CHAPTER 3

JACKAL PREDATION

Introduction

The study on the jackals of the Northern Tuli Game Reserve commenced on the 1st of September 1986. Glen Devine, then manager of Mashatu Game Reserve, reported that the local Batswana people believed that the jackals in the area were responsible for killing adult impala on a regular basis. In informal discussion he urged me to conduct the study on the jackals of Mashatu as he felt they would prove very interesting. The observations of Lind (1974), Devine, myself and many others that there were large numbers of jackals in the Reserve certainly indicated that they may be important predators in the region. The project was so launched, but I don't think that any of us suspected just how interesting the story would be.

Jackals have achieved notoriety in Africa as avid predators of small domestic stock (van der Merwe 1953, Lombaard 1971, Rowe-Rowe 1975, Ferguson 1980). In many cases this reputation may be justified (Rowe-Rowe 1975, 1976). However, all the studies on the diet of this species (van der Merwe 1953, Grafton 1965, Bothma 1966, 1971, Wyman 1967, Smithers 1971, Rowe-Rowe 1976, 1983, Stuart 1976, Lamprecht 1978, Stuart & Shaughnessy 1984, Avery, Avery, Braine & Loutit 1987, Hiscocks & Perrin 1987) have demonstrated unequivocally that the black-backed jackal is an opportunistic feeder, preying on animals ranging in size from termites to 40 kg antelope and sheep, is not averse to feeding on vegetable foodstuffs, and will feed on carrion of any origin if available. Such demonstrably opportunistic behaviour understandably is extended to those large packages of food that are almost totally defenceless against even the weakest predator - sheep. If reason were to prevail, the blame would fall not on the jackal but rather on inappropriate husbandry practices. Of course the reverse is true, and the merciless persecution of jackals has had devastating consequences for this species as well as for the other small carnivores and scavenging birds of Africa.

The adaptability and opportunistic nature of jackals means that they manage to survive under the harshest of conditions, even the intensive persecution by man. This opportunistic nature has been taken to explain the sporadic cases where jackals have been observed killing adult gazelles (van Lawick-Goodall 1970a, Kruuk 1972, Schaller 1972, Sleicher 1973, Lamprecht 1978a, Moehlman 1983, Goss 1986). The ratio of the mass of an adult jackal to an adult gazelle is approximately 1:5, and these remarkable observations have therefore been important in documenting the killing ability of this small predator. However, three of the five reports cited here noted that the victims were sick or behaving unnaturally, and one is tempted to speculate that perhaps the ever-oportunistic jackal will sieze any opportunity to prey on animals which are most easily killed.

Like the jackal, the North American coyote *Canis latrans* is a monogamous small canid. The coyote is almost twice as large as the jackal (coyote males 13,4 kg, females 11,4 kg (Andrews & Boggess 1978) cf. jackal males 7,9 kg, females 6,6 kg (Smithers 1983). Coyotes prey regularly on cervids, both adult and young (Berg & Chesness 1978, Hilton 1978, Bowen 1981, Smith, Neff & Woolsey 1986). Moreover, as shown by Hilton (1978), the predation on adults may be selective for animals in poor condition, and in all studies predation increased in winter, thus demonstrating the kind of opportunism one could expect from other medium-sized canids such as jackals. Indeed, there are remarkable similarities in the behavioural ecology of these two species which will be demonstrated by the present study, and much could be learned about the jackal by applying a comparative approach to future studies on jackals. For this reason, extensive reference is made to the coyote literature in this thesis.

To direct the study on the reported predation by jackals on adult impala the following questions were posed:

1. Do jackals indeed hunt and kill adult impala in the Northern Tuli Game Reserve?.

2. If they do hunt and kill adult impala,
   a. How is this achieved?
   b. How regularly is it undertaken?
   c. How many jackals participate in a kill?
   d. Are any changes in socioecology associated with any such predation?
   e. Is there any selectivity in the predation?

3. What space and time utilization patterns are associated with predation by jackals on adult antelope?

From the outset it was known that jackals prey on young antelope (Wyman 1967, Pienaar 1969, van Lawick-Goodall 1970a, Kruuk 1972, Stuart 1976, Lamprecht 1978a, Ferguson 1980, Rowe-Rowe 1983, Stander 1987), that jackals are monogamous, live in small family groups, and give birth to one to six pups in early spring (Ferguson 1980, Moehlman 1983, Smithers 1983). As the scope of the present study was not broad enough to cover all aspects of jackal ecology, those about which much is already known were not included. The primary goal of the study was to document as many kills of adult antelope as possible, and to relate these to the other aspects, both known and observed, of the behavioural ecology of this species.

The study had to proceed with certain constraints. First, the heterogeneous habitat resulted in jackals often being lost to sight. Radio collars were therefore an essential prerequisite, and jackals had to be captured for the purpose of fitting the collars. Second, as the Reserve was utilized for tourism purposes, impact on these activities had to be minimized. Thus a minimum number of animals could be collared, and offroad vehicle activity had to be minimized. The latter, as well as the fact that much of the habitat in the Reserve was not suitable for following and observing an animal as small as a jackal, meant that continuous behavioural observations were impossible. The questions addressed by the study thus remained brief and specific. Other information gleaned during the course of the research is recorded to supplement what little is known about the jackal rather than as a complete record of events.

Location and observation of jackals was designed to record the presence or absence of any indication of predation on adult impala. To make locations and observations as feasible as possible, the central lower floodplain of the Majale River was chosen as the site for the study - this area has sections of open, short-grass plains which fringe on the riverine bush, thus making at least some of the travelling and observation relatively easy. In addition, this area has the best developed network of tracks in the Reserve. This site was also suitable in that it included several prominent hills which would be useful for radio tracking and telemetry.

While it is generally well known that jackals are wary of human persecution, Shortridge (1934) reported that jackals in remote areas are among the easiest animals to catch. In presuming that I was dealing with a relatively unpersecuted population in a game reserve, I proceeded to select the most ethical capture technique without being too concerned about the possible wariness of the jackals.

From the outset there were significant constraints on the capture operation for the project. First, only adult jackals resident in the selected study area would be suitable - there were not enough radio-collars to mark young animals, which could be expected to range over a wide area (Ferguson 1980). Second, as the area had a population of leopards and lions it was considered undesirable to use methods which would expose trapped jackals to possible predation by these larger carnivores. As jackals had been closely approached on many occasions during the run-up to the project, it was concluded that darting would be the most feasible, selective and ethical method of capture. However, although a darting system was developed to a state of sophistication in which a 100 mm diameter target could be hit with 95% certainty at 15 m, the approachability of the jackals had been overestimated. Furthermore, the more attempts that were made to approach jackals within the study area, the more wary they became of the study vehicle. It thus became essential to experiment with other methods. In retrospect it is regrettable that the final solution - foot-hold traps - was not tried first.

Eventually an adequate number of animals were collared in March 1987.

Unfortunately, due to managerial commitments in the Reserve, the study was suspended completely between 7th July 1987 and 15th February 1988. Thereafter, intensive observations and telemetry proceeded until 15th June 1988 and again from 4th to 18th September 1988.

As the jackal study relates intimately to the subjects contained in Chapters 4 and 5, a complete discussion of the implications of the results of the jackal study are reserved until Chapter 7.

Materials and Methods

Capture

Darting

Darting was undertaken using a modified Vario 1 Telinject dart pistol (Telinject SA, Randburg, SA). The pistol was modified so as to have quick-release trigger, stock and telescopic sight. Accurate darting required a range of approximately 15 m. Close approach to jackals was attempted by: 1. Baiting with impala, wildebeest, zebra and elephant carcases were moved to suitable sites within the selected study area; 2. Driving after sighted jackals - both during the day and during the night - in an open landcruiser; and, 3. Calling jackals to a brush hide with recordings of a distressed scrub hare and with varmint callers. Reflective tape was attached to darts to facilite the following of darted jackals as well as the recovery of darts that missed their targets, as described in McKenzie (1988a) (Appendix B1)

Foot-hold traps

Foot-hold traps were used as a last resort. My reticence to use steel foot-hold traps was due in the first instance to the reported injuries caused even by padded traps (Drewek 1980, Olsen, Linhart, Holmes, Dasch & Male 1986, Olsen, Linscombe, Wright & Holmes 1988) and, in the second instance, to the fact that the numerous lions and leopards present in the study area were likely to kill trapped jackals if they were left in open traps overnight. In order to solve the first problem, the traps obtained ("Jackal",Brock-Tuchten, Johannesburg) were modified as recorded in McKenzie 1989b (Appendix B2). The modified padded traps could safely be set off against one's fingers, and I was thus satisfied that injuries would be reduced to a minimum. The second problem was overcome by complementing the bait at the trap with sounds of a distressed scrub hare to encourage immediate investigation by any nearby jackals, and thus hopefully maximize chances of capture without having to wait overnight or longer.

Trapping was finally successfully undertaken as follows:

1. Padded traps were set in one track of the road transecting the study area, at a site away from any thick bush. Traps and equipment were treated in plant extract, handled and set as described by Bodicker (1980). The set traps were then left for 1 - 2 days with a log over the trap to prevent vehicles from setting off and damaging the trap.

2. Impala meat was minced in a standard meat mincer (approximately 500 g per trap), using plastic gloves to avoid contamination with human odour.

3. One hour after sunset the vehicle was driven next to the trap. Without alighting or switching off the engine, the log was lifted and placed in the vehicle. While still in this position, the minced meat was evenly spread on the ground over approximately 1 m^2 centred on the buried trap.

4. Recorded sounds of a distressed young scrub hare were played at maximum volume from a portable cassette tape recorder for 10-15 sec while turning the recorder to cover all directions.

5. After playing was completed the vehicle was slowly driven away to a nearby hill where calls of a jackal in the trap were awaited.

6. Upon hearing a jackal in the trap, I drove rapidly to the scene, threw a blanket over the jackal and administered the immobilizing drug.

Apendix A1 is a short account of the various methods used in an attempt to capture the ostensibly unaffected jackals, together with the shortcomings of the various methods. In total, four months of nightly effort were expended trying different techniques. In general, the methods failed to yield mature jackals from within the selected study area. Only as a last resort did I turn to using steel foot-hold traps, and only then after developing an acceptably humane modification.

Immobilization and handling

Trapped jackals were injected intramuscularly with 30-60 mg of Zoletil(50:50 tiletamine hydrochloride/zolazepam hydrochloride mixture, Virbac, Carros, France) (based on mean of 5,6 mg/kg for Canidae: Boever, Holden & Kane 1977). After injection the jackal was left in the blanket until the drug took effect. Once immobilized, the jackal was released from the trap and inspected for any injuries. One ml Compropen (150 mg procaine penicillin, 142,5 mg benethamine penicillin/ml, Centaur, Johannesburg) was administered intramuscularly.

Standard body measurements and masses (Ansell 1966) were determined. The age class of the jackal was determined from tooth eruption and attrition according to Lombaard (1971), and age group was assigned according to Ferguson *et al.* (1983).

Once fitting of the radio collar had been completed, the jackal was placed on a blanket and observed until fully recovered.

Radio Collars

Manufacture: Radio collars were manufactured as described in Appendix A2.

Fitting: Initially collars were fitted so that they could not be pulled off by pulling at the transmitter compartment (ventral) or side of the collar. This method was used as some of the first jackals captured were young, and tightening of the collars had to be minimized. Later collars were fitted so that they could not be pulled over the head. Once the correct size had been determined, the collar was secured with two pop rivets, and excess belting was cut off.

Reflectors

Reflectors were manufactured and fitted to collars as described in Appendix A3.

Radio Tracking

Technique: Radio tracking equipment consisted of a Yaesu FT290R Mark II 2m transceiver (Yaesu-Musen Co. Ltd., Tokyo, Japan), a RT58U co-axial cable, and a four element Yagi antenna constructed as described by Ferguson (1980). The co-axial cable was trimmed for maximum gain as described by Parish (1981).

The transceiver was mounted in an open LWB Land Rover. An overhead shelf was used to secure a swivel mount with handle as described in Appendix A4. The Yagi antenna was strapped to the swivel mount by means of a strip of car inner tubing in such a manner that it would swing free if struck by a branch, and in such a way that it could be rapidly removed and remounted when the antenna was to be held by hand.

At the beginning of a tracking session, the approximate position of each jackal was determined from one of the several high hills in the study area. For these locations, the Yagi was removed and held by hand in a standing position in order to maximize gain and directionality. After transmitter signals had been located, the Yagi was remounted. Upon nearing the approximate location of a particular jackal, the antenna was swept from side to side using the swivel-mount with the left hand while driving. This facilitated accurate location of the jackal's position. Once a clear signal was received, a roof spotlight, also operated by the left hand, was used to search for the jackal until visual location was achieved. A hand held spotlight was used to supplement the latter from a standing position if the jackal could not be located immediately.

Hills were used whenever a jackal could not be re-located during a session.

Data Collection: Upon sighting, time, identity number, group size, habitat, activity and location were noted.

Activity was grouped into the following categories:

Resting	Social activities
Active, unclassified	Other intraspecific interaction
Zig-zag foraging	Interspecific interactions
Hunting - impala	
- other	
Feeding - own kill	
- scavenge	
- cache	

Habitat was recorded as follows, according to the classification of Joubert (1984):

01 *Boscia foetida* savanna

02 Valley bush

03 *Acacia tortilis* savanna

04 *Croton megalobotrys* thicket

05 *Colophospermum mopane/Terminalia prunoides* middle slopes

06 Erosion plains - areas of valley bush and/or *Acacia tortilis* savanna which have been denuded by sheet and donga erosion, and which have little or no ground cover.

07 *Colophospermum mopane* scrubveld (a subdivision of the above found on alluvial soils, predominated by short, stunted *C.mopane*)

08 *Salvadora angustifolia/Acacia tortilis* brushveld

Location was recorded as follows: A two-times enlargement of the aerial survey map of the study area was obtained (Department of Surveys and Lands, Gaborone, Botswana). A strong plastic overlay was adhered along the top edge of the photograph. A 1 km^2 grid was drawn onto the plastic overlay. Each square was further divided into a 12x12 grid. Fine grid size was thus equivalent to 83x83 m. Due to prominent features of the terrain (trees, rivers, hills, roads), and substantial acquaintance with the study area, the locality of the jackals could be pinpointed on the photograph to within the 83x83 m grid. The position was temporarily marked on the photograph with an adhesive pointer while the overlay was held in place and the grid reference read off.

All data were recorded on a tape recorder and later transcribed onto a data sheet.

If the located jackal was not engaged in hunting or associated activity, searching for the next jackal commenced. If the jackal was engaged in interesting behaviour, additional notes to the above were made. Detailed continuous behavioural observations were not undertaken because of the unsuitability of much of the terrain other than the open plains, and because vehicle damage to the habibat had to be minimized.

Once each jackal had been located, the process was repeated. In this way it was attempted to locate each jackal at least once every three hours. As the consumption stage of impala kills lasts 2,5-4 h, and the hunting up to 4 h (pers. obs.), this interval provided an assessment of whether or not a jackal was involved in an impala hunt on a particular night. This method was used to determine the number of jackal-nights on which impala were consumed, and was considered more productive in this regard than observing a single jackal for a prolonged period.

If a jackal was located while feeding on an impala kill additional data were collected on the prey as follows:

Sex was noted

The mandible was collected for age determination. Age was determined from attrition patterns as described by Roettcher & Hof mann (1970), Spinage (1971) and Murray (1980). Cementum annuli were not used for age determination as this method has been singularly unsuccessful in this species (Spinage 1973, Reich 1981). As dental attrition varies markedly between different geographical areas (Roettcher & Hofmann 1970, Spinage 1971) none of the ageing techniques could be used to provide a precise record of true chronological age. As the study dealt with selective predation, an index of relative physiological age was required. "Age is generally meant to be an index of the passage of time, but to a demographer it also indexes probability of death." (Dapson 1980:544). In order to obtain such an index, the technique of Roettcher & Hofmann (1970) was selected as this method allows identification of animals in which physiological function is affected by advanced or total incisor attrition. Advanced or total incisor attrition represents a situation in which ingestive processes are compromised. A similar index of advanced senescence is not evident from molar attrition, except possibly the eventual total attrition of M_1 (Spinage 1971). Such advanced molar wear was not encountered in the impala collected in the study area for baseline age structure purposes (Chapter 4, Section 1), and incisor wear was thus the only index through which the (physiologically) oldest animals could be identified. Because of the lack of precision in extrapolating from other areas, the age data as determined using the method of Roettcher & Hofmann were classified into age classes as follows:

Age class 1/Young: <5 years. Less than 50% of enamel of occlusal surface of I_1 lost.

Age class 2/Middle-aged: 6-10 years. 50 - 100% of enamel of I_1 lost.

Age class 3/Old: >10 years. Attrition of I_1 advanced beyond occlusal surface, with reduction in size of surface of I_1 and other incisors. Most extreme case represented by total absence of all incisors and canines.

One femur was collected for determination of the Bone Marrow Fat Index as described in Chapter 4.

An autopsy was performed to ascertain the presence of any pathology, and to determine the exact cause of death. The distance between canine bite marks were measured if found.

The number of jackals observed in the vicinity of the kill was recorded.

Weather and phase of the moon were noted.

Telemetry

Stations: Two six-element Yagi antennas and two telemetry stations were constructed as described in Appendix A5.

The telemetry stations were located on elevated hills within the study area. A radio transmitter was placed at a site equidistant from the stations at a point which could be located on the 1:50 000 map of the study area (see Fig. 3).

Location: Each session began and ended by taking the bearings of the fixed transmitter. All bearings were taken by determining the point of fade-on of signal strength, which was sharply demarcated with the apparatus used. For jackal bearings, each cut-off point was confirmed at least twice before recording. Bearings on all jackals were taken every 20 min throughout the tracking session. Relative bearings of jackals were calculated as the perpendicular bisector of the two cut-off bearings. Actual bearings were calculated relative to the bearing of the reference transmitter. In using this method, errors in tower conformation, movement of the compass rose and bias in the antenna were nullified. Positions were plotted at the point of intersection of bearings from the two towers. Positions thus plotted were converted to grid references and entered onto a data sheet.

Telemetric tracking sessions were undertaken between 28-3-1988 and 15-06-1988. Evening sessions were from 18h00 to 23h00, and morning sessions from 06h00 to 08h30.

Calibration: Precision of the tracking apparatus was tested using stationary transmitters, the bearings of which were recorded until a total of 41 recordings were obtained. To eliminate observer bias, the audible fade-off was determined without looking at the compass rose. Once the point was identified, the pointer was stabilized and the reading was noted.

Activity: Together with each location it was recorded whether or not the jackal was active, as determined by the activity collar (one jackal) or changes in signal strength (Ferguson 1980, Fuller, Biknevikius, Kat, van Valkenburgh & Wayne 1989).

To supplement the activity recordings between sessions, an automatic activity recording device was constructed as described in Appendix A6. This device was located at the highest station, and was activated at the end of each tracking session. Recorded data were transcribed onto data sheets.

Data Analysis: All radio-tracking and telemetry data were entered into dBase III+ files for analysis. Files were formatted for use in SEAS (Spatial Ecology Analysis System, John Cary, Department of Wildlife Ecology, 226 Russel Labs, University of Wisconsin, Madison, WI, USA.) for the determination of home range sizes and movement patterns. Using SEAS, home range was calculated using the minimum convex polygon method (Mohr 1947), and the centre of activity was determined using the harmonic mean method (Dixon & Chapman 1965).

Faecal analysis

To supplement direct observations, fresh jackal faeces were collected within the study area during April, May, June and September 1988. The scats were macerated and sieved as described by Stuart (1976).

Identification of remnants was undertaken with a dissecting microscope, and observations were recorded as follows:

Mammalia: Rodent hair and/or bone fragments were classified as 'Rodent', and were not identified further. Hair from mammals other than rodents were retained. These hairs were then later sectioned and identified as described by Keogh (1983).

Aves and Reptilia: bird and reptile remains were identified to the level of order only.

Invertebrata: Insects and arachnids were recorded separately. Insects were further separated into Isoptera and 'Other Insects', the latter including all insect remains other than Isoptera. Arachnida were separated into Scorpiones and Solifugae.

All fruit remains were classified as food items, but were not identified.

Grass and leaves were recorded, but were not considered as food items for analysis. This is contrary to Bothma (1971), but is in agreement with Grafton (1965) and Rowe-Rowe (1983).

Data were analysed to yield the relative percent occurrence of items in the diet - i.e. the occurrence of each item is expressed as a percentage of the total occurrences. This method closely approximates the proportions actually consumed (Rowe-Rowe 1983), within the limitations of faecal analysis, and facilitates comparison between the four monthly collection periods.

Population Estimation

1. Mark-Recapture Estimate: Resightings of marked animals may be used to estimate population size if certain conditions are met (Caughley 1977). During radio-tracking, numerous jackals were encountered within the study area. Date, location, group size and presence of identifying marks (i.e. radio collars) were recorded. Jackals located by radio tracking were not recorded, nor were other jackals with a jackal located by radio tracking. If, however, the jackal being tracked was located on a road, or within the arc of the vehicles's headlights in the vicinity of the road, it was recorded as a random location. Data thus obtained were analysed to determine whether or not they were suitable for population estimation (Caughley 1977).

2. Home Range Size: The mean of the minimum seasonal home range sizes derived from the home range calculations were used to determine the density of jackal family groups within the study area. A conservative estimate of two adults, one current offspring associated with the adult pair, and one juvenile jackal covering a larger area, based on the results of Ferguson (1980) and Rowe-Rowe (1982), yields a minimum of four jackals active within each adult home range. Rowe-Rowe (1982) estimated that up to eight jackals could be active within the home range of an adult pair of jackals. These estimates were used to determine minimum jackal density based on the minimum seasonal home range size.

3. Known Jackal Groups: Through extensive travelling throughout the study area the centres of activity of jackals other than the study animals were identified. These observations were used to determine the number of jackal families within the most intensively traversed part of the study area and, using the above estimate of numbers per family, to estimate jackal density within the study area.

Results and Discussion

Capture

Darting

Three jackals were captured by darting (Table 1). Darting was unsuccessful as a method for capturing adult jackals in the selected study area. This was due to wariness by the jackals upon being purposefully approached, extremely fast reaction by jackals to the sound of the dartgun being fired, and difficulty in accurately estimating range at night. In addition, only younger jackals stayed at carcases when approached, and large carcases attracted adult jackals from outside the selected study area. Jackals were attracted by varmint callers and tape recordings, but would not approach to within range of the dart gun. Two jackals were killed and one was injured by darts. Use of reflective tape facilitated the following of darted jackals as well as the recovery of many darts that missed their target as recorded in McKenzie (1989a).

Trapping

The use of padded foothold traps was extremely successful. Time from baiting traps to capture varied from 10 min to 2 h. No fractures or excessive swelling were recorded, and only a single laceration , due to self traumatization, was recorded. Mild lameness was observed for a variable period after capture, as recorded in McKenzie (1989a). One trapped jackal was attacked and killed by lions within 7 min of capture - an inherent risk in using this method in the Reserve which was taken only as a result of failure of all other methods.

Immobilization

Times to tractability, first attempts to rise and ambulatoriness are recorded in Table 1. The relatively high doses of Zoletil used could have been reduced for the trapped individuals. These doses were initially used to achieve rapid induction during darting. However, even the high dose given to animal no. 3 did not guarantee rapid induction. Intramuscular injection was guaranteed when injecting the trapped animals, thus avoiding prolonged induction.

Generally, induction and recovery proceeded smoothly, and Zoletil proved to be a useful drug for the immobilization of jackals. The only disadvantage encountered was that once the solvent is added to the dry powder, the drug expires within 4 to 5 days. Thus capture of a single jackal in the field

Table 1. Immobilization dosages and response.

ID	DATE	CAPTURE	DOSE [1]	TRACTABLE [2]	MOVE [3]	WALK [4]
01	29/10/86	Dart	50	3	47	67
02	29/10/86	Dart	50	7	59	107
03	01/11/86	Dart	70	16	84	105
04	23/11/86	Trap	90	-	140	160
05	11/04/87	Trap	70	-	-	-
07	06/03/87	Trap	60	2	52	130
17	01/03/88	Trap	50	9	84	144
18	22/04/88	Trap	50	3	50	75
19	22/04/88	Trap	50	3	63	93
20	02/03/88	Trap	40	4	56	66

1 Zoletil (Virbac, Carros, France). Total dose in mg.
2 Time till sufficiently anaesthetized for safe handling without physical restraint.
3 Time till first purposeful movements.
4 Time till successfully rises and walks.

All times in minutes.

resulted in wastage if further jackals were not caught within a few days thereafter.

One jackal, no. 15, did not recover from anaesthesia. *Post mortem* examination was inconclusive, and it was concluded that shock had resulted in the death of the animal, which died during the recovery phase.

Radio Collars

Transmitters functioned satisfactorily for a minimum of 8 months, and in one case for 16 months. The only failure experienced was due to crack in the potting fluid which admitted moisture.

Loose fitting collars were removed by the first two jackals at 4 days and 3 weeks after fitting. In both cases, the removal was as a result of snagging of the dorsal side of the collar on small branches when the jackals inserted their heads into bushes, presumably to forage. Upon pulling against the snag, the collars were pulled over the occiput and off the animals - a feat which would otherwise have been impossible. Subsequent collars were fitted with less free play so as to avoid this problem.

Reflectors

The reflectors constructed from number-plate material were extremely useful in assisting in the location of jackals with a spotlight, particularly in dense vegetation. While occasionally a reflector was lost from an animal, the majority stayed in place. Reflectors were not fitted to later collars as they were so effective that they increased the visual impact of the collars, which was undesirable from the point of view of the tourist activities in the Reserve.

Radio Tracking and Telemetry

The radio tracking and telemetry systems functioned satisfactorily, with the exception of the automatic activity recording system. While the automatic data recording device worked extremely well, wow and flutter in the recorded signals from the ordinary collars made it difficult to discriminate activity from inactivity with absolute certainty. These data were therefore discarded.

The measured precision of the telemetry towers yielded a standard deviation of 0,37^{o} (n=41). As a fixed transmitter was used as the reference bearing during tracking, the telemetry stations were thus accurate to within less than one degree. While tests on stationary transmitters are commonly used to determine accuracy of telemetry systems (Ferguson 1980, Fuller *et al.* 1989) it must be realized that acccuracy is somewhat less than that determined by this method when one is tracking moving animals. This is due both to movement of the animals relative to the observer during tracking, and to fluctuating signal strength caused by movement of the collar on the animal.

Morphometric data

Masses and measurements of the study animals are presented in Table 2.

Table 2. Jackal measurements, masses and ages.

ID	SEX	TL	E	HF	T	G	N	MASS (kg)	AGE CLASS *	AGE GROUP **
01	M	1030	105	150	305	355	210	6.0	4	2
02	F	1030	100	155	300	360	-	6.0	4	2
03	F	990	105	155	280	390	220	6.5	5	3
04	F	950	97	148	290	-	220	-	4	2
05	M	1020	105	145	290	-	235	7.0	5	2
06	F	--	-	165	290	-	200	5.5	4	2
07	M	1040	100	-	300	370	205	6.0	5	3
08	F	960	100	145	280	340	200	5.8	5	2
09	M	1120	110	145	350	420	235	8.0	6	3
10	F	1010	95	140	270	-	190	5.8	5	3
15	F	1030	105	135	285	-	225	6.5	5	3
16	M	1040	105	145	300	390	220	6.5	5	3
17	M	1110	105	155	320	420	-	8.0	5	3
18	F	920	95	142	260	380	210	5.8	5	2
19	F	1050	105	145	300	390	220	6.0	5	3
20	M	1020	100	150	280	375	225	6.5	5	2

TL = Total length, along the curve. E = Ear. HF = Hind foot. T = Tail. G = Girth. N = Neck. All measurements in mm.

* Age class according to Lombaard (1971). 4 = 6 months - 1 year. 5 = 1 - 7 years. 6 = >7 years.
** Age group according to Ferguson *et* al (1983). 1 = young. 2 = sub-adult, fully grown, < 3 years old. 3 = Adult.

Feeding ecology

Direct observations

Predation on Impala

The study confirmed that jackals in the south-central region of the NTGR do prey on adult impala. Predation by jackals on impala older than 6 months was recorded on 11 occasions. Jackals were identified as the hunters responsible by direct observation on two occasions, by autopsy results on seven occasions, and by spoor and carcase remains on the other two occasions. Autopsies revealed the site, depth and canine spacing of any bite wounds on the carcase received prior to death. The canine spacing cannot conclusively discern between the bite of a caracal *Felis caracal* and a jackal (Roberts 1986). However, the shallower nature of jackal bites, the distribution of bite wounds on the body, and the pattern of consumption, beginning with the abdomen, facilitate the identification of jackals as the responsible predator. Moreover, caracals were only seen on two occasions during three-and-a-half years of intensive nocturnal activity in the Reserve, and thus the likelihood of misidentification of the responsible predator through thorough *post mortem* examination is assessed as minimal.

If a kill was located too late to conduct a meaningful autopsy, other characteristics indicated that jackals were the responsible agents. The kills of jackals were located in moderate to dense bush cover, in contrast to the open areas where cheetah kills were observed. The skeleton was always intact, as described below, eliminating lions and spotted hyaenas as possible agents. The absence of the spoor of other carnivores also assisted in determining the responsible agent. Finally, a frenzied activity was noticed when jackals had made their own kill, as opposed to where they were scavenging remains from other predators.

Kills located and their characteristics are recorded in Table 3.

In addition to kills located, jackals were seen to run after impala on seven occasions, and on another occasion a group of five jackals was observed unsuccessfully attempting to kill an impala over a period of more than four hours.

Out of a total of 186 jackal-nights monitored, five involved killing or consuming of an adult impala.

Several facets of the recorded predation of are particular interest:

Selectivity

In discussing the selectivity of predation it is pertinent to review the method of age estimation used on impala in the present study - i.e. incisor wear was used to provide an index of relative physiological age of the prey animals. Predators, with the possible exception of man, cannot make use of chronological age as a selection criterion for predation - rather, old age represents a physiological state which may increase the likelihood of death (Dapson 1980), particularly vulnerability to selective predation. Partial or complete absence of incisor teeth, as represented by Age class 3 impala in the present study, represents a condition - related to but not necessarily exclusively the result of old age - which compromises feeding ability,

Table 3. Details of impala killed by jackals.

Date	Est. time of kill	Circumstances *	Sex	Age Class **	Habitat density ***	No. of jackals seen	Bone Marrow Fat Index	Notes
04/06/85	20h00	Feeding	F	3	Moderate	7	-	
05/11/86	19h15	Feeding	F	3	Low	8	2,70	Extensive alopecia
26/11/86	19h00	Feeding	F	3	Moderate	6	3,24	Extensive alopecia
04/12/86	20h00	Feeding	M	1	Moderate	7	-	Mild alopecia
27/02/87	20h00	Remains	F	3	Moderate	-	0,50	
20/03/87	20h00	Harassing	M	1	Moderate	6	-	Compound #, r. metacarpus
27/04/87	21h00	Harassing	F	3	Moderate	12	2,14	
23/06/87	21h00	Feeding	M	3	Dense	5	0,25	
03/07/87	20h00	Feeding	F	3	Moderate	8	2,10	Moderate alopecia
15/09/88	01h00	Feeding	M	1	Dense	12	-	
18/09/88	24h00	Remains	F	3	Moderate	-	19,15	
							4,29 ± 6,64 Mean (std. dev.)	

Only impala over 6 months of age included.
* Harassing = jackals harassing and attempting to kill impala. Feeding = jackals feeding on fresh kill. Remains = jackals with remains of kill.
** Age Class 1 = young, < 5 years, 2 = middle aged, 5 - 10 years, 3 = old, > 10 years.

contributing to a loss in condition and thereby increasing susceptibility to selective predation.

Chasing of impala was always seen to occur while jackals were engaged in foraging for smaller prey. While foraging on the open plains at night for small prey items, including *Hodotermes sp.*, jackals encountered herds of impala which emerge from the valley bush at sunset to rest/graze on the open plains or at the fringes of the plains during the night (See Chapter 4). The majority of such encounters seen were followed by the jackals continuing with their foraging session. However occasionally the jackal, or pair of jackals, would discontinue their foraging to observe the impala. Suddenly the jackal(s) would rush towards the resting herd, which scattered in alarm. The jackal(s) then stopped and sniffed at the ground in the vicinity of the previous position of the herd. Following this sniffing the chasing was repeated two or three times. The impala stopped after each short chase, but progressively moved into the thicker vegetation fringing the plains. On all occasions on which this behaviour was seen, the jackals resumed their previous foraging pattern. On only one occasion was a jackal heard to vocalize during this chasing process, and this vocalization was of the repeated type emitted when mobbing large predators (Bearder 1975, Goss 1986, pers. obs.).

The behaviour recorded here is strongly reminiscent of the "testing" behaviour exhibited by wild dogs (Estes & Goddard 1967, van Lawick-Goodall 1970b), spotted hyaenas (Kruuk 1972) and wolves (Mech 1970, Allen 1979, Carbyn, & Trottier 1987) when approaching herds of potential prey, and has been recorded in jackals by Lamprecht (1978a). Like these larger predators, it is likely that the jackal is far more adept than the human observer at detecting any debilitated, sick or injured animal within the group. Even jackal predation on sheep is selective for the most vulnerable individuals (van der Merwe 1953). The repeated chasing is thus likely to be the initial stages of a hunt whereby, by inducing a flight reaction, identification of potential prey animals is facilitated. Unlike the testing in wolves, however, the jackals did not invariably pursue any animal which ran. However, in all the cases observed, the entire herd of impala would flee the charge by the jackal(s), thus making such a relationship impossible.

This selection hypothesis is supported by the highly selective nature of the eventual predation. Of the eleven impala killed by jackals, condition (Bone Marrow Fat Index, BMFI) only the seven fully grown animals could be determined. The mean BMFIs of these seven adult animals killed by jackals was $4,3 \pm 6,6$ (Mean $\pm$ std deviation) (Table 3), significantly less than the mean value of $87,0 \pm 2,74$ ($t=28,3$, $p<0,001$, d.f.=11) obtained from the control sample of six impala shot in September 1988 (Chapter 4). All of the full-grown impala killed by jackals had extremely worn incisor teeth and belonged to the old age class. Of the three young impala killed by jackals, one had a compound fracture of the right metacarpus. No signs of pathology were detected in the other two young impala, which were also too young for BMFI determination. However, in both cases, *post mortem* examination was inconclusive as much of the carcases had been consumed by the time they were located.

Selectivity for age was tested as follows:

Hypothesis: animals from the oldest age class are selected.

Null hypothesis: there is no selection for old animals.

A complete age structure for the population under consideration was not available (see Chapter 4). The data which are available indicate that there are approximately equal numbers of impala in each age category over 3 years old in the southern impala population within the Reserve. It is highly unlikely that there would be fewer of the youngest age class than of the older age classes. If is thus assumed that the number of animals in each age class in the population is the same and that there are three age classes, then one would expect each age class to be represented in the kills in the proportion of 1:3 of the total (= 3.33 animals in 10). This assumption favours the Null hypothesis as old animals are almost always scarcer than younger animals (Caughley 1977).

The old age class in the kills was represented by 8 animals, the rest by 2 (excluding the animal which had a fractured leg). Testing for association, X^2=28,8, d.f.=1, p<0,001; with Yate's correction X^2=24,5, d.f.=1, p<0,001 - i.e. the frequency of old animals in the sample was significantly higher than expected, indicating a strong selection for advanced (physiological) age by the jackals.

From data presented in Chapter 4, it is evident that there is a relatively high proportion of old impala in the population in the study area. However, as all of the eight adult animals killed by jackals were from the oldest component of the population, it can be concluded that the jackal predation on adult impala is highly selective with respect to age.

The condition of old impala declines significantly during winter (Dunham & Murray 1982). The present study has also shown (Chapter 4) that old impala with worn incisor teeth are in poorer condition than animals with effective incisor teeth at the end of winter. Without functional incisor teeth, and with worn cheek teeth, this loss in condition is probably due to compromised ingestive and masticatory functions, as well as to increased energy expended on futile grooming efforts (Chapter 4). These factors are likely to play a critical role at times of maximum nutritional stress - during peak lactation and during winter (Dunham & Murray 1982). As all the adult impala killed by jackals were in extremely poor condition, occurrence of the selective predation may be linked to environmental conditions, such as rainfall, which influence the loss in condition by impala during these periods. Selective predation by coyotes on old deer in poor condition has similarly been shown to increase during winter (Hilton 1978).

The selective predation by jackals on impala with advanced incisor attrition, in extremely poor condition or, in one case, with severe injury, indicates an overall selection for vulnerability. As shown by Temple (1987), selectivity for vulnerability by predators is linked to the relative difficulty of subduing and killing the prey. The large size of the impala prey would suggest that jackals should be selective for vulnerability, as is evident from the data obtained in the present study.

Harassment, teamwork and joining in

Prolonged harassment of an intended prey animal was observed in detail on two occasions. On one occasion, the prey escaped after 4 h, while on the other, the animal with the broken leg, was captured and consumed.

On the first occasion, three jackals were observed harassing an adult male impala. The impala had its hindquarters backed into a low bush, and was fending off the attacks by jackals from all sides. The impala did occasionally manage to break away and move to another bush where it was again cornered and harassed. After two hours, the number of jackals had grown to five. It was observed that some of the jackals would rest while others continued to harass the intended prey. This "relay" system of harassment has also been observed when wolves corner a moose (Allen 1979).

On the second occasion (Table 3, 20/03/87) the impala was eventually killed. Over a period of approximately 2 h, the size of the jackal group grew from three to six. Resting by some of the jackals, as described above, was also observed.

On neither of the above occasions were the jackals heard to vocalize loudly, but a low "wuffing" call was heard as the jackals harassed the cornered impala.

On the first occasion, calls by nearby jackals and a lion were not followed by a response by the jackals involved in harassing the impala.

Harassment by the jackals was continuous. Individual jackals rushed towards the cornered prey which turned to fend off the charge. The jackals broke off the attack without physical contact. One or more other jackals were at this stage attacking from another angle, and the impala turned to fend of this attack. This process was repeated continuously, and was only interrupted when the impala broke from cover and ran to another bush where it was again cornered.

Wolves have been reported to harass prey prior to the kill (Mech 1970, Allen 1979, Carbyn & Trottier 1987). As both jackals (present study) and wolves select sick, weak or old animals, this harassment, by depleting the already reduced energy reserves of the selected animal, is likely to have a marked influence on the ability of the animal to fend off any physical attack when it finally occurs. The prolonged chase by wild dogs and hyaenas in open habitat (Estes & Goddard 1967, van Lawick-Goodall 1970b, Kruuk 1972) also leads to physical exertion by the prey, and would thus be most successfully applied to compromised animals.

Purposeful harassment with delayed physical contact is only likely to be advantageous if the prey in good physical condition would be difficult or dangerous to kill. This is an extension of the observation that selection by predators for old or weak animals is correlated to the difficulty with which the prey is subdued and killed (Temple 1987). Thus jackals harass adult impala (present study) and gazelles (Sleicher 1973) but not young impala (present study), young gazelles (Wyman 1967, Lamprecht 1978a) or springhaas *Pedetes capensis* (Ferguson 1980); wild dogs harass zebra and wildebeest (Estes & Goddard 1967, Kruuk & Turner 1967, Malcolm & van Lawick 1975, van Lawick-Goodall 1970b) but not impala (Reich 1981), and wolves harass moose and bison but not beavers (Mech 1970, Carbyn & Trottier 1987).

The co-operative nature of harassment by social carnivores allows the efforts of the group to exceed the stamina of the selected prey. This may be the factor alluded to when hunting ability is cited as an advantage of group living in carnivores (Kruuk 1972, 1975, Lamprecht 1981, Packer & Ruttan 1988). This is, however, the first time that mammalian predators which do not live in a cohesive group have been recorded to co-operate temporarily for the achievement of a mutually beneficial goal. The described temporary co-operation is observed under circumstances where a particular resource is available which could not otherwise be utilized.

Immobilization and Coup de grace

The method of killing of the cornered impala was deduced from two observations and seven necropsies on fresh jackal kills.

One of the jackals bites the impala on the thoat in the vicinity of the angle of the mandible. The bite is a single, holding bite without any chewing or laceration of the overlying skin. Upper and lower canines penetrate the larynx, trachea and/or surrounding fascia. On only one occasion was the jugular vein found to have been penetrated. While the bite is deep, there was never any evidence of crushing of the larynx or tracheal rings.

The throat bite immobilizes the prey, which is pulled down by the weight of the jackal. What follows is a swift penetration of the abdomen via the thin skin and abdominal wall just cranial to one of the hind legs by another jackal. One or more jackals then enter their heads via the flank wound into the abdomen. It is important to note that the animal is not disembowelled immediately. Purposefully or otherwise, the biting severs the major arteries in the dorsal part of the abdomen - aorta, hepatic artery, cranial mesenteric artery - and associated veins. The kidneys are removed in this process, but other abdominal organs remain *in situ* until after the impala is dead. After administering the *coup de grace* the heads of the responsible jackals are covered in blood. This is removed by immediately rubbing the face and head vigorously on the ground, accompanied by rolling. Signs of such behaviour at the site of coyote kills has been recorded by White (1973). This observation raises the possibility that coyotes may also use this method to dispatch large prey. As in the case of the jackal, direct observations of such kills are extremely rare.

The method used results in rapid death of the prey animal - the loss of blood pressure following the severing of these major blood vessels is certain to result in almost immediate unconciousness. The blood released into the abdomen is richly oxygenated, confirming that the throat bite does not result in asphyxiation of the prey. In one case in which the jugular vein was penetrated, there was minimal perivascular haemorrhage, confirming the short interval between the throat bite and loss of blood pressure. Minimal haemorrhage was also recorded from jackal kills by Rowe-Rowe (1975) and Roberts (1986) - nevertheless these authors assumed that the throat bite was the killing bite. These authors did, however, document that the flanks of the victims were always opened by the jackals and that this was one of the first sites of eating by the jackals. Both these authors also noted that jackals kill large prey (sheep) in a far more efficient and neat manner than do feral dogs. Whether the flank penetration method of dispatching the prey used by jackals arose for this purpose or whether it is a reflection of a preference for feeding on the abdominal organs remains to be determined.

The pattern of immobilization and killing was sufficiently consistent to indicate that the technique of killing is applied by most, if not all, jackals in the region. The organized nature of the process may be as a result of the large numbers of impala preyed upon in this region. Other reports of predation by jackals on adult antelope have suggested that the prey is disembowelled (van Lawick-Goodall 1970a, Sleicher 1973, Lamprecht 1978a). While in areas where jackals are less experienced in the killing process the *coup de grace* may not be as cleanly administered as described here, the implication of a slow and agonizing death by disembowelling may be a misrepresentation of the events. Observations in other areas may one-day indicate whether the efficient killing method described here occurs within jackal populations elsewhere in Africa.

While the throat bite does not result in the death of the animal, it does facilitate administration of the killing method. Another effect of the throat bite is likely to be inhibition of vocalization by the prey. Antelope being killed by predators emit a distinctive, loud moan which can be heard over a considerable distance. The response of lions, hyaenas, and even leopards upon hearing the sound is to run rapidly towards its source (Bearder 1977, pers. obs.), and in the case of lions and hyaenas this could result in the loss of the carcase to these larger predators, as reported by Kruuk (1972) and Lamprecht (1978a). Of the two impala killed within earshot, one emitted a single loud bleat, and the other was killed with only a slight rustling sound. The results of the study are thus inconclusive regarding the effectivity or otherwise of the throat bite in silencing the prey during the kill. However, it would be of distinct advantage to the jackals to prevent the prey's death rattle which would undoubtedly attract larger predators within earshot. The hypothesis that the immobilizing throat bite may also serve to silence the prey awaits confirmation from other studies.

Total consumption

A distinctive feature of the jackal predation is that the large group of jackals present results in the consumption of every edible part of the prey. If undisturbed, the only remains of the impala are the contents of the rumen/reticulum, some intestinal contents, and the skeleton. The skeleton is picked clean to such an extent that each individual vertebra and rib is visible. However, apart from the removal of the unattached forelegs, the skeleton remains intact and, if encountered when fresh, can be fully articulated as the ligaments remain associated with the joints. The intactness of the skeleton is a distinctive feature of a jackal kill - i.e. compared to a lion or hyaena kill where bones are crushed and the skeleton dismembered. Another distinctive feature is that the ribs are not damaged, cf. cheetah which may chew the ribs considerably (Brain 1981, pers obs.).

As jackals are disturbed by the presence of a human observer and spotlights (as also reported by Lamprecht (1978a)), one kill (27/4/87, Table 3) was observed for short periods at regular intervals to determine the rate of consumption:

Time of kill 21h04.

By 21h34 - hindquarters, lower spinal muscles and all viscera consumed.

By 22h00 - Shoulder muscles consumed and ribcage exposed.

By 23h00 - Only muscle tissue remaining is on first four neck vertebrae. Forelimbs separated from rest of body, clean. Approximately half of body skin remains.

By 23h30 - Skeleton, small scraps of skin, and forestomach contents are all that remain.

Feeding by jackals on a fresh kill was noted to be extremely rapid, in contrast to more leisurely feeding when scavenging. This was also noted by Lamprecht (1978a).

The mean mass of female impala collected during the baseline data collection (Chapter 4, Section 1) was 43,5 kg. Only the skeleton and the contents of the rumen remain when jackals are finished with a kill, as noted above. Viscera constitute approximately 20% of the body mass of impala (van Zyl, von La Chevallerie & Skinner 1969), approximately half of which consists of the rumen contents (pers. obs.). If the skeleton constitutes 15% of the carcase mass (from Buttock bone %, [Monro 1979:100], von La Chevallerie pers. comm.), then jackals obtain approximately 32,6 kg of food from an adult female impala. In the case above, as 12 jackals were present, each jackal potentially obtained 2,7 kg of high quality food from the impala kill - none of which would have been available without the co-operative hunting effort. Jackals, like many other canids, are known to be able to consume large quantities of food in a short time (Kleiman & Eisenberg 1973, Lamprecht 1978b), and are adept at caching surplus food for later use (MacDonald 1976). Thus, whether consumed immediately or later, involvement by a group of 12 jackals in an impala kill provides each individual jackal with a substantial meal equivalent to 35 to 45% of its own bodyweight, or to approximately 38 000 harvester termites *Hodotermes mossambicus* (71 mg/worker [van der Westhuizen, Hewitt & van der Linde 1985]), the main alternative food source during winter (see below). Furthermore, as 12 was the largest group recorded at an impala kill, this is a minimum estimate of the direct advantage of co-operative hunting of impala by the jackals in the NTGR.

Silence and wariness

With the exception of the low "wuffing" sound sometimes heard during harassment, and occasional bickering and yelping at the carcase, there is no vocalization by the jackals at the site of the kill. On thirteen occasions loud calls by jackals heard in the vicinity, but not at the kill, were not answered by jackals at the kill. This is in contrast to the usual response elicited in jackals by the calls of conspecifics (pers. obs.).

Jackals on an impala kill were observed to be highly excited and nervous, and were less approachable than usual, as reported by Lamprecht (1978a). After a short feeding session, individual jackals would run at a fast trot in the vicinity of the carcase before returning to feed. Feeding was interrupted by frequent pauses during which jackals would look around with an alert expression. On some of the excursions away from the carcase pieces of meat were carried off and buried as is typical of the caching behaviour of jackals (Wyman 1967, Kruuk 1972).

Group size

Group sizes of jackals at impala kills were significantly larger than observed during random observations i.e. $7,9 \pm 2,5$, n=9 cf. 1.6 ± 0.7, n=489 ($t=22,5$, $p<0,001$, d.f.=496). As observed group size during the chasing/testing phase was $1,3 \pm 0,5$, n=7, the larger group accumulated during harassment and after the kill. Jackals were observed to join in during the harassment phase as well as during the feeding phase. On all occasions, the newcomers were accepted at the feeding site, and no agressive interactions were observed, nor were any signs of overt submissive behaviour by the newcomers apparent.

The method whereby group size increased between selection and the kill was never unequivocally determined by the present study. Two alternative hypotheses were, however, formulated:

1. As reported above, on one occasion when two jackals were seen chasing a herd of impala, one of the jackals emitted a call similar to the mobbing call heard when large predators are encountered (Bearder 1975, Goss 1986, pers. obs.). On the six other occasions when jackals were observed chasing impala no vocalizations were heard. A call of the type heard may be used to congregate a group of jackals once a potential prey animal has been located by one or two foraging jackals. In the case described, no additional jackals were observed to arrive, and the initiators did not continue with the hunt.

2. The process of harassment and feeding are accompanied by the "wuffing" vocalization mentioned above. The former is also accompanied by noises made by the impala in backing into a bush and fending off attacks. Feeding is also accompanied by the sounds of bickering and feeding. The sounds of these activities were audible to the human ear for up to 100 m on a still night. Jackals are very aware of any hunting or feeding activity (as evidenced by incidents recorded by Eaton 1969, Pienaar 1969, van Lawick-Goodall 1970a, Sleicher 1973, Hiscocks & Perrin 1987). Any jackals in the vicinity could thus be attracted to a hunt in progress, and would thus swell the size of the group.

If indeed the latter is the means whereby group size is increased, this may account for the observed trotting behaviour (see Activity below). The seasonal increase in home range size is largely due to excursions (see Home Range and Movement Patterns below) from the core area in the form of extensive trotting along established paths and roads. Many of these excursions were not observed to result in any feeding activity. On some of these excursions jackal no. 11 was observed to sleep before returning to his core-area i.e. he rested in an area occupied by another jackal pair. However, on five occasions, study jackals were located while participating in impala kills far outside their core area - Figs 4 and 5. In covering the vast distances at a fast trot, the jackals are without doubt exposed to a far greater possibility of encountering an impala kill in progress than if they remained within their own core area, or moved at a walk through adjacent territories. The fact that fast-trotting is only observed at the time of the year when the jackals hunt adult impala indicates that the phenomena may somehow be related.

Whilst highly speculative, the latter is felt to be the most likely explanation for the aggregation of a large group of jackals at a kill following initial selection and cornering by one or two jackals.

Seasonality

Extensive rains in February 1988 resulted in a green flush of vegetation throughout the study area which was apparent until late April. In contrast, the poor rains of 1986/1987 resulted in little greenery being seen after March.

Over the two years studied, the onset of predation was clearly linked to the rainfall and veld condition: Despite 118 jackal-nights of intensive

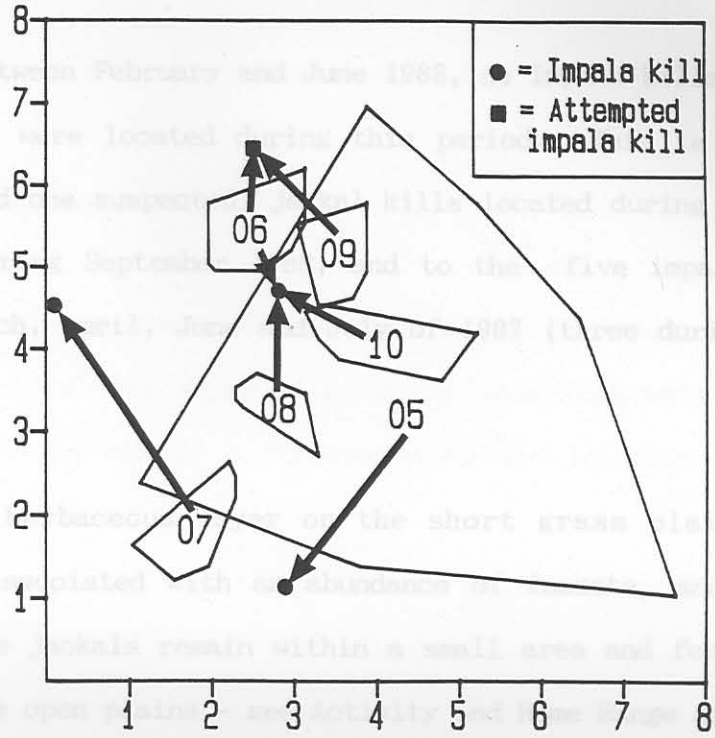

Figure 4. Location of jackals on impala kills relative to their 95% home ranges: 1987.

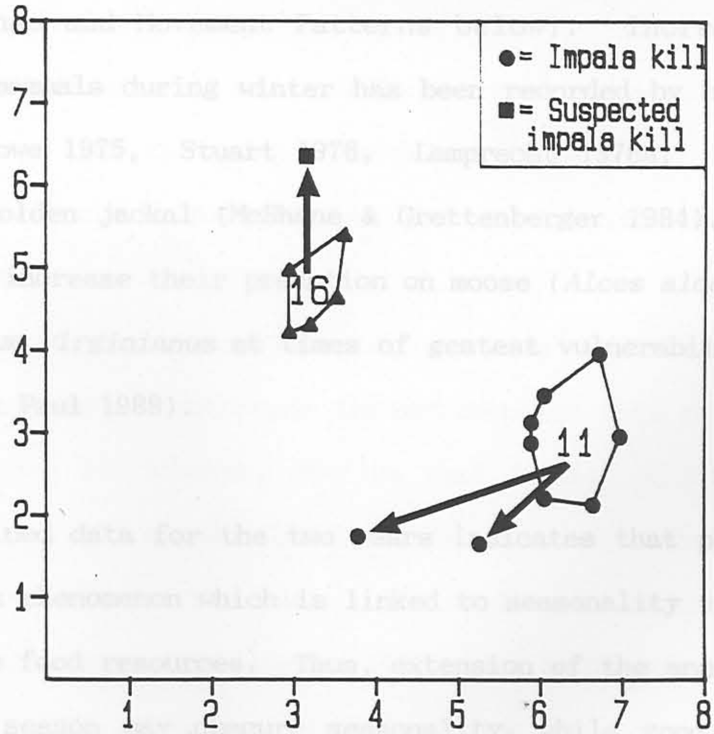

Figure 5. Location of jackals on impala kills relative to their March seasonal home ranges: 1988.

monitoring between February and June 1988, no impala kills, or even suspected impala kills, were located during this period. This is in contrast to two confirmed (and one suspected) jackal kills located during 24 jackal-nights of monitoring during September 1988, and to the five impala kills located in February, March, April, June and July of 1987 (three during 44 jackal-nights monitored).

A green herbaceous layer on the short grass plains following good rainfall is associated with an abundance of insects, and during periods of such abundance jackals remain within a small area and forage extensively for insects on the open plains - see Activity and Home Range and Movement Patterns below. Dessication of the herbaceous layer after summer is accompanied by increased foraging by jackals in the greener valley areas (See Habitat Use below). As winter progresses, jackals forage over a wider area, and eventually commence extensive excursions far outside their core activity areas (see Home Range and Movement Patterns below). Increased predation on medium/large mammals during winter has been recorded by other authors (Wyman 1967, Rowe-Rowe 1975, Stuart 1976, Lamprecht 1978a, Rowe-Rowe 1983) and also in the golden jackal (McShane & Grettenberger 1984). Wolves have also been shown to increase their predation on moose (*Alces alces*) and white-tailed deer *Odocoileus virginianus* at times of geatest vulnerability (Peterson 1977, Mech, Fritts & Paul 1988).

The combined data for the two years indicates that predation by jackals on impala is a phenomenon which is linked to seasonality via the availability of alternative food resources. Thus, extension of the annual drought through a poor rainy season may obscure seasonality, while good rains, such as in February 1988, may confine adult impala predation to the later part of the hot dry season, as was recorded by the latter part of the present study.

Other prey/food items

Quantifiable observations on utilization of other prey items did not constitute part of the study. However, some observations were made both during the two periods of intensive study and at other times. These are recorded here.

Mammalia

Impala < 6 months old Jackals were found feeding on young impala on seven occasions. Similar observations were reported by numerous other people from various parts of the Reserve. All of the occasions witnessed and reported were in December, January and February. In addition, jackals were seen actively chasing impala lambs on four occasions. On all of these occasions two jackals were involved in the chase, and on all occasions the participants were lost to sight. The latest of these incidents was in March 1988, when a particularly young impala lamb was the intended prey.

As neither of the intensive study periods coincided with the impala breeding season, the present study did not document this phenomenon in detail. These observations do, however, confirm that jackals do hunt impala lambs in the NTGR, and it would appear that the hunting is concentrated at the time of greatest vulnerability of the lambs. The ability of jackals to capture young antelope is well documented (Wyman 1967, van Lawick-Goodall 1970a, Kruuk 1972, Lamprecht 1978a, Ferguson 1980, Rowe-Rowe 1983, Stander 1987) and it is highly likely that impala lambs are an important component of the diet of jackals in the NTGR between December and February.

As pairs of jackals are considerably more successful than single jackals in hunting young antelope (Wyman 1967, Lamprecht 1978), and as group hunting is demonstrably well developed in the NTGR population (the present study), predation by jackals on young impala in the Reserve is likely to be of considerable importance in the population dynamics of the two species.

Scrub hare *Lepus saxatilis* A single jackal was found with the remains of a recently killed scrub hare in April 1987.

Small-spotted genet *Genetta genetta* Two jackals were seen attempting to capture a small-spotted genet, which escaped into a tree.

Warthog *Phacocoerus aethiopicus* In December 1987 a group of four jackals were seen harassing a female warthog with three piglets. Unfortunately the participants were surprised by the sudden appearance of my vehicle, and the interaction was disrupted. The jackals were highly excited, and the piglets were separated from the mother in their attempts to escape. Unless a suitable hole was nearby it was apparent that this attempt could have been successful if it had not been disturbed. This incident was seen during the day in the northern parts of the Reserve near Kgwedi camp (see map).

Carrion

Jackals were seen scavenging from carcases on many occasions both during the periods of study and at other times. Sources of carrion recorded in the study included: four elephants (two died of wounds inflicted by poachers, one was euthanased, and the other was shot by a landowner), one zebra (lion kill), one wildebeest (wounded by poachers, later died), two kudu (one died of old age, one lion kill), one waterbuck (victim of intraspecific agression), four impala (cheetah kills) and one impala lamb (abortus).

In February 1988 a group of six jackals were observed investigating a cheetah on an impala kill. After approximately half-an-hour, all of the jackals left the site of the kill. One of the jackals, no.11, was followed and was seen to forage for insects for several hours without returning to the site of the kill. This jackal was found with remains from the kill the next day, but the abundance of insects appeared to make scavenging a secondary activity even in the presence of such a large source of food.

Aves

Jackals were seen to snap at birds flushed from vegetation on three occasions. None of these were successful.

Reptilia

Jackal no. 5 was seen eating geckos *Pachydactylus bibroni* on three occasions. In all instances the geckos were extricated from the bases of dense bushes with considerable difficulty. On one occasion four jackals were observed unsuccessfully attempting to catch a large brown house snake *Boaedon fuliginosus*. The snake escaped into a rodent burrow.

Invertebrata

Insects Jackals were seen to consume a wide variety of insects including caterpillars, moths, ground crickets (*Hetrodes sp*, Orthoptera:Tettigonidae)(*koringkrieks*), grasshoppers, beetles, flies and maggots. After the heavy rains in February 1988 the green vegetation supported a wide variety of insects in large numbers. Jackals were seen consuming vast numbers of insects within short periods of time, as described by Lamprecht (1978a), and these observations were reflected in the predominance of insect remains in faeces observed at this time of the year (see below). Jackals were also often seen scratching open elephant dung piles and feeding on insects located within and underneath the dung.

Jackals were only observed to consume termites in winter, although faecal analysis demonstrated termites in the diet in April. On the occasions when termites were confirmed to be the source of food, inspection of the foraging site showed many harvester termites *Hodotermes mossambicus* (Isoptera:Hodotermitidae) active on the soil surface. Termites were typically fed upon in open spaces during foraging bouts which were interspersed with the wide movements typically observed in winter (see Movement Patterns and Home range below). Jackals were observed to simply lick termites off the ground while moving slowly in a zig-zag fashion. Bothma (1971) recorded 1250 termites from the stomach of a single jackal. From observations and faecal analysis (below), it is apparent that termites constitute an important part of the jackal's diet in the NTGR in winter.

Arachnida Jackals were seen successfully capturing large solifuges (Solifugae) on six occasions. Hunting invariably involved rapid movement to match the agility of the prey. On one occasion a solifuge took refuge in a hollow stick. The jackal systematically broke the stick apart with its teeth to expose the solifuge. After eight minutes of gnawing and pawing the solifuge was left to fight another day.

Coprophagia

Two jackals were seen consuming fresh baboon droppings. This behaviour was accompanied with much excitement. Only parts of the faeces were consumed.

Faecal Analysis

A total of 106 complete jackal faeces were collected and analysed. Results of the analyses are presented in Table 4.

Examinations of the diet of black-backed jackals have revealed that a wide array of food items, both of animal and vegetable origin, are utilized by this species (Grafton 1965, Bothma 1966, Bothma 1971, Smithers 1971, Rowe-Rowe 1976, 1983, Stuart 1976, Stuart & Shaugnessy 1984, Avery, Avery, Braine & Loutit 1987, Hiscocks & Perrin 1987). The conclusion reached through these various studies is that the jackal is an opportunistic feeder, making use of whatever food resource is most readily available. Large carcases are an example of a readily utilizeable source of food, and this no doubt gave rise to the early reputation of the jackal as a lowly scavenger. Utilization of carrion is, however, merely one example of the ability of the jackal to vary its diet both spatially and temporally in response to availability. The results of the analysis of the total faecal sample therefore constitute a