

ASPECTS OF THE ECOLOGY AND THE BEHAVIOUR OF THE LEOPARD *Panthera pardus* IN THE KALAHARI DESERT

J. DU P. BOTHMA

*Eugène Marais Chair of Wildlife Management
Department of Zoology
University of Pretoria
Pretoria
0002*

E. A. N. LE RICHE

*Kalahari Gemsbok National Park
Private Bag X5890
Gemsbokpark
8815*

Abstract – Tracking in sand revealed data on hunting and kill rates, range, movements, activity, cover and water use, reproduction and interactions with other carnivores, by the leopard *Panthera pardus* in the Kalahari Gemsbok National Park. For leopards in the interior, 812,5 km of tracks were followed for 54 days, and 205,1 km for 15 days for females with cubs. In the Nossob riverbed 30,2 km of tracks were followed in eight days. Medium-sized mammals featured prominently in the diet of all leopards, with prey used influenced by habitat type. Leopards in the interior moved greater distances than those in the Nossob riverbed. Leopards rested frequently at the onset and end of activity and used dense vegetation and aardvark *Orycteropus afer* and porcupine *Hystrix africae australis* burrows as daytime cover. Leopards are independent of water, and females apparently have no definite breeding season. Lions *Panthera leo* dominate leopards, but the outcome of leopard/spotted hyaena *Crocuta crocuta* encounters depend on the size of the leopard and the number of hyaenas in the pack. Leopards in the Kalahari Desert are opportunists which occupy this harsh environment successfully.

Introduction

Tracking leopards *Panthera pardus* by spoor in soft sands reveals step by step details on the ecology and behaviour of leopards in the Kalahari Desert. These data expand the existing meagre known information on the life and habits of

leopards from wherever these large cats occur.

This paper forms part of the proceedings of a review symposium on the Kalahari Ecosystem. Thus some aspects presented here are merely a review of information in an earlier paper (Bothma & Le Riche 1982). However a 26% increase in sample size for male leopards in the interior areas has led to a re-evaluation of existing knowledge, while data for leopards in the Nossob riverbed are presented here for the first time. In addition other aspects of the ecology and behaviour of leopards in the Kalahari Desert are reported on, many for the first time.

Study area

Our current study was confined to the northern sections of the Kalahari Gemsbok National Park, South Africa. The park of some 9 500 km² lies between 24°15'S and 26°30'S latitudes, and 20°00'E and 20°45'E longitudes. The main study was done in the interior areas near the windmill Dankbaar, while some observations were also made near the Nossob rest camp along the Nossob River.

Basically the interior areas consist of arid, open dune sandveld with scattered shrubs and trees; while the Nossob riverbed is usually dry and forms an open *Acacia erioloba* woodland. The average annual rainfall is less than 250 mm. In years of abundant rainfall, an extensive grass cover is present in the interior and riverbed areas, but in years of low rainfall the grass cover is sparse to absent. The fauna of the area include seven species of antelope, and several carnivore species, with the lion at the top of the food chain.

Material and methods

For male leopards in the interior 11 visits were made, and three visits for females with cubs. In the Nossob riverbed area two visits yielded data on female leopards with cubs there. In the study, new data are presented for male leopards in the interior areas, and for females with cubs in the Nossob riverbed. Data for females with cubs for the interior areas were taken from Bothma & Le Riche (1982) for comparative purposes. Leopards were sexed on the basis of spoor size and by visual observation during each period of tracking. Due to small sample sizes for female leopards, data for male and female leopards are presented separately until valid statistical comparisons can be done when larger sample sizes for data on females become available.

From a base camp the surrounding area was searched for fresh leopard tracks. Fresh tracks were followed on foot until the leopard involved was spotted; with the tracker giving details of what was found to observers following closely behind in a vehicle. All activities of the leopard were noted *en route* and the distances involved were recorded. Upon finding evidence that the trackers had caught up with the leopard, the team withdrew, to return to that spot early the next morning to resume tracking of the leopard's movements of the previous period of activity. The technique involved is described in detail in Bothma & Le Riche (1982).

A prey contact occurred when a leopard became aware of a prey, and reacted to it through a stalk, a chase or a kill, or a combination of these. A stalk is defined as an approach in stalking posture for at least 10 m; a chase is a rush of at least 5 m towards a potential prey (Schaller 1972).

A small prey is any animal up to and including the size of a springhare *Pedetes capensis*, while a large prey is an animal of the size of an adult springbok *Antidorcas marsupialis* and larger.

Results

For male leopards in the interior 771,6 km of tracks were followed for 54 complete 24-hour periods (here called days), plus 40,9 km more on six days of incomplete tracking. Data for females with cubs in the interior involve no increase in sample size from that of 201,4 km on 15 complete days, plus 3,7 km on one incomplete day as reported in Bothma & Le Riche (1982). In addition, however, new data are presented on 30,2 km of tracks followed on eight complete days for female leopards with cubs in the Nossob riverbed, plus 4,3 km for two days of incomplete tracking. In total we thus present data on 1 052,1 km of tracks followed for 77 complete days in both the interior and the Nossob riverbed areas.

Prey selection and use

Prey Selection

Elsewhere in Africa the leopard is a known opportunist (Eltringham 1979). Increased sample sizes still support the conclusion (Bothma & Le Riche 1982) that in the Kalahari Desert, leopards are equally opportunistic in terms of hunting behaviour.

In the interior, male leopards made contact with 14 potential prey types, ranging in size from a striped polecat *Ictonyx striatus* to an adult gemsbok *Oryx gazella*. Of these they killed seven prey types. Females with cubs contacted 15 prey types, of which they killed seven. Combined, leopards in the interior made contact with 19 prey types and killed 12.

The greatest frequency of contact was made with the porcupine *Hystrix africaeustralis*, steenbok *Raphicerus campestris*, aardvark *Orycteropus afer* and gemsbok calves, in descending frequency of contact. Prey of medium size, i.e. from bat-eared fox *Otocyon megalotis* size to less than an adult springbok are contacted most frequently. In male and female leopards respectively, small prey consisted of 4 and 11% of all contacts, medium prey 64 and 50%, and large prey 24 and 30%.

In the Nossob riverbed, only female leopards with cubs were followed, and they contacted ten prey types, killing five types. Medium and large prey only were contacted, both consisted 50% of all contacts, with a clear abundance of springbok adults and lambs.

Prey-use

In the interior only two of 30 kills were large enough to detain the leopard involved at the carcass for more than one day. An aardvark was fed upon for three successive days, and a gemsbok calf for two successive days. Both were killed by a male leopard. An adult red hartebeest cow *Alcelaphus buselaphus* was used until two spotted hyaenas *Crocuta crocuta* disturbed the leopard. As the carcass was too heavy to be dragged into a tree, the leopard abandoned it during the night of the

Table 1

Prey used and percentages of prey killed for male leopards in a dune-woodland habitat (interior) in the Kalahari Desert, based upon 54 days of tracking and 812.5 km of tracks followed from 1976-1983

| PREY SIZE | PREY TYPE | CONTACTS WITH PREY TYPE | PERCENTAGE OF ALL CONTACTS | KILLS | PERCENTAGE OF ALL KILLS | KILLS AS A PERCENTAGE OF CONTACTS FOR PREY TYPE |
|-----------|-------------------------|-------------------------|----------------------------|-------|-------------------------|---|
| Unknown | Unknown | 14 | 9 | 0 | 0 | 0 |
| Small | Hare | 4 | 3 | 0 | 0 | 0 |
| Small | Striped pole-cat | 1 | 1 | 0 | 0 | 0 |
| Small | Genet | 1 | 1 | 1 | 5 | 100 |
| Medium | Bat-eared fox | 10 | 6 | 2 | 10 | 20 |
| Medium | Black-backed jackal | 3 | 2 | 1 | 5 | 33 |
| Medium | Porcupine | 30 | 19 | 8 | 40 | 27 |
| Medium | Aardvark | 20 | 12 | 1 | 5 | 5 |
| Medium | Steenbok | 28 | 17 | 1 | 5 | 4 |
| Medium | Duiker | 13 | 8 | 2 | 10 | 15 |
| Large | Red hartebeest calf | 8 | 5 | 0 | 0 | 0 |
| Large | Red hartebeest adult | 5 | 3 | 1 | 5 | 20 |
| Large | Gemsbok calf | 18 | 11 | 3 | 15 | 17 |
| Large | Gemsbok adult | 4 | 3 | 0 | 0 | 0 |
| Large | Ostrich adult | 3 | 2 | 0 | 0 | 0 |
| — | All small prey | 6 | 4 | 1 | 5 | 17 |
| — | All prey of medium size | 104 | 64 | 15 | 75 | 14 |
| — | All large prey | 38 | 24 | 4 | 20 | 11 |
| — | All prey | 162 | 100 | 20 | 100 | 12 |

kill, but after having fed on it. In both the interior and the Nossob River female leopards with cubs never kill prey large enough to detain them for more than one day. Of the 30 known kills in the interior, 16 (53%) were adult; in the Nossob River four of eight kills were adult. All prey, except the one adult red hartebeest of approximately 180 kg, weighted < 70 kg. Other carnivores formed 30% of the combined 30 kills of male and female leopards in the interior.

Using the technique of Bothma & Le Riche (1982), male leopards were estimated to have consumed 3,5 kg of meat per day (n = 54 days) in the interior and females with cubs 4,9 kg per day (n = 15 days). In 30 kills the hair was removed in 6 (20%), all of which had relatively woolly fur, *i.e.* carnivores and antelope young. In the interior five of 30 kills (17%) were stored in trees, and in the Nossob River one of eight. Prey storage in trees always was the result of disturbance of leopards at the carcass by scavengers. Thus seven of 38 known kills (18%) were stored in trees.

Hunting efficiency and methods

Contact Rates

In the interior areas male leopards made 152 contacts with prey in 54 complete days at a rate of 2,8 per day; females with cubs made 2,9 per day. Of all 162 known contacts of male leopards, incomplete days of tracking included, they killed 20 (12%) as opposed to 23% for females with cubs. Males, and females with cubs killed more medium-sized prey than small or large ones (Table 1; and Bothma & Le Riche 1982).

For male leopards we recorded fewer contacts (2,4 per day) with prey on the first night after having killed and fed, than on days of kills (3,4 per day) or on second and more days after the last known kill (3,6 per day). Subdivision of contacts into stalks and chases further suggests that leopards show relatively less interest in stalking on the first day after a kill, whereas chases occurred at similar rates regardless of timing relative to the last known kill (Table 2). When the stalking frequencies for the days of kills, the first day after a kill, and for the second or more days after a kill are compared to an expected 1:1:1 ratio, a significant difference (chi-square = 16,52; df = 2; $P < 0,01$) existed, whereas for chases it did not (chi-

Table 2

Stalk and chase frequencies for male leopards in a dune-woodland habitat (interior) of the Kalahari Desert as compared for nights on which kills were made, first nights after a kill, and second and more nights after a kill was made. Based upon 812,5 km of tracts followed from 1976-1983

| TIME RELATIVE TO KILL | DAYS TRACKED | STALKS | | CHASES | |
|-------------------------------|--------------|--------|----------------|--------|----------------|
| | | n | Stalks per day | n | Chases per day |
| Night of kill | 12 | 24 | 2,0 | 17 | 1,4 |
| First night after kill | 13 | 12 | 0,9 | 19 | 1,5 |
| Second plus nights after kill | 18 | 41 | 2,3 | 24 | 1,3 |

square = 1,30; $df = 2$; $P > 0,05$). In total, males moved 5 km per contact, females with cubs 4,7 km per contact. No comparative data were available for females with cubs from the Nossob River.

Kill Rates

In the interior male leopards killed prey once every 3 days, females with cubs once every 1,5 days. Medium-sized prey were killed mainly. The longest known interval between kills was 5 days for males and 4 days for females. The mean distance between known kills was 28,1 km (SD = 27,7 km; $n = 14$) for males as opposed to 20,8 km (SD = 12,8 km; $n = 5$) for females with cubs. The minimum mean known interval from one kill to the next one was 1,9 days (SD = 1,6 km; $n = 18$) for male leopards and 0,9 days (SD = 1,4 km; $n = 8$) for females with cubs.

In the Nossob riverbed female leopards with cubs killed once every 1,3 days. Of all known records of leopard kills along the Nossob riverbed, 69% were large prey and 31% medium-sized prey; and adult springbok formed 56% of the 16 kills recorded.

The kill rates ($n = 20$ kills) of male leopards in the interior were also compared on a prey basis to those expected from the relative contact frequencies ($n = 162$ contacts) of the prey. In all cases kill rates did not differ significantly from the contact rates, indicating that whereas medium-sized prey are abundant in the diet of male leopards, this is a reflection of the frequency with which medium-sized prey are encountered rather than actual prey preference. Porcupines, however, may eventually prove to be selected for if the current trend persists in a larger sample size (Table 1).

Reactions After Prey Contact

Of 162 prey contacts by male leopards in the interior, 3% consisted of the full stalk-chase-kill sequence (Table 3); 2% for females with cubs (Bothma & Le Riche 1982). In the interior only 2 of all 206 contacts recorded for male and female leopards consisted of a stalk and kill without an intervening chase.

Stalks

Of all stalks by male leopards in the interior, 55% involved medium-sized prey (Table 3), compared to 35% for females with cubs (Bothma & Le Riche 1982). Kills followed 7% of the stalks by males, and 4% by female leopards with cubs. Chases followed 24% of all stalks by male leopards, and 30% of those by females with cubs. Small prey are seldom stalked.

When stalking frequencies ($n = 71$ stalks) are compared on a prey basis with the kill frequencies ($n = 20$ kills) for male leopards in the interior, no significant differences exist, except for:

- (1) The aardvark was significantly stalked more frequently (stalk:kill ratio = 2,8:1) than killed (chi-square = 9,67; $df = 1$; $P < 0,01$).
- (2) The steenbok was significantly stalked more frequently (stalk:kill ratio = 4,4:1) than killed (chi-square = 53,67; $df = 1$; $P < 0,01$).

Table 3

Behaviour related to stalking by male leopards in dune-woodland habitat (interior) in the Kalahari Desert, as based upon 54 days of tracking and 812,5 km of tracks followed from 1976-1983

| PREY SIZE | PREY TYPE | STALKS RECORDED | | STALKS ENDING IN KILLS | | STALKS LEADING TO CHASES | |
|-----------|-------------------------|-----------------|--------------------------|------------------------|--|--------------------------|--|
| | | n | Percentage of all stalks | n | Percentage of all stalks for prey type | n | Percentage of all stalks for prey type |
| Unknown | Unknown | 11 | 11 | 0 | 0 | 0 | 0 |
| Small | Hare | 2 | 2 | 0 | 0 | 0 | 0 |
| Small | Striped pole-cat | 1 | 1 | 0 | 0 | 0 | 0 |
| Medium | Bat-eared fox | 2 | 2 | 0 | 0 | 0 | 0 |
| Medium | Porcupine | 20 | 20 | 1 | 5 | 5 | 25 |
| Medium | Aardvark | 10 | 10 | 1 | 10 | 5 | 50 |
| Medium | Steenbok | 16 | 16 | 1 | 6 | 5 | 31 |
| Medium | Duiker | 6 | 6 | 0 | 0 | 0 | 0 |
| Large | Red hartebeest calf | 8 | 8 | 0 | 0 | 1 | 13 |
| Large | Red hartebeest adult | 4 | 4 | 1 | 25 | 2 | 50 |
| Large | Gemsbok calf | 13 | 13 | 3 | 23 | 4 | 31 |
| Large | Gemsbok adult | 4 | 4 | 0 | 0 | 1 | 25 |
| Large | Ostrich adult | 1 | 1 | 0 | 0 | 1 | 100 |
| — | All small prey | 3 | 3 | 0 | 0 | 0 | 0 |
| — | All prey of medium size | 54 | 55 | 3 | 6 | 15 | 28 |
| — | All large prey | 30 | 31 | 3 | 10 | 9 | 30 |
| — | All prey | 98 | 100 | 7 | 7 | 24 | 24 |

Table 4

Known stalking distances (metres) for leopards in dune-woodland (interior) and Nossob riverbed habitats in the Kalahari Desert. Data are based on 54 days of tracking and 812,5 km of tracks for male leopards, 15 days of tracking and 205,1 km of tracks for females with cubs in the dune-woodlands (Bothma & Le Riche 1982), and 8 days of tracking and 30,2 km of tracks in the Nossob riverbed from 1976-1983

| PREY SIZE | PREY TYPE | DUNE-WOODLANDS (INTERIOR) | | | | | | | | | | NOSSOB RIVERBED | | | | | |
|-----------|-------------------------|---------------------------|---------|----|----------|---------|---------------------------|----|----------|-------|-------|---------------------------|--------|------|----|---|-------|
| | | Male leopards | | | | | Female leopards with cubs | | | | | Female leopards with cubs | | | | | |
| | | Mean | SD | n | Range | Mean | SD | n | Range | Mean | SD | n | Range | Mean | SD | n | Range |
| Unknown | Unknown | 35,0 | 13,8 | 7 | 20-50 | 42,5 | 9,6 | 4 | 30-50 | 40,0 | 0,0 | 3 | 40-40 | | | | |
| Small | Hare | 25,0 | 21,2 | 2 | 10-40 | — | — | — | — | 40,0 | — | 1 | — | | | | |
| Small | Striped pole-cat | 10,0 | — | 1 | — | — | — | — | — | — | — | — | — | | | | |
| Small | Springhare | — | — | — | — | 36,7 | 15,3 | 3 | 20-50 | — | — | — | — | | | | |
| Medium | Bat-eared fox | 132,5 | 95,5 | 2 | 65-200 | 45,0 | 7,1 | 2 | 40-50 | 26,5 | 19,1 | 2 | 13-40 | | | | |
| Medium | Aardwolf | — | — | — | — | 2 500,0 | — | 1 | — | — | — | — | — | | | | |
| Medium | Porcupine | 80,7 | 69,7 | 18 | 10-200 | — | — | — | — | — | — | — | — | | | | |
| Medium | Aardvark | 82,2 | 90,6 | 9 | 10-300 | — | — | — | — | 32,5 | 24,8 | 2 | 15-50 | | | | |
| Medium | Steenbok | 59,5 | 51,4 | 17 | 10-200 | 130,0 | 147,3 | 3 | 40-300 | 300,0 | — | 1 | — | | | | |
| Medium | Duiker | 42,1 | 29,6 | 7 | 15-100 | — | — | — | — | 320,0 | 396,0 | 2 | 40-600 | | | | |
| Medium | Springbok lamb | — | — | — | — | 100,0 | — | 1 | — | — | — | — | — | | | | |
| Large | Springbok adult | — | — | — | — | 505,0 | 365,3 | 3 | 20-900 | 53,3 | 5,8 | 3 | 50-60 | | | | |
| Large | Blue wildebeest calf | — | — | — | — | — | — | — | — | 70,0 | — | 1 | — | | | | |
| Large | Red hartebeest calf | 188,8 | 293,1 | 8 | 45-900 | 96,7 | 89,6 | 3 | 40-200 | 100,0 | — | 1 | — | | | | |
| Large | Red hartebeest adult | 108,8 | 194,2 | 4 | 10-400 | — | — | — | — | — | — | — | — | | | | |
| Large | Gemsbok calf | 445,5 | 917,5 | 13 | 26-3 400 | 200,0 | — | 1 | — | — | — | — | — | | | | |
| Large | Gemsbok adult | 855,0 | 1 630,6 | 4 | 10-3 300 | 50,0 | — | 1 | — | — | — | — | — | | | | |
| Large | Ostrich adult | 1 800,0 | — | 1 | — | — | — | — | — | — | — | — | — | | | | |
| — | All small prey | 20,0 | 17,3 | 3 | 10-40 | 36,7 | 15,3 | 3 | 20-50 | 40,0 | — | 1 | — | | | | |
| — | All prey of medium size | 71,0 | 65,5 | 53 | 10-300 | 440,0 | 913,1 | 7 | 40-2 500 | 151,1 | 222,2 | 7 | 13-600 | | | | |
| — | All large prey | 431,9 | 876,4 | 30 | 10-3 400 | 284,4 | 312,0 | 8 | 20-900 | 66,0 | 20,8 | 5 | 50-100 | | | | |
| — | All prey | 181,6 | 518,6 | 95 | 10-3 400 | 257,4 | 537,4 | 22 | 20-2 500 | 96,8 | 149,7 | 16 | 13-600 | | | | |

Table 5

Behaviour related to chases of prey by male leopards in a dune-woodland habitat (interior) in the Kalahari Desert, as based upon 54 days of tracking and 812,5 km of tracks followed from 1976-1983

| PREY SIZE | PREY TYPE | CHASES RECORDED | | CHASES ENDING IN KILLS | | CHASES WITHOUT PRIOR STALKING | |
|-----------|-------------------------|-----------------|--------------------------|------------------------|--|-------------------------------|--|
| | | n | Percentage of all chases | n | Percentage of all chases for prey type | n | Percentage of all chases for prey type |
| Unknown | Unknown | 2 | 3 | 0 | 0 | 2 | 100 |
| Small | Hare | 2 | 3 | 0 | 0 | 2 | 100 |
| Medium | Bat-eared fox | 6 | 8 | 0 | 0 | 6 | 100 |
| Medium | Black-backed jackal | 2 | 3 | 0 | 0 | 2 | 100 |
| Medium | Porcupine | 8 | 11 | 1 | 13 | 3 | 38 |
| Medium | Aardvark | 15 | 20 | 1 | 7 | 10 | 67 |
| Medium | Steenbok | 17 | 23 | 1 | 6 | 12 | 71 |
| Medium | Duiker | 5 | 7 | 0 | 0 | 5 | 100 |
| Large | Red hartebeest calf | 2 | 3 | 0 | 0 | 0 | 0 |
| Large | Red hartebeest adult | 2 | 3 | 0 | 0 | 1 | 50 |
| Large | Gemsbok calf | 9 | 12 | 2 | 22 | 5 | 56 |
| Large | Gemsbok adult | 1 | 1 | 0 | 0 | 0 | 0 |
| Large | Ostrich adult | 3 | 4 | 0 | 0 | 2 | 67 |
| — | All small prey | 2 | 3 | 0 | 0 | 2 | 100 |
| — | All prey of medium size | 53 | 72 | 4 | 8 | 38 | 72 |
| — | All large prey | 17 | 23 | 2 | 12 | 8 | 47 |
| — | All prey | 74 | 100 | 6 | 8 | 50 | 68 |

Stalking distances varied from prey to prey (Table 4), but increased as prey size increased for male leopards in the interior. However, in females with cubs in the interior and in the Nossob riverbed, medium-sized prey had longer stalking distances than large prey, but this may be due to small sample sizes. Leopards in the Nossob riverbed apparently show shorter mean stalking distances than those in the interior.

Chases

For male leopards in the interior 8% of 74 known chases ended in a kill (Table 5) compared with 28% for females with cubs (Bothma & Le Riche 1982). Few small prey were chased, and most chases involved medium-sized prey. In both sexes, 68% of all chases were not preceded by a stalk.

Chase distances increased with increased prey size from medium-sized to large prey in male and female leopards in the interior, but decreased from large to medium-sized prey in Nossob riverbed female leopards (Table 6) and (Bothma & Le Riche 1982). However, in both the interior and Nossob riverbed areas, sample sizes for female leopards with cubs are relatively small.

Kills

In male leopards in the interior, 25% of 20 kills followed a full stalk-chase-kill sequence; in females with cubs the frequency was 10% ($n = 10$ kills) in the interior and 25% ($n = 8$ kills) in the Nossob riverbed. In the interior 65% of the kills by male leopards were not stalked or chased; in females with cubs this happened in 30% of the cases in the interior, and 50% in the Nossob riverbed (Table 7 and Bothma & Le Riche 1982). The sample sizes for the data on females with cubs in both habitat types, however, are still too small for definite conclusions.

Except once when a male leopard killed an adult red hartebeest cow in the interior, prey was always dragged underneath a bush or tree offering suitable cover. The hartebeest was presumably too heavy for the leopard to move it. Only when disturbed in 5 of 30 cases (17%) were prey later moved into a tree by leopards in the interior. In the Nossob riverbed females with cubs moved one of eight kills into a tree.

Prey was often dragged or carried for considerable distances to suitable cover. Male leopards in the interior dragged prey for a mean distance of 410,0 m per kill ($SD = 1\ 049,7$ m; $n = 20$; range = 0 – 4,9 km), females with cubs did so for a mean of 742,0 m ($SD = 1\ 028,1$ m; $n = 10$; range = 40 m – 2,9 km) in the interior, and 57,0 m ($SD = 102,0$ m; $n = 8$; range = 0 – 300 m) in the Nossob riverbed. In the case of the males, the maximum range of 4,9 km involved a bat-eared fox killed, and carried for that distance before being eaten.

In the interior there are also some indications that male leopards kill more prey of relatively large size than females with cubs. However, sample sizes of especially kills by females are still too small to allow definite conclusions.

When the kills of females with cubs and of all leopards combined are compared on a habitat basis, it is clear that the habitat and its associated prey differences are reflected in the kills by leopards. It is particularly noticeable that the larger prey

Table 6

Known chase distances (metres) for leopards in dune-woodland (interior) and Nossob riverbed habitats in the Kalahari Desert. Data are based on 54 days of tracking and 812,5 km of tracks for male leopards, 15 days of tracking and 205,1 km of tracks for females with cubs in the dune-woodlands (Bothma & Le Riche 1982), and 8 days of tracking and 30,2 km of tracks in the Nossob riverbed from 1976-1983

| PREY SIZE | PREY TYPE | DUNE-WOODLANDS (INTERIOR) | | | | | | | | | | NOSSOB RIVERBED | | | | | | | | | |
|-----------|---|---------------------------|-------|----|--------|--|---------------------------|----|---|-------|-------|---------------------------|--------|--------|-------|-------|---------------------------|----|----|-------|--|
| | | Male leopards | | | | | Female leopards with cubs | | | | | Female leopards with cubs | | | | | Female leopards with cubs | | | | |
| | | Mean | SD | n | Range | | Mean | SD | n | Range | | Mean | SD | n | Range | | Mean | SD | n | Range | |
| Unknown | Unknown | 30,0 | 20,0 | 3 | 10-50 | | | | | | | | | | | | | | | | |
| Small | Hare | 32,5 | 3,5 | 2 | 30-35 | | | 1 | | | 10,0 | | | | | 10,0 | | | 1 | | |
| Small | Springhare | | | | | | | 2 | | 17,5 | | | | 5-30 | | | | | | | |
| Small | Yellow mongoose, <i>Cynictis penicillata</i> | | | | | | | | | | | | | | | | | | | | |
| Medium | Bat-eared fox | 24,5 | 13,9 | 6 | 12-40 | | | 3 | | 55,0 | 47,7 | | 5-100 | | | 50,0 | | | 1 | | |
| Medium | Black-backed jackal | 25,0 | 7,1 | 2 | 20-30 | | | 2 | | 70,0 | 42,4 | | 40-100 | | | 20,0 | | | 1 | | |
| Medium | Aardwolf | | | | | | | 2 | | 30,0 | 28,3 | | 10-50 | | | | | | | | |
| Medium | Porcupine | 15,6 | 13,5 | 8 | 5-40 | | | | | | | | | | | | | | 2 | 5-20 | |
| Medium | Aardvark | 40,7 | 23,7 | 15 | 10-100 | | | 1 | | 5,0 | | | | | | 12,5 | 10,6 | | 1 | | |
| Medium | Steenbok | 31,1 | 45,7 | 14 | 5-180 | | | 1 | | 300,0 | | | | | | 50,0 | | | 1 | | |
| Medium | Duiker | 30,6 | 22,4 | 5 | 5-50 | | | 3 | | 40,0 | 20,0 | | 20-60 | | | 20,0 | | | 1 | | |
| Medium | Springbok lamb | | | | | | | 5 | | 100,0 | | | | | | 400,0 | | | 1 | | |
| Large | Springbok adult | | | | | | | | | 55,0 | 35,4 | | 30-80 | | | 50,0 | 17,3 | | 3 | 40-70 | |
| Large | Red hartebeest calf | 33,5 | 40,3 | 2 | 5-62 | | | 2 | | 300,0 | | | | | | 11,0 | | | 1 | | |
| Large | Red hartebeest adult | 9,5 | 2,1 | 2 | 8-11 | | | 2 | | | | | | | | | | | | | |
| Large | Blue wildebeest calf | | | | | | | | | | | | | | | 5,0 | | | 1 | | |
| Large | Gemsbok calf | 207,8 | 140,2 | 9 | 50-450 | | | 9 | | 10,0 | | | | | | | | | | | |
| Large | Gemsbok adult | 17,0 | | 1 | | | | 1 | | 50,0 | | | | | | | | | | | |
| Large | Eland calf | | | | | | | | | 50,0 | | | | | | | | | | | |
| Large | Ostrich adult | 40,0 | 20,0 | 3 | 20-60 | | | 3 | | 10,0 | | | | | | | | | | | |
| | All small prey | 32,5 | 3,5 | 2 | 30-35 | | | 2 | | 30,0 | 20,0 | | 3 | 5-30 | | 30,0 | 28,3 | | 2 | 10-50 | |
| | All prey of medium-size | 30,4 | 29,6 | 50 | 5-180 | | | 50 | | 68,5 | 77,7 | | 13 | 5-100 | | 85,8 | 154,6 | | 6 | 5-400 | |
| | All large prey | 123,1 | 136,5 | 17 | 5-450 | | | 17 | | 75,7 | 102,0 | | 7 | 10-300 | | 33,2 | 26,1 | | 5 | 5-70 | |
| | All prey | 52,3 | 79,9 | 72 | 5-450 | | | 72 | | 63,7 | 80,8 | | 23 | 5-300 | | 57,0 | 105,0 | | 13 | 5-400 | |

Table 7

Behaviour related to kills by leopards in dune-woodland (interior) and Nosob riverbed habitats in the Kalahari Desert. Data are based on 54 days of tracking and 812.5 km of tracks for male leopards in the dune-woodland, 15 days of tracking and 205.1 km of tracks for females with cubs in the dune-woodlands (Bothma & Le Riche 1982), and 8 days of tracking and 30.2 km of tracks of females with cubs in the Nosob riverbed from 1976-1983. In the dune-woodland no kills by males were chased only, and no kills by females with cubs in the Nosob riverbed from 1976-1983.

| PREY SIZE | PREY TYPE | DUNE-WOODLANDS (INTERIOR) | | | | | | | | | | NOSOBI RIVERBED | | | | | | | | | |
|-----------|-------------------------|---------------------------|----------------|--------------------------|----------------|--------------------|----------------|-------------------|----------------|-----------------------------|----------------|-----------------|----------------|--------------------------|----------------|--------------------|----------------|-----------------------------|----------------|----|--|
| | | Kills Recorded | | Kills Stalked And Killed | | Kills Stalked Only | | Kills Chased Only | | Kills Not Stalked Or chased | | Kills Recorded | | Kills Stalked And Chased | | Kills Stalked Only | | Kills Not Stalked Or Chased | | | |
| | | n | % of all kills | n | % of all kills | n | % of all kills | n | % of all kills | n | % of all kills | n | % of all kills | n | % of all kills | n | % of all kills | n | % of all kills | | |
| Small | Genet | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| Small | Springhare | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| Medium | Bat-eared fox | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 100 | 1 | 50 | 100 | 1 | 50 | 0 | 0 | 0 | 0 | |
| Medium | Black-backed jackal | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 100 | 1 | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| Medium | Aardwolf | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 50 | 1 | 50 | 1 | 100 | 0 | 0 | 0 | 0 | 0 | |
| Medium | Porcupine | 8 | 0 | 1 | 13 | 0 | 0 | 0 | 0 | 7 | 88 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| Medium | Aardvark | 1 | 0 | 1 | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| Medium | Steenbok | 1 | 0 | 1 | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| Medium | Duiker | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 50 | 2 | 100 | 1 | 50 | 0 | 0 | 0 | 0 | 0 | |
| Medium | Springbok lamb | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| Large | Springbok adult | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| Large | Red hartebeest calf | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| Large | Red hartebeest adult | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| Large | Blue wildebeest calf | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| Large | Gemsbok calf | 3 | 0 | 2 | 67 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| Large | Eland calf | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| — | All small prey | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 100 | 1 | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| — | All prey of medium size | 15 | 8 | 3 | 20 | 1 | 13 | 0 | 0 | 4 | 50 | 12 | 80 | 3 | 38 | 4 | 1 | 25 | 1 | 25 | |
| — | All large prey | 4 | 1 | 2 | 50 | 0 | 0 | 2 | 50 | 1 | 100 | 0 | 0 | 0 | 0 | 4 | 1 | 25 | 1 | 25 | |
| — | All prey | 20 | 10 | 5 | 25 | 1 | 10 | 2 | 10 | 6 | 60 | 13 | 65 | 3 | 30 | 8 | 2 | 25 | 2 | 25 | |

types, and especially adult springbok, which are abundant in the Nossob riverbed but relatively scarce in the interior (Bothma *unpubl. data*) are frequently preyed upon by leopards in the riverbed, whereas leopards in the interior kill a wide range of small to medium-sized prey, some of which are rare in the riverbed areas. However, larger samples are still needed before concrete conclusions can be reached in this regard.

Other aspects

Home Range

Data on home range still await publication. However, in an interior area of approximately 800 km², we have proof that the area was used by two adult males and by three females with cubs. We have never witnessed contact between leopards of the same sex in this area, although a red hartebeest cow carcass was visited by two separate male leopards on the same night, but at different times. Different male leopards also used the same watering point in the interior on successive days. These data are still being examined further.

The home range of the leopard is presumably marked olfactorily on a regular basis. Four types of urination occur: one is the usual copious urination without any apparent significance for marking the area. The other three types all involve urination in squirts of small volume scattered throughout the area at regular intervals, *i.e.*

- (1) Urination on low shrubs or grass tufts, followed by raking with the hind feet;
- (2) Hindward-directed squirts onto the low branches of larger shrubs, especially witgat trees *Boscia albitrunca*;
- (3) Hindward-directed squirts onto the trunks of larger trees, but especially witgat and camel-thorn trees.

Leopards also frequently roll in places where other wildlife, including carnivores and antelope, have urinated or defecated and they often stop to rake the trunks of large trees with the claws of the forefeet. In addition Kalahari leopards rub their bodies against tree trunks. These phenomena are also being investigated further and will be dealt with in more detail in a later paper.

Movements

Leopards in the interior move considerably longer distances than those in the Nossob River. In the interior, male leopards moved a mean distance of 14,3 km (SD = 7,9 km; n = 54 days) per 24-hour period (day); and females with cubs 13,4 km (Table 8, and Bothma & Le Riche 1982) on all days, including days of kills. However, killing of prey limited further movements because of the time taken to feed. In the interior, male leopards moved a mean of 9,9 km per day (SD = 5,9 km; n = 16 days) on days of kills and females with cubs 10,2 km (SD = 5,3 km; n = 8 days). On days when no kills were made, male leopards in the interior moved a mean of 16,1 km per day (SD = 8,0 km; n = 38 days) and females with cubs 17,1 km (SD = 5,9 km; n = 7 days). By contrast, female leopards with cubs in the Nossob riverbed only moved a mean of 3,8 km per day (SD = 1,7 km; n = 8 days) on all days followed. This distance differs significantly from that of females with cubs in the interior areas ($t = 12,15$; $df = 21$; $P < 0,01$). On days of kills, female leopards

Table 8

Actual daily distances (km) moved by male leopards in a dune-woodland (interior) habitat in the Kalahari Desert from 1976-1983 to show increased distances moved with increased time lapse since last known kill. Based on 812,5 km of tracks followed in 54 days

| TYPE OF MOVEMENT | DISTANCE MOVED | | | | Nights in Sample |
|--|----------------|--------------------|------------------------------------|--|------------------|
| | Mean | Standard Deviation | Coefficient of Variation (percent) | | |
| Night of kill | 9,9 | 5,9 | 60 | | 16 |
| First night after night of kill | 11,3 | 9,9 | 88 | | 9 |
| Second night after night of kill | 16,0 | 10,7 | 95 | | 7 |
| Third night after night of kill | 17,7 | 4,4 | 25 | | 2 |
| Fourth plus nights after night of kill | 20,9 | 2,4 | 12 | | 4 |
| All nights without kills | 16,1 | 8,0 | 50 | | 38 |
| All nights moved: nights of kills included | 14,3 | 7,9 | 55 | | 54 |

with cubs in the Nossob riverbed likewise moved significantly shorter distances ($\bar{x} = 3,1$ km; $SD = 1,0$ km; $n = 5$ days) than those in the interior areas ($t = 9,03$; $df = 11$; $P < 0,01$). These data probably reflect prey density differences though we have no quantitative data on relative prey abundance in the two habitat types yet. The maximum distance moved in a 24-hour period was 33,0 km ending in mating for a male leopard in the interior; 27,3 km on a day when mating did not occur. Female leopards with cubs moved a maximum of 24,6 km per day in the interior and 7,4 km in the Nossob riverbed. Male leopards in the interior moved increasingly longer distances as the period since a previous kill increased (Table 8), as did females with cubs (Bothma & Le Riche 1982).

Activity

Leopards rest frequently soon after the onset of their nightly movements, and again when they approach the end of such movements. In the middle of the active period they seem to be more intent on moving (hunting?) than on resting. A postulated resting pattern of leopards during their active period appears in Fig. 1. The total distance moved by a given leopard in a night is divided into four equal parts. This aspect will be analysed in more depth in a later paper.

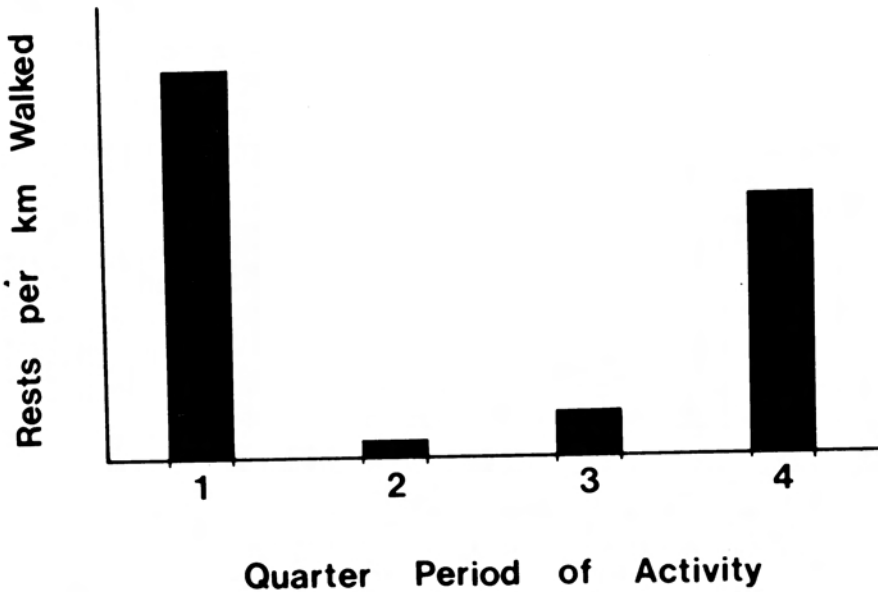


Fig. 1. Relative postulated resting in the Kalahari Desert leopard.

Cover-use

When resting during the heat of the day, leopards lie-up under suitable vegetation *i.e.* cover-use, or use aardvark and porcupine burrows. Male leopards in the Kalahari used plant cover in 78% of 58 cases, and burrows in the rest. Of the 45 plants involved, 69% were low, dense witgat trees, and of the 13 burrows used, 11 were the large excavations of the porcupine and two of the aardvark. Female leopards with cubs used plant cover in 50% of 16 cases, and burrows in the rest. Witgat trees were used in seven of eight cases of plant cover, and aardvark burrows in seven of eight burrow cases (Bothma & Le Riche 1982).

In the Nossob riverbed, plant cover was used in five of seven cases, and aardvark burrows in the rest. There was no clear preference for the type of plant cover, and witgat trees (twice), a camelthorn tree and blackthorn shrubs *Acacia mellifera* (twice) were used. Leopard cubs in the interior used aardvark burrows as daytime cover in 57% ($n = 7$) cases in the interior and 66% ($n = 6$) in the Nossob riverbed area. The rest of the time they used witgat trees in the interior, and witgat (once) and blackthorn shrubs (once) in the Nossob riverbed area.

Water-use

Male leopards in the interior drank water once every 3,9 days or 58 km moved. Females with cubs in the interior were never observed to drink in 15 days in the interior (Bothma & Le Riche 1982) or 8 days in the Nossob riverbed. Male leopards in the interior moved a mean distance of 33,0 km ($SD = 41,1$ km; $n = 6$) between successive drinks of water, with a minimum known distance moved between drinks of 2,0 km and a maximum of 113,4 km. The known mean period without water for male leopards in the interior was 3,0 days ($SD = 3,2$ days; $n = 13$) and a maximum period between successive known drinks of 10 days for male leopards, and for females with cubs in the interior (Bothma & Le Riche 1982). In the Nossob riverbed, female leopards with cubs never drank water in a known maximum period of four successive days.

Reproduction

All females followed in the interior and the Nossob riverbed ($n = 6$ occasions) were accompanied by cubs. Cubs estimated to be less than 3 months old were found in January, March, April, June, July, October, November and December in various parts of the park. Litter sizes observed ranged from 1–2, with a mean of 1,5 ($SD = 0,5$ cubs; $n = 13$). Cub ages were difficult to assess accurately and were estimated based on their physical size. In four cases, tracking revealed that a mating pair stayed together for a maximum of 24 hours before separating.

Interaction with other leopards

No contact was observed between leopards of the same sex, and mating as observed on four occasions lasted a maximum of one night. After mating the pair rested under suitable cover and separated as soon as the next period of activity started. Based on track evidence, mating is characterized by considerable chasing over a limited area before apparent (track arrangements) copulation takes place.

Interaction with other carnivores

Black-backed jackals *Canis mesomelas* may follow leopards and are sometimes killed and eaten as a result of this. Brown hyaenas *Hyaena brunnea* at times also follow the tracks of leopards. Jackals and brown hyaenas do so to scavenge from the leopard kills. A spotted hyaena once drove a female leopard away from her kill, but on at least two known occasions larger male leopards successfully defended kills against two spotted hyaenas. Two adult lions *Panthera leo* also once took away the prey of a large male leopard. Finally, smaller carnivores such as the genet *Genetta genetta*, bat-eared fox, aardwolf *Proteles cristatus* and the black-backed jackal are all preyed upon by the leopard in the Kalahari.

Discussion

The leopard in the Kalahari Desert is also an opportunistic killer, and although it will attempt to kill any potential prey as leopards do elsewhere (Smith 1978; Eltringham 1979), our data nevertheless indicate the development of individual tastes as found by Kruuk & Turner (1967) and Eltringham (1979). The abundance in our data of especially porcupines in the diet of male leopards in the interior has been accentuated by a specific male leopard tracked in January 1983 who killed six times in 12 days, four of the kills being porcupines ambushed as they emerged from their burrows.

A large variety of prey types are contacted, consisting mainly of mammals of medium size which are widespread especially in the interior areas. However, with medium-sized mammals so important in their diet, leopards in the Kalahari seldom spend long at a given carcass and usually have to move and even hunt again following a kill. Prey storage in trees, often considered a dominant feature of leopard hunting behaviour (Turnbull-Kemp 1967), is probably especially done when disturbed by scavengers at the kill site (Schaller 1972). As scavengers are fairly low in density in the Kalahari, and as leopards usually kill medium-sized prey which are consumed quickly, they are not bothered by scavengers to the same extent as they would normally be in more humid areas. Data in Smith (1978) from the Matobo National Park (formerly Rhodes Matopos National Park) of Zimbabwe, where leopards also rarely stored kills in trees in an area apparently devoid of scavengers such as the black-backed jackal and spotted hyaena, support this conclusion further.

The feeding behaviour of the leopard in the Kalahari, including hair removed from woolly prey, inedible parts left uneaten, and use of putrid meat, coincides with that elsewhere (Smith 1978). However, in the Kalahari, prey was usually eviscerated at the eating site and not *en route*, and no evidence was found of leopards attempting to cover prey with brush or plant litter as found by Smith (1978). In the open interior Kalahari habitat, the mean distances of 410 m (males) and 742 m (females) which leopards dragged or carried prey to suitable cover were greater than the averages of 120 m (wet season), 260 m (dry season) and 1 600 m (maximum) reported by Smith (1978) in Zimbabwe leopards.

Analysis of the contact rates for male leopards in the interior clearly shows that while such leopards will always show an interest in any potential prey they do not nearly attempt to stalk prey as frequently following a recent kill as they would at

other times. Thus leopards will chase prey seen after a recent kill, but will attempt to stalk them less than at other times.

Leopards in the Kalahari rarely use the full stalk-chase-kill sequence in hunting. Prey is often simply encountered, and killed without a stalk or a chase. Although all leopards in the Kalahari apparently kill prey more frequently than those from elsewhere (Schaller 1972; Hamilton 1976; Eltringham 1979), they only frequent the same general area of their range every 4–6 days. This seems to support Turnbull-Kemp (1967) in that where game is light on the ground the leopard makes a regular patrol, unconsciously giving prey time to settle down after the passage of the predator.

Kill rates reveal that whereas male leopards in the Kalahari interior kill less frequently than females with cubs, the former kill larger prey. There is no apparent difference in kill rate between females with cubs in the interior areas and those in the Nossob riverbed. These data support the view of Ewer (1973) that felids in general are killers par excellence.

The type of prey killed is clearly influenced by what is available, as is seen in the Kalahari by the comparison of kills from the interior leopards with those of the Nossob River. This aspect will be analysed in more detail in a later paper.

Analysis of the events following a contact also clearly reveals that some prey types evoke different reactions. Thus the aardvark appears to be a relatively difficult prey to catch, yet it is frequently encountered by leopards in the interior. The porcupine is often ambushed as it leaves its burrow, or is taken inside the burrow. The bat-eared fox is chased frequently, but stalked infrequently, and the steenbok is stalked and chased frequently but appears to be too wary and fleetfooted to be caught easily. These differences in predator-prey interaction, and not merely habitat differences, may be as important reasons why steenbok, for example, although common in Matobo National Park in Zimbabwe, occurred in only 2% of the leopard scats from that area (Grobler & Wilson 1972). Our data also support the conclusion of Bertram (1974) that most killing attempts by leopards fail.

It is also commonly believed that leopards rarely hunt in the open, and that they are relatively ineffective as hunters in open areas (Kruuk & Turner 1967; Ewer 1973). The hunting success of leopards in the open Kalahari habitat conclusively proves that leopards can adapt to be equally efficient there.

The hunting technique of leopards in the Kalahari varies and stalking does not feature as prominently as a prerequisite to successful hunts there as it appears to do elsewhere, *e.g.* Kruuk & Turner (1967). The open habitat of the Kalahari also requires chases of much longer distance than suggested by Kruuk & Turner (1967) for East African leopards. These differences emphasize the adaptability of the leopard (Ewer 1973).

Leopards in the interior areas of the Kalahari appear to wander over areas considerably larger than anything known to date for other leopards. The home range of approximately 800 km² of a male leopard in the Kalahari, for example, far exceeds that of 10 – 19 km² in Zimbabwe (Smith 1978), 13 km² in the Serengeti (Seidensticker 1976), 10 – 60 km² in Tsavo (Hamilton 1976), 15.9 km² in Serengeti (Bertram 1982) and even the maximum range of 260 km² suggested by Schaller

(1972) for Serengeti. As leopard ranges overlap in the Kalahari, with approximately five leopards per 800 km² area, *i.e.* one leopard per 160 km², the density of leopards in the Kalahari is less than the density of one per 29 km² of those in the Kruger National Park (Pienaar 1969).

As in Tsavo (Hamilton *op. cit.*), a male's home range in the Kalahari apparently overlaps that of several females; and the females probably have smaller home ranges with greater stability than the males. As elsewhere too, there appears to be resident leopards and transient ones, and a leopard has a core area of its range where it spends most of its time, although it visits the greater part of its range frequently (Hamilton 1976; Smith 1978; Schaller 1972). Kalahari evidence also tends to support the observations of Eisenberg & Lockhart (1972) that leopard ranges overlap, and that although male leopards seldom meet, they can at times be quite close to each other. The large ranges of leopards in the Kalahari probably also reflect food scarcity, as postulated by Schaller (1972) for leopards in Serengeti. However, more detailed analyses will be done later in this regard to examine this topic further.

Scent-marking in leopards in the Kalahari follow the same pattern as found for example by Schaller (1972) in Serengeti and Hamilton (1976), in Kenya including the fact that faeces does not seem to be used in any special manner. There is no evidence yet that leopards in the Kalahari use specific trees as scent posts, as leopards do in Sri Lanka (Eisenberg 1970), but this aspect can only be studied in detail by marking individual trees. Scrapes seem to be associated with squirts of small quantities of urine on low shrubs or grass tufts. Such scrapes occur frequently during the movements of a leopard and agree with the observations of Eisenberg & Lockhart (1972). Although the data on tree-scratching in leopards in the Kalahari still need more detailed analysis, they certainly do occur relatively frequently, in contrast with the view of Turnbull-Kemp (1967) that tree-scratching is rare in African leopards, and of Hamilton (1976) who never observed tree-scratching in Tsavo leopards. According to Ewer (1973) tree-scratching has a definite communicatory function, but may also serve to neaten the claws. She also suggests that tree-scratching is often combined with urinating and rubbing the body on tree trunks by leopards. The backward spraying of urine onto the leaves of shrubs or the trunks of trees is widespread in felids (Ewer 1973). Both sexes of leopards in the Kalahari • scent-mark and these observations agree with those of Baker (1982) for East African leopards. Eltringham (1979) believes that it is likely that the urine and faeces of mammals have an individual odour which identifies the owner and allows its territory to be individually marked.

Female leopards with cubs in the interior moved much greater distances than those in the Nossob riverbed. This aspect needs more study but it is probably linked to a different prey distribution and density in these two habitat types. Extensive movements in the interior areas reduce predator pressure on any given locality. Leopards in the Kalahari Desert also seemed to move less in the daytime than those in forested areas (Seidensticker 1976), but also rested extensively during the heat of the day.

The numerous rests of leopards early in the activity period are probably at least the result of the previous period of inactivity during the heat of the day. The late

activity increase in resting must be due to weariness and the need to select suitable cover in which to lie up for the day. During the middle portion of activity, rests are infrequent and this must coincide with the period of most determined hunting. The type of cover used depends on a combination of heat escape and escape from observation (Bothma & Le Riche 1982).

The limited data on reproduction and mating support the overall leopard picture, *i.e.* no permanent pair bond, with cubs being produced at any time of the year (Eltringham 1979). Although Baker (1982) describes the actual copulation of leopards in East Africa, there is no evidence in the literature that leopards chase each other extensively as a foreplay to copulation as was suggested by tracks observed before copulation in leopards in the Kalahari. There is also no evidence yet of a mating association of more than 24 hours in the Kalahari as was found in the Serengeti where a mating pair stayed together for four days (Bertram 1982).

Our data on the interactions of leopards with other carnivores tend to support the overall view that lions dominate leopards (*e.g.* Bertram 1974; Eaton 1979) although we have not yet found evidence of lions actually killing leopards as in Serengeti (Schaller 1972). It seems that lions and leopards in the Kalahari are separated ecologically by using different sizes of prey (adults versus young) as was suggested by Bothma & Le Riche (1982) for the Kalahari and Bertram (1982) for Serengeti. In the Kalahari, other predators also formed 30% of the kills of leopards in the dune-woodland area, as opposed to 9% in Serengeti (Bertram 1982).

Thus the overall picture of the leopard in the Kalahari conforms in many ways to that of leopards elsewhere. However, the harsh Kalahari Desert environment, in comparison with the more humid areas inhabited by leopards elsewhere, has apparently led to some specific adaptations such as extensive movements, which, together with the leopard's inherent opportunistic prey use, enables these felids to inhabit the Kalahari Desert successfully. In the Kalahari, as elsewhere, the leopard remains an unobstrusive but integral part of the ecosystem, but especially of the food chain as suggested by Bertram (1974).

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