

Winter food and foraging behaviour of the aardwolf *Proteles cristatus* in the Namib-Naukluft Park

by

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ABSTRACT

Food of *Proteles cristatus* in the Namib Desert during two years consisted mainly of termites *Trinervitermes* sp. with other insects playing a subsidiary role. Foraging involves patch utilisation, with up to 15 min. feeding in one patch resulting. Patches can be up to 100 m apart, and time spent in patches and distance between patches probably reflect patterns of food abundance. Aardwolves cover just over 1 km h⁻¹ while foraging and home ranges overlap extensively.

1 INTRODUCTION

Few quantified data exist on the diet or foraging behaviour of the aardwolf *Proteles cristatus* (Sparman, 1783). Smithers (1971), Kruuk and Sands (1972), Dean (1978) and Cooper and Skinner (1979) have shown that even in widely separated geographical areas, termites form the bulk of aardwolves' diet, but that the dominant species differ; Kruuk and Sands (1972) and Cooper and Skinner (1979) also pointed out that the contribution by various termite and other invertebrate species to the diet changes from the dry to wet season.

As pointed out by Kruuk and Sands (1972) the aardwolf is probably one of the most specialised carnivores, as far as food is concerned, in Africa. We would, therefore, expect that local patterns in abundance of preferred prey items would have a marked influence on food, and the foraging and to a lesser extent social behaviour of the aardwolf. Published data on these aspects of aardwolf biology are compared

below to our findings in the Namib-Naukluft Park, South West Africa/Namibia, during winter.

2 STUDY AREA AND METHODS

The Namib-Naukluft Park covers some 22 836 km² and includes gravel plains to the north, mountains to the north and east and shifting sand-dunes to the south. All observations reported below were made to the east of Heinrichsberg or Tumasberg in the vicinity of Ganab (23°10'S, 15°32'E), 110 km from the coast (Fig. 1) on flat gravelly-sandy plains at 1 000 m a.s.l. between low mountains and in areas of sparse vegetation, mostly low-growing perennial or annual grasses, e.g. *Stipagrostis ciliata*. Annual rainfall is ca 97.0 mm, falling mostly from January to March (Seely 1978). The 1978 study period was preceded by relatively abundant rain and good habitat conditions, whereas the 1979 study was done after several dry months resulting in relatively sparse ground cover.

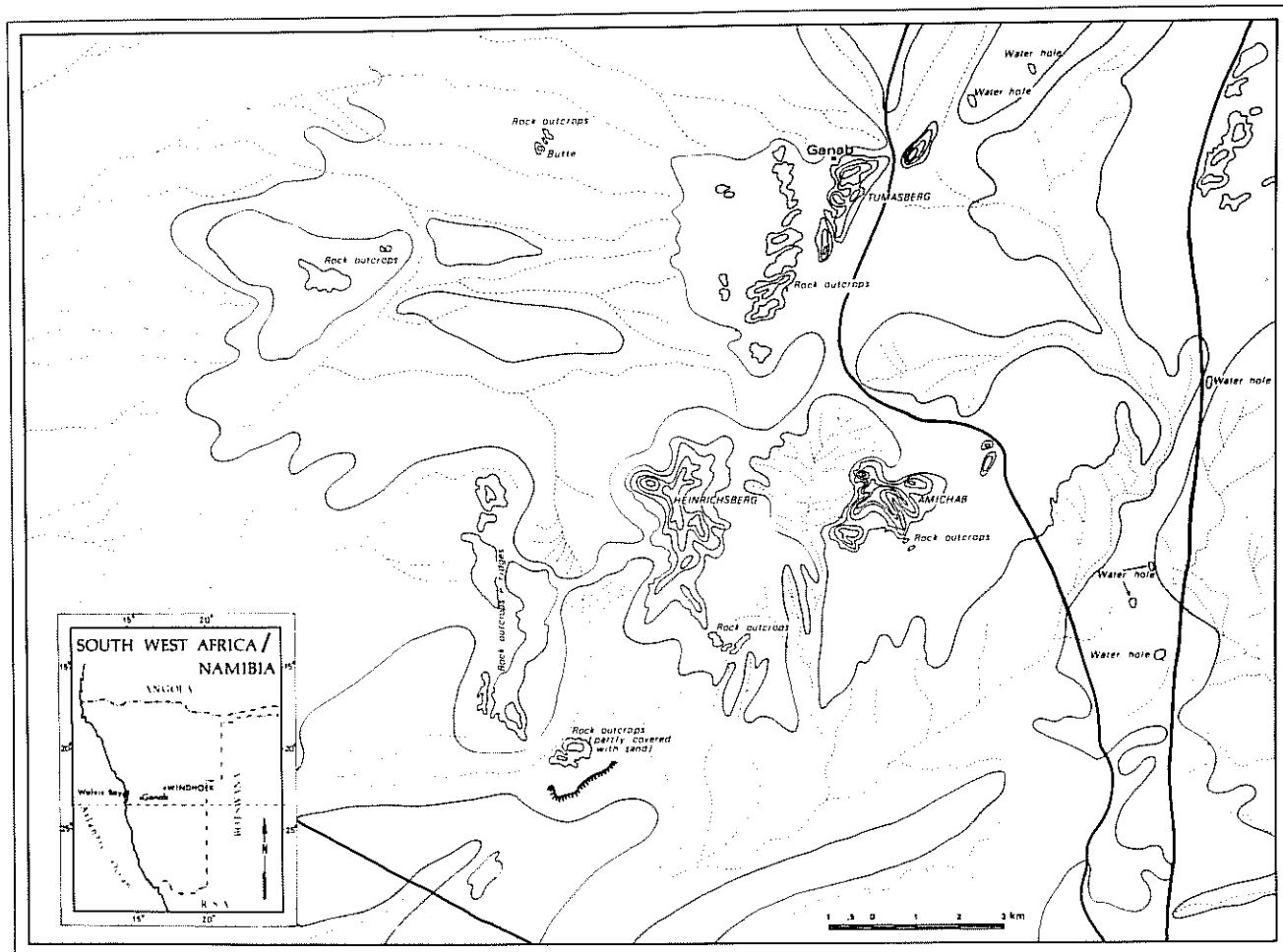


FIGURE 1: Map of the study area in the Namib-Naukluft Park.

From 25 to 31 May 1978 seven, and from 27 July to 3 August 1979 five different aardwolves were observed from high vantage points or were followed closely in a vehicle for a total of 35 h 40 min. Continuous observations on individuals ranged from 20 min. to 7 h 27 min. Only individuals which allowed close approach (<15 m) were followed.

Binoculars, and at night the vehicle's head-lamps and spot-lights aided in observations which were put on tape and later transcribed. Timing of events was by stopwatch and distances covered were taken from the vehicle's odometer. Size of feeding patches and distances between patches were estimated visually, or for longer distances, obtained from the vehicle's odometer.

Information on the diet of the aardwolves was obtained from faeces collected immediately after being passed or early the next morning, when it was still fresh and moist; 15 deposits of faeces in 1978 and 18 in 1979 were individually put in plastic bags which were sealed after air-drying the contents. Later 2–6 sub-samples were taken from each sample and analysed, using the method of Cooper and Skinner (1979) in which presence and absence only were recorded for all items which contributed less than 1 percent to the total organic mass in a specific sample or sub-sample.

3 RESULTS

3.1 Faecal analysis

1978: The average dry mass of 9 deposits of fresh faeces was $201,77 \pm 171,93$ g. These 9 samples plus another 6 samples of old faeces revealed an abundance of *Trinervitermes* sp. in the aardwolf's diet (Table 1). *Trinervitermes* spp. from the area are poorly known and could not be accurately identified (Coaton *pers. comm.*). Of the total dry organic mass 95,9 percent was *Trinervitermes* and of these, soldiers contributed 53,2 percent of the total mass. *Hodotermes mossambicus* occurred in 68,8 percent of the samples, usually as traces only, except for four scats in which *Hodotermes* formed an average of 3,6 percent of the total dry organic mass. Sand was abundant and formed 42,4 percent of the total dry faecal mass. Other items were: Formicidae (found in 37,7 percent of the sub-samples), Dictyoptera (2,2 percent occurrence), Coleoptera (10,0 percent occurrence), other Insecta (1,1 percent occurrence), Diptera pupae (12,2 percent occurrence) and Hemiptera (1,1 percent occurrence). Plant material formed 3,1 percent of the total dry organic mass.

Faeces collected within 2 min. after deposition already contained small live beetles (Coleoptera). These were two unidentified species of the Histeridae known to predate on Diptera larvae, and one unidentified species of *Aphodius* (Scarabaeidae) often found abundantly in dung.

1979: The average dry mass of 14 fresh faeces was $251,74 \pm 187,77$ g. The major food source was again *Trinervitermes* sp. (Table 2), but *Hodotermes mossambicus* was relatively more abundant in the diet than in 1978. Faeces collected within 2 min. of deposit contained numerous live Diptera (Cyclorrhapha-Drosophilidae) buried alive when the faeces were covered in sand by the aardwolf after defaecation. These faecal samples had live pupae five hours after deposition.

Of the *Trinervitermes*, soldiers formed an average of 63,1 percent of the total mass. Sand was even more abundant than in 1978, forming 65,5 percent of the dry faecal mass in 1979. Of the other organic matter, some plant material and (species unidentified) Coleoptera and Acarina were found. The Acarina were mites of which 1, 2, 4 and 8 individuals were found in four of the scats. The Coleoptera consisted of (species unidentified) Scarabaeidae (Caprinae) in three and Tenebrionidae in one scat.

The mean diameter of 11 dry scats was $29,88 \pm 5,15$ mm and the mean length of 4 dry scats was $56,80 \pm 6,75$ mm.

3.2 General foraging pattern

During the study periods sunset was at ca 18h20, and from 18h53 it became too dark for observations without the aid of lights. At 06h30 dawn broke and at 07h15 it was fully light with sunrise at 07h35 – 07h40.

Aardwolves were active from 17h12 (17h05 in 1979) to 06h36, but with a great deal of variation, especially in times of emergence from dens, in an individual or between individuals. For example, during 1978 two individuals on different nights emerged from dens at 17h37 and 17h45, and 17h49 and 18h10, respectively. Others were seen emerging at 18h00 and 18h05. During 1979 one individual emerged on consecutive nights at 17h05, 18h12 and 18h33. Another emerged close by at 17h55 and 17h36 on the first and last nights. In cases where specific dens were monitored, individuals usually emerged some 20 min. or more after the dens passed into shade caused by inselbergs on the west. As aardwolves normally foraged at least a short time in sunlight, however, shade does not seem a prerequisite for activity to commence. On the other hand aardwolves normally entered dens for the day during darkness, or at first daylight. No aardwolves were seen active following daybreak, but some were seen in the entrances of dens at 07h53 and 10h30 and others were flushed from short grass at 08h45 and 09h20. Emergence from dens was abrupt without any preliminary reconnaissance. On emergence an aardwolf would either start feeding immediately, indulge in a number of marking bouts (Nel and Bothma *in prep.*), or else run rapidly to a midden, defaecate, and then start feeding or marking. Only one aardwolf occupied a particular den at a particular time, except in one instance when two were found together, but dens can be less than 500 m apart.

TABLE 1: Faecal analysis of 9 fresh and 6 old samples of aardwolf *Proteles cristatus* faeces from the vicinity of Ganab in the Namib-Naukluft Park, collected in May 1978.

ITEM	SAMPLE NUMBER															Total sub-samples	Mean SD	C.V (%)
	1	2	3	4	5	6	7+	8+	9+	10+	11+	12+	13+	14+	15+			
<i>Trinervitermes</i> sp.*	97,8	97,0	94,7	95,2	97,2	95,7	97,7	93,0	97,3	97,5	98,1	91,7	92,0	95,5	98,5	6	95,9	2,22
<i>Hodotermes mossambicus</i> **	83,3	83,3	83,3	66,7	100,0	100,0	0,0	100,0	0,0	50,0	0,0	100,0	100,0	83,3	83,3	6	68,8	—
Formicidae**	33,3	33,3	0,0	50,0	33,3	33,3	16,7	33,3	66,7	33,3	50,0	50,0	50,0	66,7	16,7	6	37,7	—
Diclyoptera**	33,3	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	6	2,2	—
Coleoptera**	16,7	0,0	0,0	0,0	0,0	0,0	16,7	33,3	16,7	33,3	33,3	0,0	0,0	0,0	0,0	6	10,0	—
Hemiptera**	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	6	1,1	—
Diptera pupae**	0,0	50,0	0,0	33,3	0,0	0,0	0,0	0,0	66,7	16,7	16,7	0,0	0,0	0,0	0,0	6	12,2	—
Other Insecta**	16,7	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	6	1,1	—
<i>Trinervitermes</i> percentage workers	30,5	36,5	46,5	45,7	41,7	52,2	40,7	52,0	41,8	59,3	39,0	56,8	63,7	49,3	46,5	6	46,8	8,97
Plant material*	2,2	2,7	5,3	4,8	2,8	4,3	2,3	3,7	2,7	2,3	1,8	6,8	2,2	1,2	1,5	6	3,1	1,56
Sand as a percentage of faecal mass	46,5	47,5	57,5	57,5	44,0	35,5	47,0	29,0	39,0	35,5	27,5	41,0	37,5	40,0	51,5	2	42,4	9,04
Dry mass (g) of fresh faeces	—	—	—	—	—	—	91,5	125,0	89,0	54,5	145,0	547,0	156,0	165,0	443,0	1	201,77	171,93

* Percentage food composition

** Percentage occurrence in sub-samples

+ Fresh faeces

TABLE 2: Faecal analysis of 14 fresh samples of aardwolf *Proteles cristatus* faeces from the vicinity of Ganab in the Namib-Naukluft Park, collected from 27 July to 3 August 1979. + = present, — = absent.

ITEM	SAMPLE NUMBER															Total sub-samples	Mean SD	C.V (%)
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	sub-samples per sample			
<i>Trinervitermes</i> sp.*	40,0	65,0	92,0	70,0	60,0	75,0	90,0	60,0	50,0	92,0	85,0	90,0	90,0	60,0	5	70	72,79	17,40
<i>Hodotermes mossambicus</i> *	60,0	30,5	8,0	20,0	40,0	20,0	10,0	0,0	0,0	0,0	0,0	10,0	0,0	0,0	5	70	14,89	17,95
Coleoptera	—	+	—	—	—	—	—	+	+	+	—	—	—	—	5	70	—	—
Diptera	—	+	—	—	+	—	+	+	—	—	—	—	+	—	5	70	—	—
Acarina	—	+	—	—	—	—	+	—	—	+	+	—	—	—	5	70	—	—
<i>Trinervitermes</i> percentage workers	33,3	42,4	33,3	39,8	18,2	33,3	43,0	25,0	42,9	66,7	28,6	39,8	48,1	22,2	5	70	36,9	12,24
Sand g per 20 g faeces	13,2	5,7	17,6	15,8	12,4	11,3	12,5	17,1	14,6	18,1	12,9	11,4	11,0	9,2	5	70	13,05	3,42
Sand as percentage of faecal mass	66,0	28,5	88,0	79,0	62,0	56,5	62,5	88,5	73,0	90,5	64,5	57,0	55,0	46,0	5	70	65,5	17,40
Dry mass of faeces (g)	20,8	27,9	359,1	61,1	256,4	203,7	293,7	259,0	348,7	48,5	173,5	402,3	712,5	357,1	1	14	251,74	187,77
Diameter of dry faeces (mm)	21,0	35,0	—	28,1	27,7	32,0	36,6	—	34,8	—	26,0	25,0	27,0	35,5	1	11	29,88	5,15
Length of dry scat (mm)	—	57,0	—	—	53,0	—	—	—	66,2	—	—	51,0	—	—	1	4	56,80	6,75

* Percentage food composition

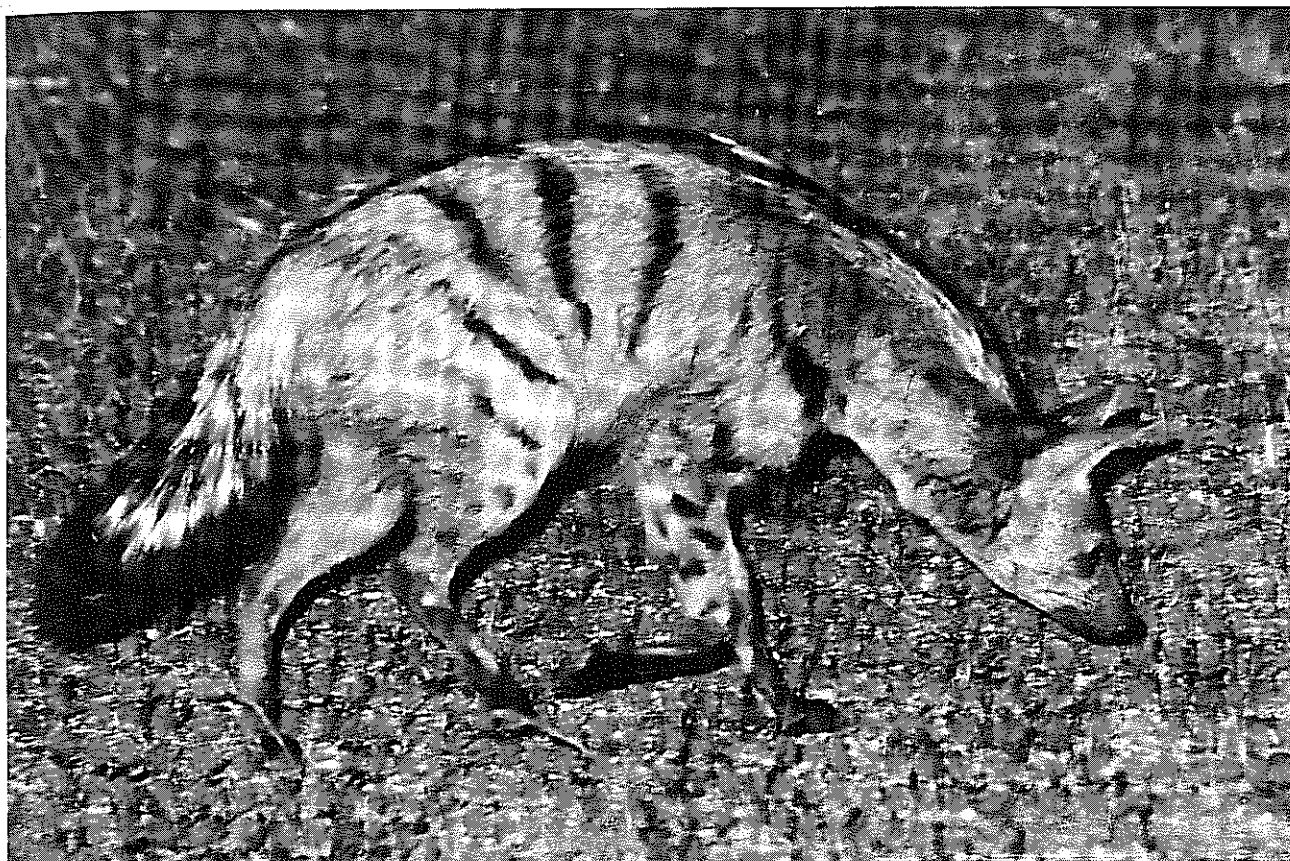


PLATE 1: Aardwolf foraging. Note especially position of head and ears.



PLATE 2: Aardwolf feeding. Ears are pulled back and face sideways.



PLATE 3: Aardwolf habitat, looking SW towards Heinrichsberg.

When foraging, aardwolves move slowly and noiselessly, head bent down and ears cocked forward (Plate 1). An irregular route is followed, although it appears that an individual follows a zig-zag pattern, up- or down-wind, with considerable turning and casting around. Cross-wind movements, with up- or down-wind turns (usually twice as often the former) predominate. At times an aardwolf would deviate from its foraging path for up to 15 m (usually 2–3 m) to run to a particular patch and start feeding there. This could result from either hearing or smelling concentrations of termites. Otherwise it would move directly from one patch to another. These patches probably reflect local areas of high termite abundance. When feeding, the ears turn sideways and are pulled back somewhat (Plate 2), only to return to the original position as the head is lifted (when chewing could be discerned on a few occasions). This shift in the position of the ears suggests that termites are primarily located by hearing. The protruding tongue can often be seen both as termites are lapped up, and when the head is lifted as the insects are being removed from the lips. All aardwolves we observed, except for one sub-adult, foraged in sparsely vegetated short grass areas only (Plate 3) and all foraged singly although at times two individuals could be feeding at <100 m from each other. During 1979 (but not 1978) aardwolves frequented and fed for long periods, in areas where subterranean termite mounds had been opened by aard-

varks (*Orycteropus afer*). This searching for left-overs (but long after the aardvark had departed) was suggested long ago by Brockmann (1911, in Kingdon 1977).

During both years, foraging areas of at least three aardwolves observed east of Heinrichsberg overlapped to some extent spatially, although not temporally. On occasion, two individuals would forage within 70 m of each other without any signs of being disturbed by the other's presence. Individuals also utilised only part of their foraging range in a night. To some extent this may result from changes in wind direction during a night, or between nights, as hearing and perhaps smell play such an important role in prey detection.

On four occasions foraging "speed" could be determined. One individual covered 2,8 km during 2 h 35 min., including rest periods; another 4,9 km during 7 h 27 min. and a third 3,3 km during 4 h 35 min. In 1979 one covered 6,4 km during 4 hours. These are minimum distances as the frequent twists and turns could not be measured. While actually actively foraging (i.e. excluding rests of >5 min.) slightly more than 1 km was covered in an hour. Usually foraging was interspersed with a number of marking bouts which varied greatly between individuals, or one individual on successive nights (Nel and Bothma, *in prep.*). Also, defaecation and urination can take place before, or during foraging.

All individuals followed for a number of hours (3 h 33 min. to 7 h 27 min.) rested for various lengths of time, which ranged from brief grooming bouts (30 s to 1 min.) to rests of up to 2 h 17 min. Such long duration rests usually occur at or in dens. During the longer rest periods (>2 min., $n = 11$, $\bar{X} = 35,7$ min.) individuals would stand up to look around briefly, or indulge in extensive grooming. Of the 24 resting periods seen, 11 were spent in short grass, and 13 in or at dens, in the latter case normally for the longer rest periods. The individual followed for 7 h 27 min. one night rested in seven different dens in its foraging range.

When foraging in specific patches individuals cast around extensively while feeding, and after finishing, trot off purposefully to the next patch. More time was spent in patches earlier in the night, before 23h30 ($n = 24$, $\bar{X} = 9,2$ min., range 3–15 min.) than later ($n = 11$, $\bar{X} = 4,6$ min., range 1–15 min.). In 1979, during 4 h of foraging (18h00–22h00) mean time spent by one individual per patch was 1,77 min. ($n = 71$, range 15 s to 8,15 min.). In 1978, during the whole foraging period distances between foraging patches ranged from 10–100 m ($n = 25$, $\bar{X} = 53,1$ m). In 1979 patches were 2–80 m apart ($n = 34$, $\bar{X} = 26$ m). Patch size diameter was estimated only in 1979 and ranged from 2 to 40 m ($n = 51$) with a mean of 16 m.

3.3 Interactions with other species

Proteles shares its habitat with black-backed jackal (*Canis mesomelas*), silver fox (*Vulpes chama*), bat-eared fox (*Otocyon megalotis*) and aardvark (*Orycteropus afer*). Although up to three aardwolves were at times simultaneously foraging in our field of view, no interactions apart from staring at each other or one running towards the other at night, were noted. Bat-eared foxes and an aardwolf at times overlapped in their feeding ranges, but even though they approached each other closely (<10 m) no aggression was evident. (The aardwolf would shake itself, and the bat-eared foxes slightly lift their tails to the incipient inverted U position). On one occasion an aardwolf and two silver foxes briefly chased each other, but this was more in the context of play, as immediately afterwards the foxes continued chasing one another. In order of den emergence as the day waned, *Canis mesomelas* was active first, followed by *Otocyon megalotis*, then *Proteles cristatus*, with *Vulpes chama* only emerging when it was totally dark. However, these observations were too few to allow definite conclusions. The emergence of *Canis mesomelas* was from 15h00 onwards; *Otocyon megalotis* was first seen active at 16h45 and *Proteles cristatus* at 17h05. Two *Vulpes chama* emerged only at 18h43 from the same den. As mentioned above, sunset occurred at ca 18h20.

4 DISCUSSION

As this study and others have shown, Isoptera form the main portion of aardwolves' food — *Trinervitermes*

sp. in the Namib, *Fulleritermes contractus* in southern Angola (Dean 1978), *T. trinervoides* in the Transvaal (Bothma 1965, Cooper and Skinner 1979), *Trinervitermes rhodesiensis* in Botswana (Smithers 1971) and *T. bettonianus* in Serengeti (Kruuk and Sands 1972). In years of relatively poor habitat conditions, e.g. 1979 of our study, a larger percentage of *Hodotermes mossambicus* in the diet seems to indicate the use of alternate food resources, possibly due to a relatively lower prey density. Kruuk and Sands (1972) consider reports of carrion and small mammals in the diet of aardwolves as probably the result of mistaken identification of the predator since the occurrence of such items in their opinion is not substantiated by any studies on gut and faecal contents. Although carrion and rodents are rare in aardwolf diets, Bothma (1965) did find one stomach of an aardwolf in which 80,1 percent of the food volume was carrion. Additionally this stomach contained the remains of a rodent and some pieces of tortoise shell.

The percentage soldiers in the *Trinervitermes* component was high in both years compared to the results of Kruuk and Sands (1972) in Serengeti and Cooper and Skinner (1979) in the Transvaal. Whether this reflects different defence mechanisms in the termite species involved (Kruuk and Sands 1972) or overall less food abundance in the Namib is unknown, but during 1979 when food seemed less abundant the mean percentage soldiers was 9,9 percent higher than in 1978 (Tables 1 and 2).

As pointed out above, a particular aardwolf or different ones emerge at different times on consecutive nights or the same night. This probably reflects the amount of food taken on the previous night, with early emergence following a less successful night, and vice versa. Certainly all individuals closely monitored emerged and fed every night, although in captivity (with probably excess food provided) up to 48 h can be spent in the den (von Ketelhodt 1966).

Density of termites also seems to affect both the foraging mode, and the area covered in a night or successive nights. During the 1978 rainy season (January – May) precipitation was 104 mm at Ganab, while in 1979 only 81,1 mm were recorded, but with 36,8 mm falling in May and June. This had a marked effect on primary productivity (Seely 1978) and in the Heinrichsberg area the grass cover was markedly poorer (in fact nearly non-existent) than the previous year. The lower primary productivity seems to have affected termite density — in 1978 the mean feeding time per patch was 9,2 min. with a range of 3–15 min., and patches were a mean distance of 53,1 m apart. In 1979 comparable figures were 1,77 min. per patch, range 15 to 8,15 min., with patches on average 26 m apart. The majority of patches were abandoned after less than 2 min. and all small aggregations sampled in 1979, while in 1978 only larger concentrations, and those further apart, were exploited. Although it can be argued that a poorer grass cover (as in 1979) should favour a higher termite density, termites and especially

Trinervitermes are a time-exhausted food supply: disturbance of foraging columns increases the percentage of unpalatable soldiers, and the termites go underground. Because of this, and the high selectivity of aardwolves for *Trinervitermes* sp., longer foraging in patches should equate with higher termite density, and vice versa. Energetically speaking the strategy adopted by an aardwolf would be to exhaust a particular food patch (the time to exhaustion depending on the number of termites and how soon an unfavourable soldier:worker ratio is reached) before moving on to the next patch. Moreover, the amount of sand in the faeces was also much higher in 1979 than in 1978 (Tables 1 and 2), again indicating a lower termite density in 1979. Foraging areas of certain individuals also differed: in 1978 all three aardwolves regularly encountered east of Heinrichsberg foraged nightly in an overall area of ca $3,0 \times 1,75$ km; in 1979 only one individual regularly used part of this area, and the other two were present only on alternate nights, pointing to a much larger foraging range. Only in 1979 were aardwolves seen to forage intensively in areas dug over by aardvark to expose subterranean termite nests. This low density of preferred prey would also mitigate against grouping in aardwolves, although small aggregations have been reported (Kingdon 1977).

Location of surface-moving termites is probably mainly auditory although smell could play a role, as evidenced by the predominant upwind turns, and the different dominant species of termites in the diet probably reflect local patterns of abundance. The manner of foraging (slow movements across and mostly upwind) would enhance prey detection and the local density of preferred prey items (*Trinervitermes* sp.) probably dictate the foraging strategy — slow, continuous search or feeding in particular patches with faster, non-stop movements between patches. The same would apply to the speed of foraging which in the Serengeti (Kruuk and Sands 1972) seems somewhat faster than in the Namib. This slower foraging speed, higher incidence of soldiers in the food of aardwolves in the Namib, and more time spent in a food patch (9,2; 1,15 or 4,6 min. vs. 22 s in Serengeti) could point to lower food availability due to lower rainfall (ca 100 mm vs. ca 700–800 mm) and thus lower primary productivity, which is low in the Namib (Seely 1978). The number of feeding bouts per unit time in Serengeti was also much higher than in the Namib (44 times in 65 min. vs. 25 times in 60 min.) which points to prey concentrations being further apart in the latter area. As in the Serengeti, Namib aardwolves, in winter at least, are only active during the last few hours of daylight and at night. Although this is probably correlated with the activity of their preferred prey, thermoregulatory requirements cannot be overlooked.

The presence of Histeridae beetles in the faeces seen after deposition and the observation of the live burial of Drosophilidae (Diptera) reveals an interesting possibility of an adaptation to harsh desert conditions. The beetles are known to predate on Diptera larvae and the

presence of these beetles in scats within a few minutes after deposition indicates that the beetles must remain in or near the middens of aardwolves, ready to occupy faeces after deposition. Cooper and Skinner (1979) also mention the presence of Coleoptera in aardwolf faeces but do not state whether these had been eaten as food or had occupied the faeces later. The burial of the Drosophilidae with fresh faeces indicates a rapid occupation of a possible breeding stratum and the heat and moisture of buried fresh faeces results in successful completion of the breeding cycles. The Diptera pupae which result in turn serve as food for the Histeridae beetles.

Foraging behaviour of aardwolves in Serengeti and the Namib differ somewhat. Most nights during our observations a slight wind or breeze was present, and although upwind turns were more common, frequent down-wind movement and down-wind turns were also seen, in contrast to the findings of Kruuk and Sands (1972). This might be related to the volume of noise or intensity of smell of the particular termite (*Trinervitermes bettonianus* in Serengeti and *Trinervitermes* sp. in the Namib) which allowed down-wind location of termites.

Although we lack data on the number of middens a particular aardwolf uses, or whether different individuals use the same one, middens in the Namib are far larger than in the Serengeti and Transvaal (Nel and Bothma *in prep.*, Kruuk and Sands 1972, Skinner *pers. comm.*). The reason for this larger size is unknown, but as Kruuk and Sands (1972) point out the concentration of strongly ammoniacal smelling faeces in discrete localities would interfere less with prey detection, if smell plays a role, than scattered faeces. As in other areas of southern Africa (Cooper and Skinner 1979), middens seem to be concentrated in specific areas in the Namib, but lacking data on local dispersion of aardwolves, the reason for this is obscure.

The biggest possible difference between our data and that of Kruuk and Sands (1972) lies in the possible existence of territories of aardwolves. Certainly in our area of observation, and during both years, home ranges of at least some individuals overlapped (as was found for a male and female in Serengeti). However, these could have been related and as such this could explain the observed overlap. If food is scarcer in the Namib than in Serengeti, as our data seem to suggest, the point may have been passed in the Namib where it would be profitable to defend widely dispersed and locally low density food resources and under such a strategy territories would be unlikely to occur.

As Kruuk and Sands (1972) pointed out, the aardwolf shares its short-grass, termite-rich habitat with other, possibly competing, species. In the Namib at least some temporal and also spatial separation exists between *Proteles* and the bat-eared fox, *Otocyon*, as well as with the aardvark *Orycteropus*. In the same general area (Heinrichsberg) as that frequented by some of the aardwolves in our study, for example, analysis of two

Otocyon megalotis scats revealed Coleoptera (30 and 20 percent of the dry faeces mass), *Microhodotermes* (40 and 45 percent of the mass), *Orthoptera* (5 percent of the mass of one scat) and plant material (30 and 30 percent of the mass) (see also Bothma and Nel *in prep.*). Although the dens of silver fox *Vulpes chama* occur intermingled with those of the aardwolf, separation of feeding areas exists, and the same applies to the black-backed jackal *Canis mesomelas*. Enough separation in food niche and habitat-niche dimensions therefore occurs to make coexistence of these sympatric carnivores possible.

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