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**Aspects of the behaviour of the African lion
(*Panthera leo*) in an extreme environment**

by

Yanna Smith

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Department of Zoology and Entomology at the
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Supervisor: Prof. O.B. Kok

For my father, Hannes Smith

Dankie pa, dat jy die pad vir my oopgetrap het.

*“Errors are costly”
en
“Arbeid maak vry”*

“One evening we came on a magnificent lioness on a rock, gazing out across the plains. She was sculptured by the setting sun, as though she were part of the granite on which she lay. I wondered how many lions had lain on the self-same rock during countless centuries while the human race was still in its cradle. It was a thought which made me reflect that civilised man has spent untold treasure on preserving ancient buildings and works of art fashioned by the hand of man, yet he destroys these creatures which typify the perfection of ageless beauty and grace. And he does so for no better reason than to boast of a prowess achieved by means of a weapon designed by man to destroy man, or to use its skin to grace some graceless abode. In my mind’s eye I could see the vast herds of wild creatures on these great plains swept away by progress, as they have been swept away in other lands, and, in their stead, herds of degenerate livestock. It was a depressing vision.”

George Adamson



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ABSTRACT

Aspects of the behaviour of a small pride of African lions (*Panthera leo*) under semi-free ranging conditions were investigated in the southern Kalahari in Namibia. Fieldwork involved continuous daytime and nighttime observations, and was conducted during winter and summer of 2003 and 2004 respectively. Behavioural patterns commonly observed included scent marking, territorial patrols, raking of specific trees, tree-climbing, covering of carcasses with sand and grazing, all of which can be considered conventional Kalahari lion behaviour. Unconventional behaviour, possibly as a result of the biased sex ratio favouring the males, included frequent dominance/submission reactions and incessant scent marking and flehmen responses. Association indices were also skewed, the younger male not only demonstrating strong kin selection for the cubs as a result of his bond with the female, his sister, but also assuming the role of "Auntie". Differentiation of behaviour in the cubs was observed from an age of four months. Time-energy budgets demonstrated a negative relationship with increasing temperature during both seasons, aptly demonstrated by extensive early morning sunbathing on dune crests during winter, as opposed to summer. Except in the tail region which is amply vascularised as established by dissection, neck and loin surface temperature readings from Thermocron iButtons™ implanted subcutaneously, demonstrated relative constancy. Thermoregulatory "escape" behaviour and loin exposure were observed mostly between 25 and 33 °C, indicating that the thermoneutral zone may lie within this range. On full bellies, these behaviours were more evident and during summer, grooming and bonding were sacrificed for heat dissipation. Observations under extreme temperatures indicate that African lions demonstrate sizeable thermal inertia under a wide range of ambient temperatures.

1 INTRODUCTION

The African lion (*Panthera leo*) is one of the greatest drawcards this continent has for tourists and hunters alike owing to its ability to capture the imagination of people across the globe. In African culture, the lion is regarded as the supreme of all beasts - powerful, fearless, enduring and imposing. Lions form part of countless myths and folk stories and embody a mysticism not seen in any other animal. People are naturally drawn to lions and one easily captures their attention when the subject of lions is broached. But it is precisely these characteristics that has reduced the numbers of the African lion in sub-Saharan Africa from 100 000 in 1996 to 25 000 in 2001, causing these animals to be listed by the IUCN as vulnerable (McCarthy, 2004). Across the continent, lions are in conflict with commercial and subsistence farmers and as a result, many are shot.

A case in point is the killing in 1996 of 13 members of the 20-strong Mata Mata pride in the south of Namibia on a farm bordering the Kgalagadi Transfrontier Park. The pride entered the sheep farm and when the rancher, Mr. Willem Kotze, contacted the authorities of the then Kalahari Gemsbok Park, he learned that tranquiliser darts for only three lions were available. Nighttime was approaching and no assistance was forthcoming and as a result, 10% of the roughly 120-strong lion population of that park was eradicated (Smith, 1996). Research currently underway in Kenya and spearheaded by the University of California, Berkley, is investigating the co-existence of African lions and cattle ranches on the same tract of land (McCarthy, 2004).

Owing to the economic power of the African lion, private ownership of lions is on the increase. The overall popularity of zoo-type captive institutions with the foreign tourist is declining and free-range self-sufficient lions on small, private reserves have become desirable across southern Africa. Many of these animals are translocated from one ecosystem to another. In the case of animals sourced from zoo-type institutions, the animals are rehabilitated and released. Often,

individual lions from different reserves are translocated to another ecosystem and rehabilitated into one pride such as was the case at Lowhills Safari's in northeastern South Africa (pers. obs.). The impact of these translocations from, for example, Pilanesberg Nature Reserve to the lowveld or a savanna ecosystem to the Kalahari, has not been adequately studied in the African lion. Adaptations not only to the climate, but also the water and differing vegetation conditions must be made, and the influence of these on the general health and well-being of the African lion is unknown. This is well exemplified by a personal observation in 1995. A farmer from the Witvlei district, Namibia, purchased cattle at an auction in Windhoek. After translocating the cattle to his farm, the entire herd died as a result of the high nitrate content in his water while the cattle reared on his land showed no negative effects.

Much has been published on the etho-ecology and biology of the wild populations of the African lion, focusing on east Africa (Bertram, 1975; Packer & Pusey 1997; Packer *et. al.*, 2001; Schaller, 1972), the southern Kalahari (Eloff, 2002; Owens & Owens, 1984) and larger game parks such as Etosha National Park in northern Namibia (Stander, 1992). The bulk of published data that can be sourced on the African lion, however, focuses on the lions in savanna and bushveld ecosystems. There is a general paucity of publications on the Kalahari lion in relation to the lions from East Africa, for example. Studies on the thermoregulation of this species are absent except for one article by West & Packer (2002).

Lions throughout Africa are confined to reserves and for viability, populations must be large. In southern Africa, the Kalahari lion occurs in the smallest numbers in the Kgalagadi Transfrontier Park, averaging roughly 120 individuals (Laws, 1999; Smith, 1996). The population is relatively small and as a result, research on these animals becomes paramount if they are to be conserved. According to Laws (*op. cit.*), the lions in the Kgalagadi Transfrontier Park occur at very low densities (1,5 lions per 100 km²) which could translate into "real threats to population demography and reduced genetic variation, leading

eventually to social instability or extinction. Conservationists have asked: what is the status of the Kalahari lion in terms of numbers and genetic isolation and can the population sustain the problem animal take-off along the borders?"

The pride studied in the southern Kalahari in Namibia is under rehabilitation and is scheduled for release in the future. The aims of this study were to:

- Investigate the general behaviour of the Kalahari lion under rehabilitation conditions,
- Study the adaptation of time-energy budgets in relation to temperature,
- Examine the use of behaviour for the purposes of thermoregulation and
- Survey ecto- and endoparasite numbers.

Behavioural studies, according to Wilson (1997), "take us closest to the true nature of the species encountered in the wild. If you know an animal's behaviour well, you know its essence." If one is to study animal adaptation the stereotypical behaviour patterns demonstrate these. Therefore, the importance of behavioural studies cannot be overemphasised. Behaviour is intricately related to thermoregulation and represents a mechanism by which thermal balance can be maintained without energy costs. Behavioural adaptations in relation to thermal balance are ecosystem unique because the organism and its environment form a single functional unit (Pantin, 1964). It would be presumptuous to assume that the response to heat and cold in the subtropical lowveld lions and the temperature thresholds at which these would occur are no different from the responses encountered in the Kalahari. Temperature has a powerful effect on an animal's ability to survive and reproduce since it reaches into the biochemistry of the body and as a result, the coping mechanisms of the species represent a large portion of its fitness.





2 STUDY AREA

2.1 LOCATION

The Kalahari is the world's largest continuous mantle of sand stretching over nine countries from the Orange River in South Africa through to the central parts of the Democratic Republic of the Congo (Grove, 1978). Approximately a fifth of the total surface area of 896 000 km² is known as the southern Kalahari which represents the southernmost variant. Southeastern Namibia occupies the western fringe of this system. Owing to the fact that the quartzite grains have a well-rounded appearance, the formation of the Kalahari sand mantle could only have occurred by wind (Van der Walt & Le Riche, 1999). The erosion of the rocks of the pre-Kalahari surface was apparently promoted by climatic extremes and the low rainfall, coupled with the cold Benguela Current, further enhanced the accumulation of sand (Van der Walt & Le Riche, *op. cit.*).

Dunes run from southeast to northwest in a parallel formation (Fig. 2.1) as a result of the prevailing winds that formed the ecosystem (Van der Walt & Le Riche, 1999). Characteristically, the sand has a red-brown hue owing to the presence of iron oxide which is leached out by water. There is a grading from red, predominantly on the highest points such as dune crests, to pink in the dune streets and pale grey in the well-known pans and saline depressions (Fig. 2.1). This is dependant on the stabilising effect of the vegetation (Van der Walt & Le Riche, *op. cit.*).

The system is classified as a semi-desert as a result of an average annual rainfall below 250 mm (Grove, 1978). The western Kalahari is drier than the eastern parts due to the prevailing cold Benguela Current off the coast of Namibia. Rainfall moves in from the Indian Ocean in the east.

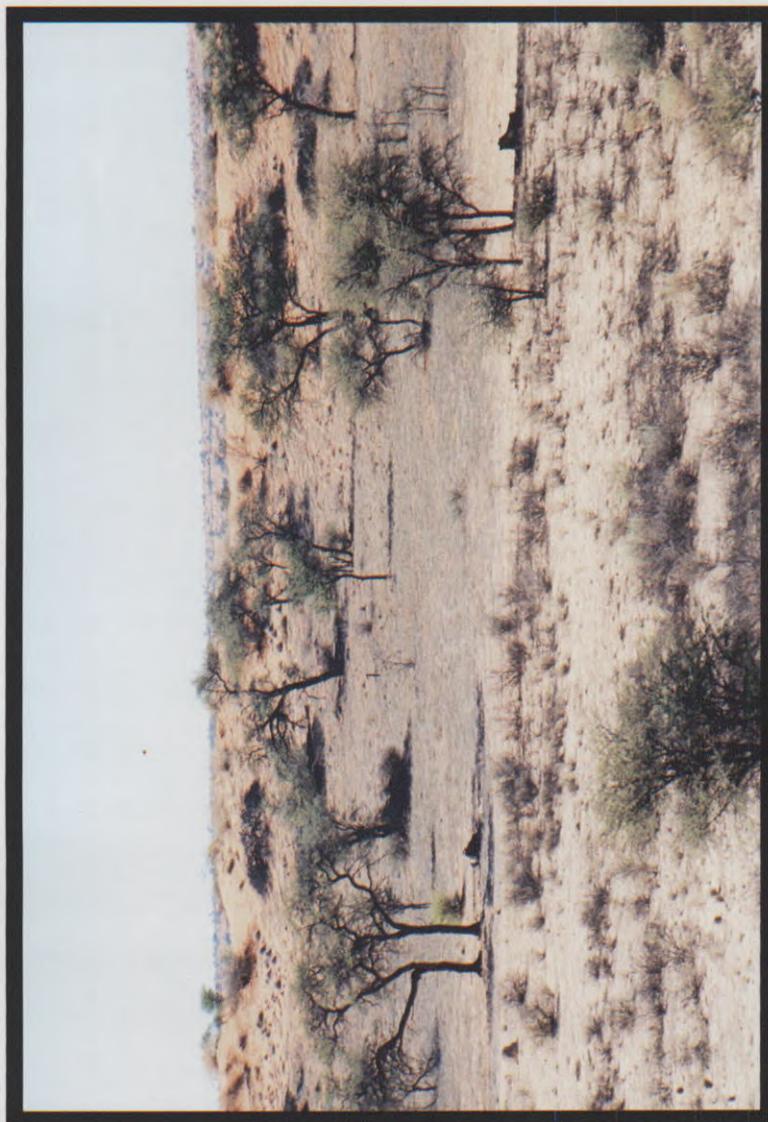


Figure 2.1 Typical Kalahari landscape. The grading from red on the dune crests to white in the saline depressions can be seen clearly.

Fieldwork on the behaviour and aspects of thermoregulation of Kalahari lions was conducted in southeastern Namibia at Intu Afrika Kalahari Game Reserve. The reserve (24° 06.33' S; 17° 56.31' E) is situated approximately 60 km northeast from Mariental (Fig. 2.2). It is a privately-owned reserve and covers an area of 10 000 ha where the lions are held in a 500 ha enclosure (Fig. 2.3) on the southwestern perimeter. As in the reserve, the vegetation in the enclosure is entirely natural and indigenous. Fencing of the enclosure is 2,4 m high and electrified to a height of 1,4 m. Four dunes with six peaks run through the enclosure. A permanent waterhole, fed by a pump with a reserve tank, is situated in the centre of the enclosure in a dune street. Three gates provide access on the northern, southern and eastern perimeter fences. For purposes of veterinary work, a separate area (ca 50 x 50 m) is cordoned off on the northern perimeter.

No large game is kept in the enclosure as the lions are fed regularly. As a result of a prolonged drought and due to good grazing in the enclosure, several steenbok (*Raphicercus campestris*) and a springbok ram (*Antidorcas marsupialis*) have taken up voluntary residence, successfully avoiding the lions for approximately three years. A solitary Cape fox (*Vulpes chama*) and the yellow (*Cynictis penicillata*) and banded mongoose (*Mungos mungo*) are also present.

2.2 CLIMATE

Most of the world's deserts are seasonal. There is a predictable wet season, but not a predictable amount of precipitation. The Kalahari, as a semi-desert, is not strongly seasonal. More than half of the annual rainfall occurs during November to April, but there is some probability of rainfall in every month of the year (Whitford, 2002). Capricious rainfall is characteristic of a semi-desert. This is coupled with temperature extremes during both summer and winter. The hottest months are December and January and the average daily maximum for

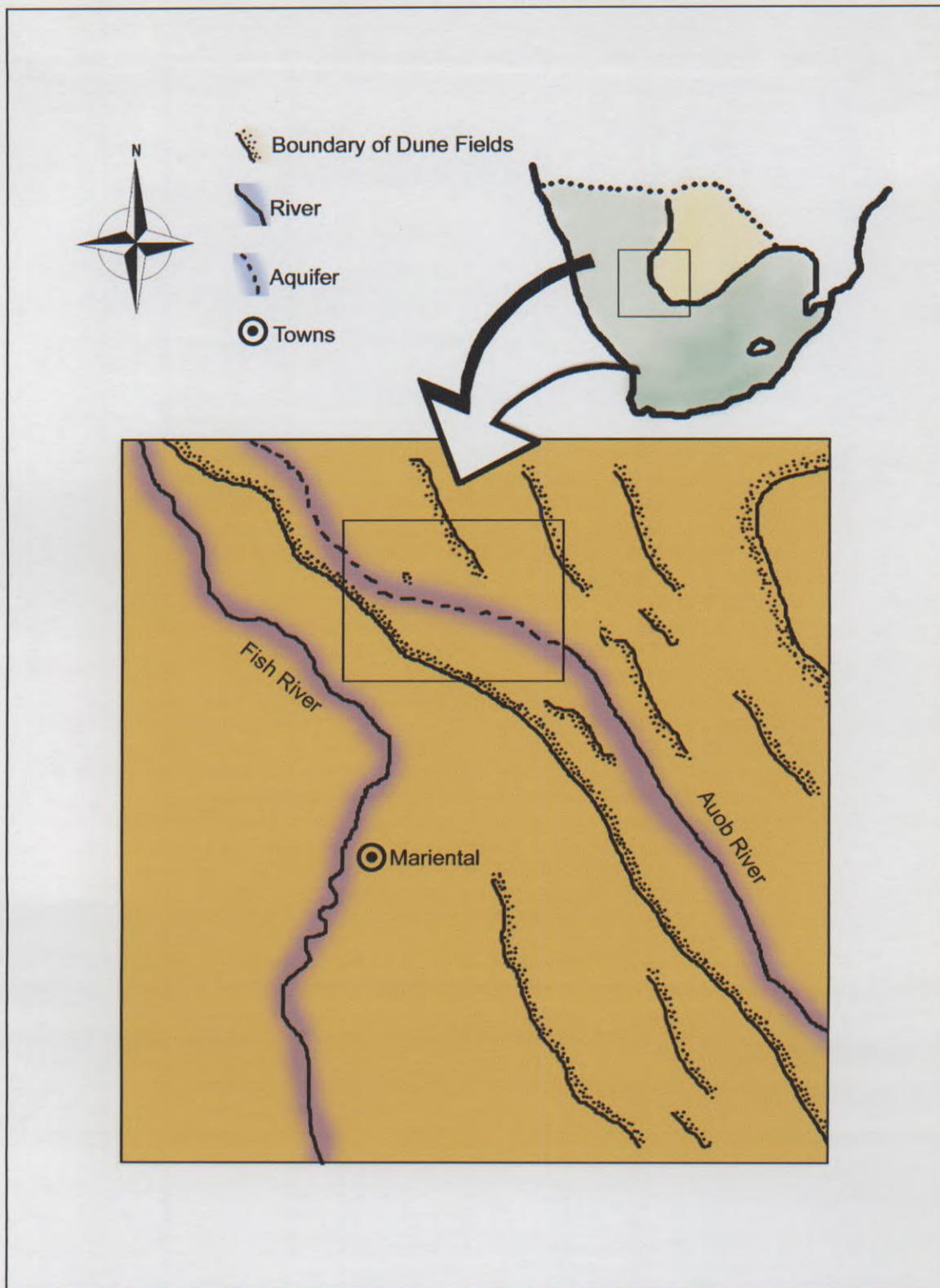


Figure 2.2 Location of the study area in the Kalahari. The reserve is situated north of the dune boundary in the region of the Auob River aquifer.

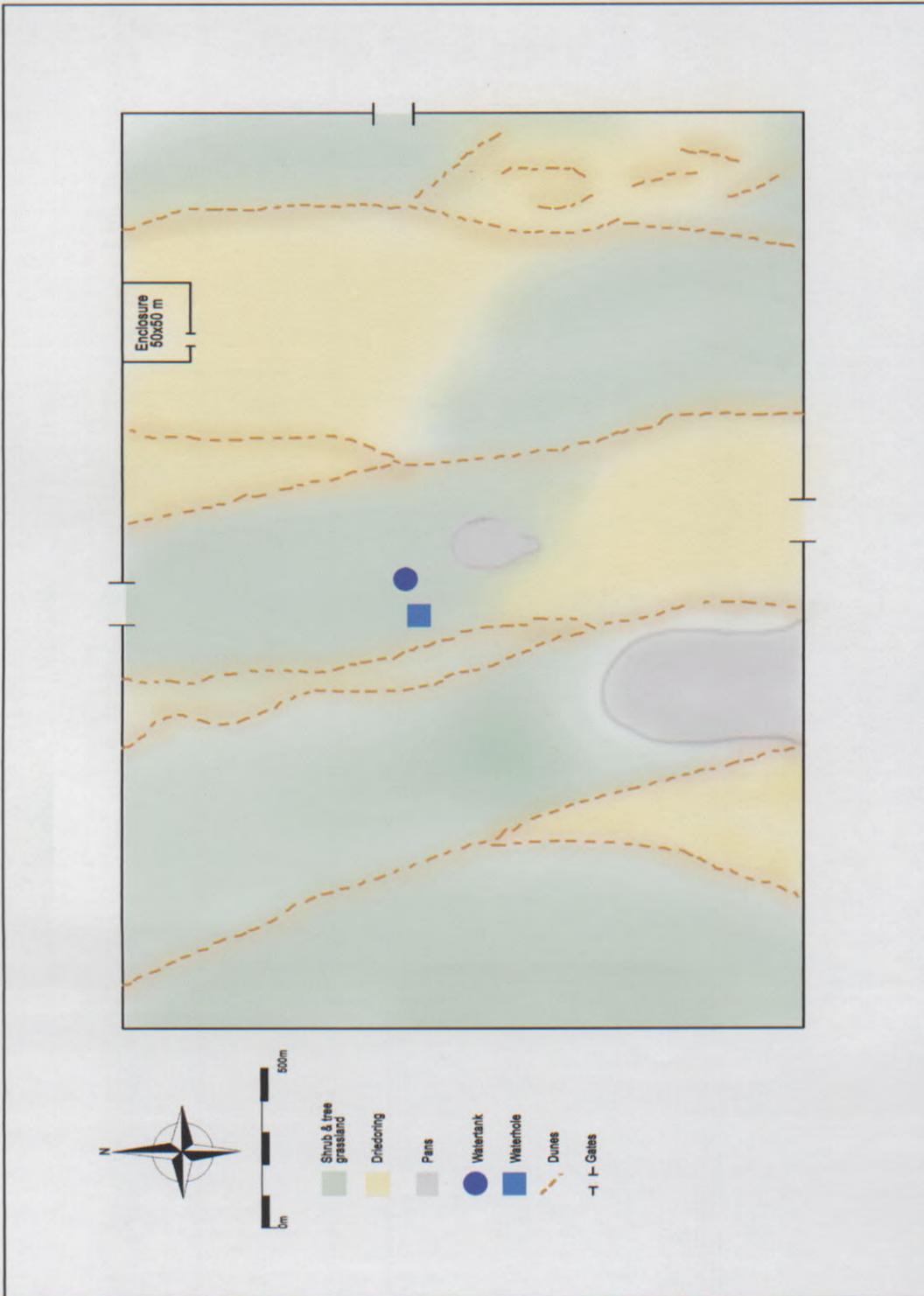


Figure 2.3 The 500 ha lion enclosure where fieldwork was conducted during winter, 2003 and summer, 2004.

Intu Afrika Kalahari Game Reserve is 35,1 °C during this time. July is the coldest month and the average daily maximum is 22,9 °C (Namibia Meteorological Service, unpublished data). Nighttime temperatures during winter are very cold and generally drop below zero, with the lowest recorded temperature at Intu Afrika being -15 °C (Howard Hebbard, pers. comm.). During fieldwork daily temperature peaks occurred at 15:00 and nighttime lows between 05:00 and 06:00, just prior to sunrise. The temperature of the sand also fluctuates greatly. The hottest measured during the winter study period in the sun was 40 °C and the maximum for summer was 59 °C. The highest temperature recorded for Kalahari sand during the summer months is 75 °C (Apps & Du Toit, 2000).

A climatogram (Fig. 2.4) of the study area was compiled with information supplied by the Namibia Meteorological Service (unpublished data) using the method described by Walter (1964). As shown in the figure, the wet season (December to April) is represented by the period when the rainfall curve exceeds the temperature curve on the climatogram for the study area. The remaining part of the year is then considered as the dry season. The total rainfall recorded during the period of study (2003 – 2004) is also illustrated on the climatogram. Table 2.1 shows the mean temperatures recorded during the study period.

According to Van der Walt & Le Riche (1999), three climatic phases dominate the ecological functioning of the Kalahari. The first is the wet phase when rainfall exceeds the standard annual mean. This phase occurs every 10 - 20 years. The arid phase is much more extensive than the former since drought is synonymous with the Kalahari. Rainfall during this phase is generally far below the standard annual average. Finally, there is the transitional phase with rainfall that varies around the annual mean. This phase acts as a prelude to a wet or arid phase and demands various adaptations from the animals and plants that inhabit the Kalahari.

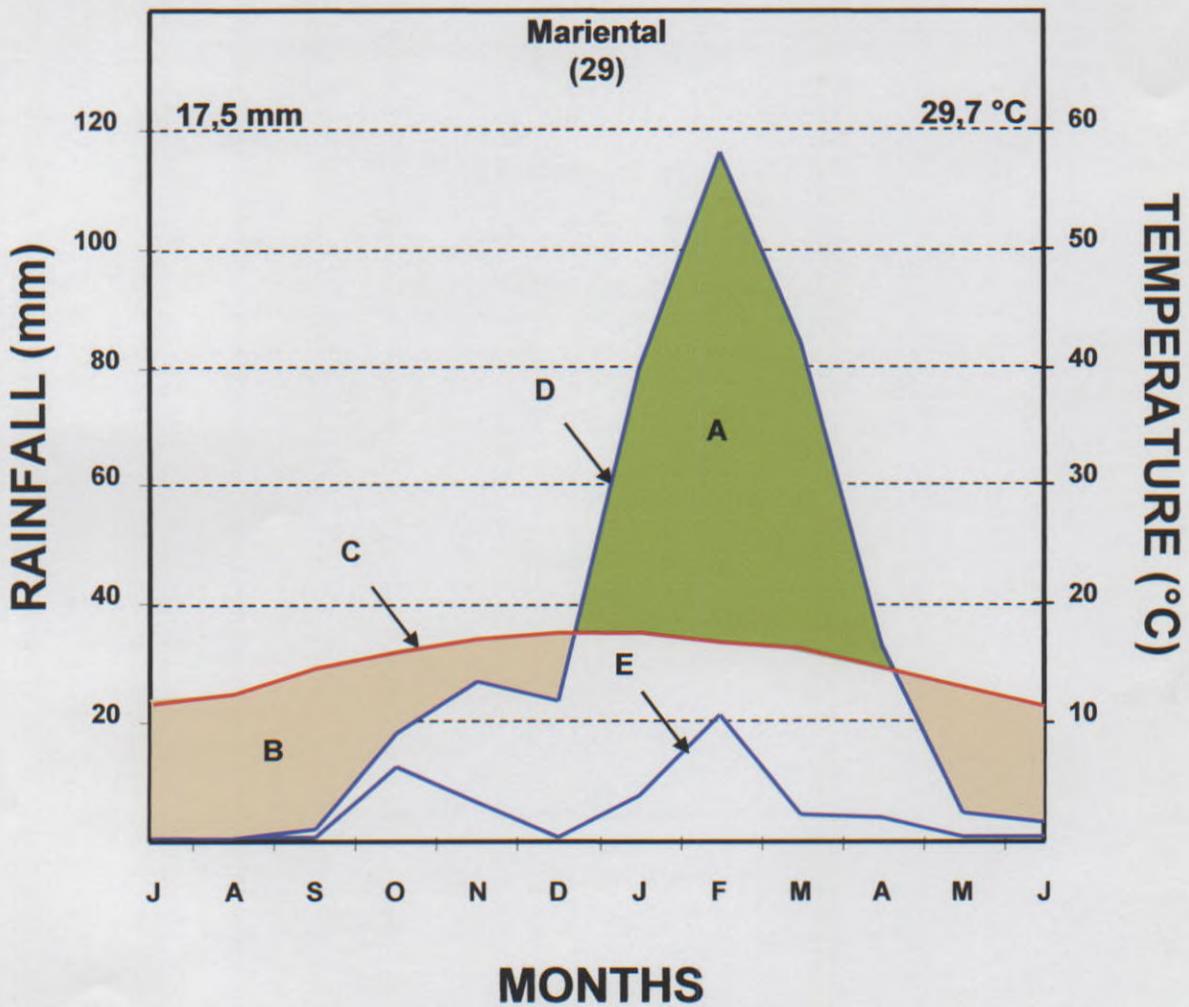


Figure 2.4 Climatogram of Intu Afrika Kalahari Game Reserve using the method of Walter (1964). A, wet season; B, dry season; C, monthly mean temperature; D, monthly mean rainfall; E, monthly mean rainfall during study period.

Table 2.1 Seasonal variation in temperature (°C) during the period of study in the Kalahari.

Week	Winter 2003			Summer 2004		
	Day	Night	Day	Night	Day	Night
	Mean	Range	Mean	Range	Mean	Range
1	21,7	(6,0 - 31,6)	32,2	(15,4 - 39,7)		
2					18,6	(15,6 - 29,2)
3	22,1	(3,8 - 31,8)	29,9	(12,7 - 39,5)		
4					23,7	(16,6 - 34,6)
5	18,8	(-2,8 - 29,7)	29,5	(10,8 - 36,7)		
6					23,8	(11,1 - 37,0)

2.3 VEGETATION

The southern and central Kalahari is classified by Lovegrove (1993) as a part of the Arid Savanna Biome. According to this classification the dominant plant life forms are the grasses, which constitute more than 50% of the canopy cover, followed by woody trees or shrubs. The Kalahari is known to have few endemic species and flowering plants, and in this ecosystem, only the hardiest species from the neighbouring Karoo Biome and grassland regions have survived rigorous selection.

Intu Afrika Kalahari Game Reserve meets its water requirements by means of the strong flow of the Auob River aquifer through the reserve. As a result, there are a large number of trees of which the camelthorn (*Acacia erioloba*) is the most dominant (Fig. 2.5A). Other acacia species include the candle thorn (*A. hebeclada*), false umbrella thorn (*A. luederitzii*) as well as the endemic grey camelthorn (*A. haematoxylon*). The well-known shepherd's tree (*Boscia albitrunca*), along with the wild green-hair tree (*Parkinsonia africana*) and the worm-bark false-thorn (*Albizia anthelminitica*), are scattered across the area in the dune streets as well as on the dune faces. Only the shepherd's tree occurs on the dune crests and when found here, it is more shrub-like in appearance.

Black thorn (*Acacia mellifera*) is the most prevalent shrub in the dune streets. Other shrubs include blue bush (*Monechma incanum*), blue pea (*Lebeckia linearifolia*) and trumpet thorn (*Catophractes alexandri*). The driedoring (*Rhigosum trichotomum*), good karoo (*Pentzia incana*) and perdebos (*Monechma foliosum*) are mostly limited to the pans and saline depressions while the dune faces and crests are home to the besembossie (*Crotalaria spartioides*) and the January bush (*Gnidia polycephala*).

Grasses dominate a large area of the Kalahari especially after copious rains. The reserve's principal grass species is the Kalahari sour grass (*Schmidtia*

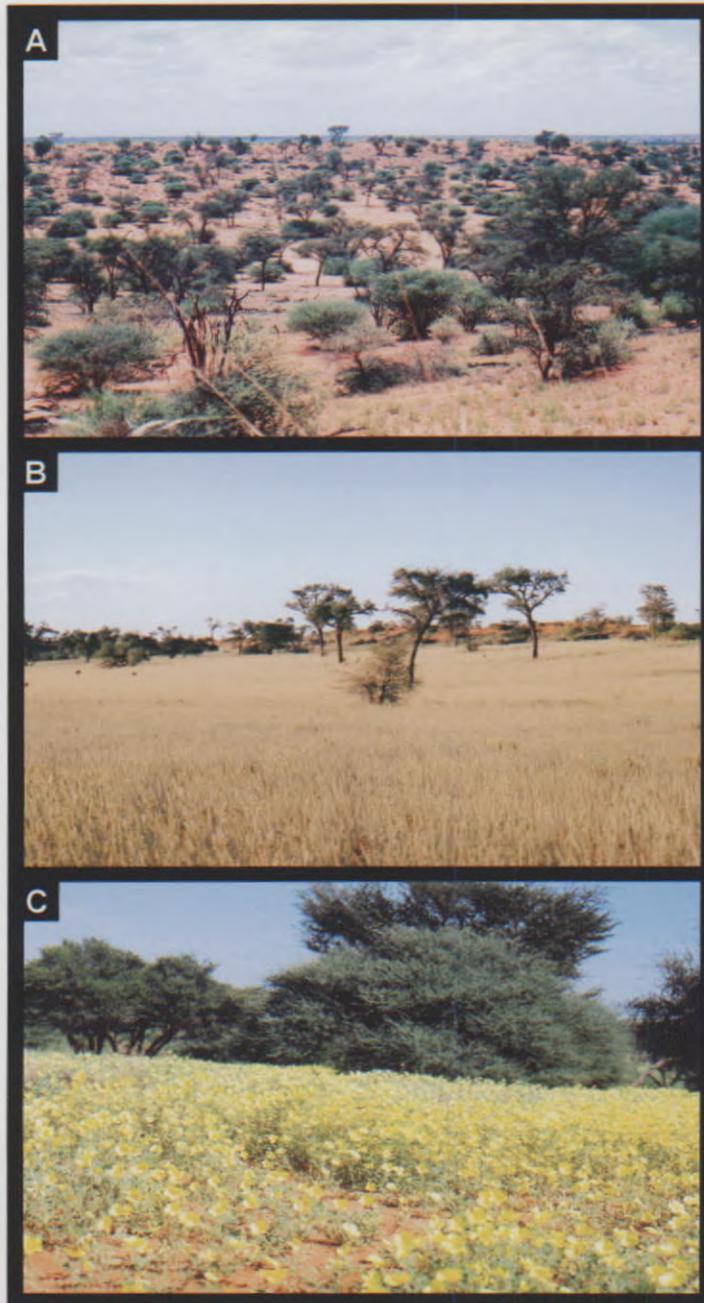


Figure 2.5 Typical Kalahari vegetation. A, the dominant tree (*Acacia erioloba*) and shrub (*A. mellifera*) species in the study area; B, Kalahari sour grass (*Schmidtia kalahariensis*) is the primary grass species; C, devil's thorn (*Tribulus zeyheri*) covers major areas of the reserve after copious rains.

kalihariensis) (Fig. 2.5B). This species, along with gha (*Centropodia glauca*) and nine-awned grass (*Enneapogon cenchroides*), as well as silky (*Stipagrostis uniplumis*), small (*S. obtusa*) and tall bushman grass (*S. ciliata*), covers the dune streets and the dune faces. Only Kalahari dune grass (*S. amabilis*) grows on the dune crests.

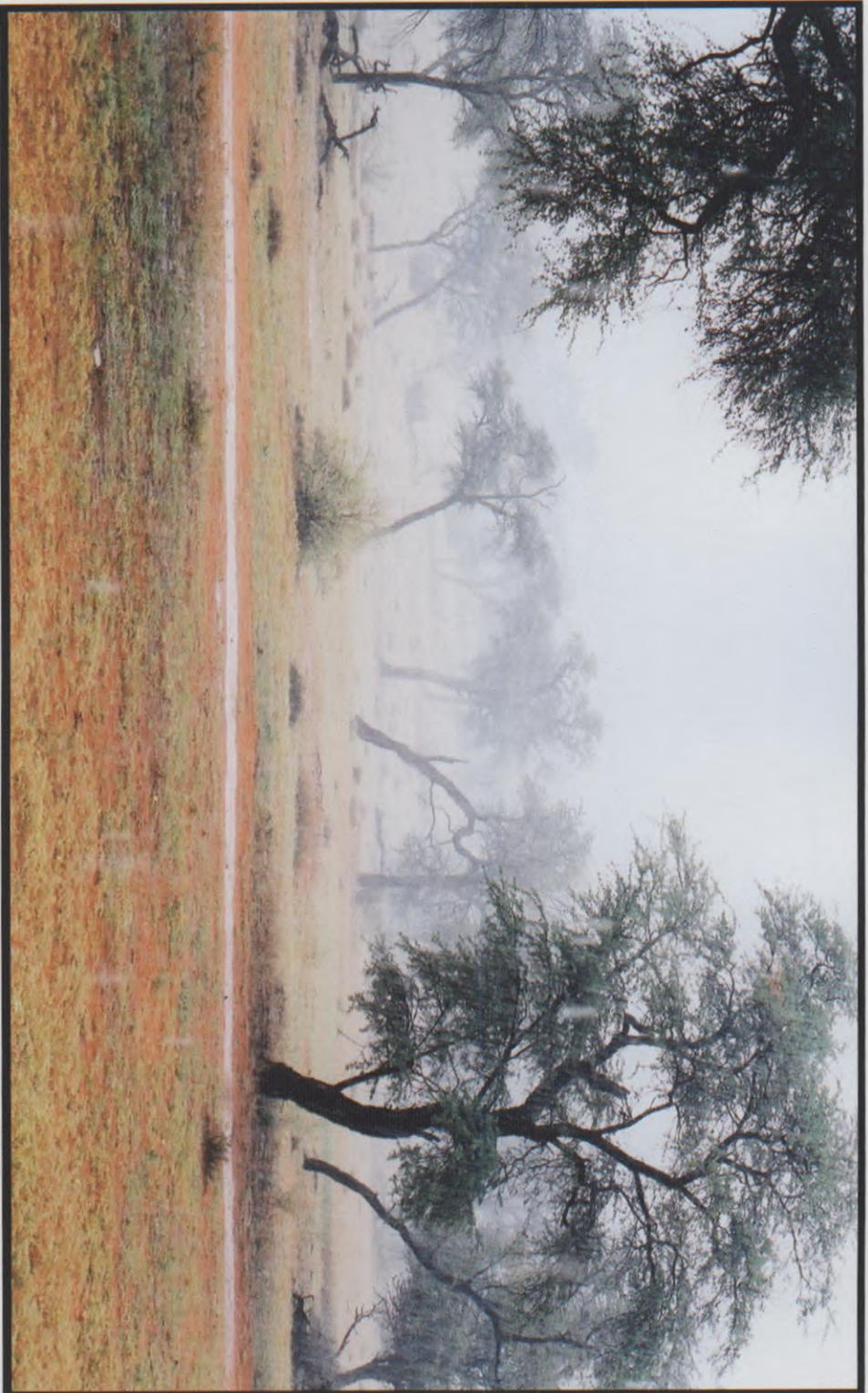
A large variety of bulbs and creepers occur in the Kalahari, most of which are only seen after rainfall. This is the time they normally bloom and set seed. Well-known ephemerals present on the reserve are the devil's thorn (*Tribulus zeyheri*) (Fig. 2.5C), pretty lady (*Cleome angustifolia*), springbokopslag (*Indigofera alternans*) and thunderbolt flower (*Sesamum triphyllum*). Important food and water sources for carnivores and ungulates alike are the tamma (*Citrillus lanatus*), small wild cucumber (*Cucumis africanus*) and gemsbok cucumber (*Acanthosicyos naudiniana*).

2.4 WILDLIFE

Prior to 1989 the reserve area was used for commercial livestock farming. As a result, there is a strategic system of boreholes driven by windmills and this is used to water the wildlife on the reserve. Subsequent to its purchase, it was converted to a game reserve and a number of animals were re-introduced or introduced for the first time. Excluding the lion enclosure, all internal fences were removed and the wildlife on the reserve is free-roaming. These include an estimated 20 blue wildebeest (*Connochaetus taurinus*), three eland (*Tragelaphus oryx*), 100 Cape oryx (*Oryx gazella*), 20 Burchell's zebra (*Equus burchelli*), five giraffe (*Giraffa camelopardalis*) and 520 springbok. A small herd of 15 impala (*Aepyceros melampus*) and 26 black wildebeest (*Connochaetes gnou*) were also introduced. Smaller species of ungulates such as the steenbok, common duiker (*Sylvicapra grimmia*) and warthog (*Phacochoerus aethiopicus*), as well as carnivores like the African wildcat (*Felis silvestris*), small spotted genet (*Genetta genetta*) and the bat-eared (*Otocyon megalotis*) and Cape fox also abound. Black-backed jackals (*Canis mesomelas*) have been heard at

night and it is presumed that a family group may be present. Two leopards (*Panthera pardus*), one free-roaming and the other held in a 2 ha enclosure, are present on the reserve. A variety of mice, mongooses, some 80 species of birds, including some 70 reintroduced ostriches (*Struthio camelus*) can also be seen.





3 MATERIALS AND METHODS

3.1 RESEARCH SUBJECTS

A small pride of lions was studied in the Kalahari. It consisted of three adults, two males and a female, and two cubs (Fig. 3.1). The younger male and the female are siblings. They were sourced from an animal sanctuary when they were approximately six months old. They are the fourth generation sired by lions from Port Elizabeth Zoo. Their lineage is captive and hunting skills were learnt at Intu Afrika. The larger male, although sourced from the same sanctuary, was wild-born and entered Namibia from Botswana as a nomadic male aged roughly 18 months. He was held at the sanctuary for three months. Relocation to the 500 ha enclosure at Intu Afrika was roughly three years ago. The lions were capable of effective hunting at the inception of the study. Two cubs, sired in all probability by the older male, were born in November 2003 and were included in all the trials during summer 2004. The older male was approximately four and the female and younger male 3½ years of age during the winter trials of 2003. During the summer trials of 2004, the older male was five and the sibling pair adult at roughly four years. The two cubs were 2½ months old at the start of the summer trials. Morphometric measurements of the older male and female were taken during the winter trials. The total length of the older male was recorded at 2,87 m, with a shoulder height of 0,97 m and chest circumference of 1,34 m. The female's total length was 2,33 m with a shoulder height of 0,80 m and chest circumference of 1,08 m. During the summer trials both these animals were weighed with the older male recording a mass of 226 kg and the female 126 kg. According to Eloff (2002) and Schaller (1972) these results fall within the means recorded for African lions except for the female's total length which may be as a result of her age, 3½ at the time.

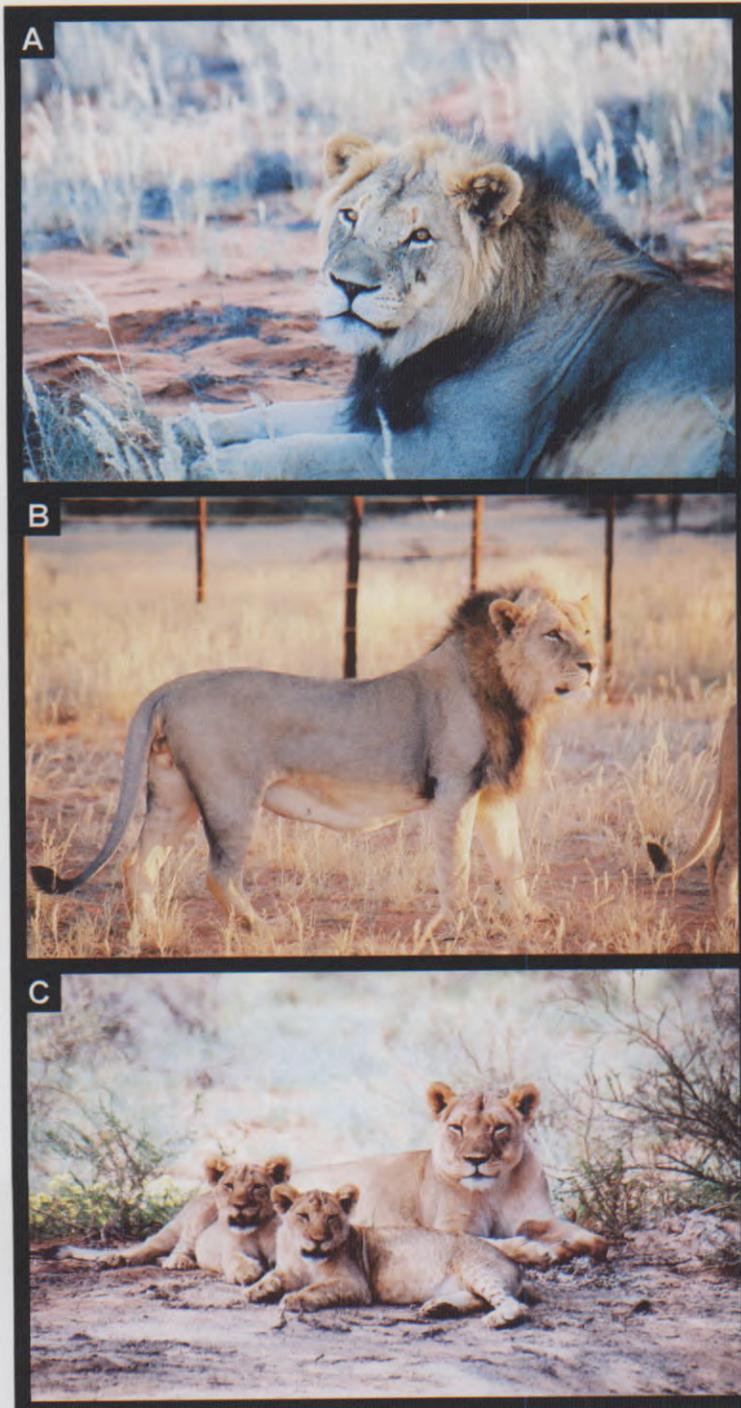


Figure 3.1 Small pride of African lions studied in the Kalahari. A, the older male; B, the younger male; C, the female with the two cubs.

3.2 FIELDWORK

Behavioural studies require qualitative and quantitative observations of the animals in their natural environment, coupled with the collection of quantitative data of abiotic factors. Fieldwork was carried out during winter 2003 and summer 2004 to enable the gathering of data that is specifically aimed at temperature balance. The winter trials lasted five weeks and the summer trials six weeks, alternating between day and night shifts lasting six consecutive days each. Winter trials were conducted during the period 11 - 29 May and again from June 23 - July 5, 2003. The summer trials began on February 16 and lasted until March 27, 2004. Continuous daytime and nighttime observations of the animals were made. Daytime shifts began at sunrise and ended at sunset, while nighttime shifts began one hour prior to sunset and ended at sunrise. The extra hour was essential for establishing the change of behaviour and climate pattern during the transition from day to night.

All field observations of the lions were made from a vehicle while following the animals as closely as was viable. During day shifts, the activities of the focal animals were timed with the use of a stopwatch, while the activities of the remaining members of the pride were also noted. All movement and stationary activity were recorded. Selection of site in the enclosure, positioning of the animals and selection of sun and shade were taken into account. Interaction amongst members of the pride such as play, allogrooming and nuzzling were observed and timed as was the use of vocals, both inter- and intrapride, auto-grooming and territorial behaviour. The intensity of panting and duration of loin exposure, both activities which indicate thermoregulation, were documented. Focus was also placed on activity patterns and variables such as enclosure usage and activity with empty or full bellies were taken into account. The extent and intervals of feeding and drinking were observed. Other behavioural data was also collected such as association within the pride, tree climbing and dominance behaviour. The latter included the frequency of scuff and spray marking in relation to urination.

Nighttime shifts presented difficulties in terms of detailed observations. The use of the headlights of the vehicle as well as a hand-held spotlight powered by two separate car batteries could not be employed for the entire time of darkness. When the animals were asleep, light was used every 30 minutes and when there were periods of interaction or activities such as grooming or feeding, light was used every ten minutes. During active nights such as when border patrols occurred, the animals were followed and light was used for the entire time. A red filter on the light source was not deemed necessary and the lions demonstrated no discomfort or disturbance when the light was used. It was never directed at the animals, but shone slightly above them.

For the purposes of documenting behavioural thermoregulation, ambient temperature and relative humidity were recorded hourly with the use of a MCS 120-02 Data Logger, during both the nighttime and daytime shifts. The sensor was fixed outside the vehicle to allow for full acclimation and immediate and correct readings. The temperature of the sand was measured at hourly intervals by suspending a thermometer from the vehicle and allowing the mercury tip to penetrate the surface of the sand. It was held in that position for one minute. Sand temperature readings were taken at the site where the vehicle was parked, which was normally close to the pride in the shade. When an opportunity arose for readings in both sun and shade without disturbing the lions, such as the proximity of sunlight or movement of the pride, this was done. The general direction of the wind was recorded. During summer trials, wind speed on the dune crests and in the dune streets was measured with a handheld anemometer.

3.3 IMMOBILISATION

For the purposes of surface temperature measurement of the animals, they were immobilised and Thermocron iButtons™ were implanted. The lions are limited to a 500 ha enclosure and are fully habituated to vehicles. The female

and the oldest male were selected for implantation. The focal animals were darted from a game drive vehicle and immobilised using 250 mg Zoletil and 100 mg Xylazine per dart. For the purposes of implantation of iButtons, combing for ectoparasites and weighing, the animals were removed from the enclosure. The trials were conducted during two seasons and, therefore, iButtons were implanted at the start of each trial and removed at the end of the trial. The immobilisation lasted some three hours each time. As a result, the animals required top-up of anaesthesia, done every 30 to 60 minutes with 100 mg Zoletil.

Implantation of iButtons to record the surface temperature of the animal was done at three sites on the body, namely the right side of the neck, the base of the tail and in the loin (Fig. 3.2A – C). A subcutaneous pouch was created to hold the iButton in position. The wounds, after being stitched, were treated with 20 ml Peni LA and Terramycin topical spray, both antibiotic treatments. The surface of the animals was combed and searched for the presence of ectoparasites. Finally, the animals were individually weighed by suspending them in a tarpaulin attached to a Salter™ scale (Fig. 3.2D). Prior to reversal of anaesthesia using a 25 ml i/v dosage of Tolazoline, the animals were placed in the cordoned-off area on the northern perimeter of the enclosure. Once they were fully alert, the gate was opened and the animals could move back into the enclosure. The older male was collared for the duration of the research.

3.4 CARCASS DISSECTION

Owing to the variation in the results of the iButton data during loin exposure, panting and drinking, a lion carcass was dissected. A male African lion carcass, sourced from Sandhurst Safari's in the Kalahari in the Northwest Province, South Africa, was collected. The lion was five years old and was trophy hunted which prohibited access to the skin and skull. The paws, although skinless, were obtained. The entire dermis was examined for the presence of surface



Figure 3.2 Immobilisation procedure at the inception of the study. A - C, implantation of the iButton into the neck, tail and loin region respectively; D, the weighing procedure of the focal animals.

blood vessels and larger veins and arteries. The kidneys were removed, weighed and measured with a pair of calipers. After making a longitudinal section, the cortical and medullary thicknesses were measured at ten intervals along the periphery. Relative medullary thickness was calculated as:

$$\frac{\text{Absolute medulla thickness} \times 10}{\text{Kidney size}}$$

where kidney size = $\sqrt[3]{\text{length} \times \text{width} \times \text{depth}}$ (mm)
(Cloete & Kok, 1986).

The paw pads were examined for the presence of sweat glands. They were preserved in 10% formalin and sections were made courtesy of the Department of Anatomical Pathology, Medical Faculty at the University of the Free State.

3.5 PARASITES

3.5.1 Ectoparasites

While immobilised for implantation or removal of iButtons, the external surfaces of the animals were combed with a parasite comb. All areas, including the paws and inner ears, were checked for ectoparasites. Collected parasites were preserved in 70% ethanol.

Ectoparasite collection included sampling for tsetse flies (*Ornithodoros savignyi*). Sampling was carried out to determine whether ectoparasites had any effect on the selection of shade by the lions. Sand samples were collected mainly under the shepherd's tree as well as camel- and candle thorns. Excluding a control sample collected under a tree not utilised by the lions, six samples were collected during winter and eight during summer. Collection was always carried out at 12:00 in the shade under the trees in the four wind directions around the circumference of the tree. This was repeated at 1 m

intervals from the tree trunk. Samples were collected at a depth of 5 cm and at 30 cm. The sand samples were sieved through a standard 2 mm flour sieve.

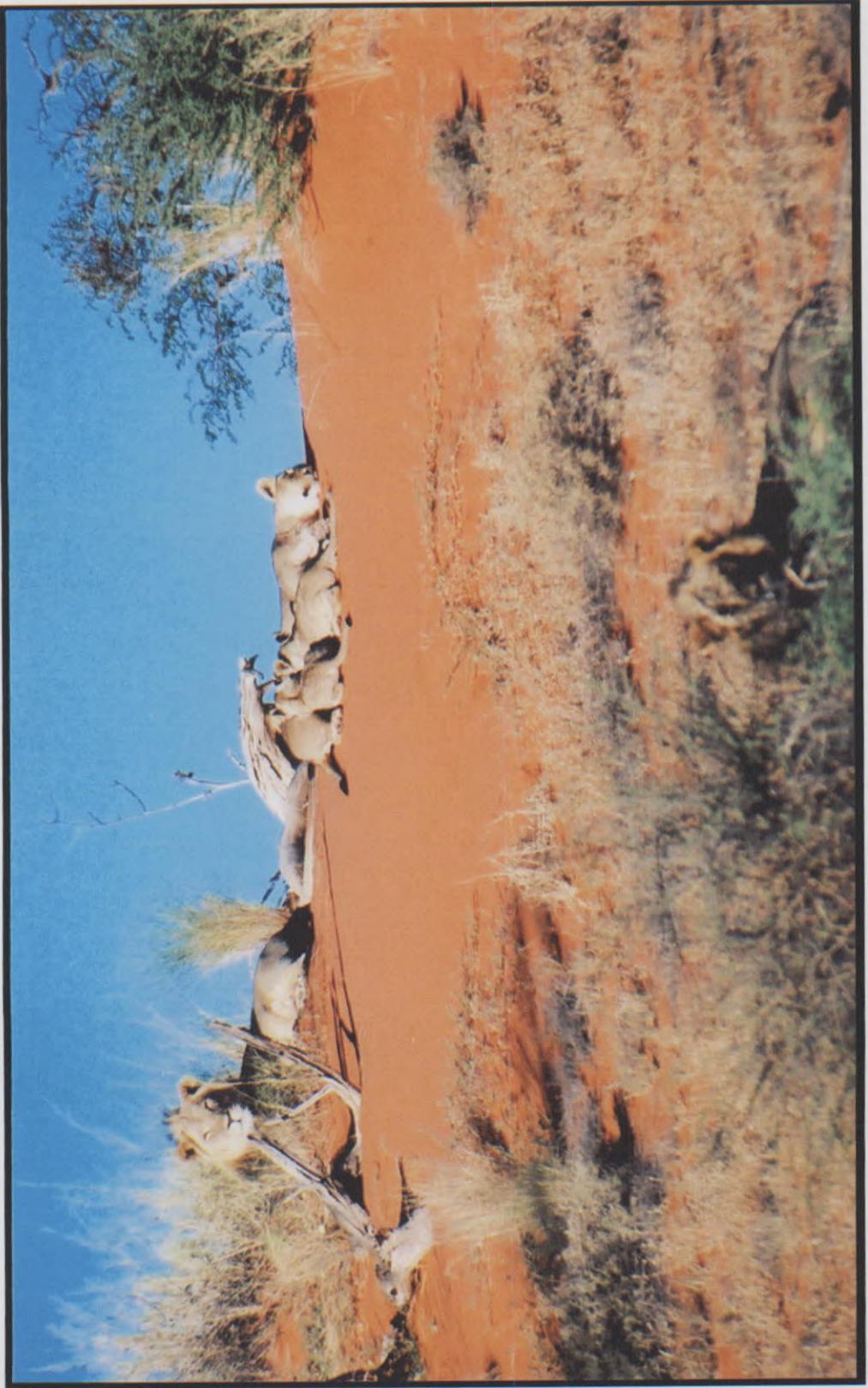
3.5.2 Endoparasites

Intestinal parasite surveys were conducted by opportunistic collection of scat during field observations. A total of 23 samples were collected from the adult lions during both summer and winter. During the summer trial, six samples of scat from the cubs were also obtained, four from the male and two from the female. All collected scat was halved. For the preservation of cestode eggs and proglottids, as well as nematode and trematode eggs, the faeces were preserved in 10% formalin, while 2.5% potassium dichromate was used for the preservation of coccidian oncospheres. Preservation in 750 ml glass bottles was carried out within 12 hours after collection.

A standard operating procedure (SOP CVII/07/02/014 Faecal Examination: Diagnostic and Quantitative) obtained from ClinVet International (Pty.) Limited was used for identification of endoparasites. A flotation technique using egg flotation kits was employed for the diagnosis of nematodes and coccidia. The technique is based on the principle that parasite eggs are less dense than the fluid flotation medium (saturated salt solution) and will, therefore, accumulate at the top of the container. Particles on the top layer were collected on a microscope slide cover, placed on a standard slide and examined under a light microscope for identification. Cestode eggs (oncospheres) such as *Taenia* spp. could also be identified with the use of the flotation technique. Infections with other tapeworms were diagnosed with the use of a sieving technique to locate expelled proglottids. Faeces were washed consecutively through sieves with apertures of 1 mm, 0.5/0.3 mm and 150 µm, respectively. The residues were suspended in a small amount of water and examined under a stereo microscope for the presence of proglottids. Proglottids and eggs were not observed after the winter trials and as a result, sieving was not employed after the summer trials.

The McMaster method (ClinVet International, unpublished data) was used for quantification of eggs. A 2 g sample of faeces was suspended with the aid of a magnetic stirrer in 58 ml of 67% sucrose solution. The latter was prepared by adding 400 g granulated sugar to 600 ml warm water. Eggs were floated in the McMaster slide. This slide has a counting chamber constructed of two perspex slides separated by strips of perspex 1.5 mm thick. A 1 cm² area is ruled over the chamber. Egg numbers are expressed as eggs per gram faeces (EPG). The EPG is calculated by multiplying the number of eggs counted in the square of the slide by 200. The volume under the 1 cm²-ruled area of the McMaster slide is 0.15 cm³. The calculation is as follows: egg count in 0.15 ml x 200 = 30 ml, the volume in which 1 g of faeces was suspended. McMaster slides with three chambers were used and the mean of the three counts were multiplied by 200.





4 GENERAL BEHAVIOUR

4.1 INTRODUCTION

The behaviour of the African lion has been well documented since the early Sixties (Bertram, 1975; Eloff, 2002; Owens & Owens, 1984; Packer & Pusey, 1997; Schaller, 1972; Stander, 1992). Of these, Eloff and Owens & Owens specialised in the research of the Kalahari lion. The pride of lions in the present study also occurs in the Kalahari. The animals are held under semi-artificial conditions, but are scheduled for release in the future. During the fieldwork unusual behaviour not previously recorded was observed, possibly as a result of the semi-captive holding facility. Some behavioural data, however, conforms to what is known about the Kalahari lion and the African lion at large. Since much of behaviour is reaction as it is influenced by the outside world (Tinbergen, 1967), the causes underlying some of the behaviours observed differ from those observed under natural conditions. This chapter serves to record both the conventional and unconventional behaviour of the research subjects, including that of the cubs.

4.2 CONVENTIONAL BEHAVIOUR

In many respects and in spite of the unnatural conditions, the pride conformed to conventional lion behaviour. Activity patterns and time-energy budgets for the pride concurred with published data. (Thermoregulatory aspects of activity patterns and thermoregulatory behaviour are discussed in Chapters 5 & 6). Activity was reduced to a minimum as temperature peaked. Daytime levels differed during summer and winter, but both correlated negatively with temperature increase. Nighttime activity was low, but the pride did not need to, and was not able, to move in search of prey. For the bulk of the daytime hours, the pride stayed in the shade and during early morning and late afternoon, they were found on the dune crests. Scanning, especially towards the east, was

common during this time. The direction of the scanning was based on conditioning (the "food" always arriving from the east), but the behaviour of scanning from an elevated point for prey is recorded by Schaller (1972) as well as Eloff (2002). The latter states that Kalahari lions are often found on dune crests where they scan the habitat for prey and that this is an important aspect of the Kalahari lion's *modus operandi* in hunting. It is well-known that lions use elevation to secure food.

Interaction within the pride also corresponded to published accounts (Estes, 1997; Schaller, 1972; Skinner & Smithers, 1990). Play was common during the crepuscular hours. All the members of the pride would join, but the older male played less frequently. Nuzzling, especially at the arrival of a pride member, was common with no visible preference of individual. Grooming was frequent and took place between all the members of the pride.

Scent marking behaviour was similar to what is known about these elements in lion behaviour. African lions are known to claw trees. Some authors believe that this is for claw sharpening, but Estes (1997) states that the raking of trees may not only assist in removing loose claw sheaths, but also leaves visual and "possibly scent marks (assuming glands described in the feet of domestic cats exist in other cats as well)." The pride was observed to specifically mark two trees in the enclosure. This concurs with results obtained by Schaller (1972). He reports that lions will scratch a particular tree and return to it repeatedly for this purpose. Marks were both high on the tree and lower along the stump (Fig. 4.1). When these two trees were raked, the animal would stand up against the tree. The lions often raked a tree in a stretch posture after sleep (Fig. 4.2), and when this was observed, the raking was never on the two trees visually marked. In the stretch posture, the "consummatory expression" as described by Estes (1997) as one of pleasure, was evident, as demonstrated in Figure 4.2. It is possible then, that lions also rake trees simply to stretch after long periods of inactivity.



Figure 4.1 A signpost tree (*Acacia* spp.) raked by African lions in the Kalahari. Areas of bark removal are indicated.



Figure 4.2 Stretch posture and typical consummatory expression in the older male African lion during tree raking often observed after periods of inactivity.

Scuff marking and spray marking occurred often, increasing in frequency during summer due to the increased competition between the two adult males (Fig. 4.3). The female was observed to scuff mark once during winter, at the site of a carcass, and four times during summer, three times at the carcass and once on the urine of the male cub. Anal glands are present in the African lion (Estes, 1997), but whether secretions are included in the urine has as yet not been tested. Lion Aid is currently researching several prides in Botswana and has managed to successfully collect urine (Website 2). It is expected that this will be tested soon.

Patrols occurred twice during winter and on six occasions during summer. These were incited by the older male and all but once when it commenced at 03:12, they began between 04:00 and 04:17. The males would lead the way and patrol the northern perimeter fence calling, scent marking, playing and resting until shortly after sunrise. A patrol along the southern perimeter was observed only once, during winter. Schaller (1972) reports that territorial calls prior to 17:00, and after 08:00 were rare in the Serengeti. Data collected in the Kalahari indicates that territorial calls by the older male during the first trials in winter totaled 17 with 13 echoed by the younger male, and these occurred between 04:43 and 08:28. During summer, 67 calls were heard with 47 echoed between 19:47 and 07:38. The range was between 15 and 34 with a mean of 20 calls lasting on average 49 seconds. The female joined in the calls twice. In terms of voice and vocal use, Tinbergen (1967) states that calling is contagious. This may explain why the territorial calls are generally in chorus. During these periods, the animals often rubbed their necks against the corner fence poles and often wandered precariously into the cordoned-off area (used for veterinary work), scent marking the fences and rubbing their necks against the poles. The female was reluctant to accompany the males on patrol during summer and often joined them only after an hour or so had passed, lagging behind during the entire period. This may be ascribed to the presence of the cubs during the summer trials. Females do not assist males in territorial patrol and defence.

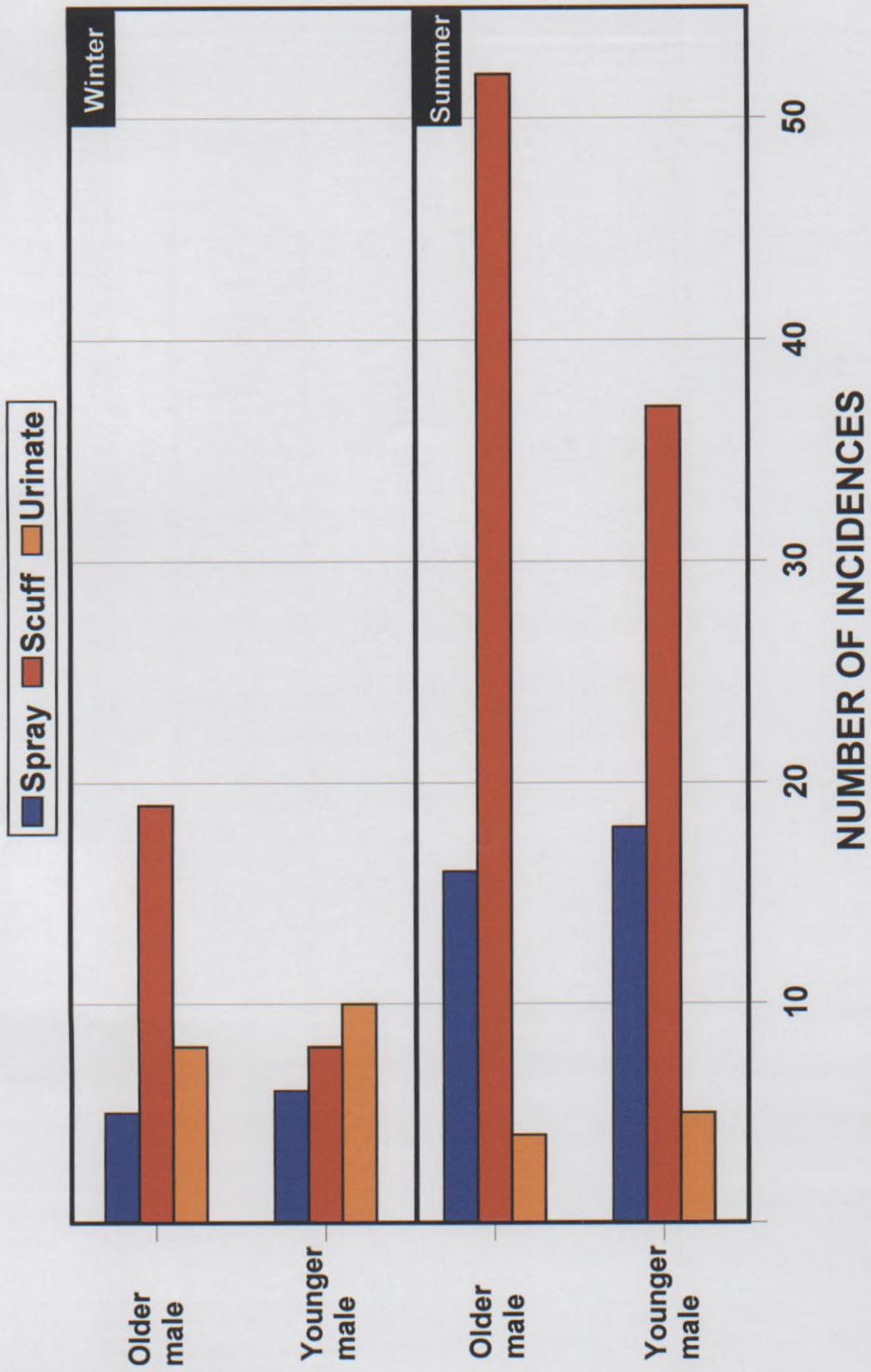


Figure 4.3 Seasonal number of urinations for two adult African lions in the Kalahari.

Dominant males do not spend the bulk of their time with the pride, joining the females only when food has been secured and if the amount is scanty, they will take possession of the carcass (Bertram, 1975). They are also known to be impatient with cubs and do not allogroom frequently. The larger male conformed in all the above aspects to traditional lion behaviour. Unrelated males will form a coalition and will co-operate in the same way as brothers or close relatives do (Owens & Owens, 1984; Packer & Pusey, 1997). The older and younger male behaved in this manner. The younger male accompanied the older on patrols and assisted with scent marking and territorial calling, always echoing the older male and never inciting calling.

Bertram (1975) and Eloff (2002) state that lionesses trigger the pride's movement and direction. The results attained during both the summer and winter trials are in agreement. Conditioning played a large part of the behaviour and the lions were aware of the relative day and time when food would be brought into the enclosure. The sound of a vehicle on these so-called "hungry days" always incited the older male to move "forward" in the enclosure, east, the direction from which the vehicle would approach. It was only on these days that the female did not cause the movement or direction of the pride. During the winter trials, the female broke out of the enclosure four times, three times hunting and killing an ostrich and once when she walked over a large area of the reserve and returned to the enclosure at sunrise. Bertram (1975) and Schaller (1972) report that lionesses in a pride are related and have close social bonds. They also spend the majority of their time together in social activities and interaction. The female in the Kalahari was alone and as a result of the lack of resource limiting factors within her immediate environment, boredom may have played a large part in this behaviour. She often tried to engage the males in play, without success. During the summer trials when the cubs were present, she did not try to escape from the enclosure even when ostriches were moving along the perimeter.

Tree climbing in lions is common in the Kalahari. Eloff (2002) reports that the prides he observed not only climbed trees during play, but also utilised trees for rest. Fosbrooke (1963) describes a severe outbreak of *Stomoxys* biting flies in the Ngorongoro Crater in 1962 which caused the resident lions to climb *Acacia* trees and hide in spotted hyaena (*Crocuta crocuta*) holes to evade the flies. The habit of Kalahari lions of climbing trees can be ascribed to play, the avoidance of a variety of biting flies, tsetse flies (*Omithodoros* spp.) or to escape the heat. Kalahari sand can reach temperatures of up to 75 °C in summer (Apps & Du Toit, 2000). During the study period, the female often climbed trees (Fig. 4.4). This was observed during play and once, during the immobilisation procedure, both her and the younger male climbed trees to escape the vehicles.

According to Estes (1997), members of the family Felidae “tend to be frugal with their food, caching remains of a kill by covering it with leaves or grass and returning to feed on it as long as it lasts.” Eloff (2002) concurs, stating that Kalahari lions not only cover the carcass, but that they bury the intestines and stomach. Schaller (1972) and Skinner & Smithers (1990) report the same. The pride in the Kalahari buried the intestines and stomach immediately after the kill and would scrape sand on the carcass when it was left while they moved to drink or when they left the carcass in the shade for the day (Fig. 4.5). Vultures were present twice during the study period and on both these occasions, the frequency and intensity of covering the carcass increased. This suggests that this behaviour is as a result of competition and that the scent of the carcass is reduced by the sand cover.

The lions were fed once weekly and on occasion, live prey would be brought into the enclosure to reinforce their hunting skills for their rehabilitation. In total, three kills were observed. On all occasions, the lion that was closest to the prey would make the kill and the other two held back standing up only once the prey was pulled down and the kill guaranteed. Co-operative hunting is reported by



Figure 4.4 Tree climbing behaviour of the African lion. The female is seen in a camelthorn (*Acacia erioloba*) tree.

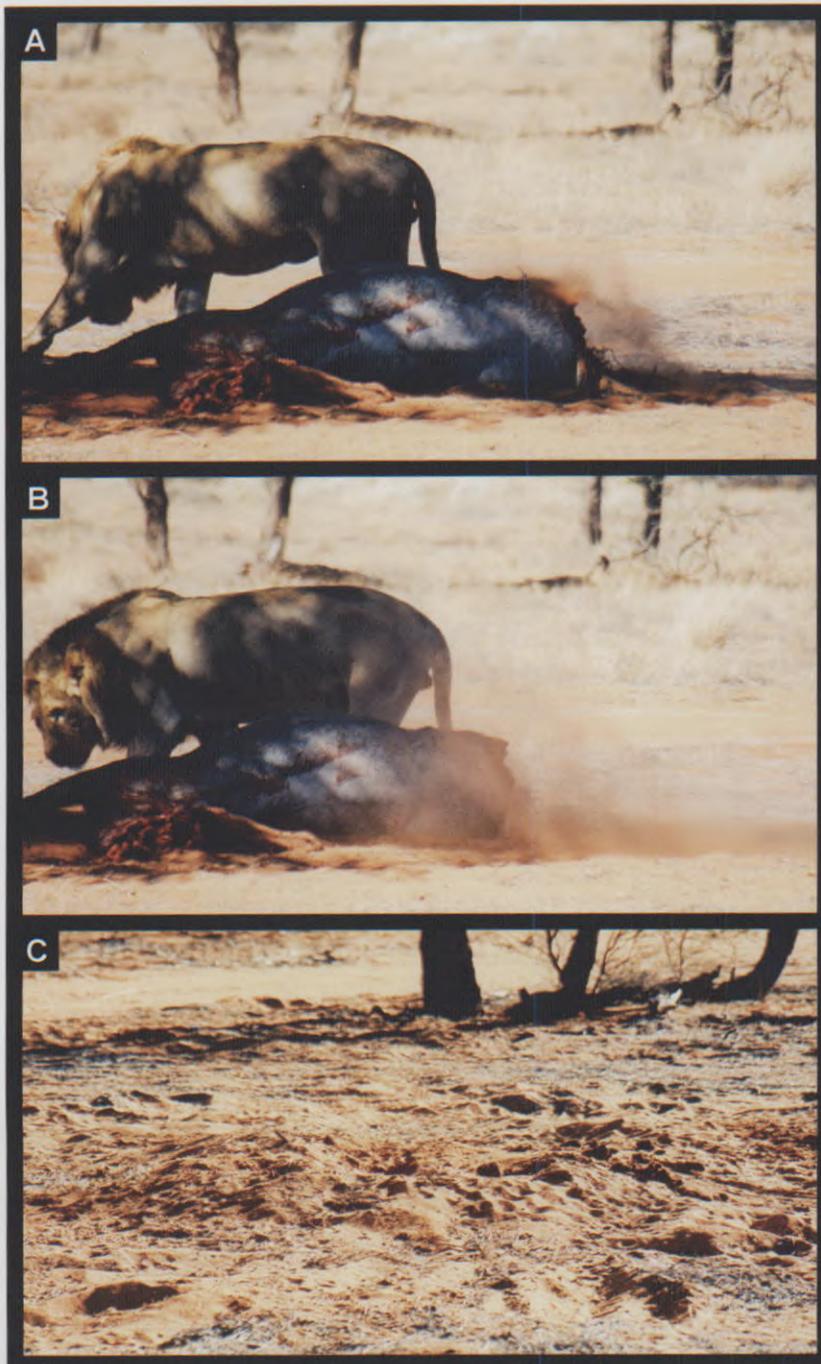


Figure 4.5 Covering of the carcass by the older male African lion in the Kalahari, seen in A and B; C, the intestines and stomach, buried under a mound of sand.

Eloff (2002), Owens & Owens (1984), Packer & Pusey (1997) and Stander (1992).

Ownership of the carcass was taken by either of the males, the female and cubs waiting. When the younger male had possession of the carcass, the female and during summer, the cubs were permitted to feed. On those occasions when only half a carcass was fed, the older male would take ownership and the younger male, female and cubs would feed very little. The results published by Packer & Pusey (1997) are in accordance. With large carcasses, the adults often took turns feeding during the night, the average time for each feeding being 28 minutes. The entire pride was seen feeding together on a carcass twice. Some authors report that kills are sometimes made by breaking the back of the prey (Eloff, 2002; Schaller, 1972). All the kills observed during the trials were by asphyxiation. Feeding on the carcass lasted up to 48 hours during winter and only 36 hours during summer. This could be as a result of the remaining meat putrefying faster during summer. Dragging of the carcass was always the prerogative of the older male. At his first possession of the meat, he dragged the carcass into the nearest shade and proceeded to feed there. He was observed once taking the carcass up the dune face and wrapping it around the base of a tree, fixing it. The two males were seen to play with the carcass and to re-enact the kill during three feeds.

Kalahari lions will consume plant material for moisture and/or roughage (Eloff, 2002). Digestibility trials performed at Bloemfontein Zoo over a period of three years support this. During these trials, collected scat from each feeding cycle held plant material, specifically when bone and hair were voided. Grazing was observed once, by the older male, and his next defecation was photographed (see Fig. 4.6).

Lions are not dependent on water and will drink after feeding if water is available (Eloff, 1973 & 2002; Skinner & Smithers, 1990).



Figure 4.6 Scat voided by the older male African lion after he was observed to graze. Grass material and bone are indicated in the faeces.

Owens & Owens (1984) observed a lioness that had not drunk in nine months. According to Eloff (1973), Kalahari lions "will drink regularly where water is available, they may become completely independent of water under extreme desert conditions." During this study, the lions would drink every second or third day, but often passed the waterhole without drinking. After feeding, the animals drank and the data shows that more drinking took place on a full stomach during both seasons (Figs 4.7 & 4.8), except in the case of the younger male during winter. This may be as a result of his reluctance to leave the carcass site because of competition with the older male.

4.3 UNCONVENTIONAL BEHAVIOUR

According to Wilson (1976), "behavioural scaling is the variation in magnitude or the qualitative state of a behaviour which is correlated with stages of the life cycle, population density or certain parameters of the environment." It is adaptive and its response is appropriate to the situation. Aggressive behaviour and its scaling are dependent on density. As was previously mentioned, the conditions in which the pride was held are artificial. Keeping two adult male lions in a pride with one female has repercussions for behaviour. When fighting and mating behaviour appeared in a husky (*Canis familiaris*) pack, pups learned to avoid strange territories and underwent an adaptation in behaviour (Tinbergen, 1968). The same author also states that in the case of the snow bunting (*Plectrophenax nivalis*), territorial fights space out breeding pairs.

As a result of the imbalance in sex and the semi-captive conditions, avoidance behaviour and spacing effects were not possible for the males in the pride and the impact of dominance and its effects were evident in the Kalahari. Winter trials demonstrated some dominance from the older male with the younger male always submitting. During the subsequent summer trials the younger male, who had become adult at roughly four years of age, began to resist the dominance of the older male.

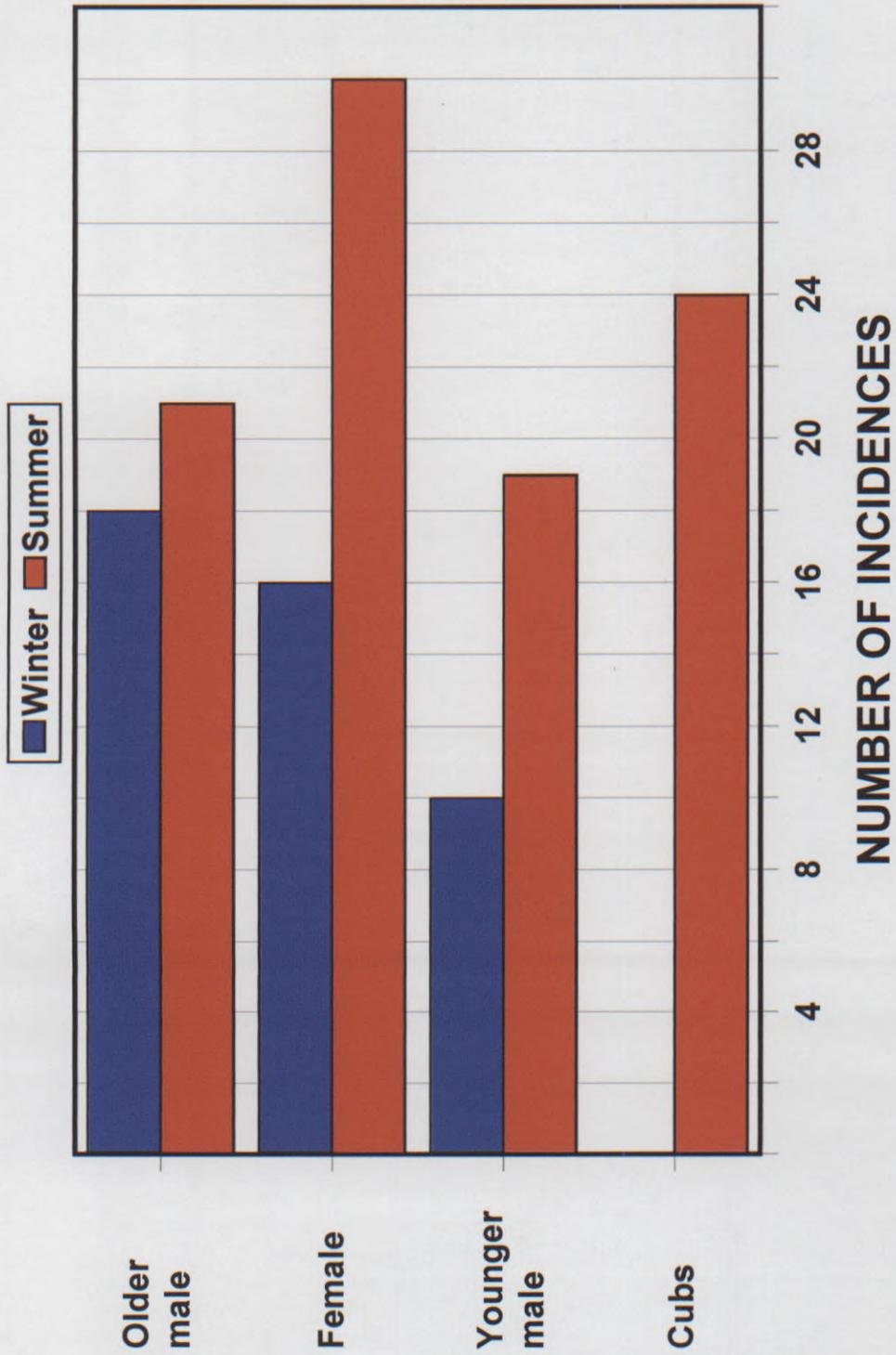


Figure 4.7 Seasonal variation in incidence of drinking in African lions in the Kalahari.

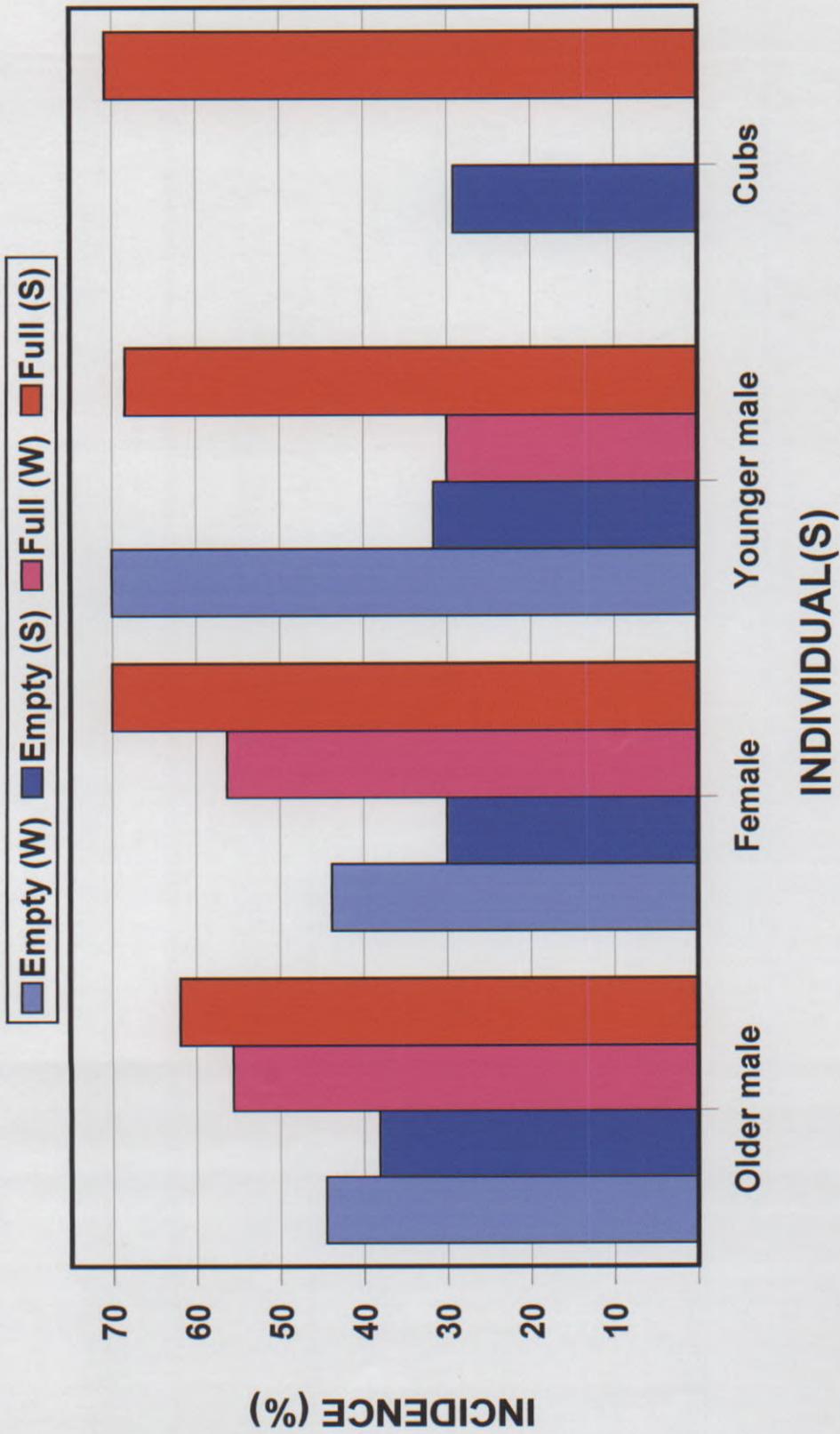


Figure 4.8 Seasonal incidence of drinking at empty and full bellies by African lions in the Kalahari. W, winter; S, summer.

This resulted in significant tension during the summer trials with a corresponding increase in scent marking, flehmen response and dominance behaviour. These behaviours became incessant. The frequency of scuff and spray marking is indicated in Figure 4.3. There was a substantial increase from winter to summer with a marked decrease in urination. Territorial scent marking in the African lion is accompanied by rubbing the head against the scent post. In winter, the older male was observed to rub his head against a grass tuft prior to scuff marking twice, the younger male never exhibiting such behaviour. During the following summer, the older male always rubbed his head against the scent post prior to spray marking and once for 25 seconds without spraying (Fig. 4.9). The younger male exhibited the same behaviour five times, but sprayed each time after the rubbing action. According to Schaller (1972) Serengeti lions rub their heads against scent posts prior to marking, possibly to ascertain whether the object had been marked. Rubbing the head after the marking serves the purpose of anointing the male with the scent (Estes, 1997). This was not observed in the males in the Kalahari.

The males in the Kalahari marked en route to a destination and no particular selection for scent posts was seen. They often marked black thorns and would penetrate the bush deeply with their heads prior to marking, often hooking themselves on the thorns and leaving small tufts of hair on the bush. Estes (1972) postulates that prides have their own scent and that individuals of the pride all carry that scent. It is plausible that this scent is left on the scent post in this action. This may also explain why lions often urinate on themselves or their fellow pride members during midday rest periods. Urine is also deposited on the hind legs and paws during scuff marking, again, possibly, to anoint the animal with the scent. Scuff marking included treading the ground four to six times with two to four squirts of urine. Spraying and scuffing may serve as a visual sign to pride members and may also be an assertion of the "right to be there" (Estes, 1997). Observations in the Kalahari support this. Scent marking was seen mostly in conjunction with clawing, feeding, male to male interaction and in male



Figure 4.9 Head rubbing against a scent post prior to spray marking, performed by the older male African lion.

to female interaction. It also coincided with dominance between the males. During spray marking, the lions would only spray three or four squirts of urine.

Head rubbing against trees was observed three times, only during winter. On these occasions, the lion would "nuzzle" the tree stump. The older male was observed doing it twice, once on patrol and once en route to drinking after feeding, and the female once during morning play after a night of feeding. All the observations were made between 05:15 and 06:25. This behaviour may be explained in terms of the specific scent of a pride, as mentioned earlier, and the deposition of that scent in the territory. Brown & Macdonald (1985) report that histological investigation of the inner left thigh, cheek and ear region of three adult domestic cats (*Felis silvestris*) by Rieger & Walzkoenig (1979), revealed small sebaceous glands connected to the hair follicles. As a result of cheek rubbing being common on odorous objects by both sexes, they concluded that such behaviour in cats is a form of scent rubbing. Whether such glands are present in the African lion remains to be shown, but the behaviour is indicative of their presence. Both Estes (1997) and Schaller (1972) mention lions following the scent of their pride mates when on the move. The latter author specifically mentions an incident when a lion walked while keeping its nose to the ground and sniffing. Similar behaviour was seen once when the female walked low, sniffing the ground.

Scent marking is linked with territoriality which, in turn, can be related to dominance. According to Brown & Macdonald (1985), the dispersion of territorial marks is patterned to increase the chances of intercepting an intruder which suggests that the patterns will, in turn, reflect that of resources in the territory. The same authors state that there is no evidence that scent marks deter intruders. In field experiments, female red foxes (*Vulpes vulpes*) turned back when an alien mark was encountered, but other vixens invariably over-marked on it. In the case of the pride in the Kalahari, it seems likely that animals mark in their territory for no better reason than they spend all their time within its borders. The chances of intruders are slim, no feedback is received on territorial

calls and no other scents are encountered. The increase in scent marking from winter to summer indicates that rather, in this case, scent marking was as a result of the dominance struggle between the two males over the one female.

In felids the sense of smell is highly developed. Along with taste, there is a third sense, which utilises the vomeronasal organ known as Jacobson's organ (Macdonald, 1999). This organ is situated in the anterior roof of the mouth and is associated with a distinctive facial gesture known as the flehmen response. It consists of a pouch lined with receptor cells and opens by a duct into the mouth. During the response, shown in Figure 4.10, the lips are curled up, the nose is wrinkled and drawn back and the head is raised, as also described by Ewer (1973). According to Romer (1956) this organ functions in olfactory sensations linked to food, but Macdonald (*op. cit.*) links it to sexual communication. Since flehmen is normally associated with mating it is usually performed by the male of the species (Ewer, *op. cit.*). Observations in the Kalahari of the flehmen response included responses to old carcass sites, urine, anogenitals and sniffing of the habitat. (Personal observations under zoo conditions have included responses to perfume, plastic containers and other odd objects, so it is plausible that flehmen is used not only for feeding and mating, but also to identify foreign scents). The frequency of this response by the males is shown in Figure 4.11. As indicated, the response, observed on a daily basis, occurred incessantly. In some cases, the male would repeat the response up to five times on the same site. On one occasion, the older male lay over the urine site of the female, growling at the younger male when he attempted to come close. The female was seen to flehmen five times on three occasions during summer. She responded twice to male cub's urine, twice to his scuff mark site and once when she sniffed his anogenital area. The decrease in the older male's sniffing of the female's anogenital area during summer may be as a result of the hormonal implant the female received at the start of the summer trials. During the winter trials she had had several periods of oestrus. Further to this, the younger male consorted with the female often and also, as a result of his increasing age, he



Figure 4.10 Typical flehmen response posture and facial grimace in the African lion, performed by the older male.

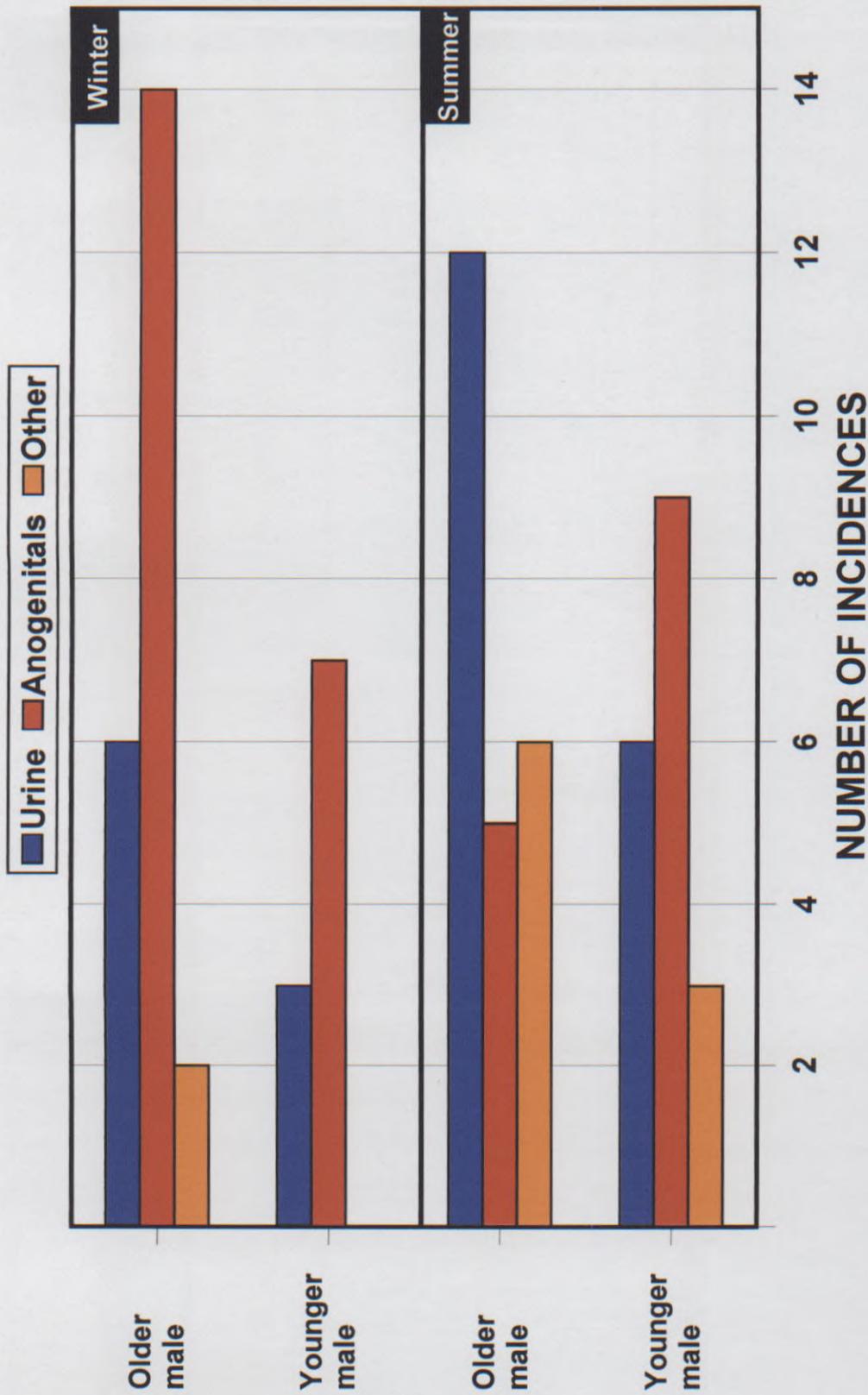


Figure 4.11 Seasonal variation of the flehmen response in adult African lions in the Kalahari. The responses are indicated for the female's urine and anogenital area. Other includes elements such as carcass sites and scent marking sites.

had days where he was dominant in the enclosure and would not permit the larger male to come close to her.

Dominance behaviour includes not only scent marking and other visual displays such as clawing, but also strutting (Fig. 4.12), facial expressions and aggression (Estes, 1997). As mentioned earlier, the younger male and female are siblings. The result of their continued contact since birth, an unnatural scenario, has led them to become very strongly bonded (Fig. 4.13). Male lions will begin to dissociate from their female siblings between four and six months (pers. obs.) and are expelled from the pride by 20 to 24 months of age (Bertram, 1975; Packer & Pusey, 1997). This can be related to kin selection as discussed by Wilson (1976) and will be extrapolated on in the following section on the cubs. Schaller (1972) used a formula:

$$a = \frac{2N}{n_1+n_2}$$

for determining association amongst pride members in the Serengeti, where a is the association, $2N$ is the number of times two animals were seen together and n_1 and n_2 , the number of times the animals were seen. This formula was adapted by replacing the n_1 and n_2 with the total hours of observation during daytime and nighttime hours. The results are shown in Figure 4.14. The association is clearly skewed towards greater association between the female and the younger male, more so during winter than summer. A large portion of the younger male's time was spent with the older male, especially during the summer nights, which supports the assertion that as a result of his age, the younger male began to form a strong coalition with the older male and assisted not only in territorial behaviour, but also began to bond with him. Data collected by Packer & Pusey (1997) and Packer *et al.* (2001) concurs. Males do not spend large amounts of time with the pride. According to Owens & Owens (1984) and Schaller (1972) males form coalitions even when they are not related, specifically so in harsh environments. The chances of survival for two

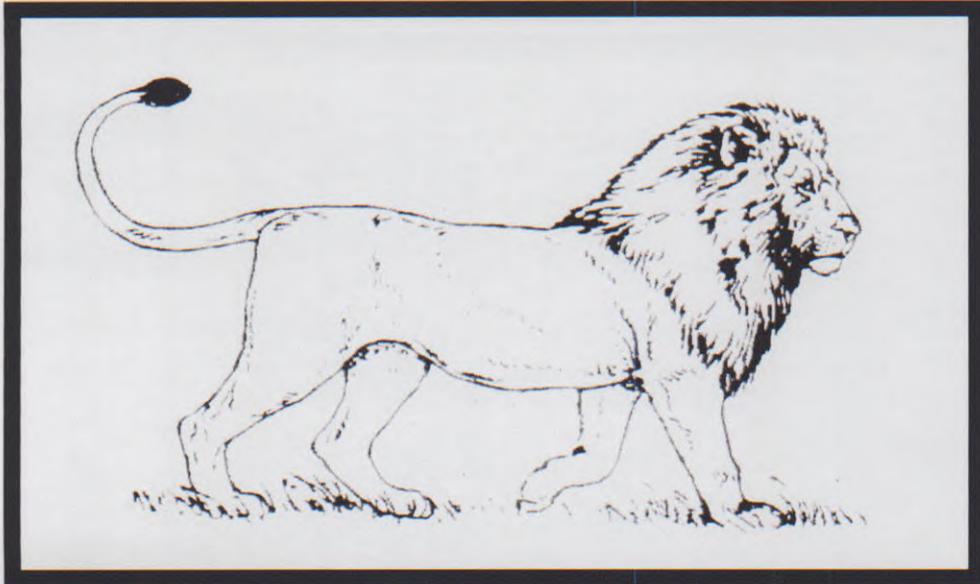


Figure 4.12 Strutting posture of a dominant male African lion. The body is held erect with the tail raised. (From Schaller, 1972)



Figure 4.13 Illustration of the close bond of the sibling pair, the female and younger male.

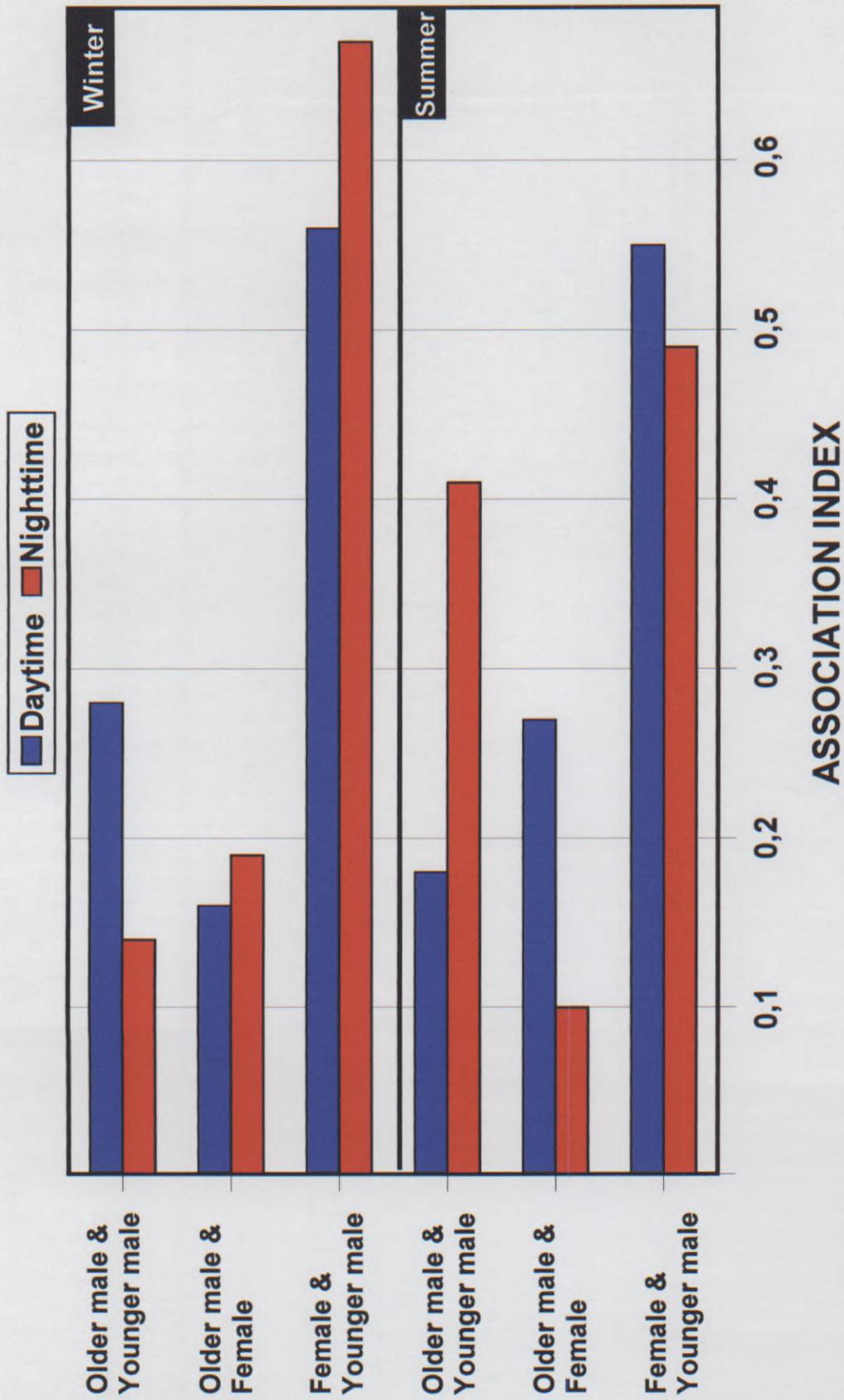


Figure 4.14 Seasonal variation in association of African lions in the Kalahari.

males are greatly enhanced versus being alone. The greater association between the female and younger male during daytime in summer is not as a result of greater dominance by the younger male, but the selection of the female to spend time with her brother. The older male would often attempt to prevent this, but the female would simply ignore him as he tried to block her movement towards her brother. Owing to the effects of high ambient temperature, the older male repeatedly abandoned his attempts to secure the female's company.

It is consistently reported (Owens & Owens, 1984; Packer & Pusey, 1997) that lions will avoid direct contact, hence the complicated and ritualised signals indicating dominance and submission. Conflict between males can escalate to full contact, but rarely does, unless a dominant male is directly challenged. During the winter trials, dominance from the older male would include charging, growling and a slap. At the approach of the older male, including simple strutting or a direct stare, the younger male exhibited submissive behaviour typical of domestic cats as demonstrated by Leyhausen (1956) and shown in Figure 4.15. The face was turned away from the aggressor (1), hindquarters dropped with the tail held low and ears pulled back. This was followed by lying down in the same position with the tail held under the body (2 & 3). The eyes were always held closed. During the winter trials, the younger male submitted after dominance behaviour from the older male 15 times and was able to dominate the older male three times. In all instances of the latter, the older male approached a carcass owned by the younger male. The younger male growled and the older male stepped back, but did not exhibit the submissive posture. Posturing in social animals is an important aspect of communication and the movement, however slight, is understood by members of the group (Tinbergen, 1967). This holds true for the pride. Dominance by the older male included looking directly at the younger male, with no discernable body movements, causing the younger male to lie down, take a detour or avoid the female.

Dominance from the older male during the winter trials was frequent. The younger male had consistently broken out of the enclosure for a period of a year

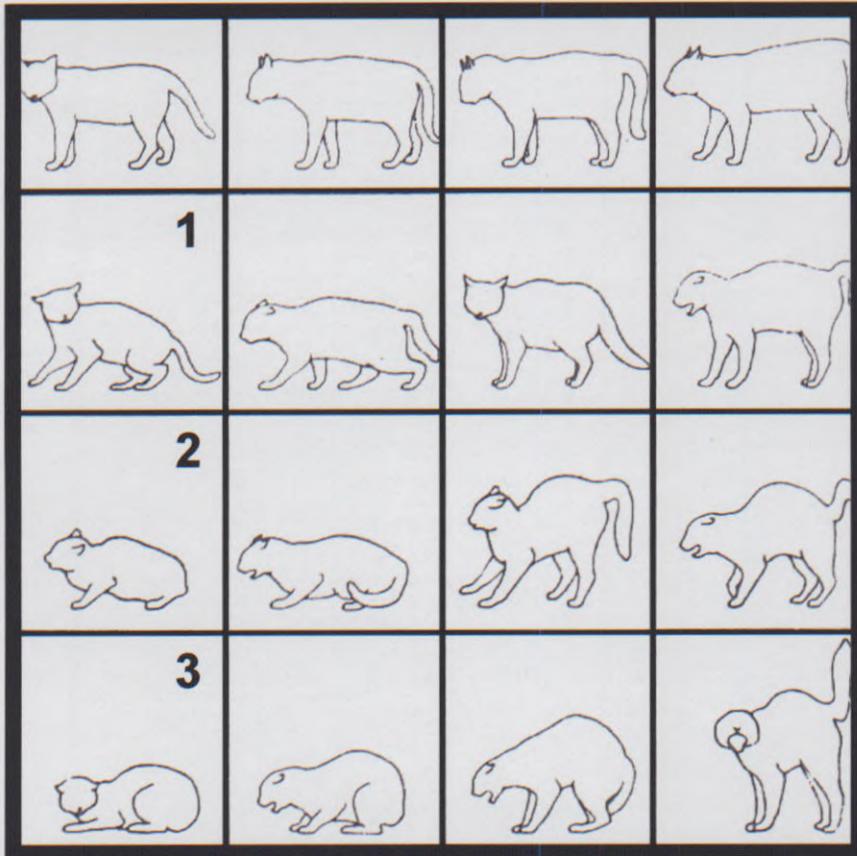


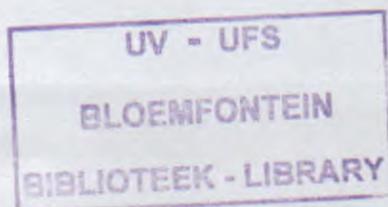
Figure 4.15 Submissive and aggressive behaviour in the domestic cat (*Felis silvestris*) adapted from Leyhausen (1956). The submissive postures marked 1 - 3 were performed by the younger male.

prior to the winter trials (Howard Hebbard, pers. comm.). This is indicative of the younger male's instinct to, at the age of 2½ to 3½ years, leave the pride. According to Wilson (1976), emigration is programmed into an animal in such a way as to "take the individual from one locality when the odds favour that greater success will come from settling in another locality." As a result of returning the younger male to the enclosure each time, the pressure on him increased and pent-up aggression was evident. Twice he turned that aggression towards the research vehicle. On the first occasion, he stood in front of the vehicle with his ears pulled back and snarled while swishing his tail. As the vehicle moved back, he ran to the back of the vehicle and placed his forelegs on the bumper. This was repeated three times until the female approached and pulled him to the ground around his neck in a play gesture. The second time he repeated the same behaviour, but on this occasion the vehicle moved towards him. The older male approached him, strutting, as demonstrated in Figure 4.12. The younger male lay down in typical submission posture, the older male standing over him. No vocals were heard. This illustrates the dominance hierarchy in male coalitions, the ultimate authority resting with the older male.

During the summer trials, the younger male was old enough to withstand and resist the dominance from the older male and the authority lines became blurred. A total of 36 instances of dominance towards the younger male were observed (the total number of observations were 36 days/nights during summer). Of these, two ended up in fights, lasting five and 15 seconds each, and in two instances, there was no obvious provocation such as the female approaching the males and food. The younger male dominated the older male a total of nine times. On one occasion there was contact, the younger male slapping the older male three times. The older male was lying down and turned onto his back, exposing his belly in a rollover self-defence posture (Fig. 4.16) and demonstrated the facial expression marked 1 in Figure 4.17 which is listed by Leyhausen (1956) as a purely defensive threat. On no other occasion did the older male demonstrate submissive or defensive behaviour.

Much of the dominance/submission interactions were caused by the positioning of the female. During the first trial in winter these interactions escalated as the female went into oestrus, but during summer they were more complex. As previously mentioned, the female received a hormonal implant for the purposes of birth control at the start of the summer trial. Further to this, she was nursing 2½-month-old cubs. Mating during winter was, therefore, a matter of reproduction with the older male covering her five times, the younger male once. During summer, however, 24 pseudocopulations were observed, 18 from the older and six from the younger male. Two of these copulations occurred at night, the remainder during daytime. The majority were caused by the female repositioning during daytime rest or when the female nuzzled one of the males. The males did not position themselves such that penetration was at all possible. The female was mounted over her lower back. There was ejaculation during some of these pseudocopulations which lasted between eight and 11 seconds. The female resisted seven times, resorting to slapping the male in question and when there was no resistance, there was no response from her. No published account could be found on this behaviour in lions, but it is well-known for other species, especially primates, which use it to express rank amongst males where the dominant male mounts the subordinate. Male to male pseudocopulation was not observed in the pride although it has been observed in free-range wild lions (Sarel van der Merwe, pers. comm.).

Finally, two examples of other unconventional behaviour were observed. When on patrol, the lions utilised the northern perimeter all the time except once when they walked the southern perimeter. They were never seen to call into a dune face and always called towards the north. No other prides are held near to the reserve and on both the southern and northern borders, game is present. In fact, during the winter trials, the female broke through the fence three times and successfully caught game. On all of these occasions, she exited the southern perimeter. That the animals do not call into a dune face is reasonable since it reduces the distance the sound will travel. The rationale behind the



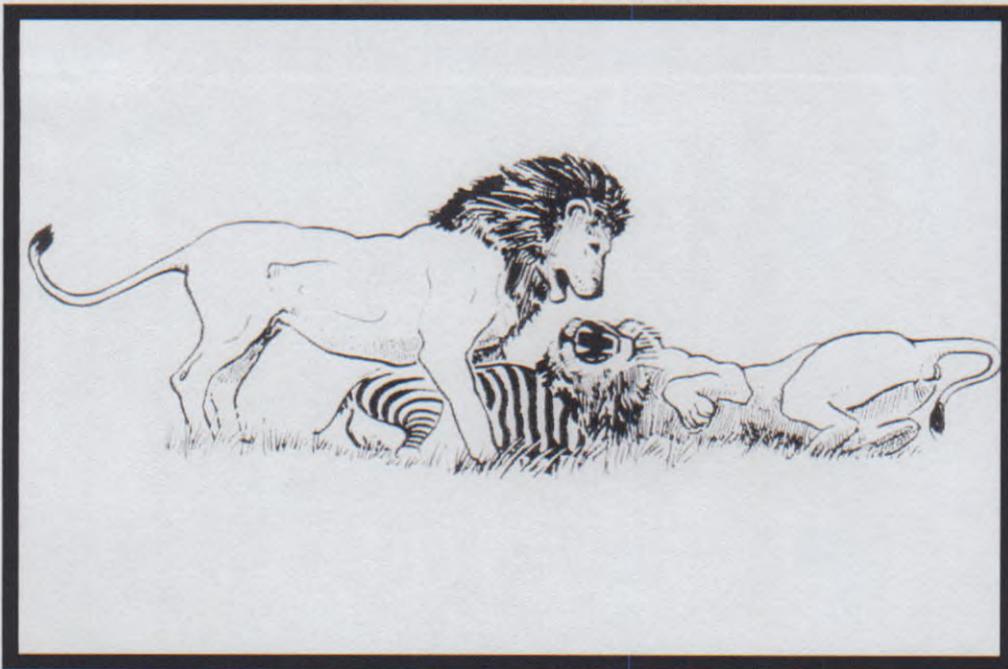


Figure 4.16 Rollover self-defence posture, characteristic of felids, which inhibits an attack from the aggressor. (From Schaller, 1972)

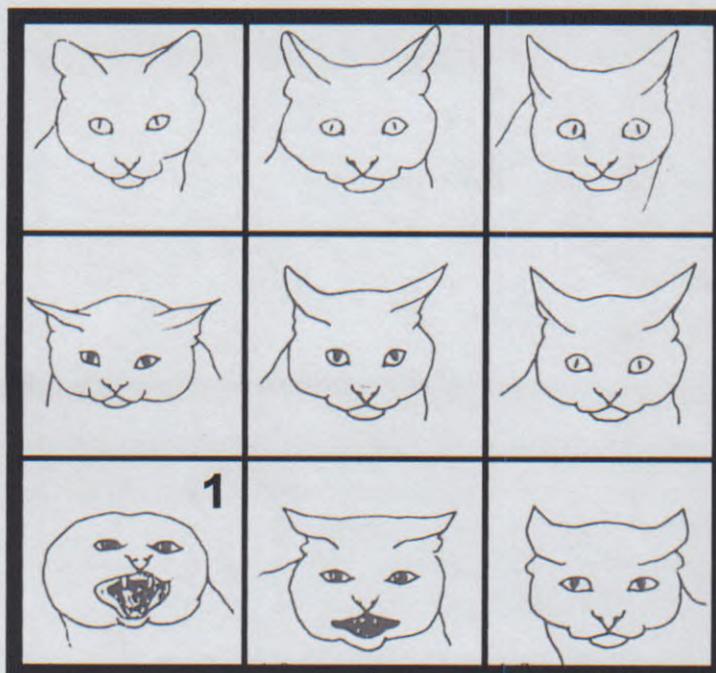


Figure 4.17 Defensive facial expression of a felid under threat (1). Adapted from Leyhausen (1956).

predominance of patrolling the northern perimeter is not understood.

The older male was seen chewing twigs, twice during the winter trials and three times during summer. One observation was on the dune crest during the morning and it appeared as if the twigs were in his way. The second time, however, was on a "hungry day" when the feeding vehicle arrived, but did not bring a carcass. He ran after the vehicle and when no food was forthcoming, he turned towards a black thorn and began to chew on the twigs. During the ensuing summer trials, he demonstrated the same behaviour while playing with the younger male once, once when the feeding vehicle did not deliver a carcass and he had run after the vehicle, and once while he was waiting for the female to finish feeding. The distinct impression was that excepting for play or when the twigs were in his way, frustration caused the behaviour. This is referred to as a redirected response where the animal aims its response at a substitute object (Tinbergen, 1967).

4.4 CUBS

Two cubs, one male and one female, were born during mid-November 2003. They were included in the summer trials of this study. As a result of the younger male's age and the time of conception, the cubs were most likely sired by the older male. He was effective in dominating the younger male and did not permit copulation except for once, when the younger male managed to cover the female while the older male was patrolling the northern border. Summer trials began when the cubs were 2½ months old. Cubs survive on milk only up to the age of two months and begin to feed on meat at this time (Skinner & Smithers, 1990). The female was a primiparous mother. Eloff (2002) reports that Kalahari lionesses vary in terms of their ability or inclination to raise cubs. Some females are excellent mothers while others simply abandon their cubs and stay with the pride. The female in the Kalahari fell into the first category. Although she did not have cause to aggressively defend her cubs against the males, she fed them well, called them immediately after the kill was made, regularly groomed them,

and frequently played and bonded with them. Whenever the pride was moving through the enclosure, she would not go forward unless the cubs were with her and always waited for them to catch up.

Daily activity patterns or time-energy budgets of the cubs reflect a pattern similar to that of the adults in terms of being stationary. Interaction, feeding and movement differ slightly in that there is an increase versus that of the adults. This is as a result of the nature of young animals. Much of their time is spent on play and exploration and suckling at regular intervals. Play and exploration increased during the early morning hours and again during late afternoon, correlated with temperature and not the behaviour of the adults. The cubs tottered around and played regularly while the adults were resting. This is discussed in detail in Chapter 5 and is shown in Figure 5.4. It is well known that animals demonstrate differences in temperament and personality. In the domestic cat, Mendl & Harcourt (2000) measured this in terms of responses to novel situations, boldness and behaviour types. Likewise, the cubs demonstrated distinct differences in their behaviour. The female cub explored further from the female and always did so first, the male cub following her after a few minutes and then regularly looking back to the female. During feeding from the carcass, the female cub twice demonstrated such aggression towards the female that she abandoned the carcass, leaving the cub to feed alone. On another occasion, the female cub held a piece of meat that the female wanted and did not release it until she was slapped. On all these occasions, the cub had her ears pulled down, swished her tail and woofed (Estes, 1997) repeatedly. She also demonstrated curiosity towards the research vehicle, coming very close while the male cub stayed back and responded with aggression if the vehicle came too close with the male cub retreating.

Suckling and feeding occurred throughout the day, the female not always permitting the cubs to suckle each time they attempted to. The male cub regularly suckled for a few minutes longer than the female. This may be as a result of his greater nutrition requirements, males growing larger than females with large protein requirements for muscle and mane development.

During the trials, the cubs spent 8% of their time hidden. A Serengeti lioness left her four-month-old cubs under a tree from 19:05 to 06:00 the next morning (Schaller, 1972). The cubs in the Kalahari, when hidden, were never left in the open, but always in shrubbery. This normally occurred when the pride was alerted to something and moved in response to it, or when a vehicle, including the feeding vehicle, entered the enclosure. They hid six times during the trial and only during the day. The longest time was six hours and the shortest, 14 minutes. The frequency and duration of hiding decreased as they grew older. At the start of the summer fieldwork during February, the cubs hid four times and from one to six hours. During March they hid twice, 14 and 20 minutes respectively. When reunited with the pride after hiding, the cubs would greet the adults with nuzzling and play lasting up to ten minutes.

The cubs did not hide from the research vehicle, possibly as a result of the adults' response. They were fully habituated and did not respond to its arrival or presence. No specific indication from the female was seen to prompt the cubs into hiding, but grunts from her, varying from five to 18 depending on how far away they were, called the cubs out of hiding. Deag *et al.* (2000) state that ultrasonic communication exists between the domestic cat and her kittens, but whether such communication exists in lions is unknown. The cubs are cryptically coloured. On one occasion it was known where they were hidden, but even with the use of binoculars at a distance of about 50 m, they could not be seen inside the bush. Colour and behaviour work together for camouflage (Tinbergen, 1968) and while hiding, the cubs lay still.

It was mentioned earlier in the chapter that the female and younger male are siblings and developed a strong bond and that the younger male was subordinate to the older male. Much of the dominance from the older male towards the younger male was as a result of his bond with the female. They sought out each other's company as was demonstrated by the association index in Figure 4.14. The compensation of being subordinate may lie in kin selection where it could play out a genetic benefit. "If an animal that has little

chance of succeeding on its own chooses instead to serve a close relative, this strategy may raise its inclusive fitness" (Wilson, 1976). The younger male conforms to this in terms of his bond towards the female. Twice during the winter trials, he assisted the female in securing the carcass from the older male. Packer *et al.* (2001) report that lionesses have egalitarian relationships within a pride: "Female pridemates do not harass each other or assert themselves during social interactions." There is no discernable feeding hierarchy among females, never supplanting each other from a substantial quantity of meat. This holds true for the feeding style of the female and the younger male. They fed together during each feed at least once and always did so in harmony. The young male did not demonstrate aggression towards the female when she approached the carcass and always permitted her to feed with him. On one occasion when the female had escaped from the enclosure and caught an ostrich, the grunts of the younger male brought her down from a tree outside the enclosure and lured her back. She responded to the younger male by grunting back and moving into the enclosure toward him, ignoring the older male. "As a rule, the closer the genetic relationship of the members of the group, the more stable and intricate the social bonds of its members" (Wilson, 1976). Upon the arrival of the cubs, the younger male assumed the role of an "Auntie", a term coined by Schaller (1972). The latter author states that lionesses within a pride will assist with the care and education of the cubs and allow suckling.

The association index used for the adults was applied also to the cubs. The results are shown in Figure 4.18. The majority of the time was spent with the female although this would generally include the younger male since his association with the female was also in the majority. The cubs fed with the female, allogroomed with her, suckled from her, played with her and moved with her. When the young male was present, he was included in all these activities except for suckling. The nighttime results for the female cub support the assertion that she was bolder, spending slightly more time with the older male who, in turn, spent his nights some distance from the other members of the pride. Both cubs, however, spent a lot of time with the younger male. He

demonstrated great patience with them, permitting them to clamber over him, play with his mane and his tail and they allogroomed often. In general, male lions repulse the advances of the cubs (Bertram, 1975; Eloff, 2002; Schaller, 1972). This was observed in the enclosure. One afternoon, the lioness was on the dune crest in the shade with the cubs and the two males were lying down some 50 m away from her, across a road. The older male lay approximately 5 m closer to the female. The female cub first made her way towards the males, the male cub following a minute or so later. They walked slowly and deliberately and upon approaching the older male, he pulled up the right side of his lip. Both cubs took a detour around him towards the younger male who fell flat and began to paw and play with the cubs.

One of the feedings observed during the summer trials further supports the "Auntie" role by the younger male. During late afternoon, the older male was feeding on a carcass that had been killed the night before. The younger male approached and after a short scuffle, took ownership of the carcass. The female and cubs were lying nearby under a tree waiting to feed. The older male moved away and the younger male lay down by the carcass, but did not feed. The female and cubs moved in and began to feed, the younger male still lying by them, but without eating. When the older male moved, the younger male reacted with aggression towards him, growling. On another occasion, the younger male waited for the cubs to finish feeding before he moved in on the meat. This behaviour implies a distinct dual role played by the younger male – one of coalition partner to the older male and one of "Auntie" to the cubs. Wilson (1976) refers to this as polyethism, the differentiation of behaviour among categories of individuals of the society and states that the adaptive significance of this lies in the optimisation of work. In the case of the pride in the Kalahari, the behaviour is, however, most likely as a result of kin selection and the captive conditions. Under natural conditions, sub-adult and adult males stay back with the cubs while the females hunt (Graham Hemson & Luke Hunter, pers. comm.) They agree that this may have ancillary cub-minding effects, but is

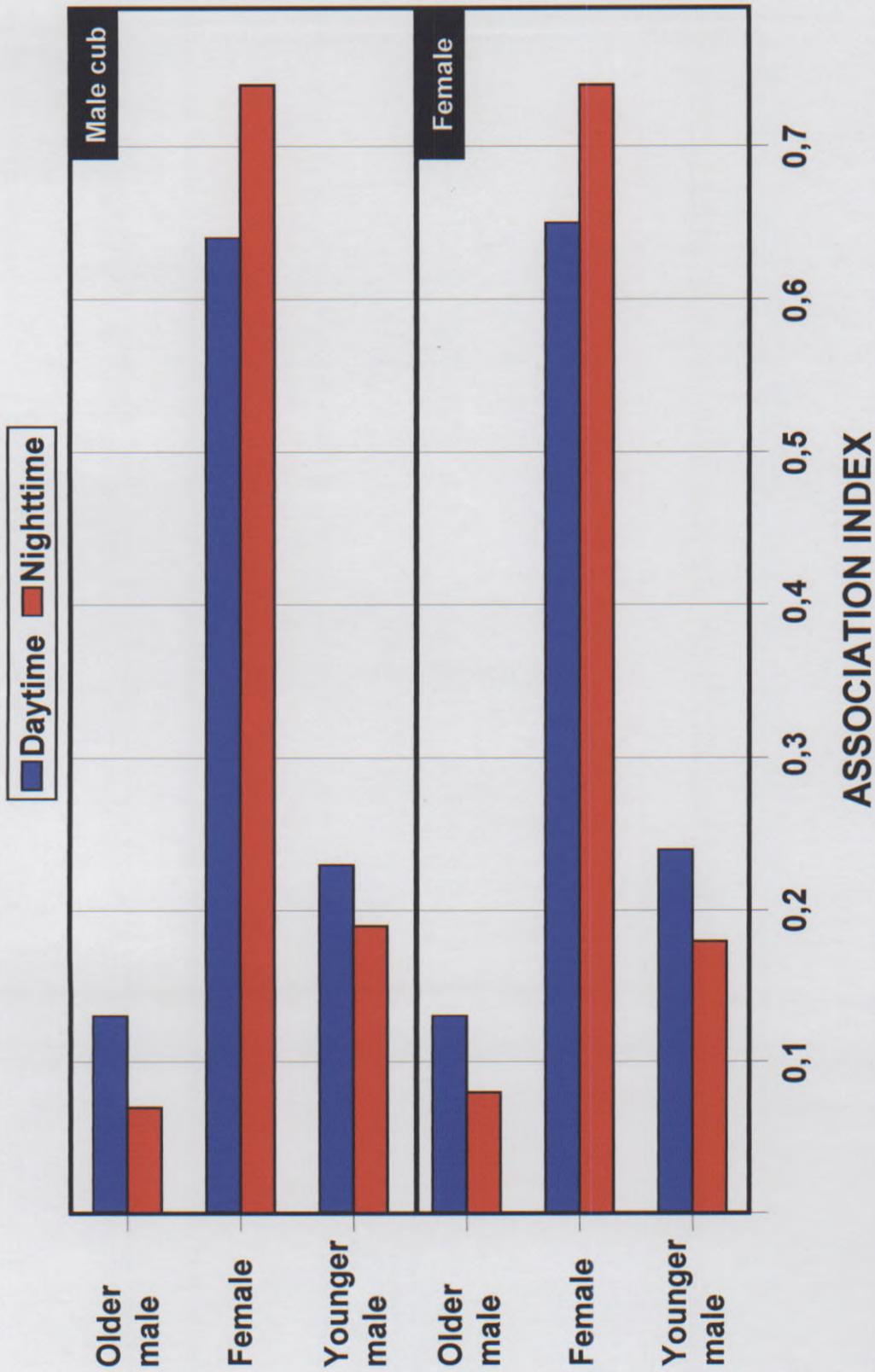


Figure 4.18 Variation in association of African lion cubs in the Kalahari.

most likely as a result of the females securing food for the pride. Therefore, the behaviour of the younger male in the Kalahari has not been previously recorded.

The co-operation between the female and the younger male is termed reciprocal altruism (Wilson, 1976). Prior to the arrival of the cubs, they shared resources and defended them successfully from the older male. The alloparental care of the cubs observed in the younger male can be taken a step further with the observation of his taking custody of the cubs during both darting procedures. Where he generally would react with aggression to the vehicles during darting, especially when they came close to the female as was observed during the first trials in winter, during summer, he ran with the cubs, positioning himself between the vehicle and the cubs. Further to this, he moved to the "back" (west) of the enclosure with the cubs and did not come close to the small enclosure where the work was being done. During the winter darting, he remained close to the enclosure during the entire procedure. Alloparental care has advantages for the young as well as for the inclusive fitness of the mothers. In situations where the males are less likely to be the fathers of the young, this behaviour may serve other ends. Research done on primate troops has caused this kind of alloparental care to be called "agonistic buffering", since the presence of infants consorting with a male inhibits aggression among the adult members (Wilson, 1976). This may apply to the pride in the Kalahari since the older male was never seen to react with aggression to the younger male when the cubs consorted with him.

As a result of the support offered by the younger male in the enclosure, the cubs appeared to have become oblivious to the superiority of males within the pride. This was demonstrated one morning when only half a carcass was fed. The lions were hungry and, as a result, aggression was high. The larger male secured the meat and moved it to a large tree, the pride joining him later. Excessive dominance was observed that afternoon, the older male reacting with violence when either of the other adults moved. At approximately 15:45, after

relative calm under the tree, the female cub first, followed by the male cub, made their way towards the older male who was still feeding. He responded with growling and tail swishing. The cubs continued to move forward and the older male lunged at them. They ran back to the female. After roughly five minutes, the cubs moved towards the older male again. The female made no attempt to call them back. The older male reacted violently, slapping the cubs away from him with such force that one flew through the air. He then lunged at the younger male who submitted immediately, followed by the female, who also submitted. He returned to feeding. The other members of the pride lay together, allogrooming and nuzzling. Lion cubs of 3½ months generally demonstrate respect for adult males and do not repeat the same behaviour they have received discipline for after such a short interval (pers. obs.).

From the age of roughly three months, the cubs began to copy the behaviour of the adults. It is known that young animals learn by imitating adults. The female cub began to cover the carcass and chase away birds in response to the female doing so. When the female climbed a tree one morning, the female cub followed suit (Fig. 4.19). The male cub was never seen to attempt to climb a tree, but did follow the older male along the northern perimeter while he was on patrol. Schaller (1972) reports that male cubs begin to scent mark at eight months. At four months, the male cub was observed to scuff mark after watching the younger male scuff close to the carcass. At this age, the cubs began to differentiate in their association. The male cub consorted with the older male, lying down with him and walking with him. The female cub stayed with her mother and the younger male. This occurred during the last week of the fieldwork and as a result, no data is available to support this, but it appears that differentiation in male and female lions may begin at approximately four months.





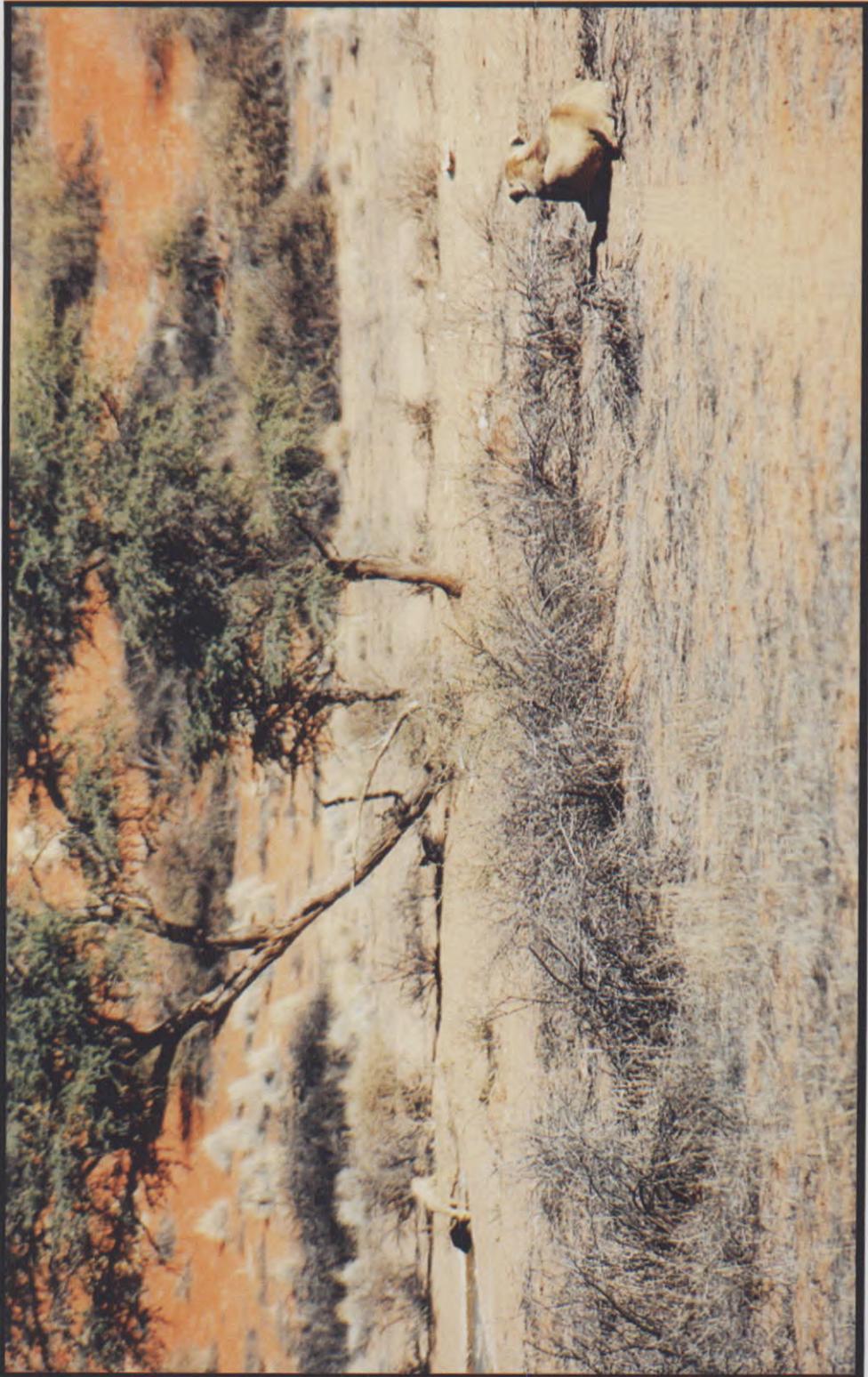
Figure 4.19 Imitation of tree-climbing behaviour by the female African lion cub in the Kalahari.

5 TIME-ENERGY BUDGETS AND TEMPERATURE

5.1 INTRODUCTION

No animal can survive independently from its environment. Excluding migratory species, all animals are confined to their specific habitats during all seasons. As a result, they are subjected to the weather patterns of the area. The Kalahari is an extreme environment with typical desert attributes such as high daytime summer and low nighttime winter temperatures (Lovegrove, 1993). The African lion, unlike small mammals, cannot escape into a microclimate with the use of burrows and underground shelters and, therefore, is exposed to all the natural elements.

The distribution range of the African lion in sub-Saharan Africa reflects a variety of ecosystems from savanna biomes to sub-tropical ecosystems to semi-deserts (Skinner & Smithers, 1990). "Regardless of the area of Africa a lion is found today, their DNA analysis has shown them to be the same, whereas there is a difference between the African and the Asian lion." (Website 3). This implies that the African lion's ability to maintain heat balance and temperature homeostasis relies heavily on behavioural mechanisms. According to Cabanac (1972), thermoregulation has no specific organ of its own and, therefore, thermoregulatory behaviour is a mechanism by which to achieve a physiological goal. This chapter serves to document the broad behaviour patterns related to thermal balance.



5.2 RESULTS

5.2.1 Ambient and sand temperature

Ambient temperature and relative humidity are important abiotic factors for the determination of behavioural thermoregulation. Figure 5.1 shows the median values for temperature and humidity during the study period. Values are indicated for a natural day (24 hours) for both winter and summer. Noticeable is the negative relationship between ambient temperature and relative humidity as well as the intersects between the two factors in both seasons. During winter, air is notoriously dry and although there was some rain in the Kalahari during the summer, the humidity remained relatively low during the daytime as a result of the high ambient temperature and reached its peak just prior to sunrise when temperature was at its lowest. Relative humidity has implications for evaporation in animals, but for the purposes of this study this factor may be ruled out as an influencing variable since high humidity was never coupled with high temperature.

The temperature of Kalahari sand can become very hot in summer. Measurements were taken at hourly intervals during both summer and winter. They were taken from the vehicle which was parked close to the pride and was normally in the shade. Readings in the sun were only taken when it was feasible. During the winter trials, daytime sand temperature in the sun ranged from 3 to 41 °C and during summer, from 20 to 59 °C. Winter daytime sand temperature in the shade ranged from 1 to 33 °C and in summer, from 16 to 52 °C. At night, the winter sand temperature ranged from 1 to 32 °C and in summer, from 18,5 to 41,5 °C. This wide range of sand temperature has implications for thermoregulation since the animals are constantly exposed to the sand and the short and long wave radiation emitted from it.

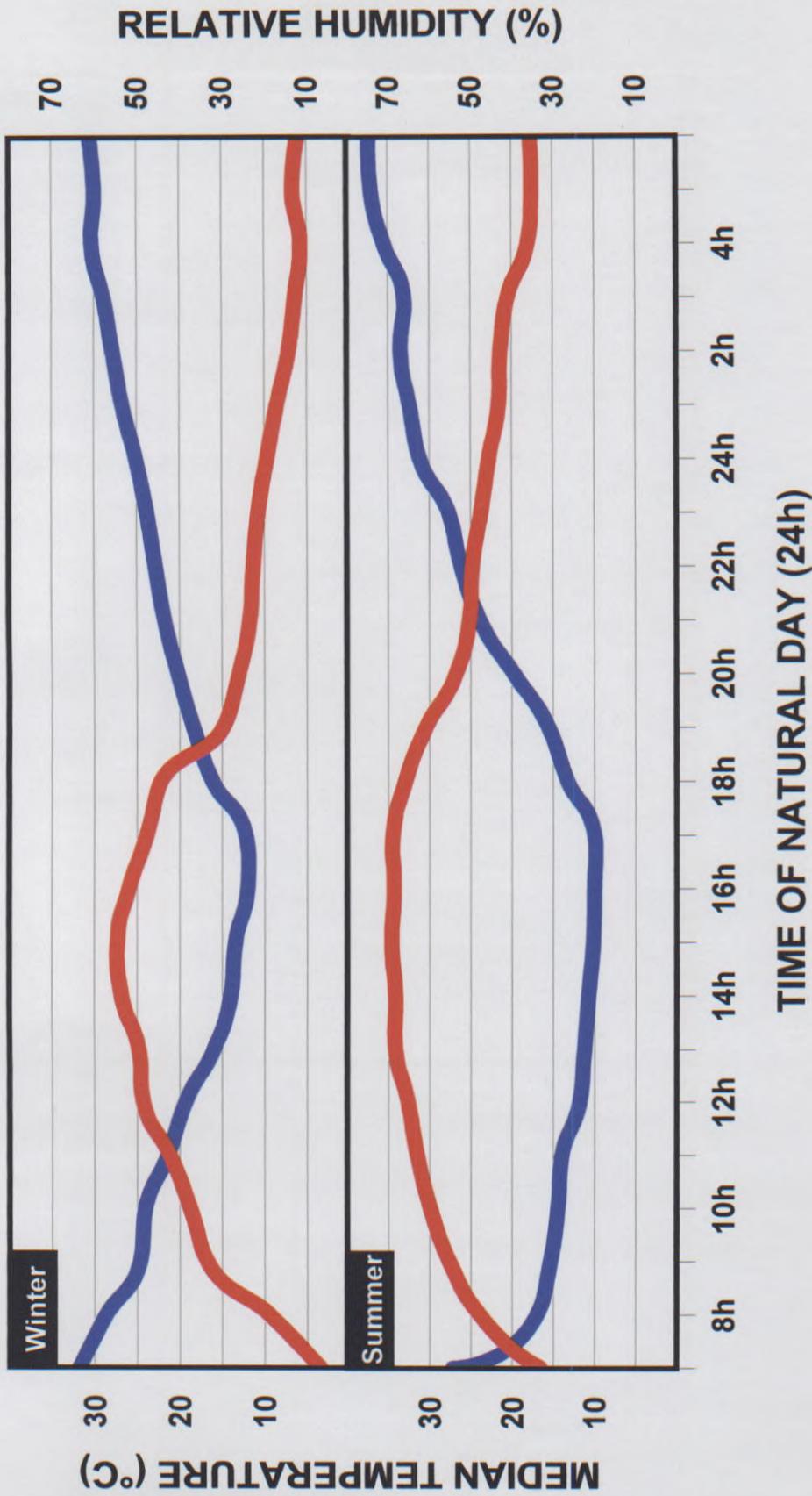


Figure 5.1 Main climatic conditions during the period of study (winter and summer) in the Kalahari. Red, ambient temperature; blue, relative humidity.

5.2.2 Activity patterns

A comparison between winter and summer diurnal activity patterns or time-energy budgets for the adult African lions is shown in Figure 5.2. Categories of activity discerned are feeding, interaction, movement and stationary. Feeding includes drinking, interaction includes all play, bonding and grooming, while movement involves walking and running and stationary refers to lying down and sleeping. During both winter and summer, the bulk of the daytime hours were spent on lying down and sleeping, as the figure indicates. There is a distinct inverse relationship between activity and temperature increase. Movement peaked during the early morning hours and steadily decreased until the late afternoon, when an increase was seen again. There was an increase in movement around midday during winter which was not seen in summer, apparently as a result of the lions moving into the shade after sunbathing on the dune crests. The movement seen during the day in summer was as a result of movement to different or denser shade. Feeding and interaction, albeit low, occurred throughout the day except for the summer season, where interaction all but disappeared during the heat of the day. The time for diurnal activity was taken from sunrise to sunset for both seasons. In winter, sunrise was at 07:00 with sunset at 18:00, while in summer, sunrise was at 06:00 and sunset at 19:00.

The same subsets of behaviour were applied to nocturnal activity patterns (Fig. 5.3), with nighttime hours being taken from sunset to sunrise. During winter this was from 18:00 to 07:00 and in summer, from 19:00 to 06:00. The trend in the nighttime activity patterns was similar for both seasons with the predominant activity being sleep. There was a difference in feeding and interaction between winter and summer, the pride being involved in these activities to a greater extent during summer nights.

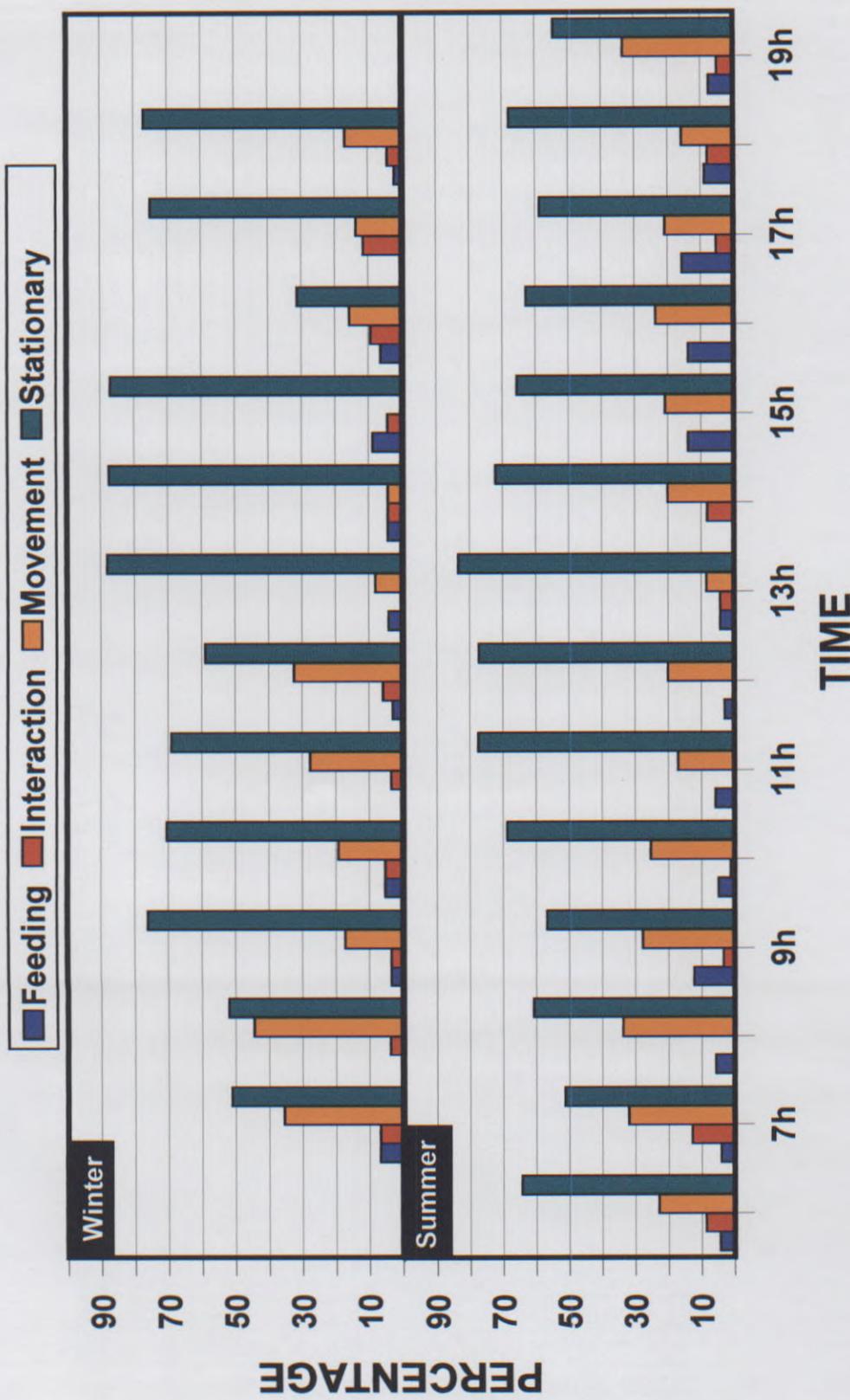


Figure 5.2 Seasonal variation in diurnal activity patterns of African lions in the Kalahari.

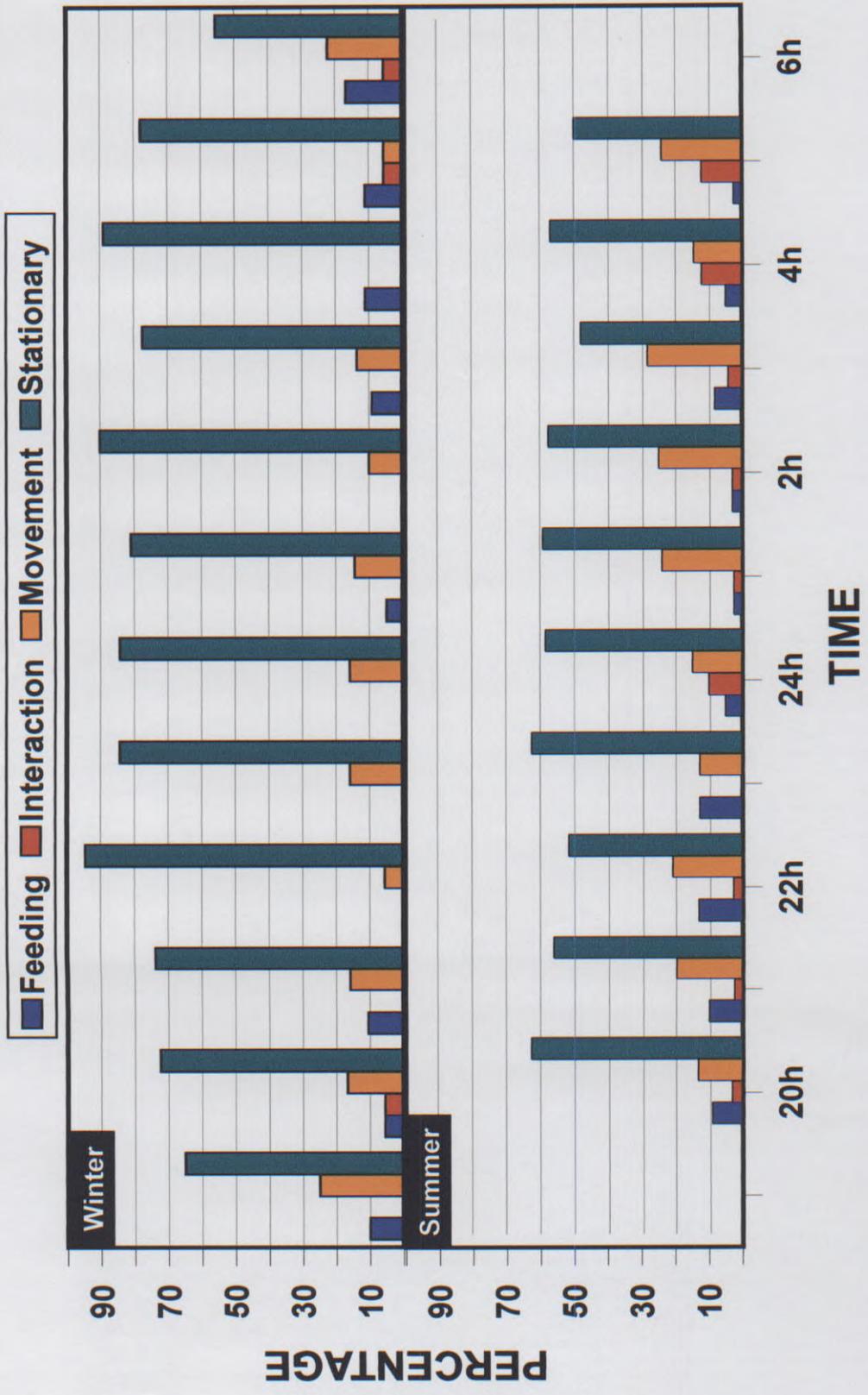


Figure 5.3 Seasonal variation in nocturnal activity patterns of African lions in the Kalahari.

Figure 5.4 indicates the activity patterns for the two cubs. The cubs were born in November 2004 and were included only in the summer trials and, therefore, their results are indicated for diurnal and nocturnal activity patterns during summer. The same subsets of activities and time used for the adults were applied to the cubs. Their results vary in relation to the adults with more activity and feeding throughout the day, although the negative correlation of activity and ambient temperature can still be seen. During nighttime, however, with pleasant ambient temperature, all the activities were more evenly spaced. Feeding took place at most hours during both the day and night. Interaction was somewhat scattered during nighttime hours and after 22:00 no interaction occurred until after dawn, except at 01:00.

5.2.3 Sunbathing

As was mentioned earlier, the lions sunbathed on dune crests in the enclosure during the early morning. Attempts to calculate variation between the two sexes with the use of a Two-way Anova test failed as the data could not be converted into frequencies. Figure 5.5 indicates a marked difference in the total amount of time spent sunbathing between winter and summer for all the individuals concerned. During both seasons, there was a distinct preference for exposing the belly towards the sun (Fig. 5.6). Movement in direct sunlight on the dune crests was absent during summer, as was tail orientation. There was a distinct difference in the total amount of time spent in the sun and the shade between summer and winter. The results are shown in Figure 5.7. An average of 33% of the total winter daylight hours was spent in the sun versus 17% of the summer daylight hours.

5.2.3 Body surface temperature

Body surface temperature measurements of the older male and female were made with the use of iButtons implanted in the neck, tail and loin regions. Median values of these readings are shown in Figures 5.8 to 5.11. The winter results (Figs 5.8 & 5.9) for the female demonstrate a relative constancy within

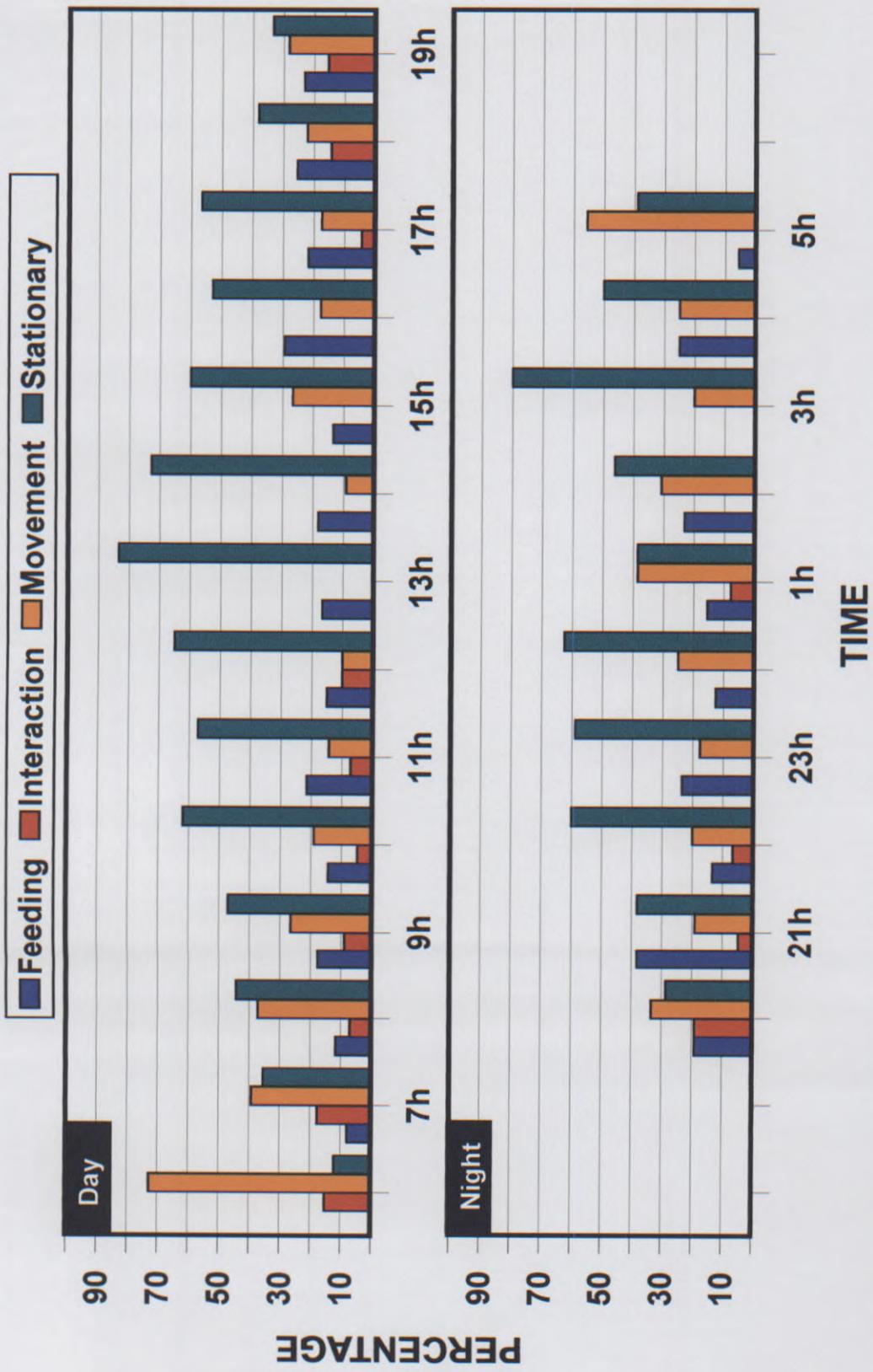


Figure 5.4 Summer variation in diurnal and nocturnal activity patterns of two African lion cubs in the Kalahari.

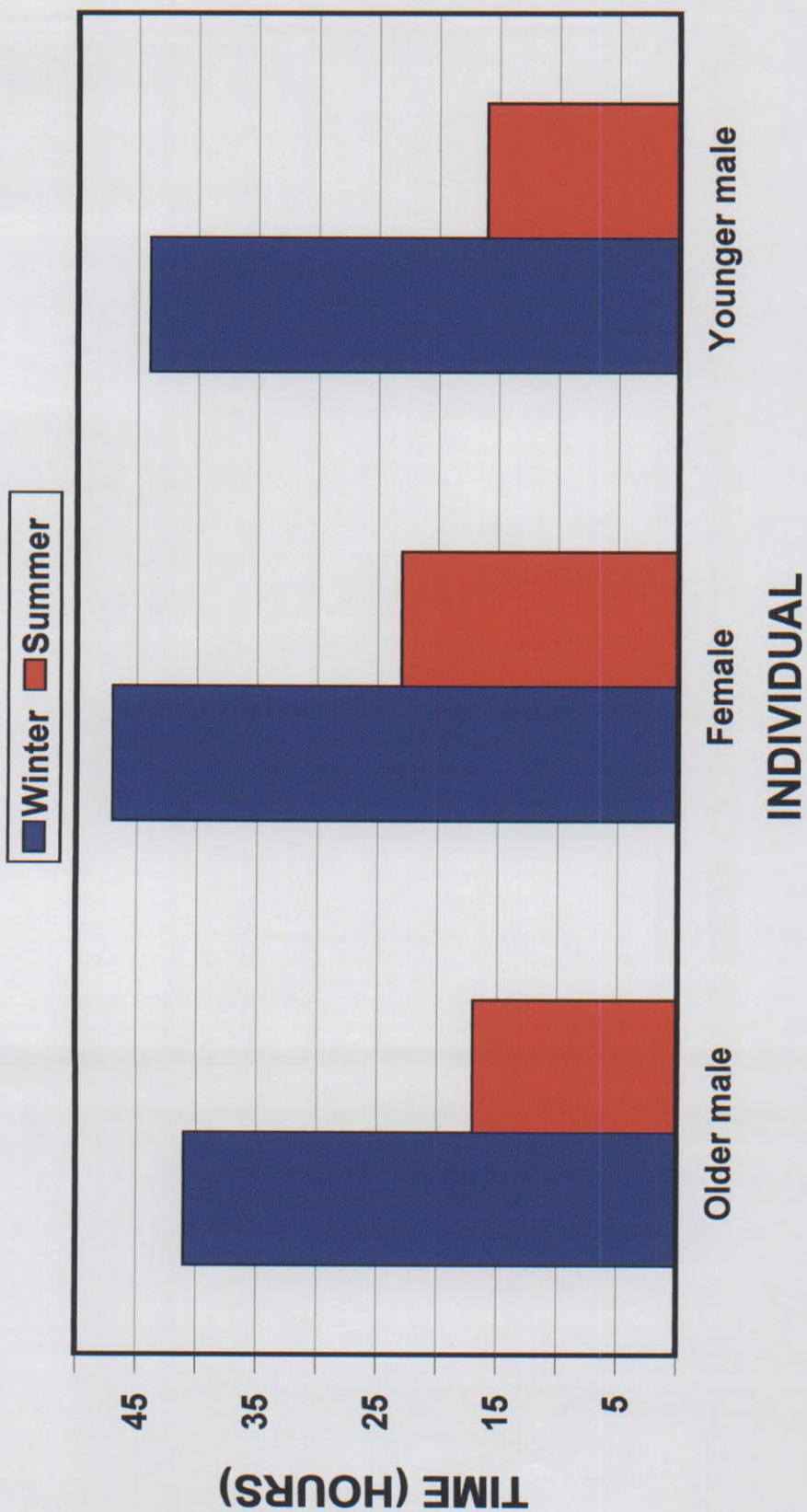
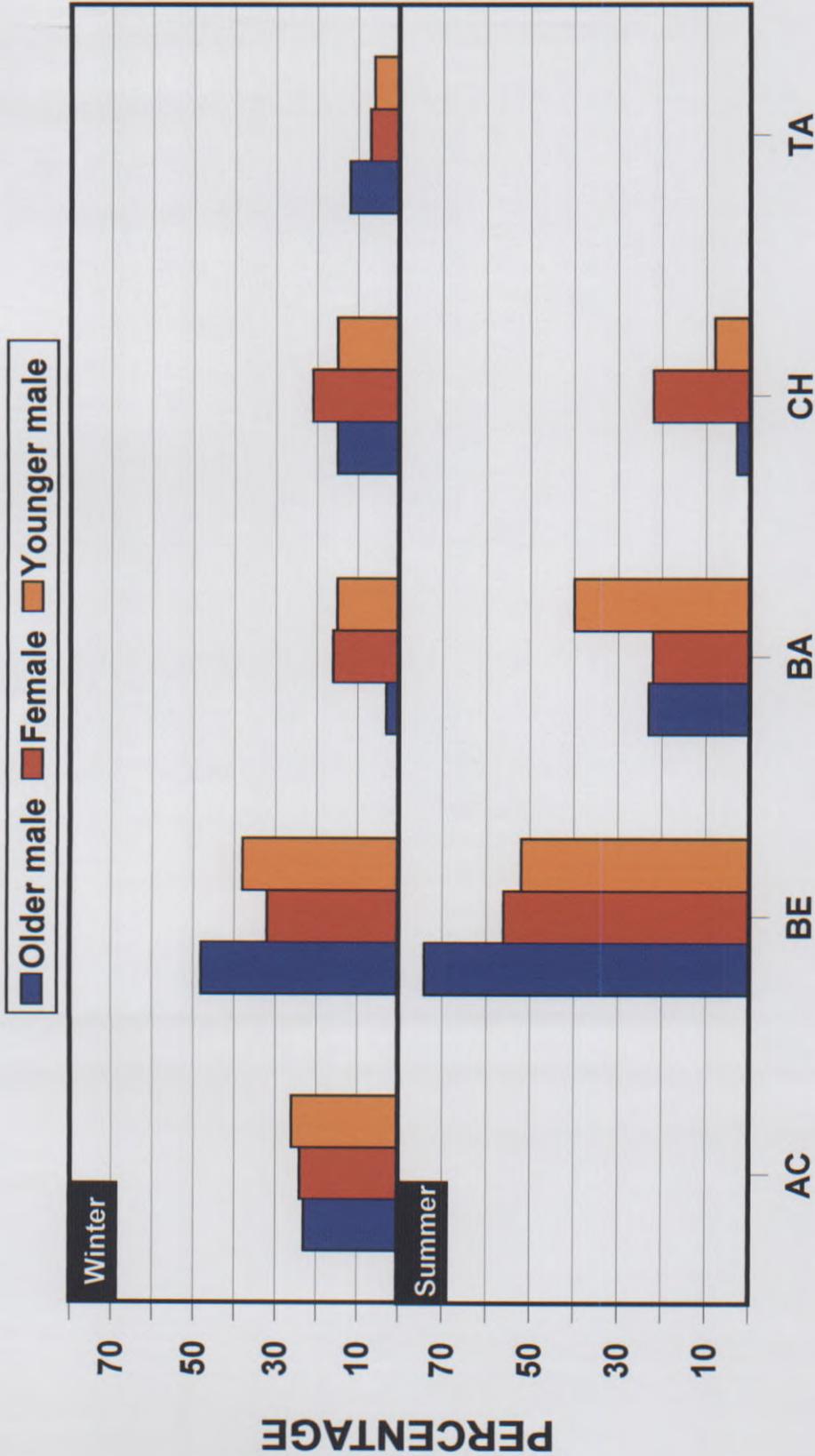


Figure 5.5 Seasonal variation in time spent sunbathing on dune crests during the early mornings by African lions in the Kalahari.



MOVEMENT & BODY ORIENTATION

Figure 5.6 Seasonal variation in movement and body orientation during sunbathing on dune crests in the early mornings by African lions in the Kalahari. AC, activity in direct sunlight; BE, BA, CH and TA indicate belly, back, chest and tail respectively, directed towards the sun.

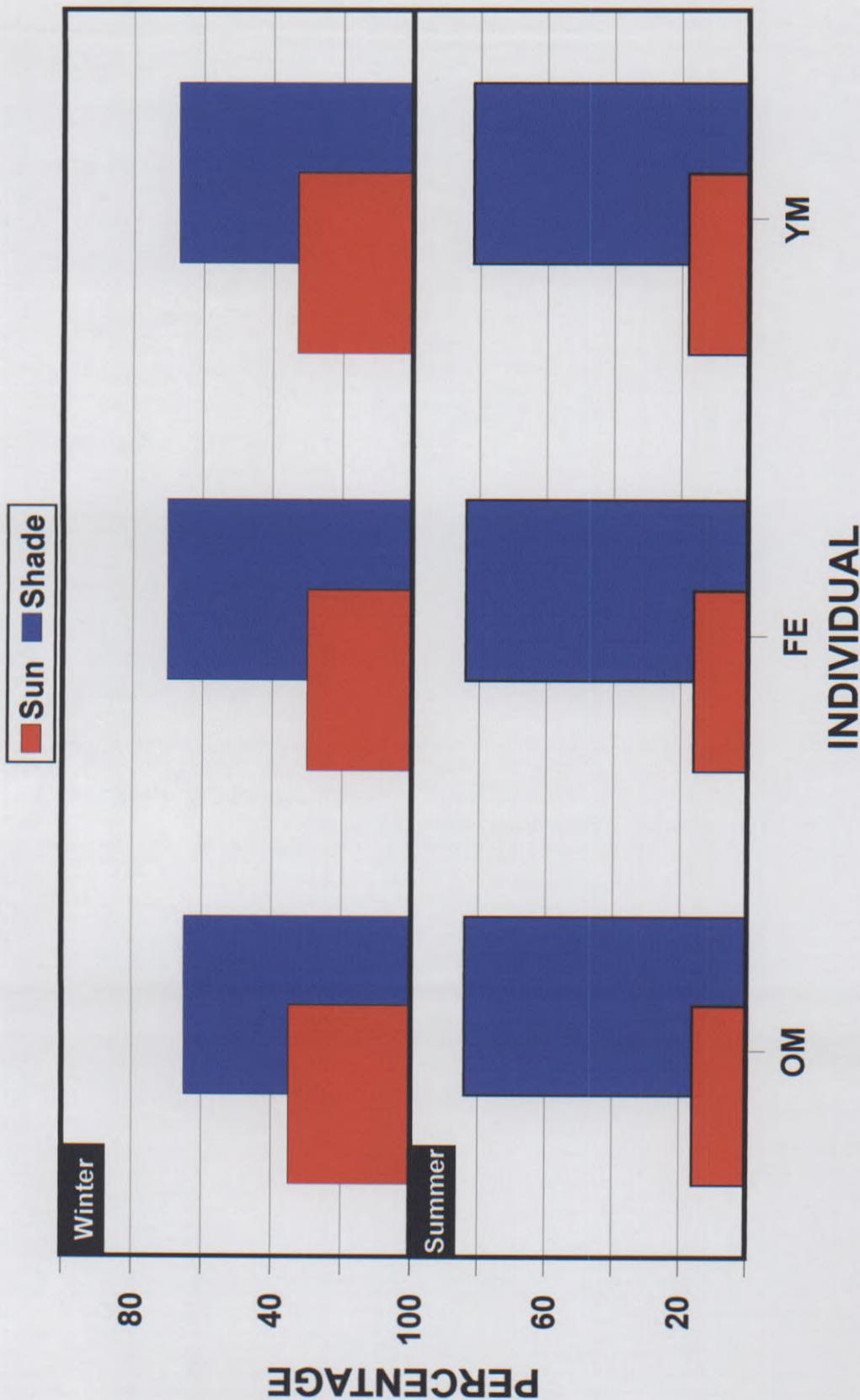


Figure 5.7 Seasonal variation of the total percentage of the time the adult African lions spent in the sun and the shade in the Kalahari. The results are indicated for daylight hours during the two seasons. OM, older male; FE, female; YM, younger male.

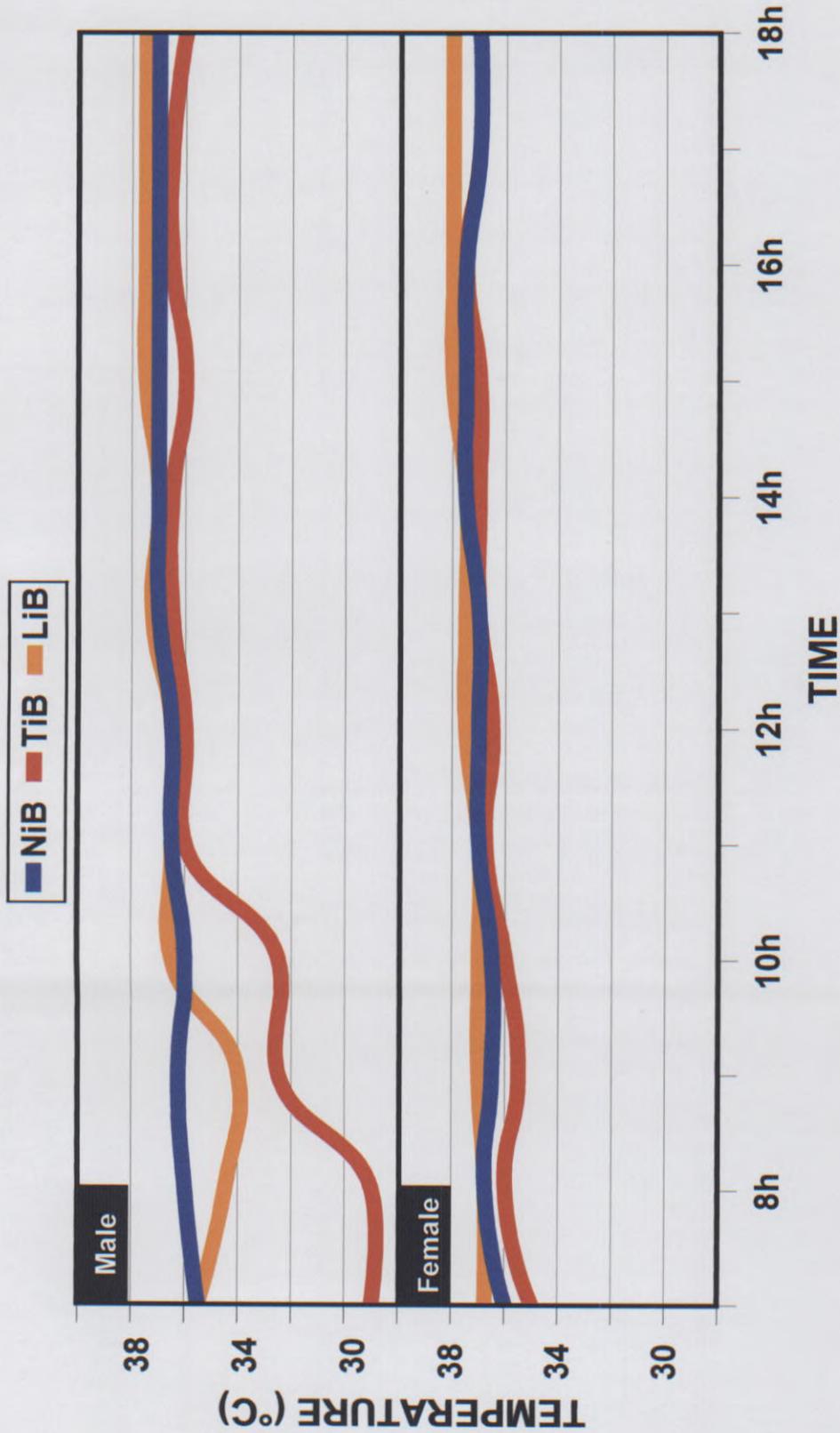


Figure 5.8 Diurnal variation in median temperatures of iButtons implanted in adult African lions in the Kalahari during winter. NiB, neck; TiB, tail; LiB, loin.



Figure 5.9 Nocturnal variation in median temperatures of iButtons implanted in adult African lions in the Kalahari during winter. NiB, neck; TiB, tail; LiB, loin.

three degrees, between 35 and 38 °C. The male, however, manifested variation, especially in the tail iButton which decreased steadily along with ambient temperature during nighttime, reaching a low of 28 °C just before dawn. Summer results, indicated in Figures 5.10 & 5.11, were slightly different. The male demonstrated less variation during the day and the female slightly more. At nighttime, the tail iButton in both lions varied, although the extent of variation in summer was less than that observed in winter, being between 32 and 35 °C. The iButton implanted in the loin region of the female failed one week into the summer trials and, therefore, no data for the period of sunset to 07:00 is available.

It is known that metabolism increases when an animal is well-fed and as a result, total body heat production also increases. If this heat is to be dissipated to the environment, surface temperature increases accordingly. Median values for the iButtons at empty or full bellies for the two lions were calculated for both winter and summer (Fig. 5.12). At full bellies, surface temperature increased by an average of 0,5 – 1,0 °C during both seasons. In the female, the tail iButton during winter showed no difference and in summer, the loin iButton showed no difference. The tail iButton of the older male varied the most during winter with a range of approximately 2 °C.

Observations of the sleep posture of the lions was made during nighttime *vis-à-vis* open or hunched up. The latter is an indication of thermoregulatory behaviour as it implies a reduction in surface area exposed to the environment. The results showed that the female and younger male hunched up four times, all during the same period. The older male hunched up seven times, of which four were shared with the other two lions. In all incidences during winter, the animals had full bellies. The time ranged from 20:00 to 04:00 and the temperature, from 5,4 to 16,5 °C. The sand temperature ranged between 9,5 and 19,5 °C. The older male slept alone only three out of the seven times, the female twice and the younger male once. During summer,

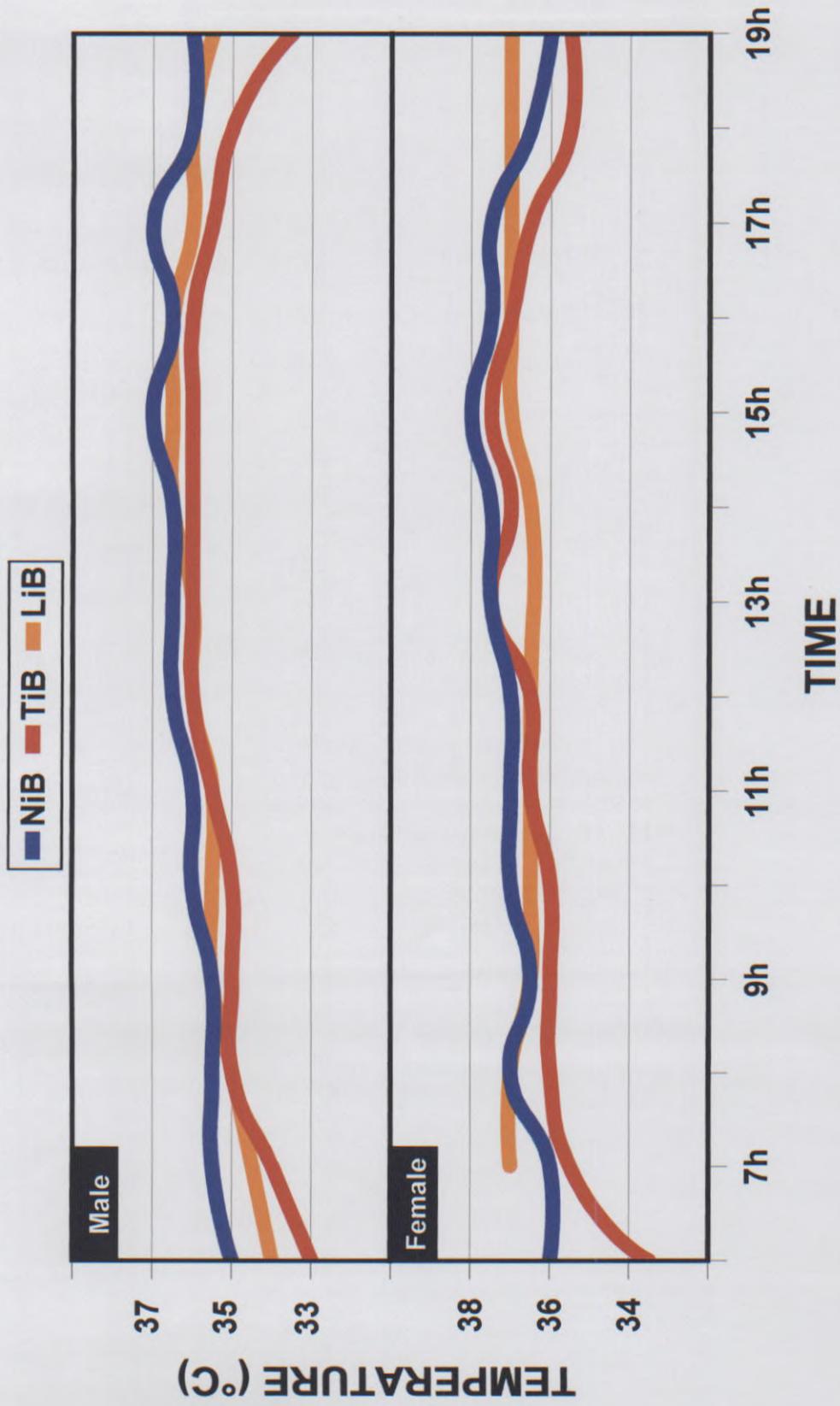


Figure 5.10 Diurnal variation in median temperatures of iButtons implanted in adult African lions in the Kalahari during summer. NiB, neck; TiB, tail; LiB, loin.



Figure 5.11 Nocturnal variation in median temperatures of iButtons implanted in adult African lions in the Kalahari during summer. NiB, neck; TiB, tail; LiB, loin.

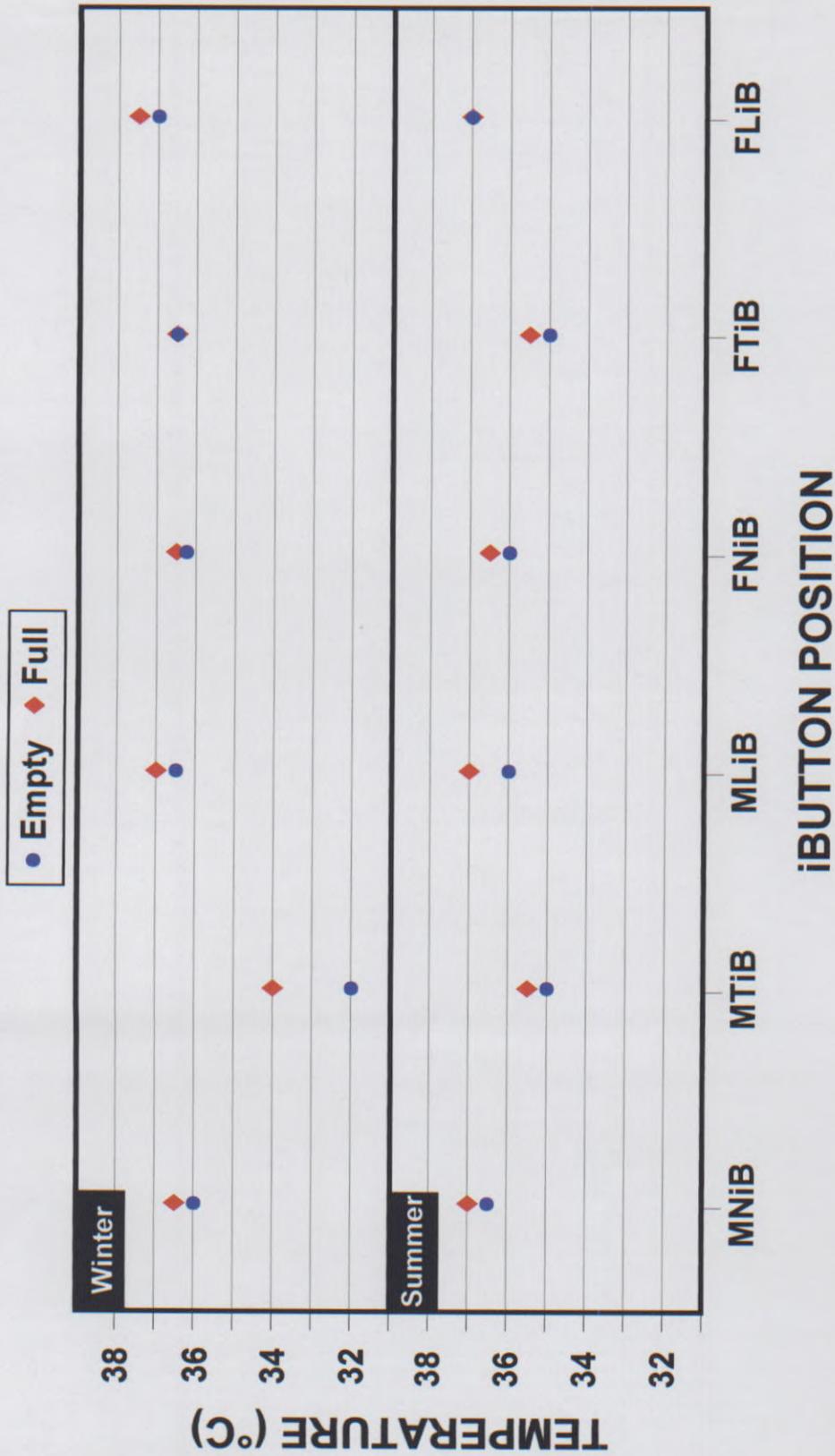


Figure 5.12 Seasonal variation in median temperatures of iButtons for empty and full bellies in adult African lions in the Kalahari. Neck (NiB), tail (TiB) and loin (LiB) iButtons for male and female indicated by prefix M or F respectively.

the adults hunched up three times and all of these incidences were shared. In all the cases, the lions were had empty bellies. The males were alone twice during these observations and the female was alone on all three occasions. The time ranged from 21:30 to 04:00 and the temperature from 16,4 to 19,8 °C. The sand temperature ranged between 19 and 24 °C.

Copious rains fell during the summer season, but these were not evenly spread across the reserve. The lion enclosure received rain three times during the summer trial period. The median temperature of the iButtons during this time, when the lions were wet, indicate that the surface temperature decreased between 0,5 and 5,5 °C (Fig. 5.13). In the case of the female neck iButton, one reading of the wet neck at 36,5 °C was the same as the reading when the neck was dry.

5.2.4 Enclosure usage

During the winter trials, the lions spent the majority of their time in the southern half of the enclosure (Fig. 5.14) and on top of the second dune from the eastern side under a small shepherd's tree. They were frequently seen along the southern perimeter and also on the dune crest in the north-eastern corner of the enclosure. In the subsequent summer trials, however, the animals concentrated more to the northern half of the enclosure and rarely moved along the southern side and that perimeter (Fig. 5.15). The pride also never spent their days near the small shepherd's tree, but opted for a large arup tree (*Albizia anthelmintica*) and black thorns towards the northern half. They also spent a lot of their time along the northern perimeter.

5.2.5 Grooming

The frequency of grooming by the pride demonstrated distinct differences between the two seasons and indications are that when thermoregulation mechanisms are employed, certain behaviours are sacrificed. Figure 5.16 illustrates the diurnal and nocturnal incidences of both auto- and allogrooming

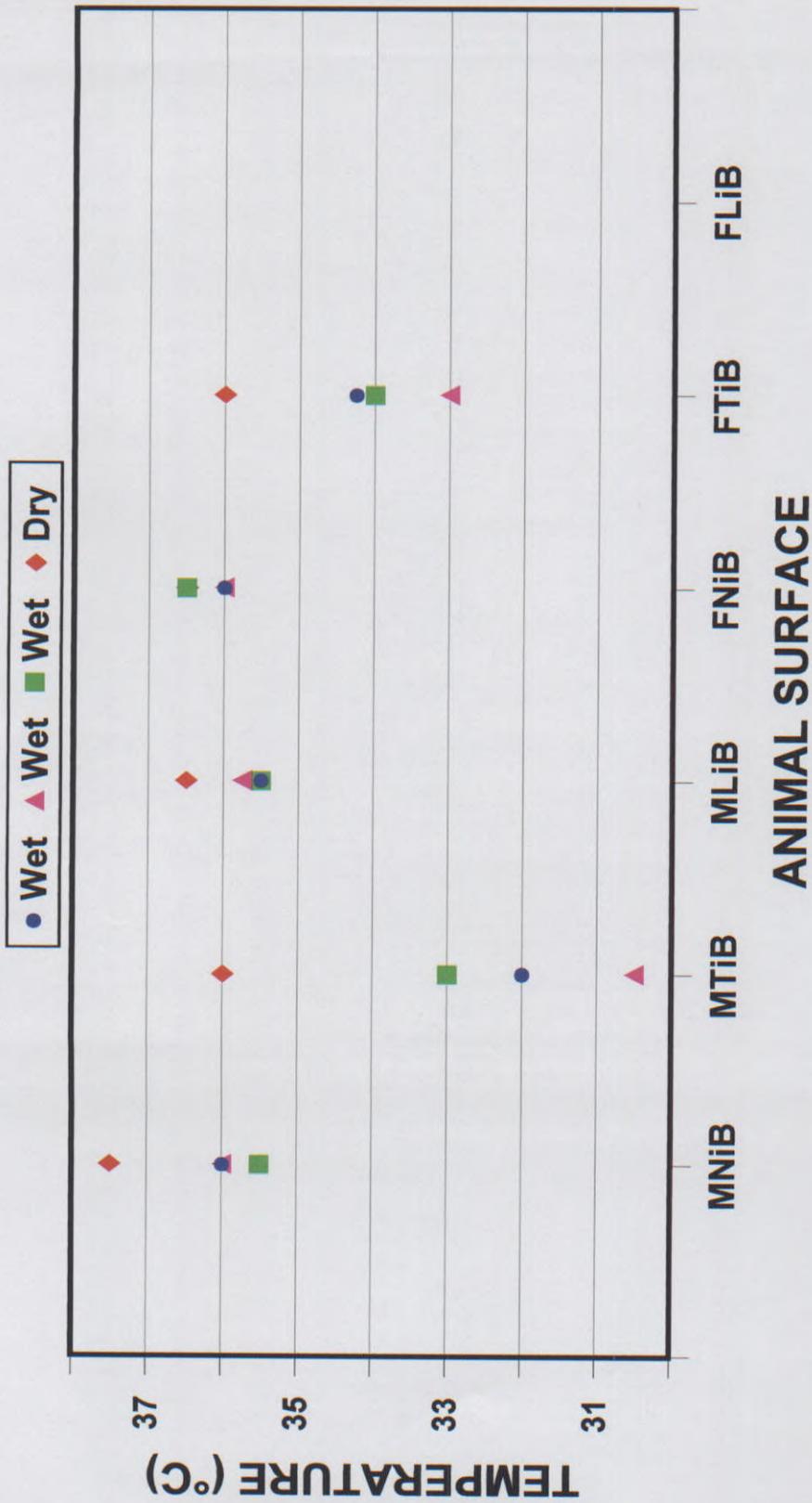


Figure 5.13 Comparison of iButton values during summer when the lions were wet after three rain showers and on one sunny day. Neck (NiB), tail (TiB) and loin (LiB) iButtons for male and female indicated by prefix M or F respectively. Due to the failure of the loin iButton of the female, no data is indicated.

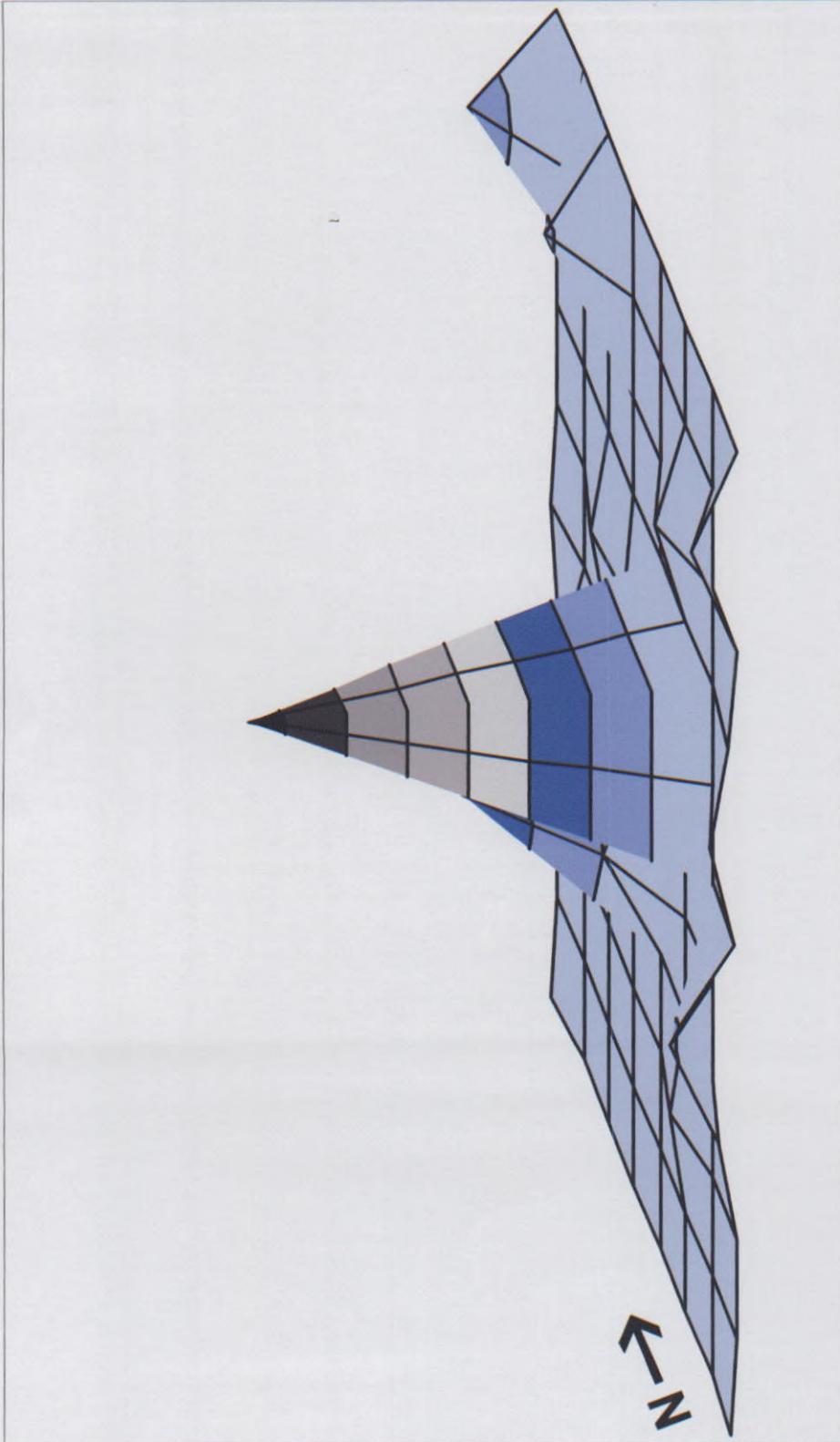


Figure 5.14 Use of the enclosure by the pride of African lions in the Kalahari during the winter study period. Peaks indicate where the majority of the time was spent.

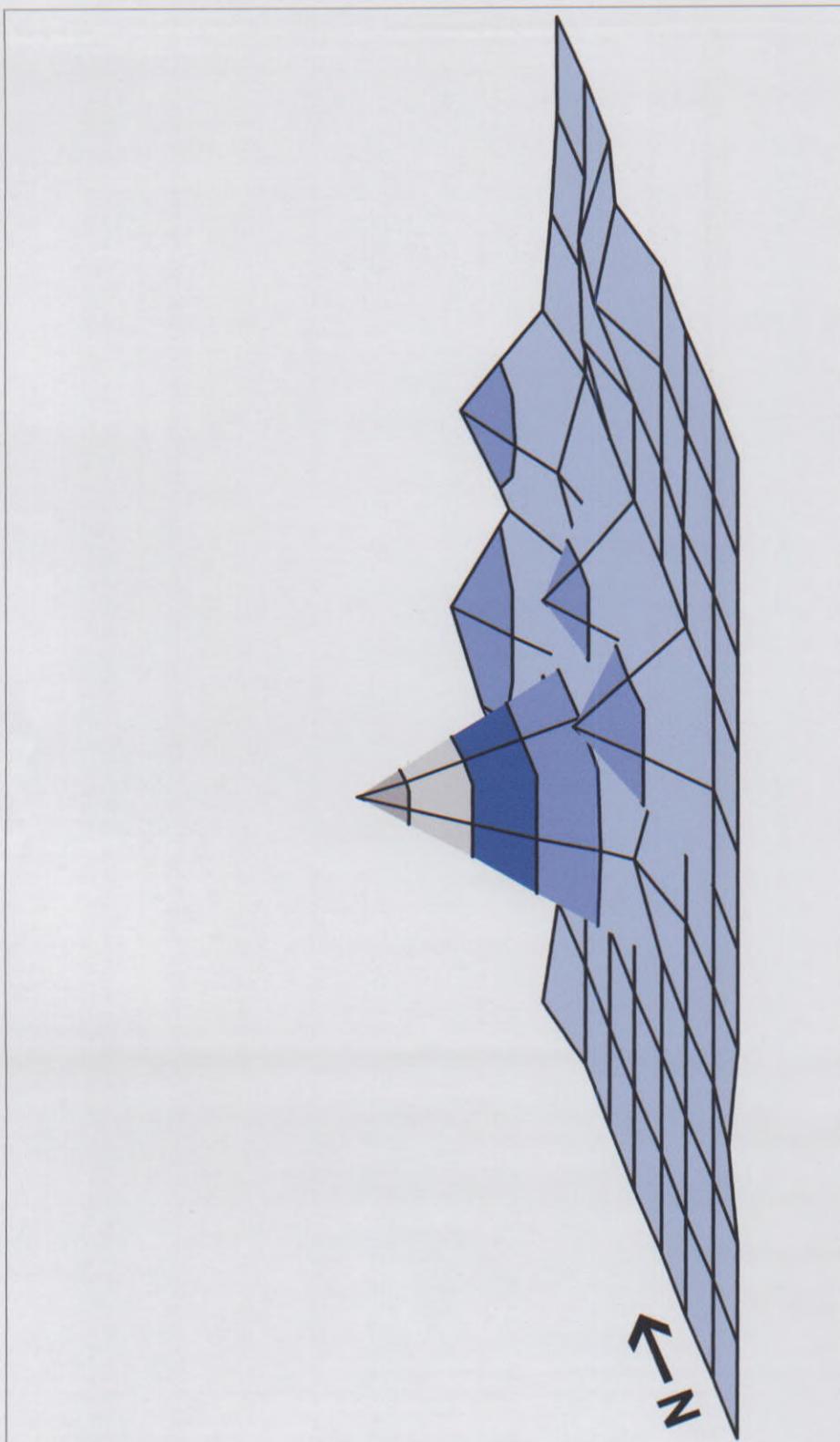


Figure 5.15 Use of the enclosure by the pride of African lions in the Kalahari during the summer study period. Peaks indicate where the majority of the time was spent.

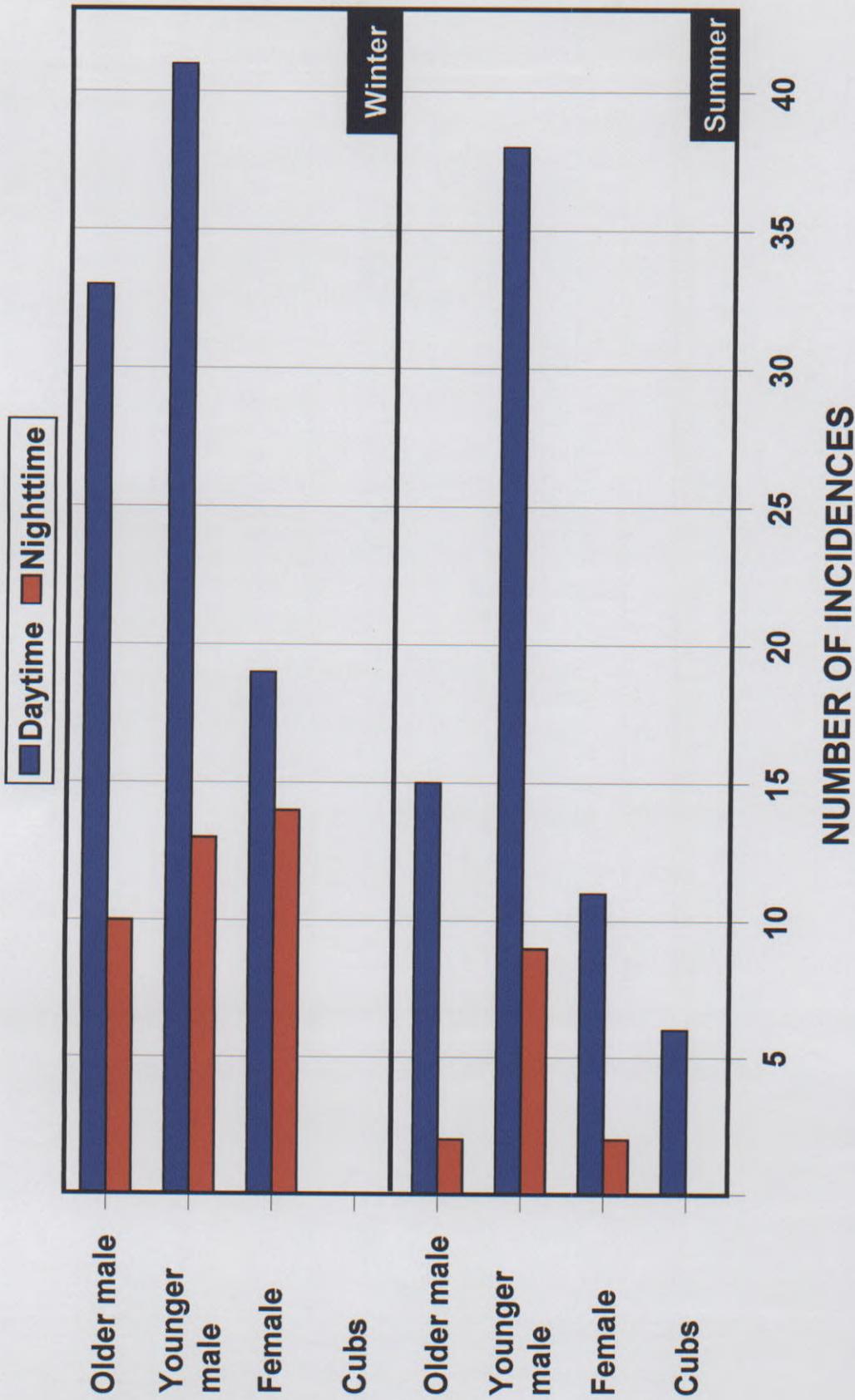


Figure 5.16 Seasonal incidence of diurnal and nocturnal grooming of African lions in the Kalahari.

during both summer and winter. As can be seen in the graph, there was a distinct decrease from winter to summer, especially in the case of the males. The female's results did not demonstrate dissimilarity to the same extent, but it should be taken into account that during summer she was mother to two cubs which was not the case during the previous winter, and as a result, the incidence of grooming should have increased. Table 5.1 indicates all the incidences of allogrooming observed within the pride during both seasons. Except for the increase in allogrooming between the female and the cubs, there was a more even spread in summer as compared to winter.

5.3 DISCUSSION

Large mammals enjoy thermal advantages over small mammals as a result of their relatively smaller surface area through which to absorb or lose heat and their increased capacity for heat storage (Schmidt-Nielsen, 1984). Within the pride, the size of the animals varied as the males were much larger than the female not only as a result of their sex, but also due to the fact that they were overweight. For the calculation of the surface area, Schmidt-Nielsen (*op. cit.*) quotes Meeh's 1879 formula, $S = k M_b^{0.67}$, where k is the Meeh coefficient, which for cats is 10, and M_b is body mass. The surface area of the older male was calculated as 3,77 m² and the female's, 2,55 m². The difference in surface area between the male and female is large. Taking into account this difference and the excess weight carried by the male which affords a greater insulation and added heat burden, there should be implications for thermoregulation on an individual level. Large animals, unlike their smaller counterparts, lose and gain heat slowly and do not have great fluctuations in body temperature. Larger endotherms have a high thermal inertia (Louw, 1993).

All eutherian mammals regulate their internal or core temperature within a narrow range, between 36 and 38 °C (Schmidt-Nielsen, 1998). To achieve this, a balance of its net thermal exchange must be maintained where heat content is

Table 5.1 Seasonal incidence of allogrooming by African lions in the Kalahari. OM, older male; FE, female; YM, younger male; CU, cubs.

	Winter (n = 13)					Summer (n = 46)				
	OM	FE	YM	CU		OM	FE	YM	CU	
OM	■	0	2	0		■	1	2	1	
FE	1	■	4	0		1	■	6	21	
YM	2	4	■	0		2	3	■	2	
CU	0	0	0	■		3	2	2	■	

equal to metabolism and heat exchange. Heat content is the sum of conduction, convection, radiation and evaporation, of which the latter is the only element which represents heat loss. The former three are passive forms of heat exchange with the environment and rely solely on temperature gradient. It is known that heat moves from a high to a low and when ambient temperature increases to beyond that of the surface temperature of the animal, the animal gains heat. This scenario is reversed when ambient temperature drops to below that of the animal's surface temperature and heat is consequently lost to the environment. Endotherms have various physiological mechanisms for temperature regulation and these will be discussed in Chapter 6, but there are various behavioural mechanisms that these animals can employ to thermoregulate. The most elementary of these are reduction or increase of activity, reduction or enlargement of surface area and "escape" behaviour.

5.3.1 Ambient and sand temperature

The winter trials in the Kalahari had mild ambient temperatures, including those at night. Temperature under zero degrees was experienced only twice during the trial. Daytime median temperatures peaked at 27 °C and nighttime median temperatures dropped to just under 5 °C. Maximum daytime temperature reached 31,9 °C with minimum nighttime temperature dropping to -2,9 °C (see Fig. 5.1). The sand temperature was mild during winter, especially in the shade. Therefore, a temperature gradient for passive heat exchange was almost always available. Humidity during winter was not a factor; the air was dry and at the lowest temperatures, the median value for relative humidity was just over 60%. Summer, however, had high ambient temperatures with medians peaking at just below 35 °C and dropping to 16 °C. The hottest daytime temperature recorded was just under 40 °C and the lowest at nighttime was 11 °C. Sand reached a maximum of 52 °C in the shade during summer. As a result, temperature gradients that favoured the animals during winter were no longer available. Humidity was a little higher during summer, especially when rain was present, but vapour pressure was never at levels that became uncomfortable. Much of the humidity was driven off by increasing ambient temperature.

5.3.2 Activity patterns

The diurnal activity patterns of the lions did not differ much between the seasons, especially from approximately 11:00 to 17:00. Movement varied between the two seasons at each hour and no discernable decrease from winter to summer can be seen. The type of movement, however, was different. During winter, the pride often exerted themselves by running after the feeding vehicle or with constant movement in response to the sound of a vehicle on "hungry" days. They also moved across greater distances during the daytime in winter, which was not seen in summer. During the latter trials, movement was typical "escape" behaviour, from shade to shade, the pride seeking out denser trees. They often ran over the sand and paused in shade while en route. They were also more precise regarding shade, moving when the sun penetrated only slightly. Inactivity during both seasons demonstrates that the bulk of daytime is spent at rest. During winter, two peaks can be seen, the first between roughly 08:00 and 12:00 and the second from 13:00 to 16:00. The summer results indicate only one peak, from roughly 09:00 to 17:00. Similar curves in ambient temperature during winter and summer were seen (see Fig. 5.1). "Escape" behaviour, therefore, directly correlates with ambient temperature increases. The movement to a more densely shaded site is indicative of behavioural thermoregulation. Movement and activity correlate well with what is known about free-range lions. The sighting of lions resting in shade during daytime hours is renowned. Muscular work produces heat and the intensity of this work is correlated with the amount of heat produced (Brafield & Llewellyn, 1982). The increases in rest during the daytime hours in both summer and winter compare well with increasing temperature and this is the means by which lions maintain thermal balance, what Louw (1993) refers to as thermal inertia.

Nighttime inactivity occurred as a result of the captive conditions. Free-range lions patrol territories and hunt at night which was not possible for the pride in the Kalahari. During summer nights, movement was higher than in winter. When ambient temperatures are low, movement may be inhibited to decrease surface area so as to prevent further exposure of the body and consequent loss of heat

to the environment (Hull, 1973). Ambient temperature during the winter nights did not drop low enough for movement to become necessary for survival and the inactivity was as a result of the cold. During summer nights, pleasant temperatures were experienced which may be the cause of the higher active periods during this trial.

Feeding occurred at every hour during the day except for 11:00 in winter and 12:00 in summer. As a result of the captive conditions with the lions being fed, this differs somewhat from the feeding behaviour of free-range lions. Lions are known to feed at night and depending on pride size, will finish a kill during one feed and move away from it after feeding (Packer & Pusey, 1997). As a result of competition between the two males in the pride and the specific ritual of this pride in taking turns for feeding, the incidence of this behaviour throughout the day is explained. During winter nighttime hours, feeding was absent from approximately 22:00 to 01:00. This is as a result of the time the lions fed during winter, usually at roughly 18:00. By approximately 22:00, the older male secured the carcass and fed and rested at his leisure. Due to ambient temperature, the animals may also have opted for less movement to conserve body heat. During summer, as a result of the higher ambient temperature and the age of the younger male, competition for the carcass was fiercer and the entire pride fed throughout the night. The general feeding behaviour of the pride in the Kalahari was discussed in Chapter 4.

Interaction was present at all daytime hours during winter except for 13:00 and 15:00. During summer, it is absent for the bulk of the day from roughly 09:00 to 17:00, except for a small percentage at 13:00. Play, bonding and nuzzling are behaviours that are present when lions are active and in high ambient temperatures, lions reduce heat production by resting. Grooming does not involve high levels of physical work and during daytime in winter, ambient temperatures were comfortable. During summer, however, much of the grooming activity was sacrificed for panting. The latter is discussed in Chapter 6.

The results of the diurnal activity patterns demonstrate that when temperature gradients are reduced and conduction, convection and radiation imply heat absorption, the pride retreated to the shade and reduced activity and body heat production to a minimum by resting. During the winter nights, the lions reduced activity so as to limit heat loss to the environment and during summer, total activity, including northern perimeter patrols, increased. The results for the cubs indicate the same patterns except for slightly more movement than the adults, especially at night. Higher levels of activity are typical for young animals as exploration and play make up most of their active hours.

5.3.3 Sunbathing

Sunbathing is a common feature of behavioural thermoregulation in both ecto- and endotherms and significantly lowers energy demands (Morse, 1980). The pride in the Kalahari was found to sunbathe on dune crests (see Figs 5.5 & 5.6). The total amount of time spent in the sun during winter is significantly longer than the time recorded in summer (see Fig. 5.7), as a result of the colder winter nights and lower morning temperatures. During the winter trials, the lions settled on the crest every morning at roughly 07:30 and oriented their bodies east. When they were well fed they moved to shade early, between 09:00 and 10:00, and when their bellies were empty they moved into the shade later, between 11:00 and 13:00. This supports the assertion that feeding increases metabolism, and as a consequence, total body heat. During the summer trials, the pride spent only 54% of the mornings they were observed on the dune crests and on these occasions, they moved into the shade between 07:00 and 09:00. Taking into account median temperatures during these times in both seasons, indications are that the ambient temperature cutoff for sunbathing is 25 °C (see Fig. 5.1). On two occasions when the lions were clearly hungry, having not fed well six days earlier, they remained on the crest, looking east, until approximately 11:00. This may be as a result of conditioning rather than behavioural thermoregulation. The animals demonstrated a distinct preference for orienting the belly *eastwards*, towards the sun. The belly has the largest

surface area and is the part of the body with the lowest insulation (Schmidt-Nielsen, 1998). This allows for deeper penetration of irradiation and due to the white fur, heat gain is less affected by the movement of air and wind (Louw, 1993). The older male sunbathed for the shortest period during winter and the younger male, during summer. According to Louw (*op. cit.*), animals with a rotund shape such as the polar bear, have maximum heat gain. As previously mentioned, larger animals also store more heat and both the males in the Kalahari were overweight. Excess fat has advantages not only as insulation during cold, but also leads to excess overheating in direct sunlight, as described by Morse (1980). The darker colour of the older male's fur and mane, being adult during the winter trials, may also have caused greater heat uptake during the winter study period (Schmidt-Nielsen, *op. cit.*). Experiments on the black lateral stripe of the springbok by Louw (*op. cit.*) showed that that specific area heated up faster and maintained heat for longer.

Desert animals like Cape oryx utilise wind and hilltops or dune crests to thermoregulate, moving onto the tops or crests during late afternoons to catch the breeze which is intensified on higher ground (Louw, 1993). The pride in the Kalahari was not observed doing this. Just prior to sunset the female in particular lay on the crests, scanning, and never oriented her body such as to maximise the effect of the breeze. Wind speed was measured in summer with a hand-held anemometer. The wind speed was greater on the crest than in the streets roughly 50% of the time. The lions, however, did not lie on the dune crests during summer, but rather somewhat below it. This may be due to greater shade on the dune faces since large trees do not grow on the dunes. During winter, as was mentioned, the lions utilised a small shepherd's tree on the crest, but during summer the demand for shade was too great. On several occasions during the study period the lions were observed to avoid the wind, even though it was not of high speed. For example, if the wind was easterly, they lay on the western face of the dune. The loose surface sand of the dunes blowing into the animals possibly made it unpleasant for them to lie on the dunes in the wind.

5.3.4 Body surface temperature

Median values of the Thermocron iButton readings for both daytime and nighttime during the entire winter and summer study period were calculated. Body surface temperature related well with ambient temperature. There was a distinct leveling of the temperature around 10:00 during the winter daytime hours with very little variation. Throughout the winter nighttime hours, however, variation was seen, especially in the older male. This may be clarified in terms of the role of the pride male. He almost always slept alone, thereby having the tail iButton constantly exposed, and regularly exposed his loins during the night. It has been previously mentioned that the males were more overweight and, therefore, some heat storage would have occurred during the daytime, being offloaded at night. Further to this, confidence and personality would also assist in loin exposure during darkness. The neck iButton remained relatively constant throughout the 24-hour cycle as a result of the insulating capacity of the mane, preventing both heat loss and heat gain. West & Packer (2002) report that the surface temperature of maned males was consistently higher than that of females, suggesting the added heat burden of the mane. The results of the iButtons do not show this, the levels being similar. The female's iButtons remained more even. She was normally accompanied by the younger male during winter, often sleeping in close proximity and unless she was well-fed, loins were not exposed at night.

The summer results for nighttimes show more variation, but the temperature range is smaller. During winter, the range for the older male's tail iButton was 23 to 38,5 °C whereas the range for summer was 29 to 38,5 °C. The lions were more active during the summer nights, moving often. Further to this, the cubs often suckled at night, the female then exposing her loins. She also slept alone with the cubs more often, the males not far, but not in close proximity to her. Movement during both seasons exposed more surface area and heat loss to the environment is increased, probably causing the flux in the summer results. Humidity increased at night and dew was frequently present. The lions were

exposed to this moisture on the vegetation and the wetting of the area of the iButton would have assisted in causing a temperature drop.

In rats, thermoregulation is affected by reserves in the body, and on food deprivation the average body temperature is lower (Yoda *et al.*, 2000). As a result, cold-escape behaviour is facilitated by food deprivation, but heat-escape behaviour is unchanged. The results found in the Kalahari are in agreement. The median surface temperature of the male and female (see Fig. 5.12) was almost always higher when the animals were well-fed. According to West & Packer (2002), males decrease their food intake substantially during the hottest months of the year. This was not observed in the Kalahari and may be as a result of the increased competition between the two males during the summer trials. The higher body temperature during full-bellied periods had implications for thermoregulatory behaviour. Lions were never exposed during winter nights on an empty belly, for example. The entire pride moved substantially less when they were well-fed. On one occasion during winter, the adults did not move once from sunset to sunrise, only turning over throughout the night. Daytime activity during both seasons was also substantially decreased when the lions were well fed.

No correlation between hunching up and temperature or full versus empty bellies could be found. It is plausible that lions hunch up their bodies simply because it is comfortable. Colder temperatures were experienced during the winter nights where the animals did not hunch up. Sand temperature was also recorded at lower temperatures than that measured during the times the animals hunched. Hunching up is a posture utilised in behavioural thermoregulation and whether the observations in the Kalahari may have been caused by metabolic heat changes is probable, but not known. The fact that most of the incidences are shared by the members of the pride further supports the assertion that indeed, they hunched up as a result of thermoregulation, but the reasons for this are not clear.

Water assists in cooling the body down as a result of evaporation (Schmidt-Nielsen, 1998). Rains fell in the lion enclosure three times and on these occasions, the surface temperature measured by the iButtons, decreased (see Fig. 5.13). On one particular occasion, the storm was particularly heavy and the lions were very wet and when they shook themselves, water spray was evident. During this time, they licked water off each other's body's, played exuberantly and the female exposed her loins. The observation time for this was from 16:00 to sunset and this level of activity was not seen on normal days during this time. It was clear that the reduction in not only ambient temperature, but also that of their bodies, allowed for the high levels of activity.

5.3.5 Enclosure usage

The total use of the 500 ha enclosure by the pride differed between the two seasons. There was a marked increase of usage during summer with more activity towards the northern half unlike winter, where movement was concentrated to the central-southern area. The reason for this was in all likelihood shade density. The enclosure has more black thorns and bigger and denser trees towards the northern half. The pride in the Kalahari had a propensity for resting at an elevated point. During winter, a small shepherd's tree on a dune crest sufficed, but a large arup tree offering dense shade was a preferred site during summer, while it was never used during winter. Black thorns in the dune streets were also well utilised by the pride during summer, while in winter they never lay under these bushes.

5.3.6 Grooming

The incidence of grooming (see Fig. 5.16) declined during summer as compared to winter, particularly in the case of the older male and the female who had the added burden of the cubs during summer. The latter were regularly seen after feeding with their faces dark from blood stains for the entire day without the female grooming them. Further, on one occasion, she attempted to groom the female cub who was panting. The cub resisted the female's attempts. The majority of the summer daytime hours were spent panting or simply lying

still. It appears as though the behaviour of grooming was sacrificed in favour of thermoregulation. During winter while the lions were in the shade, they lay and groomed one another, bonding and relaxing together. Summer, however, showed a different picture. The adults did not lie touching one another and became aggressive if touched or bumped by another member of the pride. No nuzzling or bonding occurred during these times. They either lay flat or lifted their heads to pant during the daytime, indicative of the burden of heat load compounded by increasing daytime ambient temperature. In the case of only allogrooming (see Table 5.1) a slight increase and spread of allogrooming between the two seasons is seen, most likely as a result of the cubs.

Saliva spreading is common in rats as a behaviour mechanism for thermoregulation (Cabanac, 1972). Hull (1973) also reports on its use by animals to cool down. During the summer trials, both the female and younger male were observed to lick their own chests for between 3 and 6 seconds on 12 occasions. These incidences were included in the total grooming, but may be considered as saliva spreading. The particular lion, when licking the chest, always lay upright, exposing the chest. The use of saliva to assist in evaporation and subsequent cooling down would be effective in reducing surface temperature.

As previously mentioned, the most basic of thermoregulatory behaviours is the reduction of activity during times of ambient heat and the change in total surface area, either an increase or decrease, depending on the demands of the ambient temperature. Pantin (1964) states that due to the fact that the physiology and anatomy of vertebrates changes extremely slowly, "vertebrates are in a type of phylogenetic trap as regards the kinds of physiological and anatomical adjustments they can make to temperature conditions." Behaviour then, becomes vital in thermal balance. Further to this, the distribution and abundance of animals is not limited by physiological adaptation, something which is clear in the case of lions taking into account their distribution range, and hence, distribution cannot be predicted on the basis of thermal physiology

alone. The importance of behavioural adjustments rather than physiological adaptations in overcoming thermal stress would, therefore, appear to be greater than in the case of nutritional or water stress (Louw, 1993).





6 THERMOREGULATORY BEHAVIOUR

6.1 INTRODUCTION

Temperature has a profound effect on life. If physiology is fine control of thermoregulatory processes in animals, then behaviour is broadband control (Cabanac, 1972). In extreme environments such as the Kalahari where ambient temperature ranges are significant, homeostasis becomes increasingly challenging and once behavioural mechanisms for heat balance fail, biothermal defences must be initiated. Within the thermoneutral zone, heat balance is well maintained without any physiological effort and is complemented by behavioural adaptations. The width of the thermoneutral zone is dependent upon the size and conductance of the animal concerned (Louw, 1993). In the case of the African lion, both its size and insulation imply that the zone may be wide. Consideration of the wide range of habitats within which it survives, supports the above assertion. Adams (1971) refers to changes in core and surface temperatures within this range as the thermoregulation dead zones. Outside of this range, physiological mechanisms must be activated. Inputs regarding changes in ambient temperature are via warm and cold receptors in the body. Responses to these receptors include sweating, panting, shivering, non-shivering thermogenesis, cardiovascular adjustments, piloerection and behaviour (Louw, *op. cit.*).

The importance of behaviour in thermoregulation was aptly described by Whittow (1973): "Behavioural thermoregulation is common in invertebrates and vertebrates, conformers and regulators, poikilotherms and homeotherms. In all groups, examples of a sophisticated and sensitive nervous control system can be adduced."

6.2 RESULTS

6.2.1 *Thermocron iButtons and body surface temperature*

The median values and the deviation around the median for the three implanted iButtons during both the winter and summer study periods are shown in Figures 6.1 & 6.2. During winter, the greatest variation was observed in the older male's tail and loin iButtons, while the summer results showed that both the older male and the female's tail iButtons had the greatest variation. The female's loin iButton failed one week into the summer trials and, therefore, no data for the nighttime is presented in Figure 6.2.

6.2.2 *Loin exposure*

The data provided by the iButtons implanted in the loin regions of the two adult lions did not withstand the rigours of statistical testing. Efforts to determine associations by means of Chi-squared tests failed as calculations could not be completed. Further, no significant patterns could be found as temperature increases and decreases in the iButtons were volatile. In addition to this, due to the positioning of the iButton, the temperature increased immediately after the legs were closed which often occurred shortly before the hour, the time at which the temperature recording was made. The iButtons were programmed to measure surface temperature at hourly intervals. There are a limited number of readings that can be stored in the iButton, and as a result of the duration of the two study periods, hourly intervals were the shortest that could be selected. On account of the erratic nature of the results of the loin iButtons, the natural day (24h) was divided into early morning, midday, late afternoon and nighttime periods which correlate well with daily ambient temperature curves. During the winter season, early morning was from 07:00 to 12:00, midday from 12:00 to 16:00, late afternoon from 16:00 to 18:00 and nighttime from 18:00 to 07:00. For summer, the time for early morning was from 06:00 to 11:00, midday from 11:00 to 16:00, late afternoon from 16:00 to 19:00 and nighttime from 19:00 to 06:00.



Figure 6.1 Variation in the median temperature of iButtons implanted in adult African lions in the Kalahari during winter. Standard deviation around the median is indicated in blue. Neck (NiB), tail (TiB) and loin (LiB) iButtons for male and female indicated by prefix M or F respectively.

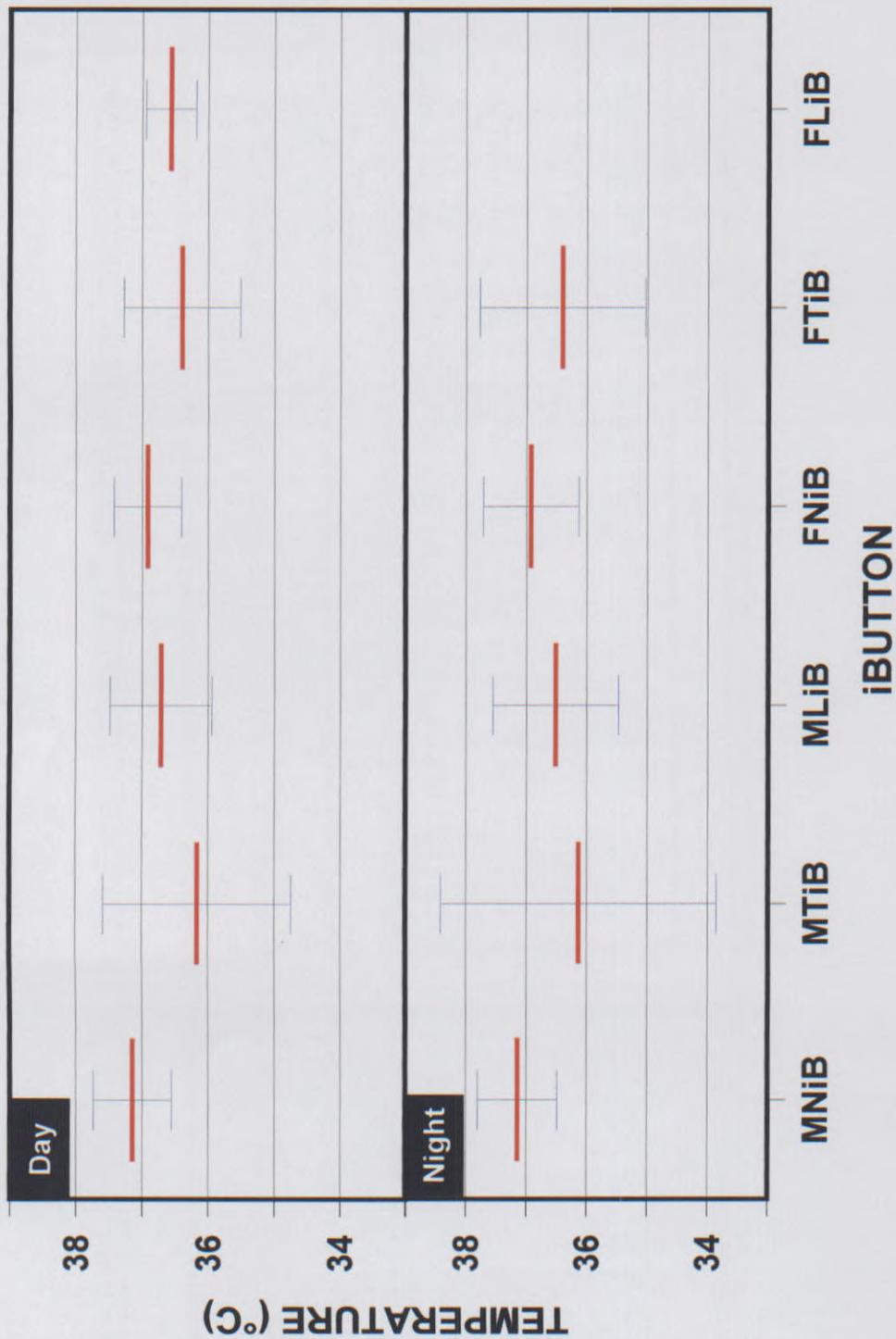


Figure 6.2 Variation in the median temperature of iButtons implanted in adult African lions in the Kalahari during summer. Standard deviation around the median is indicated in blue. Neck (NiB), tail (TiB) and loin (LiB) iButtons for male and female indicated by prefix M or F respectively.

The number of loin exposures with empty or full bellies for each of the adults in the pride was counted for each of the natural day periods. The results are indicated in Figures 6.3 to 6.5.

Throughout the winter study period, the older male (Fig. 6.3) did not expose his loins on an empty belly except during the midday period when ambient temperature peaked. Exposure on a full belly, however, occurred throughout the 24-hour period, peaking during the night when temperature dropped to its lowest. Throughout the summer trials, no exposures occurred during early morning. Excluding late afternoon when exposure took place only on an empty belly, both midday and nighttime showed exposure on both an empty and full belly, with a peak during midday. The female (Fig. 6.4) demonstrated a greater number of loin exposures during both seasons and did so on both an empty and full belly during the natural day periods, except for nighttime during winter, when she did not expose on an empty belly. A peak was reached during late afternoon in summer, when she exposed most on an empty belly. The remaining peaks are for full belly exposures, mostly during winter, except for midday in summer. The results for the younger male (Fig. 6.5) demonstrate a very different curve with a low number of exposures during all natural day periods in both seasons and a large peak on an empty belly during late afternoon in summer. Again, as with the other adults, no empty belly loin exposures during winter nighttimes were seen.

The frequency of loin exposure of all the adults during both seasons was merged and demonstrated a distinct relationship with ambient temperature. The frequencies were calculated to correct for differences in total observation time at the different ambient temperatures. The results are shown in Figure 6.6. The frequencies for winter indicated that from 16 °C and below, all exposures were on a full belly. The lowest ambient temperature during the winter trials at which loin exposure on an empty belly occurred was 17,6 °C. During summer, the frequency of loin exposure increased up to 34 °C with a sharp decline above

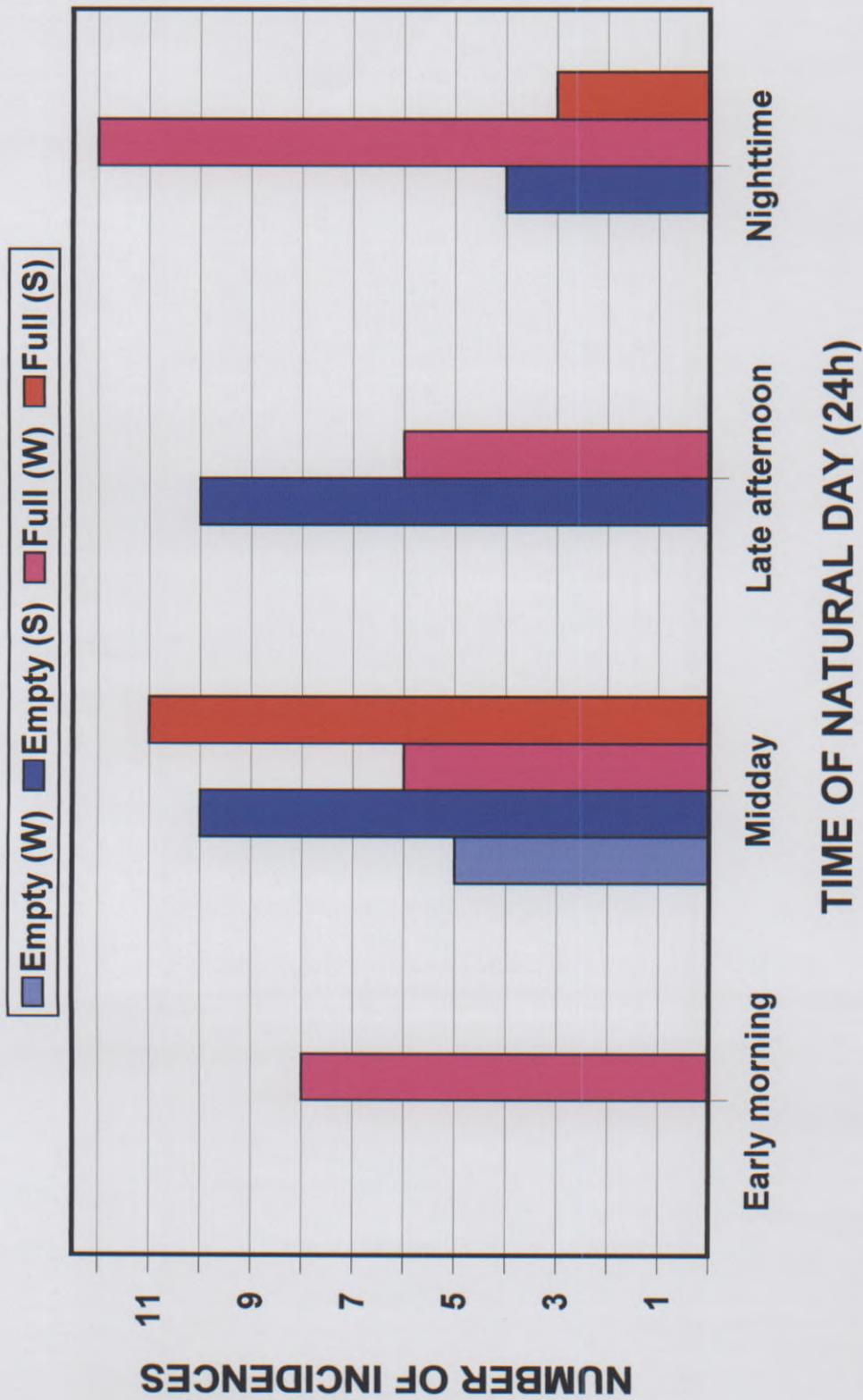


Figure 6.3 Seasonal and temporal incidences of loin exposure at an empty or full belly by the older male African lion during a natural day (24h). W, winter; S, summer.

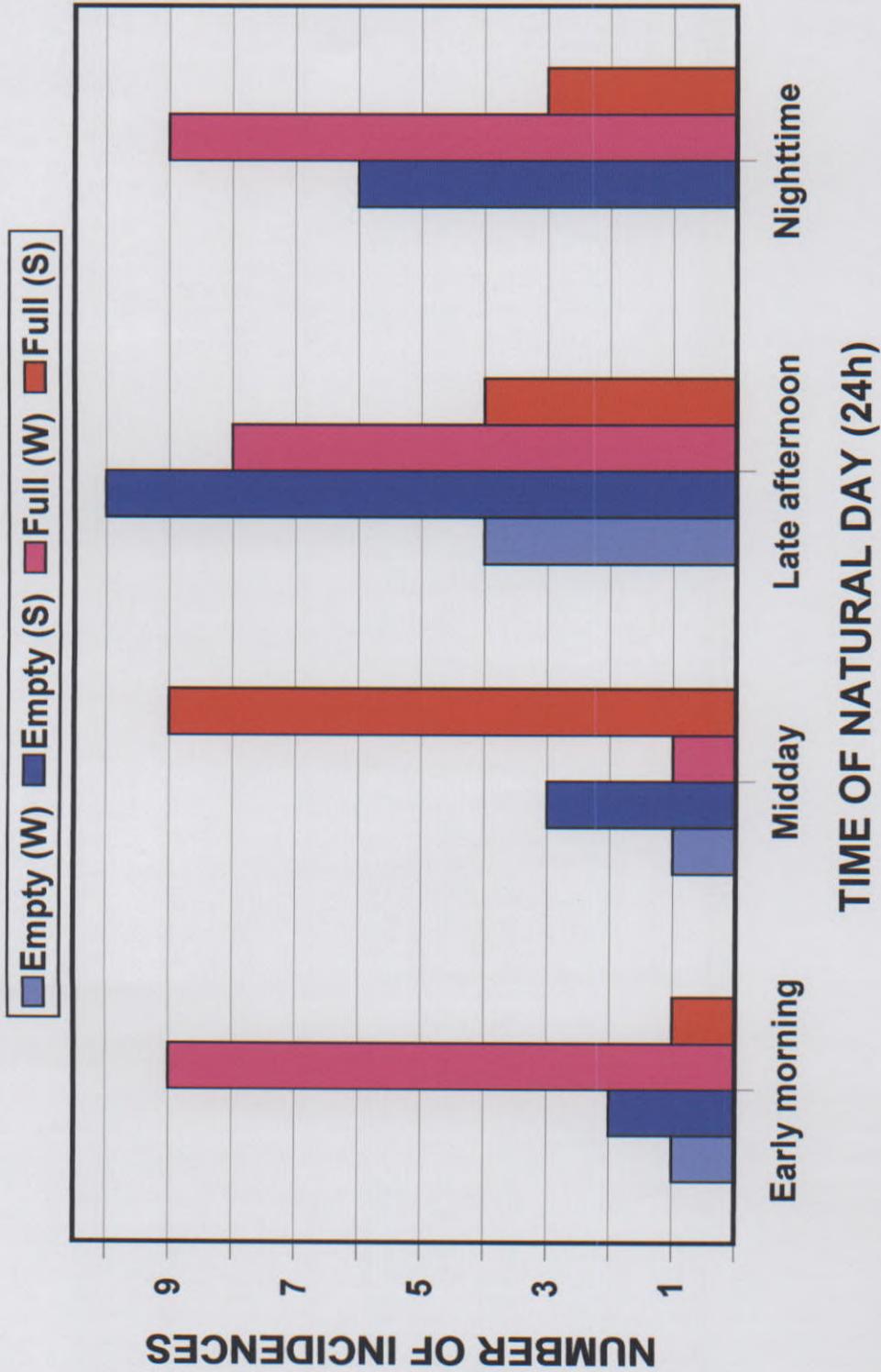


Figure 6.4 Seasonal and temporal incidences of loin exposure at an empty or full belly by the female African lion during a natural day (24h). W, winter; S, summer.

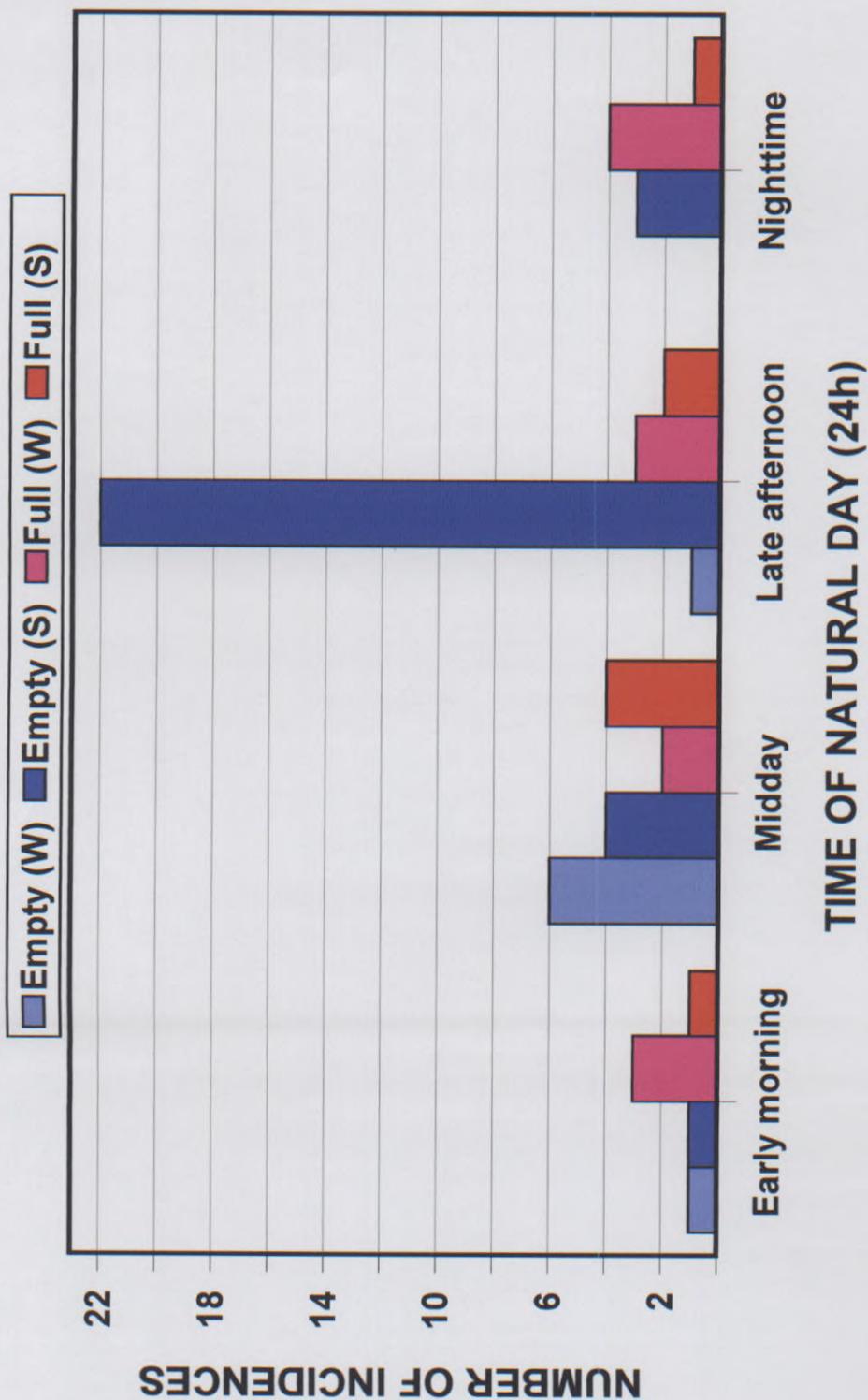


Figure 6.5 Seasonal and temporal incidences of loin exposure at an empty or full belly by the younger male African lion during a natural day (24h). W, winter; S, summer.

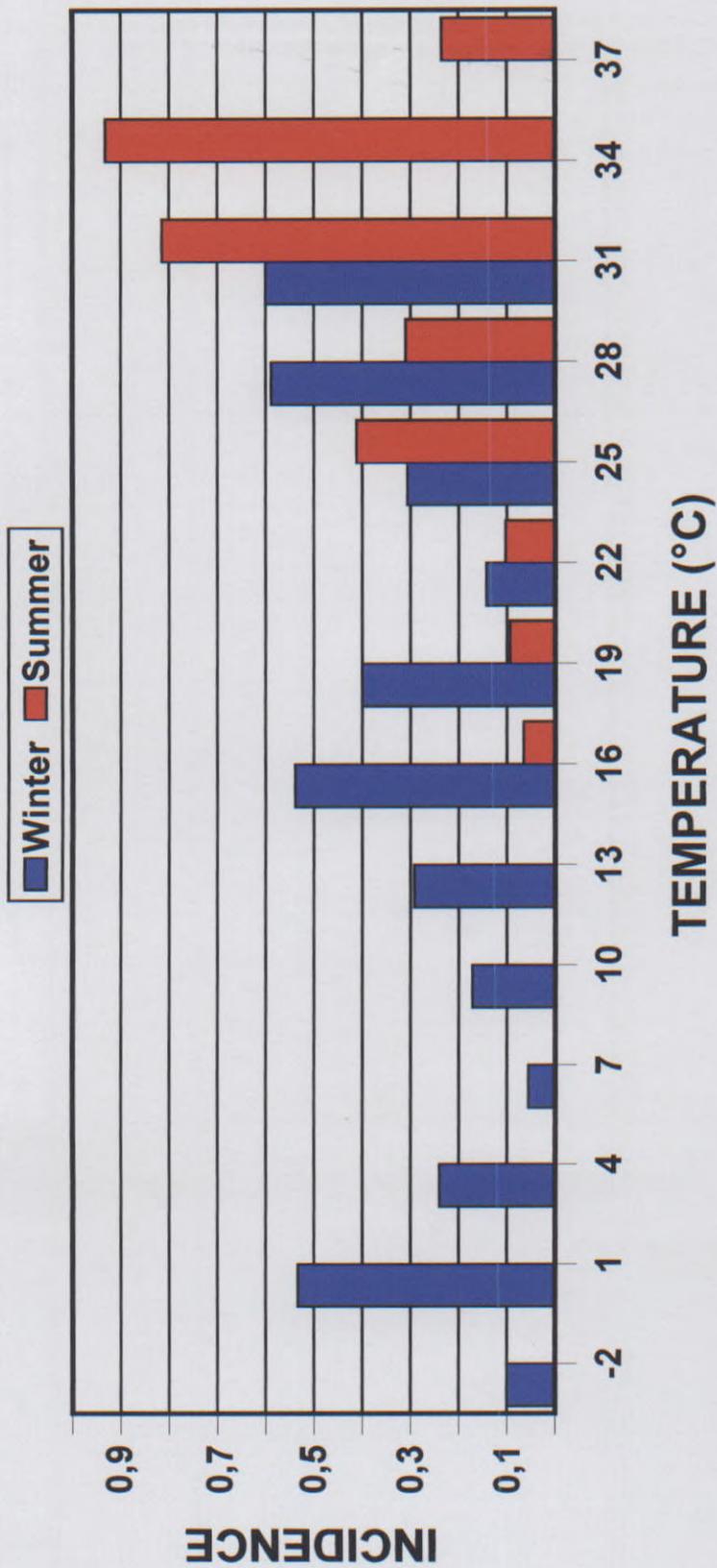


Figure 6.6 Seasonal incidence of loin exposure by adult African lions at the range of temperatures observed during the period of study in the Kalahari.

this. There was an area of overlap between summer and winter and the frequencies for summer for 16 °C are, as with winter, also indicated for a full belly. As with winter, the pride did not expose loins on an empty belly at ambient temperatures below 17,7 °C, a difference of 0,1 °C from winter.

There was a large variation in the range of temperatures at which individual pride members exposed their loins on either an empty or full belly during both the seasons. Figure 6.7 indicates the ranges for both winter and summer. The lowest ambient temperature observed for loin exposure was for the female at -1,7 °C during winter, and the highest was 38,5 °C for the older male during summer.

The probability of loin exposure at an ambient temperature greater than 25 °C during winter and 30 °C during summer was calculated for the three adults. The formula used was:

$$P(E) = m / s$$

(Kemp, 1998)

where m is the number of observed loin exposures at the said temperature, and s the total number of loin exposures for the animal concerned. The results for the winter study period are 0,16 for the older male, 0,15 for the younger male and 0,09 for the female. The summer results are 0,24 for the older male, 0,23 for the younger male and 0,18 for the female.

6.2.3 Panting

The incidence and frequency of panting of the pride in the Kalahari was closely observed and the results of the two seasons, winter and summer, were compared.

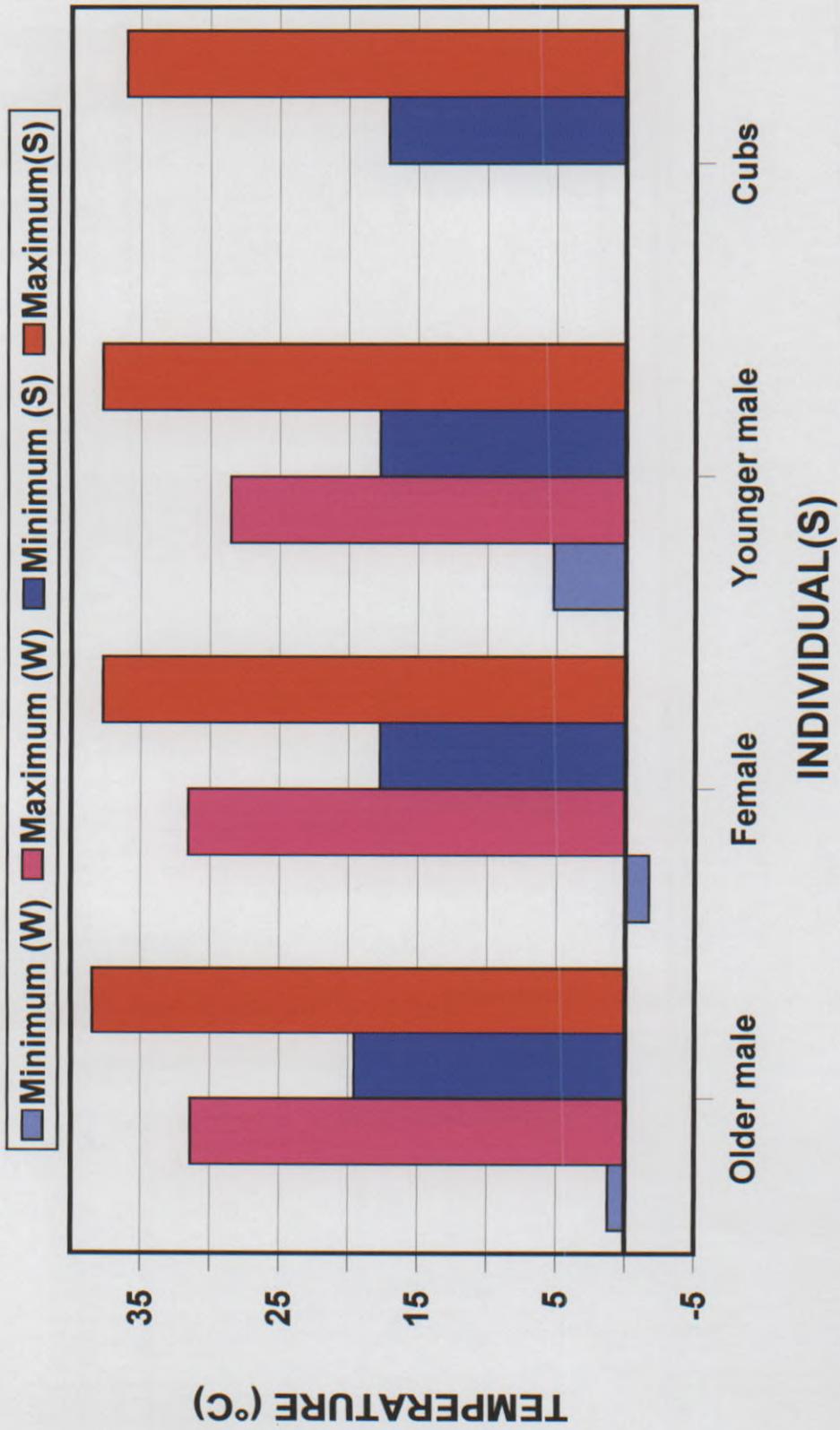


Figure 6.7 Seasonal variation in ambient temperature extremes at incidence of loin exposure by African lions in the Kalahari. W, winter; S, summer.

Panting was recorded when rapid oscillation of the floor of the mouth was observed. The natural day periods as applied for the loin exposure results were also used for panting. The number of panting incidences with empty or full bellies for each of the adults in the pride during the natural day periods is indicated in Figures 6.8 to 6.10. For all three adults concerned there is a prominent peak during midday, while during late afternoon the peaks are either equal to or higher than those observed during early morning. No panting was observed during nighttime, nor did panting occur on a full belly during winter. All the panting observed during these trials was after bursts of activity, specifically on "hungry days" when the pride moved in response to the sound of vehicles. During summer, however, panting behaviour was observed while the animals were static and resting in the shade. The female demonstrated the highest number, and the older male the lowest. In all three adults, panting at a full belly during summer was most frequent.

The frequency of panting of all the adults during both seasons was merged and compared to ambient temperature (Fig. 6.11). The frequencies were again calculated to correct for differences in total observation time at the different ambient temperatures. The occurrences indicated for winter, as previously mentioned, all apply to empty bellies and were recorded after active periods. During summer, however, this was not the case, with the highest frequency occurring on full bellies and increasing towards an ambient temperature of 37 °C. The lowest temperature at which panting was observed on an empty belly was 31,6 °C and on a full belly 28,4 °C. The mean ambient temperature during this season for panting was 34,5 °C. The range of temperatures for panting during both seasons was not as pronounced as with the loin exposures. As illustrated in Figure 6.12, the range for winter and summer was roughly 10 °C (21,4 – 31,9) and 11°C (28,4 – 39,5) respectively. The older male panted at a maximum rate of 92 per minute during winter and 138 during summer, while the female panted at 156 pants per minute during winter and 240 during summer. The younger male's results are 156 pants per minute during winter and 174

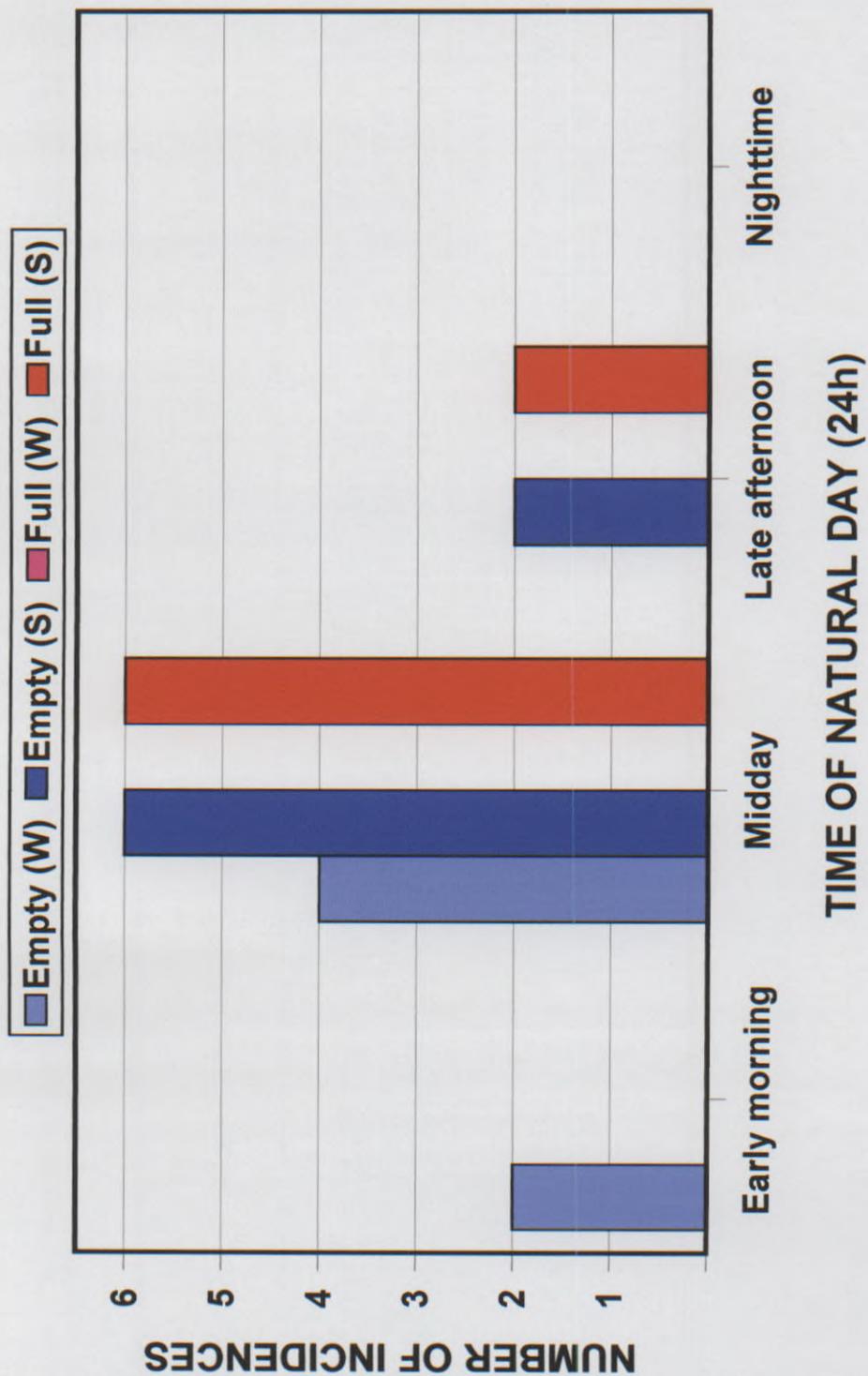


Figure 6.8 Seasonal incidence of panting at an empty or full belly by the older male African lion during a natural day (24h). W, winter; S, summer.

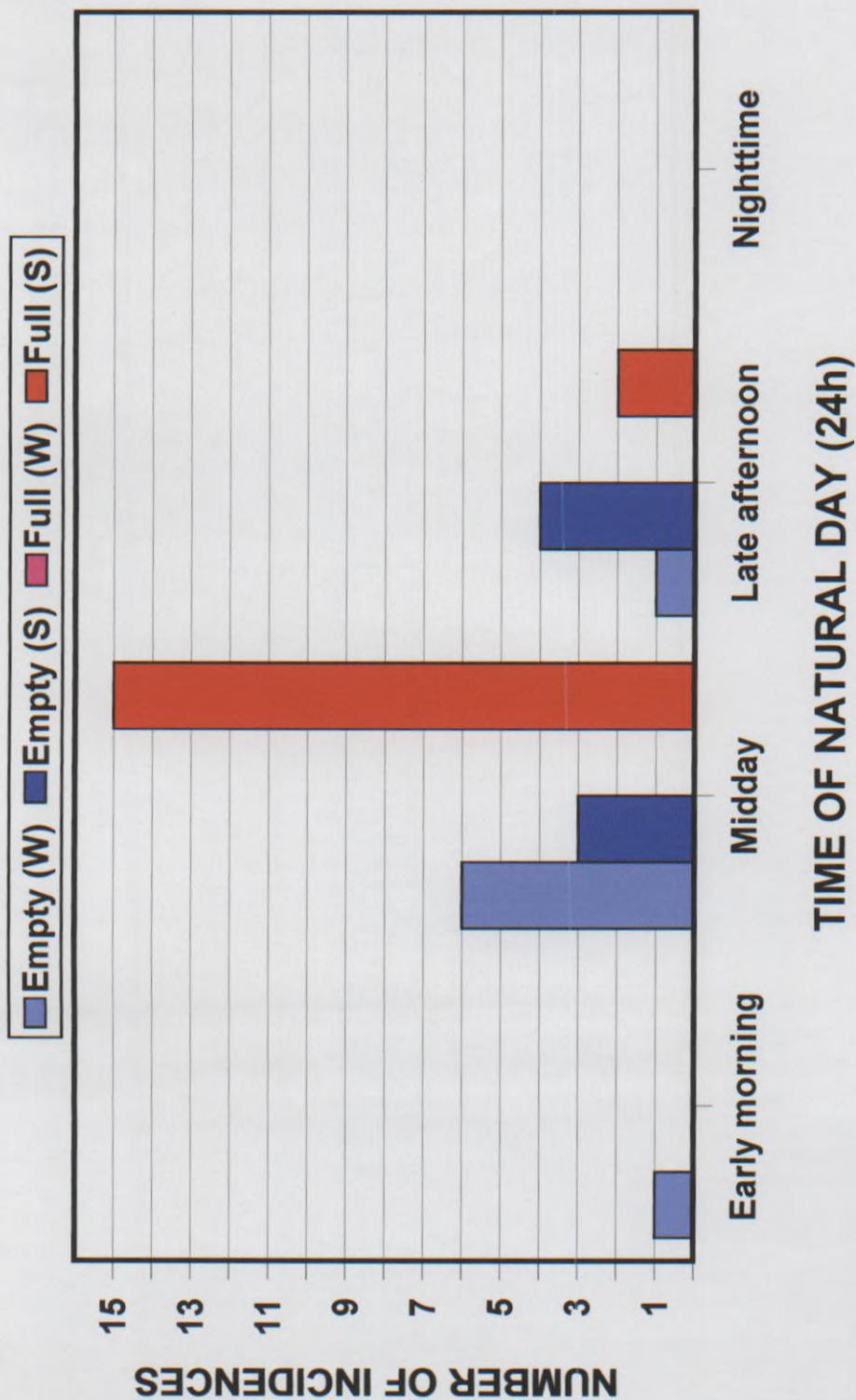


Figure 6.9 Seasonal incidence of panting at an empty or full belly by the female African lion during a natural day (24h). W, winter; S, summer.

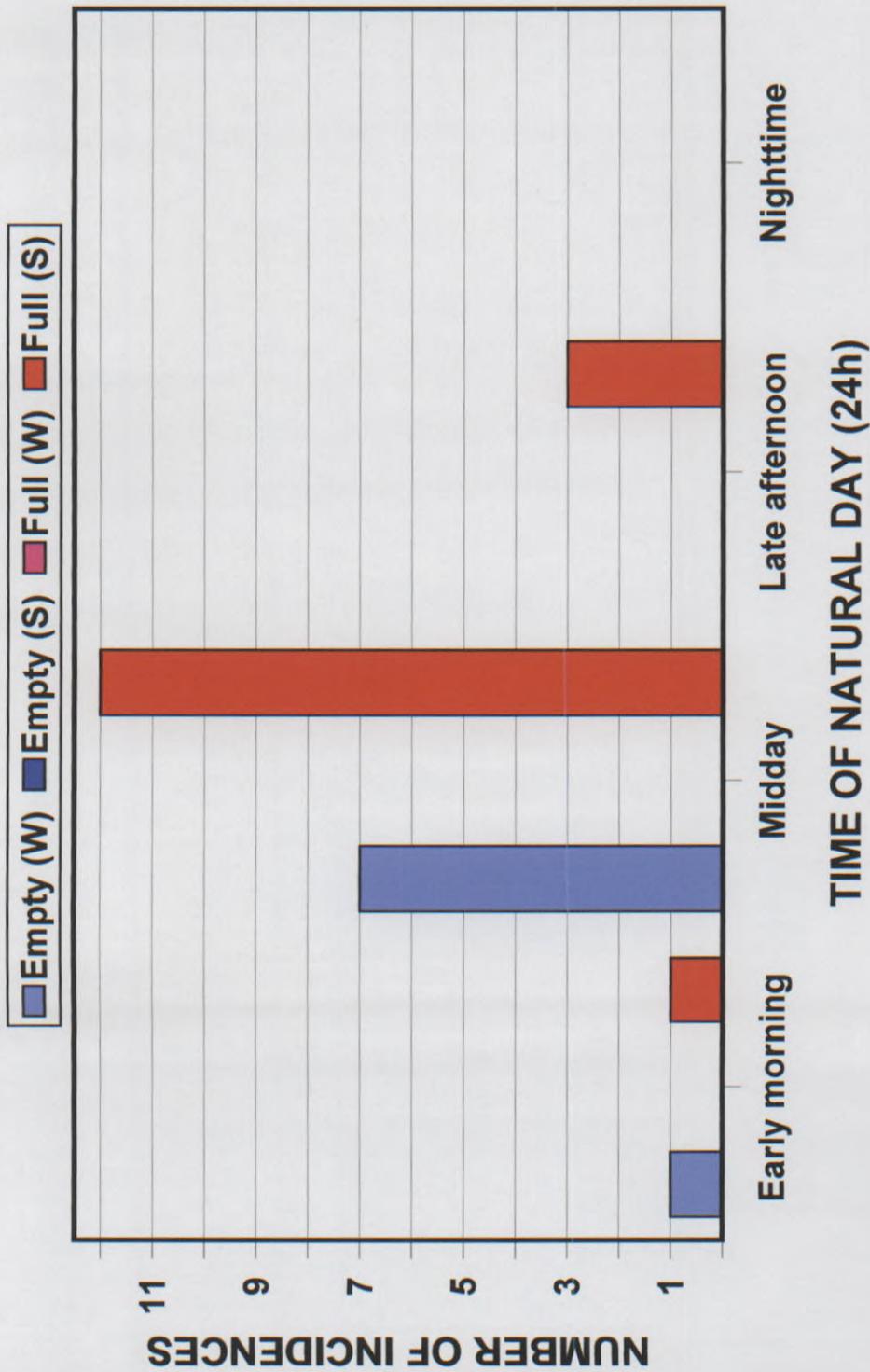


Figure 6.10 Seasonal incidence of panting at an empty or full belly by the younger male African lion during a natural day (24h). W, winter; S, summer.

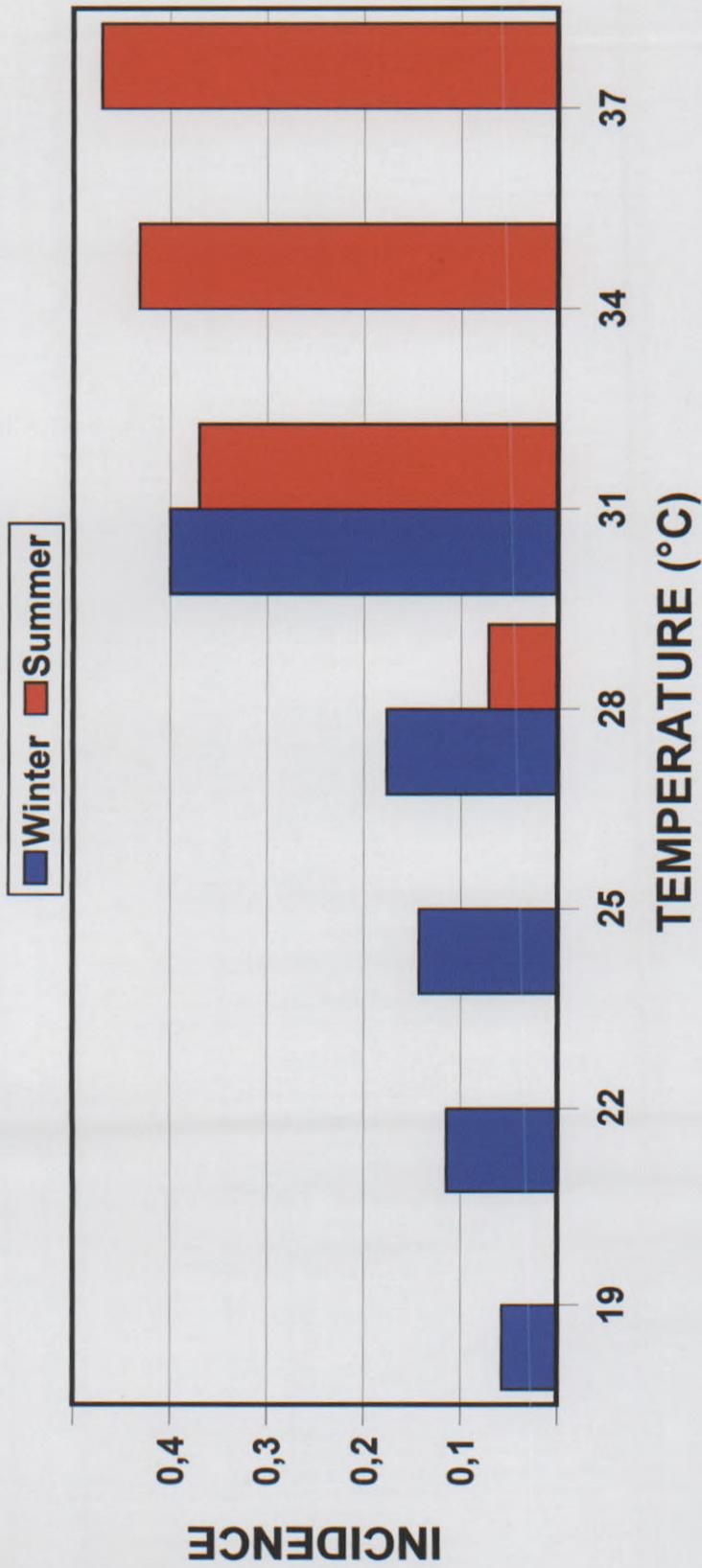


Figure 6.11 Seasonal incidence of panting by adult African lions at the range of temperatures observed during the period of study in the Kalahari.

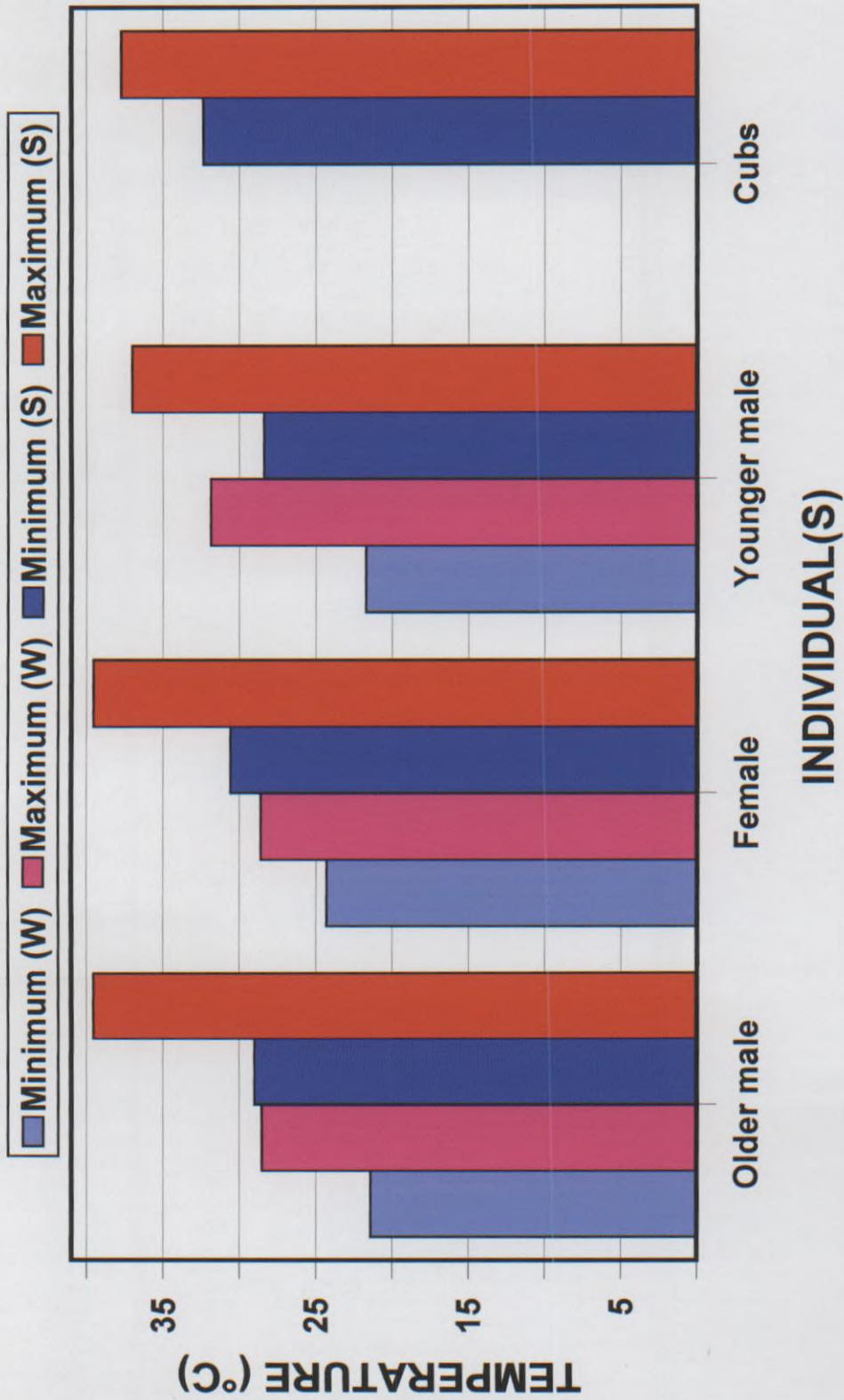


Figure 6.12 Seasonal variation in ambient temperature extremes at incidence of panting by African lions in the Kalahari. W, winter; S, summer.

during summer. The cubs were observed to pant on three occasions during the summer study period with pants per minute ranging from 77 to 162.

Breathing rates differed greatly between winter and summer. Throughout the daytime shifts ($n = 18$) of both the winter and summer study periods, the average breathing rate of the resting lions was counted when the opportunity arose. The average rate for the winter study period was 9 breaths per minute and during summer, 55 breaths per minute.

6.2.4 Carcass dissection

A multitude of superficial and integrating network of blood vessels, approximately 1 – 2 mm in diameter, were found along the dorsal and lumbar areas of the carcass (Fig. 6.13A), extending laterally as far as is demonstrated in Figure 6.13B. In the region of the sternum extending to the lateral thorax, larger vessels of roughly 2 – 4 mm in diameter were found and ventrally, still larger vessels of 5 – 8 mm in diameter (Fig. 6.13C). The parasacral and perineal areas were found to be well-supplied with both small and larger blood vessels, illustrated in Figure 6.14A. The very small superficial 1 - 2 mm blood vessels were also present, but were sparser than in the dorsal and lumbar regions. Superficial small-diameter blood vessels in the neck region were very sparse, the surface covered mostly with muscle tissue. The area where a few small-diameter vessels were found is indicated in Figure 6.14B. The foreleg demonstrated some shallow blood vessels with diameters of 2 - 4 mm.

According to Eloff (1973), the Kalahari lion appears to be entirely independent of drinking water, relying primarily on fluids obtained from the blood and body fluids of their prey and the small amount of plant material they consume. As a result of this, the relative medullary thickness of the African lion's kidney was calculated. The length of the loops of Henlé, situated in the medulla, determines the water resorption/concentration ability of the kidney (Ryke, 1982). The relative medullary thickness of the gerbil (*Gerbillus gerbillus*)

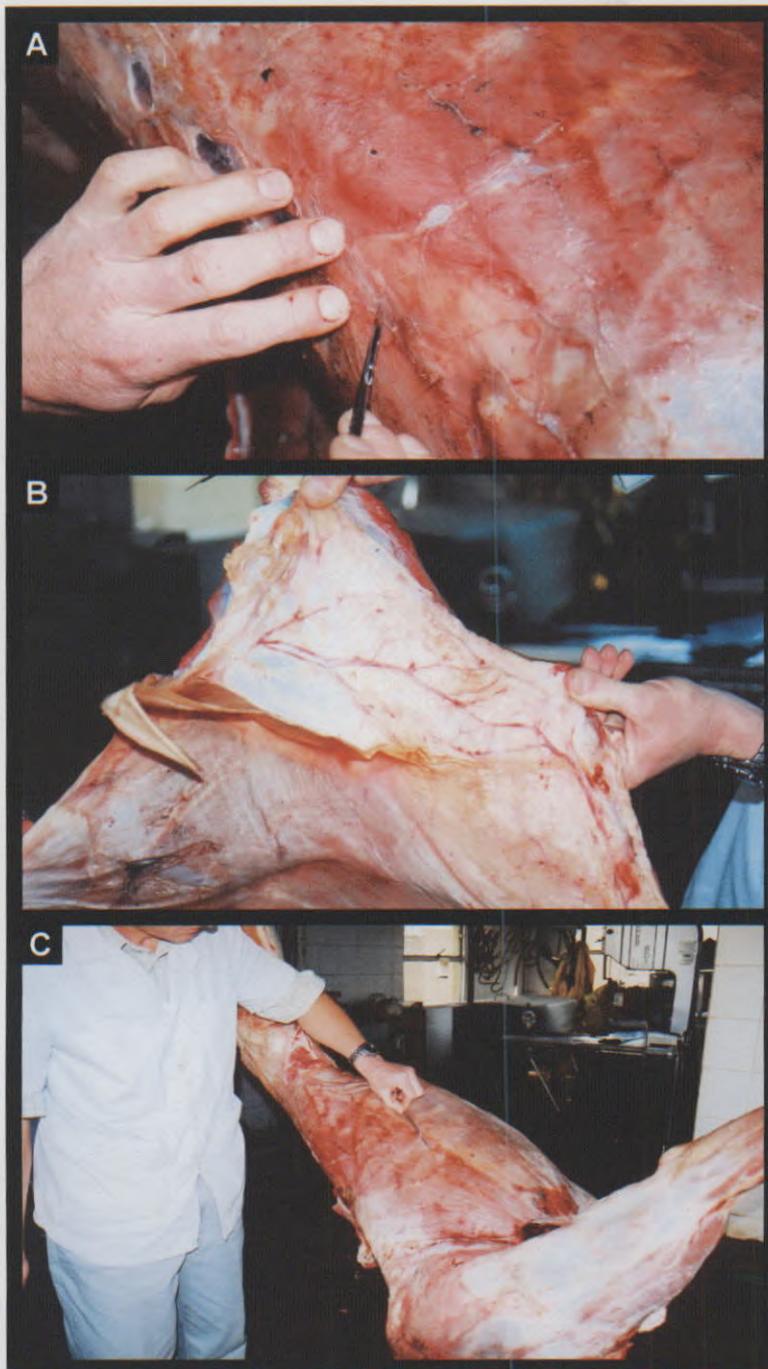


Figure 6.13 Dissection of the male African lion carcass. A, dorsal superficial blood vessels; B, lateral area to which the superficial vessels extend; C, larger vessels in the belly and loin region which, although primarily functioning in lymph drainage, assist with thermoregulation.

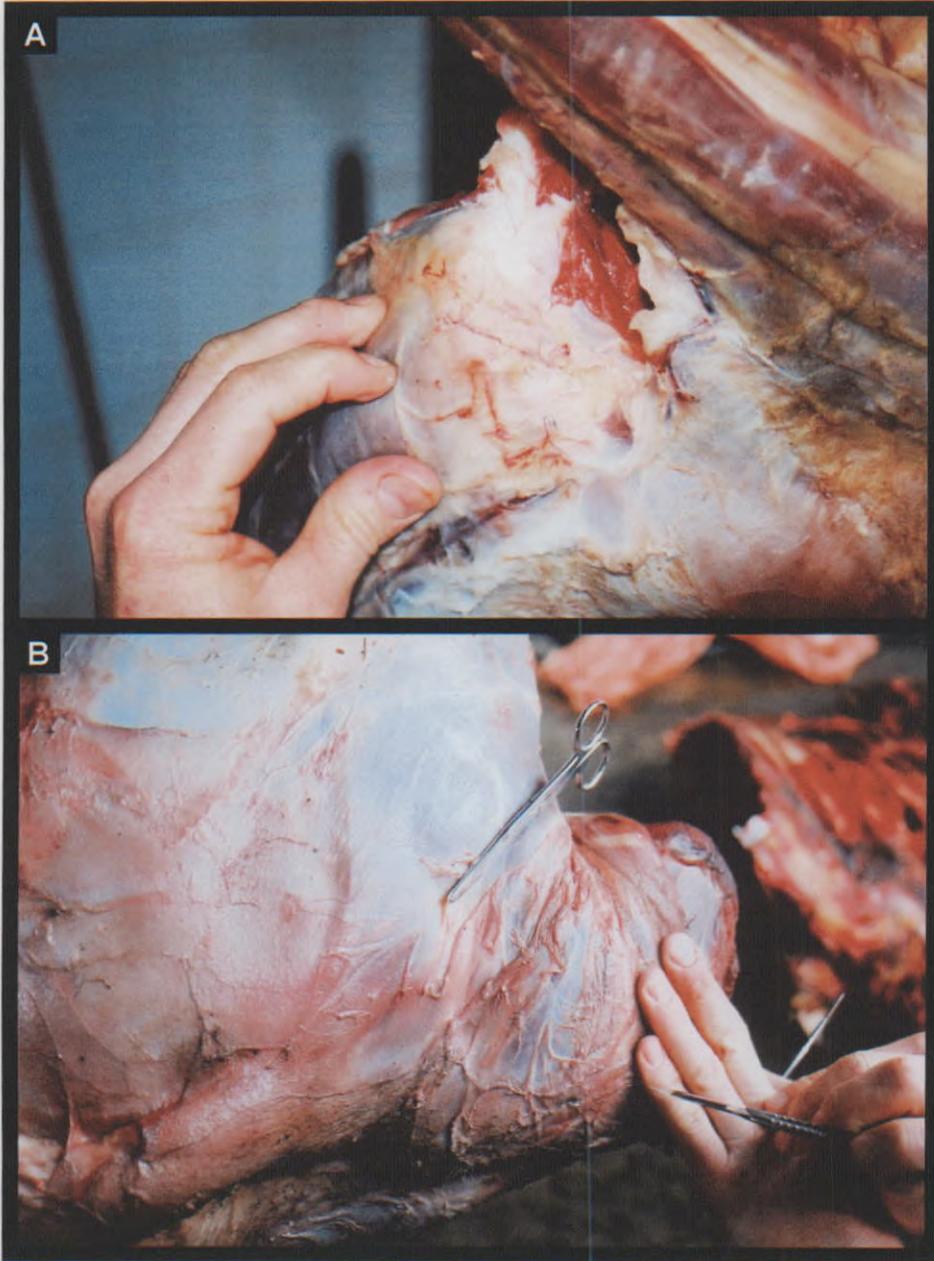


Figure 6.14 Examination of the tail and neck regions of the carcass. A, multitude of vessels in the parasacral and perineal area; B, muscular reinforcement of the neck with some superficial vessels in the area, as indicated.

is 10,5 mm (Gordon, 1972) and that of the desert mouse (*Psammomys obesus*) is 12,9 mm (Chew, 1965). Both of these animals have excellent water resorption ability and are adapted to dry conditions. By contrast, the relative medullary thickness of the male African lion's kidneys were 4,3 mm for the right kidney, and 4,2 mm for the left.

According to Ewer (1973), felids possess sweat glands in the interdigital area of the paws. No other sweat glands are present except those in the paws and these are situated in the skin (Dr. Ryan Niemand, pers. comm.). Sweat glands were found in only two of the slides prepared of the four paw pads of the lion (Fig. 6.15), in all likelihood as a result of the fact that the glands are found in the interdigital region in the skin and are not present in the deeper tissues. The sweat glands found were of the simple, coiled, tubular type eccrine glands (Krause & Cutts, 1981).

6.3 DISCUSSION

The development of endothermy, although advantageous in many respects, has resulted in an increased energy cost for the animal. According to Louw (1993), endotherms require a metabolic rate four to eight times greater per gram of tissue than that of most ectotherms. This in turn, requires an increase in respiratory ventilation rate and food requirements. Therefore, endothermy has conferred advantages only to certain taxa of animals within their specific niches. The African lion has clearly benefited from this development, being able to inhabit any open ecosystem where its prey base is present, surviving intense heat and high humidity as well as the obvious advantage of nocturnal activity. Desert-adapted animals such as the Cape oryx and ostrich have specific mechanisms by which they survive. These include the ability to expire air which is not saturated with water, efficient renal function and the ability to increase body temperature to 45 °C without any negative effects (Louw, *op. cit.*). Although many of these aspects must still be tested in the African lion, these mechanisms appear not to be present.

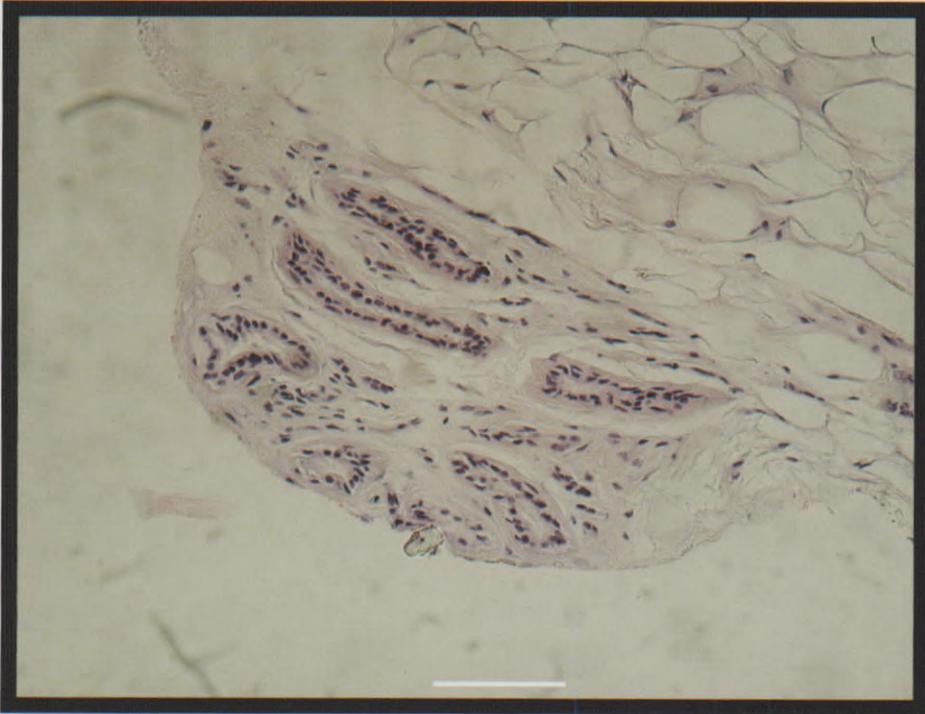


Figure 6.15 Eccrine sweat gland on the surface of the hind paw pad. Scale indicated is 140 μ .

6.3.1 Thermocron iButtons and body surface temperature

The results for the iButton readings during daytime and nighttime in both seasons indicate that during winter, the deviation from the median values are greater than those seen in summer. Further, the temperatures during winter were also consistently higher than those seen in summer, especially during the daytime. This may be explained by the extended periods of sunbathing and lack of “escape” behaviour observed during the winter study period. As discussed in Chapter 5, at least a third of the winter daylight hours were spent in the sun, while less than a fifth was spent in the sun during summer (see Fig. 5.7). The nighttime results indicate similarity for the neck iButton for both the older male and female. The tail iButton data for the older male demonstrated greater variation during winter and for the female, greater variation during summer. The larger deviation of the tail iButton in the older male during both seasons and the female during summer may be ascribed to the area being constantly exposed, and as a result of the high vascularisation of the parasacral and perineal regions, the temperature varied. The tail region is richly endowed with blood vessels, supplying the genital areas and specifically the scrotum in the males (see Fig. 6.14A). The increased variation in the female during the summer nights may be as result of increased activity during this time. Neck temperatures remained fairly constant during both seasons. As the results of the dissection demonstrated, few superficial vessels were found in this area and thick muscle layers were seen. The neck of the male African lion is protected by the thick mane which insulates and prevents both heat loss and gain. The females also have thicker and longer hair in the neck region and this may assist in buffering against temperature fluctuations. The absence of large blood vessels in this region is necessary to prevent serious injury during fights as well as hunts and the thick muscle layers are required for strength. In adult uncastrated domestic tom cats, the skin of the neck is roughly four times thicker than that of the rest of the body (Dr. Ryan Niemand, pers. comm.). The same may apply to the male African lion.

Neck temperatures during both study periods show a striking similarity. The maximum for the older male during both winter and summer was 39,5 °C and the minimum 31,5 °C. The maximum recorded for the female was 40,0 °C during winter and 39,5 °C during summer, while the minimum for winter was 32,0 °C and 31,5 °C for summer. The results for summer, being the same for both lions, indicate physiological thermoregulation control mechanisms especially in case of the female owing to the lack of insulation conferred by the mane. The results attained in the Kalahari show that the mane, or lack thereof, has no real implication for thermoregulation during both winter and summer seasons. African lion males in the Ngorongoro Crater were found to be darker during cold periods and had higher surface temperature and lower food intake during the hottest months of the year (West & Packer, 2002). Maximum mane growth and darkness in male African lions peaks between five and eight years (Skinner & Smithers, 1990) and as a result of the age of the males in the Kalahari, mane darkness increased from the winter trials to the subsequent summer trials. The surface temperature of the older male was not higher on average than that of the female and may be due to the semi-captive holding facility and the accompanying adaptations in behaviour. The coverage by the manes of both the males was typical of fully-maned adult male lions (Kays & Patterson, 2002), covering the throat, chest, upper neck and forehead with elbow tufts also present. The shoulder area was bare.

Increased insulation during winter seasons in furred animals is reported by Hull (1973) and Schmidt-Nielsen (1998). Figure 6.16 shows the difference in winter (A) and summer pelage (B) in the female. During winter, thicker fur is clearly present in the belly and loin region, the chest, elbow, shoulder and perineum. No investigation of undercoat against the skin was made, but the proliferation of fur during the colder season implies development of this. Personal observations of lion cubs during winter under zoo conditions have shown extensive undercoat on the skin and the presence thereof in adults can, therefore, be inferred. During summer periods fur may not necessarily be a

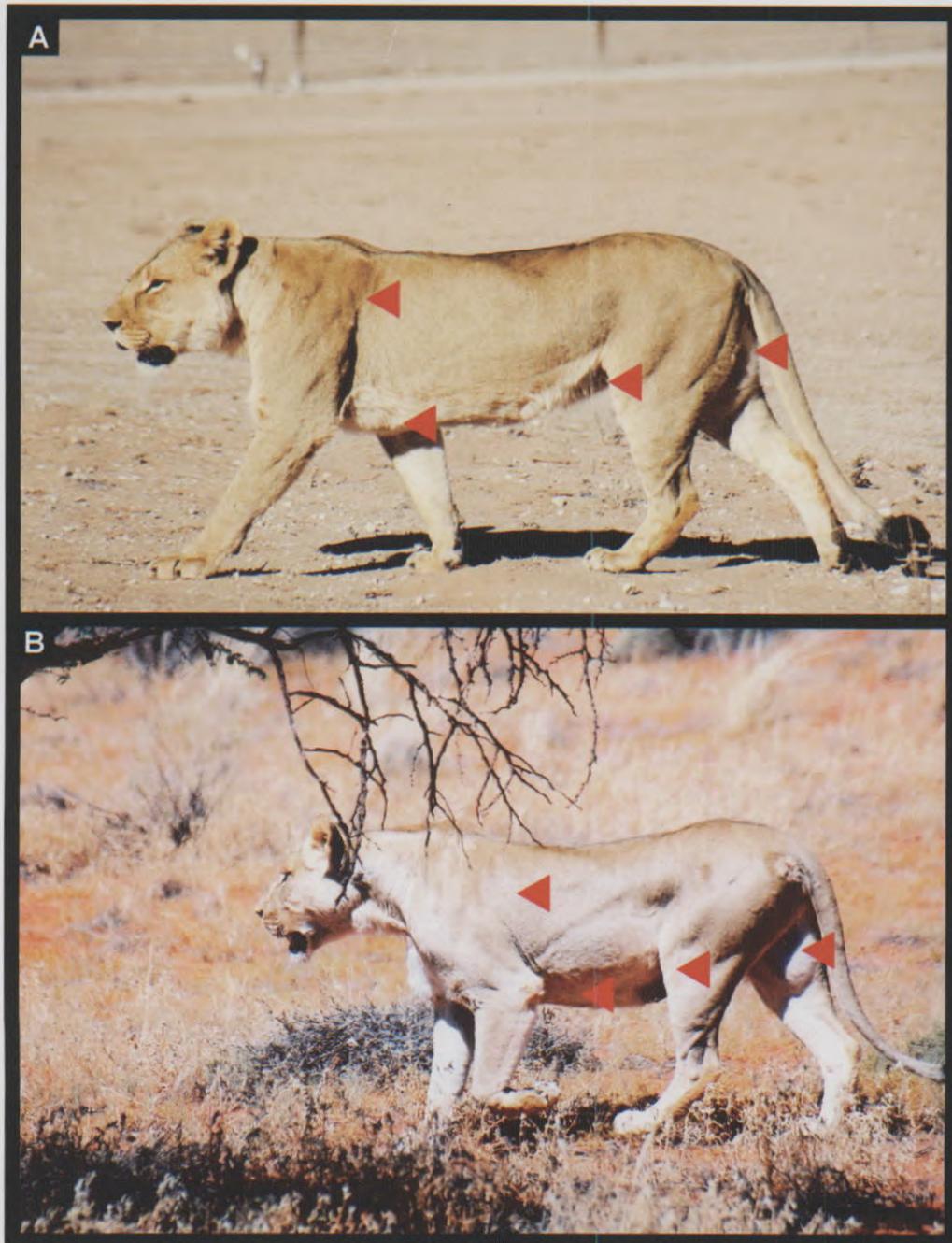


Figure 6.16 Seasonal difference in pelage in the lioness, as indicated. A, winter; B, summer.

burden for thermoregulation, but may, in fact, be an "equally important biothermal protection by reducing the rates at which heat is gained" (Adams, 1971). This is supported by the relative constancy of the neck temperatures of the older male during both the seasons. Figure 6.16 also demonstrates slightly darker fur during winter as compared to summer, but this may be as a result of the density of the fur. The pride members were not noticeably darker during the winter study period. Colour, although important in the absorption of short-wave radiation, has no effect on long-wave radiation. In deserts, large amounts of short-wave radiation are absorbed by the desert surface which then heats up and re-radiates this energy as long-wave radiation (Louw, 1993). For animals living close to the substrate, colour becomes less important. This applies to the African lion, spending more than 80% of their days resting. In the Kalahari, the temperature of the sand will influence thermoregulation since it impacts greatly on the temperature gradient between the environment and the animal.

The data provided by the iButtons showed great variation, specifically in the region of the loins. No definite patterns could be established. During the carcass dissection, a large number of superficial small diameter vessels were found along the dorsal and lateral areas (see Fig. 6.13B). The skin, although not examined, would have demonstrated the same number of vessels. Since this is the largest surface area, these vessels are very effective in dissipating heat when vasodilation occurs. The distal legs, ears and paws undergo the greatest change in temperature due to vasodilation. When ambient temperature is still higher than that of the surface, the animal is still in a gradient by which it gains heat and under these circumstances vasodilation does not increase heat loss rates, but decreases heat uptake rates (Adams, 1971). Control of body temperature and the subsequent thermal responses are controlled by the hypothalamus. The bulk of these receptors are situated in the spinal cord region (Adams, *op. cit.*; Cabanac, 1972). Thus, the presence of these vessels is necessary for thermal balance. No iButtons were implanted in this region and as a result, the data from the neck, tail and loin iButtons was not conclusive in terms of thermoregulation. Vasodilation in high ambient temperatures is a

common mechanism for dissipation of metabolic heat. The reverse, vasoconstriction, is in turn applied in cold to retain body heat (Bullard, 1966). Figure 6.17, taken from Eloff (2002), demonstrates vasodilation in the Kalahari lion well. The obvious swelling of veins and arteries under the skin was not observed in the pride researched in this specific study. The members were overweight and this may have caused the dilation not to be seen. The dilation and constriction of veins, arteries and other blood vessels is a very effective mechanism for the maintenance of heat balance. In cold conditions, this reduces surface temperature and, therefore, also the gradient between the body and the environment. This is referred to as “first line defence” by Adams (*op. cit.*) and leads to cooling in the legs and ears as extremity blood flow is reduced during acute whole body cold stress.

Other thermal defences in times of cold include shivering, involuntary muscle activity. According to Louw (1993), animals will go to great behavioural lengths to avoid employing it. It costs work and produces heat effectively, but as a result of increased blood flow, the retention of the heat generated is not very effective, being around 50% in humans. It is calorically expensive and “unequally effective for different size animals of the same species of carnivore” (Adams, 1971). Shivering, however, is more effective in generating heat than movement during cold, the latter allowing only for 20% storage of heat generated. As mentioned in Chapter 5, the lions did move during the winter nights, allowing for decreased heat loss. Shivering, however, was never observed, but in overweight animals and when not employed to a large degree, it is not always visible (Dr. Tony Booysen, pers. comm.). Piloerection, another well-known cold thermal defence, was in all likelihood also employed by the pride in the Kalahari, but as with shivering, it was never seen.

6.3.2 Loin exposure

Loin exposure in the African lion is a common sight. Seasoned travelers to game parks in Africa have all seen the sight of lions, “spread out like honey”

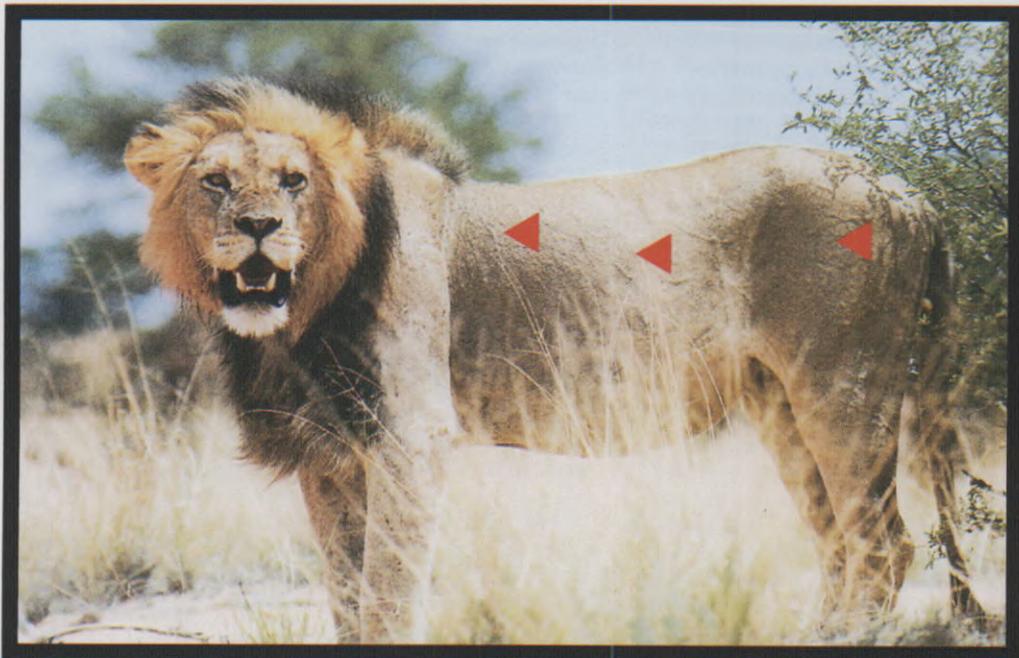


Figure 6.17 Male Kalahari lion demonstrating vasodilation, as indicated. (From Eloff, 2002).

(Unknown), with their hind legs in the air, loins and bellies exposed. Although the readings from the iButtons implanted into the loin region were not conclusive in that a definite pattern of temperature decrease was seen, indications are that loin exposure is used as a thermoregulatory behaviour. The loin and belly has a large surface area and has sparse insulation. Examination of the carcass showed large veins and arteries, especially around the belly region, which, although assisting with heat dissipation, mainly function in lymph drainage. No vessels were found near the position of the iButton and a large vein/artery was found some 15 cm posteriorly to the iButton position. This probably explains the lack of conclusive data from this iButton.

Occurrence of exposure with empty and full bellies during the four periods of the natural day show definite peaks during the midday and late afternoon period, demonstrating a positive relationship with increasing ambient temperature (see Figs 6.3 – 6.5). During the cooler times of the day, specifically early morning during winter and nighttime during both seasons, exposure was high when the belly was full. The highest peaks for early morning during winter, while the lions were sunbathing, are only for full bellies. During summer, ambient temperature climbed quickly in this time period and exposure was low or absent. The results across the board for both seasons at the different temperatures show that from 28 °C, the frequency of exposure increased up to 34 °C (see Fig. 6.6). Above this temperature, panting was employed and loins were not exposed. Metabolic heat increases when digestion takes place. Lions are obligate carnivores and consume large amounts of raw protein, skin and fats in one feeding. In experiments done with domestic dogs, “oxygen consumption rose after a meal to a maximum of about twice the resting rate, returning to a normal level after 24 to 72 hours” (Braithwaite & Llewellyn, 1982). The specific heat of combustion for fats is twice that of carbohydrates with protein in between these values. Further to this, experiments performed by Max Rubner (Braithwaite & Llewellyn, *op. cit.*) on the domestic dog, revealed that heat production was greater on days when meat was fed than when the diet was of fat or sugar. The uptake of nutrients on a protein diet is also very high, at 84%,

as compared to that of carbohydrates which averages 45% in herbivores (Brafield & Llewellyn, *op. cit.*).

During the winter and summer study periods, the minimum temperature for loin exposure on an empty belly differed by 0,1 °C. This indicates that below this temperature, metabolic heat on a full belly was such that loins could be comfortably exposed for heat dissipation and further supports the assertion that loin exposure is related to thermoregulation. Loin exposure during sunbathing may also have functioned in heat uptake after cold winter nights. Another contributing factor to this assertion is the percentage of perpendicular or parallel orientation towards the breeze during loin exposure. During the winter study period, the older male oriented his exposure 55% of the total, the female 46% and the younger male 52%. The subsequent summer trials showed orientation in the older male at 65%, the female at 51% and the younger male at 57%. The cubs oriented their loins 44% of the nine total exposures. The increase in oriented loins during the hotter summer trials shows that the African lion uses wind to cool the surface area exposed. It is not a form of evaporative cooling since no sweat glands are present in this area.

The close relation of the probability results for loin exposure in the two males also supports the assertion that loin exposure is related to thermoregulatory behaviour. The two males were similarly overweight and, therefore, have similar rotund shapes. If the surface area of the younger male was calculated, it would in all probability have been close to that of the older male. Therefore, their sex, shape and excess weight cause the probability that thermoregulatory mechanisms will be employed at similar times, indicated by the probability calculations. The results for the female, on the other hand, are very different from that of the two males.

Different grades of loin exposure were observed during both the study periods in the Kalahari. Figure 6.18 illustrates these. The lions often lay flat on

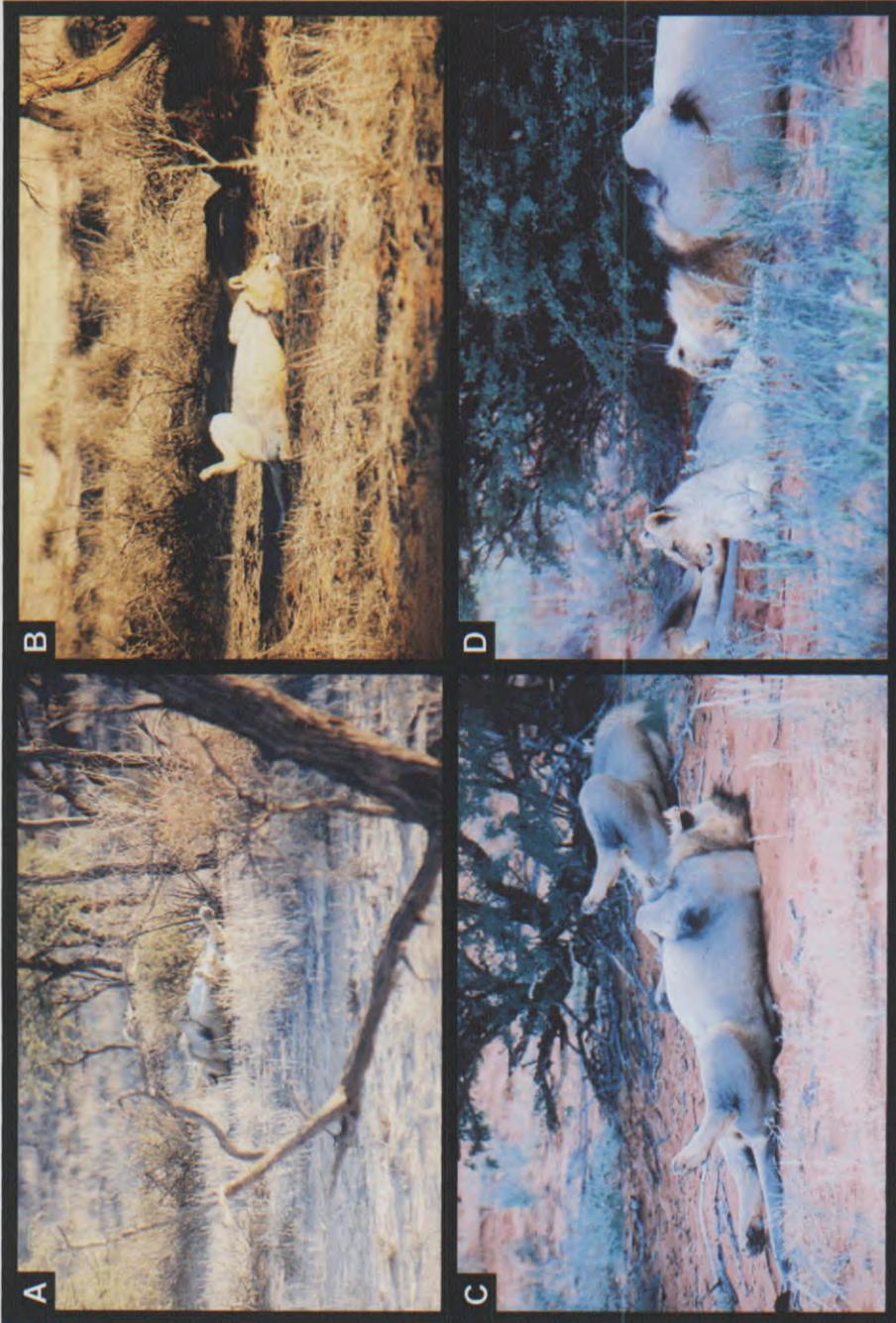


Figure 6.18 Different positions in loin exposure by the pride members in the Kalahari. A, full belly exposure on the back; B, one leg lifted while lying on the side; C, exposure while not lying fully on the back or the side; D, exposure of the neck, head thrown back entirely.

their backs (A) and when this position was assumed, they lay for long periods of time. When a leg was raised (B), often into an oncoming breeze, the exposure was for less than eight minutes. The posture shown in Figure 6.18C was also held for long periods. Figure 6.18D demonstrates only exposure of the neck. In this particular incident, the loins were not exposed whereas when the loins were exposed, the neck was included, the head thrown back, as can be seen in the photographs. Further, on four occasions, once during the winter trial and three times during the subsequent summer trial, the lions were observed to raise a leg and rest it either on another animal or against a tree (Fig. 6.19). This was always observed during late afternoon when temperatures were high and mostly when a breeze was present. The increase of surface area and corresponding changes in posture are of the most obvious behavioural mechanisms used for thermoregulation.

Other explanations for loin exposure can be mentioned. Domestic cats, when ill, do not lie on their backs (Prof. O.B. Kok, pers. comm.). The exposure of loins in the African lion may simply be as a result of confidence and a relaxed attitude. Looking at the winter trial data, the younger male, under duress from the older male, exposed his loins a total of 15 times during daytime as opposed to the 25 times for the older male. During the subsequent summer trials, when the younger male turned adult and began to defend himself from dominance, he exposed his loins a total of 36 times versus the 30 times of the older male. During nights, exposure of loins may indicate high levels of confidence since the most vulnerable area is exposed in the dark. The older male did so 11 times during winter and the younger male only four times. The summer results show seven nighttime exposures for the older male and two for the younger, again supporting the assertion of total confidence. Another factor which may be taken into consideration is the large amounts consumed during feeding. Lying on the back is simply more comfortable than lying on the side or the belly. The range of temperatures at which loins were exposed (Fig. 6.7) supports the above. The exposure of the loins may also assist in the cooling of the scrotum in the males, necessary for fecundity.

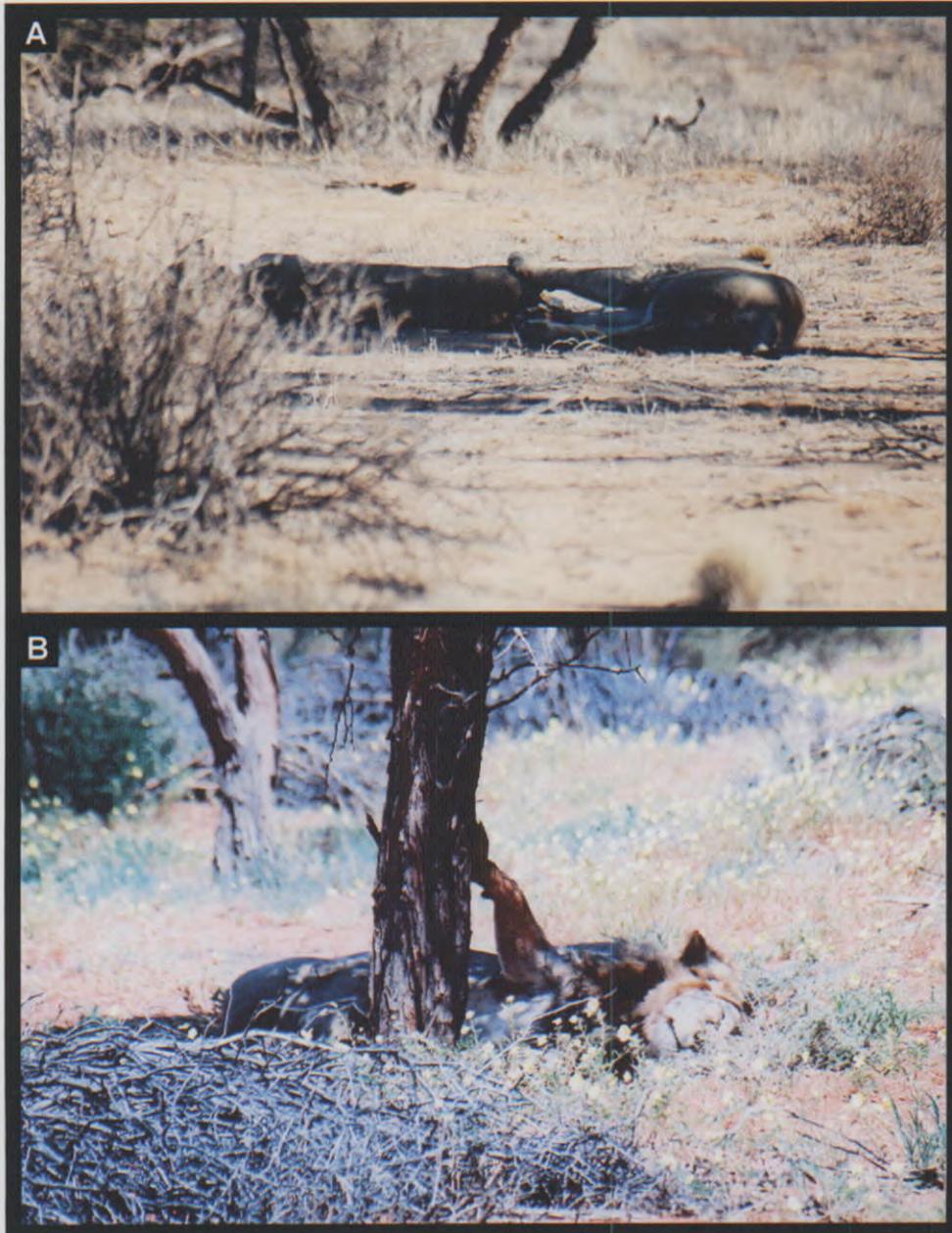


Figure 6.19 Enlargement of the surface area, a typical response to heat. A, resting the foreleg on another pride member; B, the placement of the leg against a tree.

6.3.3 Panting

When heat load can no longer be decreased by behavioural and circulatory mechanisms, heat balance can only be maintained by evaporative cooling. Evaporation is the only element in the heat balance equation which always represents heat loss. There are two principal pathways for evaporative cooling: panting and sweating. In high humidity coupled with high ambient temperature, the effectiveness of evaporation is reduced. Dry air increases evaporation (Website 4).

Animals that do not possess a large number of sweat glands generally employ panting as a means of evaporative cooling. The family Felidae and, therefore, the African lion, fall into this group as they only possess sweat glands in the paws (Ewer, 1973). Panting is the rapid oscillation of the floor of mouth and the upper part of the throat, known as gular flutter. (Schmidt-Nielsen, 1998). The breathing is fast and shallow and concentrated in the respiratory tract reducing the muscular work and, consequently, the heat produced. The threat of alkalosis is minimised since the tidal volume of the lungs is not filled - only the dead space is utilised and, therefore, no hyperventilation takes place. The pride in the Kalahari, when observed to pant, lay upright on their bellies, flat on the ground with the head leaning slightly forward. The ears were always drawn back, the eyes slightly closed and the face extended (Fig. 6.20A & B). Salivation increases somewhat with panting. This is necessary since evaporative cooling requires water. Figure 6.20B actually shows a small white speck of saliva on the lower lip of the younger male. This was always seen when the animals panted.

There is a striking positive relationship between the incidence of panting and increasing ambient temperature (see Figs 6.8 to 6.10). No panting was observed during nighttimes. All the incidences of panting observed during winter were after periods of activity and on empty stomachs when on so-called "hungry days" the sound of a vehicle caused bursts of running. During summer,



Figure 6.20 Panting posture exhibited by the younger male African lion in the Kalahari. A, head is pushed forward, eyes closed and ears drawn back; B, open mouth to allow for rapid oscillation for airflow across the mucous membranes. Note the speck of saliva on the lower lip.

however, sustained periods of panting occurred, especially during midday and late afternoon and specifically on full bellies. The usual pattern observed was periods of lying with the head down alternating with periods of lying upright, panting. When the lions were well-fed, panting always occurred at lower temperatures, beginning at approximately 28 °C.

The carotid rete is well-developed in felids (Mitchell *et al.*, 2001). According to Schmidt-Nielsen (1998) the rete is present only in animals that pant, but Mitchell *et al. (op. cit.)* state that research done with domestic goats (*Capra hircus*) suggests that panting is not required for selective brain cooling as normal breathing is adequate. Traditionally, the carotid rete was believed to cool the brain via the nasal cavities and mucous membranes during exertional hyperthermia. Mitchell *et al. (op. cit.)* however, report that in rete ungulates such as Cape oryx and springbok, selective brain cooling is employed under moderate heat load in order to switch body heat loss from evaporative to non-evaporative means. The possession of the carotid rete by felids in general and lions in particular is succinctly explained by Louw (1993) who wrote: "It would seem that if an animal possesses a fur coat and is obliged to either sprint from a predator or after prey, it requires a carotid rete to selectively cool the brain. Alternatively, profuse sweating must be employed." Owing to the semi-captive facility, the pride was never observed to exert themselves on a level that can be related to free-range lions. They did, however, pant during summer while at rest, but during the previous winter trials panting only took place after exertion. Further research on the employment of selective brain cooling and activation of the rete is required for conclusive results in the case of the African lion, but that it cools arterial blood flowing to the brain via veins from the nasal cavity through either passive breathing or panting is certain.

Average temperature when panting was employed during summer was at 34 °C and above. Taking into account the results of the sunbathing (see Chapter 5) where the pride moved into the shade at an average temperature of 25 °C and the inception of panting at 34 °C, it appears as though, in the case of the pride

in the Kalahari, the thermoneutral zone can be set between 25 and 33 °C, the same as for humans (Louw, 1993). Motivation for this is the fact that the thermoneutral zone is the temperature range where the animal can rely on slight cardiovascular changes and behavioural adjustments to maintain thermal balance. Outside of this zone, physiological adaptations must be employed to either conserve or dissipate body heat. If sunbathing is required under 25 °C and panting is initiated over 33 °C, the thermoneutral zone may very well lie in this region. Laboratory tests that measure metabolic rates and oxygen consumption are not practical in the case of the African lion and as a result, the thermoneutral zone remains to be tested.

6.3.4 Carcass dissection

Discussion of the surface area of the carcass has been included in the sections on Thermocron iButtons and body surface temperature as well as in loin exposure. In this section, the discussion focuses on the presence of the sweat glands and the kidneys.

Lions do not require drinking water as a constant supply, drinking when water is available and more often than not, after feeding (Eloff, 1973). They are able to meet much of their water requirements from metabolic sources and further to that, they do not utilise water for the bulk of their thermoregulatory processes. They sweat only from the interdigital area of the paws and utilise evaporative cooling only with panting. The kidney of one five-year-old male was examined and according to the relative medullary thickness, renal function is not specifically designed to concentrate urine and thus, conserve water. Only one specimen was obtained and this requires further examination. Figure 6.21 illustrates the frequency of drinking and urination for the pride during the winter and summer study periods. The urination is indicated for normal urination, not scent marking (see Chapter 4). As can be seen in the figure, the frequency of drinking increased from winter to summer, markedly in the female and in her case also, the frequency of urination decreased in relation to the occurrence of

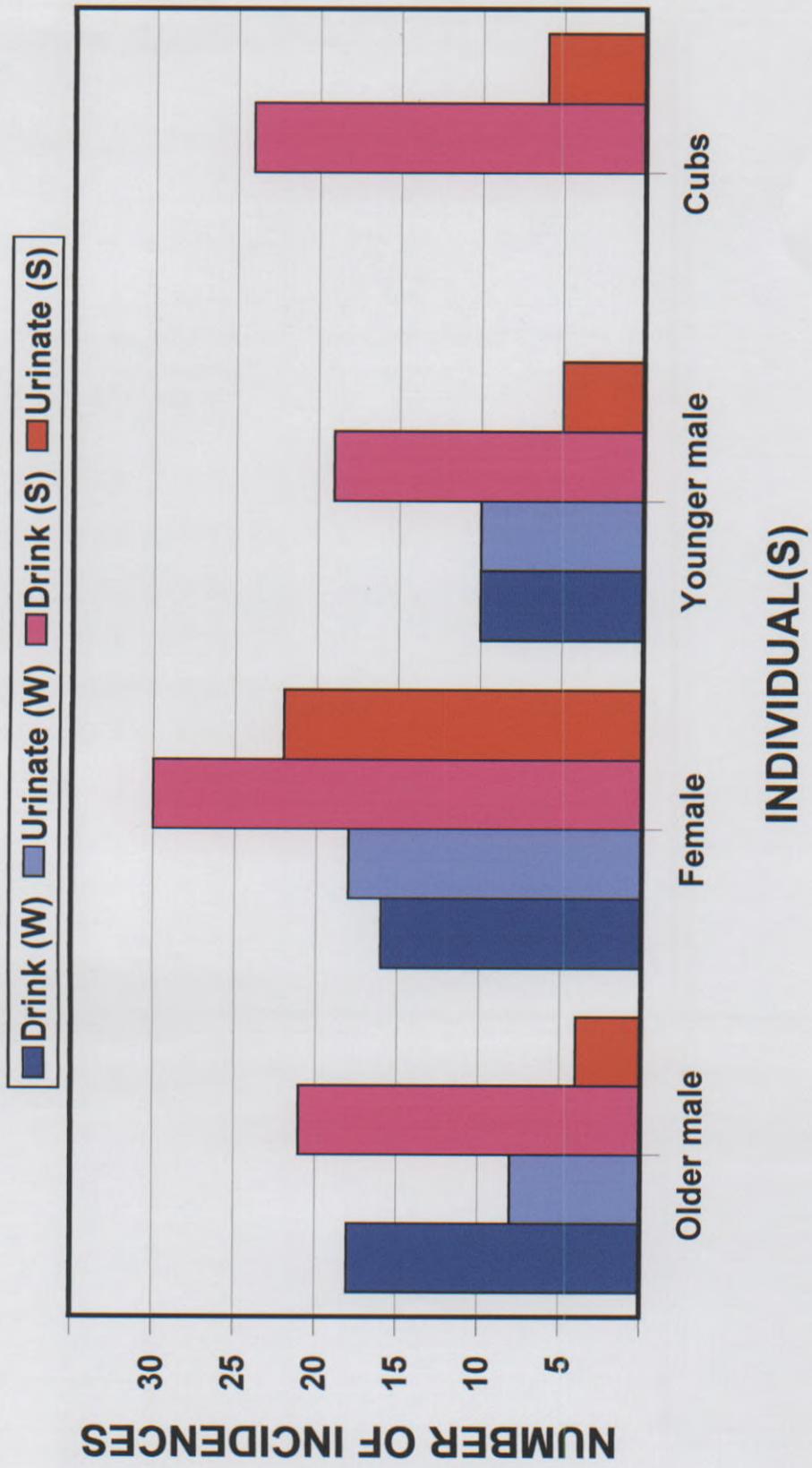


Figure 6.21 Seasonal variation in drinking and urination in the pride of African lions in the Kalahari.

drinking between the two seasons. The results of urination for the two males are skewed by the incessant scent marking during the summer season, supported by the winter data for the younger male who turned adult during the subsequent summer trials. The cubs also showed a marked lower rate of urination versus the incidence of drinking. The older male demonstrated the lowest increase in drinking between the two seasons and taking into account the high rate of scent marking, the older male demonstrated a substantially low water requirement. The overall increase in drinking for the summer season indicates an increased water usage as a result of panting and sweating for maintenance of thermal balance.

Desert-adapted animals have a reduced sweating ability as a result of water stress in these ecosystems (Whitford, 2002). A large number of felids have invaded desert systems including the African wild cat, leopard, caracal (*Caracal caracal*), serval (*Felis serval*) and the small spotted cat (*Felis negrispis*) (Skinner & Smithers, 1990). Whether the sweating ability via the paws only has developed as a result of this is not known, but is plausible. The eccrine sweat glands in the interdigital area of the paws cannot be highly effective since this is not an exposed area. This may explain why lions lie with the forepaws upturned when positioned upright and when on the left side, for example, only the right forepaw is turned down, and vice versa. The toes are also often extended. When panting was employed, however, the forepaws were mostly turned down, but if raised, only one paw was upturned (see Fig. 6.20B), presumably as a result of the work done by the respiratory tract for the purposes of balance of the body. The pride in the Kalahari was seen to move their forequarters forwards and backwards while panting.

During the summer trials, sand was observed to adhere to the bodies (Fig. 6.22), paws and heels of the pride members, something not seen during the winter trials. Kalahari sand is notoriously static and clings to clothing and skin, something seasoned visitors to the Kalahari will attest to. However, owing to the

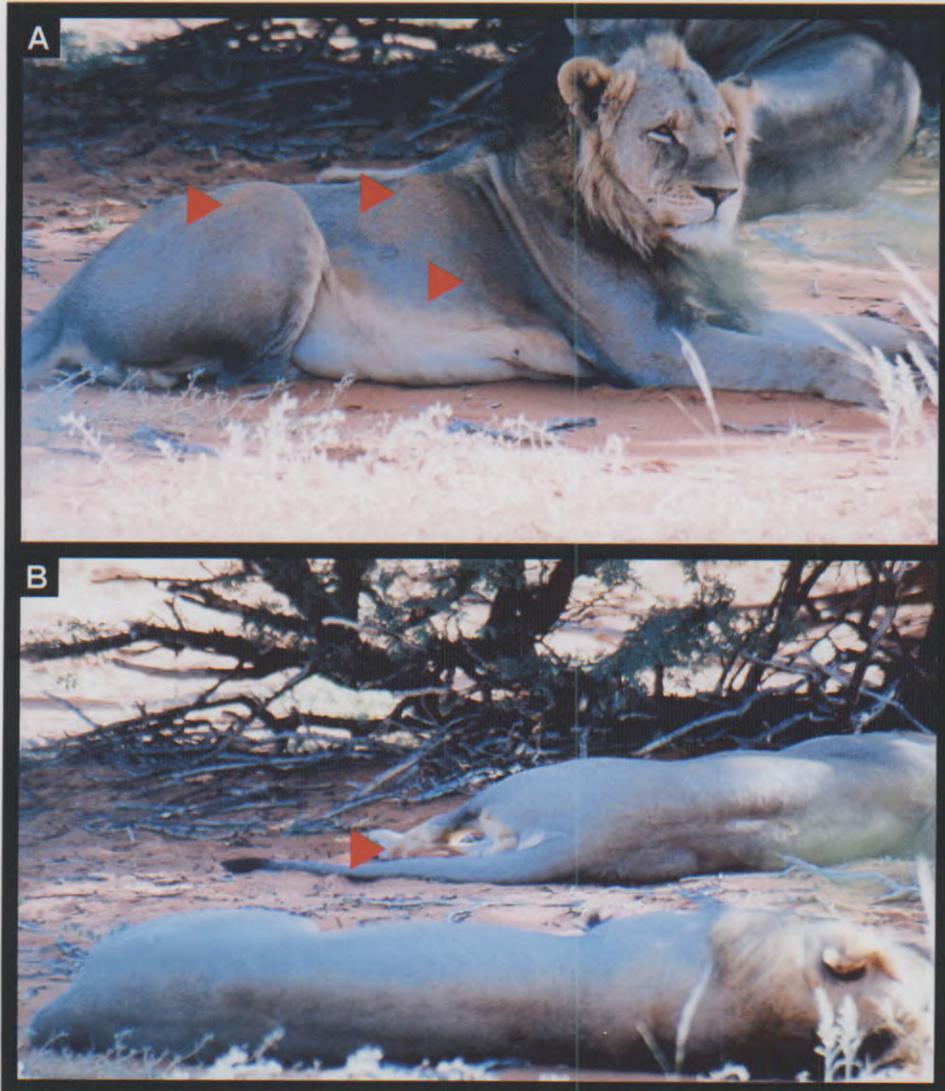


Figure 6.22 Kalahari sand adhering to the bodies of the lions during the summer study period in the Kalahari. A, sand on the body on the younger male; B, sand on the hind leg of the older male, as indicated.

fact that this was not observed during the winter study period, temperature must be assumed to play a role. The African lion does not sweat on its body. The only plausible explanation for this phenomenon is the sand temperature. During the summer trials, the sand was almost always hotter, even in the shade, than the surface temperature of the animals. Heat travels from a high to a low and when temperature drops, condensation occurs and this may have resulted in the sand sticking to the bodies of the lions. It was always observed after long periods of rest during the late afternoon and often the lions employed grooming to remove it, especially from the face. This was observed on a few occasions when the female groomed the cubs to remove sand from their faces and necks.

As a result of its social structure, the African lion's prey base is medium and large-sized ungulates. Exploitation of this prey base requires survival in habitats where temperatures can reach extremes. The African lion has successfully invaded all the open habitats where its prey occurs and has managed to adapt to the varying climates of these habitats. Due to its large size and endothermy, it demonstrates thermal inertia to a sizeable degree and uses behaviour to manage thermal balance, complemented by physiological mechanisms. Although further research is required, the African lion in the Kalahari does not seem to possess any specific desert adaptations to survive extreme environments. The obvious conclusion then must be that behavioural adaptations are the principle means by which this African carnivore has managed to invade the Kalahari Desert.





7 PARASITE SURVEY

7.1 INTRODUCTION

There is a paucity of published data on the parasites carried by Kalahari lions. Owing to extensive field observations and the opportunity to collect faeces, a parasite survey on the small pride of lions was conducted. Scat samples were collected opportunistically from all the individuals in the pride. Parasites are known to influence fitness and more recently, have also been shown to influence behaviour (Zimmer, 2000). Further, as social animals, the taxa carried by the different individuals in the pride are influenced by their association, the general health of the individual, the size of the parasite suprapopulation and ecological factors.

7.2 RESULTS

7.2.1 *Ectoparasites*

During both the summer and winter immobilisations, one species of ectoparasite fly, *Hippobosca longipennis*, was found on the focal animals. In both seasons, the number of flies recovered per lion ranged from zero to four, with a mean of two. During the winter immobilisation, the older male had the highest infestation, namely four, and during summer, the female, with three.

No tampsans were collected throughout the study period.

7.2.2 *Endoparasites*

Nematode species recovered in the scat were *Ancylostoma braziliense*, *Gnathostoma spinigerum* and *Uncinaria stenocephala*. Two coccidians were present, *Toxoplasma gondii* and *Isospora felis* (Fig. 7.1). Table 7.1 indicates the parasite species found during both seasons. The cubs were born during November 2003 and are, therefore, not included in the winter trials.

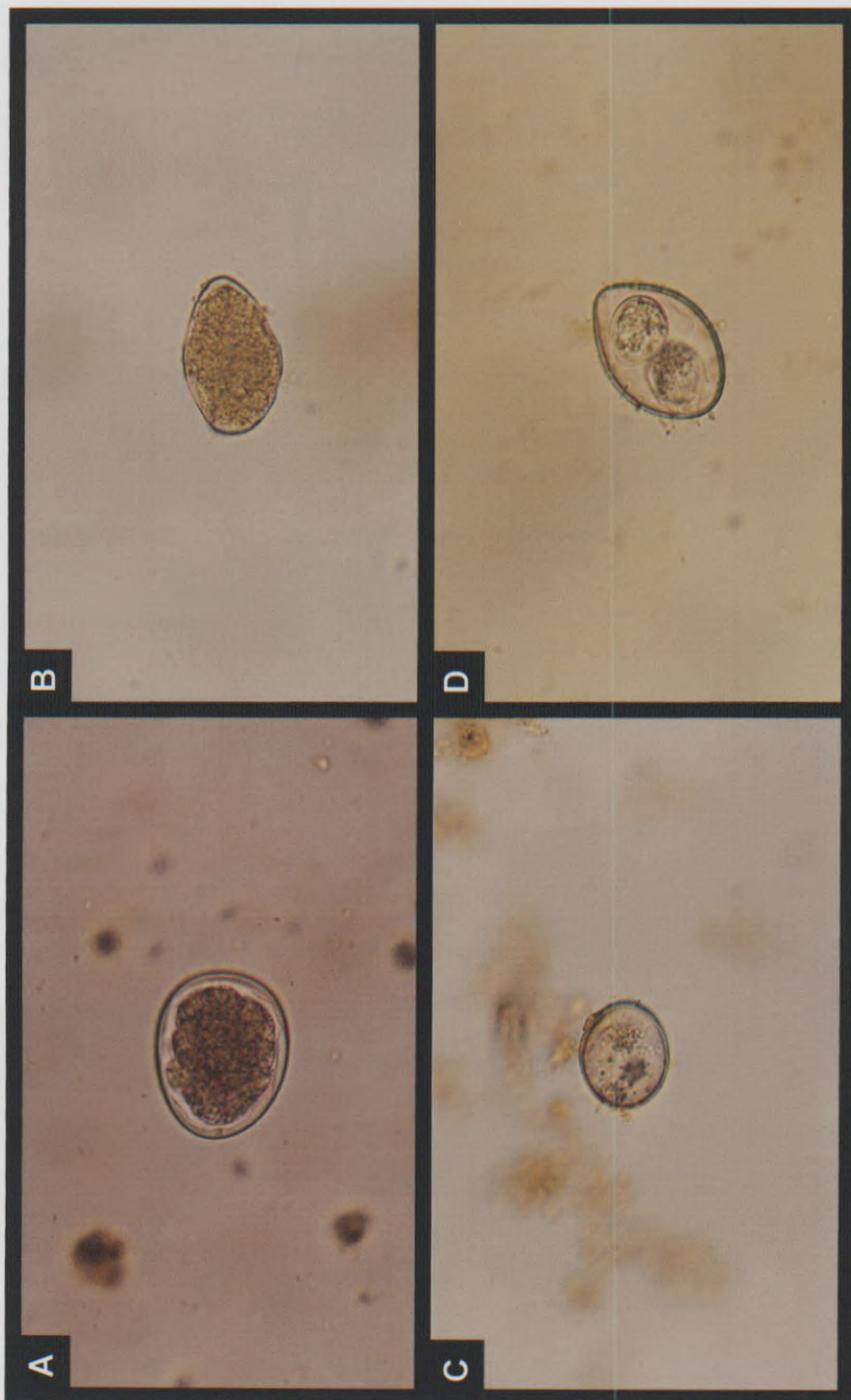


Figure 7.1 Eggs of endoparasite species found in the scat of the pride of African lions in the Kalahari. A, *Ancylostoma braziliense*; B, *Gnathostoma spinigerum*; C, *Toxoplasma gondii*; D, *Isospora felis*.

Table 7.1 Endoparasite suprapopulation in three adult African lions during the winter study period and three adult and two cub African lions during the summer study period.

	<i>A. braziliense</i>	<i>G. spinigerum</i>	<i>U. stenocephala</i>	<i>T. gondii</i>	<i>I. felis</i>
Winter					
Older male	✓	x	x	✓	✓
Female	✓	✓	x	✓	✓
Younger male	✓	x	✓	x	✓
Summer					
Older male	✓	x	x	✓	x
Female	✓	✓	x	✓	✓
Younger male	✓	x	x	✓	x
Male cub	✓	✓	x	✓	x
Female cub	✓	x	x	✓	✓

Mean intensity of eggs per gram (EPG) of faeces for all the endoparasites were reduced during the summer trial except for the hookworm *A. braziliense* which demonstrated an increase. The results of the EPG counts are presented in Table 7.2.

Nematodes (Fig. 7.2) were found in the scat after the summer trial. See Table 7.3 for the results. Worms were present in each flotation performed. A total of six samples, three from each season, were negative for any eggs or worms when EPG counts were done with the McMaster slide. All of these were collected from the adult lions.

7.3 DISCUSSION

7.3.1 Ectoparasites

Parasite species recovered from both the ecto- and endoparasite analyses are known to parasitise the African lion. There are few published reports on the parasites of free-roaming lions and the bulk of the research was done in East Africa with the focus on endoparasites. Information on the ectoparasites of wild lions is limited for obvious reasons. Regular collection of this information is not only very expensive but also impractical. Research underway in Botswana under the auspices of Lion Aid in Kent, United Kingdom, has included endoparasites, but species identification is still underway (Website 2). Much of the information on the variety of ecto- and endoparasites of lions has been sourced from zoos and other captive institutions.

Lions are known to be hosts to a variety of ectoparasites including ticks, fleas and mites (Boomker *et al.*, 1997). The authors list seven genera of ticks, two of fleas and one of the mites. Publications such Heyman (2001), and various issues of wildlife magazines have ticks and dog flies clearly visible on photographs of lions. The dipteran, *Hippobosca longipennis*, is a known

Table 7.2 Mean and maximum intensity EPG counts of endoparasites in the pride of African lions during both the winter and summer study periods.

	Sample size	Infected hosts	Infected samples	Mean intensity (EPG)	Maximum intensity (EPG)
Winter					
<i>A. braziliense</i>	11	3	4	133	200
<i>G. spinigerum</i>	11	1	1	666	666
<i>T. gondii</i>	11	2	4	233	400
<i>I. felis</i>	11	3	7	3 320	14 866
Summer					
<i>A. braziliense</i>	17	3	4	173	600
<i>G. spinigerum</i>	17	1	1	66	66
<i>T. gondii</i>	17	4	7	173	200
<i>I. felis</i>	17	1	1	66	66



Figure 7.2 Unidentified intact nematode found in the scat of the African lion pride in the Kalahari. Scale indicated is 20 μ .

Table 7.3 Number of intact and fragmented nematodes found in African lion scat samples during the summer study period.

Individual	Samples	Intact worms	Worm fragments
Older male	1	1	0
Female	2	22	3
Younger male	3	14	3
Male cub	2	10	0
Female cub	1	3	0

ectoparasite of carnivores (Haeselbarth *et al.*, 1966) and since they are the only effective breeding host (Website 2), they are semi-permanently associated with carnivores. It is a winged fly and is, therefore, not reliant on the host for transport. They are avid blood suckers and have a high irritation value, exacerbated by high levels of infestation (Website 2). The relatively low numbers of *H. longipennis* collected from the focal animals may be as a result of their motility. Once the lions were immobilised they were handled and this surface irritation may have caused some of the flies to move away.

The absence of *Ornithodoros savignyi* was not expected. Theiler (1962) reports that the tampan is present and even abundant in the Kalahari in southern Namibia. "It is ubiquitous and exceedingly plentiful everywhere to the south of Rehoboth," the author writes. She adds that it is not found in the shadeless clay soils of the pans and prefers the camelthorn, grey camelthorn and shepherd's tree for shelter, but will use any dense shade that is also utilised by its hosts. It responds to CO₂ (Eugene Marais, pers. comm.) as well as vibrations in the soil, and as a result, it parasitises larger mammals only. It is found at a depth of up to 31 cm in the ground and laboratory experiments have shown that it avoids ground temperature exceeding 26 °C. Theiler (*op. cit.*) states that in adverse conditions, the starvation-survival period for *O. savignyi* can be presumed to be six months to one or two years for nymphs, and two to eight years or more for adults.

Excessive moisture levels in the sand, veld fires and natural enemies such as game birds, including the sandgrouse (*Pterocles* spp.), will act to reduce the occurrence and prevalence of the sand tampan. According to Theiler (1962), laboratory experiments have shown that rats prey on the nymphs although this has not yet been demonstrated in the field.

Intu Afrika Kalahari Game Reserve received copious rains during the season of 1999/2000. Much of the reserve was in flood. The pans and dunes alike were saturated with water and this may have reduced tampan density. Strict control is

exercised over the entire area and, therefore, the influence of veld fires is diminished. The double-banded (*Pterocles bicinctus*) and Burchell's sandgrouse (*P. burchelli*) are widespread and this may have impacted on the incidence of sand tampans in the sampling area. Finally, the large number of trees in the reserve (Fig. 2.5A), including the camelthorn, grey camelthorn and shepherd's tree, could result in a more even distribution and hence, lower numbers of sand tampans in the shaded areas. The relative low number of viable hosts in the form of game as well as the lions in the enclosure combined with the high density of trees may also have had an effect on the numbers of tampans in the area. For a period of four years only three lions were held in the enclosure and although small mammals, including springbok, also occurred there, this may have not been a viable source of hosts to support the tampan population. The results indicate that the selection of shade by the pride is not affected by the occurrence of tampans.

7.3.2 Endoparasites

Boomker *et al.* (1997) list *Ancylostoma* as well as *Gnathostomum* species among the helminth parasites of lions. Among the coccidians, both *Toxoplasma* and *Isospora* species are named by the same authors as found in lions.

The egg counts during both the winter and summer trials indicate a low rate of infection. Research in the Serengeti and Ngorongoro Crater (Müller-Graf, 1995) indicates that median values per gram faeces may reach up to 5 700 for coelozoic helminths with no apparent ill-effects to the host. With the exception of *Ancylostoma braziliense*, all egg counts decreased from the winter to the summer trials (Table 7.2). The scope of the increase is reduced by the increase in sample size since two cubs were included in the summer trials. The results, however, may be attributable to the high egg production of *A. braziliense* which permits a higher fecundity (Hinz, 1988). Schmidt & Roberts (1985) state that some 25 000 to 30 000 eggs may be produced per day by a female in the gastrointestinal tract. In respect of the histozoic coccidians and specifically *Isospora felis*, egg count subsides after initial infection which explains the

substantial decrease in egg count from winter to summer. Cysts persist in the tissue, egg production all but ceases and immunity responses after the first infection is normally permanent (Schmidt & Roberts, *op. cit.*). The high egg count for *I. felis* during the winter trials indicate a new infection for the female. Further to the former, the pride was de-wormed one year prior to the inception of the fieldwork and the animals are fed, reducing exposure to various endoparasites. The specific habitat experienced drought conditions for two years before the research and this would have assisted in reduction of viable parasite eggs in the environment. According to Stear *et al.* (1998), high densities of endoparasites occur when artificially high densities of hosts are held together. It is further well-known that in captive conditions, sanitation is essential to reduce infestation. These variables are not at play in the study area and, therefore, have no bearing on the results.

Results differed during the flotation and the McMaster slide investigations. Two species of parasite, *Ancylostoma braziliense* and *Toxoplasma gondii*, were present in both the males. Flotation results for the older male indicated *A. braziliense* and the McMaster slide results showed only the presence of *T. gondii*. The younger male's flotation results indicated only *T. gondii* while the McMaster slide demonstrated the presence of *A. braziliense*. The female had the highest egg counts during both the flotation as well as the McMaster slide counts. Schmidt & Roberts (1985) calls this phenomenon overdispersion and states that parasite infrapopulations are not randomly dispersed, but that a minority of the hosts will harbour a majority of the parasites. Flotation showed that the female harbours *Isospora felis* but the eggs were not present in the McMaster slide. Results for the female cub's flotation included *A. braziliense* and *I. felis*, whereas the former and *T. gondii* were present in the McMaster slide. In the case of the male cub, flotation indicated the presence of *A. braziliense*, *T. gondii* and *Gnathostomum spinigerum*, while the McMaster slide showed only *T. gondii*. The female cub had a higher egg count than the male cub. *Uncinaria stenocephala* was not present during the summer trials.

A relative large number of nematodes were found in the scat samples (Table 7.3). In the case of both the hookworms present, the eggs, after voiding, require warm and moist conditions to hatch into J1 larvae (Schmidt & Roberts, 1985). The majority of scat collected was in the form of diarrhoea (Fig. 7.3). The lions were fed sporadically during the summer trials and engorged themselves when large carcasses were provided. The scat was left for a day or two prior to being collected to permit drying. During this time, nematode eggs could have hatched. In the alternative, nematode eggs also hatch in warm, moist soil and as a result of the rains, the nematodes found in the scat may also have been present in the environment (Schmidt & Roberts, *op. cit.*).

All of the endoparasites found are transmitted either via the environment or by transplacental transmission. According to Noble & Noble (1988) hookworm congenital transmission has been demonstrated in domestic dogs, but not in domestic cats. However, this has not been tested in lions and remains to be proved or disproved. The male cub is host to *Gnathostomum spinigerum* and the female to *Isospora felis*, both endoparasites present in only the female. Transmission of *G. spinigerum* to the male cub may be congenital or could have occurred due to the large amount of time spent with his mother with allogrooming quite common. The infection of the female cub with *I. felis* was most likely via the placenta.

Curio (1988) reported that egg counts in faecal matter correlate positively with dominance rank in the yellow baboon (*Papio cynocephalus*). The data collected on the Kalahari lion does not support this. Although feeding of the larger male should support greater exposure to parasites, especially *Toxoplasma gondii* which has the herbivore as an intermediate host, behaviour may play a more prominent role in terms of the parasite burden. The larger male spent most of his time alone and did not allogroom often and as a result, his exposure to endoparasites from other members of the pride was reduced.

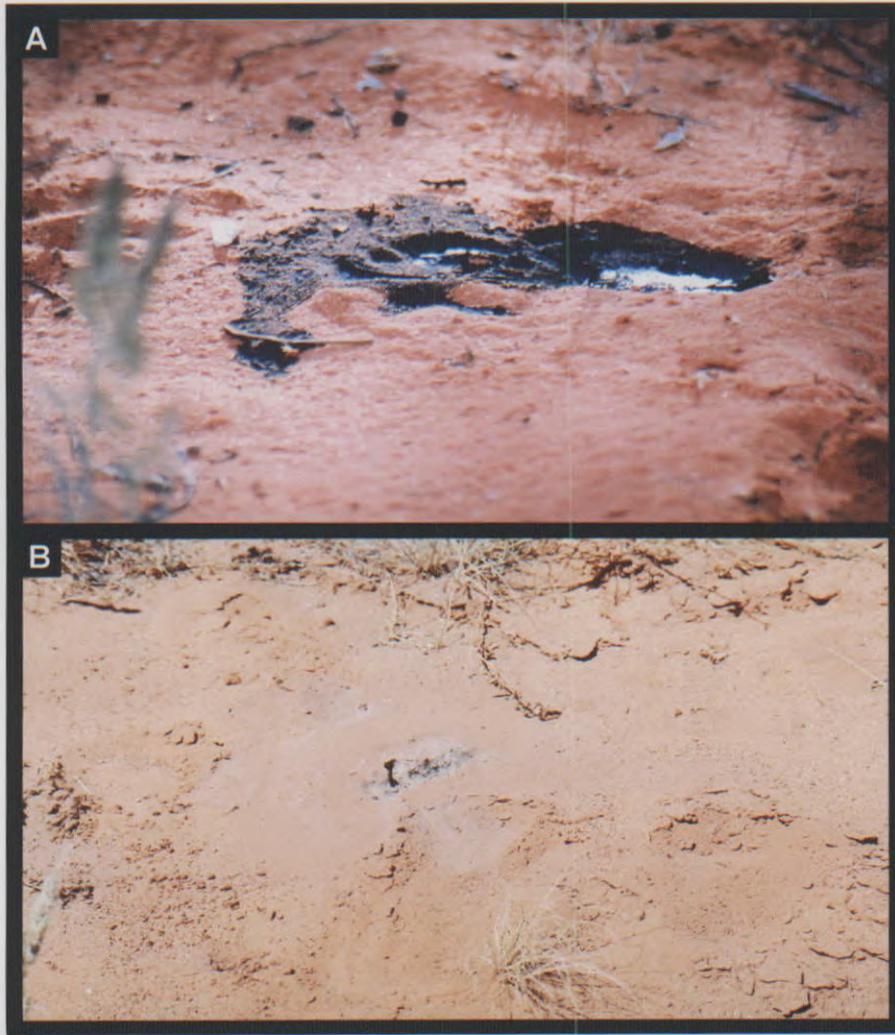


Figure 7.3 Scat voided during the summer trials was mostly in the form of diarrhoea. A, dark-coloured liquid; B, colourless diarrhoea. Note the small cavity in the soil filled with hair.

Results for the younger male indicate the lowest egg counts and contradict published data. The circumstances in which the lions are held are unnatural. Further to this, in natural conditions, the younger male would have left the pride for a nomadic lifestyle. All the behaviour of the younger male indicates that he was under pressure. Dominance from the larger male was constant and turned violent as the younger male grew older and began to resist. When an animal is under stress, adrenal glands become hyperactive and corticosteroids are released (Henk Bertschinger, pers. comm.). This impacts negatively on the animal in question and reduces resistance to parasites (Esch *et al.*, 1975). Wilson (1976) makes mention of what Hans Selye called the General Adaptation Syndrome (GAS) in 1956. There is a sequence of three stages, namely the alarm stage when adrenal corticotropical hormones (ACTH) are released, followed by the stage of resistance. Here the adrenal glands enlarge due to a continuous increased demand for corticosteroids. Aggressive interactions are named as the most potent of stressors. Finally, a stage of exhaustion is reached where the body is not able to withstand the increased corticosteroid levels and in the long run, this increases the chances of infection. Exposure to infection in the younger male was also increased by the protracted periods spent with the female and later, the cubs.

The positive response seen in the younger male in terms of resistance to the parasites could be as a result of his response to the pressure. In all cases, the younger male consumed the largest amount of muscle tissue, in one case feeding for four hours and 22 minutes with an average consumption of 50 kg, and also drank for the longest time recorded, 8.39 minutes. Although he was not weighed, he was the most overweight of the lions and as a result, he may have the physiological resources to resist infestation.

The relatively low egg counts and corresponding infestation levels are as a result of a variety of factors. Firstly, the habitat is clean and parasites present in the environment would have been reduced by two years of drought prior to the inception of the study. Sporadic de-worming was done before the study.

Isolation of the lions from the greater reserve may also cause a bottleneck in terms of taxa diversity and finally, the relative safety and lack of natural pressure on the animals permits a well-functioning immune system allowing for a strong defense response to the endoparasites.





8 SUMMARY

Aspects of the behaviour of a small pride of African lions (*Panthera leo*) were investigated at Intu Afrika Kalahari Game Reserve in the southern Kalahari in Namibia. The full pride consisted of three adults, two males and a female, as well as a cub of each sex. Fieldwork was conducted for periods of six weeks during midwinter (May to July 2003) and again during midsummer (February and March 2004). Trials consisted of alternating continuous observational periods during daytime (sunrise to sunset) and nighttime (sunset to sunrise). Body surface temperatures of the lioness and the oldest male were measured by Thermocron iButtons™, implanted subcutaneously into the neck, tail and loin regions of each individual.

Behavioural patterns which commonly occurred and can be considered conventional Kalahari lion behaviour, included scent marking, territorial patrols, raking of specific trees, tree-climbing, co-operative hunting, covering of carcasses with sand and grazing. Unconventional behaviour, possibly as a result of the skewed sex ratio favouring the males, included frequent dominant/submissive interactions as well as incessant scent marking and flehmen responses. Calculated association indices were disproportionate, the younger male not only demonstrating strong kin selection for the cubs as a result of his bond with the female, his sister, but also exhibiting alloparental care by assuming the role of "Auntie".

Time-energy budgets demonstrated a negative relationship with increasing temperature during both seasons, being more prevalent during the hotter summer months. A distinct decrease in activity set in around midday during winter and during early morning (9 - 10 h) in summer. During the latter season, behaviours such as grooming and bonding between individual pride members were sacrificed for panting. Nighttime activity during winter was very low, probably as a result of the low temperatures, whereas greater activity was shown during summer. Periods of sunbathing on the dune crests during early

mornings were generally more extensive during winter than in summer. The results for the time-energy budgets of the cubs were in accordance with that of the adults.

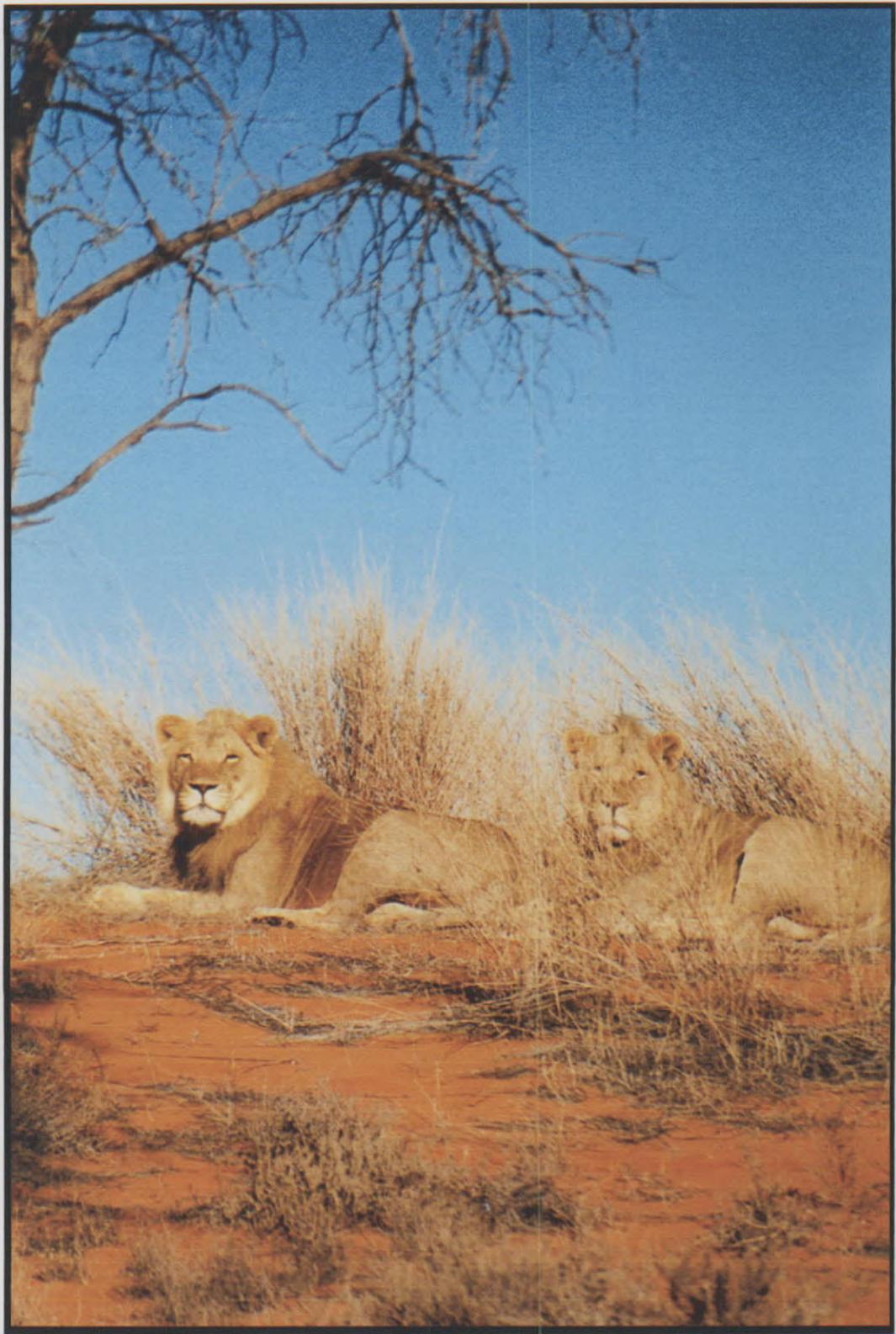
Temperature measurement by the iButtons indicated relative constancy in surface temperature particularly in the neck region, most likely due to the thicker skin and greater muscularisation. The tail region demonstrated greater temperature variation possibly as a result of its constant exposure and extensive vascularisation as demonstrated by dissection. A large number of superficial small-diameter vessels were found dorsally and laterally on the carcass, probably used for thermoregulation. The loin iButton data was not demonstrative, but exposure of loins increased as temperature increased, specifically with full bellies during summer. Loins were not exposed with empty bellies under 17 °C during both winter and summer. Thermoregulatory “escape” behaviour was observed at temperatures greater than 25 °C during both seasons. At ambient temperatures above 33 °C thermoregulatory behaviour was abandoned in favour of physiological mechanisms (panting), thereby indicating that the thermoneutral zone of the Kalahari pride lies between 25 and 33 °C.

Behavioural adaptations, a low use of water for evaporative cooling and the apparent sourcing of water from prey blood and body fluids indicate that the African lion may be independent of drinking water. Measurements to determine of the relative medullary thickness and thus the extent of kidney function, did not show a specific capacity for water resorption. Sweat glands are only present interdigitally in felids and examination of the paw pads showed these to be eccrine glands.

Ecto- and endoparasite numbers of the lions were found to be relatively low when compared to published data, probably as a result of the arid habitat and the original deworming of the adult individuals prior to the inception of the present study. Only one species of ecto- (biting fly) and four species of

endoparasite (nematodes and coccidians) were collected, all of which are typical African lion parasites. No tampsans were collected and, therefore, had no impact on the behaviour of the pride.





9 OPSOMMING

Aspekte van die gedrag van 'n klein trop Afrika-leeus (*Panthera leo*) in die Intu Afrika Kalahari Wildreservaat is in die suidelike Kalahari van Namibië ondersoek. Die voltallige leeutrop het uit drie volwassenes, twee mannetjies en 'n wyfie, asook 'n welpie van elke geslag, bestaan. Veldwerk is oor tydperke van ses weke gedurende die midwinter (Mei tot Julie 2003) en weer gedurende die midsomer (Februarie en Maart 2004) uitgevoer. Veldopnames het alternatiewelik gedurende die dag (sonop tot sononder) en nag (sononder tot sonop) plaasgevind. Liggaamsoppervlaktemperatuur van die leeuwyfie en oudste mannetjie is deur middel van Thermocron iButtons™ wat onderhuids in die nek, stert en lieste van elke individu ingeplant is, bepaal.

Gedragspatrone wat algemeen voorgekom het en as normale gedrag van Kalahari-leeus beskou kan word, sluit reukafbakening, territoriale patrolling, krap van spesifieke bome, boomklim, koöperatiewe jag, sandbedekking van karkasse en grasbenutting in. Ongewone gedrag, moontlik as gevolg van die ongelyke geslagsverhouding ten gunste van mannetjies, het herhaalde dominante/onderdanige interaksies, asook aanhoudende reukafbakening en lipkrulreaksies, ingesluit. Berekende assosiasie-indekse was ook oneweredig aangesien die jonger leeumannetjie weens sy hegte band met die wyfie, sy suster, nie alleen 'n duidelike familievoorkeur vir die welpies getoon het nie, maar ook allotrope ouersorg deur die rol van "Tante" te vervul.

Aktiwiteitspatrone toon 'n negatiewe verwantskap met toenemende temperatuur gedurende beide seisoene, maar heers veral gedurende die warm somermaande. 'n Duidelike afname in aktiwiteite kom teen die middel van die dag gedurende die winter, maar vroegoggend (9 – 10 h) gedurende die somer voor. Tydens laasgenoemde seisoen vind hyging ten koste van liggaamsversorging en die vorming van bondgenootskappe tussen individuele lede van die trop plaas. Aktiwiteite gedurende die winternagte was baie beperk, waarskynlik as 'n gevolg van die lae temperature, terwyl verhoogte aktiwiteite

tydens die somer voorgekom het. Vroegoggend sonbadperiodes op die kruine van duine was oor die algemeen meer omvattend gedurende die winter as in die somer. Resultate met betrekking tot die aktiwiteitspatrone van die welpies is in ooreenstemming met dié van die volwassenes.

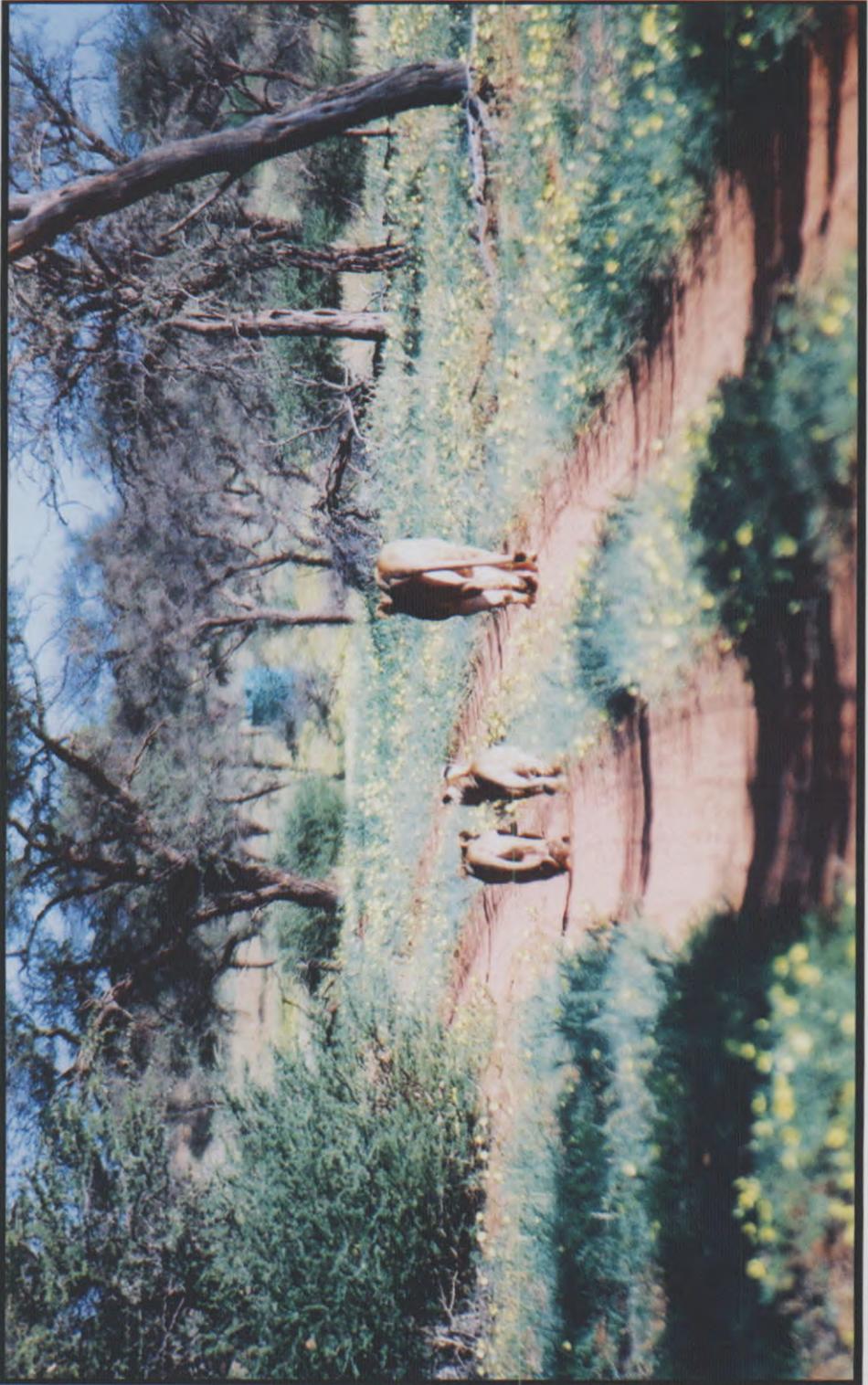
Temperatuurlesings van die iButtons dui op relatief stabiele oppervlaktemperature, veral in die neksone met sy dikker vel en groter mate van gespierdheid. Die stertstreek toon groter temperatuurvariasie, moontlik as gevolg van die voortdurende blootstelling en uitgebreide bloedvatvoorsiening soos deur disseksie bepaal. 'n Groot aantal oppervlakkige maar kleiner bloedvate is dorsaal en lateraal op die karkas aangetref en is waarskynlik by termoregulering betrokke. iButton-data van die lieste kan nie as afdoende beskou word nie, maar blootstelling van die lieste het toegeneem namate temperature gestyg het, veral met vol pense gedurende die somer. Met leë pense is die lieste nooit onder 17 °C gedurende die winter of somer blootgestel nie. Termoregulerende vermydingsgedrag is by temperature hoër as 25 °C tydens beide seisoene waargeneem. By omgewingstemperature bo 33 °C is gedragstermoregulering ten gunste van fisiologiese meganismes (hyging) laat vaar, voldoende aanduiding dat die termoneutrale sone van die Kalahari-leeutrop tussen 25 en 33 °C geleë is.

Gedragpatrone, die geringe gebruik van water vir verdampingsafkoeling en die klaarblyklike benutting van prooibloed en -liggaamsvloeistowwe as waterbron dien as aanduiding dat die Afrika-leeu nie van drinkwater afhanklik is nie. Afmetings om die relatiewe dikte van die medulla en dus die nierfunksie te bepaal, dui nie op 'n besondere vermoë tot waterresorpsie nie. Sweetkliere van katagtiges kom slegs tussen die tone voor, en ondersoek van die pootkussinkies toon dan dat dit uit ekkriene kliere bestaan.

Vergeleke met gepubliseerde data was die ekto- en endoparasietgetalle van die leeus relatief lag, waarskynlik as gevolg van die ariede habitat en die oorspronklike ontworming van volwasse individue vóór die aanvang van die

huidige studie. Slegs een ekto- (steekvlieg) en vier endoparasietsoorte (nematodes en koksidiëë) is versamel, almal tipiese parasiete van Afrika-leeus. Geen tampan is versamel nie, en het dus geen invloed op die gedrag van die leeutrop uitgeoefen nie.





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