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Table 4. Total occurrence and relative percent occurrence of remains in jackal faeces, 1988.

	April		May		June		Sept.		Total	
Mammalia	10	24	16	24	25	42	27	44	78	34
Rodentia	7	17	11	16	12	20	13	21	43	19
Impala	1	2	4	6	10	17	13	21	28	12
Scrub hare	-	-	-	-	1	2	-	-	1	.4
Unidentified	2	5	1	2	2	3	1	2	6	3
Aves	2	5	3	5	-	-	9	15	14	6
Reptilia	-		2	3	-	-	-	-	2	1
Invertebrata	26	63	45	67	35	58	26	42	132	57
Insects	26	63	30	45	32	53	21	34	109	47
Isoptera	2	5	8	12	11	18	15	24	73	32
Other insects	23	59	22	33	21	35	6	10	36	
Arachnids	-	-	15	22	3	5	5	8	23	10
Scorpiones	-	-	-	-	3	5	-	-	3	1
Solifugae	-	-	15	22	-	-	5	8	20	9
Fruit	3	7	1	2	-	-	-	-	4	2
Grass (non food)	24		18		24		30		96	
Leaves (non food)	1		-		3		-		4	
No. of scats	23		24		26		33		106	

First column: Total occurrence in sample.
Second column: Relative percent occurrence (percent of all food item occurrences).

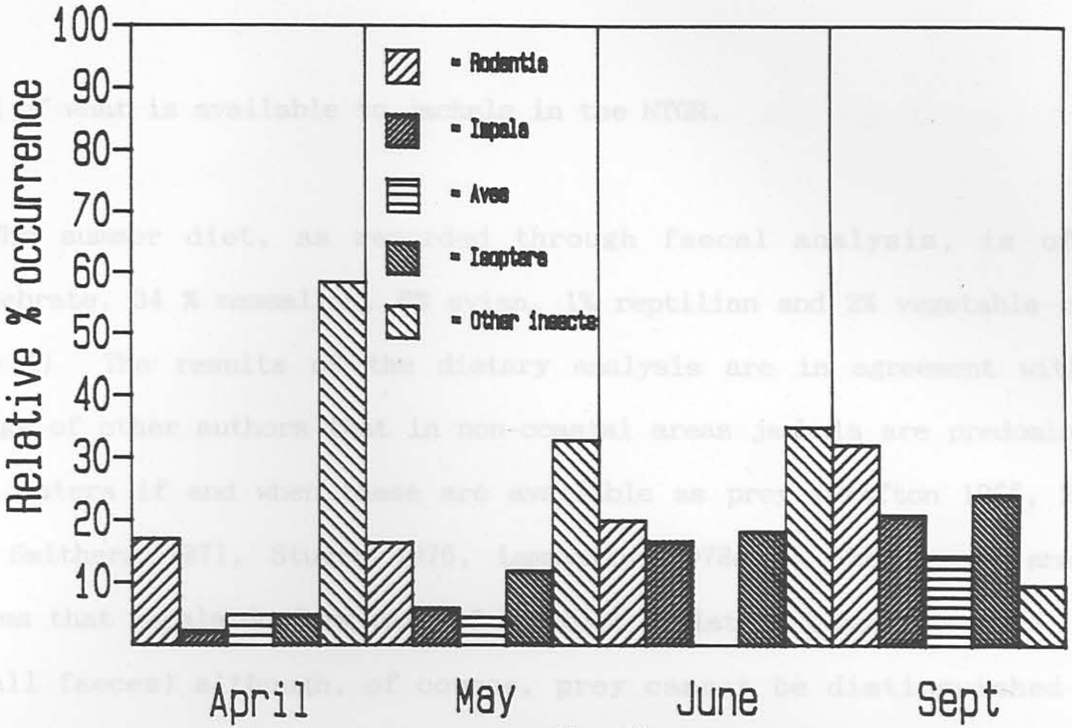

Figure 6. Relative percent occurrence of animal remains in jackal faeces: April - September 1988.

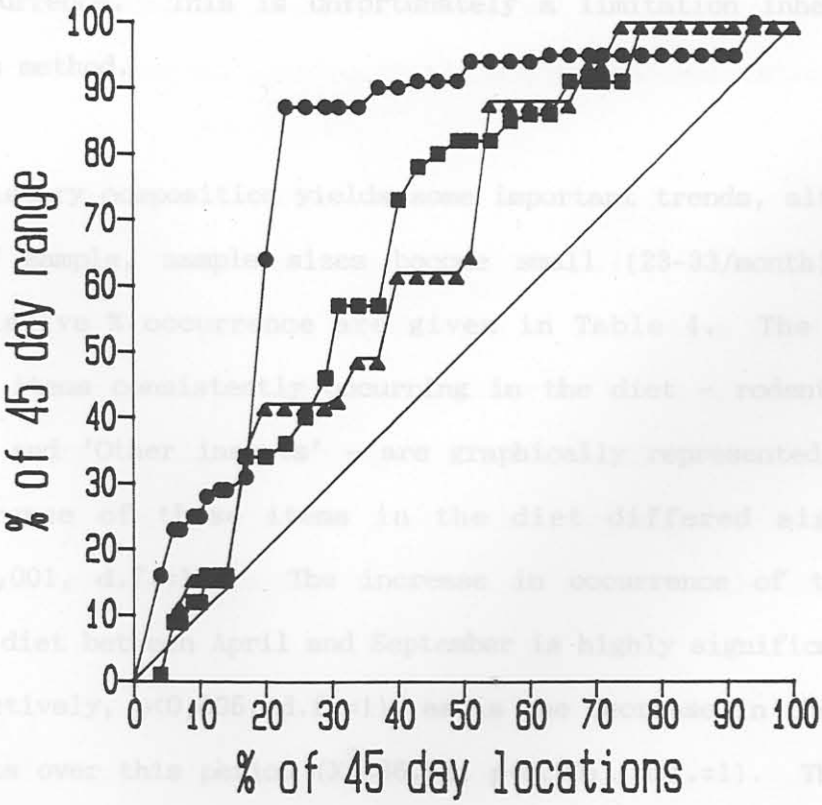

Figure 7. Relationship between the number of locations and home range size: first 45 days, 1988.

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record of what is available to jackals in the NTGR.

The summer diet, as recorded through faecal analysis, is of 57% invertebrate, 34 % mammalian, 6% avian, 1% reptilian and 2% vegetable origin (Table 4). The results of the dietary analysis are in agreement with the findings of other authors that in non-coastal areas jackals are predominantly insect eaters if and when these are available as prey (Grafton 1965, Bothma 1971, Smithers 1971, Stuart 1976, Lamprecht 1978a). The faecal analysis confirms that impala do form part of the diet (relative % occurrence 12, or 26 % of all faeces) although, of course, prey cannot be distinguished from scavenged material. At a relative % occurrence of 18,7%, rodents are the mammals most commonly represented in faecal remains. If, however, the size of a meal composed of impala, whether scavenged or killed, is considered in relation to a meal of rodents or insects, the occurrence of impala in the diet represents a source of food of greater importance than is indicated by the relative % occurrence. This is unfortunately a limitation inherent in the faecal analysis method.

Monthly dietary composition yields some important trends, although in so separating the sample, sample sizes become small (23-33/month). Monthly totals and relative % occurrence are given in Table 4. The relative % occurrences of items consistently occurring in the diet - rodentia, impala, Aves, Isoptera and 'Other insects' - are graphically represented in Fig. 6. Monthly occurrence of these items in the diet differed significantly (X^2=81,69, p<0,001, d.f.=12). The increase in occurrence of termites and impala in the diet between April and September is highly significant (X^2=9,15 and 9,31 respectively, p<0,005, d.f.=1), as is the decrease in the occurrence of other insects over this period (X^2=36,62, p<0,001, d.f.=1). The increases in rodents and bird remains during this period are not significant (X^2=0,64 and 3,20 respectively).

The results of this seasonal comparison agree with the reported increase in importance of mammalian prey in the diet of the jackal during winter (Wyman 1967, Stuart 1976, Lamprecht 1978a, Rowe-Rowe 1983). In particular, the increased proportion of impala in the diet (to 40% of all samples in September) supports the conclusion made from direct observations during the present study that impala predation is associated with the annual winter dry season (see above). The impala present in the diet in June may be accounted for by either scavenging or unobserved hunting during this month. While the increased percentage of impala in faecal remains does not prove that jackals hunt impala more frequently, there was also no evidence to suggest that scavengeable resources accounted for this increase.

The only other medium sized mammal identified in faeces, a scrub hare, is also the only other mammalian prey recorded from direct observations.

The marginal increase in bird remains in September may indicate that utilization of birds increases concomitantly with mammals as winter progresses. Lind (1974) expressed the concern of landowners in the NTGR that jackals may prey heavily on ground-nesting birds in the Reserve. The present study does not record a high percentage of birds in the diet, but this does not mean that birds are not preyed upon - their appearance in the diet is likely to reflect their availability to the jackals as with the other items in the diet.

The seasonal decrease in abundance of insect remains in the faeces also

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confirms the results of direct observations (see above) and agrees with the findings of other authors (Wyman 1967, Stuart 1976, Lamprecht 1978a, Rowe-Rowe 1983). The increase in Isoptera (termites) also corroborates the observation that jackals did forage extensively for termites on the open plains during winter. This was also the only insect which was observed to occur in high numbers in the study area during the winter months.

Solifuges form a small part of the diet as reported by Grafton (1965), Smithers (1971) and Stuart (1976).

Grass was found in 89% of all faeces examined. The grass in some of the faeces was fresh, while in others it was dry. In many of the scats the grass appeared to have been derived from the dung of herbivores, as it was digested and finely ground. Jackals were often seen foraging in dung heaps, as recorded above and as reported by Lamprecht (1978a). These observations, as well as observations on foraging for other insects in vegetation, indicate that most grass is ingested accidentally, and thus does not comprise a food item as claimed by Bothma (1971).

Movement Patterns and Home Range

The objective of the present study was to determine the presence or absence of predation on impala by jackals in the NTGR. Data collected on movement patterns and home ranges were collected incidentally, and the data collection was not designed with detailed home range analysis in mind. Nevertheless, sufficient data are available to discern at least some trends in the home range and movement patterns of the jackals studied.

Table 5. Total home ranges of study jackals for which sufficient locations were obtained.

Age* group	ID no	Sex	Total range (sq.km.)**	Monitored From	To	Method ***	Locations
2	5	M	32,7	11/04/87	05/07/87	DIR	119
2	18	M	51,0	27/04/88	15/06/88	TEL	282
3	11	M	9,7	01/03/88	19/09/88	DIR	269
3	16	M	11,0	01/03/88	19/09/88	DIR	258
3	17	M	10,4	01/03/88	19/09/88	DIR	262
3	19	F	12,7	27/04/88	15/06/88	TEL	402

* According to Ferguson *et al.* (1983).
** Minimum convex polygon (Mohr 1947).
*** DIR = Direct observations. TEL = Telemetry.

Total Home Range

Subject to the requirement of Bowen (1982) of a minimum of 42 locations over a minimum period of 45 days, total home ranges could be determined for five of the jackals studied. These data are presented in Table 5. Note that jackal no.5 in 1987 is the same as jackal no.11 in 1988 - changing from an age Group II jackal in 1987 to a mated age Group III jackal in 1988 which is accompanied by a reduction in range size from 32,7 to 9,7 km^2. Roy & Dorrance (1985) recorded a similar reduction in home range of a male coyote from 34,0 to 6,4 km^2 upon attaining breeding status. . The larger home ranges of the Group II jackals from the present study conforms to the results obtained by

Rowe-Rowe (1982) and Ferguson *et al.* (1983). While the sample size is small, the absolute size of the group II ranges (32 & 51 km^2) from the present study are closer to the values of 33 and 32,8 km^2 obtained by Rowe-Rowe than to the mean value of 85,2 km^2 obtained by Ferguson *et al.*(1983).

The size of the home ranges of the Group III jackals are approximately half of the mean of 20 km^2 obtained by Rowe-Rowe. The 95% ranges are similar to the 4,2 km^2 obtained for Group III jackals in the Kalahari Gemsbok National Park by Ferguson *et al.* (1983). While home range size of carnivores may to some extent be determined by metabolic needs and diet (Gittleman & Harvey 1982), the dispersion and abundance of resources may be expected to determine the absolute home range sizes observed within these constraints (MacDonald 1983). As speculated by Ferguson *et al.* (1983) regarding the Kalahari jackals, the small total home ranges recorded in the present study probably can be ascribed to an abundance of available food greater than in the Natal montane regions studied by Rowe-Rowe, and the Transvaal regions studied by Ferguson *et al.* This is discussed further in Chapter 7.

In the study by Hiscocks & Perrin (1988), the presence of a super-abundant food resource in the form of a seal colony probably accounts for the extremely high density of jackals recorded - 22 km^{-2}. However, under these conditions of super-abundance, the mean adult home range was found to be 27,4 km^2 (n=3). The authors concluded that "Habitat structure and prey distribution are therefore not necessarily parameters affecting home range size." (p99). However, the authors also recorded nightly fog and the use of hummocks and hills by the jackals for shelter. Without further evidence I suggest that the above conclusion is unjustified: the spatial distribution of sheltered habitat on this exposed coastline is likely to account for the relatively large home ranges in the presence of a super-abundant food resource. For example, golden jackals, in the presence of a super-abundant food source, have been recorded to remain within an area of 0,11 km^2 (MacDonald 1979).

The mean total home range of 1,8 km^2 (n=6) reported from Kenya by Fuller *et al.* (1989) is not directly comparable with the results of the present study. First, outlying points were discarded, second, only one month (June - after peak rainfall) was considered, and third, the mean number of locations used for the home range determinations was 21.

Seasonal Home Range

To date, none of the studies on jackal home ranges have addressed the possibility that home ranges may change seasonally (Rowe-Rowe 1982, Ferguson *et al.* 1983, Hiscocks & Perrin 1988, Fuller *et al.* 1989). Fortunately, sufficient data are available to compare the home ranges of the three adult jackals studied during 1988 on a monthly basis. The sizes of the respective ranges for the months of March, April, May, June and September are presented in Table 6. As can be seen from the Table, home range sizes increase steadily from March to June. The values for September must be regarded as minimum values, as the data were collected over only a 14 day period. If expressed as a percentage of the total home range, or of the September home range, Table 7, the seasonal increase is readily apparent.

Because of the study methods used, locations were only recorded every 4 - 5 h during the night. Many more observations could have been made, but it was readily apparent in March that the jackals were moving over very small areas while foraging for insects. Thus it is felt that the 48-52 observations used to obtain the initial ranges provide a true reflection of the jackal's ranges at that time. The increasing range with the seasonal changes results in a situation wherein a true asymptote (Bowen 1982) is not reached during the course of the study except in the case of jackal no. 11. However, a reasonable levelling off is achieved after 45 days (approximately 70 locations per animal) as shown in Fig. 7. Thus, the monthly increases in home range shown in Table 6 reflect a true increase in home range from summer to winter in all three of the jackals studied.

The small absolute size of the March and April home ranges in all the jackals is worthy of note.

The coyote is known to increase its home range during winter (Andelt & Gipson 1979, Laundré & Keller 1981, Bowen 1982, Springer 1982, Roy & Dorrance 1985, Parker & Maxwell 1989). For the coyote, this time of year co-incides with the breeding season as well as with changes in food availability - as it does in the case of the jackal in southern Africa. The reason for the increased winter home range could thus be related to food procurement or to the seeking of extra-pair copulations as postulated for the coyote (Laundré & Keller 1981). As all three animals in the present study were males, no comparison can be drawn between the sexes, and no unequivocal conclusion can be drawn in this regard. However, Gittleman & Harvey (1982) suggest that 10-fold increases in carnivore home range can be accounted for by changes in diet.

Feeding observations indicated that the very small ranges recorded in March, after the February rains, were linked to an abundace of insects which

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Table 6. Monthly and total home range sizes, 1988.

Jackal no.	Month						
	March	April	May	June	Sept	Total	Total (95%)*
11	1,4 (48)	1,2 (42)	1,4 (40)	6,4 (77)	5,8 (40)	9,7 (247)	4,8 (234)
16	0,5 (53)	0,7 (46)	2,4 (34)	5,6 (83)	6,8 (42)	11,0 (258)	2,1 (245)
17	1,0 (49)	1,3 (45)	1,4 (40)	3,7 (87)	9,5 (41)	10,4 (262)	2,8 (248)

All areas in sq. km. Number of locations in parentheses.
All areas calculated by minimum convex polygon method (Mohr 1947).
* Derived by removing each point which contributes most to area until 95% of points remain.

Table 7. Home Range overlap.

Vertical = Monthly range as % of total range.
Horizontal = Monthly range as % of September range.
Diagonal = % of range shared with other jackal.

	11T	113	114	115	116	119	16T	163	164	165	166	169	17T	173	174	175	176	179
11T																		
113	24,8																	
114	21,4	.																
115	25,2	.	.															
116	79,9	.	.	.														
119	75,3	23,7	19,9	23,7	110													
16T	9,9	.	.	.	.	.												
163	.	0	.	.	.	.	8,6											
164	.	.	0	.	.	.	11,7	.										
165	.	.	.	0	.	.	36,2	.	.									
166	.	.	.	.	0	.	67,2	..	.	.								
169	.	.	.	.	.	8,1	76,6	7,4	10,0	35,7	81,5							
17T	61,2	.	.	.	.	.	37,2	.	.	.	.	.						
173	.	0	.	.	.	.	.	0	.	.	.	.	17,9					
174	.	.	15,1	.	.	.	.	.	0	.	.	.	22,2	.				
175	.	.	.	2,2	.	.	.	.	.	0	.	.	23,3	.	.			
176	.	.	.	.	42,2	.	.	.	.	.	0	.	53,0	.	.	.		
179	.	.	.	.	.	40,1	.	.	.	.	.	46,2	95,7	10,6	13,6	14,4	39,3	

11, 16, 17 = jackal nos. 3 = March, 4 = April, 5 = May, 6 = June, 9 = September, T = Total were relatively evenly distributed throughout the study area. The only other study which demonstrates such small ranges is that of Fuller *et al.* (1989) who obtained a minimum seasonal home range of 1,8 km^2 (n=6) in Kenya in June. Importantly, this period follows one of the periods of peak rainfall in that region (Fuller *et al.* 1989).

As discussed above, the hunting of impala necessitates movement over a wide area and, as this phenomenon is linked to the annual winter dry period, the change in feeding habits is certain to play some role in the changes in home range. This conclusion is reinforced by the observation that on most occasions when marked jackals were observed feeding on or harassing impala they were not within their core areas (Figs 4 and 5). Increases in coyote range - both male and female - is also accompanied by increased predation on deer (MacCracken & Uresk 1984, Andelt, Kie, Knowlton & Cardwell 1987, Parker & Maxwell 1989).

Moehlman (1983) reported a reduction in jackal territory sizes in Serengeti, Tanzania, between 1974 and 1976. This was ascribed to demonstrably increased prey abundance following a period of higher rainfall, and shows that jackal home range or territory size is sensitive to temporal changes in resource availability.

Whatever the underlying cause, the present study indicates that flexibility in home range size according to seasonal changes in prey type and availability may be an important aspect of jackal biology.

Centre of Activity and Core Area

Seasonal changes in home range could be related to changes in the centre of activity. However, as illustrated in Fig. 8, centres of activity did not change significantly despite the large changes in absolute range size. In all cases, centres of activity were located in open habitat on the short grass plains. Because of this faithfulness to a single core area, the centres of activity of the study jackals as well as of other jackal families active in the study area could be identified. These are shown in Fig. 9.

All adult jackals spent most of their time in a single core area at the centre of their range, with the single exception of no. 19 who appeared to have two distinct core areas. The relative utilization of core areas is illustrated in Figs 10 and 11. Unlike coyotes (Springer 1982), all jackals returned to their core areas after their nightly forays.

Overlap

A natural consequence of increasing home ranges through winter is that overlap of home ranges must increase. The three jackals studied resided in sub-adjacent home ranges, with at least one jackal family between nos 11 and 17, and and between nos 16 and 17 (Fig. 9). During the time of minimum home range, there was thus no overlap at all between the home ranges of the study animals. However, as winter advanced, overlap increased as shown in Table 7 to reach a maximum in mid to late winter in all cases. The overlap *per se* is a natural consequence of the increasing home range sizes. However, the fact that the study area was saturated with jackal family groups implies that overlap is an immediate consequence of any increase in range over and above the minimum summer range. Tolerance of other jackals within the home range is thus closely linked to increasing overlap in movements. Whether the tolerance is as a result of the inability to effectively exclude a large number of

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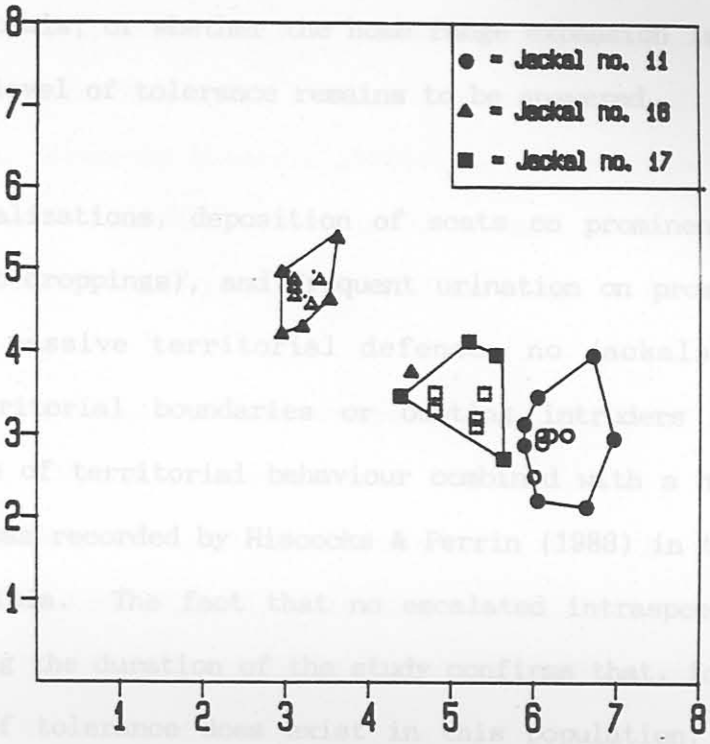

Figure 8. Monthly harmonic mean centres of activity (Dixon & Chapman 1980) relative to March seasonal home range.

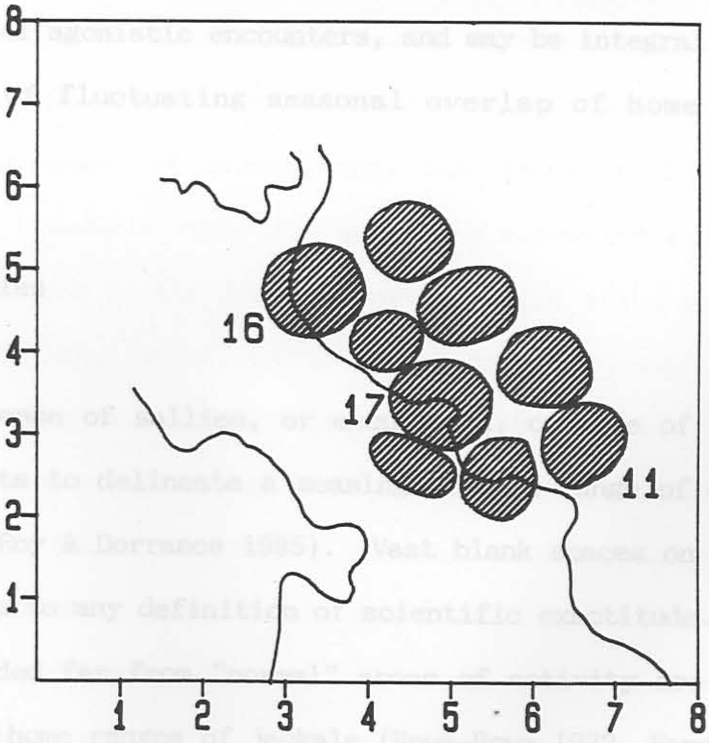

Figure 9. Jackal activity centres within study area. Sites where jackal pairs or families were regularly seen circumscribed by hand. Activity centres of nos 11, 16 and 17 indicated.

trespassing jackals, or whether the home range expansion is facilitated by an innately high level of tolerance remains to be answered.

While vocalizations, deposition of scats on prominent objects (bushes, rocks, elephant droppings), and frequent urination on prominent objects were indicative of passive territorial defence, no jackals were ever found patrolling territorial boundaries or ousting intruders during the study. Similar absence of territorial behaviour combined with a high degree of home range overlap was recorded by Hiscocks & Perrin (1988) in the Cape Cross Seal Reserve in Namibia. The fact that no escalated intraspecific agression was ever seen during the duration of the study confirms that, for whatever reason, a high level of tolerance does exist in this population. The co-operative predation recorded during the present study also reflects this high degree of mutual tolerance. As suggested by Springer (1982) for an undisturbed population of coyotes, proximity of relatives and known individuals may result in a low level of agonistic encounters, and may be integral to the maintenance of the system of fluctuating seasonal overlap of home ranges in jackal society.

Excursions/Sallies

The phenomenon of sallies, or excursions, outside of the "normal" range bedevils attempts to delineate a meaningful home range of canids (Burt 1943, Hibler 1977 in Roy & Dorrance 1985). Vast blank spaces on a map of locations does not conform to any definition of scientific exactitude. For this reason, locations recorded far from "normal" areas of activity are often excluded in calculations of home ranges of jackals (Rowe-Rowe 1982, Ferguson *et al.* 1983, Hiscocks & Perrin 1988, Fuller *et al.* 1989) and coyotes (Andelt & Gipson 1979,

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Bowen 1982, Roy & Dorrance 1985). Alternatively, the modified minimum area method (Harvey & Barbour 1965), which reduces the influence of outlying points, is used (Hiscocks & Perrin 1988). The methods used eliminate outlying points, or reduce their influence, until a neat group of locations remains which is then measured and is termed the home range.

As demonstrated above, the centres of activity of the three jackals remained almost unchanged between March and September. The enlarged ranges were due exclusively to sallies/excursions far from the minimum summer home range. If the 95% home range is calculated by excluding those locations which contribute most to the home range size (Ferguson 1980, Bowen 1982), resulting home ranges are 25 - 50% of the total range - Table 6.

Sequential monthly locations are plotted in Fig 10. As can be seen, the activity centres contain the highest number of locations, but the extensive sallies account for the increasingly larger winter ranges. Eliminating the 5% of the observations results in a tidier group of locations which suits the scientific requirement of orderliness, but denies a fundamental aspect of jackal biology. Jackals regularly undertake extensive excursions in winter. These excursions are in the form of fast trotting along paths and roads (see Activity below), and cover extensive areas in a short period of time. Whatever the primary reason for these forays (above), they are are a regularly observed phenomenon which should not be excluded by statistical manipulation. For this reason, total home ranges are used in the present study as opposed to 95% home ranges or some other artificial construct. Moreover, it is apparent that measurement of jackal home range size over a short period, or by using a few data points, or by lumping all data to obtain a high total number of locations does not give a true reflection of the total picture.

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If indeed reduced ranges are used, the larger area should be retained as an "impact area: an area through which an animal travels and on which it impacts occasionally" (Springer 1982:196). This definition is highly suitable for the present study, with one of these impacts being predation on impala outside of the core area (Figs 4 and 5).

The progressive nature of the excursions is illustrated by the telemetric data presented in Fig. 11 a,b,c & d. Some of the zig-zagging is as a result of telemetric error, but the excursionary nature of the peripheral locations is apparent from the overall out-and-back movement pattern during excursions. These patterns are of the type defined as "ranging" movements for coyotes (Laundrė & Keller 1981).

Extensive sallies by jackals were recorded only from May onwards. The longest such excursion recorded through direct observation was by jackal no. 16, and involved a round trip of 7,1 km over 8,5 h. Jackal no. 11 was observed sleeping while out on excursions on nine occasions. However, as with the other jackals, no. 11 always returned to his core area folowing an excursion.

Mean distances moved per night should provide an indication of the increasing length of sallies through winter. However, due to the fact that only three jackals were monitored, and that continuous 24 h monitoring was not used, no comparisons can be drawn. Direct observations were spaced 3-4 h apart, and it is known from the present study, and from Ferguson *et al.* (1983), that jackals can travel several kilometres in this period. If this is of the out-and-back pattern recorded here, then part or all of the excursion could be missed. The telemetric monitoring did not reveal any significant

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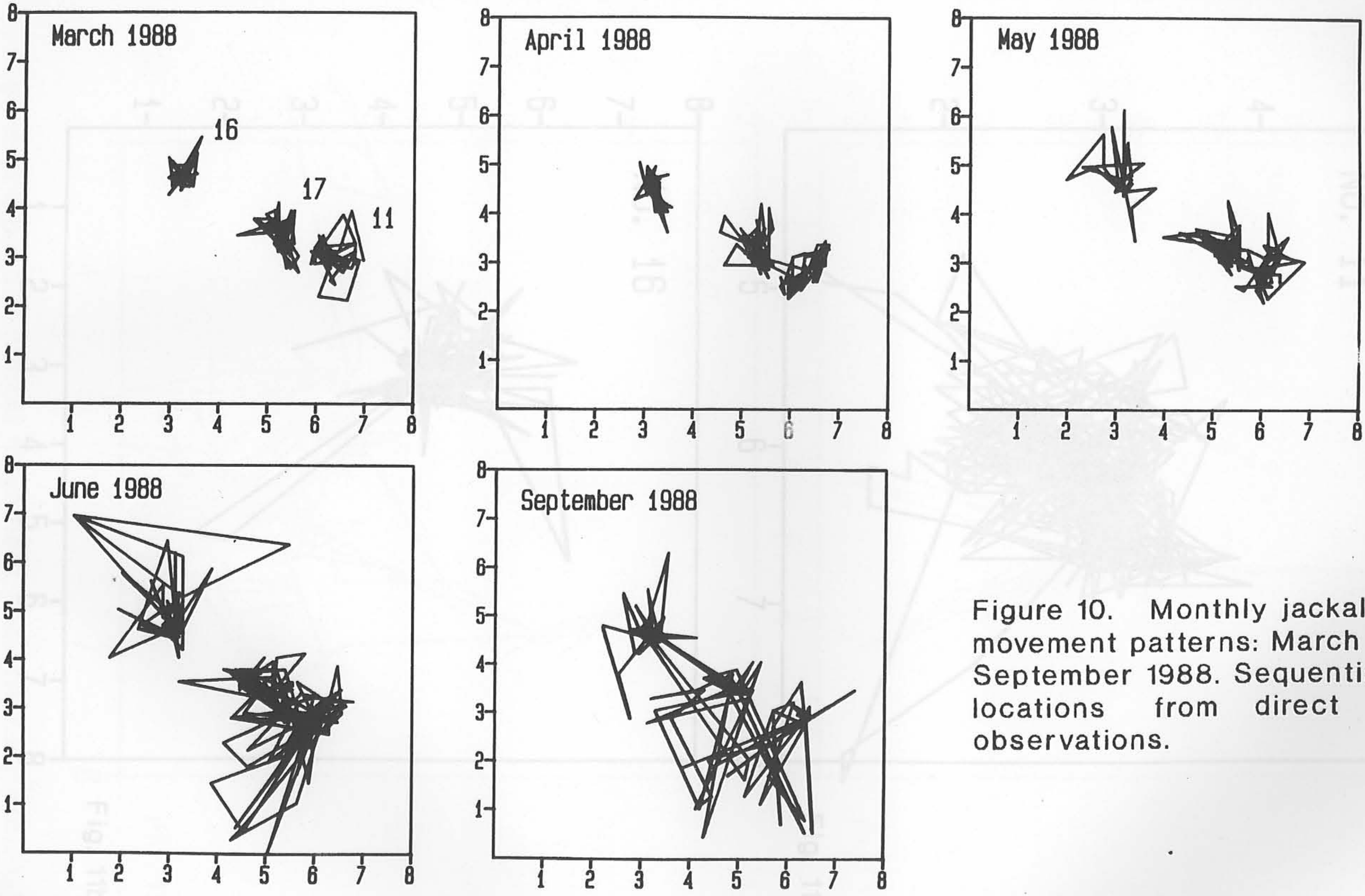

Figure 10. Monthly jackal movement patterns: March - September 1988. Sequential locations from direct observations.

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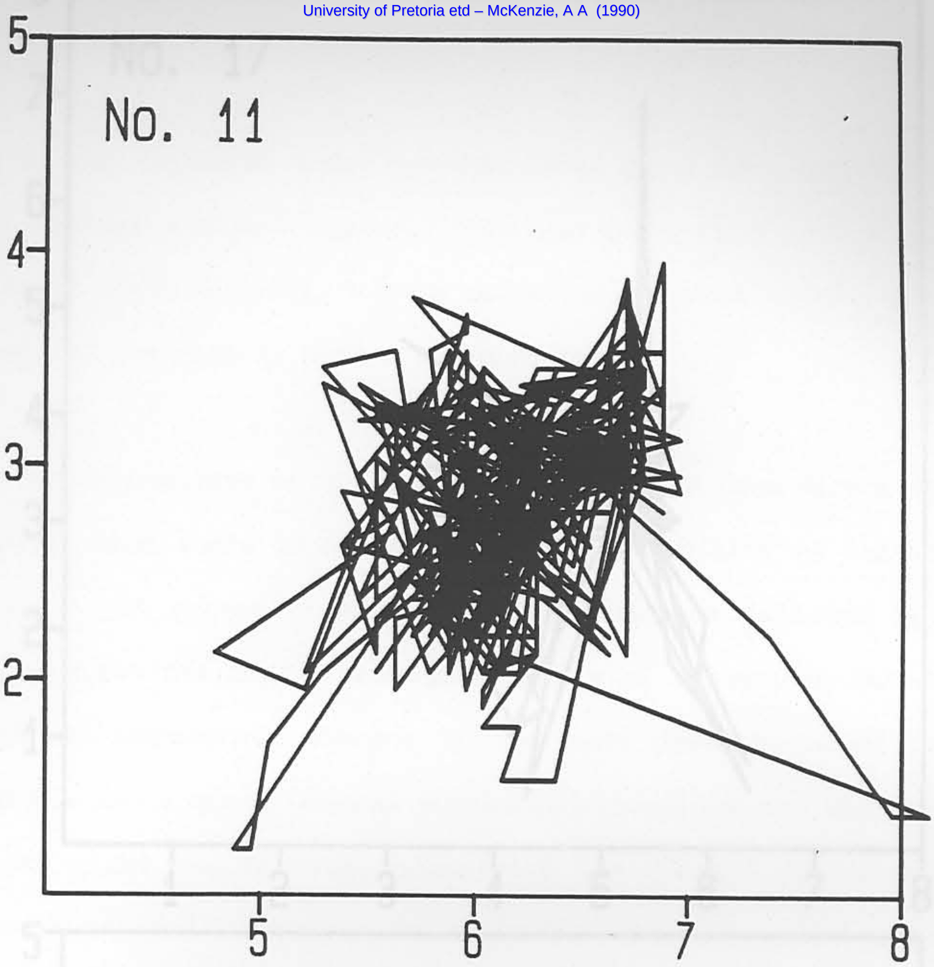

Fig. 11a

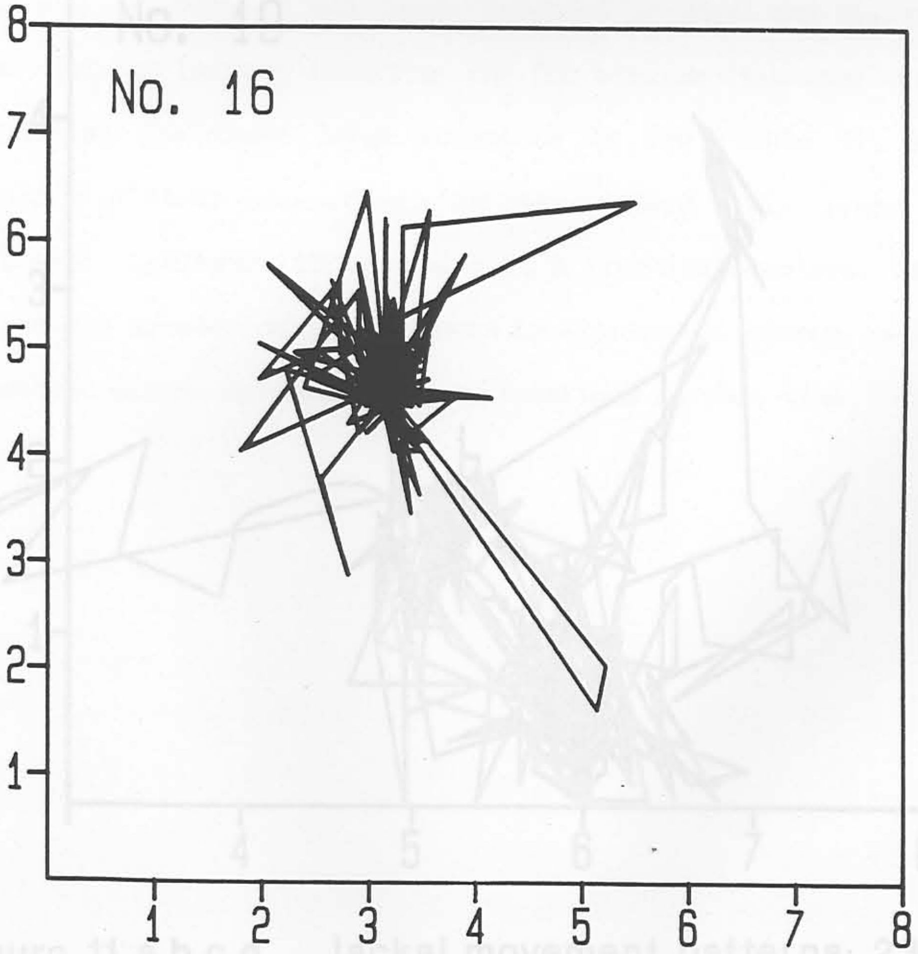

Fig. 11b

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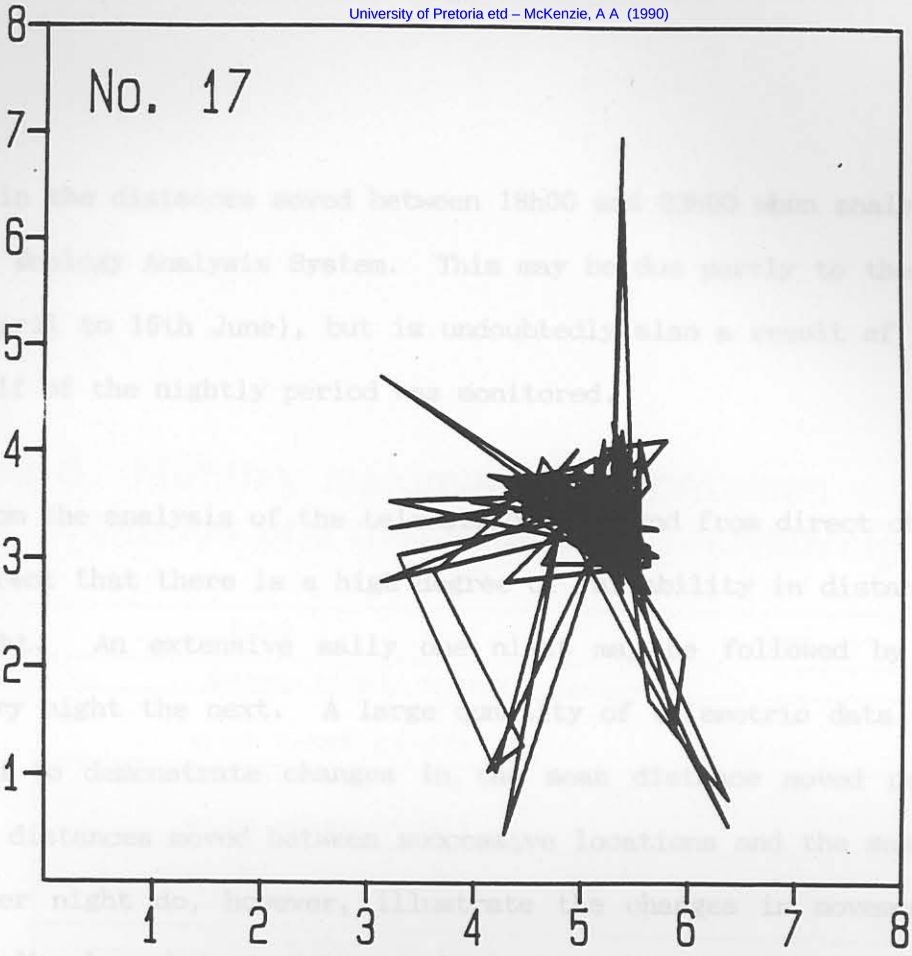

Fig. 11c

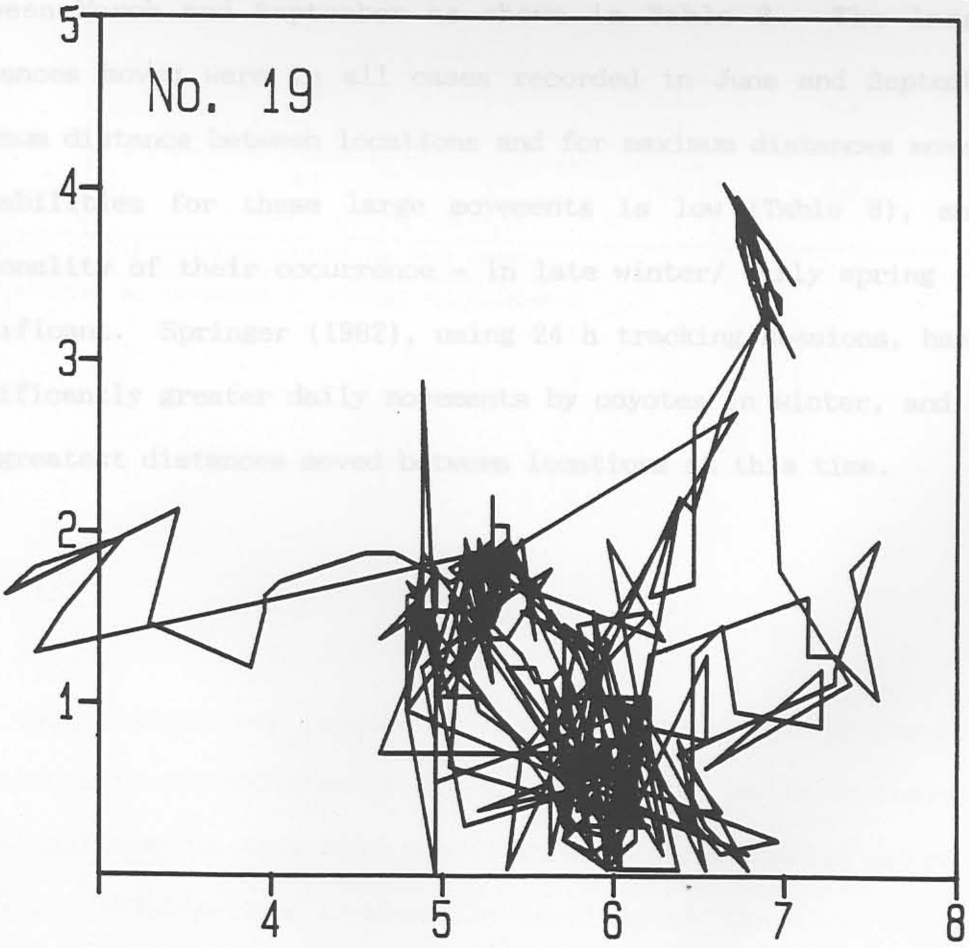

Fig. 11d

Figure 11 a,b,c,d. Jackal movement patterns: 23 April - 15 June 1988. Sequential locations, 20 min intervals, 18h00-23h00 and 06h00-08h00.

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trends in the distances moved between 18h00 and 23h00 when analysed using the Spatial Ecology Analysis System. This may be due partly to the short period (23rd April to 15th June), but is undoubtedly also a result of the fact that only half of the nightly period was monitored.

From the analysis of the telemetric data, and from direct observation, it is apparent that there is a high degree of variability in distances travelled per night. An extensive sally one night may be followed by a relatively sedentary night the next. A large quantity of telemetric data would thus be required to demonstrate changes in the mean distance moved per night. The maximum distances moved between successive locations and the maximum distance moved per night do, however, illustrate the changes in movement parameters between March and September as shown in Table 8. The largest maximum distances moved were in all cases recorded in June and September, both for maximum distance between locations and for maximum distances moved/night. The probabilities for these large movements is low (Table 8), and the marked seasonality of their occurrence - in late winter/ early spring - is therefore significant. Springer (1982), using 24 h tracking sessions, has demonstrated significantly greater daily movements by coyotes in winter, and also recorded the greatest distances moved between locations at this time.

Table 8. Monthly maximum dist. between successive locations and maximum dist. moved/night.

Jackal number		March	April	May	June	Sept.
	Distance between successive locations					
11		0,9	1,3	1,2	3,4	2,7
		n=147, x=0,66, s.d.=0,63			p=0,025	
16		1,2	0,8	2,4	3,2	3,5
		n=135, x=0,62, s.d.=0,70				p=0,040
17		1,1	1,1	1,8	2,0	3,3
		n=168, x=0,64, s.d.=0,60				p=0,023
	Distance moved per night.					
11		2,0	1,8	2,3	3,8	5,4
		n=46, x=2,11, s.d.=1,42				p=0,042
16		1,9	2,0	3,8	9,6	7,2
		n=46, x=1,84, s.d.=1,93			p=0,0001	p=0,0023
17		2,5	2,4	2,7	3,5	5,3
		n=51, x=2,04, s.d.=1,16				p=0,038

Monthly figures represent maxima for that month.
All distances in km. Data from direct observations.
Probabilities (p) calculated for Poisson distribution of data.

Activity

While obtaining telemetric movement data, the opportunity was used to monitor activity patterns of the study jackals. While extensive activity data were collected in this way, the failure of the automatic activity recorder to provide reliable data resulted in sampling at the times of greatest jackal activity - i.e. 18h00 to 23h00 and 06h00 to 08h00. These data alone were thus of no use in determining daily activity patterns, and were discarded. However, sufficient data are available from direct observations to make some deductions concerning the activity patterns of jackals in the NTGR.

As 45% of direct observations did not detail the activity type due to limited visibility and accessibility and limited offroad travelling, detailed analysis of time-budgets falls beyond the scope of the present study.

Total Activity

The definition of total activity used here is "... the actions of an animal while it is not resting or sleeping" (Ferguson *et al.* 1983).

An analysis of the times at which jackals were found to be active reveals a bigeminus pattern of activity as described by Ferguson *et al.*, and as reported by Hiscocks & Perrin (1988) (Fig. 12). However, the results from the present study reveal a smaller trough of activity between 24h00 and 06h00 compared to the abovementioned studies. As recorded by Fuller *et al.* (1989), activity between 00h00 and 05h00 remained substantial in contrast to observations by Ferguson (1980) in the Kalahari Gemsbok National Park and as revealed by the activity graphs of Hiscocks & Perrin (1988) and Fuller *et al.* (1989). In addition, the peak of evening activity lasts approximately 4 h in the present study cf. 1-2 h in Ferguson *et al.* These differences may, however, be due to the different methods used.

Jackals appear only to become strictly nocturnal when persecuted (van der Merwe 1953, Smithers 1983, Goss 1986). The jackals in the present study were not persecuted and were often seen to be active during daylight. Times of inactivity during daylight were almost invariably spent in the shade of a tree or bush (see below), indicating that temperature plays at least some role in the maintenance of the largely nocturnal activity of the jackal.

Insufficient data are available to test for the influence of season, age, sex and light conditions on activity as reported by Ferguson *et al.* (1983). However, it was noted from observations and during telemetric tracking that peak activity, and particularly the most extensive ranging movements, occurred during nights of medium lunar intensity vs full moon and new moon, as noted by these authors.

Inactivity

Periods of inactivity, both during the day and at night, were largely confined to open habitat types (see Habitat Use below).

During daylight, jackals were observed to make use of trees and bushes for shade. However, these favoured resting places were also elevated and open, thus providing a good view of surrounding areas as observed by Ferguson (1980) in the Kalahari Gemsbok National Park. Many other non-study jackals were noted to have the same choice as regards resting places. The few occasions when jackals were seen resting within or underneath low bushes were associated with cold windy weather. The jackals would shelter in the lee of the bush as described for jackals from the coastal areas of Namibia which shelter behind sand hummocks while feeding (Avery *et al.* 1987).

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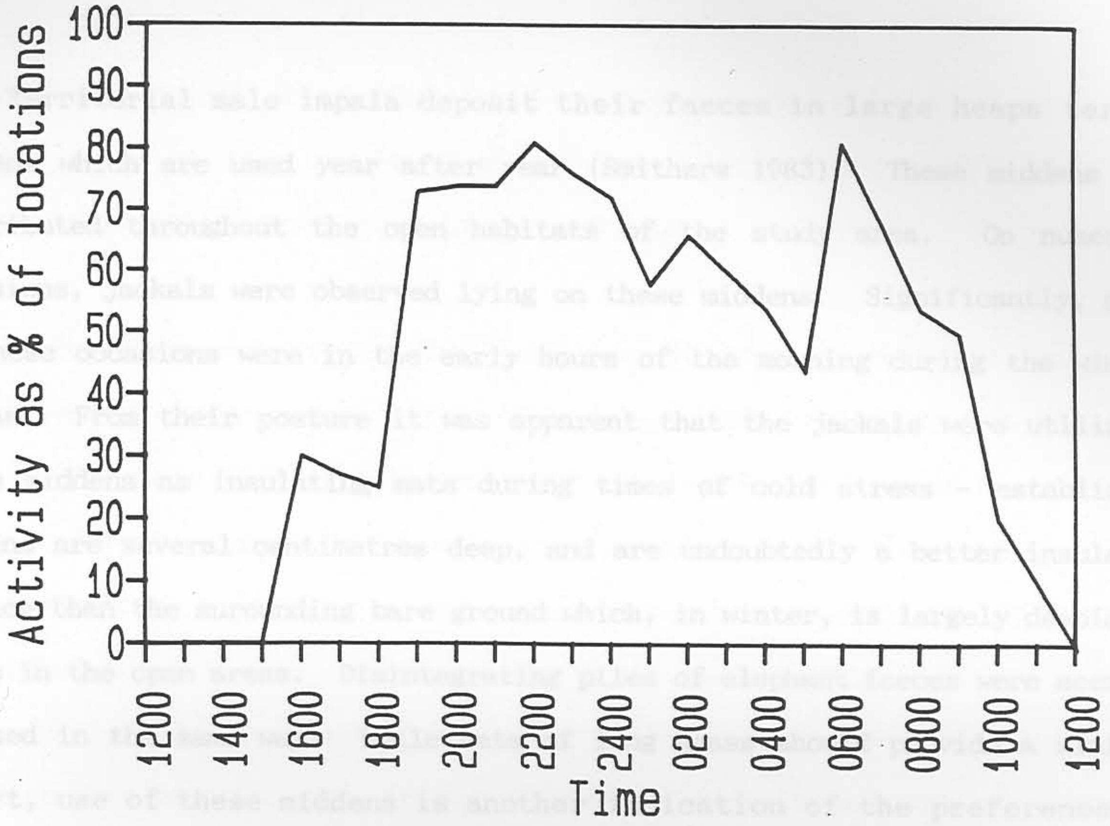

Figure 12. Hourly activity levels of jackals as determined by direct observation. n = 528.

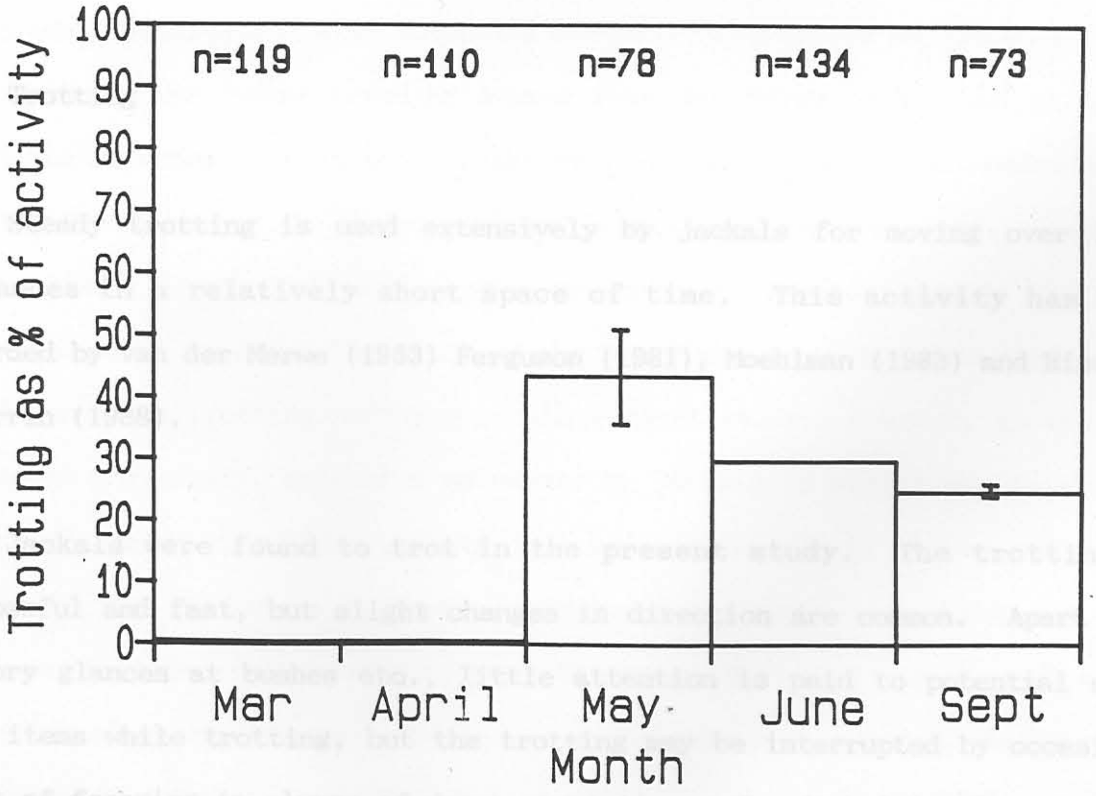

Figure 13. Relative frequency of trotting activity by jackals: March - September 1988. Vertical bars represent standard deviations.

Territorial male impala deposit their faeces in large heaps termed middens which are used year after year (Smithers 1983). These middens are distributed throughout the open habitats of the study area. On numerous occasions, jackals were observed lying on these middens. Significantly, most of these occasions were in the early hours of the morning during the winter months. From their posture it was apparent that the jackals were utilizing these middens as insulating mats during times of cold stress - established middens are several centimetres deep, and are undoubtedly a better insulated surface than the surounding bare ground which, in winter, is largely devoid of grass in the open areas. Disintegrating piles of elephant faeces were seen to be used in the same way. While mats of long grass should provide a similar effect, use of these middens is another indication of the preference by jackals for open habitat (see Habitat Use below). Extensive use of the middens by jackals is indicated by the collections of bones on these heaps (pers. obs.).

Fast Trotting

Steady trotting is used extensively by jackals for moving over large distances in a relatively short space of time. This activity has been recorded by van der Merwe (1953) Ferguson (1981), Moehlman (1983) and Hiscocks & Perrin (1988).

Jackals were found to trot in the present study. The trotting is purposeful and fast, but slight changes in direction are common. Apart from cursory glances at bushes etc., little attention is paid to potential small prey items while trotting, but the trotting may be interrupted by occasional bouts of foraging in clumps of dense vegetation. The jackal is alert, and it trots at a fast pace along established paths and roads, and the extensive use made of roads by this species (van der Merwe 1953, Bearder 1975, Ferguson 1980) can probably be ascribed to this activity.

While no seasonality in the occurrence of trotting activity was noted during 1987, a distinct seasonality occurred in 1988. Following the extensive rains of February 1988, hunting activity was largely restricted to leisurely foraging for the insects which were super-abundant during this period. Thus fast trotting as a specific activity pattern was not observed during March or April, but suddenly increased to 43,3% of all observations of active jackals in May - Fig. 13. Despite the subsequent decline to (29,7 and 24,7%) in June and September respectively, frequency of this activity remained considerably higher than in the earlier months of the year. While the decline in occurrence between May and June is significant ($t=2,86$, $p<0,05$), this cannot be ascribed to any sudden changes in environmental conditions over and above the gradual dessication with advancing winter. However, as May is known to be the onset of the jackal breeding season (van der Merwe 1953), and as jackal movements increase at this time of the year (present study), the sudden advent of fast trotting may be linked to this aspect of jackal biology. Andelt & Gipson (1979) found that wide-ranging movements by coyotes precede the onset of the breeding season. The onset of the breeding season may thus explain the initial peak in trotting activity in the present study. However, as was also discussed previously, extensive movements by jackals in winter may be related to the change in diet from insects in summer to impala in winter. With the supply of the latter in discrete, dispersed packages, trotting may be a response to the need to cover large distances during foraging excursions. Extension of coyote ranges in winter is associated with a rapid, ranging type of movement pattern (Laundré & Keller 1981, Roy & Dorrance 1985), and the winter extension of jackal home range recorded in the present study may be linked to the simultaneous change in the mode of activity recorded here.

Habitat use

The eight habitat types within the study area are so intricately interwoven that any demarcation of boundaries on a map would be contrived. Any trends or conclusions based on such an attempted demarcation would thus be of no use at all. From observations made during the study it became apparent that jackals made preferential use of open areas within each habitat type. As visual cues are important both in foraging and in predation avoidance in this species, open habitat, from a jackal's perspective, must comprise a habitat which provides good visibility. The eight habitat types cannot be clearly distinguished on this basis, as each consists of a mosaic of shorter and longer vegetation. However, each habitat type is clearly either predominantly open or predominatly closed. For the purpose of habitat preference analysis, the predominantly open habitats (*Boscia foetida* savanna, *Colophospermum mopane/ Terminalia prunoides* middleslopes, *Colophospermum mopane* scrubveld, and *Salvadora angustifolia* brushveld) and the predominatly closed habitats (Valley bush, *Acacia tortilis* savanna, and *Croton megalabotrys* thicket) were lumped together. These comprise a mean of 38% and 62% of the home ranges covered by the 3 jackals respectively (Fig. 14).

Activity and Habitat Use

In March a mean of 73% of observations on active jackals were made in the open habitats - depicting a significant selection for open habitat (X^2=25,3, p<0,001, d.f.=1). This confirms the observation that, during this time, the jackals foraged extensively in open areas for the abundant insect prey. As dessication advanced, and insect prey became noticeably scarcer in the dry open areas, jackals were seen to spend more and more time in the denser, greener parts of the respective habitats. This is reflected in the decreased overall use of open habitats as winter advanced - Fig. 15. The use of open habitat differs significantly over the period of observation (X^2=33,09, p<0,001,d.f.=4), with the preference for open habitat in March contributing most to the difference (X^2=23,09, p<0,001).

The results of the direct observations and the habitat use analysis indicate that, where possible, jackals are active in open habitat. Even when observed in dense habitat, jackals made extensive use of open areas, especially roads and paths, and a microhabitat analysis would possibly reveal an even stronger preference for open areas. Furthermore, Ferguson (1980) found that mixed bushveld habitat in the western Transvaal was used more extensively than open grassveld. This was ascribed to greater prey availability in the bushy areas. However, the persecution of jackals was noted to be a possible confounding factor, forcing jackals to remain within relatively closed habitat.

The discrepancy in findings of these two studies can possibly be ascribed to the phenomenon of risk-sensitive foraging. Jackals are preyed upon by leopards (Estes 1967, Lind 1972, Ferguson 1980, present study), and leopards were present in the study area (Lind 1974, pers. obs.). Leopards preferentially hunt in closed habitat, as they use concealment to facilitate close approach to potential prey (Smithers 1983). During the present study jackals were observed to mob leopards on many occasions (as described by Goss

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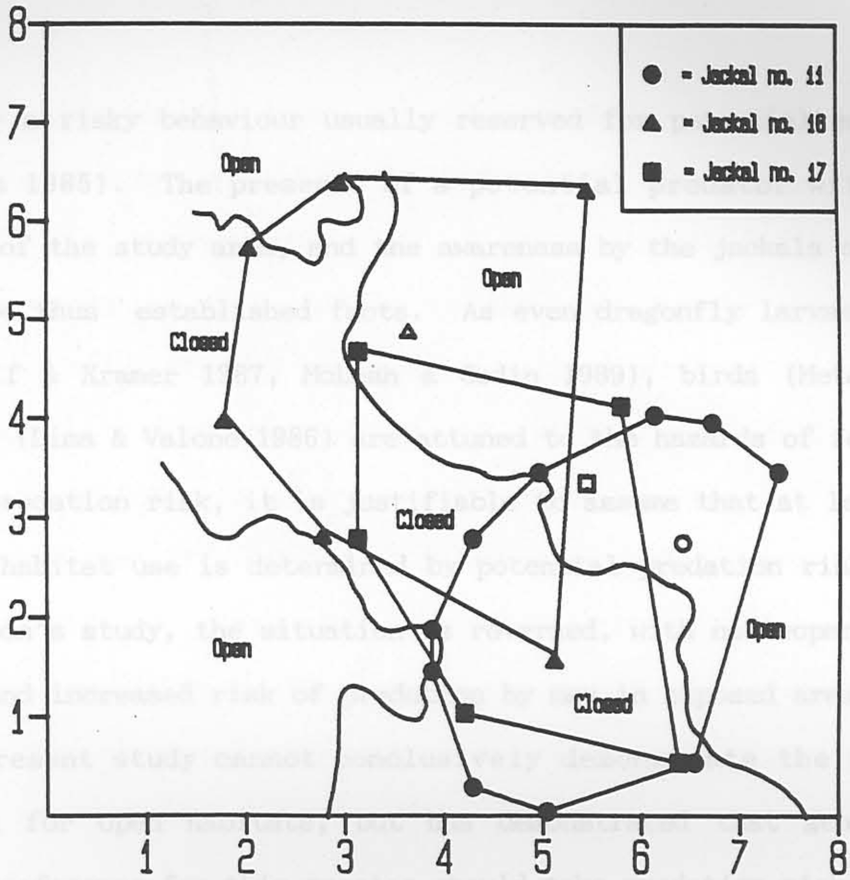

Figure 14. Total jackal home ranges relative to open and closed habitats: 1988.

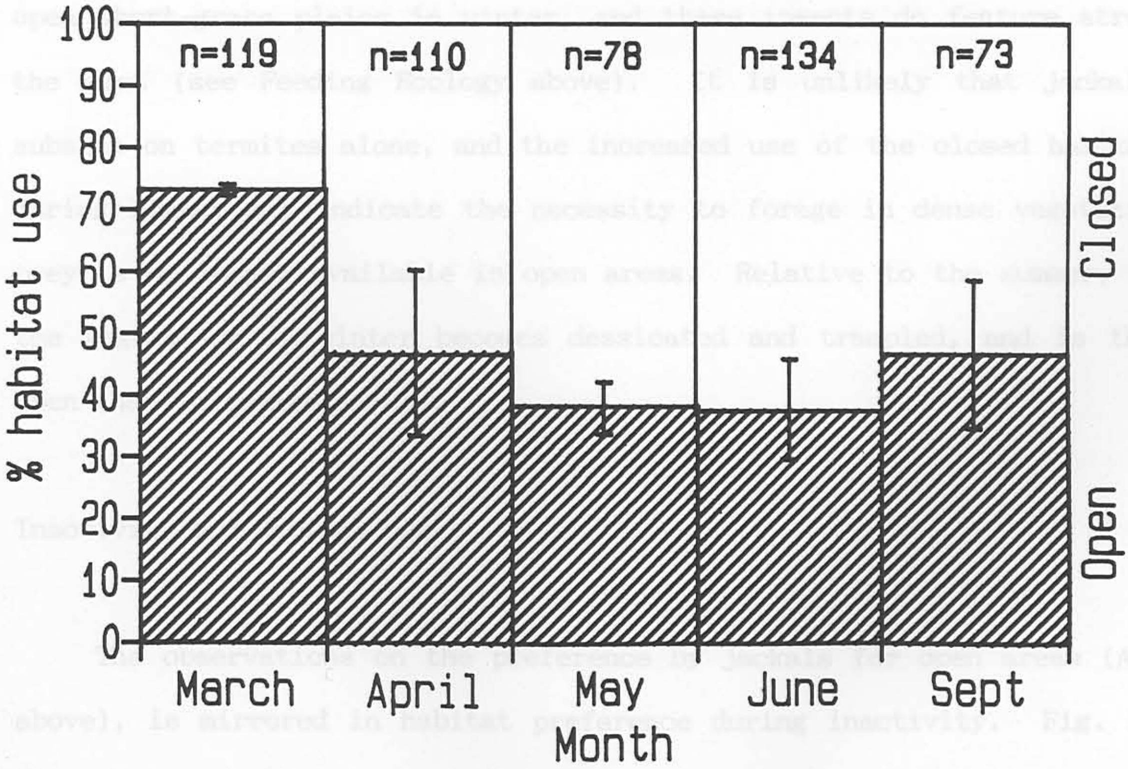

Figure 15. Use of open vs. closed habitat types by jackals during activity: March - September 1988. Vertical bars represent standard deviations.

(1986)) - a risky behaviour usually reserved for potential enemies (Curio & Regelmann 1985). The presence of a potential predator within the dense habitats of the study area, and the awareness by the jackals of the potential threat are thus established facts. As even dragonfly larvae (Pierce 1988), fish (Wolf & Kramer 1987, McLean & Godin 1989), birds (Metcalfe 1984) and squirrels (Lima & Valone 1986) are attuned to the hazards of foraging in areas of high predation risk, it is justifiable to assume that at least some of the jackal's habitat use is determined by potential predation risk. In the case of Ferguson's study, the situation is reversed, with no leopards in the dense habitat and increased risk of predation by man in exposed areas. The results of the present study cannot conclusively demonstrate the reason for the selection for open habitats, but has demonstrated that generalizations on habitat preference for this species should take predation risk into account.

Harvester termites were the only insects observed in large numbers on the open short-grass plains in winter, and these insects do feature strongly in the diet (see Feeding Ecology above). It is unlikely that jackals could subsist on termites alone, and the increased use of the closed habitat types during winter may indicate the necessity to forage in dense vegetation when prey is no longer available in open areas. Relative to the summer, however, the vegetation in winter becomes dessicated and trampled, and is thus more open than in summer anyway.

Inactivity and Habitat Use

The observations on the preference by jackals for open areas (Activity, above), is mirrored in habitat preference during inactivity. Fig. 16 shows that the most open habitat, *Boscia foetida* savanna, is preferentially selected

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above all other habitat types for all periods of inactivity. This habitat comprises approximately half of the open habitat utilized by the three jackals (Fig. 14), i.e. approximately 19% of the available habitat. The 76% of resting activity in this habitat is therefore highly significant (X^2=105, p<0,001, d.f.=1). Use of the open vs. closed habitats during inactivity by the jackals is illustrated in Fig. 17, with a mean utilization of 83% vs availability of 38%. In all cases, selection for open vs. closed habitat is highly significant (X^2, p<0,001). Sites where jackals were found resting are depicted in Fig. 18. As can be seen, the majority of these sites fall in open habitat and are within the March minimum seasonal range. Jackal no. 11 is the only exception in having some of his resting sites in closed habitat far away from his core area. However, these observations account for only 5% of inactivity observations on no.11.

The selection for open habitat during inactivity supports the above suggestion that risk-sensitive activities may determine habitat use by jackals in the presence of a potential predator. In the case of inactivity, habitat preference is not complicated by factors such as food abundance. The strong selection for open habitat during rest is therefore a significant aspect of jackal biology recorded during the present study. On the other hand, this contrasts with the observations by Ferguson (1980) of jackals in the Transvaal resting in dense clumps of vegetation, and highlights the impact that persecution by man has on micro- and macro-habitat use by this species.

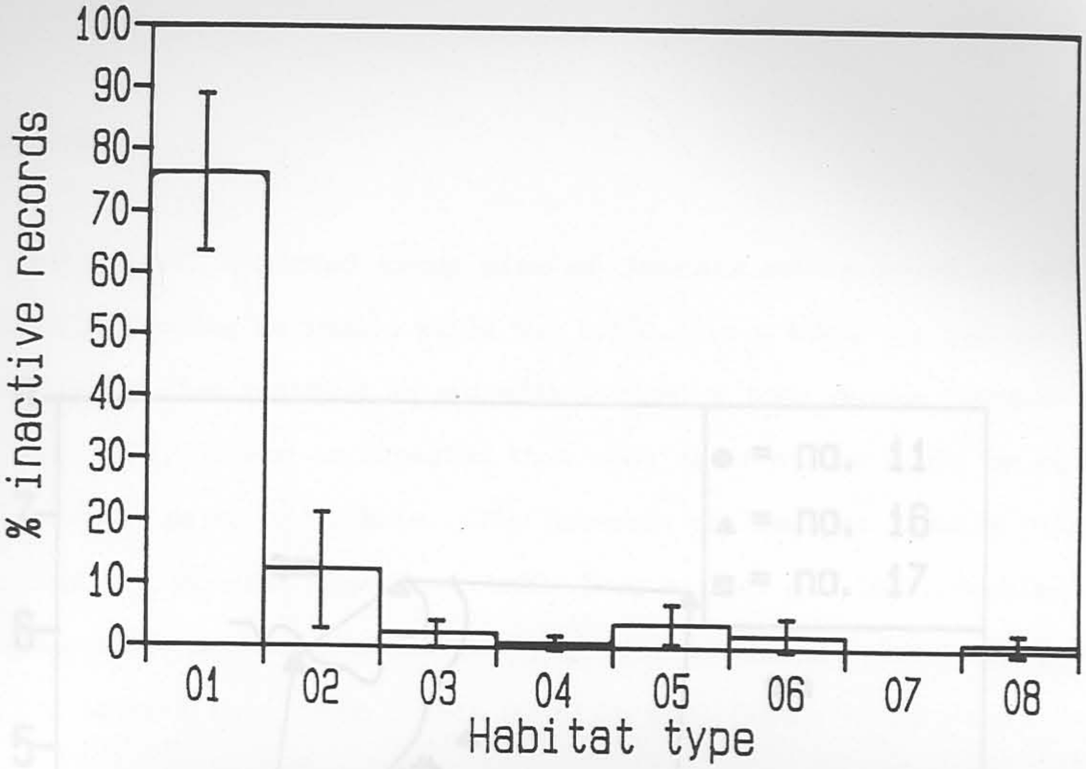

Figure 16. Use of habitat types by jackals during inactivity. 01= B.foetida savanna (O), 02=Valley bush (C), 03= *A.tortilis savanna (C),* *04=* C.*megalobotrys* thicket (C), 05=*C.mopane/T.prunoides* middle slopes (O), 06=Erosion plains (O), 07=C.mopane *scrubveld (O)*, *08= S.angustifolia / A.tortilis* brushveld (O). O= open, C= closed. Vertical bars represent standard deviations.

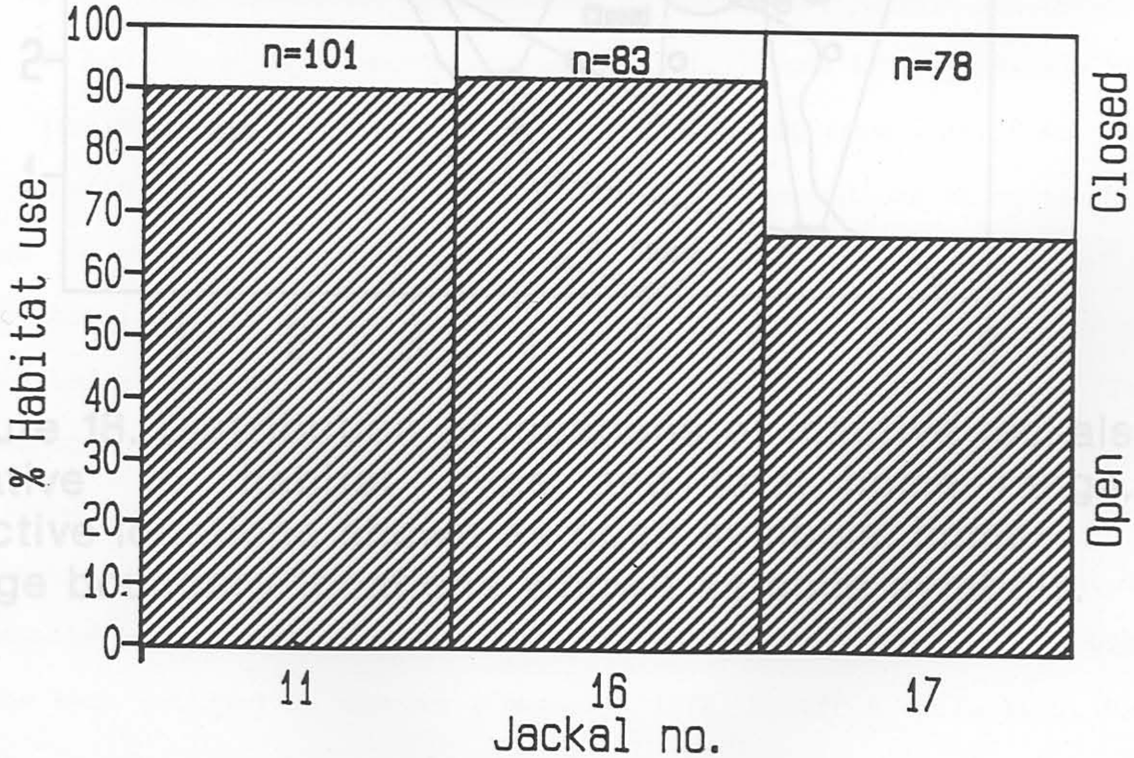

Figure 17. Individual use of open vs. closed habitat types by jackals during inactivity.

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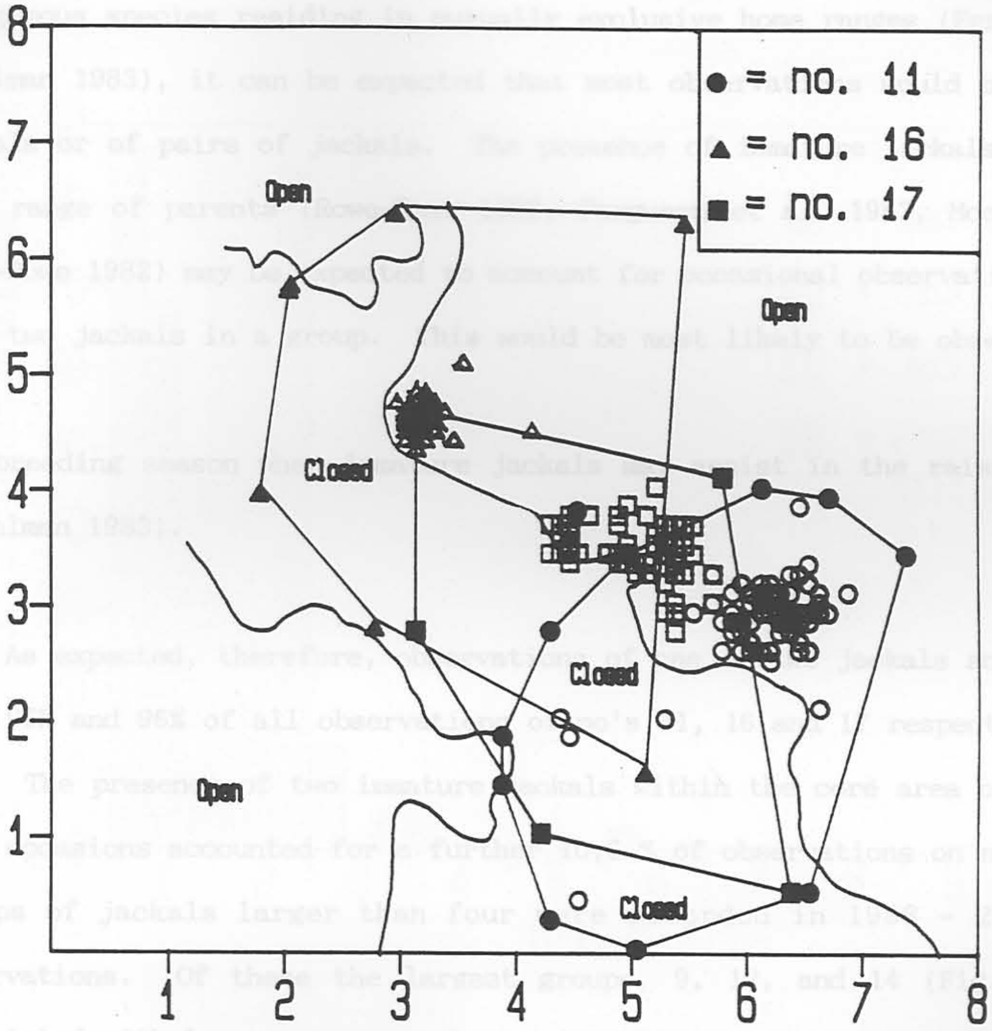

Figure 18. Distribution of locations of inactive jackals relative to habitat type and total home range. Inactive locations shown as open symbols, home-range boundary locations whown as solid symbols.

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Group Size

The overall observed group size of jackals not scavenging at large carcases or feeding on impala kills was 1,6±0,7 (n = 489). As the jackal is a monogamous species residing in mutually exclusive home ranges (Ferguson 1980, Moehlman 1983), it can be expected that most observations would be of single jackals or of pairs of jackals. The presence of immature jackals within the home range of parents (Rowe-Rowe 1982, Ferguson *et al.* 1983, Moehlman 1983, Rowe-Rowe 1982) may be expected to account for occasional observations of more than two jackals in a group. This would be most likely to be observed during the breeding season when immature jackals may assist in the raising of pups (Moehlman 1983).

As expected, therefore, observations of one or two jackals accounted for 86%, 95% and 96% of all observations of no's 11, 16 and 17 respectively (Fig. 19). The presence of two immature jackals within the core area of no. 11 on many occasions accounted for a further 10,6 % of observations on no. 11. Ten groups of jackals larger than four were recorded in 1988 - 2,1% of all observations. Of these the largest groups, 9, 12, and 14 (Fig. 19), were associated with large carcases of animals killed by lions or cheetahs. Three of the groups of 6 jackals were associated with feeding on large carcases. The remaining large groups of 5, 5, 6, and 7 could not be explained by the presence of a large scavengeable resource or a jackal kill. Insufficient data are available to indicate whether the larger groups occur more often in winter as has been recorded in coyotes (Camenzind 1978, Bekoff & Wells 1980, Bowen 1981).

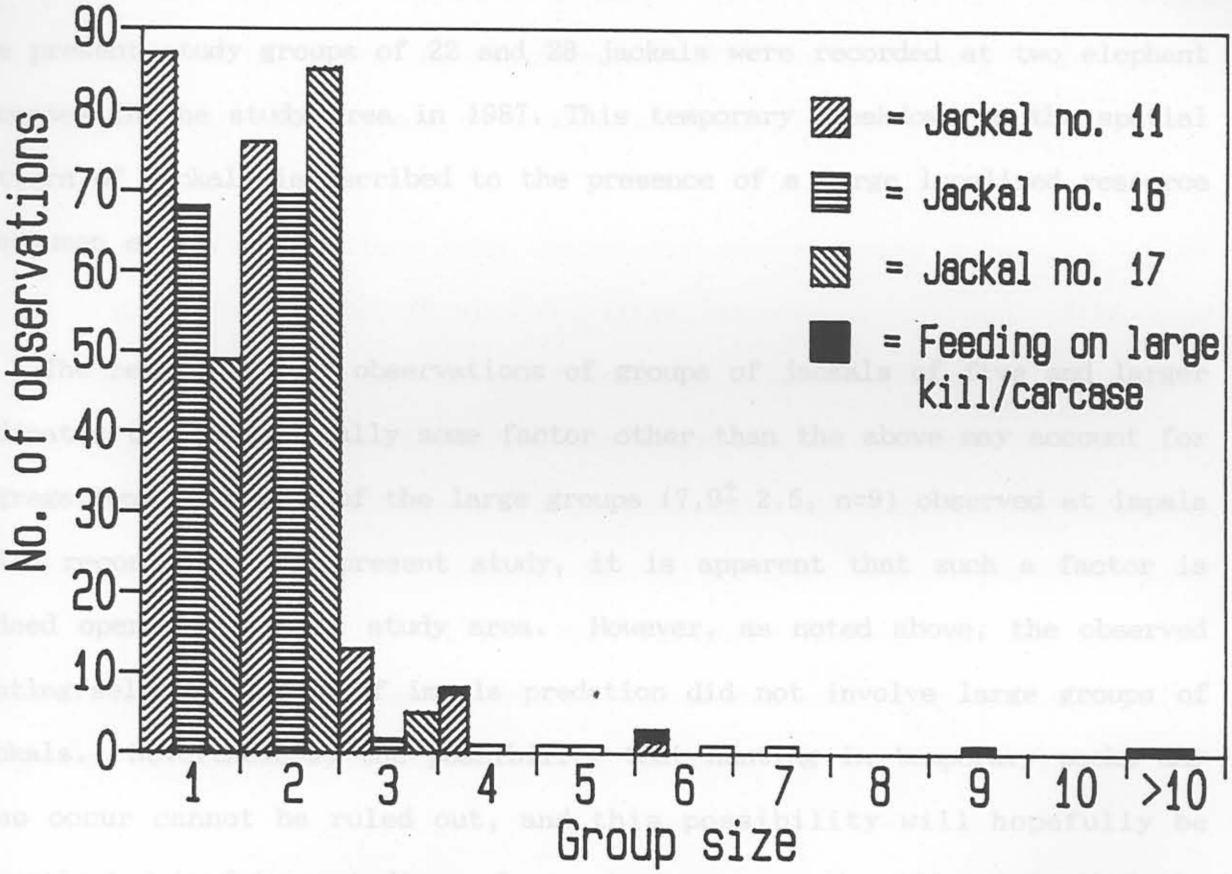

Figure 19. Group size frequency distribution. n = 489.

It is readily apparent from the predominance of observations of one or two jackals that the jackals of the NTGR do not live in packs, nor do they regularly forage in packs. Occasional aggregations of large numbers of jackals at large carcases is well known (van Lawick-Goodall 1970a, Schaller 1972, Ferguson *et al.* 1983, Moehlman 1983, Hiscocks & Perrin 1987). During the present study groups of 22 and 28 jackals were recorded at two elephant carcases in the study area in 1987. This temporary breakdown in the spatial pattern of jackals is ascribed to the presence of a large localized resource (Ferguson *et al.* 1983).

The remaining four observations of groups of jackals of five and larger indicates that occasionally some factor other than the above may account for aggregations. In view of the large groups (7,9 ± 2,5, n=9) observed at impala kills recorded in the present study, it is apparent that such a factor is indeed operative in the study area. However, as noted above, the observed hunting/selection phase of impala predation did not involve large groups of jackals. Nevertheless, the possibility that hunting in temporary packs may also occur cannot be ruled out, and this possibility will hopefully be investigated in future studies. I can, however, unequivocally state that the "packs" which were observed were ephemeral aggregations. There is thus no evidence that the jackals in the NTGR have resorted to pack living as has been reported for coyotes (Camenzind 1978, Hilton 1978, Bekoff & Wells 1980, Bowen 1981, 1982, Smith, Neff & Woolsey 1986) and even golden jackals (MacDonald 1979). In the light of the results of the present study and the study of Hiscocks & Perrin (1988), it would appear that black-backed jackals do not resort to living in packs in densely populated areas as observed in coyotes (Bowen 1981).

Population Density

1. Mark-recapture estimate

Resighting frequency varied by a factor of 3,3 between the five marked jackals included in random observations in 1988. The data thus could not be used for a meaningful estimate of population density.

The random observations made during the present study were made on an opportunistic basis to fit in with the other research activities. With some of the roads passing through the favoured resting areas of some of the marked jackals (eg. no. 16), biased sighting frequency was inevitable. In addition, the core area plus excursion movement pattern makes the likelihood of sighting jackals unequal at different times of the day. These limitations would have to be overcome in order to utilize mark-recapture methods on this species. Regular traversing of a fixed route at a fixed time would possibly enable the conditions for mark-recapture analysis to be met.

2. Home Ranges

From the analysis of home ranges it was apparent that the March home ranges represented minimum seasonal home ranges with minimal overlap between ranges of adjacent family groups (above). As such, these represent the area exclusively occupied by an adult pair of jackals with their associated offspring.

The mean minimum seasonal home range determined in the present study was

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$0{,}97\pm0{,}45$, n=3). (This figure may appear small, but is well above the estimated minimum home range size of 0,11 km^{2} estimated for golden jackals by MacDonald (1979). At an estimated minimum of 4 jackals/family, the density of jackals in the study area is thus 4 km^{-2}. If the figure of 7 - 8 jackals/adult home range used by Rowe-Rowe (1982) is applied, a density of 7 - 8 jackals km^{-2} is obtained.

3. Known Jackal Groups

The core areas of known jackal family groups within the part of the study area most intensively traversed are plotted by hand in Fig. 9. This map yields a total of 9 jackal families in an area of 10,3 km^{2}. Using the above estimates of the numbers of jackals/family, an estimate of between 3,5 and 7 jackals per km^{2} is obtained.

Jackal population densities have been calculated by Rowe-Rowe (1982) (0,3-0,4 km^{-2}) and Hiscocks & Perrin (1988) ($22\pm2{,}23$ km^{-2}). The results of the present study therefore fall within the range of these data, the former from a conserved montane region of Natal and the latter from the coast of Namibia. In the case of the latter, the high densities are ascribed to the presence of a super-abundant food resource in the form of seal carcases from a nearby seal colony.

In view of the fact that the two coarse estimates used here are in close agreement, an estimate of 4 - 7 jackals km^{-2} of the study area is justified. While absolute density is thus not determined (and indeed does not exist, given the wide-ranging movements of the young jackals which can cause chaotic fluctuations in density), the estimate remains high in comparison with the results of Rowe-Rowe (1982). This author used total home ranges for his calculations, and thus may have underestimated the density. A high population of jackals was reported in the Reserve by Lind (1972). This observation was confirmed by casual observations made by myself as well as many other residents and visitors to the Reserve.

Studies by MacDonald (1979) and Hiscocks & Perrin (1988) indicate that in the presence of a super-abundant food supply, jackal population density can become extremely high. In the former study, a density of 195 golden jackals km^{-2} was recorded where abundant food was supplied at an artificial feeding point on a constant basis. The present study records the availability of an abundant food supply in the form of old impala which lose condition following the end of summer (Chapter 4). While the old impala are not a source of scavengeable food, their extremely poor condition (Table 3) indicates that they are probably relatively easily subdued by a pack of jackals, and thus consitute a reliable source of high quality food at a time of the year when food supply might otherwise be limiting. With the demonstrated ability of jackal populations to reach densities of more than 20 km^{-2}, the 4 - 8 km^{-2} estimated in the present study is acceptable. The consequences of the presence of this high jackal population in the Reserve are discussed in Chapter 7.

Conclusion

The present study has demonstrated that jackals in the Northern Tuli Game Reserve do prey on adult impala. It has shown that this predation:

1. Is regularly undertaken by jackals in the study area;

2. Is highly selective for vulnerability as reflected in advanced physiological age, poor condition, and/or injury;
3. Is opportunistic, in that the impala are preyed upon when they are most available (i.e. vulnerable);
4. Is seasonal, the seasonality depending on the abundance of other prey; and
5 Is co-operative, being undertaken by temporarily co-operating groups larger than the average social group in the population.

Opportunistic predators capture prey according to (an often unmeasurable index of) relative availability (Jaksic 1989). Old impala occur in the Reserve where the present study was conducted (Chapter 4). Old impala lose condition more markedly than other impala during late winter (Dunham & Murray 1982). Relative vulnerability is a measure of availability of prey to a predator which is selective for vulnerability - selective predators being those predators which prey disproportionately on a certain component of the available prey population (Jaksic 1989). Availability of old impala to jackals, through loss of condition, therefore increases in winter. Increased predation at a time of increased availability reflects a component of opportunism. Availability is only rarely measurable, therefore often limiting the use of the term opportunistic (Jaksic 1989). However, the results of the present study indicate that jackals are both opportunistic and selective predators.

The demonstrated ability of black-backed jackals to capture medium sized antelope is yet another parallel between this species and the coyote. Seasonal changes in home range size and movement patterns also show a strong similarity between these two species in responding to environmental cues. The wealth of information available on coyote biology could therefore be consulted

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to assist further research on the black-backed jackal.

In ending the speculation (Sleicher 1973, van Lawick-Goodall 1970a, Lamprecht 1978a, Smithers 1983) on the ability of jackals to regularly hunt such relatively large prey, the present study opens an array of questions which cannot be adequately adressed in this thesis. Some of these are discussed in Chapter 7. Others, based on the findings presented here, will require further specific investigations to be satisfactorily resolved.

Meanwhile, the co-operative, selective predation by black-backed jackals on the impala in the Northern Tuli Game Reserve continues. That this is the first description of regular predation on adult antelope may be due partly to the fact that little direct observation of jackal behaviour has been undertaken, particularly nocturnal observation. There is strong evidence to suggest, as discussed in Chapter 7, that this predation is the acquired result of a specific set of circumstances peculiar to the NTGR at this particular time. Therefore jackals in all regions, at all times, may not be concluded to be regular predators of medium sized adult ungulates and, in particular, the present study does not provide any evidence that jackals should be regarded as wanton or destructive predators. In fact, as is demonstrated in Chapter 7, jackals may play a pivotal role in maintaining some semblance of resilience in stressed ecosystems.