.00	3.50	13.8	0.60	-1.20	0.32	3
Small									

Table 2: *Continued*

Prey	Component	Time-frame	Mean distance		Standard error of the mean		t-value	*P*-value	Degrees of freedom
			Successful	Unsuccessful	Successful	Unsuccessful			
All	Hunt	Year-round	16.38	20.98	3.70	2.40	1.08	0.29	65
Large			23.90	63.70	6.50	10.90	-3.16	0.0020 *	69
Small			8.90	11.80	2.20	0.90	-1.24	0.23	21
All		Hot season	7.26	19.75	1.00	3.30	-3.76	0.0002 *	175
Large			6.80	63.40	1.80	16.50	-3.40	0.0002 *	26
Small			7.50	11.50	1.50	1.20	-2.17	0.0390 *	25
All		Cold season	23.60	22.40	6.30	3.40	-0.17	0.86	32
Large			31.00	64.00	8.20	14.20	-1.98	0.055	38
Small			10.90	12.20	5.10	1.30	-0.25	0.81	7

* Significant difference within rows
~ Insufficient data

On a year-round basis there was no significant difference between the mean distances of successful and unsuccessful hunts for all prey. When the data for large and small prey are separated, unsuccessful hunts for large prey take place over significantly longer distances than successful ones. However, hunts not ending in a kill are not significantly longer than those ending in a kill when hunting small prey on a year-round basis. In the hot season, unsuccessful hunts take place over significantly longer distances than successful ones. This is true for all prey combined and for both large and small prey independently. In the cold season, the hunting distances for successful and unsuccessful hunts were similar. This is true for hunts for all prey combined and for hunts for large and small prey independently (Table 2).

On a year-round basis, both successful and unsuccessful hunts for large prey take place over significantly longer distances than hunts for small prey. There was no significant difference between the distances over which successful hunts for either large or small prey took place in either the hot or cold season. However, in both the hot and the cold seasons, unsuccessful hunts for large prey took place over significantly longer distances than unsuccessful ones for small prey (Table 3).

The hunting technique of the caracals in the Kgalagadi Transfrontier Park is highly varied. In the present study, 43 different behavioural sequences were identified as part of hunting. The traditional stalk, chase and kill sequence that has been described by Schaller (1972), was only observed once during this study (Table 4). The most frequently used hunting tactic involved a sequence of behaviours that began with a crouch, to be followed by a powerful take-off that culminated in a chase. Of the 327 observed hunts, 146 (44.6 %) began with this behavioural sequence. Another 73 (22.3 %) hunts started with a take-off followed by a chase. Only 31 (9.5 %) of the hunting sequences began with a stalk and 11 (3.4%) began and ended with

Table 3: *The mean hunting distances (m), comparing the distances of caracals hunting large and small prey in the Kgalagadi Transfrontier Park from June 2000 to August 2002.*

Season	Hunting success	Mean		Standard error		t-value	*P*-value	Degrees of freedom
		Large prey	Small prey	Large prey	Small prey			
Year-round	Yes	23.90	8.90	6.50	2.20	2.20	0.0400	20.00
Year-round	No	63.70	11.80	10.90	0.86	4.80	< 0.0001	54.00
Hot season	Yes	6.80	7.50	1.80	1.50	-0.31	0.7600	9.00
Hot season	No	63.40	11.50	16.50	1.20	3.14	0.0040	25.00
Cold season	Yes	30.90	10.90	8.20	5.10	2.06	0.0550	16.00
Cold season	No	64.00	12.20	14.20	1.30	3.56	0.0010	27.00

a pounce with no other preliminary behaviour. Five (1.5 %) of the hunts began with a crouch, followed directly by a pounce and four (1.2 %) of the hunts began with a caracal crawling to begin the hunting sequence (Table 4).

The number of behavioural components that form a hunt is highly variable. A hunt could also consist of only one behavioural component. The highest number of consecutive distinct behavioural components that comprised a single hunt was 11. The most successful strategy seems to be a sequence of five behavioural components starting with a stalk, followed by a crouch, a take-off, a chase and a pounce. This sequence had a success rate of 66.7 %. A sequence of four behavioural components starting with a crouch, followed by a take-off, a chase and a pounce resulted in 10 kills in 19 attempts at a success rate of 52.6 %. On three occasions a single repetition of a distinct behavioural sequence resulted in a kill. In these cases no success ratio was calculated because of the inadequate sample sizes involved. The least successful strategy involved three behavioural components that had a success rate of 2.2 % (Table 4).

Hypothetically, the behavioural sequence that is most likely to end in a kill is the crawl - stalk - crouch - take-off - chase - pounce sequence. However, no behaviour sequence starting with a crawl was successful. When plotted along a gradient from failure to success, the crawl and stalk components are orientated closer to failure on a gradient of success. The crouch, take-off and chase components, however, are orientated more centrally between success and failure on the gradient, while the pounce is orientated closest to the kill because it usually preceded the kill immediately. The behavioural components that are most closely associated with one another are the take-off and chase. The crouch behaviour is also associated with the take-off and chase, but not as closely related as are the take-off and chase with one another.

e 4: *Hunting sequences of caracals in the Kgalagadi Transfrontier Park from June 2000 to August 2002.*

Number of components	Number of repetitions	Sequence of components*	Number of successful hunts	Number of unsuccessful hunts	Percentage hunting success
1	9	6	3	6	33.3
1	29	5	3	26	10.3
1	6	2	1	5	16.7
1	7	3	0	7	0.0
1	5	4	1	4	20.0
2	1	6-6	1	0	100.0
2	1	6-5	1	0	100.0
2	1	5-6	1	0	100.0
2	4	2-6	3	1	75.0
2	1	2-5	0	1	0.0
2	1	2-3	0	1	0.0
2	4	3-6	0	4	0.0
2	1	3-3	0	1	0.0
2	7	3-4	0	7	0.0
2	1	3-1	0	1	0.0
2	1	4-6	0	1	0.0
2	61	4-5	4	57	6.6
2	1	1-1	0	1	0.0
3	1	2-4-6	0	1	0.0
3	1	2-4-5	0	1	0.0
3	126	3-4-5	1	125	0.8
3	1	3-4-6	0	1	0.0
3	1	3-1-3	0	1	0.0
3	5	4-5-6	2	3	40.0
3	1	4-5-5	0	1	0.0
3	1	1-4-5	0	1	0.0
4	1	2-3-4-5	0	1	0.0
4	8	2-3-4-5	0	8	0.0
4	1	3-6-4-5	0	1	0.0
4	2	3-2-4-5	0	2	0.0
4	19	3-4-5-6	10	9	52.6
4	1	3-4-5-4	0	1	0.0
4	1	4-5-4-5	0	1	0.0
5	3	2-3-4-5-6	2	1	66.7
5	1	3-4-5-4-5	0	1	0.0
5	4	4-5-3-4-5	0	4	0.0
6	1	2-3-3-3-4-5	0	1	0.0
6	1	3-3-4-5-4-5	0	1	0.0
6	1	4-5-2-3-4-5	0	1	0.0
7	1	2-2-2-3-4-5-6	0	1	0.0
7	1	1-1-3-4-5-4-5	0	1	0.0
8	1	1-2-2-2-3-4-5-6	0	1	0.0
10	1	3-4-5-6-3-4-5-3-4-5	0	1	0.0
11	1	2-3-4-5-4-5-4-5-3-4-5	0	1	0.0

*1: crawl 2: stalk 3: crouch 4: take-off 5: chase 6: pounce

Stalks

A stalk is a behavioural component that is found in a number of hunting sequences. On 39 occasions stalking was observed in relation to hunting. During a specific hunt, a caracal can stalk more than once, and on two occasions, stalking occurred three times during a single hunt. In all the other instances, stalking was recorded only once in a specific hunting sequence. Stalking was a component of seven (21.2 %) of 33 hunts that ended in a kill. Moreover, successful hunts never included more than one stalking sequence. Of the 39 stalks that were recorded, 13 were recorded in the cold season and 26 in the hot season. Stalking took place in 34 (10.4 %) of all 327 hunts (Table 4).

Caracals stalk their prey over variable distances. They also stalk them over significantly longer distances in the cold season than in the hot one (Fischer's exact test = 0.023, df = 1, $P \leq 0.05$). In the hot season the longest stalking distance was 27 m, but in the cold season it was 61 m. The mean stalking distance in the cold season was 12.9 m (SE = 5.5 m; range = 3 – 61 m) and 4.2 m (SE = 1.1 m; range = 1 – 27 m) in the hot season. Caracals stalk small prey significantly more often than large prey ($\chi^2 = 5.56$, df = 1, $P < 0.05$) (Table 5).

Caracals do not stalk large prey over significantly longer distances than small prey or vice versa, either on a year-round (t = 1.21, df = 22, $P > 0.05$) or a seasonal basis (hot season: t = 2.13, df = 6, $P > 0.05$; cold season: t = -0.24, df = 13, $P > 0.05$) (Table 5).

Chase

The chase is an integral component of most hunts, and during the present study 293 chases were recorded. Although chases were not recorded in every hunting

Table 5: *The mean ± standard error of the stalking distances (m) of caracals when hunting different types of prey in the Kgalagadi Transfrontier Park from June 2000 to August 2002*

Prey	Season	Stalks ending in kills			Stalks not ending in kills			All stalks			
		Number	Mean	Standard error	Number	Mean	Standard error	Maximum distance	Minimum distance	Mean	Standard error
Bat-eared fox	Cold	1	10.0	0.0	1	2.5	0.0	10	2.5	6.3	3.8
	Hot	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0.0
Brant's whistling rat	Cold	0	0.0	0.0	1	4.0	0.0	4	4.0	4.0	0.0
	Hot	2	3.0	0.0	5	2.5	0.8	5	1.0	4.3	2.2
Cape fox	Cold	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0.0
	Hot	0	0.0	0.0	3	18.0	4.5	27	13.0	18.0	4.5
Kori bustard	Cold	2	31.0	29.1	0	0.0	0.0	61	3.0	31.0	29.1
	Hot	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0.0
Scrub hare	Cold	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0.0
	Hot	0	0.0	0.0	1	2.0	0.0	2	2.0	2.0	0.0
Springhare	Cold	0	0.0	0.0	3	3.8	0.6	5	3.0	3.8	0.6
	Hot	0	0.0	0.0	2	2.5	0.5	3	2.0	2.5	0.5
Steenbok	Cold	1	6.0	0.0	0	0.0	0.0	6	6.0	6.0	0.0
	Hot	0	0.0	0.0	1	7.0	0.0	7	7.0	7.0	0.0
Striped polecat	Cold	1	39.0	0.0	0	0.0	0.0	39	39.0	39.0	0.0
	Hot	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0.0
Unidentifiable	Cold	0	0.0	0.0	3	19.0	15.8	50	1.0	19.0	15.8
	Hot	0	0.0	0.0	14	2.2	0.2	3	1.0	2.2	0.2
All small prey	Hot	2	3.0	0.0	19	2.3	0.3	5	1.0	2.3	0.2
	Cold	1	39.0	0.0	6	10.2	8.2	61	2.5	12.9	7.6
	Both	3	15.0	12.2	25	4.2	1.9	61	1.0	5.3	2.1
All large prey	Hot	0	0.0	0.0	7	9.7	3.5	27	2.0	9.7	3.5
	Cold	4	20.0	13.8	4	3.5	0.6	61	2.5	11.8	7.2
	Both	4	20.0	13.8	11	7.5	2.4	61	2.0	10.8	3.9
All prey	Cold	5	19.1	11.5	8	9.4	5.9	61	3.0	14.9	5.7
	Hot	2	3.0	0.0	26	4.3	1.1	27	1.0	4.2	1.0
	Both	7	17.9	8.8	34	5.2	1.6	61	1.0	7.2	2.0

sequence, at least one chase was recorded in 270 (82.6 %) of the 327 hunts. In 10 (3.1 %) of 327 hunts more than one chase was recorded per hunt. The distances over which caracals chased their prey varied greatly, and there was no significant seasonal difference in these distances (t = -0.94, df = 286, $P > 0.05$). The mean chase distances for large and small prey and for individual prey species appear in Table 6. Of the 293 chases, 134 (45.7 %) were recorded in the cold season. There was no significant preference for chasing small prey rather than large prey ($\chi^2 = 2.9$, df = 1, $P > 0.05$).

Caracals chased large prey over significantly longer distances than small ones, both year- round (t = 4.83, df = 66, $P < 0.05$) and seasonally (hot season: t = 2.97, df = 28, $P < 0.05$; cold season: t = 3.80, df = 37, $P < 0.05$). The mean chase distances reflect this trend (Table 6).

On a year-round basis the distances of chases ending in kills and those that did not do so for the combined prey data set were similar. However, when the prey data are divided into small and large prey, chases ending in kills take place over significantly shorter distances than unsuccessful ones. In the cold season there is no significant difference between the distances of successful and unsuccessful chases, but in the hot season the chases ending in kills are significantly shorter than unsuccessful ones (Table 2).

Pouncing

During the present study pouncing was observed on 58 occasions occurring in 55 (16.8 %) of the observed hunts. On two occasions more than one pounce was recorded in a single hunt. Caracals pounced in similar frequencies when trying to catch small and large prey, doing so in 15.9 % of their attempts to catch small prey

Table 6: *The chase distances (m) of caracals when hunting different types of prey in the Kgalagadi Transfrontier Park from June 2000 to August 2002*

Prey	Season	All chases				Chases ending in kills			Chases not ending in kills		
		Mean	Standard error	Maximum	Minimum	Number	Mean	Standard error	Number	Mean	Standard error
African wild cat	Hot	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Cold	35.00	32.50	38.00	32.00	1.00	32.00	0.00	1.00	38.00	0.00
Bat-eared fox	Hot	24.50	17.80	56.00	5.50	1.00	5.50	0.00	2.00	34.00	22.20
	Cold	47.50	18.90	97.00	12.00	0.00	0.00	0.00	4.00	47.50	18.90
Black-backed jackal	Hot	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Cold	302.00	0.00	302.00	302.00	0.00	0.00	0.00	1.00	302.00	0.00
Brant's whistling rat	Hot	7.00	1.20	18.00	1.00	5.00	7.60	1.60	12.00	6.75	1.50
	Cold	9.83	3.20	23.00	3.00	2.00	11.50	1.50	4.00	9.00	4.80
Cape fox	Hot	82.63	45.60	379.00	4.00	2.00	8.50	3.60	6.00	107.33	58.70
	Cold	318.00	0.00	318.00	318.00	0.00	0.00	0.00	1.00	318.00	0.00
Ground squirrel	Hot	22.50	18.70	41.00	4.00	0.00	0.00	0.00	2.00	22.50	18.70
	Cold	15.00	10.10	25.00	5.00	0.00	0.00	0.00	2.00	15.00	10.10
Scrub hare	Hot	63.00	24.80	125.00	16.00	0.00	0.00	0.00	4.00	63.00	24.80
	Cold	60.00	15.00	122.00	0.50	0.00	0.00	0.00	8.00	60.00	14.96
Springhare	Hot	51.50	19.20	181.00	4.00	1.00	4.00	0.00	9.00	56.78	20.90
	Cold	43.13	9.50	111.00	12.00	1.00	107.00	0.00	11.00	37.32	8.50
Steenbok	Hot	22.80	18.70	64.00	9.00	0.00	0.00	0.00	3.00	22.75	18.70
	Cold	17.50	2.50	20.00	15.00	0.00	0.00	0.00	2.00	17.50	2.50
Unidetifiable	Hot	12.53	1.10	52.00	1.00	4.00	3.50	1.90	101.00	12.89	1.21
	Cold	12.93	1.10	50.00	2.00	2.00	2.70	0.80	94.00	13.14	1.10
Yellow mongoose	Hot	1.00	0.00	1.00	1.00	1.00	0.00	0.00	0.00	0.00	0.00
	Cold	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
All small prey	Hot	19.76	3.40	59.00	1.00	10.00	5.30	1.30	121.00	12.48	1.10
	Cold	12.67	1.00	50.00	2.00	4.00	7.13	2.60	99.00	12.89	1.10
	Both	12.30	0.70	59.00	1.00	14.00	5.80	1.20	220.00	12.60	0.80
All large prey	Hot	55.22	14.50	379.00	4.00	4.00	6.63	1.80	25.00	63.00	16.40
	Cold	56.01	11.30	318.00	8.50	8.00	7.13	1.90	29.00	62.02	14.00
	Both	55.70	9.00	379.00	4.00	12.00	25.00	7.80	54.00	62.50	10.70
All prey	Hot	19.78	3.20	379.00	1.00	14.00	5.68	1.10	133.00	21.13	3.50
	Cold	24.13	3.60	318.00	2.00	3.00	25.21	16.10	127.00	24.02	3.70
	Both	21.81	2.40	379.00	1.00	17.00	22.48	10.00	260.00	14.69	1.30

and 18.9 % of those to catch large prey. In the hot season 37 pounces were recorded as opposed to 21 in the cold season (Table 7).

Pouncing distances did not differ seasonally ($t = 0.84$, $df = 32$, $P > 0.05$) nor did they differ when hunting large or small prey year-round ($t = 1.31$, $df = 20$, $P > 0.05$) or seasonally (hot season: $t = 1.33$, $df = 7$, $P > 0.05$; cold season: $t = 0.96$, $df = 14$, $P > 0.05$) (Table 7).

Kills

Of the 327 hunts observed, 33 (10.1 %) ended in a kill. However, the method of killing could only be identified in those cases where the prey remains were found. It was assumed that for smaller prey, a throat-bite in conjunction with claw-raking was used, as was described by Leyhausen (1979). The only visual evidence that a small prey item had been killed was the visceral remains (n = 19 kills) that the caracals removed before eating the prey. In one case a caracal consumed a Brant's whistling rat *Parotomys brantsii* completely without evicerating it, and its identity was only confirmed because the caracal regurgitated the entire rat 10 m from where it had killed it. Caracals therefore do not always eviscerate smaller prey. In two cases where a caracal killed an African wild cat *Felis sylvestris*, two sets of teeth puncture marks were visible on each carcass, one set at the nape of the neck and one on the throat. The same killing method was used by caracals when killing two bat-eared foxes *Otocyon megalotis*, a scrub hare *Lepus saxatilis*, two springhares *Pedetes capensis*, a yellow mongoose *Cynictis penicillata*, two striped polecats *Ictonyx striatus*, a steenbok *Raphicerus campestris* and two Cape foxes *Vulpes chama*. On one occasion a caracal killed a Cape fox by biting it on the head, penetrating the skull with its canines. A caracal also killed two kori bustards *Ardeotis kori* by severing the spinal cord of each with a nape bite.

Table 7: *The distances (m) from which that caracals pounced on prey in the Kgalagadi Transfrontier Park from June 2000 to August 2002.*

Prey animal	Season	Number of pounces			Distance of all pounces				Distance of pounces ending in kills			
		All	Ending in Kills	Not ending in kills	Maximum	Minimum	Mean	Standard error	Maximum	Minimum	Mean	Standard error
African wild cat	Hot	0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Cold	1	1	0	2.0	2.0	2.0	0.0	2.0	2.0	0.0	0.0
Bat-eared fox	Hot	1	1	0	2.0	2.0	2.0	0.0	2.0	2.0	0.0	0.0
	Cold	1	1	0	1.0	1.0	1.0	0.0	1.0	1.0	0.0	0.0
Brant's whistling rat	Hot	6	4	2	2.0	1.0	1.5	0.4	2.0	1.0	1.1	0.3
	Cold	3	2	1	2.0	1.0	1.7	0.4	2.0	1.5	1.8	0.2
Cape fox	Hot	2	1	1	2.0	2.0	2.0	0.0	2.0	2.0	2.0	0.0
	Cold	0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Kori bustard	Hot	0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Cold	2	2	0	2.5	2.0	2.3	0.3	2.5	2.0	2.3	0.3
Scrub hare	Hot	2	1	1	3.0	1.0	2.0	1.4	1.0	1.0	1.0	0.0
	Cold	0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Springhare	Hot	1	1	0	2.5	2.5	2.5	0.0	2.5	2.5	2.5	0.0
	Cold	2	1	1	3.0	2.0	2.5	0.7	3.0	3.0	3.0	0.0
Steenbok	Hot	0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Cold	1	1	0	2.0	2.0	2.0	0.0	2.0	2.0	2.0	0.0
Striped polecat	Hot	0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Cold	2	2	0	2.0	1.0	1.5	0.5	2.0	1.0	1.5	0.5
Unidentifiable	Hot	23	4	19	3.0	1.0	1.7	0.1	2.0	1.0	1.4	0.3
	Cold	8	2	6	3.0	1.0	1.3	0.4	1.0	1.0	1.0	0.0
Yellow mongoose	Hot	2	2	0	3.0	2.0	2.5	0.5	3.0	2.0	2.5	0.5
	Cold	0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
All small prey	Hot	31	10	21	3.0	1.0	1.7	0.1	3.0	1.0	1.6	0.2
	Cold	12	6	7	3.0	1.0	1.4	0.3	2.0	1.0	1.5	0.2
	Both	44	16	28	3.0	1.0	1.6	0.1	3.0	1.0	1.5	0.2
All large prey	Hot	6	4	2	3.0	1.0	2.1	0.3	3.0	2.0	2.5	0.4
	Cold	8	7	1	3.0	1.0	1.8	0.3	2.5	1.0	1.9	0.2
	Both	14	11	3	3.0	1.0	1.9	0.2	3.0	1.0	1.8	0.2
All prey	Hot	37	14	23	3.0	1.0	1.8	0.1	3.0	1.0	1.7	0.2
	Cold	19	8	11	3.0	1.0	1.7	0.2	3.0	1.0	1.8	0.2
	Both	56	26	30	3.0	1.0	1.7	0.1	3.0	1.0	1.7	0.1

Table 7: *Continued*

Prey animal	Season	Number of pounces			Distance of pounces not ending in kills			
		All	Ending in Kills	Not ending in kills	Maximum	Minimum	Mean	Standard error
African wild cat	Hot	0	0	0	0.0	0.0	0.0	0.0
	Cold	1	1	0	0.0	0.0	0.0	0.0
Bat-eared fox	Hot	1	1	0	0.0	0.0	0.0	0.0
	Cold	1	1	0	0.0	0.0	0.0	0.0
Brants whistling rat	Hot	6	4	2	2.0	1.5	1.8	0.3
	Cold	3	2	1	2.0	2.0	2.0	0.0
Cape fox	Hot	2	1	1	2.0	2.0	2.0	0.0
	Cold	0	0	0	0.0	0.0	0.0	0.0
Kori bustard	Hot	0	0	0	0.0	0.0	0.0	0.0
	Cold	2	2	0	0.0	0.0	0.0	0.0
Scrub hare	Hot	2	1	1	3.0	3.0	3.0	0.0
	Cold	0	0	0	0.0	0.0	0.0	0.0
Springhare	Hot	1	1	0	0.0	0.0	0.0	0.0
	Cold	2	1	1	2.0	2.0	2.0	0.0
Steenbok	Hot	0	0	0	0.0	0.0	0.0	0.0
	Cold	1	1	0	0.0	0.0	0.0	0.0
Striped polecat	Hot	0	0	0	0.0	0.0	0.0	0.0
	Cold	2	2	0	0.0	0.0	0.0	0.0
Unidentifiable	Hot	23	4	19	3.0	1.0	1.7	0.2
	Cold	8	2	6	3.0	1.0	2.0	0.4
Yellow mongoose	Hot	2	2	0	0.0	0.0	0.0	0.0
	Cold	0	0	0	0.0	0.0	0.0	0.0
All small prey	Hot	31	10	21	3.0	1.0	1.7	0.1
	Cold	12	6	7	3.0	1.0	1.8	0.3
	Both	44	16	28	3.0	1.0	1.7	0.1
All large prey	Hot	6	4	2	2.0	2.0	2.0	0.0
	Cold	8	7	1	3.0	3.0	3.0	0.0
	Both	14	11	3	3.0	1.0	2.3	0.4
All prey	Hot	37	14	23	3.0	1.0	1.8	0.1
	Cold	19	8	11	3.0	1.0	1.9	0.2
	Both	56	26	30	3.0	1.0	1.8	0.1

Caracals often cached the carcasses of large prey. After the caracals had killed the kori bustards, bat-eared foxes, scrub hare and the steenbok, the prey were cached under a dense bush. In all these cases the caracal came back to where it had cached its kill to feed even after it had been disturbed, by the tracking.

DISCUSSION

Hunting variation

All hunts consist of a sequence of behavioural components that aim at a kill. These behavioural components do not necessarily follow a specific sequence. Traditionally, hunts by large wild cats are regarded to consist of either a combination of a stalk, a chase and a kill (Schaller 1972, Eltringham 1979, Bothma & Le Riche 1984). Caro (1994) extended this behavioural combination in cheetahs *Acinonyx jubatus* to include trotting, crouching and rushing. Because of the further inclusion of pouncing, take-off and crouching in the combination of behavioural components of hunting used here, the variability of the hunting sequences is high when compared with other types of cat. A caracal's hunting sequence does not necessarily consist of the repetition of any one behavioural sequence. The potential for variation of a behavioural sequence that could consist of six different behavioural components and any number of repetitions of these components, suggests a huge potential for adaptation of the hunting strategy of a caracal to specific situations. This potential supports the conclusion that caracals also use an adaptable hunting strategy, as was found by Schaller (1972) and Mc Bride (1990) for lions, and for leopards *Panthera pardus* by Bothma & Le Riche (1989). Mc Bride (1990) goes so far as to suggest that the hunting tactics of lions are so varied that they defy classification.

Moolman (1986) identified two distinct hunting strategies that were displayed by captive caracals in the Mountain Zebra National Park. The most frequently observed strategy involved the caracal stalking the prey to within 5 m, and then chasing it.

Grobler (1981) observed the same stalking technique in a captive caracal. The second, and less frequently observed, hunting strategy involved the caracal lying hidden in ambush of the prey, and then chasing it down from behind. In the Kgalagadi Transfrontier Park, the most frequently applied hunting strategy was an adaptation of the ambushing technique that was described above, and 44.5 % of the hunts that were recorded involved a caracal waiting in a crouched position in ambush and then chasing its prey. The stalking strategy was used less frequently than was reported by Moolman (1986).

Unlike the hunting behaviour of lions as reported by Schaller (1972) and Elliot *et al.* (1976), stalking does not appear to be the most important component of the hunting strategy of caracals in the Kgalagadi Transfrontier Park. Stalking was only used in 10.1 % of the observed hunts, and of these only 21.2 % ended in kills. This success rate is even less than that reported by Bothma & Le Riche (1984) for male leopards and for females without cubs. There does not seem to be any difference between the distances stalked when hunting large or small prey, but there is a trend towards stalking all prey over longer distances in the cold season when compared with the hot season. This may be a response by caracals to optimise their chances of killing prey in times when prey availability is more limiting (Nel *et al.* 1984, Begg 2001), and when energy conservation may be more important. Caracals were never observed to stalk either specific prey or any prey size group over excessively long distances. There is therefore no evidence of caracals using optimal positioning for specific prey that are difficult to hunt in the manner that Bothma & Le Riche (1989) described for some prey of leopards.

Caracals expend proportionally more energy on failed hunts in the hot season than in the cold season (Table 2). This suggests that in the hot season there is sufficient prey available to allow caracals to expend energy on extravagantly long hunts in the hope of killing large prey. This is surprising because the hot season is a time of relatively high prey abundance in the Kgalagadi Transfrontier Park (Begg 2001). Under these conditions it was expected that caracals would abandon long hunts in the hot season because there are enough other hunting opportunities, and theoretically excessive energy expenditure should be avoided.

It appears that although the available food resource is more limiting for caracals in the cold than the hot season, the seasonal energy expended whilst chasing prey is higher in the cold than in the hot season, based on mean hunting distances (Table 2). This is not surprising because it is expected that caracals would expend more energy in attempting to kill prey in the cold than in the hot season because of the lower prey abundance. It was also expected that the higher maintenance energy requirements of a caracal in the cold season, would induce them to expend more energy on attempts at killing large prey that would provide greater energetic gains per kill, especially in the cold season.

Caracals in the Kgalagadi Transfrontier Park seem to expend considerable amounts of energy on unsuccessful hunts of large prey, especially in the hot season. This situation is similar to that found by Mills (1990) for spotted hyaenas *Crocuta crocuta* in the Kalahari. Bothma & Le Riche (1984) reported that leopards in the Kalahari chase large prey more frequently than small ones, but there is no evidence caracals doing this.

Caracals chase large prey over longer distances than small prey in both seasons, as was also observed for leopards in the Kalahari (Bothma & Le Riche 1984). This supports the optimal foraging theory that stipulates that energy expenditure in acquiring a particular type of prey should be proportional to the expected energy gained from that prey item (Begon *et al.* 1990, Smith 1990, Brewer 1994). It also indicates an adaptation in hunting behaviour when hunting large prey. The importance of the potential energetic gain from hunting large prey is highlighted further by the fact that caracals tend to chase large prey over relatively long distances before giving up the chase, especially in the hot season.

It appears that caracals often surprise their prey, in a similar manner to that described by Bothma & Le Riche (1984) for leopards and Geertsema (1985) for serval, because only 9.4 % of all chases were preceded by stalks in which caracals could be regarded to be premeditating a potential hunting opportunity.

Hunting success

Burton (1962) contended that predators are unlikely to succeed in killing more than 50.0 % of the prey animals that they chase. The results of the present study support this conclusion. The overall hunting success rate of caracals in the Kgalagadi Transfrontier Park was 10.1 %. This is considerably lower than the success rate recorded for most other predators in this area. Bothma and Le Riche (1986) found that male leopards in the Kalahari kill 18.5 % of the animals that they hunted, while females killed 21.8 % of the animals that they hunted, for a mean hunting success rate of 20.2 % for both sexes. Eloff (1984) found that lions in the Kalahari had a hunting success of 38.5 %. Mills (1990) found that spotted hyaenas hunt with a success rate that varies between types of prey, as did Bothma and Coertze (2004) for leopards in the Kalahari.

Schaller (1972) and Kruuk (1986) suggested that hunting success in lions was reliant on sufficient cover. Lions tend to be most successful in areas of dense cover where they can stalk to within a close striking distance of the prey. Bothma *et al.* (1997) suggest that the ability of a male leopard to stalk certain prey is less than that of a female because of size differences and the general lack of large cover in the southern Kalahari. This is unlikely to be the case for caracals because they are small in stature and there is sufficient vegetation of the required height to ensure that they can stalk efficiently. It is therefore suspected that the low hunting success of caracals in the Kgalagadi Transfrontier Park is due to factors other than a lack of cover.

Caracals are more successful when hunting large than small prey, killing 20.2 % of the large prey that they attempt to hunt. This rate is similar to the hunting success of leopards in the same region (Bothma & Le Riche 1984). The low hunting success of caracals when hunting small prey may in part be due to the strict protocol that was used in the present study for the verification of a kill. In areas such as the Kgalagadi Transfrontier Park, where there is a low abundance of prey, the hunting efficiency of a leopard is influenced by the availability of its prey (Bothma & Le Riche 1986). It was expected that a similar hunting success for small prey would be recorded as that for other predators that utilise small mammals as a food resource elsewhere. However, Geertsema (1985) found that servals in the prey-rich Ngorongoro Crater in Tanzania killed 48.6 % of the small mammals that they hunted. It is probable that prey distribution and abundance limit the hunting success of caracals in the Kalahari region. This would require the caracals in the Kgalagadi Transfrontier Park to hunt more often than in prey-rich environments to satisfy their energy requirements. In the semi–arid southern Kalahari it therefore seems that a high level of energy expenditure is required by caracals per unit of energy gained.

Hunting model

A hunting model was developed here, based on the differential likelihood of a particular behavioural component resulting in a kill. It was hypothesised that behavioural components would have to occur in a specific sequence for the best hunting success rate. The gradient of success from no likelihood of a kill (failure) to high likelihood of a kill was plotted, as was the behavioural components that are associated with hunting.

Of the behavioural components of hunting, the crawl was least likely to be associated with a kill, and most often led to the failure of a hunt. The stalk was less likely to end in failure. However, the crawl and stalk components were not closely associated with one another. The take-off and chase components were closely and logically associated, no matter what behavioural component preceded the chase. This is logical because for a chase to develop from any other component of behaviour it has to be preceded by a take-off. The crouch was associated with both the take-off and chase components but not as closely as was the take-off with the chase. The crouch, take-off and chase components were all positioned centrally along a gradient from success to failure, suggesting that they did not dictate either the success or the failure of a hunt. The pounce was oriented close to the kill on the gradient because it often is part of the conclusion of a successful hunt.

It was indicated previously that the most successful hunting sequences contained five behavioural components, but any given sequence could repeatedly contain various behavioural components. Using the sequences that were modelled here, a commonly used five-component behavioural sequence would start with a stalk, followed by a crouch, then by a take-off, then by a chase and finally by a pounce. This was found to be the most successful hunting sequence that is used by caracals in the Kgalagadi Transfrontier Park (Table 4). The model does not dictate the number of behavioural components or the number of repetitions of a component within a sequence, but rather indicates that a certain sequence of behavioural components is most likely to result in a kill. Therefore the hunt does not have to begin with a crawl, and all the other behavioural components do not have to follow in a specific sequence to end in a kill. A hunting sequence could just as easily begin with a crouch and progress directly to a pounce without a chase. However, the model does confirm that a logical sequence of any number of goal-orientated behavioural components has the best chance of ending in a kill.

Killing prey

Caracals in the Kgalagadi Transfrontier Park kill their prey in a similar way as elsewhere. When killing large prey, caracals tend to subdue the prey first by capturing it and then applying a nape bite that is not fatal. A final throat bite is then used to suffocate the prey. This agrees with the killing method as described by Grobler (1981), Stuart (1981, 1982), Moolman (1986) and Stuart & Hickman (1991) for caracals elsewhere. In doing so, caracals kill their prey in much the same way as the other larger felids of Africa (Estes 1995). Pringle & Pringle (1978) and Skinner (1979) stated that caracals can kill large prey with a nape bite, but the only evidence of it happening in the Kgalagadi Transfrontier Park was when two kori bustards were killed in this way. These birds were each despatched by a bite to the nape of the neck that appeared to sever the spinal cord. This is much more easy to do with a bird with a slender and fragile neck than with a mammal, and could be a further indication of prey-specific hunting behaviour.

The method of killing a small prey such as a rodent could not be examined in the present study because of the method of observation. However, it is likely that caracals in the Kgalagadi Transfrontier Park use the same methods to kill small prey as were reported in other caracal studies (Grobler 1981, Stuart 1981, 1982, Moolman 1986, Stuart & Hickman 1991).

Pringle and Pringle (1978) indicated that caracals do not usually return to their kills for a second feeding bout once they have moved off or have been disturbed, but Grobler (1981), Stuart (1982), Moolman (1986) and Stuart & Hickman (1991) all found that caracals would return to a kill, provided that it was still fresh. In the present study the caracals also returned to fresh kills of large prey to feed again. This may be especially important in terms of energy balance in prey-poor areas where the use of the prey resource must be optimised (Bothma & Le Riche 1989). Small prey was usually consumed too quickly and completely to allow a second feeding bout. Even in areas in the vicinity of the Namibian border, where the caracals are often persecuted by farmers, they regularly returned to fresh kills to feed again after having been disturbed.

Caracals in the present study regularly cached remains of 42 % of larger kills under dense bushes such as *Boscia albitrunca* and *Acacia mellifera*, as was also described for leopards by Bothma & Le Riche (1986). This supports the observations of Grobler (1981) and Stuart (1982) that caracals do cache their kills. Mills (pers. comm.)[2] also observed caracals to cache prey remains, and on one occasion he observed that a caracal carried the carcass of a springhare up a tree. However, no evidence of caracals caching kills in trees was found in the present study, and it seems to be a rare event. When it does happen, it is likely to be in response to an immediate threat from a competing predator for the kill. In areas where the density of predators is high and the likelihood of interspecific competition is higher than in the Kgalagadi Transfrontier Park, leopards also take their prey into trees more frequently than in the more prey-poor Kalahari (Bothma & Le Riche 1984).

On a number of occasions the caracals carried their kills from the killing site to areas of more dense cover. The distance over which the caracals did so was highly variable, with the longest distance being a scrub hare that was carried for 160 m. The behaviour of carrying kills has also been recorded by Grobler (1981) for

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[2] Dr. M.G.L. Mills. Specialist Scientist, Kruger National Park, Private bag X402, Skukuza 1350, South Africa.

caracals. It probably happens to prevent other predators, including raptors, from spotting and competing for the kills.

CONCLUSIONS

Although a hunt is often interpreted as a single activity for African predators generally, it is not a single behaviour in a caracal. Rather it is a sequence of behavioural components that are adapted to the prevailing conditions and the prey target. There is no strict sequence of behavioural components that comprises a hunt. Hunting behaviour in a caracal is therefore a fluid situation without a pre-ordained sequence. It is a constant adaptation to a specific situation and type of prey, with the sequence developing as a specific hunt unfolds. As for other felids in the Kgalagadi Transfrontier Park, opportunism is an important component of hunting. In the caracal, hunting behaviour is therefore both flexible and adaptable.

When caracals hunt large prey, they do so with a greater intensity and expend more energy in the hunting process than when hunting small prey. The relatively high hunting success rate of caracals when hunting large prey might justify the increased effort because of the greater amount of energy gained, although more energy is expended when hunting large prey than small ones as is revealed by the longer mean hunt distances for the large prey. Moreover, more effort is required to overpower large prey than small ones. There also is an increased likelihood of a caracal being injured when killing a large prey.

The sequence of behavioural components that forms a hunt, varies. Yet, the hunting behavioural components follow a logical order, ending in a kill, although not all the components appear in all the hunts. A hunting model for a caracal therefore should rather emphasizes the sequence in which the various behavioural components must occur for a kill, and not the full complement of each sequence. Nevertheless, there is an ideal sequence of behavioural components for the best kill rate. The overall killing technique of caracals when hunting large prey supports what has been found in other studies elsewhere.

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