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THE ECOPHYSIOLOGY OF
BABOONS LIVING IN THE
KUISEB RIVER CANYON, NAMIBIA
CONRAD BRAIN
1993

The eco-physiology of baboons living in the Kuiseb River Canyon, Namibia

Conrad Brain

A dissertation submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfilment of the requirements for the degree of Doctor of Philosophy

Okaukuejo 1993

Abstract

This study was designed to investigate the eco-physiology of baboons (Papio cynocephalus ursinus) in a troop living in the Kuiseb River canyon of the central Namib desert, Namibia. Answers were sought for two major questions: what were the baboons prospects for survival and were there special adaptations allowing for their survival in their desert environment? To answer the former, life history phenomena of individuals and demographic changes within the troop were studied over a six year period. Results showed that the troop was not self-sustaining. Ectoparasite infestations killed the majority of infants born to high ranking female baboons while infant kidnapping by high ranking females killed most lower ranking females' infants. The high infant mortality appeared to affect the behaviour of adult male baboons in the troop, causing non-paternal males to fight harder to maintain a rank with reproductive opportunities, usually with serious wounding or death as a consequence. Answers to the latter question involved investigations into the baboons feeding patterns and diet, body temperature regulation, water flux rates and methods of body water conservation. Despite their desert environment, the baboons had access to plants of high water content and were not dependent on free water intake. Plant foods also had low electrolyte concentrations. Body temperatures of three free-ranging baboons recorded by intraperitoneal radio telemeters were remarkably labile, indicating an adaptive heterothermy. The baboons appeared to employ evaporative cooling

only when water was available to drink and used cool sub-surface sand to slow their body temperature rises. Water flux rates determined using tritiated water of three free-ranging baboons were not different to those of baboons from elsewhere. Acquisition of free water at times of water scarcity was strictly rank related. Body water conservation was apparently achieved through a combination of factors: urine concentration of Kuiseb baboons increased significantly when they were water deprived. The kidneys of the Kuiseb baboons, obtained from baboons that died naturally, were anatomically significantly different and head greater urine concentrating abilities than the kidneys of baboons from the northern Transvaal, South Africa. Kuiseb baboons showed efficient faecal water conservation, similar to other desert adapted mammals. Body water also was apparently conserved by engaging in water conservative behaviour, predominantly inactivity.

Research described in this thesis has been published or presented as follows:

Scientific publications

Brain, C. 1992. Deaths in a desert baboon troop. *International Journal of Primatology*, 13: 593-595.

Brain, C. and Bohrmann, R. 1992. Tick infestation of baboons (Papio ursinus) in the Namib desert. *Journal of Wildlife Diseases*, 28: 188-191.

Brain, C. 1991. Activity of water deprived baboons (Papio ursinus) during inter-troop encounters. *South African Journal of Science*, 87: 221-222.

Brain, C. 1990. Spatial usage of a desert environment by baboons (Papio ursinus). *Journal of Arid Environments*, 18: 67-73.

Brain, C. 1990. Aspects of drinking by baboons (Papio ursinus) in a desert environment. In: *Namib ecology: 25 years of Namib research*, M.K. Seely (ed.), pp. 169-172. Transvaal Museum Monograph No. 7, Transvaal Museum, Pretoria.

Brain, C. 1988. Water gathering by baboons in the Namib desert. *South African Journal of Science*, 84: 590-591.

Abstracts

Brain, C. 1991. Annual Congress of the Physiology Society of Southern Africa. Sandbathing: the alpha's answer? *South African Journal of Science*, 86: 540.

Appleton, C.C. and Brain, C. 1991. Annual Scientific Meeting of the Parasitological Society of Southern Africa. The gastro-intestinal parasites of the baboon, Papio cynocephalus ursinus, in the Namib Desert. *Journal of the South African Veterinary Association*, Vol. 63, No. 2: 85.

Brain, C. and Bohrmann, R. 1991. Annual Scientific Meeting of the Parasitological Society of Southern Africa. Tick infestation of baboons, Papio cynocephalus ursinus, in the Namib desert. *Journal of the South African Veterinary Association*, Vol. 63, No. 2: 87.

Declaration

I declare that the work reported in this dissertation was carried out by me at the Desert Ecological Research Unit, Gobabeb, Namibia and in the Department of Physiology, University of the Witwatersrand. Where help was received, it has been acknowledged. This work has not been submitted before for any degree or examination at any other university.



C. Brain

Signed on this the tenth day of June 1993, Okaukuejo, Namibia

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Chapter One

General introduction, study area and the process of habituating the baboons

This introductory chapter is not a literature review as each subsequent chapter provides its own. Instead it identifies the relevance of the work contained in this thesis and provides a breakdown of the structure and specific questions posed prior to their investigation.

If abundance, breadth of distribution and habitat diversity are measures of evolutionary success, baboons (genus Papio) are indeed successful. Savanna baboons are distributed throughout sub-Saharan Africa and occupy habitats including desert, savanna, woodlands, rain forest, high altitudes and low-lying coastal areas (Wolfheim, 1982). Amongst non-human primates, this distribution indicates the unique ability of baboons to successfully colonize a range of ecological settings.

The phenotypic variation of savanna baboons between and within this range of habitats is partially responsible for the current confusion regarding their taxonomic classification. The most widely accepted classification of Thorington and Groves (1970) considers all savanna baboons as one species, Papio cynocephalus, and separate from hamadryas baboons, Papio hamadryas. Savanna baboons include Papio cynocephalus cynocephalus (yellow baboons), Papio cynocephalus ursinus (chacma baboons), and Papio cynocephalus anubis (olive baboons).

Amongst savanna baboons, the development of any adaptations promoting survival in a particular habitat is likely to be

more conspicuous in those conspecifics at the habitat extremes, both environmental and spatial. For baboons living in the Namib desert (Hamilton, 1985), the most arid habitat yet known to be occupied by non-human primates, physiological and behaviourial adaptations (Louw, 1990) could be important factors to their survival in a desert habitat.

The Namib baboons described by Hamilton (1985) were living in the seasonally dry Kuiseb River canyon where it crosses the central Namib desert, Namibia. Within the canyon an alluvial floodplain supported a riparian forest that formed a linear oasis crossing the desert (Seely, Buskirk, Hamilton and Dixon, 1981). Baboon movements were restricted to approximately 1 km from the canyon edge as it was bordered by vegetationless desert into which the baboons did not venture.

In a short-term study, Hamilton and colleagues outlined the peculiarities of the desert baboons' habitat (Hamilton, Buskirk and Buskirk, 1976) and provided preliminary results on the demographic status and behaviourial ecology of these baboons (Hamilton, 1985). From Hamilton's study it became clear that the environmental variables that are of the most interest as determinants of baboon behaviourial ecology in most other habitats (Dunbar, 1992) were, for the most part, conspicuous through their extreme values in the Kuiseb canyon habitat. Chief amongst them was annual rainfall. In the area occupied by the Kuiseb baboons, rainfall was so low and variable that it was considered negligible. There were also no permanent water

sources in the baboons range and they depended on the unpredictable floods of the Kuiseb River for water.

Other than baboons, most mammals living in the Namib desert or in similar desert habitats are known to demonstrate major eco-physiological adaptations, especially in their means of body water conservation. Indeed, the most common mammal living alongside the Kuiseb baboons is gemsbok, Oryx gazella, and the abilities of this animal to cope with desert conditions, particularly in terms of its body water conservation and thermoregulation are legendary (Taylor, 1969).

Striking amongst many desert adapted animals is their ability to exist without drinking (Louw and Seely, 1982). Whether terrestrial primates in arid/desert habitats have this ability has not been investigated because the animals appear dependent on free water intake (Altmann and Altmann, 1970). Physiological data obtained from captive baboons under manipulated experimental conditions has provided information as to how the animals are able to respond physiologically under extreme conditions, including water deprivation (Zurovsky, Shkolnik and Ovadia, 1984; Zurovsky and Shkolnik, 1982; Hiley, 1976). There is, however, an absence of such data obtained from free-ranging animals indicating what non-human primates *really* do to cope with desert conditions.

In this dissertation I examine various ecophysiological questions concerning the chacma baboons (Papio cynocephalus ursinus) living

in the Kuiseb River canyon. How successful are the baboons, and what are their prospects for survival? This question is addressed in Chapter 2 through an examination of life history phenomena of these baboons and the demographic changes within the baboon troop over a six year period.

Results in Chapter 2 indicated that the baboon troop I studied was not self-sustaining, mainly because of an exceptionally high neonatal mortality. The circumstances surrounding these mortalities are addressed in Chapters 3, 4 and 5. I examined two components when considering the reasons for these mortalities, an abiotic and a biological one. In Chapter 3 I analyzed short term changes in the abiotic environment of the baboons and how these changes affected the baboons' lifestyles. I placed emphasis on how the changes in lifestyle might predispose the baboons, especially neonates, to ectoparasite infestations which were found to be the cause of the majority of infant deaths. Besides killing most infants, ectoparasites infested all the baboons. The parasites involved and the pathology associated with the parasite infestations are examined in Chapter 4.

The next highest cause of infant mortality to tick infestation is infant kidnapping by adult females. In Chapter 5 I present the circumstances surrounding the incidence of fatal infant kidnapping. This is the first time such behaviour has been observed to occur regularly and repeatedly in a non-human primate population.

Also peculiar to this troop of baboons was the high incidence of serious wounding and fatal fighting amongst adult male baboons. In Chapter 6 I examined the adult male baboon dynamics of this troop, analyzed the incidence of wounding during dominance fights, and compared my result with those from a similar baboon population in Botswana.

The major question of whether these desert baboons have any special adaptations allowing their survival in their extreme habitat is the subject of the rest of this dissertation, Chapters 7 through 10.

In Chapter 7 the baboons feeding habits and diet were examined. Through analysis of their feeding patterns and year-round food sources, I attempted to determine periods of possible nutritional deficiencies or of unusually high electrolyte loads.

Desert adapted mammals have different ways of coping with daytime heat: small mammals escape the heat by retreating into burrows and large mammals store large amounts of body heat (Louw and Seely, 1982) and/or possess a carotid rete for brain cooling (Mitchell and Laburn, 1985). Baboons are of intermediate mass. They can neither burrow nor store excessive amounts of heat, nor do they have any known mechanisms for brain cooling. The body temperatures exhibited by baboons and the fluctuations in body temperatures of baboons under free-ranging conditions were thus examined. Body temperature changes of three Kuiseb baboons were examined using radio-telemeters that I surgically implanted

intraperitoneally. This was the first time this procedure was used in free-ranging primates, and the results appear in Chapter 8. Baboon body temperature changes obtained in this way provided new insights into interpretation of certain baboon behaviours.

Baboon thermoregulation and body temperature changes appeared to be integrally linked to the availability and intake of water. Water use and conservation by the baboons are the subjects of Chapter 9 and 10. Chapter 9 addresses the water flux rates (using tritiated water) of three of the Kuiseb baboons. The intake of preformed water is also examined in Chapter 9.

In Chapter 10 I examined aspects of baboon water conservation. The anatomy of the kidneys of the Kuiseb baboons, urine concentrations, faecal water conservation and behaviourial modifications promoting water conservation were investigated. The anatomy of the kidneys of Kuiseb baboons (kidneys were obtained from animals that died naturally) was also compared with kidney anatomy of baboons from the Northern Transvaal, South Africa to determine if any differences existed between the two populations.

A summary of the conclusions of this work is discussed in Chapter 11.

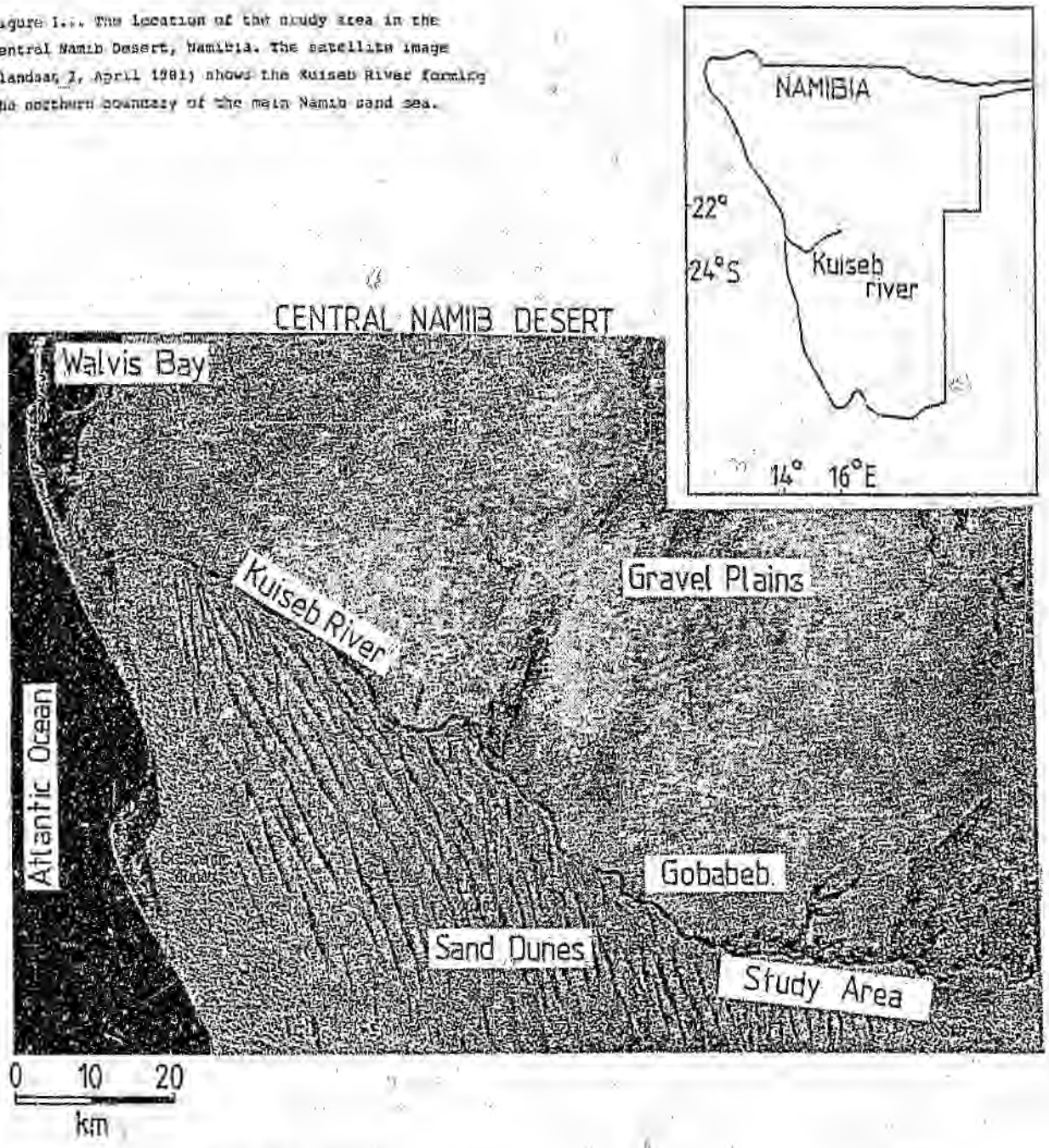
STUDY AREA

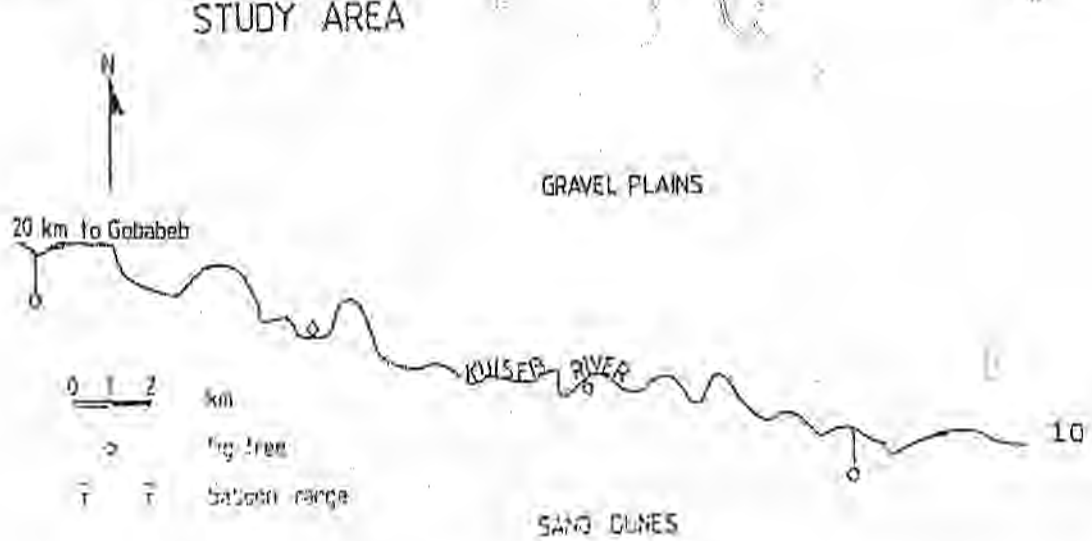
The baboon troop that I have studied, originally described by Hamilton (1985) as the "Lower" troop, was the most westerly or downriver of three troops of baboons living along the seasonally dry Kuiseb River canyon that crosses the central Namib desert (Fig. 1.1). The downriver limit of the Lower troop's range was approximately 20km upriver from the Desert Ecological Research Unit of Namibia at Gobabeb (23'34°S, 15'03°E). From here the Lower troop's range stretched approximately 30km upstream within the canyon (Fig. 1.1).

The linear range occupied by the Lower troop had an approximate 7 km overlap with the linear range of the neighbouring troop, the Middle troop, at the upriver extent of the Lower troop's range (Hamilton, 1985; Brain, 1990). The Middle troop's range extended for a further 25 km upriver from the end of this overlap zone. The Middle troop's range had a 5 km overlap with a third troop's range, the Upper troop, at the Middle troop's upriver range extent. The Upper troop's range extended for approximately 20 km further upstream from the upriver extreme of the Middle troop's range. The Lower, Middle and Upper troops have maintained these ranges from 1972 to present time (Hamilton, 1985; Brain, unpub. data). No record of these baboons' ranges exists prior to 1972, but baboons were first recorded in the Lower troop's current range in 1837 (Alexander, 1838). Details of troop structures and sizes are provided in subsequent chapters.

Although the Lower, Middle and Upper troops occupied adjacent linear ranges that partially overlapped, the following range description was specific to the Lower troop. The section of Kuiseb River occupied by the Lower troop formed the northern boundary for the main Namib sand sea, creating a clear definition between the sand sea and the near vegetationless gravel plains (Seely, Buskirk, Hamilton and Dixon, 1981). The baboons were restricted to the canyon confines for food, water, shelter and sleeping cliffs. Within the canyon an alluvial floodplain supported a riparian forest (Fig. 1.2) dominated by Faidherbia albida, Acacia erioloba, Euclea pseudebenus trees and Salvadora persica bushes. As one moved upriver in the Lower troop's range, the canyon gradually narrowed so that in the upriver section of their range both canyon floor area and total vegetated space were less than one quarter of that in the downriver section (Hamilton and Tilson, 1982). Baboon plant food was abundant in the downriver extent of the Lower troop's range but this was the first area to lose surface water following the short annual flood (river flow is dealt with in the following chapter). Thus within their range, the gradient of resources included an increasing downriver gradient of food and a seasonal gradient of water increasing in the opposite direction (Hamilton and Tilson, 1982; Brain, 1990). Lower troop baboons had therefore to choose between eating and drinking, especially at times of water shortage when water was localised at the extreme upriver limit of their range (Brain, 1988).

Figure 1... The location of the study area in the Central Namib Desert, Namibia. The satellite image (Landsat 2, April 1981) shows the Kuiseb River forming the northern boundary of the main Namib sand sea.





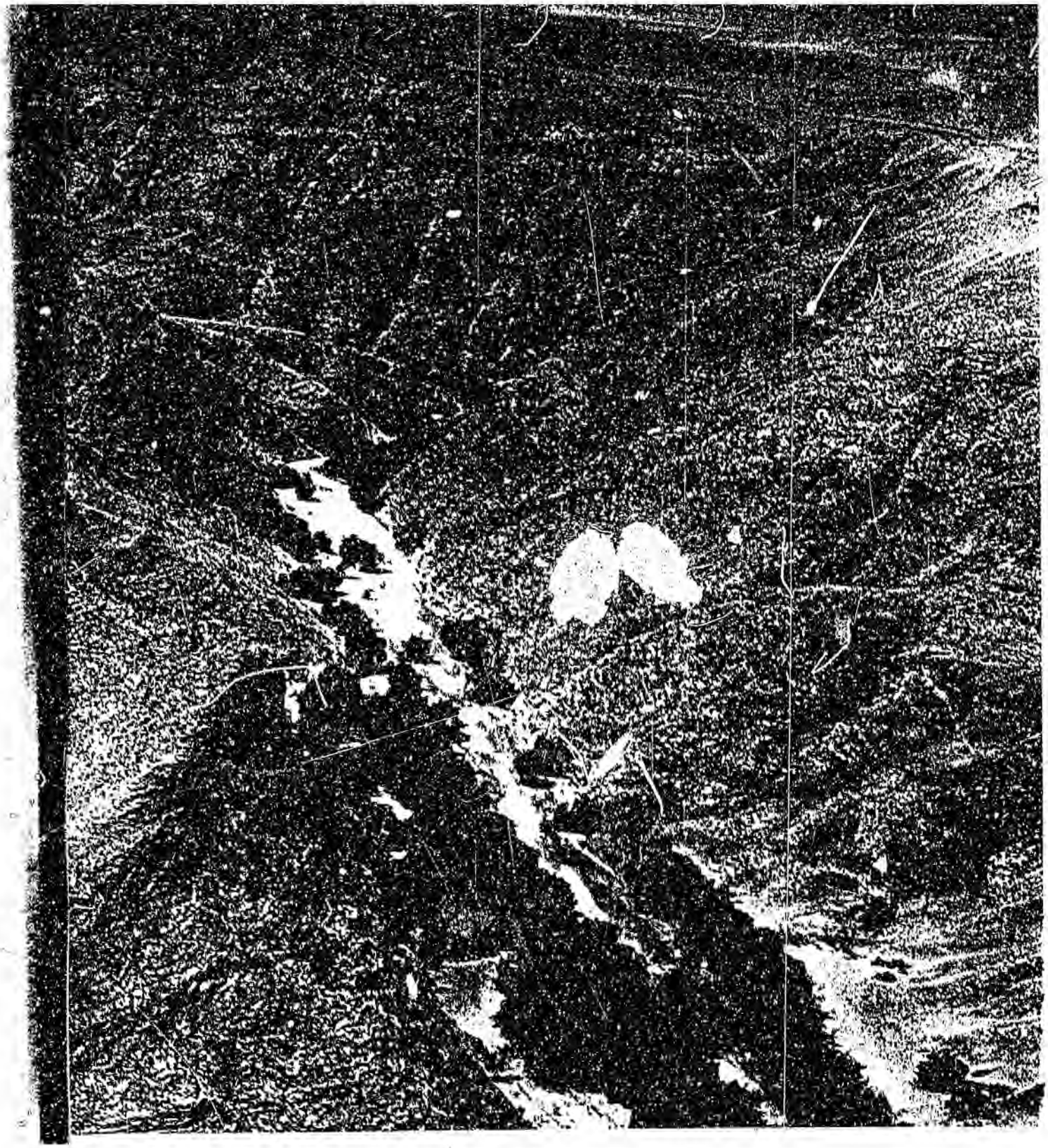


Figure 1.2. Aerial view of a section of the Kuiseb River canyon occupied by the baboons. (Scale: one cm= approximately 20m.)

Spotted hyaenas (Crocuta crocuta) were the only large predators coinhabiting the baboons' range but were not observed to prey upon the baboons. Other medium to large sized mammals living alongside the baboons included jackal (Canis mesomelas), African wildcat (Felis lybica), gemsbok (Oryx gazella), steenbuck (Raphicerus campestris) and klipspringer (Oreotragus oreotragus).

The climate of the study area is moderate for a desert area with little seasonal temperature variation (Lancaster, Lancaster and Seely, 1984). A climatic summary of the study area is provided for the study period (1987 through 1992) in Table 1.1. Climatic data were recorded at Gobabeb, the nearest first order weather station.

Table 1.1 (pages 13, 14 and 15). Climatic summary of the study area for the period 1987-1992. Temperatures are in °C and rainfall in mm.

1987	Mean Temperature		Mean Temperature			Rainfall
	Max	Min	08H00	14H00	20H00	
Jan	30.4	13.2	14.8	28.2	24.4	0
Feb	32.8	16.3	17.7	30.7	27.2	0
Mar	33.2	15.4	16.3	31.3	26.6	0
Apr	33.0	17.2	17.7	31.6	26.2	12.3
May	33.0	16.9	24.9	39.6	10.4	0
June	28.8	12.3	13.3	27.9	21.4	0
July	25.4	10.4	11.6	25.2	19.4	11.2
Aug	29.2	11.6	13.1	27.9	21.7	0
Sept	27.6	9.5	11.3	25.5	19.7	0
Oct	31.1	12.5	14.1	28.9	23.1	0
Nov	31.0	13.2	15.1	19.7	14.8	0
Dec	30.2	13.7	15.6	29.4	23.8	0
Mean	30.5	13.5	15.5	29.7	22.4	Total 23.5
SD	2.4	2.5	3.6	3.7	4.6	

1988	Mean Temperature		Mean Temperature			Rainfall
	Max	Min	08H00	14H00	20H00	
Jan	33.1	15.9	17.3	32.2	26.3	0.7
Feb	30.9	16.2	17.0	28.9	25.9	0
Mar	31.3	16.3	17.0	30.4	25.6	6.7
Apr	30.9	15.6	16.6	30.7	24.8	0
May	32.6	17.7	18.6	31.1	25.2	0.6
June	29.0	12.9	13.7	28.0	21.0	0
July	26.2	9.2	10.4	24.5	19.2	0
Aug	27.9	11.2	12.5	25.7	20.3	0
Sept	29.6	9.7	11.5	26.6	22.8	0
Oct	28.1	9.7	11.5	27.1	20.5	0
Nov	31.6	13.3	15.5	30.4	23.9	0.6
Dec	31.1	14.6	16.6	30.9	26.6	0.2
Mean	30.2	13.5	14.9	28.9	23.5	Total 8.8
SD	2.1	3.0	2.8	2.5	2.6	

1989	Mean Temperature		Mean Temperature			Rainfall
	Max	Min	08H00	14H00	20H00	
Jan	29.9	15.3	16.4	27.8	24.0	0.3
Feb	29.3	15.5	16.4	28.2	24.2	1.2
Mar	34.1	17.3	17.7	32.9	27.1	0
Apr	32.8	17.0	18.0	31.6	25.9	1.3
May	30.2	16.0	16.6	29.2	23.7	11.7
June	25.4	10.5	11.2	24.2	18.0	0
July	28.0	10.4	11.8	26.9	20.7	0
Aug	26.9	9.5	10.7	25.5	19.5	0
Sept	30.1	11.5	12.8	28.5	22.5	0
Oct	30.3	10.3	12.6	28.3	22.4	0
Nov	29.5	11.3	13.2	28.6	23.5	0
Dec	29.7	13.1	14.7	28.5	24.2	0
Mean	29.7	13.1	14.3	28.4	23.0	Total 14.5
SD	2.3	2.9	2.6	2.3	2.6	

1990	Mean Temperature		Mean Temperature			Rainfall
	Max	Min	08H00	14H00	20H00	
Jan	32.3	16.2	17.3	30.7	26.5	0
Feb	32.4	16.9	17.9	29.8	26.1	11.7
Mar	33.8	17.1	18.3	33.1	28.2	0
Apr	31.7	14.8	15.9	30.4	24.3	0
May	31.8	16.0	17.6	31.5	25.7	0
June	25.8	11.4	12.1	24.5	19.4	0
July	26.0	10.1	11.0	25.2	18.8	0
Aug	29.0	10.1	10.9	27.2	21.4	0
Sept	28.4	9.5	10.5	26.5	20.6	0
Oct	29.5	11.0	12.9	27.7	22.1	0.7
Nov	32.4	13.4	15.6	29.9	25.2	0
Dec	30.9	13.6	15.2	29.2	24.1	0
Mean	30.3	13.2	14.6	28.8	23.5	Total 12.4
SD	2.6	2.8	3.0	2.6	3.0	

1991	Mean Temperature		Mean Temperature			Rainfall
	Max	Min	08H00	14H00	20H00	
Jan	31.7	15.3	16.6	29.8	26.4	0
Feb	31.7	15.8	16.6	29.5	26.0	0
Mar	34.1	16.8	18.0	32.9	27.1	2.7
Apr	34.7	18.0	19.3	33.9	27.7	7.0
May	31.8	15.6	16.7	31.5	25.4	0
June	25.0	10.1	11.3	24.3	18.6	0
July	25.6	11.5	12.1	23.9	19.0	0
Aug	27.4	9.5	10.6	26.1	20.1	0
Sept	26.6	9.1	10.4	25.0	18.6	0
Oct	28.0	10.7	12.3	26.5	20.4	0
Nov	32.6	14.0	16.5	31.2	25.7	6.3
Dec	31.2	15.1	16.8	29.7	25.5	1.2
Mean	30.0	13.5	14.8	28.7	23.4	Total 17.2
SD	3.3	3.1	3.2	3.4	3.7	

1992	Mean Temperature		Mean Temperature			Rainfall
	Max	Min	08H00	14H00	20H00	
Jan	34.3	17.0	18.9	32.7	28.3	0
Feb	33.0	14.8	16.6	31.0	26.8	0
Mar	30.7	14.0	14.8	28.9	24.3	0
Apr	33.3	15.5	16.3	31.9	26.3	0
May	32.0	15.6	16.5	30.4	24.5	0
June	27.6	11.9	13.5	26.9	20.6	0
July	28.8	17.3	13.7	28.1	21.4	0
Aug	27.3	9.9	10.9	24.8	19.1	0
Sept	27.9	9.8	11.0	26.4	20.9	0
Oct	27.8	10.1	11.5	25.9	19.8	0
Nov	30.9	12.0	14.1	30.2	24.1	0
Dec	31.3	12.9	14.6	29.6	24.3	0
Mean	30.4	13.4	14.4	28.9	23.4	Total 0.0
SD	2.5	2.7	2.5	2.5	3.0	

The process of acceptance of humans by the baboons (Habituation)

The baboons studied for this thesis were habituated by Ginger Mauney and myself. Initially the baboons would not tolerate humans on foot at less than 300m and had not had any regular human contact since a brief period in 1972 (Hamilton, 1985). Our approach to gaining acceptance by the baboons without obviously affecting their behaviour was to maintain a presence only and not to provision or interact with the baboons. We spent a period totalling around 10 months between December 1986 and June 1990 (see Chapter 2) habituating the baboons to our presence, of which approximately 20 days of each month were spent moving on foot with the troop. We gradually moved closer and closer to the baboons until we were accepted by them at close range (Fig. 1.3). At this stage our presence did not appear to influence the baboons' behaviour as they appeared to eat normally, move in an unafraid manner and continued to breed despite our presence. This tolerance was maintained as the study progressed, but the baboons were only moderately tolerant of other human individuals and then only towards the latter stages of the study.

The method of habituation of baboons in this study was similar to that used by Hamilton (pers. comm.) in Botswana and in both studies near complete habituation was achieved without

provisioning the animals. In Botswana, however, unlike in the Kuiseb, many different people were involved in the habituation process and the baboons came to accept any human being at close range.

At all stages of the Kuiseb study we exercised the utmost caution not to damage our acceptance by the baboons. This precaution placed certain limitations on some of the invasive physiological procedures carried out (Chapters 8, 9 and 10) in terms of sample sizes and methodology. These limitations are discussed in the relevant chapters. All procedures were carried out in ways least likely to damage the baboons' acceptance of us as this acceptance was essential to the successful completion of this study.



Figure 1.3. Within ten months we had habituated the baboons from their original wild state and intolerance of humans to one of near complete acceptance of us. We were able to study the baboons at close range without obviously affecting their behaviour. Here Ginger Mauney and three Lower troop baboons catch the morning sun.

Chapter Two

Demographic changes and causes of death in the Lower troop



INTRODUCTION

The study of demographic and life history variables is important in wild populations as a means to predict their prospects for survival. While data on demographic structure are available for most non-human primate species, only a few studies have been of sufficient duration (> 20 years) for the construction of life tables concerning the fate of an entire cohort. However, life history data can be meaningful from shorter studies by determining mortality rates within age specific classes (Dunbar, 1987; Dittus, 1975). These data, however long or short term, suffer from the fact that as environmental conditions fluctuate from year to year so too do birth and death rates and are therefore population and time-specific.

When non-human primate populations suffer heavy mortalities under natural conditions, mortality does not usually fall evenly on all age-sex classes. Extreme environmental conditions have produced disproportionately high juvenile and infant mortality among cercopithicines [vervets (Struhsaker, 1973), macaques (Dittus, 1977)] and for baboons living in nutritionally poor habitats, the proportion of infants surviving to an age of 18 months can be as low as 40 per cent (Altmann, Altmann, Hausfater and McCuskey, 1977). Food shortage and malnutrition appear to be major causes of death (Dittus, 1977; Mori, 1979) with disease, temperature stress and predation implicated as lesser causes (Dunbar, 1980; Cheney, Lee and Seyfarth, 1981). Water shortage during dry seasons and drought has been considered an important factor in

non-human primate population crashes mainly through restricting the area accessible to the primates thereby decreasing food availability (Wrangham, 1981; Hamilton, 1985).

From Dec. 1986 to Dec. 1992, I recorded the death of 29 of 36 infants born in one desert baboon (Papio cynocephalus ursinus) troop. Further, I established the cause of death for 27 of the infant deaths and have also discovered the cause of death for most individuals in various other age groups. In this Chapter I present the demographic changes within this troop and use this to determine the prospects for their survival.

STUDY AREA AND METHODS

This study was conducted on the Lower troop of Kuiseb baboons (Chapter 1) and details of the study area are provided in Chapter 1.

I recorded the demographic changes of the Lower troop over a 72 month period of which results for 48 months appear in Brain (1992). I individually identified all baboons in the troop within two weeks after the onset of the study in December 1986. Thereafter, changes in numbers of baboons in the troop resulting from births, deaths, immigrations, emigrations and disappearances were recorded. I used the age-sex classification of Altmann and Altmann (1970) in categorising infants (0 - 1 year), juveniles (1 - 4 years), adult females (> 4 years), subadult males (4 - 6

years) and adult males (> 6 years). The use of this classification was facilitated in this study because the birth dates of all infants were known, at worst to within two weeks and there were no juveniles or infants in the troop at the onset of the study (see Results). Intermittent observation periods by myself between 1986 and 1989 (12 Dec 1986 - 21 Jan 1987, 4 June 1987 - 3 July 1987 and 9 Dec 1987 - 3 Jan 1988) were augmented by regular demographic observations on the baboons by staff members at the Desert Ecological Research Unit of Namibia (D.E.R.U.N). From Sep 1989 to Dec 1992 I spent 18 ± 6 days per month for 39 months in permanent close contact with the baboons. Complete habituation of the baboons (Chapter 1) was only achieved during the intensive study period. Prior to habituation, observations were made mainly through binoculars while for the intensive study period observations were made with the naked eye and binoculars. Staff members of the D.E.R.U.N. were not able to individually identify baboons but were able to count individuals in the various age/sex groups. I am confident that most births during the intermittent observation periods have been accounted for because the reproductive state of individual females was monitored. Predictions of birth dates worked out from estimated conception (detumescence minus two to three days [Gillman and Gilbert,1946]) were made only during the intensive observation period when a gestation period for each adult female in the Lower troop had been estimated. Predictions of birth dates thereafter were accurate to within two days (n=20). The ages of other infants were known, at worst, to the nearest fortnight. Infants' sex was determined at the first available

opportunity by observing external genitalia through binoculars.

RESULTS

There were no juveniles in the Lower troop in December 1986 with only one sub-adult male (Table 2.1). Since then, with one juvenile female reaching adulthood, no adult female transfers from elsewhere (eg. Anderson, 1981) and with one adult female death (Fig 2.1), the number of adult females has remained unchanged (Table 2.1 and Fig 2.1). Although there were a large number of adult male immigrants (Fig 2.1 and see Chapter 6) the number of adult males in the troop has remained reasonably constant (Table 2.1).

	Adult and subadult males	Adult females	Juveniles 1-4 years	Infants 0-1 year	Total
December 1986	5	7	0	0	12
Immigrants	12	0	0	0	12
Emigrants	4	0	0	0	4
Births	-	-	-	36	36
Deaths	5	1	0	29	35
Disappearances	4	0	0	0	4
December 1992	5*	7	3	1	17

Table 2.1. Summary of the demographic changes in the Lower troop. * One subadult male (72 months old) included in total.

♀	1986	1987	1988	1989	1990	1991	1992	1993
Pa	Dec----------							
Am	Dec----------							
Co	Dec----------							died
Ha	Dec----------							
Bo	Dec----------							
Gr	Dec----------							
Sp	Dec----------							
♂	1986	1987	1988	1989	1990	1991	1992	1993
Ga	Dec----------							
Sa	Jan---left							
Kh	June------left							
Pa	Dec----------killed							
Ne	June----------killed							
Al	Dec----------killed							
Du	Oct----------							
Gr	Nov----------							
No	June--left							
Wh	June----------							
St	May------left							
Si	Aug-------killed							
Ft	Dec----------died (immobilization accident)							

Fig. 2.1. Schematic representation of changes in Lower troop structure during the study period.

Of 36 infants born, 30 died (including one still birth - Table 2.2) before reaching 1 year of age (Table 2.2). All adult females were fertile, each giving birth two or more times during the study (Table 2.2). For the seven adult females, a mean birth rate of one infant every 341 ± 68 days (x ± SD) was recorded. Infants were born during two well defined birth periods, September to January and April to July (Fig. 2.2). Of the 36 infants born, 21 were males, 14 females and one was of undetermined sex. Three males and three females survived to more than one year of age. Details regarding the cause of infant death are in Table 2.2 and the pathology associated with the ectoparasite infestations are examined in Chapter 4. Live infants born to the top three ranking adult female baboons died from tick infestation while tick infestation and fatal infant kidnapping (Chapter 5) caused the death of infants born to the four lower-ranking adult females (Table 2.2). When the number of infant deaths due to tick infestations versus infant kidnappings were compared for high (top three) ranking female baboons and lower-ranking female baboons in a contingency table, a significant deviation from the expected was found (chi-square test with Yates correction, $X^2 = 20.5$, $p < 0.001$). (Circumstances surrounding the causes of infant deaths of both high and low ranking female baboons are addressed in Chapters 4 and 5).

MOTHER	INFANT BORN	SEX	FATE	AGE AT DEATH (days)	CAUSE OF DEATH
Pa	?-12-86	M	Died	< 30	Ticks
	01-10-87	M	Died	< 90	Ticks
	?-07-88	F	Died	< 10	Ticks
	09-01-90	?	Died	0	Still-born
	28-10-90	F	Died	64	Ticks
	10-10-91	F	Survived to 31-12-92		
Am	?-12-86	M	Died	< 30	Ticks
	11-11-90	M	Died	7	Ticks
	25-07-91	M	Died	4	Ticks
	0-09-92	F	Died	13	Ticks
Co	?-12-86	M	Died	< 30	Ticks
	12-07-88	M	Died	9	Ticks
	16-01-90	M	Died	24	Ticks
	18-01-91	M	Died	32	Ticks
	24-12-91	F	Died	60	Ticks
	05-12-92	M	Died	13	Ticks
Ha	?-12-86	F	Survived to 31-12-92		
	?-06-88	M	Died	< 73	Unknown
	08-11-89	M	Died	15	Kidnapped
	11-11-90	F	Died	2	Kidnapped
	07-01-92	M	Died	6	Kidnapped
	29-09-92	F	Died	35	Kidnapped
Bo	?-12-86	M	Survived to 31-12-92		
	17-12-88	F	Survived to 31-12-92		
	29-09-90	F	Died	1	Kidnapped
	14-04-91	M	Died	4	Kidnapped
	21-02-92	M	Survived to 31-12-92		
Gr	?-12-88	M	Died	< 30	Unknown
	19-04-90	F	Died	8	Kidnapped
	18-12-90	M	Survived to 31-12-92		
	25-12-92	F	Died	2	Unknown
Sp	?-07-89	M	Died	< 153	Ticks
	03-05-90	M	Died	4	Kidnapped
	22-01-91	F	Died	26	Ticks
	25-11-91	F	Died	8	Lactation failure
	09-11-92	M	Died	19	Kidnapped

Table 2.2 Details of infants born in the Lower troop since 1986. Mothers are listed in order of rank.

An infant survivorship curve has been constructed for the Lower troop for the period from birth through approximately one year of age (Fig. 2.3). From the figure it is clear that infants surviving to three months of age will probably survive to at least one year. Stated otherwise, there was an infant mortality rate (ie, number of infant that died per 35 live births) of 0.86 for the first year.

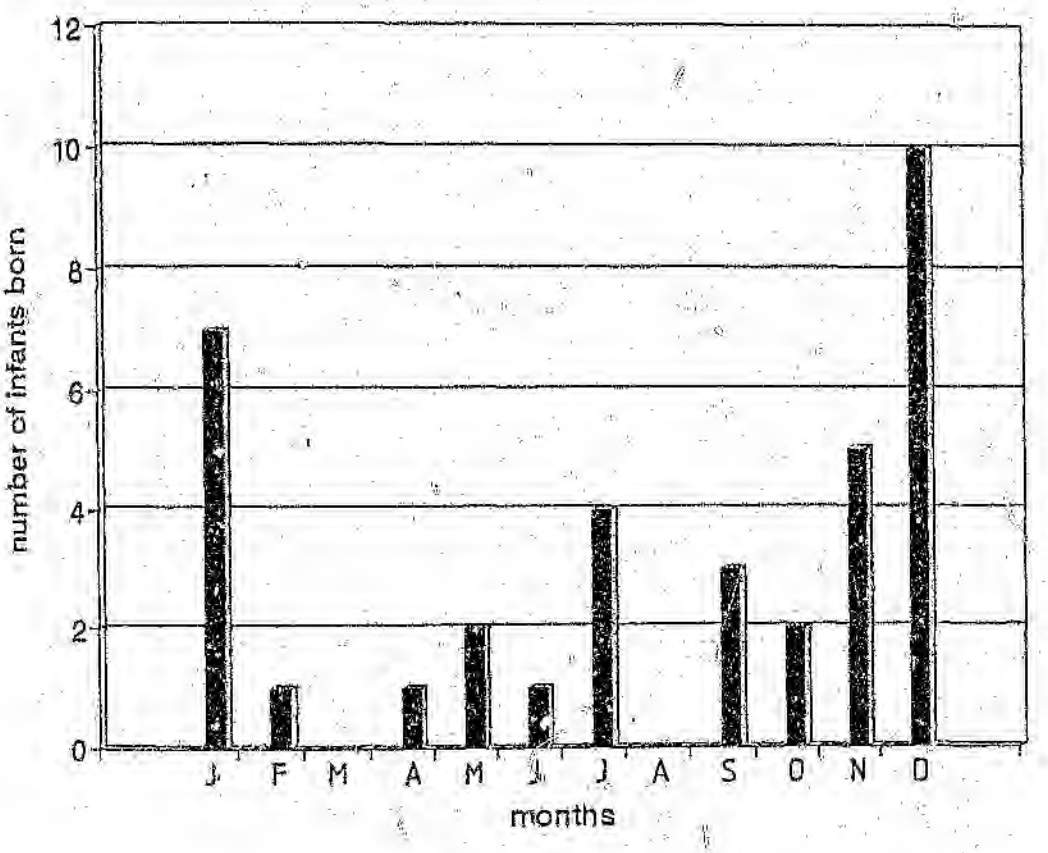


Figure 2.3 Birth periods of infants in the Lower troop.

The mean duration of the interbirth intervals (where interbirth intervals were known to the day) for adult females (n = 7) whose infants died soon after birth (see Table 2.2) was 323 ± 57 days ($\bar{x}$ ± SD). For the females whose infants survived and subsequently gave birth to another infant during the study (see Table 2.2), a mean interbirth interval of 27 ± 6 months ($\bar{x}$ ± SD) was calculated.

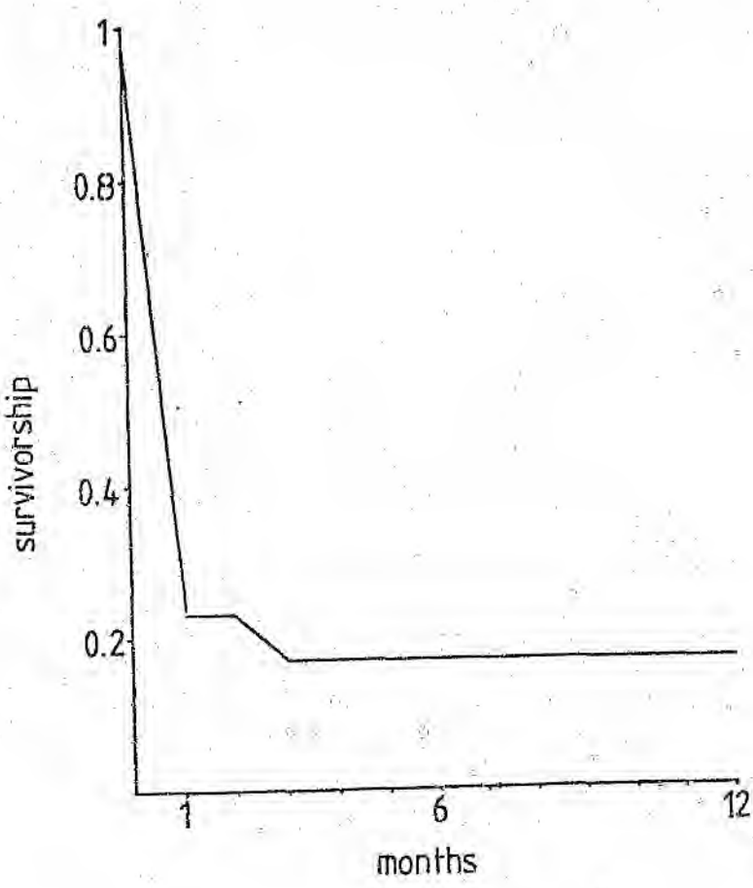


Figure 2.3. Survivorship (proportion of infants born surviving to a specific age in months) curve for infants (n=29) born in the Lower troop from December 1986 to December 1991.

Unlike the adult females in this troop, adult male numbers fluctuated as a result of immigration, emigration and death (Table 2.1; Chapter 6). Three of the four adult males who died following fights were recovered for autopsy soon after death. One male died from a severe purulent peritonitis following a left abdominal puncture wound, and another from blood loss resulting from canine-inflicted gashes to his neck, head and chest. Another died following a particularly violent fight in which a large part of his maxilla, including two incisors, a canine and a premolar was literally bitten off by his rival. He deteriorated rapidly, stumbled into a hollow and fell onto a large (1.9m) black spitting cobra (Naja nigricolis) which appeared to strike the weakened baboon twice. He died soon thereafter. One sub-adult male with particularly bad tick related lesions extending around his neck, back of his head and mandible was having difficulty eating and moving at the time of his disappearance and is presumed to have died. I subsequently discovered the remains of a sub-adult male in the nearby area matching the features of the one who disappeared.

DISCUSSION

My results show that like other species of large mammals (Smithers, 1983), the age-specific death rate was higher for infants and adult males than for juveniles or adult females.

However, an infant mortality rate over 6 years of 0.86 for the first three months of life recorded here is far in excess of the infant mortality rate of 0.3 reported for Papio cynocephalus (Altmann et al, 1977) or any other non-human primate population (Dunbar 1988). If a mortality rate for individuals between 2.5 years and 8.5 years of 0.13 - 0.17 per annum, such as reported from cercopithicine populations elsewhere (Sade, Cushing, Cushing, Dunaif, Figueroa, Kaplin , Laurer, Rhodes and Schneider, 1976; Dunbar, 1980) were to occur in the Lower troop, the number of juveniles reaching adulthood would be approximately halved. Consequently, under present conditions, it is not obvious that the troop is self-sustaining and even a slight deterioration in infant/juvenile survival could be catastrophic .

Birth rates amongst non-human primates are known to vary over short periods of time (Dunbar, 1988; Strum and Western, 1982). However, the birth rate of one infant per female every 341 days recorded for my baboons was significantly higher than the 661 days for Papio cynocephalus (Altmann and Altmann, 1970) and the 665 days for Papio anubis (Rowell, 1966) (t test with Bonferroni correction for repeated measures, $p < 0.001$ for both).

This unusually high birth rate is a result of the high incidence of neonatal mortality and corresponding decrease in duration of inter-birth intervals. The duration of corresponding inter-birth intervals for females whose infants survived to one year is consistent with findings elsewhere (Altmann and Altmann, 1970; Altmann et al, 1977) where a post-partum amenorrhea is associated

with lactation. Data on inter-birth intervals for females with surviving infants, although few, suggest an absence of other factors (eg, stress) elevating birth rate.

The demographic data presented here, especially regarding infant deaths, indicated that an unusual and possibly unique interaction of environmental and social variables were at work in this baboon troop. The troop was not in equilibrium so the factors at work were probably leading to its extinction, despite any adaptations that might have occurred. These factors were likely to include variables involving abiotic and biological components, each of which is dealt with in the following chapters.

Chapter Three

Kuiseb River flow and the effect of water availability on baboon travel

INTRODUCTION

Baboons have been living in the Namib desert in an area corresponding to that currently occupied by the Lower troop (Chapter 1) since at least 1837 (Alexander, 1838). Between 1972 and 1992 the Lower troop has maintained an identical range (Hamilton, 1985; Brain, 1990). Similarly, both the climate and vegetation of the area described for this study (Chapter 1) corresponded to that previously reported (Lancaster, Lancaster and Seely, 1984; Theron, van Rooyen, van Rooyen and Jankowitz, 1985).

A demographic study of the Lower troop of baboons in 1979 (Hamilton 1985) showed the troop to have a composition that included 8 juveniles and 2 infants and indicated that no unusually high infant mortality had occurred for the period 1972 - 1979. This contrasts sharply with the unusual troop composition in 1986 (Chapter 2, Table 2.1) and the exceptionally high infant mortality since then (Chapter 2, Table 2.2).

One highly variable factor within the baboons' range covering my years of baboon observation was the annual flooding of the Kuiseb River and the year round water availability thereafter. In turn, water availability was a major determinant of daily movement patterns of the baboons (Brain, 1990; Hamilton and Tilson, 1982). In this chapter I analyze the extent of the changes in these variables (water availability and baboon travel) and indicate how

they might be responsible for the baboons' recent demise (Chapter 2).

STUDY AREA AND METHODS

The baboons and the range occupied by them in the seasonally dry Kuiseb River canyon are detailed in Chapter 1.

Seasonal rains in the 14700 km² inland catchment (Huntley, 1985) of the Kuiseb River resulted in sporadic river flows between December and April during my study. Although flood water remained as pools in the river bed immediately after flow had stopped, pools within the downriver extent (Chapter 1) of the troop's range dried within two months. Only the upper third of the Lower troop's range extended into the section of canyon where active downcutting of the river was still taking place (Blom and Bouwer, 1985). Pools in this section persisted for two to eight months after flooding. Although permanent water was available a few kilometers upriver of the upper boundary of the Lower troop's range, there were periods before the floods when there was no water in the troop's range. As the pools dried and disappeared in the baboons' range, baboons, together with gemsbok (Oryx gazella), spotted hyenas (Crocuta crocuta) and jackal (Canis mesomelas) maintained temporary access to water by digging down to the water table (Hamilton, Buskirk and Buskirk, 1976; Brain, 1990). Each excavation allowed for only one baboon at a time to drink (Brain, 1990).

Blom and Bouwer (1985) determined that the water table in the upriver extent of the Lower troop's range declined at a rate of 0.16m per month between floods and that periods of river flow were critical in recharging the water table. By extrapolating this information into my study period, an examination of bouts of annual Kuiseb River flow would provide an indication of post flood water availability to the baboons during my study.

Timing and flow durations of floods have been measured at Gobabeb since 1966 (Seely, Buskirk, Hamilton and Dixon, 1981; Ward and Breen, 1983). Data from these studies are used here along with my data of river flow at Gobabeb since 1986. To assess the cumulative effect of successive increased/decreased periods of river flow, I took the mean period of river flow over the 1966 - 1992 period (18 days) and expressed each year's flow since 1966 as a deviation from this mean. The deviation from the mean was added to the preceding years value when greater than the mean and subtracted when less than the mean in a cumulative fashion.

To determine the number of days Lower troop baboons spent without drinking between two successive floods and the movement patterns associated with corresponding drinking and non-drinking periods, I moved with the baboons on foot for 231 days (dawn to dusk) between the successive floods in January 1991 and January 1992.

This period was selected in favour of a longer period because of the physical difficulties associated with living with baboons for long periods on end.

Because of the linearity of the baboons range (Chapter 1 - figure 1.1), I was able to accurately determine distances of daily movement. I did this by marking each 500 meters of their 30 kilometre range, and within each 500 meter stretch, measuring the distance between prominent landmarks.

In conjunction with movement data on drinking and non-drinking days, I used scan sampling procedures (Altmann, 1974) to obtain quantitative data on periods the baboons spent resting under the trees. Sampling was carried out at half hourly intervals on days when water was available (n=9) and when it was not (n=9). The two sampling periods occurred at the same time of year and when the same food sources were being used. Climatological data for the two sampling periods were recorded at Gobabeb and compared using the Mann-Whitney U test. Each half hour a sweep was made from one side of the troop to the other recording what each visible animal was doing in as near an instantaneous sample as possible. In the present context the number of animals stationary under the trees were recorded. The median number and ranges of records (counts per scan sample) obtained from half hourly scan samples for each hour (ie, two half hour samples) for the nine days each when water was and was not available were 184 (110 - 230) and 230 (202 - 238) respectively.

All data collected by scan sampling was arcsin-square root transformed prior to statistical (ANCOVA and ANOVA) analysis. Data were transformed because they were percentages with values

close to 0 and 100 percent. The Mann-Whitney U test was used to compare movement data.

RESULTS

Figure 3.1 shows the total days of Kuiseb River flow at Gobabeb each year since 1966. These data (Fig. 3.1) were used to determine the cumulative residual values plotted in Figure 3.2, and Figure 3.2 demonstrates the cumulative effect of decreased river flow in recent years.

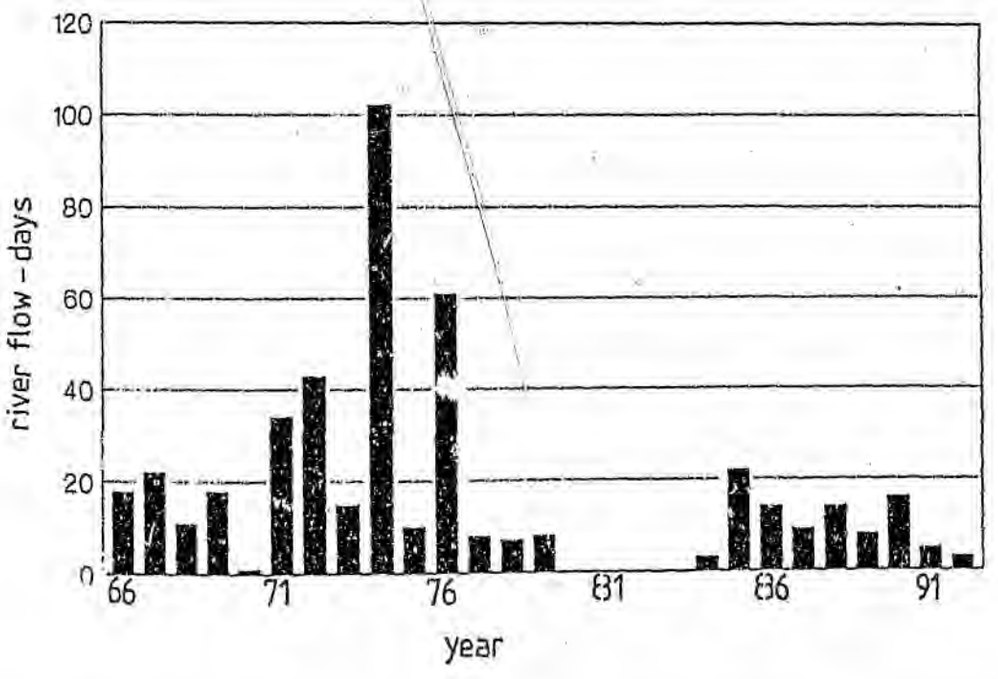


Figure 3.1. Total days of Kuiseb River flow at Gobabeb from 1966 to 1992. Data for the period 1966 to 1986 from Ward and Seely (1989). Data from 1986 to 1992 from Brain (unpub. data).

since 1986 the baboons have had to excavate for water each year for several months prior to flooding. For 1989, 1990 and 1991, unlike any previously recorded years (1972 - 1988 [Hamilton, 1985; Brain, 1988]) when excavations never dried up prior to flooding, excavations were dry by late December and the baboons were without water until the next flood. In 1992, all excavations were dry by October and the baboons were without water until the flood arrived on 29 January 1993.

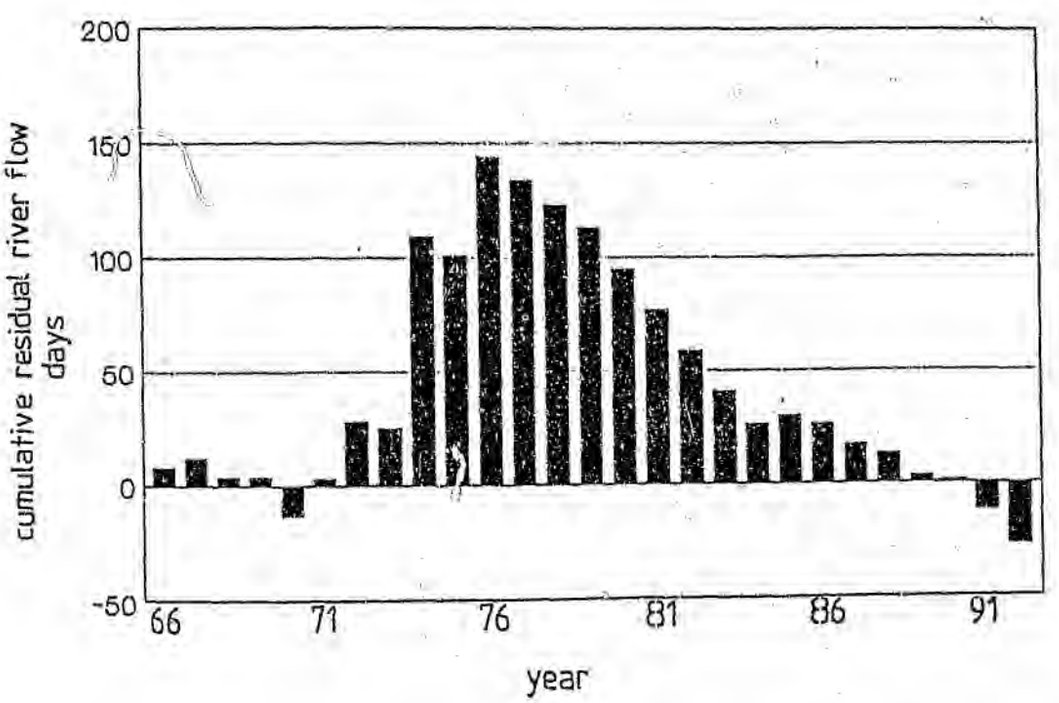


Figure 3.2. The cumulative residual river flow days for the Kuiseb River calculated from days of annual river flow from 1966 to 1992.

In 231 observation days between January 1990 to end January 1991, the baboons spent a total of 104 days (range of continuous period = 1 - 26 days) without drinking. Single day non-drinking periods occurred as early as April when the baboons left localised water sources to feed further downriver. The number and duration of non-drinking periods are shown schematically in Figure 3.3. Maximum continuous non-drinking periods of 13 and 26 days occurred only after November. In other years since 1986, non-drinking periods of 7,8,9,11 and 20 days were recorded from November onwards (Brain, 1988), but these were spot observations and do not represent a comprehensive record. In 1992, after the last water dried in October, the baboons went for 116 days without drinking (Brain, unpub. data).

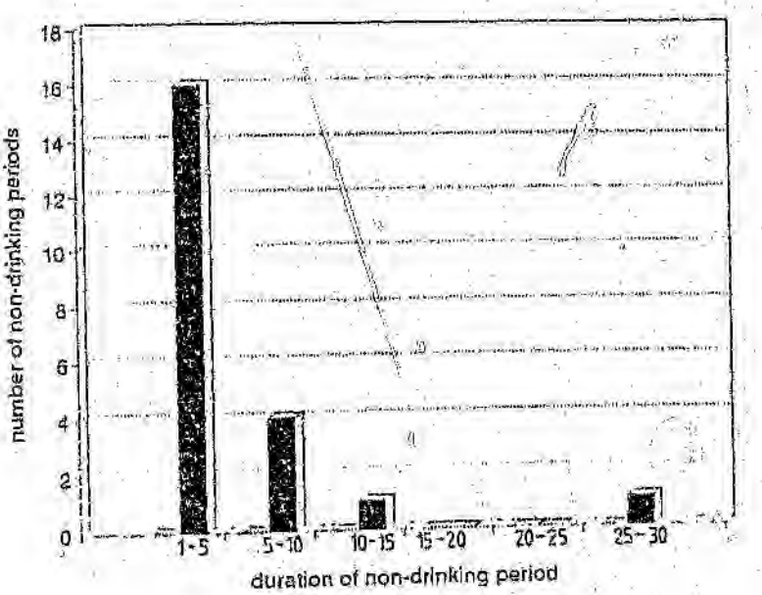


Figure 3.3. Schematic representation of the number and duration of non-drinking periods from January 1990 to January 1991.

Lower troop baboons moved shorter daily distances on non-drinking days (n = 29; median = 1.8km; range 0.7 - 4.6km) than on days when water was drunk (n = 19; median = 6.5km; range 2 - 15km) (Mann-Whitney U test, Z = 5.28, $p < 0.001$). The mean daily maximum temperature for the non-drinking and drinking periods was 28.7°C ± 6.7°C and 30.6°C ± 4°C (x ± SD). There was no significant difference between the maximum daily temperatures of the non-drinking and drinking periods (Mann-Whitney U test; Z = 0.811, $p > 0.4$). For the 26 day continuous non-drinking period, the baboons moved significantly shorter daily distances (median = 1 km; range 0.5 - 3km) than previously recorded on non-drinking days (Mann-Whitney U test; Z = 3.9, $p < 0.001$). Similarly, there was no significant difference between the maximum daily temperatures of these non-drinking periods (Mann-Whitney U test; Z = 1.4, $p > 0.1$).

Besides moving shorter distances, significantly more baboons remained stationary under trees at various times throughout the day on non-drinking days compared to drinking days (Fig. 3.4; ANCOVA; covariate = hours; F = 54.3; $p < 0.001$; residual df = 443). Using the Tukey test for ANOVA, significant ($P < 0.05$) differences were found between the two sampling periods for 10H00- 11H00, 11H00-12H00, 12H00-13H00 and 14H00-15H00 (Fig.3.4). There was no significant difference between the maximum daily temperatures of the two sampling periods (Mann-Whitney U test; Z = 1.15, $p > 0.3$).

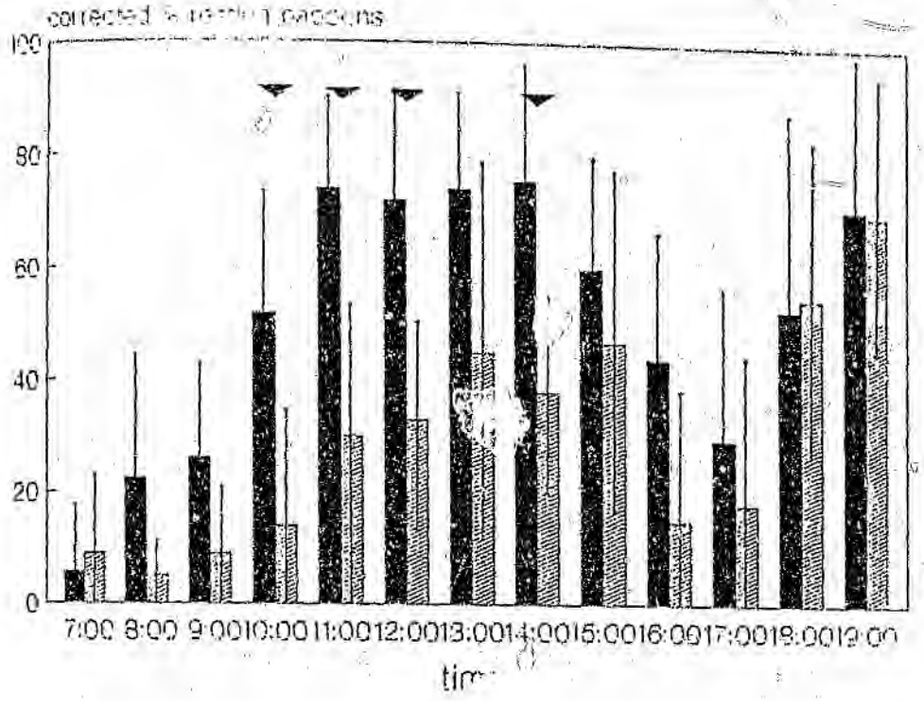


Figure 3.4. Percentage of baboons stationary under trees at various times throughout the day for periods when water was available (hatched bars, n = 9 days) and when it was not (shaded bars, n = 9 days). Vertical lines indicate SD. The values plotted at the hour are the values for the succeeding hour (eg, 7 - 8 at 7:00). Arrows indicate significant differences. See text for sample sizes and sampling procedures.

DISCUSSION

For the duration of my study and the ten years prior to it, days of Kuiseb River flow each year have been below the mean or absent (Figs. 3.1 and 3.2). Since 1986 the baboons have not had water

available to them for periods between river floods and have not been able to maintain viable excavations to water.

With the clear difference in movement patterns of these baboons associated with water availability, it could be hypothesised that in previous years when more water was available to the troop, that the troop (possibly with different individuals) moved greater daily distances and spent less time stationary under trees. Other than the problems of sufficient food and moisture acquisition that decreased movement could induce (see Chapter 7), it is not intuitively obvious that the findings of decreased water availability and movement reported here would be the major underlying factor to the unusually high infant mortality in the Lower troop (Chapter 2). Any dramatic decline in baboon food availability, quality or reduced access to food plants as a result of decreased water availability would have been expected to manifested itself in the baboons at least through loss of condition with decreased reproduction. This appeared not to be the case because the baboons apparently maintained body condition throughout the study and for adult females, reproductive performance was not affected (Brain, 1992; Chapter 2, Table 2.2).

Savanna baboons elsewhere in arid habitats, when faced with water shortages or drought increase their distance of daily travel in order to reach food and water sources (Hall, 1963; Stoltz and Saayman, 1970; Anderson, 1981). Consequently, for baboon populations in arid habitats, dry seasons have been associated with increased movements for the acquisition of sufficient food

and water. Deaths during these periods usually result from malnutrition and starvation (Dunbar, 1988). Decreased movement and lethargy under food (not water) shortages in free-ranging conditions has been reported for baboons (Hall, 1963) and macaques (Dittus 1980), but appear to have had the expected consequences of starvation and weight loss only.

It is only when the actual major cause of infant death in the Kuiseb baboon troop, ie, ectoparasite infestation (Chapter 2), is considered that a potential link between water availability and infant mortality becomes apparent. Ectoparasite infestations of animals are frequently associated with animal(s) movement, or the lack thereof, in infested areas (Howell, Walker and Nevill, 1978; Horak, 1982). Any factor resulting in more time being spent by the animal(s) in ectoparasite infested areas will increase the likelihood of the animals acquiring a greater infestation. For the Kuiseb baboons, decreased free water availability was associated with increased stationary time in certain shaded areas. However, without knowledge of the ectoparasites themselves, the pathology associated with infestation and the relative abundance and distribution of the parasites, the significance of the decreased movement can not be fully appreciated. These topics are covered in the following chapter.

Chapter Four

Tick infestation and endoparasites of the Kuiseb baboons

INTRODUCTION

Tick infestations, skin lesions and skin diseases of baboons are rare (McConnell, Basson, DeVos, Meyers and Kuntz, 1974). Findings of a near absence of ticks on baboons (Kuntz and Meyers, 1967; McConnell et al, 1974; Strum, 1987) have led to suggestions that mutual grooming may account for this near absence of ticks (Seyfarth, 1977; Silk, 1987). Tick infestations have not previously been implicated as a major cause of mortalities amongst baboons. Chacma baboons comprising the Lower troop of Kuiseb baboons (Chapter 1) were heavily infested with ticks (Brain and Bohrmann, 1992). Characteristic of this baboon troop was the exceptionally high infant mortality (Brain, 1992 and Chapter 2) where I determined that the majority of deaths resulted from tick infestations.

Factors related to ectoparasite infestation by primates under natural conditions also predispose the animals to endoparasites (Hausfater and Meade, 1982). Considering the severity of tick infestation of the Lower troop baboons I thought they might have a marked endoparasite infestation as well.

In this chapter I examine the tick infestation of the baboons, its associated pathology and the endoparasites of these baboons. Ticks were identified and their relative abundance within certain areas of the baboons range determined.

Study area and methods

The baboons studied here were the Lower troop of baboons inhabiting the Kuiseb River canyon in the central Namib Desert, Namibia (Chapter 1).

The pathology associated with tick infestations was determined by post mortem examinations. One dead infant was recovered soon after death (< 5 hours). The apparent similarity of visible gross pathology of the infant examined and other infants that died led me to conclude that the cause of death was similar in all instances. I could not physically examine all the dead infants because the dead infants were carried around by troop members and it was not possible to recover them. Three adult males were examined immediately following their deaths in dominance fights. Samples for histopathology were taken from all areas of macropathology and preserved in 10 percent formalin and blood smears from all the dead baboons (and those immobilized - Chapter 8) were examined for parasites. All adult ticks were removed from the baboons, counted and preserved in alcohol for later identification. Ticks were identified in the laboratory at the Veterinary Research Institute, Onderstepoort, Republic of South Africa, and the Central Veterinary Laboratory, Windhoek, Namibia.

Ticks were collected in June 1990 within the Lower troop's approximate 30km linear range. A $1m^2$ flannel cloth (flag)

attached to one end of a 1.8m wooden stick was dragged over shrub vegetation at a slow walk. The speed of the walk could be kept approximately constant over different terrains. Eight areas with similar plant cover, plant species composition and with similar physical features were selected for sampling within the baboons range. In each area, measuring approximately 500m by 200m, ten randomly chosen runs of 20m each were sampled. At the end of a 20m stretch ticks were picked off the cloth, counted and preserved in alcohol for later identification. The median number (and range) and total number of ticks collected was calculated for each area (n=8). The total number of ticks collected in each area was correlated to the number of days the baboons had spent in that area over the preceding three months (a period well within the lifespan of Rhipicephalus ticks [Horak, 1982]) using Spearman's Rank Correlation statistical procedure.

Tick were also sought in other areas used by the baboons and where possible, tick association with other mammal species in the area assessed. Two sleeping cliffs regularly used by the baboons were searched for ticks. Domestic goats, cattle and horses that occasionally fed in the downriver limits of the troop's range were also frequently (about twice monthly) examined for ticks and any morbidity or mortality ascribed to tick infestation noted.

To determine what endoparasites were present in the baboons, I collected ninety-four fresh scat samples from all juvenile and adult members of the Lower troop over an 11 month period from February 1990 to January 1991. A mean of 4.9 ± 2.6 replicate

samples were collected from each animal. All samples were analyzed for gastro-intestinal parasite cysts, eggs and larvae using the M.I.F. (Methiolate Iodine Formalin) technique of Sapero and Lawless (1953).

I examined blood smears from six lower troop baboons placing emphasis on the presence of blood parasites and erythrocyte dyscrasis.

RESULTS

Ectoparasites

The infant obtained for post-mortem examination harboured 70 adult ticks, most infesting the muzzle and showed acute inflammation of the nose and mouth (Fig. 4.1).

Tick infestations of infants that died all followed similar sequences. Infants acquired ticks on their muzzles while the baboons rested under trees in the river. The numbers of ticks increased rapidly as more ticks crawled on from the surroundings to a point where, after successive rest periods, the infants were observed to be unable to suckle and died, presumably from dehydration or starvation. The situation for infant suckling was worsened in some cases ($n=4$) through infestation and partial sloughing of the mother's teats, and in all such cases the infant died within a week. In no cases of tick infestation of infants did I see any attempt by the mother to groom ticks off her infant.



Figure 4.1. Tick infestation of an infant's muzzle resulted in acute inflammation of the nose and mouth inhibiting the infant from suckling.

In November 1991, the two Lower troop infants, aged two and 11 months, developed severe tick infestations of nose and mouth during a period when the baboon troop was without water and spending all their time around one fig tree (location 7.6km -

Chapter 1). These infestations visibly intensified during this period so that by the eighteenth day without water the two month old infant was having difficulty suckling. Her mother frequently had to hold the infant on her ventrum while walking and the infant's head hung down limply. On the twentieth day without water, an isolated rainstorm filled a pool up in the canyon. The baboons immediately left the fig tree and moved to the rain pool 7km further upstream, and for a week thereafter drank daily and ranged the canyon sides for food. Both infants improved dramatically as engorged ticks dropped off and infants were not reinfested with other ticks. However, once the rain pool dried, the baboons again returned to and concentrated their time around the same tree. Within two days the infants again developed massive tick infestations, and a third infant born during the week died within three days with an infested muzzle.

The two adult male baboons examined each carried more than 400 adult ticks, the majority (> 60%) attached to their ears (Figs. 4.2 and 4.3). Histopathologically the pinnae showed prominent chronic inflammation with epidermal acanthosis and exudative crusting. The number of eosinophiles was clearly increased.

Blood parasites

Blood smears examined microscopically were all negative for blood parasites.

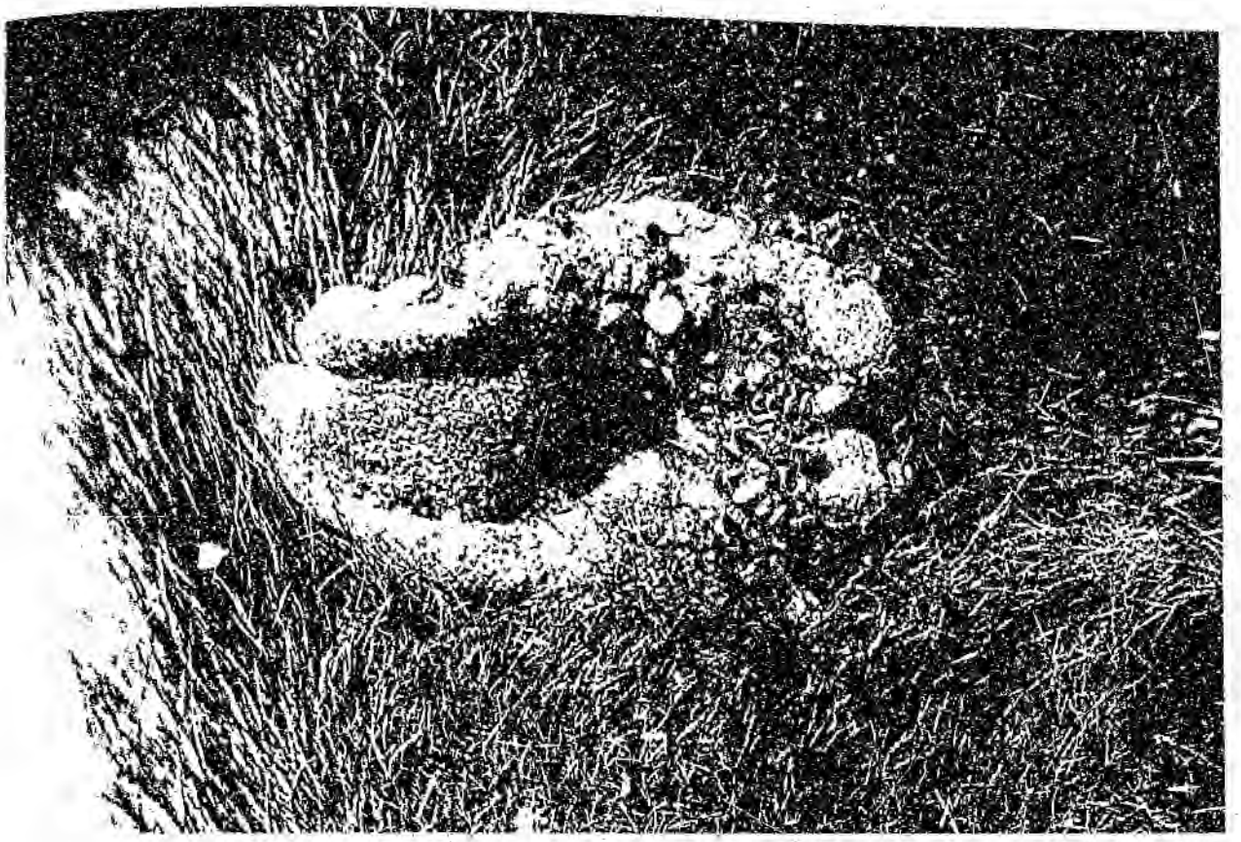


Figure 8.2. Ticks attached to the ear of an adult male baboon.

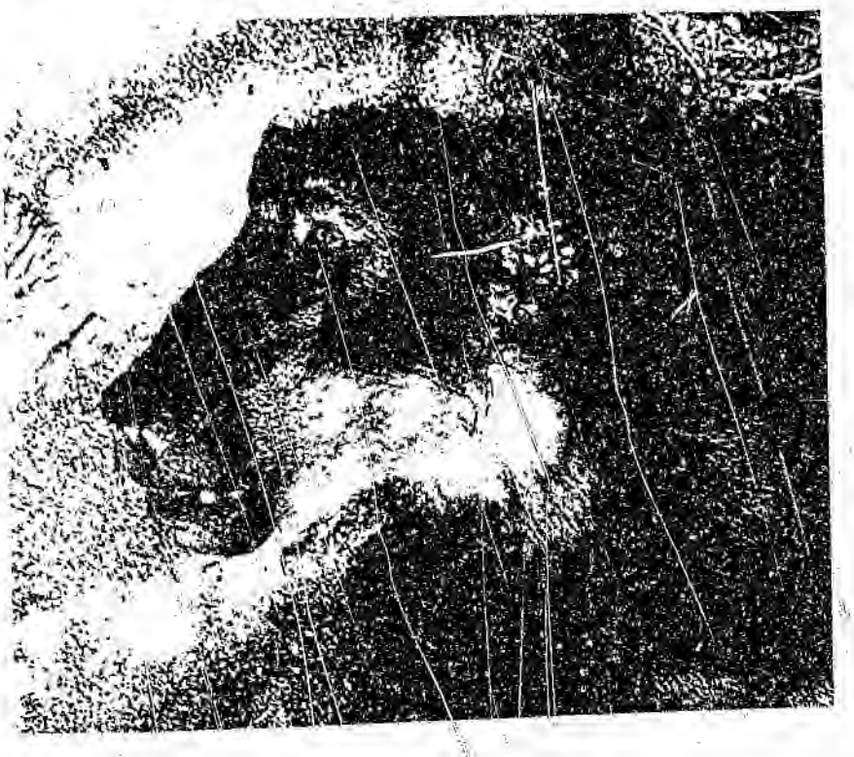


Figure 8.3. Tick infestation of the ear of an adult male baboon. (Baboon under Ketamine anaesthetic. Photo: G. Mauney).

The median and total number of ticks sampled within areas of the baboons range by flagging, the location of those areas and the number of days the baboons had spent in those areas in the preceeding three months are shown in Table 4.1. A strong correlation (r = 0.97, n = 8, p <0.05, Spearman's Rank correlation) exists between days spent in an area and the tick infestation thereof. (Total number of ticks sampled in an area, not median number, was correlated to days spent in the area because 4/8 median numbers were tied - Table 4.1)

Kilometre of range	Days in area	Median number and range (in parentheses) of ticks collected	Total number of ticks
2	2	1 (0-5)	10
7.6	17	9 (0-53)	109
9.4	15	3 (0-30)	64
13.4	2	1 (0-4)	14
17.2	18	5 (0-57)	104
22.1	6	1 (0-24)	43
24.4	4	1 (0-8)	25
26.4	0	0 (0-1)	1

Table 4.1. The location within the baboon troop's range (expressed in km upstream from the downriver limit of their range) where tick numbers were sampled, the median number and range (in parentheses) of ticks collected within an area and the number of days the baboons were observed to spend in those areas in the preceding three months, and the total number of ticks found in sampling each area.

few ticks were found on those sleeping cliffs inspected (n=4) and at no time did any of the domestic animals that were inspected yield more than 20 ticks per animal. All ticks collected, both by flagging and from baboons were, with one exception, of the same species and identified as Rhipicephalus gertrudae or a very similar species. The one exception was a specimen of Hyalomma marginatum rufipes found in the river bed within the baboon's range but not in one of the areas selected for flagging.

Endoparasites

Table 4.2 shows that 13 species of endoparasites were found in scats of baboons in the Lower troop (Appleton and Brain,pers.comm.). The majority of species (10/13) were protozoans, mostly amoebae while only three helminths were found in the scat samples. This constitutes an assemblage largely similar to that found in man (Sargeaunt, Williams and Jones, 1982).

Two protozoan exceptions to the usual assemblage of man found in the baboon scats were (i) Entamoeba chatteni, viz. mononucleate cysts with a mean diameter of 12.1 µm (see Sargeaunt et al, 1982) and (ii) the sporocysts of an unidentified coccidean, possibly Isospora sp. This species had the second highest prevalence (Table 4.2). Syporocysts recovered from faecal concentrations measured 14.2 ± 3.2 x 10.2 ± 1.7mm (x ± SD) (n=10). This was slightly smaller than those of Isospora papionis, the only coccidean known from baboons (McConnell, de Vos, Busson and de

Vos, 1971), but unlike McConnell's species, these were common in faecal concentrates.

Gastro-intestinal parasite	Number of baboons positive
Ancylostoma duodenale *	2
Balantidium coli	7
Chilomastix mesnili	10
Endolimax nana	3
Entamoeba coli	16
Entamoeba hartmanni	11
Entamoeba histolytica	4
Giardia duodenale	4
undetermined mononuclear cysts	11
Iodamoeba buetschlii	8
Isospora ?	12
Streptopharagus pigmentatus *	10
Strongyloides *	1

Table 4.2. List of gastro-intestinal parasites recorded in scats from the Kuiseb baboons (n=17) over an 11 month period from February 1990 to January 1991. Numbers indicate 'positive in every scat' and astrixes indicate nematode species.

All three helminths found in the scats were nematodes (Table 4.2). The hookworm eggs were unembryonated and relatively small, measuring 57 ± 6.5 x 45.3 ± 1.5mm ($\bar{x}$ ± SD; n = 4). Following Goldsmid (1967, 1968) they conformed to Necator americanus but it is unwise to allocate such a small sample to any genus. The

rhabdiform larvae of Strongyloides measured 252.0 x 14.4mm (oesophagus length 48.0mm). Their presence suggested S. stercoralis.

DISCUSSION

Ectoparasites

Ectoparasite data indicated that for the study period ticks were closely associated with the baboons' day to day living. The characteristic ear lesions, now known to be caused by tick infestations, were observed on all Lower troop baboons since the earliest recorded observations in 1972 (Hamilton, 1985), but only when observations resumed in 1986 were infants found to be dying as a consequence of infestations. Although the life cycle and intermediate hosts for Rhipicepalus gertrudae are not yet known, the areas of regular and repeated use by the baboons appeared to have relatively higher tick numbers (Table 4.1). It was also clear that ticks occurred in varying numbers at all the sites sampled and that the possibility existed for baboons to acquire ticks in any of these areas. Baboon tick infestation would be greatly enhanced by the baboons spending prolonged stationary time under the trees as the Rhipicephalus ticks are attracted by exhaled CO (Howell et al, 1978). The major factor affecting travel or the lack thereof during the study appeared to be water availability (see Chapter 3). The chance happening reported here, where a prolonged inactive non-drinking period for the

baboons was suddenly broken and tick infestations of infants were visibly reduced only to recur once activity ceased again, provided further evidence linking movement patterns and tick infestations.

It therefore appears that in recent years (since 1979 - Hamilton, 1985) a trend of increased infant mortality has occurred in this troop of baboons (Chapter 2). Coinciding with this period has been a steadily decreasing amount of water available to the baboons (Chapter 3). Data here provide a link between the two, not only by highlighting the incidence of the ticks, but by identifying the host attachment sites of Rhipicephalus gertrudae which proved fatal to most infants. Consequently I am proposing that ticks were a major factor regulating infant survival for this population of baboons. This is the first time such a relationship has been proposed between primates and ectoparasites.

Although many other species of large mammals, including spotted hyaena (Crocuta crocuta), jackal (Canis mesomelas), African wildcat (Felis lybica), gemsbok (Oryx gazella), steenbuck (Raphicerus campestris) and klipspringer (Oreotragus oreotragus), live in the baboons' range, none showed any visible signs of tick infestation as seen on the baboons, but none were closely examined for parasites and their possible role as hosts of Rhipicephalus gertrudae was unknown. Similarly, stock we inspected carried relatively few ticks but whether or not these

animals can maintain tick populations in the desert area is still uncertain.

Although Hyalomma sp. ticks are generally very well adapted to arid and semi-arid environments (Theiler, 1956, 1962; Knight et al., 1978), only one was collected. All other ticks collected were morphologically similar and closely related to Rhipicephalus gertrudae. Although the taxonomic status of many Rhipicephalus sp. ticks has caused problems in the past, the situation is becoming clearer (Theiler, 1950; Fedlmann-Munsam, 1960; Biggs and Langenhoven, 1984; Pegram and Walker, 1988). Rhipicephalus gertrudae-like ticks have been found in parts of the Namib desert before (J.B. Walker, pers. comm.), but the details of the life-cycle and intermediate hosts are not known for the desert environment.

Endoparasites

The protozoan-dominated parasite assemblage of the Lower troop baboons contrasts to the helminth-dominated ones of Papio cynocephalus ursinus in wetter parts of Southern Africa, viz Natal and Transvaal (Appleton et al., 1986; Goldsmid and Rogers, 1978). This difference may be explained by the specific modes of transmission of the parasites and the desert environment. All except the three helminths, Streptopharagus pigmentatus, hookworm and Strongyloides, can be transmitted without having to pass through an obligatory developmental phase outside their host.

In other words, while they may be tolerant of the prevailing environmental conditions, they can all, with three exceptions, also be transmitted from one host to another via the "hand to mouth" route. It seems probable that this transmission can be effected through allo-grooming, particularly of the peri-anal area, thus avoiding any prolonged exposure to the environment.

Streptopharagus pigmentatus

The spiruroid Streptopharagus pigmentatus, the most common helminth in the Kuiseb baboon scats, uses an arthropod intermediate host and orthopterans are likely candidates (Appleton and Brain, pers. comm.). Insect species commonly eaten by these baboons are in fact both orthopterans: the cricket Brachytrupes membranaceus and the locust Schistocerca gregaria (Hamilton, 1986; Chapter 7). During outbreaks of the latter, the baboons eat little else (Brain, unpub data).

Hookworm

Hookworm live in soil and Smith (1990) indicated shaded soil is a more likely site for hookworm transmission than exposed soil (see Smith, 1990). Shaded soil under trees in the Kuiseb was not subject to the vast temperature fluctuations of exposed soil (Appleton and Brain, pers.comm) but gives an almost constant thermal environment of approximately 24°C at a two centimeter sub-surface depth. At this temperature, eggs will probably hatch

and develop to L3 (third larval stage) within a week to 10 days provided soil moisture levels remain around 20% - 30% (Smith, 1990). In the Kuiseb, with an average annual rainfall of 27mm and the very high evaporation rates of 7-10mm day (Lancaster et al, 1984), it is unlikely that upper soil layers will retain moisture for even two weeks after rain/river flow has ceased. Also, the silt deposited under trees by the flood water becomes very compact and hard as it dries (Ward, 1987).

Transmission in situations of high soil moisture content could perhaps occur if the maturation of parasites acquired during one rainy season was to be arrested and egg-releases timed precisely to coincide with the next rainy period. Such arrested development in response to unfavourable environmental conditions has been proposed for Ancylostoma duodenale by Schad et al., (1973). Meade (1983) concluded that in Kenya, waterholes were not important in helminth transmission but could be for protozoans.

The fact that only two baboons - an adult female and her two-year-old daughter - were infected with hookworm strongly suggests an alternative mode of transmission, i.e. vertically, via the trans-mammary route, by a few infected females whose offspring rarely survive. The infant mortality rate is high (Brain 1992; Chapter 2). Clear evidence for vertical transmission of hookworm in man is scarce but Schad (1991) believes that it does occur.

The presence of hookworm and Strongyloides, albeit rare, shows that strongyles can survive here, despite the vulnerability to desiccation of their thin-shelled eggs and free-living larvae (Smith 1990).

Strongyloides

Damp sand at water sources in the Kuiseb canyon may also be a transmission site for S. stercoralis, though possibly only for the first few weeks after the brief annual flood. The conductivity of the interstitial water will be low immediately after rain but will rise with time to levels around 1425µS cm (= total dissolved solid loading of 991ppm, mostly Na) (van Wyk, Opperman and Kok, 1985). This would lower the osmotic gradient between the egg and the outside medium and so interfere with the hatching of eggs. It may also affect the growth of bacteria on which both hookworm and Strongyloides larvae must feed.

The other possible alternative route to soil transmission is trans-mammary transmission which, although not known for S. stercoralia, was reported for S. fulleborni in man by Brown and Girardeau (1977).

Trichuris

The absence of Trichuris from the Kuiseb baboons is surprising as Trichuris is a common endoparasite of baboons elsewhere in

Southern Africa (Appleton et.al., 1991). The critical period for this nematode would seem to be the 3-5 week period that its eggs need to be in soil for the morula to develop to the third larval stage and be carried to a new host. Beer (1973) showed for the closely related T. suis that this development period varied with temperature from 19 days at 34°C to 37 days at 25°C. At 20°C development was dramatically retarded and took 102 days. Infection would have to occur within the few months following development to L3 since the larvae did not survive much longer.

Soil temperatures beneath trees might thus be favourable for nematode (i.e. Trichuris, hookworm and Strongyloides) development (Appleton and Brain, pers. comm.), but the moisture levels in the upper layer of the soil are unlikely to be adequate for long enough. Soil moisture may well be the "limiting factor" accounting for the absence of many parasites infecting baboons elsewhere and which cannot be transmitted vertically, hand-to-mouth or by means of an intermediate host, but until data are available on soil moisture levels throughout the year, soil moisture as limiting factor remains speculative.

Blood parasites of baboons living elsewhere in Southern Africa appear to be rare and in 100 baboons examined from the Kruger National Park, only three showed infection of Hepatocystis simiae (McConnell et al, 1974). Also, because the life cycle of Hepatocystis is predominantly exoerythrocytic, the rings and gametocyte forms of the parasite are often scarce in the peripheral blood of infected individuals (Kuntz and Myers, 1967)

and the parasites can easily be missed in individuals with low levels of parasitaemia. Thus, the incidence of the parasite in a population is probably underestimated and I cannot be absolutely sure that baboons of the Lower troop are free from low levels of Hepatocystis parasitaemia.

Chapter Five

Fatal infant kidnapping in the Kuiseb baboon troop

INTRODUCTION

Maternal care of offspring and mother-infant relationships in non-human primates are well documented and widespread phenomena (Altmann, 1980). The relationship between primate infants and other female members of a conspecific group is more puzzling. Universally, primate neonates are objects of attention, and especially females are attracted to neonates (Altmann, 1980). If a female other than the mother takes possession of the infants for any amount of time it is referred to in the non-human primate literature as "aunting" (Rowell, Hinde and Spencer-Booth, 1964). This nomenclature does not necessarily designate any genetic relationship although it does not preclude it.

Within and between species of primates, individual mothers vary as to the freedom that they allow potential aunts (Hrdy, 1976). Four non-human primate species are remarkable for their permissiveness, Presbytis entellus (Jay, 1962), Colobus guereza (Wooldridge, 1969), Presbytis obscuros (Badham, 1967) and Pygathrix nemaeus (Hill, 1972). These primate mothers allow their infants to be held by other group members and to be carried off some distance away from them within hours after birth. In other species in which aunting is common, the first aunting episode is substantially later, approximately 8 days for Cercopithicus aethiops (Lancaster, 1971) and 2-3 weeks in Macaca mulatta (Rowell, et al, 1964). In most species where aunting has been reported, maternal supervision of aunts has also been

reported (Dumond, 1968; Bourliere, Hunkeler and Bertrand, 1970; Lancaster, 1971) and at the first sign of infant distress, the mother usually retrieves her baby. Savanna baboons (genus Papio), epitomize possessive mothers and the only interaction a baboon mother will normally allow troop members to have with her infant is "greeting" (Hall, 1963). Although aunting behaviour has been observed in baboons (Cheney, 1978), the time spent by infants with other females away from their mothers is very short (Nicolson, 1987).

Besides the possible harm or injuries an infant might suffer as a result of clumsy aunting (Gartlan, 1969; Hrdy, 1976), the most serious result of aunting occurs when females take unweaned infants and do not return them. This is referred to as "aunting to death" or fatal kidnapping (Hrdy, 1976). Such behaviour is extremely rare amongst non-human primates with only isolated reports for wild cercopithicenes (guenons - Bourliere, et al, 1970; baboons - Strum, 1975; Collins, Busse and Goodall, 1984; macaques - Quaitt, 1979).

The contrary was true for the baboons living in the Kuiseb River canyon (Chapter 2). In this troop, fatal infant kidnapping occurred regularly and was the most common cause of death for infants born to low-ranking females.

In this chapter I examine the fatal infant kidnappings that occurred in this troop and discuss the events which may have

resulted in the high incidence of this unusual behaviour in this troop of baboons.

METHODS

The data were collected as part of the demographic study detailed in Chapter 2. I monitored (see Chapter 1) each mother-infant pair closely for the first three weeks following birth. When an infant was kidnapped, I recorded the identity of the kidnapper and the events during and immediately after the actual kidnapping. The subsequent behaviour of the kidnapping female, the mother and the infant were recorded until the infant died. The sex of all kidnapped infants was determined prior to their deaths.

RESULTS

A summary of all kidnapping events taking place from 1989 through 1992 is shown in Table 5.1. Only infants of the lower four (of seven) ranking females were kidnapped and only the number two (Am) and three (Co) ranking females kidnapped infants.

Birth Date	Mother	Infant sex	Kidnap date	Kidnapped by	Birth-kidnap days	Kidnap-death days
8-11-89	Ha (4)	male	23-11-89	Am (2)	15	1
19-4-90	Gr (6)	female	23-4-90	Co (3)	4	4
3-5-90	Sp (7)	male	4-5-90	Co (3)	1	3
29-9-90	Bo (5)	female	29-9-90	Co (3)	0	1
11-11-90	Ha (4)	female	11-11-90	Co (3)	0	2
14-5-91	Bo (5)	male	15-5-91	Co (3)	1	3
7-1-92	Ha (4)	male	11-1-92	Am (2)	4	2
29-9-92	Ha (4)	female	1-11-92	Am (2)	33	2
9-11-92	Sp (7)	male	16-12-92	Am (2)	37	2

Table 5.1. Summary of infant kidnappings in the Lower troop. The rank of adult females is bracketed.

The two females who kidnapped infants had different methods of taking infants: Co forcibly removed the infants from the mother by pulling the infant from the mother's ventrum as she attacked the mother. Co would frequently bite the mother on the back just prior to grabbing the infant. Once she had the infant, she would attack and bite the mother if the mother came within her reach. Characteristically, after the kidnapping event, the mother would remain a few meters away from Co and the mother apparently communicated with her infant through lipsmacking. Co appeared to care for the infant, grooming it and allowing it to suckle but she was apparently without milk on each kidnapping occasion. Following the death of each kidnapped infant, Co carried the dead infant around for periods from 0 - 2 days and was observed eating one infant after its death. The mothers were not observed to pick up their dead infants after Co had left them.

Am kidnapped infants by waiting for them to be slightly separated from their mothers and then running by and scooping the infants up in her arms. Am's technique of kidnapping necessarily required the infants to be older than for Co and the durations of birth dates to kidnap dates for the two kidnapping females (Table 5.1) supports this and were significantly different (Mann-Whitney U test; $Z = 2.23$; $p < 0.05$; $n = 9$). After the kidnapping event, if the mother came too close to Am, she would attack the mother as was seen for Co. Similarly to Co, Am appeared to care for the kidnapped infants, but she too was apparently without milk on each occasion. Once the infants died, Am continued to

carry them for 3 - 5 days and was not observed to eat any dead infants.

Kidnapped infants, within hours after being kidnapped, would start giving distress cries as they attempted to suckle. Despite this, on no occasion was a mother observed trying to retrieve her infant from the kidnapper. Kidnapped infants quickly weakened and their skin colour turned an ashen grey prior to death, presumably as a result of starvation and dehydration. Tick infestations of infants (Chapter 4) were not implicated in any of the kidnapped infant deaths. All infants died within four days of being kidnapped.

DISCUSSION

Female-infant interactions presented here had effects on at least three individuals - the infant, its mother and the kidnapping female. The effect on the infant in this study was the clearest and always the same - death. The effects on the two adult females involved was less obvious.

Evidence from populations elsewhere suggest aunting behaviour, similar to that reported here, to be an aspect of female-female competition (Nicolson, 1987). Aggression from high ranking females towards low ranking females and their infants may serve to reinforce the status quo, especially in those species such as

baboons where daughters inherit rank from their mothers and remain in their natal groups throughout adulthood. This interpretation would require the infants who received any form of abuse or aggression such as kidnapping to survive the incident. Thereafter the infants would learn which females rank above their mothers and which females are lower ranking. This explanation seems unlikely in this Kuiseb baboon troop as all the kidnapped infants died.

Another possible function of severe aggression by adult females towards infants of other females is the reduction in the number of competitors for the perpetrator's own offspring (Hrdy, 1976). Although this theory might appear plausible in a desert habitat, especially where competition for sparse resources is often intense (Brain, 1990), it seems unlikely in this baboon troop as neither kidnapping female had any surviving offspring at any stage of this study (see Chapter 2).

In the opinion of Gartlan (1969) and Lancaster (1971), aunting behaviour is practice for motherhood. Amongst other points, this argument rests upon the predominance of nulliparous females participating in aunting behaviour (Hrdy, 1976). This appears to be the case for cercopithecines (Spencer-Booth, 1968a; Lancaster, 1971), but there is no evidence indicating such aunting resulting in infant death (Hrdy, 1976) and is thus not applicable here.

It therefore appears that not only was the occurrence of fatal kidnapping in the Kuiseb baboons unusual, but so too were the factors resulting in it. These factors remain inconclusive but there were likely possibilities. The extremely high infant mortality from causes other than fatal kidnapping was the most striking demographic feature of this baboon troop (Brain, 1990; 1992; Chapters 2 and 3). Numerous observations suggest that this might have been the root cause of the fatal kidnappings.

The females responsible for the kidnappings have to date not had one infant survive to more than a few weeks of age (see Chapter 2). In Japanese macaques and other macaque species, kidnapping may occur when a mother has lost her own infant and she attempts to steal an infant from another female before she herself gives birth to another infant (Itani, 1959). In such cases and where the infant dies, the behaviour of the adult female could best be described as an overzealous allomothering (Nicholson, 1987). Observations that Co and Am attempted to mother and nurse the kidnapped infants suggest that they did not intend to harm them. The infant kidnappings by females without milk were then in all cases lethally inopportune. Had Co been lactating, kidnapping could have meant survival for the infant. However Am suffered partial sloughing of her teats from tick infestation during this study period and would thus probably not be able to suckle an infant even if she had milk (Chapter 3). Aunting and adoption are however known to induce lactation in non-lactating macaques (Hansen, 1966), but this clearly did not happen at all or did not

happen in time in the kidnappings reported here as no infants survived beyond four days of being kidnapped (Table 5.1).

The disposition and psychology of individual females appears to be an important consideration in the context of infant kidnappings reported here. The number one ranking female baboon in this Kuiseb troop (Pa - see Chapter 2) has lost at least as many infants as each of the two females demonstrating kidnapping behaviour. If own infant death is an important factor causing kidnapping, one would expect Pa to be a kidnapper as well. I have seen no attempt by Pa to kidnap any infants. Likewise, Ha, Bo and Gr, females with at least one other female ranking below them and who have also lost at least one of their own infants to kidnapping and/or ticks (Table 5.1), have not been observed attempting to kidnap.

Thus the data presented on fatal infant kidnappings in the Kuiseb troop did not identify any obvious cause for the kidnappings but suggested that a combination of two factors were important contributing factors to the kidnappings: the repeated loss of infants born to a female and that particular female's psychological disposition. The repeated loss of infants was common to all females (Chapter 2) but not all females of sufficient rank to kidnap other females' infants did so. Also, some low ranking females suffered more kidnappings than others over the same time period (Table 5.1) although this difference could possibly be explained by something as straightforward as the number of births they had (Chapter 2). Clearly, therefore,

the kidnapping behaviour in this troop is exceptional and unexplained. A multidisciplinary approach to the problem, including the study of hormonal physiology and psychology of the female baboons, would be necessary to provide a better understanding of this fatal kidnapping behaviour.

Chapter Six

Adult male baboon dynamics in the Lower troop: Serious wounding, fatal fighting and genetic implications

INTRODUCTION

Prereproductive male cercopithecine primates hold positions in dominance hierarchies in accordance with age, mother's rank and individual ability (Hamilton and Bulger, 1990). From five years of age onwards, male baboons begin surpassing adult females in the hierarchy and from seven years exceed the declining adult males (Altmann, Hausfater and Altmann, 1988; Smith, 1986; Pereira, 1988). From 7.5 to 10 years, males are considered as "prime" (Hamilton and Bulger, 1990) and usually leave their natal troop and take up residence in other troops (Altmann, 1988). Prime males then usually attain their highest rank within 6 months of intertroop transfer (Altmann et al, 1988) or may reach the highest rank within their own troop in a similar time span (Hamilton and Bulger, 1990). During the process by means of which adult males rise in rank, damaging and lethal fighting behaviour amongst them is usually fleeting or entirely suppressed, although they are capable of wounding or killing an opponent with their sharpened canines.

In this chapter I examine the circumstances surrounding incidence of wounding and death amongst adult male baboons (Papio cynocephalus ursinus) during dominance fights. In the Kuiseb baboon troop I have studied, fatal and serious wounding was the usual outcome in adult male conflict. By comparing the behaviour of these baboons with that of an equivalent baboon troop in Botswana (Brain, Hamilton and Bulger, pers. comm.), the sequence

of life history events which may produce restraint in baboon conflict are identified. The conclusions are likely to have wide relevance in other contexts of mammalian conflict. Furthermore, this study examines the activities of immigrant males and their reproductive success, and assesses the potential for genetic isolation in this geographically isolated population in the lower Kuiseb.

STUDY AREA AND METHODS

This study was conducted in the Kuiseb River canyon over a 62 month period starting in December 1986. Details of observation schedules, the study area and the troop over this period appear in Chapter 1 and Brain (1992). The comparative data were available from a similar study in Botswana in the Moremi game reserve. The Botswana study was carried out by J. Bulger and W.J. Hamilton III over a similar time period as that in the Kuiseb.

Male rank determinations in both locations were based upon uncontested supplants at food sources or other resources. Access to females is a consequence of rank and was not used to determine it. All supplanting encounters were recorded whenever possible and during focal observations.

Namib immigrants were classified as prime based upon the appearance of their canines (observed with binoculars at <10m). Prime males have long sharply pointed canines and can also be distinguished by their lean appearance and athletic movements (Hamilton and Bulger 1990). Post prime immigrants were easily distinguished by their worn, shortened canines but not always by their physical appearance.

To assess the relationship between adult males and infants in both locations for the duration of the respective studies, I recorded which male was consorting and m[illegible]emale at the time of her probable ovulation (sexual s[illegible]detu[illegible]cence minus two days [D - 2], Gillman and Gilbert, 1946). Females were then monitored until they gave birth. If the same adult male that consorted the particular female at probable ovulation formed a persistent and exclusive association with the mother-infant pair, and supported the infant through its early (to 2 years) juvenile life, he was considered as the behaviourial father (Busse and Hamilton, 1981; Busse, 1985) of that infant. The differences between behaviourial fathers and non-paternal males (ie, did not conceive an infant or lost an infant soon after birth) regarding the outcome of conflict were analyzed. Because I knew the origin of Lower troop immigrants and their subsequent reproductive success, I also discuss the possibilities for gene transfer and the genetic diversity of the Kuiseb troop.

RESULTS

In both study sites all adult males were ordered within their own linear dominance hierarchy (Brain, 1992; Smith 1986). In the Kuiseb population, the top two ranking (alpha and beta ranks) adult males gained access to oestrus females by consorting them at the time of probable ovulation (Gillman and Gilbert, 1946). For 36 oestrus cycles, Kuiseb female baboons (n=7) were consorted by alpha (n=28 oestrus cycles) or beta (n=8 oestrus cycles) males only, and of 16 conceptive cycles 12 were attended by alpha males and four by beta males. Similarly, in the Okavango, 66 conceptive cycles were exclusively attended by alpha (n=55), beta (n=10) or gamma (n=1) males (Bulger and Hamilton, 1988). In both Kuiseb and Okavango populations at least three other adult males were always in the troops but were not involved in consorting.

In this study, in all but one case in the Okavango troop (Hamilton, unpub. data), the adult male who adopted the role of behavioral father was the individual who consorted the mother 187 days (Kuiseb) and 183 days (Moremi, [Smith 1986]) before parturition, the respective gestation periods for females in these populations.

In the Kuiseb baboon troop, putative sires were rarely behaviourial fathers because of the exceptionally high infant mortality in that troop (30 of 36 infants born between 1986 - 1992, [Brain, 1992, Chapter 2]). Table 6.1 provides details of adult male immigrants into the Lower troop. One obviously post prime male (Si) has not been included in further analyses. Of 11 Kuiseb male baboons who challenged the resident alpha male for

alpha or beta rank, one (No) was seriously wounded. Nine of 12 resident males who lost contests for alpha or beta rank sustained major (n=3) or disabling (n=3) wounds or death (n=3). By comparison during a longer interval (92 mo) only two of 17 resident Moremi males suffered serious injuries during contests for the two top ranks (Fisher exact test, two tailed, $p < 0.005$) and none of the 16 challengers was wounded (Hamilton and Bulger, unpub. data).

ID	ORIGIN	CHALLENGE DATE	WOUND SEVERITY	RANK	LOSE RANK?	INFANTS ON GROUND	BEHAV. FATHER
SA	Upper troop	JUN 87	MAJOR	β	YES	0	NO
XH	Inland	JUN 88	MAJOR	α	YES	0	NO
PA	Inland	OCT 89	DEATH	α	YES	0	NO
NE	Inland	OCT 89	DEATH	β	YES	0	NO
AL	Middle troop	NOV 89	DEATH	α	YES	0	NO
GR	Solitary	JUN 90	MINOR	α	YES	0	NO
NO	Middle troop	JUN 90	MAJOR	β	YES	0	NO
WH	Inland	JUN 90	DISABLE	α	NO	0	NO
WH		MAY 91	DISABLE	α	YES	0	NO
GA	Unknown	JUL 91	MINOR	α	YES	2	YES
DU	Middle troop	SEPT 91	MAJOR	α	YES	0	NO
ST	Solitary	OCT 91	MINOR	α	YES	0	NO

Table 6.1. Wound severity associated with adult male immigration and challenges to alpha and beta males in the Kalahari baboon Lower troop. Minor wounds are superficial cutaneous gashes of any length not causing loss of function and healing fully. Males not observed to sustain any wounds are placed in this category. Major wounds are deep soft tissue wounds with temporary loss of function, haemorrhaging and sometimes sepsis. Simple bone fractures are included. Once healed, major wounds do not effect performance in any observable way. Disabling wounds include the above plus compound or complex fractures, severed tendons or nerves, loss of any eye, teeth or other permanent function losses. Death is any wound leading directly or indirectly to death. The term 'behaviourial father' is explained in the text.

There were no statistically significant differences between the Khiseb and Okavango troops in wounding of challengers (chi-square test, $p > 0.5$). Combining paternal behaviour data for the two populations only one of 14 behaviourial fathers was seriously injured when he lost alpha or beta rank compared with serious injuries to 10 of 15 nonpaternal males who were challenged (Fisher exact test, two tailed, $p < 0.002$). Adult male baboons holding alpha or beta rank (the only two ranks affording reproductive opportunity in these two troops) who had no living offspring therefore appeared more likely to be seriously wounded in contests for high rank.

Two nonpaternal Namib males (Gr and St - Table 6.1) who received only minor wounds were both solitary males for periods of three and four years respectively prior to immigrating to the Lower troop. Both males were known to be in visual contact with the Lower troop approximately twice monthly, but, prior to immigration, made no attempt to follow the troop. Gr immigrated into the Lower troop three days after two contenders for alpha rank were injured, one fatally, in a fight. Gr then killed the wounded alpha rank holder and assumed alpha rank without sustaining any wounds. Similarly St made his only serious attempt at establishing himself as alpha in the Lower troop when the then current alpha-ranked challenger suffered a compounded fracture of his right hand.

DISCUSSION

When animals with dangerous weapons oppose one another, they might fight with restraint because individuals with lower fighting ability can identify their lower probability of winning and quit contests they probably will lose (Enquist and Leimar, 1990) before being seriously wounded. Contests may also be resolved if one contestant places a higher value on winning and fights harder or longer to gain or maintain access to a resource (Parker, 1974). An asymmetry in estimated value of resource is also a critical determinant of contest outcome when high ranking male baboons challenge one another for alpha status (Hamilton and Bulger, 1990).

In the Kuiseb and Moremi populations, prime immigrant males appeared more likely to oust resident alpha males than to be repelled by them. Among resident losers, non-fathers are less likely than behaviourial fathers to concede high status to challengers and suffer more frequent and more serious injuries in losses to new prime immigrants who displace them at the top of the hierarchy. Males from populations considered here do not form coalitions as reported for east African baboons (Bercovitch, 1988; Noe and Sluijter, 1990), eliminating one complexity in the analysis of contest outcomes.

The cost of serious injuries or death to behaviourial fathers in expected further reproductive success (Grafen, 1987) exceeds that

to non-paternal immigrant baboons because disabled and dead male baboons cannot protect infants from infanticidal intruders or provide other paternal care (Hamilton, 1984). Males who complete care of infants seldom recover high rank (Hamilton and Bulger, 1990), indicating prime status not to be a cyclical, but rather a linear and irreversible event. Males who were behaviourial fathers lost or conceded alpha status to challenges from immigrants who previously had no access to fertile females and thus could not be fathers of any infants in the troop.

The two non-paternal males (Gr and St) who received no major wounds and who immigrated following prolonged periods of solitary existence are of interest. Upon immigration, these two males who presumably emigrated from their natal troops no earlier than seven years of age and thereafter spent at least three years in solitary existence, were just beyond the considered prime age limit of males in populations elsewhere (Altmann et al, 1988). Their strategy of entering the troop only when the opposing resident males were weak or wounded suggested an unwillingness by them to confront prime, healthy males. This is possibly also the reason why, when later challenged by prime immigrants, they conceded although being of non-paternal status.

It seems unlikely, from the pattern of wounding of challengers, that fights were more violent in the Kuiseb troop than in the Okavango troop (otherwise the challengers would also have shown more injuries). Consequently, in the Kuiseb troop, residents get more seriously wounded in fights that are apparently no more

serious. Data indicate resident males to be very vulnerable and at high risk of serious injury if they do not concede to challengers. It seems that fights favour the challengers and that challengers have an enormous reserve so that, as the intensity of the conflict increases, they remain within capacity and residents who do not concede are seriously wounded. The reasons for these apparently lop-sided fights remain uncertain but the relative age of the fight contestants is likely to be a very important factor. The canines of adult male baboons reach maximum length around the age of their natal emigration and their body weights increase following natal emigration (Hamilton and Bulger, 1990). It is possible that the fighting ability of newly immigrated males is far superior to older resident males and that fighting ability (of which physical development is a component) is the major contributing factor to contest outcomes. To evaluate this hypothesis, the ages of individuals must be determined, preferably by known birth dates, and their success in contests monitored.

The high probability of being seriously injured is plausibly the reason top-ranking paternal males concede status to prime immigrants without engaging in combat. In the Kuiseb, exceptionally high infant mortality prevented the development of assymmetries in resource value based upon paternal status. As a result, debilitating injuries and death during fights to gain status and prospective fatherhood were, under the conditions of high infant mortality, the rule.

conditions of high infant mortality in the Kuiseb troop were not only important in the context of adult male conflict but were also important in considering gene transfer and genetic diversity in the Kuiseb troop. With such poor infant survival rates, factors relating to inbreeding avoidance (Packer, 1979) become irrelevant and genetic diversity will largely depend on the extent of gene homology amongst the breeding males. As indicated in Table 6.1, the large number of male immigrants originating from at least four different localities makes it unlikely that immigrants were closely related. Also, the absence of any juveniles or sub-adult males reaching adulthood in the Namib populations for at least the last eight years makes it unlikely for current breeding males, possibly originating from the Namib populations, to be closely related. Because the mean degree of relatedness between individuals born in the same troop decreases as the average tenure of the alpha male becomes shorter (Packer, 1979a) and with on average one infant surviving each year in the Namib troop, a low degree of relatedness amongst the surviving members of the Lower troop is to be expected. It is probable therefore that even with fewer adult male immigrants than recorded here that the genetic diversity of the Lower troop would be near that of the local and more inland populations.

Chapter Seven

Feeding patterns and foods of the Kuiseb baboons

INTRODUCTION

Animals living in a desert environment are frequently constrained by its low primary productivity and patchy distribution of food plants (Louw and Seely, 1982). Patchy dispersion of plants of varying nutritional quality may result in periodic energy, protein and micro-nutrient deficiencies. Electrolyte concentrations in desert plants are also known to impose severe electrolyte loads, especially potassium, on animals inhabiting desert environments (Nagy, 1972; Nagy, Shoemaker and Costa, 1976; Mitchell, Seely, Roberts, Pietruska, McClain, Griffin and Yeaton, 1987). However, the overall unpredictability of a desert environment places periodic nutritional stress on all its inhabitants. Adaptive responses of animals to nutritional stress and desert environments include the storage of energy in the form of fat, migration, decreased metabolic rate through aestivation and diapause, sun basking and selection for small body size (Louw and Seely, 1982).

Baboons are not known to demonstrate any of the above mentioned adaptations for living in a desert environment. Rather, the most striking fact about baboon diet is its variety and eclecticism (Hall, 1963; Altmann and Altmann, 1970). Baboons lack highly specialized digestive system anatomical adaptations (Dunbar, 1988), but have keen vision and manual dexterity, enabling them to exploit a wide variety of foods. Baboon omnivory is considered the major factor enabling their survival in a great

diversity of habitats (Altmann and Altmann, 1970; Hamilton, Buskirk and Buskirk, 1978).

In this chapter I examine the feeding habits and diet of desert baboons (Chapter 1) in the Kuiseb River canyon. I determined the feeding patterns of the baboons and the seasonal changes in foods used by the baboons. Chemical analyses of the various foods was conducted to determine the baboons' dietary composition and to assess whether their nutrition was unique.

STUDY AREA AND METHODS

The study area and the baboon population are detailed in Chapter 1.

Scan sampling (Altmann, 1974) was used to obtain quantitative information on feeding patterns. Sampling was carried out at half hourly intervals. For each sample I made a sweep from one side of the troop to the other, recording what each visible animal (excluding infants) was doing in as near an instantaneous sample as possible. All samples took 1-4 minutes to complete. In the present context, an animal was recorded as feeding if it was harvesting, passing food to its mouth, biting or chewing any item other than unknown objects picked off during grooming. Scan sampling was carried out during two periods of different water availability: in January 1990 when there was no free water available to the baboons and in March 1990 when water was

diversity of habitats (Altmann and Altmann, 1970; Hamilton, Buskirk and Buskirk, 1978).

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abundant (Chapter 2). I sampled every half hour from dawn to dusk for five days for each sampling period. The median number of records per hour (ie, two half-hour samples) for the respective periods was 137 (range 121-140 - January) and 135 (range 123-156 - March) and the median number of animals recorded for each half hour sample was 14 (range 8-16). During scan samples I also recorded the species and parts of plants being eaten by the baboons. In both January and March the baboons were feeding on the same food plants (see results) and used the same feeding sites. Climatic data for the two sampling periods were recorded at Gobabeb's first order weather station (Chapter 1).

Seasonal changes in food plants used by the baboons were determined. I spent three days of each month (early, middle and late part of the month) for a year (1990) during which I distinguished between feeding periods when the baboons were feeding on a single food as opposed to those when feeding was more eclectic. This distinction was abetted by the tendency of the group to enter discrete stands of fruiting trees or bushes for variable periods of time, often extending over several hours in duration. In order to evaluate the relative importance of the different food plant species to the baboons, and of the parts of the plants consumed, I distinguished between:

1. primary food sources: entire troop feeding for majority of a feeding bout on a specific plant or part of plant

2. secondary food sources: foods which typified periods when no single item was dominant

3. incidental foods: foods infrequently consumed.

(Lindberg, 1977)

In order to determine the relative importance of the different primary food sources, I estimated the amount of time the baboons spent feeding on each food source during feeding bouts. The approximate total time spent by the baboons feeding on the various primary food sources was then calculated.

Nutritional and moisture analyses were carried out on all primary and the more commonly used secondary food sources. Samples of plants for these analyses were collected fresh from trees or bushes at times when the baboons were actually feeding on them. Samples were weighed in the field upon collection. I determined water content through the mass loss following drying at 80°C for four days. Concentration of selected electrolytes was measured by atomic absorption spectroscopy at the Outspan Laboratories, South Africa. Protein content was determined using the Kjeldahl technique, gross energy was determined through bomb calorimetery, fat through ether extraction, and nitrogen free extract (NFE) was calculated through subtraction. These analyses were done by the Dairy Research Institute at Irene, South Africa.

Use of animal foods by the baboons was recorded whenever it was observed; this activity frequently coincided with weather conditions permitting the baboons to leave the Kuiseb canyon and penetrate into the Namib sand sea.

All data collected by scan sampling was arcsin-square root transformed prior to statistical analysis (ANCOVA and ANOVA). Data were transformed because they were percentages and the percentage values were close to zero or 100 percent.

RESULTS

There was a significant difference between the time spent feeding by the baboons on days when water was not available and when it was (Fig. 7.1; ANCOVA; covariate = hours; $F = 18.53$; $p < 0.001$; residual df = 257). There were no significant differences between the daily maximum and minimum temperatures recorded during the two periods in January and March when feeding behaviour was recorded (Mann-Whitney U test; maximum temperature, $Z = 0.42$, $p > 0.6$; minimum temperature, $Z = 0.31$, $p > 0.7$). The data in Figure 7.1 show that feeding activity dropped off earlier following early morning feeding bouts on the non-drinking days than on drinking days. Thereafter, during the midday period feeding activity remained low but peaked again in the late afternoon when, on non-drinking days, feeding activity exceeded that of drinking days from 17h00 to 19H00. Using the Tukey test

for ANOVA, significant ($p < 0.05$) differences were found between the two sampling periods for 09H00-10H00 and 11H00-12H00.

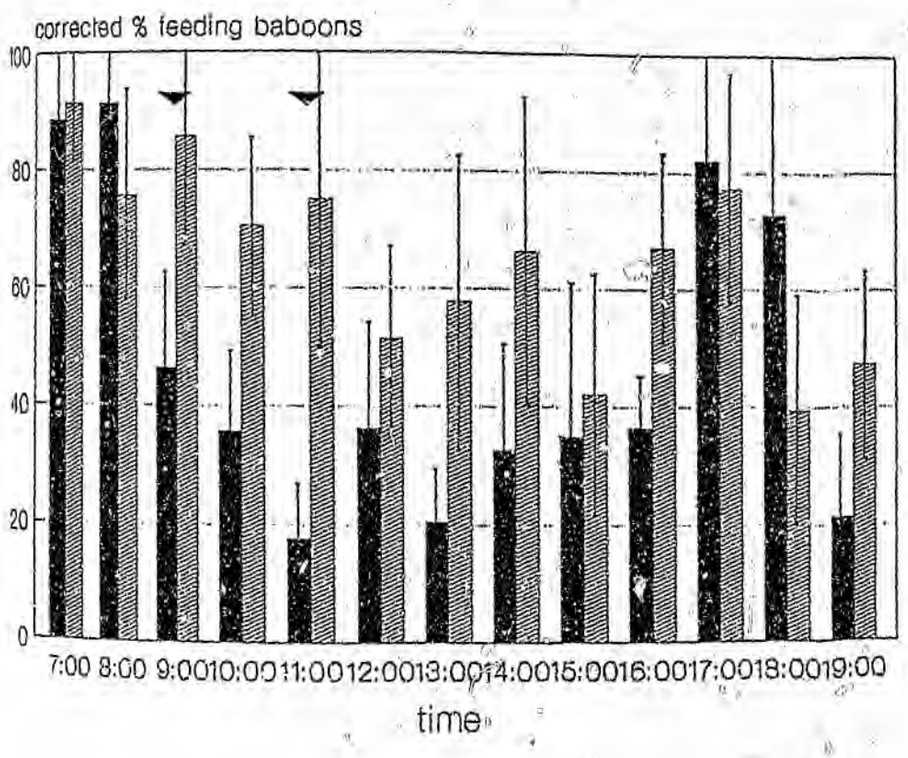


Figure 7.1. Percentage of baboons feeding during periods when water was not available (January; shaded bars) and when water was available (March; hatched bars). Arrows indicate significant differences between the two. See text for details of sampling procedures and sample sizes. (Untransformed data were used for the construction of the figure).

The plants and the plant parts eaten by the Kuiseb baboons are listed in Table 7.1. Invasive plants of known toxicity to livestock and humans, (Datura stramonium, Nicotiana glauca and Argemone ochroleuca [Watt and Breyer-Brandwyk 1962]), were eaten regularly when encountered and fall into the category of secondary food sources. The baboons showed no apparent unusual symptoms following ingestion of these plants (see discussion).

Figure 7.2 gives a schematic representation of the primary food plants eaten by the baboons on a monthly basis together with the incidence of invertebrate feeding. Feeding on primary plants coincided with the seasonal peak production of the specific phenophases of those plants (van Wyk, Opperman and Kok, 1985). Nutritional analyses of the primary plants are shown in Table 7.2, while moisture content and selected electrolyte concentrations of primary plants are included in Table 7.3.

Analyses of the protein content of the plants shows that with one exception (Acacia erioloba - green seeds) the protein values are towards the low end of the normal range for vegetable plants and much lower than the protein content of seeds or animal tissue (Diem, 1962). The use of invertebrate prey by these baboons, especially at the time of near exclusive fig feeding (Fig.7.2 and see Chapter 9) therefore enhances not only energy uptake, but also protein uptake.

Table 7.1. Plants foods - primary, secondary and incidental eaten by the baboons.

PRIMARY

Acacia erioloba	-	green pods, cotyledons of seeds only
Euclea pseudebenus	-	green and ripe berries
Faidherbia albida	-	bark strips
	-	green pod seed hulls
Ficus cordata	-	green and ripe fruits
Ficus sycomorus	-	green and ripe fruits
Salvadora persica	-	ripe berries

SECONDARY

Acacia erioloba	-	dry pods
	-	flowers
Argemone ochroleuca	-	pith
Cyperus marginatus	-	green stems and corms
Datura stramonium	-	root, pith and fresh flowers
Faidherbia albida	-	flowers
	-	dry pods
Flaveria bidentis	-	pith and flowers
Nicotiana glauca	-	pith
Stipagrostis sabulicola	-	green stems
Tribulis terrestris	-	seeds and flowers

INCIDENTAL

Adenolobus pechuelii	-	flowers
Brachiaria glomeraca	-	leaves and stem
Cladoraphus spinosa	-	leaves and seeds
Cleome suffruticosa	-	leaves and pods

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	–	dry pods
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Stipagrostis sabulicola	–	green stems
Tribulis terrestris	–	seeds and flowers
INCIDENTAL		
Adenolobus pechuelii	–	flowers
Brachiaria glomerata	–	leaves and stem
Cladoraphus spinosa	–	leaves and seeds
Cleome suffruticosa	–	leaves and pods

Cadon spp	-	stem
Euphorbia avasmontana	-	pith
Heliotropium ovalifolium	-	leaves
Mesembryanthemum spp	-	leaves
Moringa ovalifolia	-	pith
Osteospermum microcarpum	-	flowers
Pechuel-loeschea leubnitziae	-	root base
Peliostomum leucorrhizum	-	flowers
Petalidium angustitubum	-	flowers
Rogeria longiflora	-	pith
Ruellia diversifolia	-	flowers
Sesamum capense	-	flowers
Sesuvium sesuvioides	-	leaves and flowers
Setaria verticillata	-	leaves and seeds
Solanum nigrum	-	berries
Sporobolus robustus	-	leaves
Stipagrostis ciliata	-	stems and seeds
Stipagrostis namaquensis	-	stems
Stipagrostis sabulicola	-	stems
Sutera canescens	-	flowers
Tephrosia dregeana	-	pods
Vahlia capensis	-	leaves and flowers
Welwitschia mirabilis	-	cones
Zygaphyllum simplex	-	roots

Codon spp	-	stem
Euphorbia avasmontana	-	pith
Heliotropium ovalifolium	-	leaves
Mesembryanthemum spp	-	leaves
Moringa ovalifolia	-	pith
Osteospermum microcarpum	-	flowers
Pechuel-loeschea leubnitziae	-	root base
Peliostomum leucorrhizum	-	flowers
Petalidium angustitubum	-	flowers
Rogeria longiflora	-	pith
Ruellia diversifolia	-	flowers
Sesamum capense	-	flowers
Sesuvium sesuvioides	-	leaves and flowers
Setaria verticillata	-	leaves and seeds
Solanum nigrum	-	berries
Sporobolus robustus	-	leaves
Stipagrostis ciliata	-	stems and seeds
Stipagrostis namaquensis	-	stems
Stipagrostis sabulicola	-	stems
Sutera canescens	-	flowers
Tephrosia dregeana	-	pods
Vahlia capensis	-	leaves and flowers
Welwitschia mirabilis	-	cones
Zygaphyllum simplex	-	roots

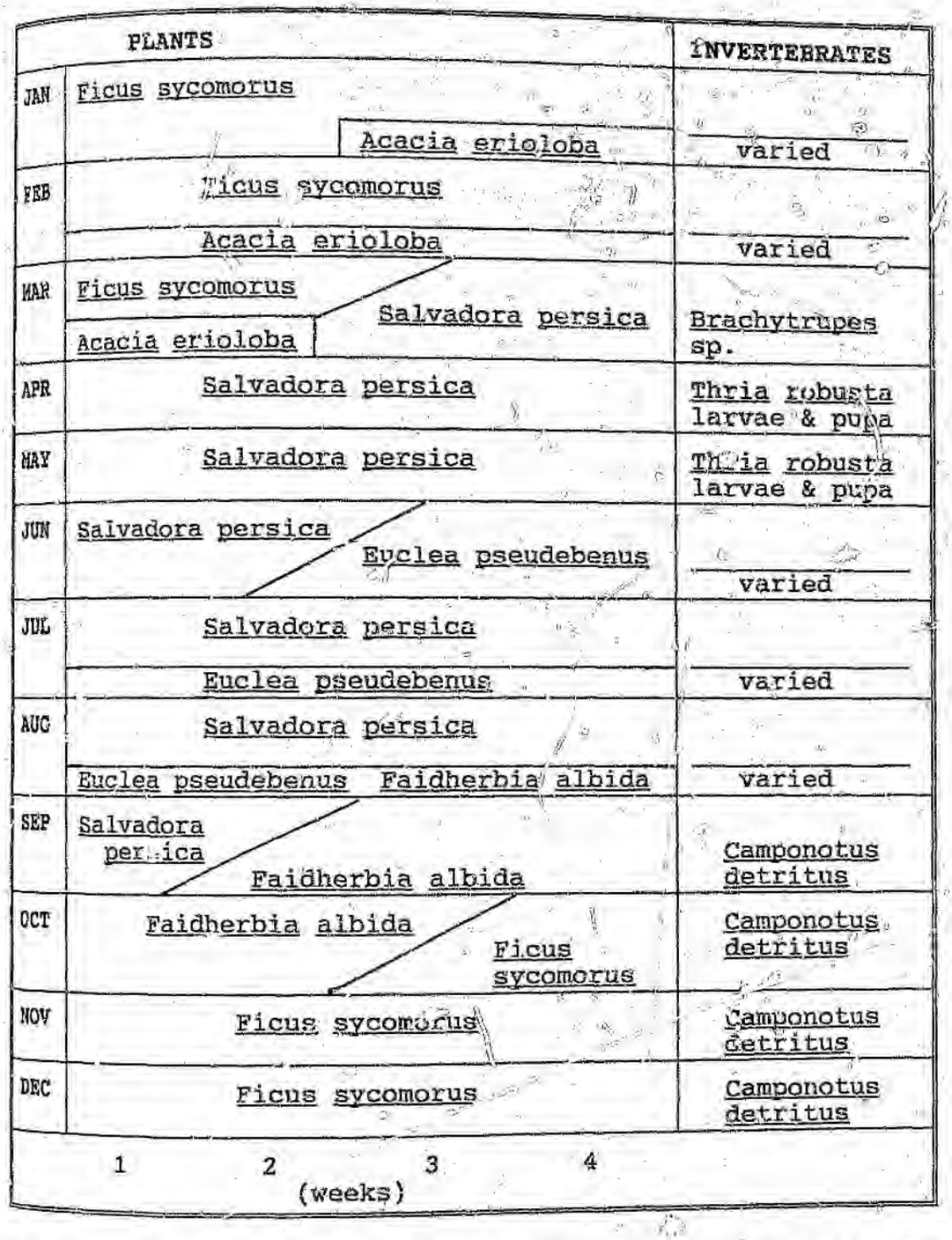


Figure 7.2. Schematic representation of primary food plants and invertebrates used by the baboons on a monthly basis in 1990. Size of area occupied by specific plant in each month block indicates approximate time the baboons spent feeding on that plant - see text for details.

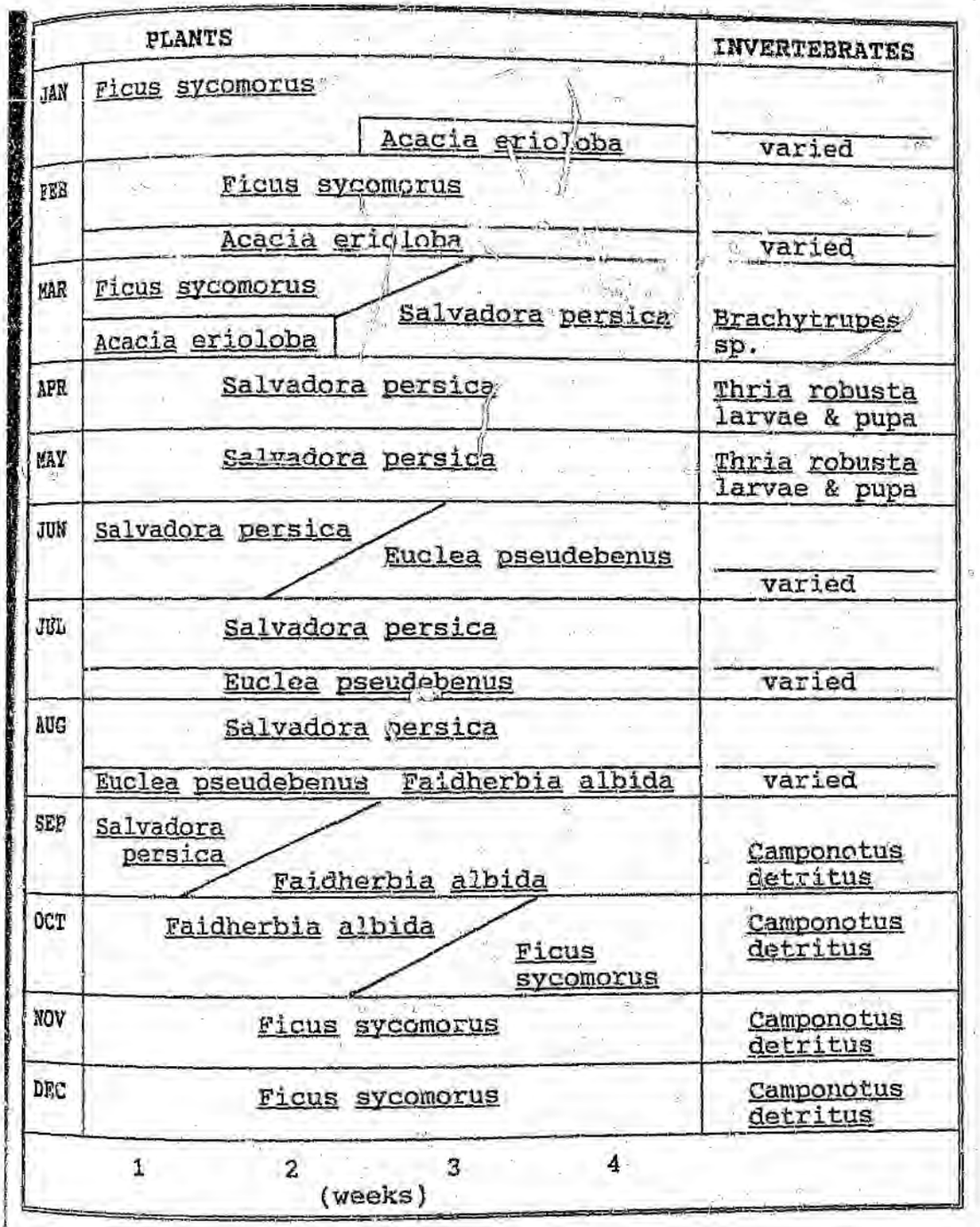


Figure 7.2. Schematic representation of primary food plants and invertebrates used by the baboons on a monthly basis in 1990. Size of area occupied by specific plant in each month block indicates approximate time the baboons spent feeding on that plant - see text for details.

Plant	Protein Content (%) wet mass / dry mass	Fat- % dry mass	Fibre- % dry mass	NFE %	Gross Energy Mj/kg dry mass
Acacia erioloba - green seed	15.7 / 40.3	6.9	6.6	35.6	17.2
dry pod	10.2 / 10.6	1.0	31.1	57.6	19.9
Euclea pseudebenus	1.2 / 2.5	0.4	17.3	63.3	17.1
Faidherbia albida - seed cover	3.7 / 13.1	2.1	16.7	59.4	17.5
dry pod	5.6 / 5.8	0.9	20.6	52.4	19.9
Ficus sycomorus - ripe fruits	1.3 / 10.0	5.4	26.8	45.9	17.0
Ficus cordata - ripe fruits	0.9 / 6.0	11.1	37.9	35.9	19.9
Salvadora persica - ripe berries	5.0 / 17.1	5.3	4.5	49.2	15.7
Argemone ochroleuca - pith	0.95 / 7.0	0.5	44.6	37.7	15.5
Datura stramonium- stem base	0.98 / 12.0	1.3	20.6	58.4	11.7
Nicotiana glauca - pith	1.4 / 23.0	1.1	46.1	10.0	13.1

Table 7.2. Chemical analyses of primary and some secondary (Argemone, Datura and Nicotiana) plant foods used by the baboons (n = 1 throughout).

With regard to water content (Table 7.3), the plants fell into three categories: the dry pods of Acacia erioloba and Faidherbia albida with 3% moisture, the seeds and berries of Acacia erioloba, Faidherbia albida, Euclea pseudebenus and Salvadora persica of between 53% and 72% water and the Ficus spp and invasive plants of between 84% and 94% water. Thus the baboons had access to plants of high moisture content. (Aspects of plant water are further analyzed in Chapter 9.)

The electrolyte concentrations in the food plants expressed as mmol/kg wet mass (Table 7.3) did not show the range of variation as seen in plants from other locations in the Namib desert (Mitchell et al., 1987). Potassium concentrations were uniformly low with the dry pods of Acacia erioloba having the highest concentration of 347 mmol/kg. Sodium concentrations of the various plants were very low with more than half the samples having concentrations of < 10 mmol/kg. The high potassium:sodium ratios of some of the plants were as a result of the very low sodium concentrations and not as a result of very high potassium concentrations as was the case with other desert plants of high potassium:sodium ratios (Nagy, 1972; Nagy, Shoemaker and Costa, 1976). However, the overall low electrolyte concentrations of the various plants are not likely to impose any serious electrolyte loads on the animals. The low electrolyte concentrations of the plants, especially sodium, is likely to be an important factor in body water conservation of the baboons and other animals eating the plants as minimal water would be needed to excrete the sodium via the kidneys (see Chapter 10).

Plant	Water content – % by mass (n=4 throughout)	Electrolyte concentration (mmol/kg wet mass) (n=1) Na	K	Ca	Mg	P	K:Na Ratio
Acacia erioloba							
green seed	60 ± 3	5.2	141.2	16	46	55.4	27.2
dry pod	3 ± 1	16.8	347.3	172.1	47.9	18.7	20.6
Euclea pseudebenus ripe berries	53 ± 3	38.8	143.4	54.1	23.2	10.6	3.69
Faidherbia albida							
green seed cover	72 ± 1	4.9	75.0	12.1	29.6	44.9	15.3
dry pod	3 ± 2	16.8	283.5	67.9	32.3	12.5	16.9
Ficus sycomorus ripe fruits	87 ± 4	22.3	90.9	24.9	18.8	12.8	4.1
Ficus cordata ripe fruits	84 ± 2	6.1	66.0	39.8	11.7	10.1	10.8
Salvadora persica ripe berries	71 ± 1	25.2	134.6	216.1	19.3	14.0	5.3
Invasive Plants							
Argemone ochroleuca pith	86 ± 3	6.5	110.3	28.9	1.7	2.2	17.0
Datura stramonium stem base	92 ± 1	4.86	101.1	43.3	42.3	4.1	20.8
Nicotiana glauca pith	94 ± 1	7.8	141.5	27.8	1.8	2.5	18.1

Table 7.3. p.97. Moisture content and electrolyte concentrations of primary and some secondary (invasive) plant foods used by the baboons.

The two plants (Ficus sycomorus and Salvadora persica) that the baboons used nearly exclusively when no water was available (Brain, 1988; 1990; Chapter 7) were important because the baboons obtained both their water and food requirements from these plants. Besides both plants having low protein content (Table 7.2), they were both of high water content and were ingested rapidly by the baboons (see chapter 9). They have relatively high fat percentage, low fibre percentage, especially Salvadora, and Salvadora is a valuable source of calcium (Table 7.2).

Animal foods

Other than catching and eating fish (Tilapia mossambica) from small pools left after flooding (Chapter 3), I did not see Kuiseb baboons hunting or eating vertebrates. Bird nests were occasionally raided and the eggs eaten. A variety of invertebrates were eaten and the incidence of seasonal feeding on invertebrates is shown in Figure 7.2. The baboons undertook trips into the Namib dunes, located south of the canyon, on days when the coastal fog penetrated as far as their range. The fog appeared to keep the sand-surface temperature in the dunes down long enough to allow the baboons to reach their feeding sites, which were up to 4km into the sand dunes and return to the river before sand surface temperatures became prohibitively hot. In the dunes the baboons fed on invertebrate larvae contained in

galls of the dune grasses, Stipagrostis seelyae and Stipagrostis sabulicola. They also dug for white lady spiders, Leuchorchestris spp. (Fig. 7.3), successfully capturing them at an observed rate of 72% (n=69). However, the main activity was the excavation of large ant nests (Camponotus detritus) and eating the eggs and larvae, especially the alate larvae, found in the nests (Fig. 7.4). The troop excavated up to 35 nests in a single two hour dune trip. All except the very young baboons appeared tolerant of the masses of ants that climbed on to them during their excavating. The baboons buried their feet in the sand during digging, presumably to protect them from being bitten by the ants.

In March, soon after the flood waters had passed and the hard silt banks were softened, the baboons dug out the large crickets, Brachytrupes m[illegible] ranaceus. In April and May, when the larvae of the moth Thria robusta droped out of the trees and buried in the sand to pupate, the baboons ate little else, as these larvae were particularly abundant. At other times, invertebrate feeding was varied and sporadic. Species eaten included the locust Schistocerca gregaria, butterflies Belenas aurota and Catopsillia florella and spiders from the Lycosidae family. The highly toxic scorpion Parabuthus villosus was not eaten while the equally large, but non-toxic Opistothalmus flavesens was.

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Figure 7.3. A young female baboon (Pa) digs out a white lady (Leuchorchestris sp) spider. (Photo: Ginger Hausey)

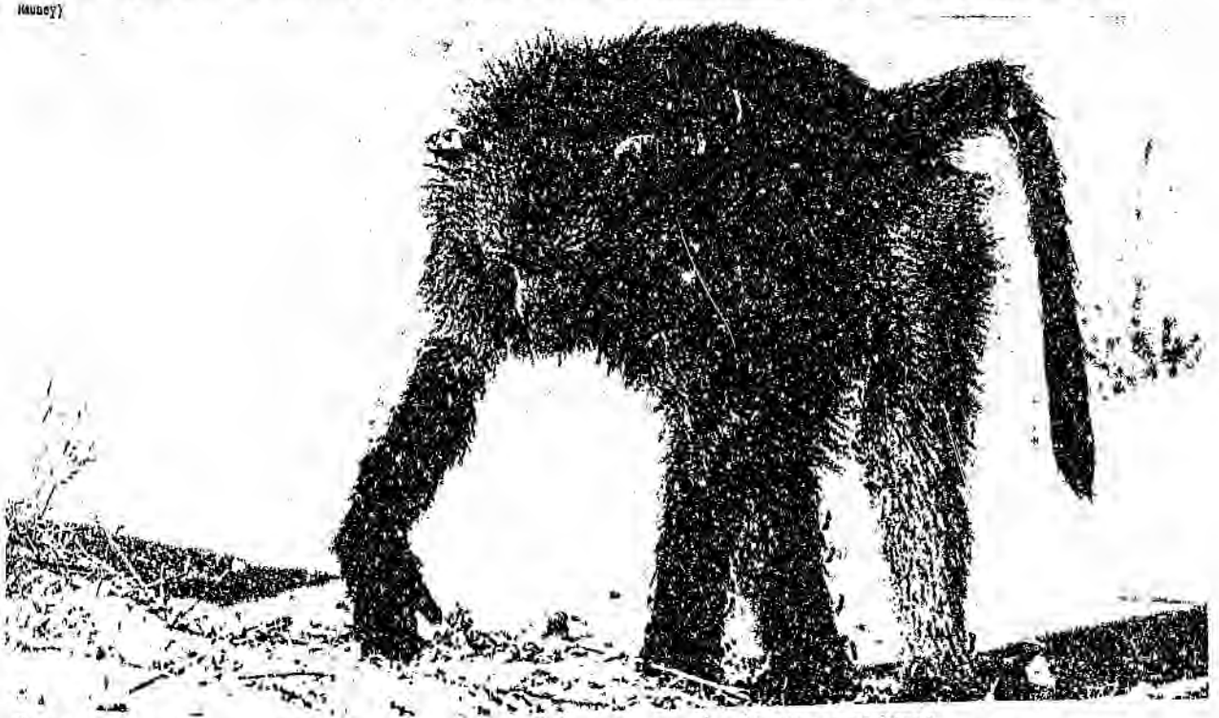


Figure 7.4. Sub-adult male baboon (Sm) eating Camponotus detritus ants in the sand dunes.

DISCUSSION

Results obtained here regarding the feeding activity of the Khiseb baboons are consistent and complimentary to those concerning movement patterns and stationary inactivity with respect to free water availability (Chapter 3). However, probably more important to consider here was the timing of the initiation and cessation of feeding activities with respect to core body temperature changes (see Chapter 8).

The decreased feeding activity on non-drinking days occured at that time when body temperature was rising. Continued feeding and associated movement, as seen on days when water was drunk, caused body temperature to exceed 39°C generally before midday before it was brought down again following drinking (Chapter 8). This situation was avoided by the baboons when no water was available, and modification of feeding activity appeared as one of the associated behavioural changes. However, the feeding pattern adopted at times of no surface water appeared to pose some other problems. There was a shorter feeding time in which not only nutritional needs must be met, but also moisture needs. Periods when free water was at a minimum or absent occur late in the year (generally Oct. until the next flood). This time coincided with the ripening of figs and data on intake rates and water content of figs together with the determined water flux rates suggest that the baboons can meet their water requirements through eating figs in the recorded feeding times (see Chapter

9). Figs do, however, have very low protein content. This was probably overcome by the eating of invertebrates occurring in the Namib sand dunes. The Namib fog season largely overlaps with this period of free water shortage and the fogs allowed the baboons temporary access to the dunes. The baboons appeared to maintain body condition throughout the year and data on the reproductive capacities of the females (Chapter 2, Table 2.2) indicated no decreases in reproduction, suggesting maintenance of body condition year round.

The feeding patterns of baboons elsewhere in arid or semi-arid habitats are unlike those recorded for the Kuiseb baboons. Baboons in arid regions other than the Kuiseb continue to feed steadily throughout the day (Altmann and Altmann, 1970; Stoltz and Saayman, 1970; Dunbar, 1977). The difference between baboons elsewhere and the Kuiseb baboons in this regard appears to be the availability of drinking water. All other baboons drank daily whereas the Kuiseb baboons did not. Because water availability was found to significantly affect feeding patterns of the Kuiseb baboons, it seems likely that water availability is probably a major factor causing the inter-population differences as well. For yellow baboons (Papio cynocephalus cynocephalus) in Tanzania, plant chemistry, especially fibre, was found to significantly affect feeding behaviour during the dry but not the wet season and baboons selected foods of lower fibre content in the dry season (Johnson, 1990). This suggests foods available in the dry season may be more restrictive in terms of chemical acceptability or that dry season vegetation spans a broader range of fibre

content. Thus it may be more beneficial for animals to select more strongly for lower fibre foods in the dry season than in the wet. Baboons feeding in the dry season in Tanzania also selected plants of high fat content (Johnson, 1990).

An obvious shortcoming of my data presented in this chapter is the lack of information concerning seasonal fluctuations of nutritive value and electrolyte concentrations of the plants. Data on electrolyte fluctuations would indicate whether the baboons were using certain plants at a specific development / nutritive phase or simply because they were available. It would also be valuable to look at urine electrolytes for the baboons at various stages of the year to assess electrolyte loads imposed by various diets and environmental conditions.

Although seasonal chemical changes of plant foods used by the Kuiseb baboons were not known, data indicated all primary and secondary food plants of the Kuiseb baboons to be of high moisture content (Table 7.3). In the absence of data regarding daily dry mass intake for the baboons, I used the allometric equation for predicting daily dry matter ingestion (grams per day) as determined by Nagy (1987). Using this equation, it is predicted that a 25kg baboon has a predicted dry matter requirement of 41.9g kg^{-1} day^{-1}. Using this and the measured water flux rate of 110ml kg^{-1} day^{-1} (Chapter 9), I can estimate the minimum dietary water content necessary to support the baboons. Assuming field animals produce about 15ml H_2O kg^{-1} day^{-1} via metabolism (Nagy 1987), the minimum water content of the diet

would be (110 - 15)ml H_2O kg^{-1} day^{-1} ÷ 41.9g dry food kg^{-1} day^{-1} = 2.2ml H_2O (per g dry food) or 68.7% water. Data presented here showed that most primary foods eaten at times other than during the flood season (Jan-April) had water contents higher than 69%. These data support the hypothesis that water content of primary food plants was probably a major factor determining their selection by the Kuiseb baboons.

The secondary compounds or toxicity of some of the plants used by the baboons were of interest. Of all three toxic invasive plants eaten, Nicotiana glauca was the most commonly eaten. These plants contain a pith of very high water content (94%) which takes minimal processing to obtain. All parts of the plant contain the alkaloid anabasine (Watt and Breyer-Brandwyk, 1962) that is an isomer of nicotine but has only about one-fifth the potency of the latter. Baboons show no ill effects or any signs associated with nicotine toxicity from eating this plant in fairly large quantities (ie, > 5 plants in 15 minutes - see Chapter 9).

Datura stramonium toxicity is known in humans (Watt and Breyer-Brandwyk, 1962). Stems and leaves are less toxic than seeds and contain the alkaloid hyoscyamine. Baboons commonly ate a section of this plant. After uprooting it, they usually took one bite from the root stem junction. Argemone ochroleuca has sharp spiny leaves that protect it from most grazers; however, the baboons dug around this plant and uprooted it by pulling on the spineless roots. The leaves were then stripped off and the moist pith

eaten. The pith contains an alkaloid berberine that is used medicinally by humans for skin diseases, and also as a narcotic and a purgative (Watt and Breyer-Brandwyk, 1962). In the absence of any obvious nutritional value of the invasive plants (Tables 7.2 and 7.3), it seems likely that they were sought after for their high moisture content.

Chapter Eight

Thermoregulation of baboons in the Lower Kuiseb troop

INTRODUCTION

No primate, other than human beings, has colonized so wide a range of habitats as the baboon. Baboon habitats include tropical forest, savanna and arid desert environments. Most studies examining adaptations to such diverse habitats have concentrated on the habitat extremes (Kummer, 1968; Whitten, Byrne and Henzi, 1987) and predominantly the arid and semi-arid environments (Hamilton, 1985; Sigg and Stolba, 1981; Brain, 1990; Zarovsky and Shkolnik, 1962). One obvious stress to animals living in African arid and semi-arid environments is daytime heat and a recent central theme of studies has been baboon thermoregulation (Stelzner and Hausfater, 1987). While behaviourial adaptations of baboons to thermal stress are documented under free-ranging natural conditions (Stelzner and Hausfater, 1987; Stelzner, 1988), data on actual body temperature changes are absent for baboons or any other non-human primate under free-ranging natural conditions.

Present understanding of baboon temperature regulation based on changes in body temperature is derived exclusively from captive animals in laboratory or enclosure studies (Funkhouser, Higgins, Adams and Snow, 1967; Hiley, 1976; Adair, 1977; Muller, Kamau and Maloiy, 1982; Dahl and Smith, 1985). The mass of adult baboons (15kg - 35kg) inhibits both rapid passive heat dissipation (as seen in the ground squirrel of mass 90-100g [Chappell and Bartholomew, 1981]) and extensive heat storage (as seen in the

gemsbok of mass > 100kg [Taylor, 1969]), and little fluctuation (usually < 2°C around a mean body temperature of 38°C) in core body temperature has been recorded for baboons in the laboratory. For mammals lacking known mechanisms for effective brain cooling (carotid rete), of which the baboon is one, ready access to water is essential to replace body water used for evaporative cooling (Mitchell and Laburn, 1985) to prevent compromises in physiological functioning and death (Shibolet, Lancaster and Danon, 1976). Considering that most mammals of similar mass and activity patterns living alongside baboons in arid habitats have effective brain cooling mechanisms (Schmidt-Nielsen, 1975; Mitchell, Laburn, Nyland, Zurovsky and Mitchell, 1987), the question as to the changes in body temperature tolerated by baboons under natural conditions and their subsequent response to these changes has remained unanswered.

I have undertaken to examine, under natural conditions, body temperature changes for the baboons in the lower Kuiseb, the most arid habitat yet recorded for non-human primates. The area is characterized by extreme aridity and scarcity of drinking water so that the baboons regularly go without drinking for periods of between one and 116 days (Chapter 2). Here I present telemetric and observational data obtained directly from these free-ranging desert baboons.

STUDY AREA

The study was conducted in the dry river bed of the Kuiseb River canyon in the central Namib desert, Namibia. Details of the area and range occupied by the baboons are given in Chapter 1 along with long term climatic data of the area. Climatic data for this study period (March to July 1992) were recorded at Gobabeb and are given in Table 8.1.

METHODS

Body temperature telemetry

To obtain direct measurements of body temperature, I surgically implanted temperature sensitive telemeters (148 - 150 MHz) into the peritoneal cavities of three baboons weighing 17-33.5kg, between April and July 1992. The telemeters were made by Mr G van Urk, Physics Department, Potchefstroom University, Potchefstroom, South Africa. The telemeters weighed < 20g when encapsulated with neoprene and inert wax for implantation and were free-floating in the peritoneal cavity. Telemeters had a transmission range of around 50m when implanted. I used a portable multichannel receiver (Yaesu FT-290R II), hand held directional antenna and head-phones for field work.

Two adult male baboons (27kg and 33.5kg) and one five and a half year old male (17kg) were immobilized at different times during the above mentioned period using a blowpipe and Telinject darts

containing ketamine at an estimated dose of 10mg/kg. Target animals were followed for a period of up to eight days until an ideal darting opportunity presented itself. This was when the unsuspecting animal was somewhat separated for the rest of the troop, facing away from the immobilizer and in an area free of vertical cliffs from which the partly immobilized animal could fall. Animals were then darted from a distance of around six metres and once fully immobilized, removed from the troop after being covered with a tarpaulin. Surgery was conducted in the field (Fig. 8.1) and all animals were returned to the troop within 1½ hours of darting.

A ventral midline approach just caudal to the umbilicus was used and prepared for surgery in the standard manner. An approximate 5cm cutaneous incision was made followed by blunt dissection to the rectus sheath which was incised as was the peritoneum. The telemeter, previously sterilized for > 24 hours in Hibicol, was rinsed with sterile saline solutions and inserted into the peritoneal cavity. The rectus sheath was sutured with simple interrupted monofilamentous 2/0 nylon. Subcutaneous 2/0 nylon sutures were used if skin apposition was not good and cutaneous incisions were closed with simple interrupted inverted sutures with 2/0 Vicryl suture material. Monitoring and care during surgery and recovery period included keeping eyes protected and moist, monitoring vital signs and rectal temperature. Baboons were treated with antibiotics (Comprapen - Milborrow) following surgery. Animals were monitored until fully recovered when they behaved normally and appeared healthy. Surgical incisions healed

quickly and cleanly with little scarring, and telemeters were not removed from the animals. The habituation of the troop to ourselves was not affected by this protocol.



Figure 8.1. Surgical implantation of radio-telemeter under field conditions (photograph by G. Mauney).

Body temperature was transduced by these telemeters as a click frequency. Each telemeter was individually calibrated in a water bath against a digital thermometer resolving better than 0.1°C. Accuracy and repeatability of the telemeters was better than 0.1° C. To obtain a body temperature measurement from a baboon with an implanted telemeter, I timed 30 clicks with a stopwatch so that repeatability of the measurement indicated an accuracy better than 0.1°C. The baboons' acceptance of me allowed me to obtain body temperature readings at any time throughout the day, but the inaccessibility of the baboons' sleeping cliffs to me and the danger of scaling the cliffs to within range of the baboons at night prevented me from recording night time body temperatures. Thus all temperatures were recorded from animals under direct observation. Telemeter battery life was around 6 weeks, and all readings taken during the five days prior to battery failure were discarded.

Behaviourial thermoregulation

The behaviour of the baboons was recorded at all times during the periods when body temperatures were being recorded. Any behaviour possibly associated with body temperature regulation was noted and thereafter body temperature changes were measured at short intervals (< 15 mins) for at least two hours. This procedure was used as body temperature changes and behaviour would be out of phase because, while behaviour is often instantaneous, body temperature changes are gradual.

RESULTS

Body temperatures of the baboons with implanted telemeters were remarkably labile over the recording periods. Early morning body temperatures of the three baboons leaving their sleeping cliffs were 36.7 ± 0.8°C (n=19 days), 36.7 ± 0.5°C (n=11 days) and 36.8 ± 0.2°C (n=11 days) respectively. The early morning body temperatures of the baboons leaving their sleeping cliffs were their lowest recorded temperatures for each day. Thereafter, depending on whether the baboons drank that day or not, there were two distinct patterns of daily temperature fluctuations in the baboons with the implanted telemeters. The greatest change in temperature occurred on days when the baboons did not drink, with a maximum temperature variation in one baboon of 5.3°C (36.8 - 42.1) being recorded. The greatest short term change in temperature was usually associated with the rapid troop movements to water or intense activity during aggression and dominance displays.

	08H00	14H00	20H00
Mean dry bulb temperature (°C ± SD) and range °C	15.0 ± 4.8 4.2 - 25.7	29.5 ± 4.9 19.6 - 39.7	23.5 ± 4.5 14.5 - 32.7
Mean relative humidity (% ± SD) and range %	48.4 ± 29.4 1 - 100	17.6 ± 12.4 1 - 47	31.2 ± 16.7 2 - 64
Wet bulb temperature (°C ± SD) and range °C	9.8 ± 3.2 0.1 - 17.6	15.8 ± 2.6 10.0 - 22.6	14.0 ± 2.5 9.7 - 20.3
Mean absolute humidity g water/m air	6.1	5.1	6.8

Table 8.1. Climatic data measured at Gobabeb weather station during the study period (March - July 1992).

Drinking periods

Figures 8.2, 8.3 and 8.4 show body temperature and activity changes for the three baboons with telemeters on each of two days. The daily peaks in temperature for each baboon were reduced by drinking which occurred around the mid-day period. Body temperature decreased more gradually in the evening as the baboons rested prior to ascending their sleeping cliff. Although periods of changing activity and temperature changes would initially be out of phase, drops in temperature, especially in late afternoon, clearly corresponded to periods of inactivity. By drinking around the midday period, the three baboons reduced their respective body temperatures by 1.6 ± 0.9°C (n=15), 2.2 ± 0.4°C (n=4) and 1.2 ± 0.5°C (n=6). For all three baboons these temperature changes occurred within 64 ± 42 minutes ($\bar{x}$ ± SD; range = 25-180 minutes).

Details of the baboons' daytime body temperatures that were recorded on days when water was available are shown in Table 8.2.

Body temperature data indicated the importance of the availability of drinking water and the timing of drinking to these baboons with regards to temperature regulation. The rapid rise in temperature just prior to drinking was associated with the rapid movements to reach water (Figs. 8.2 - 8.4). Often as far as 3 km from water, the baboons would start running and jockeying for positions in the procession. This behaviour was especially true for low-ranking baboons who attempted to get to the water first before the rest of the troop arrived when strict

rank-ordered drinking occurred and only one baboon at a time could drink (Brain, 1992; Chapter 9).

Figure 8.2. Baboon 1

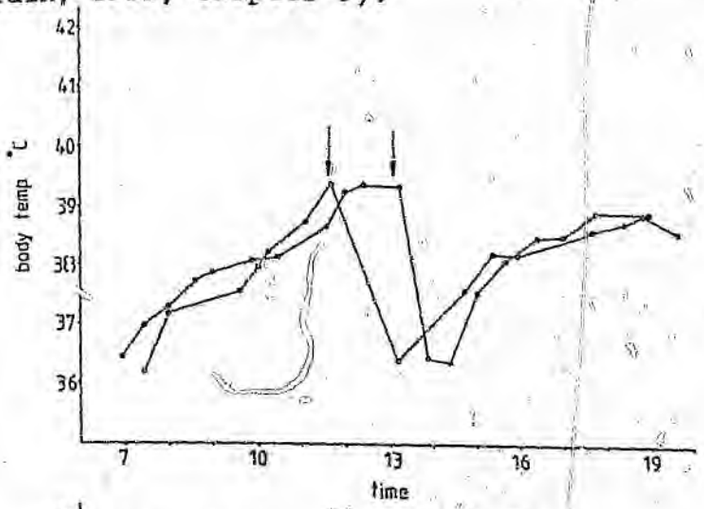


Figure 8.3. Baboon 2

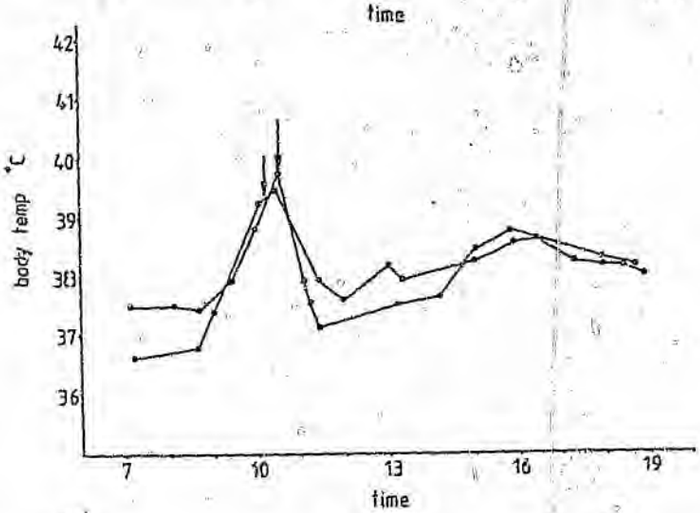
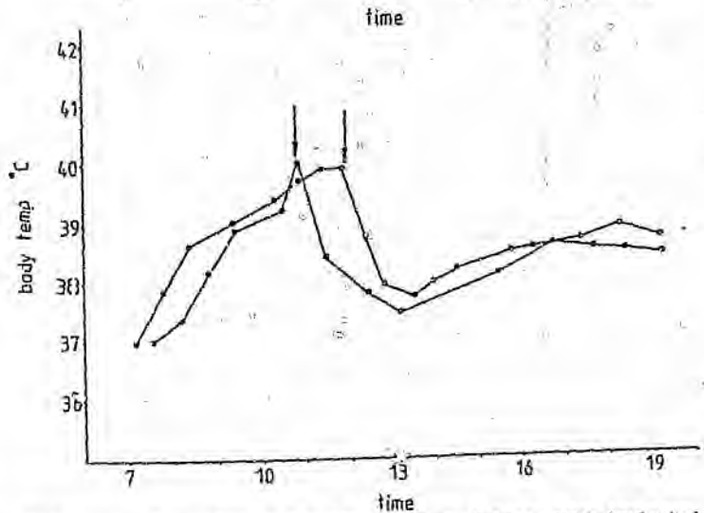


Figure 8.4. Baboon 3



Figures 8.2, 8.3 and 8.4. Body temperature changes for each of three baboons with implanted telemeters as recorded for two different days when the baboons drank water. Shaded circles indicate periods of activity and open circles periods of inactivity. Arrows indicate drinking. Baboon 1 had a mass of 27 kg, baboon 2, 17 kg and baboon 3, 33.5 kg.

DRINKING DAYS					
Baboon	Minimum daily T°	Maximum daily T°	Daily fluctuation	Highest maximum T°	Lowest minimum T°
1 x	36.9	40.1	3.2	42.7	36.1
SD	0.9	1.3	0.5		
n	12	12	12		
2 x	36.8	39.8	2.9	40.3	36.0
SD	0.4	0.5	0.8		
n	4	5	4		
3 x	36.9	39.6	2.7	40.0	36.5
SD	0.2	0.3	0.2		
n	6	6	4		
x	36.9	39.8	2.9	41.0	36.2
SD	0.1	0.3	0.3	1.5	0.3

Table 8.2. Details of daytime body temperatures recorded on days when water was drunk.

NON-DRINKING DAYS					
Baboon	Minimum daily T°	Maximum daily T°	Daily fluctuation	Highest maximum T°	Lowest minimum T°
1 x	36.7	41.1	4.3	42.7	36.3
SD	0.7	1.2	1.0		
n	4	6	6		
2 x	36.4	40.1	3.7	40.1	36.2
SD	0.4	0.2	0.4		
n	3	3	4		
3 x	36.6	39.2	2.5	40.0	36.5
SD	0.1	0.6	0.6		
n	5	5	5		
x	36.6	40.1	3.5	40.9	36.3
SD	0.2	1.0	0.9	1.5	0.2

Table 8.3. Details of body temperatures recorded on days when water was not available.

Non-drinking periods

On non-drinking days, the pattern of temperature changes in the telemetered baboons was much simpler than on drinking days. Figures 8.5, 8.6 and 8.7 show temperature changes for the baboons each for two entire days. Temperatures generally peaked in the afternoon with no major temperature drops prior to that time. The details of body temperatures recorded for the three baboons on days when water was not available are shown in Table 8.3.

Temperature drops that occurred late in the afternoon coincided with periods of complete inactivity that characterise non-drinking days when the troop rested on the sand in characteristic postures (Figs. 8.8 and 8.9). Temperature rise in the morning was quite often dramatic (Fig. 8.6) and coincided with intense morning activity on leaving the sleeping cliff. Thereafter unlike days when water was drunk, there were no dramatic decreases in body temperature with the highest body temperatures occurring between 17H00 and 18H00.

There were no significant differences in the variables recorded in Tables 8.2 and 8.3 between non-drinking and drinking days (t - tests, $p > 0.3$ for all). The differences in baboon body temperature changes for non-drinking and drinking days lay therefore entirely in the patterns of body temperature changes throughout the day (Figures 8.2 - 8.7). However, the lack of significance between the variables in Tables 8.2 and 8.3 is possibly a consequence of the small sample size and interpretations could change if more data becomes available.

Non-drinking periods

On non-drinking days, the pattern of temperature changes in the telemetered baboons was much simpler than on drinking days. Figures 8.5, 8.6 and 8.7 show temperature changes for the baboons each for two entire days. Temperatures generally peaked in the afternoon with no major temperature drops prior to that time. The details of body temperatures recorded for the three baboons on days when water was not available are shown in Table 8.3.

Temperature drops that occurred late in the afternoon coincided with periods of complete inactivity that characterise non-drinking days when the troop rested on the sand in characteristic postures (Figs. 8.8 and 8.9). Temperature rise in the morning was quite often dramatic (Fig. 8.6) and coincided with intense morning activity on leaving the sleeping cliff. Thereafter unlike days when water was drunk, there were no dramatic decreases in body temperature with the highest body temperatures occurring between 17H00 and 18H00.

There were no significant differences in the variables recorded in Tables 8.2 and 8.3 between non-drinking and drinking days (t - tests, $p > 0.3$ for all). The differences in baboon body temperature changes for non-drinking and drinking days lay therefore entirely in the patterns of body temperature changes throughout the day (Figures 8.2 - 8.7). However, the lack of significance between the variables in Tables 8.2 and 8.3 is possibly a consequence of the small sample size and interpretations could change if more data becomes available.

Figure 8.5. Baboon 1

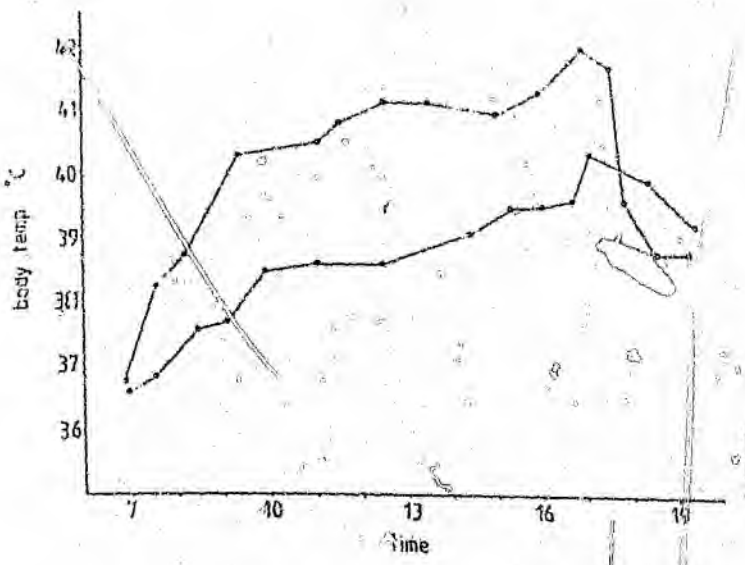


Figure 8.6. Baboon 2

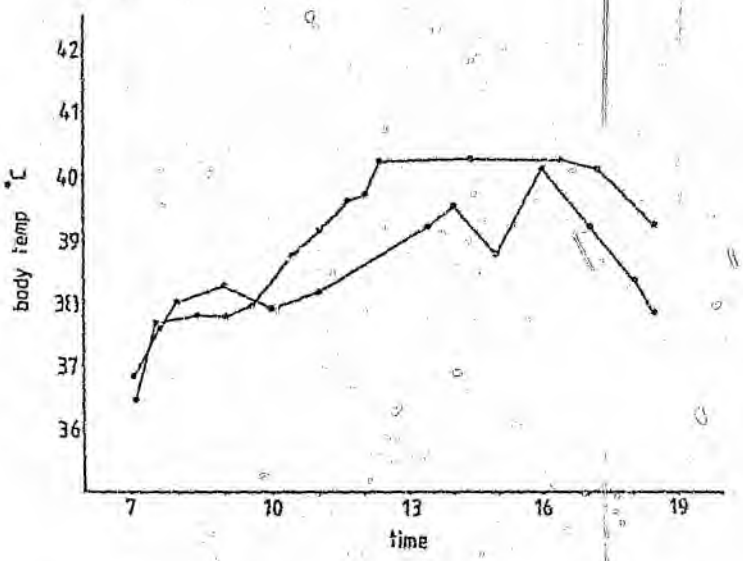
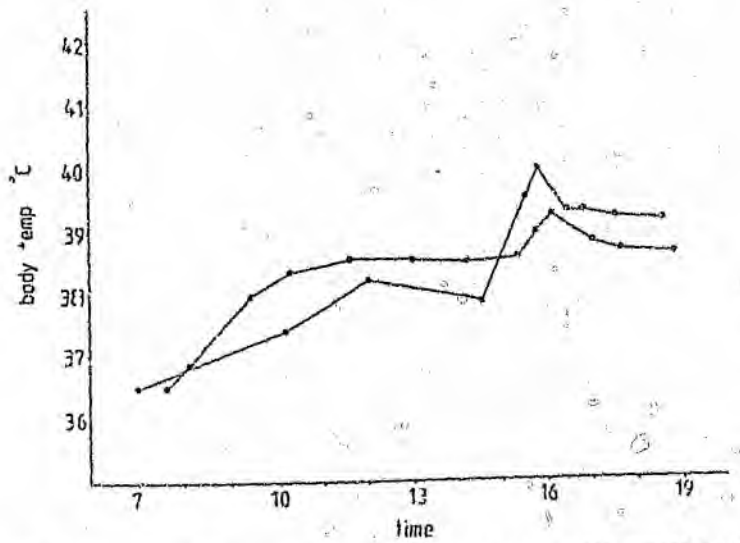
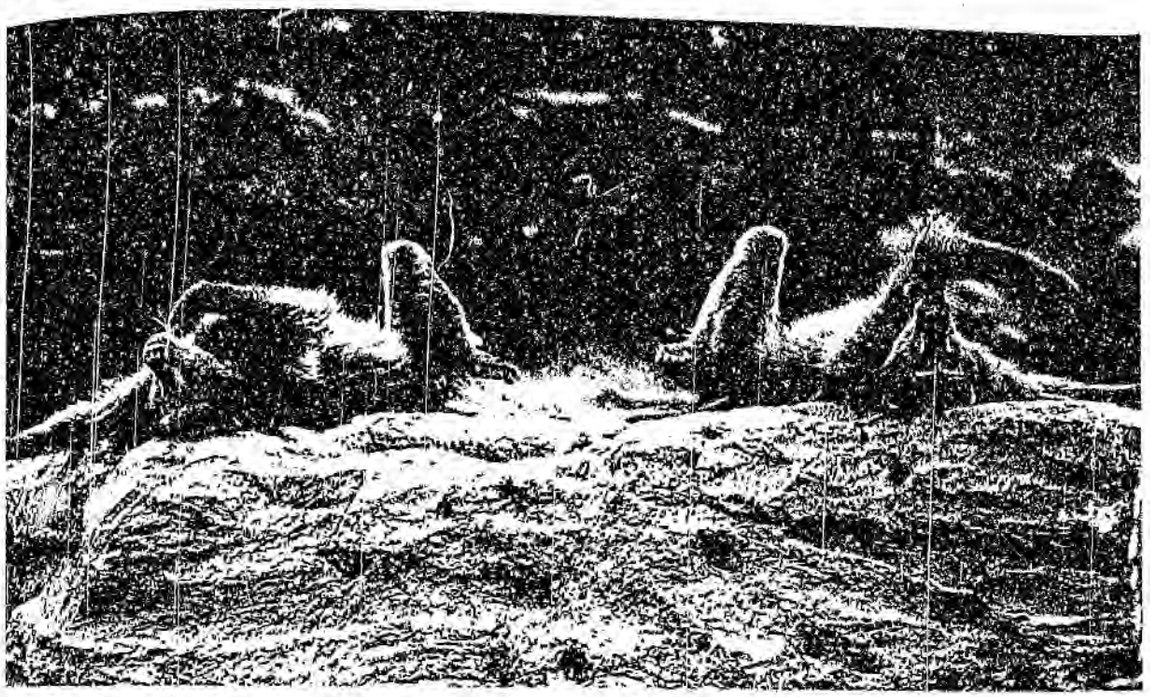


Figure 8.7. Baboon 3



Figures 8.5, 8.6 and 8.7. Body temperature changes for each of the baboons with implanted telemeters as recorded for two different days when water was not drunk. Shaded circles indicate periods of activity and open circles periods of inactivity.

Figure 8.8



Figures 8.8 and 8.9. The open postures adopted by the baboons in the late afternoons that coincided with decreases in body temperatures.

Figure 8.9



Sandbathing behaviour

The Kuiseb baboons are the only baboons known to exhibit sand bathing behaviour. Characteristically baboons scrape away surface sand in shaded areas and through wrist flicking action mobilize subsurface sand in a "plume" fashion against their ventrum (Fig. 8.10).



Figure 8.10. Adult male (Grin) demonstrates the sand bathing behaviour.

this behaviour interposes bouts of mainly morning and less frequently afternoon activity (Brain, 1990) and does not appear to be related to the ectoparasite infestation of the baboons as the body area of tick attachment (ie, mainly head and ears - Chapter 3) are not effected by the sand during sandbathing (see Fig. 8.10). Furthermore, the obvious irritation caused by the ticks (eg, scratching) is not associated with sandbathing.

For the three baboons with implanted telemeters, sandbathing occurred statistically no more frequently on non-drinking days (n=8) than drinking days (n=8) ($x^2 = 1$, $p > 0.1$). The changes in body temperature for a sandbathing baboon are shown in Fig. 8.11. In all other cases of observed sandbathing where body temperature was recorded (n=37) a similar result to that shown in Fig. 8.11 was obtained where body temperature rise was staggered following a bout of sandbathing. The duration of body temperature staggering depended upon subsequent activities: if the animals remained inactive with subsequent sandbathing (eg, Fig 8.11 - non-drinking day) up to four hours of low body temperature change was experienced. Any movement, however (eg, Fig. 8.11 - drinking day), caused rapid rise in body temperature. In all cases of sandbathing recorded here the temperature of sand used for sandbathing was between 19°C and 24°C and was thus at least 15°C below the baboons' body temperature at time of sandbathing.

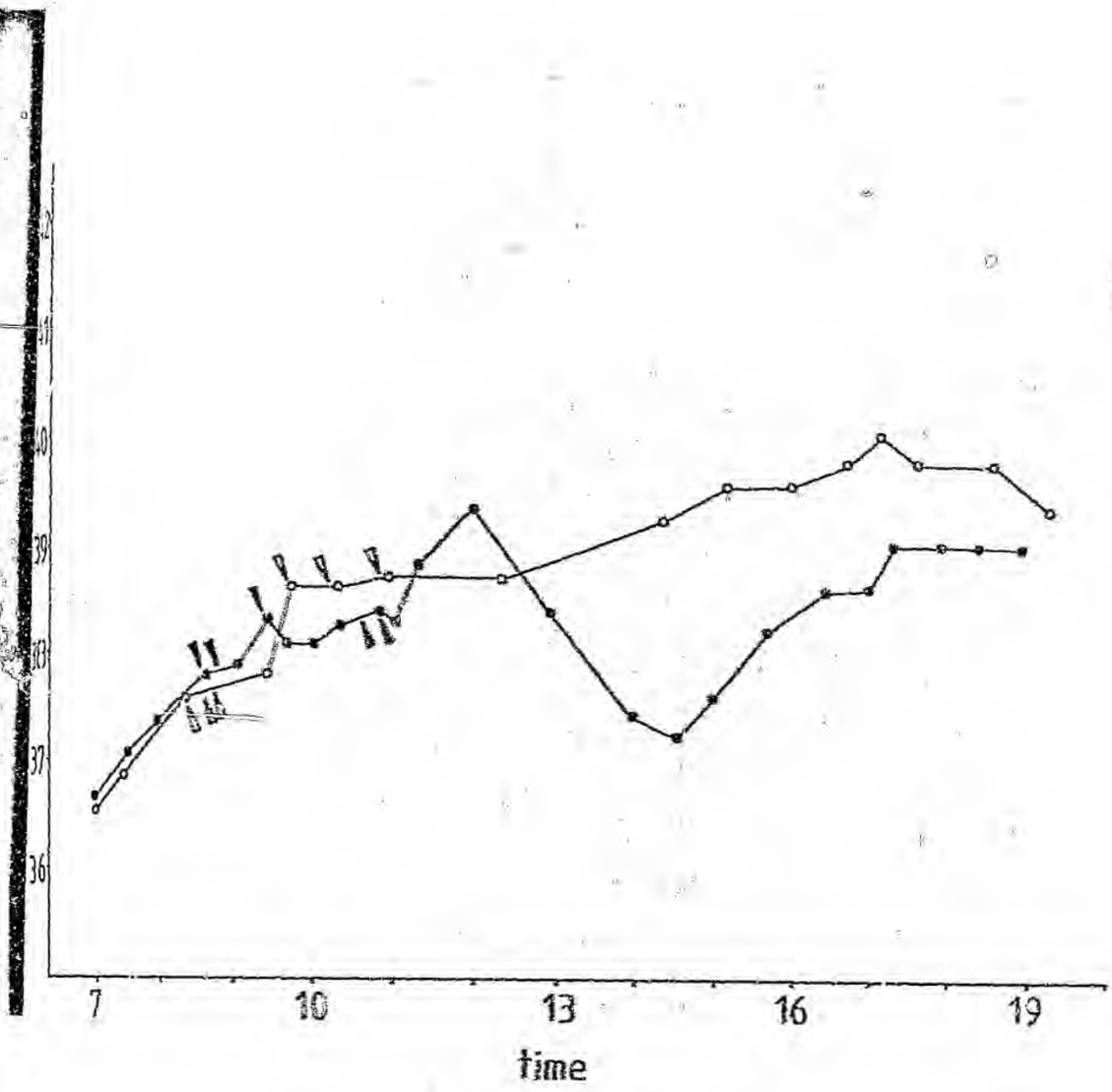


Figure 8.11. Body temperature changes associated with sandbathing behaviour in a baboon with an implanted telemeter, for a drinking day (closed circles) and a non-drinking day (open circles). Arrows indicate sandbathing. For the drinking day, the drop in body temperature after 1230 is associated with drinking that occurred at 1210.

DISCUSSION

In arid and savanna habitats, distribution of baboons' food and water resources are usually patchy. In hyper arid areas and areas with a "dry season", water availability appears to be a major factor governing range determination (Dunbar, 1992). My

telemetry data shows patterns of body temperature changes to be integrally linked to drinking water availability for the Kuiseb baboons. The drop in temperature following drinking in all cases here effectively created a midday trough of body temperature from where temperature again rose and peaked in association with afternoon activities. These data furthermore suggest calculated timing of movements by these baboons to reach water at a time of maximum benefit in terms of body and ambient temperature. By reducing body temperature around midday the day is effectively divided into two. Following each low in body temperature (ie, early morning and following drinking) the baboons were able to engage in daily activities which caused body temperature to rise and the activities could be maintained without having to employ any obvious physiological cooling measures such as evaporative cooling or operate at elevated body temperatures.

The lability of the body temperatures recorded for the three baboons was unexpected. Baboons of similar masses in laboratories have demonstrated much more stable body temperatures under manipulated laboratory conditions (see introduction and below). However, factors such as travel, water availability, water distribution and thermoregulatory behaviour in the field appear fundamental to the Kuiseb baboons' body temperature changes. It is also difficult to asertain wheather the extremes of body temperature recorded (36 °C - 42.7 °C) represent unusual body temperature elevation or depression for the species as no comparative data for free ranging animals exists.

the lability of temperature here suggests active body cooling through evaporation was noticeably employed only when water was available. The absence of any major decreases in temperature on days when water was not available and the large mean daily fluctuations in body temperature support this and would have two important consequences for the baboons. Firstly, the storage of heat which can be dissipated by non-evaporative means in the late afternoon and night would result in a saving of body water otherwise used for evaporative cooling. Considering that these baboons have been recorded to go without water for > 90 days, the recorded heterothermy could result in substantial water conservation. It seems unlikely that the decrease in body temperature of the baboons after drinking was simply a physical consequence of drinking cold water although I have no actual evidence on this. I would have expected a more varied temperature decrease after drinking within and amongst the individuals at different drinking sessions, depending on quantity and temperature of water drunk, if the water itself was responsible for body temperature decreases.

Data on activity patterns of these baboons indicate them both to be less active and to have significantly shorter day journeys on non-drinking days as opposed to drinking days (Chapter 3). Body temperature data complements these activity data, where rapid body temperature rises on non-drinking days are absent. It seems possible then that factors associated with body temperature may be the major determinants of activity patterns in these baboons. Because activity is decreased when water is not available, body

temperature could be seen as a constraint on activity. The major consequence of this apparent "thermal constraint" to the Kuiseb baboons is the tick infestation that kills most infants (Brain and Bohrmann, 1992; Chapters 2 and 3). Thus an unexpected spin off of the temperature telemetry data is a clearer understanding of the unique relationship between parasites and the baboons, and indeed, the ecology of the Kuiseb baboons. These results also emphasise the importance of obtaining measurements from animals under natural conditions if one is to contribute meaningfully to an ecophysiological study of the animals.

Sandbathing behaviour

While sand surface temperatures exposed to sun in the riverbed rose rapidly from around 21°C to 56°C, shaded sand at a subsurface depth of two centimetres ranged daily by only 3.4°C around 23°C (Appleton and Brain, pers. comm.). The baboons showering of themselves with this subsurface sand during brief periods of inactivity, especially during activity periods, appears to be a major contributing factor to the staggered body temperature rise recorded. As mentioned, sandbathing and actual temperature changes are out of phase but the steady constant rise of the temperature in absence of sandbathing (Fig. 8.11) suggests this behaviour to be an important factor to baboon temperature changes. However, this remains a tenous conclusion because of the small sample size.

While sandbathing behaviour has been recorded in many mammals (eg, Hyaena - VanLawick-Goodall, 1970; Elephant - Smithers, 1983; Zebra - Penzhorn, 1979) its function has usually been described as hygienic or for ectoparasite control. White and Odell (1971) reported Elephant seals (Mirounga anguistirostris) initiating sand flipping in response to peripheral heating while on the beach, and ground squirrel (Xerus inauris) sandbathe in hot weather, probably as a thermoregulatory measure (Herzig - Straschi, 1978). However, amongst primates, sandbathing behaviour is unique to the Namib baboons and telemetry results indicate it to be, amongst other possibilities, of a thermoregulatory nature. One observation indicating that sandbathing may be a behaviour either learnt or inherited by baboons in the Lower troop only is that adult male baboons immigrating to the Lower troop from distant inland populations (see Chapter 6) have never been seen to sandbathe.

Possibilities for comparison of these results with those from elsewhere

The obvious importance reported here of factors associated with daily living in a natural environment such as travel, drinking and range use, severely limit comparison of these results with laboratory studies. The temperature thermolability recorded for the Kuiseb baboons is a striking contrast to temperature of captive animals; Hiley (1976) recorded abdominal temperatures of baboons exposed to environmental temperature of 40°C for 120 minutes to fluctuate by less than 1.7°C. Similarly, Funkhouser

et al (1967) found baboon body temperatures to remain virtually unaltered after exposure to environmental temperatures between 10 and 40°C with maximum body temperature not exceeding 39°C and the mean rectal temperature under neutral conditions to be 38.1 °C. However, various observations on the behaviour of free ranging baboons elsewhere in arid habitats indicate some similarities to that of the Kuiseb baboons.

Foremost among these is the drinking behaviour of hamadryas baboons. Kummer (1968) reported hamadryas baboons moving to one of the isolated water holes around noon and them spending around two hours there during which the baboons drank and rested quietly. Activity was resumed thereafter. Similarly, chacma baboons in the arid Northern Transvaal region of South Africa drank during the hottest time of the day (Stoltz and Saayman, 1970) as did baboons in South West Africa (Namibia) during a severe drought (Hall, 1963). Stelzner (1988) and Stelzner and Hausfater (1986) found that Papio cynocephalus in Amboseli when faced with high ambient temperature did not prefer shaded over non-shaded microhabitats but adjusted their behaviour to opportunistic encounters with shade. Their data indicate that encounters with shade are important to Amboseli baboons, possibly for thermoregulatory reasons. The authors were not able to establish this as they were not monitoring body temperatures or using appropriate models (Chappell and Bartholomew, 1981) for estimating body temperatures. They did however predict that postural thermoregulation would be more clearly expressed by baboons engaging in low activity behaviours such as resting.

While these results and predictions are based on statistical inference from observation data, my results on temperature changes indicate even brief resting periods to be important in the overall thermal balance of the Kuiseb baboons.

The sandbathing activity of the Kuiseb baboons indicates a "fine tuning" of their behaviour to brief periods of inactivity. Sandbathing behaviour of the Kuiseb baboons suggests that in their desert environment, relatively large thermal loads are imposed on the baboons. To establish the extent of these thermal loads, telemetry data would have to be combined with "operative temperatures" obtained from appropriate models (Chappell and Bartholomew, 1981). However, the data presented in this chapter clearly show the importance of including body temperature when considering the activities of baboons.

Chapter Nine

Water flux rates of the Kuiseb baboons and the acquisition of water

INTRODUCTION

The availability of drinking water differs in different habitats; so too does the amount of water contained in different food types. Conspecific African mammals rarely inhabit an entire spectrum of habitats ranging from moist forest to hyper-arid desert (Smithers, 1983). Amongst non-human primates, baboons (Genus Papio) are the notable exception, living in habitats ranging from rain forest to desert. Baboons dependence on water might then be expected to correlate with aridity of habitat and dryness of diet.

The importance to baboons of ready access to drinking water is emphasized in studies showing that most baboons, including the semi-desert dwelling hamadryas baboon, Papio hamadryas, drink free water daily (Kummer, 1968) or sometimes once every two days (Altmann and Altmann, 1970). Irregular drinking was reported for baboons, Papio cynocephalus ursinus, on the Cape Peninsula (Hall, 1962) where baboons obtained moisture from dew and succulent plant material, but there observations were made in a high rainfall area on one day per week for a year. To date no data exist on actual water flux rates (Nagy and Peterson, 1988) for free-ranging baboons under natural conditions.

The baboons living in the Kuiseb occupy the most arid habitat recorded for any non-human primate. These baboons demonstrate a partial independence of drinking water (Brain, 1988; 1990), and

their access to water, for the most part of the year, is restricted to sources where only one baboon at a time can drink (Brain, 1990). When water is not available the baboons apparently fulfil their moisture requirements by ingesting high moisture plant food (Brain, 1990).

Considering the Namib baboons are living at the arid extreme of habitats for the species, data regarding water flux rates of these animals would be useful, both for assessing the baboons' dependence on environmental water in their habitat and for comparing with predicted values (Nagy and Peterson, 1988) of species under similar environmental conditions. In this chapter I present water flux rates of these free-ranging baboons. I also analyze their acquisition of preformed water.

MATERIALS AND METHODS

The materials and methods for the two sections of this chapter, water flux rates and water acquisition, are described separately below

Water flux

I used tritiated water to measure water flux rates of free ranging baboons in the Kuiseb River canyon (Chapter 1). However,

because it was not possible to immobilize the same baboons twice within a short period of time (< 2 weeks) to obtain a second body fluid sample for analysis without seriously risking destruction of the habituation (Melton, 1980; Hamilton and Bulger, pers. comm.), the usual procedures for water flux determinations (Nagy, 1983) were modified. To this end and to assess the accuracy of using faecal "recapture" samples in the field instead of blood samples following isotope (tritium) injection, I conducted a laboratory study prior to the field study. Tritium activity in faecal samples had been found to accurately represent tritium activity of plasma in the aardwolf Proteles cristatus (Williams, pers. comm.). However, for my baboon study, a laboratory investigation was deemed especially necessary as baboon faecal moisture in the field could be expected to vary as the availability of free water changed (Chapter 1), and factors associated with faecal water reabsorption in the large intestine and rectum (Zurovosky and Shkolnik, 1982) might prevent faecal isotope activity being a true representation of plasma activity. All experiments, laboratory and field, were approved by the Animal Ethics Committee of the University of Witwatersrand (no. 91/48/5) and were under constant veterinary supervision.

Laboratory study

Five adult female chacma baboons (Papio cynocephalus ursinus) weighing between 14 and 19 kilograms were studied at the Central Animal Service, University of Witwatersrand Medical School. The baboons were immobilized (ketamine, 100 mg/ml, 5 mg/kg) in crush

cages, removed from the cage, weighed and 2 x 3ml blood samples were taken. Each baboon was injected I.V. (femoral vein) with tritiated water (1mCi/ml) at a dose of 0.29 mCi/kg and returned to their cages. Water was withheld from the baboons for the following two days and dry pellet food was offered ad lib.

Between 21 and 23 hours later, immediately following defecation, the baboons were again immobilized and weighed. Faecal matter was collected and sealed in glass containers and 2 x 3ml heparinized blood samples were withdrawn. Time lapse between defecation and the taking of blood samples was no longer than four minutes. Microhematocrits were determined by spinning 75 µl heparinized blood in a capillary tube for 3 minutes at 12500 rpm (centrifuge head diameter = 18cm). A similar procedure was repeated on the third day (45 -48 hours after isotope injection) and thereafter the baboons were provided with water again. None of the baboons showed any signs of weakness or distress during the procedure.

Blood and faecal samples were distilled using quick-fit distillation glassware. I deposited approximately 3ml blood and approximately 3g homogenized faeces in separate distillation flasks, and fitted a distillation tube onto each flask and the sample (blood or faecal) in the flasks were frozen in liquid nitrogen. The flask and tube were evacuated to around 68 torr while the sample remained frozen. I placed the end of the distillation tube in liquid nitrogen while the flask was exposed to room temperature. Water immediately started evaporating from

the sample and the apparatus was left for 12-16 hours by which time a dry powder remained in the flask. Water, once thawed, was removed from the tube and transferred into glass vials that I flame sealed pending further analysis. For analysis, 10µl of each sample (three replicates of each) were pipetted into 10ml Packard Ustagel Scintillation cocktail using a Gelman SAFE pipette and 10µl Drummond Gold Label Microcaps. The same pipette was used for all samples to eliminate errors due to slight variance in volume between pipettes. Samples were counted in a Packard Tri-Carb 460C liquid scintillation counter until < 2% of counting error was obtained. A mean counts per minute (CPM) value was determined for the three samples and u[illegible] further analysis.

Field study

Three male baboons weighing 17, 27 and 33,5 kg were darted between March and July 1992 for water flux determinations. Baboons were immobilized only once, so I remain uncertain if the animals maintained constant body mass indicating steady state conditions during the experiment. Fortunately, water influx rates calculated with the steady-state equation are relatively close to actual water influx rates in most non-steady-state situations (Nagy and Costa, 1980). Therefore, the risk of re-immobilizing to determine steady-state was not taken and for the calculation of the water flux rates of the Kuiseb baboons I assumed that body water volumes of the baboons remained constant during the measurement period.

Baboons were immobilized using a blow-pipe and Telinject dart containing an estimated dose of 10mg/kg ketamine (100mg/ml). Baboons were darted only when the unsuspecting target animals were somewhat separated from the troop and facing away from the immobilizer. Further, the baboon had to be on flat ground > 200m from the nearest cliff, as previously a partially immobilized animal who had climbed a sheer cliff was attacked by other baboons, resulting in a fatal fall (Brain, unpub. data). It took approximately eight days of continuous following before the first darting opportunity presented itself for each baboon. Upon immobilization, the baboon was immediately covered with a tarpaulin to enable covert removal from the troop. Once removed the baboon was weighed, and two 3ml blood samples and a faecal sample for isotope background analysis were taken. At the same time, a temperature transmitting telemeter was surgically inserted intraperitoneally (see Chapter 8). Baboons were injected intramuscularly (I.M.) with tritiated water (HTO 5mCi/ml) at a dose of 0.4mCi/kg. Animals were returned to the troop within 1½ hours of darting and monitored visually until fully recovered which occurred in all cases within two hours.

Faecal samples were collected from these baboons for the following ten days. Faecal matter was sealed in a glass jar within 30 seconds of being deposited and stored at -4°C until further analysis. At least six samples were collected from each animal over the ten sampling days and the exact time of defecation was noted.

distillation, pipetting and activity counting were done in the manner as described for the laboratory study except that a mixture of dry ice and alcohol was used for freezing samples and distillation. Standards were prepared from the original injection solution and counts of duplicate standards differed by < 2.5%. Ln CPM values were regressed against time (hours) for the 10 days and activity at equilibration determined by back extrapolation of the regression line to time zero. HTO space was calculated through the equation:

$$\text{HTO space} = \frac{Vst \times Cst \times Vinj.an}{Co \times Vinj.st.}$$

(Yahav, Simon and Nevo, 1989)

where HTO space is tritiated water space (ml), Vst is volume (ml) of standard solution, Cst is the specific activity of tritium in standard solution, Co is the specific activity of tritium in body water at equilibration, Vinj.an and Vinj.st are volumes (ml) of tritium injection into the animal and standard solutions.

Water flux rate was determined by the equation:

$$\text{Water flux (ml/h)} = \text{HTO space} \times K$$

where K is the slope determined from the decreasing of $\ln[H^3]$ in faeces as a function of time (Fig. 9.1) and $T_{\frac{1}{2}} = \frac{0.693}{K}$ where $T_{\frac{1}{2}}$ is the biological half-life time of the tritium.

Acquisition of Water

Preformed water

To determine the amount of preformed water consumed by the baboons at various times throughout the year, I conducted one minute focal observations on feeding baboons. I recorded type of food being eaten and ingestion rate of the food. Ingestion rates/minute of continuous feeding on various parts of different plants were determined through observations of hand/mouth actions of randomly selected adult baboons observed at < 5m. I am confident that my observation method used in determining how much the baboons were eating was fairly accurate as the berries or fruits that were picked and eaten could be clearly seen and counted as they were put into the mouth and the whole fruit was usually eaten. Representative samples of the various foods were collected from the plants at the times that the baboons were feeding on them. Fresh plant samples were weighed immediatly upon collection and their moisture composition determined through the weight loss following drying for four days in an oven at 80°C. From these data, estimates of preformed water ingestion per minute were made. These data are combined with the chemical composition and nutritional value of the various plants as described in Chapter 7 where the overall value of these plants to the baboons in a desert environment is discussed. Plants of very low moisture content (<10%) that at times form a part of the baboons diet were not included here as these plants contributes little to the baboons intake of preformed water.

RESULTS

Water flux

Laboratory study

Changes in body mass, haematocrit and faecal moisture content that occurred during the experiments are shown in Table 9.1 together with the activity of distilled blood and faeces in counts per minute (CPM). For the baboons, a 5.9 ± 1.2% (x ± SD) decrease in body mass was associated with a 9.6 ± 6.5% decrease in plasma volume. There was no significant difference between activity in CPM of blood and faecal samples for the 21 - 23 hour samples (paired t test, $p > 0.2$, $n = 3$) or the 45 - 48 hour samples (paired t test, $p > 0.1$, $n = 5$).

Field study

A total of 23 faecal samples with a mean faecal water content of 74.6 ± 5% were collected and analyzed, 11, 6 and 6 samples from the three animals respectively. There was no significant difference (Mann-Whitney U test; $Z = 0.56$; $p > 0.5$, $n = 8$) between the moisture content of faecal samples from the field animals and those of the laboratory animals. Isotope activity of the water in faecal samples from the field animals was therefore likely to be an accurate representation of the animals plasma isotope activity.

Regression lines of LnCPM values against time for each animal are shown in (Fig. 9.1). Details of body mass Wt, calculated total body water and water influx rates are shown in Table 9.2.

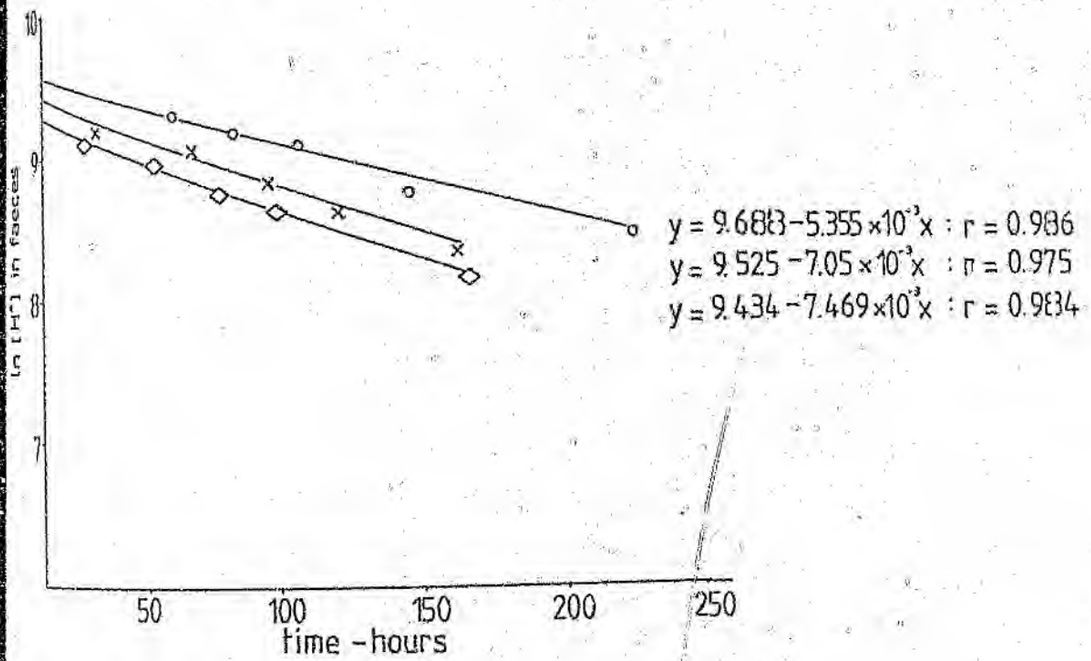


Figure 9.1. The disappearance of tritiated water from baboon faeces with time. Each line represents one baboon.

Baboon	Body mass (kg)		Hematocrit		Faecal Moisture (%H O)	CPM			
	Initial	Subsequent	Initial	Subsequent		Blood $\bar{x}$	SD	Faecal $\bar{x}$	SD
1	14.1	13.3[1]	47	50[1]	79[1]	5560[1]	44	5549[1]	51
		13.3[2]		50[2]	78[2]	5260[2]	94	5183[2]	7
2	18.7	18[1]	49	50[1]	76[1]	5667[1]	7	5516[1]	1
		17.7[2]		51[2]	74[2]	5370[2]	202	5364[2]	108
3	18.4	17.4[1]	49	51[1]	71[1]	5353[1]	53	5321[1]	104
		17.1[2]		52[2]	68[2]	5256[2]	45	5152[2]	12
4	17.9	17.2[2]	45	49[2]	66[2]	5104[2]	20	5079[2]	26
5	16.3	15.1[2]	44	44[2]	77[2]	4366[2]	4	4386[2]	79

Table 3.1. Variables recorded for captive baboons in laboratory experiment examining relationship between activity (tritium) of simultaneous blood and faecal samples obtained from the baboons. Only one faecal sample was obtained for baboons 4 and 5. Values marked with [2] were the 21 - 23 hour samples and those with [1] were the 45 - 48 hour samples. (See text for details of experiment.)

Baboon	Mass (kg)	Hematocrit	Body water (%)	Water flux ml kg^{1} day^{1}
1	27	32	73	129
2	17	38	69	117
3	33.5	41	66	82
$\bar{x}$	26	37	70	110
SD	8	5	4	25

Table 9.2. Mass specific total body water, haematocrit and water flux rates for the three free-ranging baboons.

Using the allometric equation of Nagy and Peterson (1988) where mass specific water flux rate is expressed as ml g day ^{1}, the mean water flux rate measured for the Kuiseb baboons was 0.670ml g day ^{1}.

WATER ACQUISITION

Preformed water

Plants in Table 9.3 are arranged in order of estimated quantity of preformed water ingested/minute. There was no significant difference in feeding rates (ie, hand to mouth movements per minute) between randomly selected individuals [illegible] t males, n = 3; adult females, n = 3) when feeding on the same plant species (ANOVA; F = 0.21, p = 0.95). Differences in quantities of food ingested by individuals during feeding bouts are therefore likely to be influenced by selection of prime feeding sites, ie, sites

with more food and\or better quality foods, and durations of individual feeding times. Figures in Table 9.3 were based on uninterrupted one minute feeding bouts (ie, no supplanting, moving, etc) so estimated preformed water ingestion rates are probably close to the maximum that can be achieved for the various plants.

Plant	% Moisture ± SD	Season Used	Ingestion rates/min $\bar{x}$	SD	n	Estimated H20 (preformed) ingested/min
Ficus sycomorus						
- ripe figs	87 ± 3.7	Oct-Feb	9 figs	4	33	55 ml
- green figs	78 ± 3.4	Oct-Feb	9 figs	4	33	31 ml
Nicotiana glauca - pith	94 ± 0.6	year round	1 pith	1-2	28	33 ml
Argemone ochroleuca - pith	86 ± 3.4		1 pith	1-2	12	approx 22 ml
Acacia shoots	90 ± 1.0	Jan-Apr	27	16	37	14 ml
Acacia erioloba - green seed	60 ± 2.7	Dec-Feb	3 pods (± 10 seeds/pod)	0.3	11	7 ml
Salvadora persica - ripe berries	71 ± 0.7	Dec-Jun	49 berries	12	69	6 ml
Faidherbia albida						
- bark	63 ± 2.1	yr.round	1.8 pellets	1	16	3 ml
- seed covers	72 ± 2.1	Sept-Dec	9 pods	3	23	3 ml
Euclea pseudebenus - green berries	53 ± 2.9	Oct-Mar	23 berries	1[illegible]	38	2 ml

Table 9.3. Plant moisture, ingestion rates and estimated preformed water ingested by the baboons; n = feeding observations.

DISCUSSION

Water flux in animals can be extremely variable (Nagy and Peterson, 1988). In any species, changes in water content of food, increased need for evaporative water loss at times of heat stress, degree of activity and drinking frequency all contribute to the complexity of water flux rates. My study was conducted during a period when free water, although restricted to one excavation, was drunk daily by the baboons and it is likely that the recorded water flux rate of 110 ± 25 ml kg^{-1} day^{-1} would be within the higher range of values characteristic for these individuals and the species as a whole under natural conditions. Other factors of importance here when considering water flux were increased daily movement and activity associated with foraging (Brain, 1990; Chapter 3) and the subsequent decrease in body temperature (Chapter 8) presumably through evaporative water loss exhibited only when free water was available.

The only other study of water flux of non-human primates under natural conditions is that of the Howler monkey (Alouatta palliata) where a water flux rate of 118 ml kg^{-1} day^{-1} was recorded (Nagy and Milton, 1979). Zurovsky and Shkolnik (1982) reported a water flux rate of 140 ml kg^{-1} day^{-1} for captive hamadryas baboons (Papio hamadryas). If these values are corrected for body mass using the allometric equation of Nagy and Peterson (1988), the free-ranging howler monkey had a water flux rate of 0.583 ml $g^{-0.819}$ day^{-1} and the captive hamadryas baboon 0.701 ml $g^{-0.819}$

day^{-1} . The Kuiseb baboons water flux rate of 0.670 ml $g^{-0.819}day^{-1}$ falls between the two. It therefore appears that there was nothing unusual about the Kuiseb baboons water flux rate. However, one should not draw comparisons between captive and wild animals as these values vary widely (Nagy and Peterson, 1988).

Comparison of data presented here with that of other free ranging non-human primates is therefore severely limited by the virtual absence of data from conspecific or other species. Nagy and Peterson (1988) however have derived an equation relating water flux to mass in a variety of free living eutherians. According to this equation, predicted water flux for a 25 kg desert animal = 90 ml kg^{-1} day^{-1}. The factors related to free water intake and moisture composition of the diet during the study of the Kuiseb baboons could easily account for the 17% increase in water flux recorded for the Kuiseb baboons. However, when compared to the predicted value and on a t test, the value of 110 ± 25 ml kg^{-1} day^{-1} for the Kuiseb baboons was not significantly different from 90 ml kg^{-1} day^{-1} ($p > 0.5$). Therefore, in spite of the clear behaviourial adaptations of the baboons to the arid environment recorded in the previous chapters of this thesis, there appears to be no evidence of physiological adaptation (ie, reduced water turnover) on this most crucial of physiological functions.

The hematocrits of the laboratory and Kuiseb baboons are given in Tables 9.1 and 9.2. The hemotocrits of the laboratory baboons at the first sampling (21 - 25 hours, Table 9.1) were significantly higher than the Kuiseb baboons hematocrits (Mann-

Whitney U test; $Z = 2.1$, $p < 0.05$). However, the values from both groups are within the range (30 - 49) of hematocrit values reported for wild chacma baboons in Botswana (Melton and Melton, 1981). The mean (± SD) hematocrit of 63 male baboons Papio anubis from the Awash National Park, Ethiopia was 36.8 ± 3 (Phillips-Conroy, Jolly and Rogers, 1987), which is similar to the Kuiseb baboons' mean hematocrit value of 37 ± 5. It seems likely that the higher hematocrit values of the laboratory baboons in my study were the result of factors associated with captivity such as stress and dehydration. There appeared to be no obvious factors affecting the Kuiseb baboons that are associated with low hematocrits in primates; Kuiseb baboons had few endoparasites and no obvious blood parasites (Chapter 4), they were not emaciated or suffering from acute starvation nor were any suffering from septic wounds.

The acquisition of preformed water appears essential for survival of baboons in the Namib considering the scarcity and distribution of free water. While plants of reasonably high water content (> 70%) were available to the baboons, moisture content of plants were not the only factor determining their consumption. While alien invasive plants (Nicotiana glauca, Argemone ochroleuca) have a year round high supply of moisture (Table 9.3), they are of known toxicity to livestock and humans alike (Watt and Breyer-Brandwyk, 1962). Whether the baboons were eating them for some other reason (eg. electrolytes, nutritional value) is discussed in Chapter 7.

The seasonality of fruit production by the plants forming the major part of the baboons' diet is important. Free water scarcity increases from April of each year until the following flood (Chapter 3). When water was not available, Salvadora persica berries and Ficus sycomorus figs formed the major part of the baboons' diet (Brain, 1988, 1990), and supply was abundant (Brain, 1988). According to Table 9.2, on average, even when the baboons were drinking regularly, they turned over 2860 ml/day. According to Table 9.3, by eating figs the baboons can get 55 ml/minute of water when the figs are ripe. It would then be possible for the baboons to get their full days water in 52 minutes of continuous fig feeding. Because the baboons do not feed uninterruptedly for 52 minutes at a time, it would take them longer than 52 minutes to acquire their daily water, but in an approximate four hours of feeding a day, it was likely that they were easily able to acquire their full days water. Figs were especially important because their main fruiting time coincides with the periods of maximum water shortage (Chapter 7, Figure 7.2) and the baboons were recorded to spend 116 days without water eating mainly figs.

Chapter Ten

Water conservation by baboons in the Kuiseb River canyon

INTRODUCTION

Adaptive responses to minimise water loss in animals include the storage of heat (adaptive heterothermy), efficient reabsorption of water from faecal material in the rectum, production of highly concentrated urine, low metabolic rate, escape to favourable micro-environments and specialized integuments and pelages (Louw and Seely, 1982). Animals adapted to desert environments usually show advanced development in one or more of these spheres. However, only few desert animals qualify to be termed truly "special" in terms of the differences in their physiological functioning compared to conspecific or similar species from other environments. While profound physiological differences do exist in some desert animals, many show no qualitative differences to species from other environments. In this regard, behaviourial adaptations form an important adjunct to physiological ones for desert animals (Seely, 1989).

Physiological and behaviourial changes within a species could be expected to be found at the habitat extremes inhabited by the species (Louw and Seely, 1982). To what extent such changes might be considered "different" ultimately depends on interpretation of the word "different"; but if a population has a physiological adaptation without which it could not survive in its habitat but which is not evident in conspecifics or similar species in other habitats, it could be considered different.

studies of captive hamadryas baboons (Papio hamadryas) originating from the desert area of the horn of Africa and southern Arabia provided some evidence of baboon adaptation to a desert environment. Findings concerning body water conservation and body fluid distribution appear most important (Zurovsky, Shkolnik and Ovadia, 1984; Zurovsky and Shkolnik, 1981). Most striking is the ability of this baboon to maintain its plasma volume even at 10 per cent dehydration. This ability complements the baboon's capacity to conserve water at times of water shortage as seen by its renal performance in terms of increased urine concentration, reduced sweating rates and decreased faecal water loss.

The aim of this chapter is to examine aspects of body water conservation by the Kuiseb baboons in an attempt to assess whether there is anything "different" or special about their conservation of water. The measured water flux rate for these desert baboons of 110 ml kg^{-1} day^{-1} (Chapter 9) falls within the range one would expect for baboons and is nearly identical to water flux rate of baboons elsewhere in southern Africa (Buffenstein, unpub data). However, because of the difficulties associated with free water acquisition in their desert environment (Chapter 9) and the prolonged periods these baboons spend without drinking, I would expect them to conserve body water.

STUDY AREA AND METHODS

The study was conducted in the dry river bed of the Kuiseb River canyon in the central Namib desert, Namibia. Details of the area, the baboons and the range occupied by the baboons are given in Chapter 1.

The aspects of water conservation examined here are renal (kidney anatomy and urine concentrating ability), faecal water conservation and modified behaviourial activity.

Renal

I divided the study of renal water conservation into two parts:

1. The examination of kidney anatomy with determinations of relative medullary thickness (RMT), absolute medullary thickness and body mass specific metabolic rate for the predicting of maximal urine concentration (Umax). Similar parameters were obtained from a baboon population in the northern Transvaal, South Africa for comparison with the Kuiseb baboons.
2. Determinations of changes in urine osmolality for the Kuiseb baboons obtained from free flow urine samples at various stages of [illegible] water deprivation. This was augmented by simultaneous urine/plasma samples obtained from immobilized or dead baboons.

Kidney anatomy and dimensions

In the Kuiseb, baboon kidneys were obtained from three adult male baboons immediately after their deaths in dominance fights (see Chapter 6). The mass of the baboons and the individual kidneys was determined. The length, width and depth of each kidney was measured with a pair of callipers to the nearest 0.5mm. Kidney size was calculated as the cube root of the product of these dimensions (Sperber, 1944). The kidneys were medially bisected and the width of the cortex and medulla measured at ten intervals along the periphery and the mean determined. The relative medullary thickness was determined using the formula:

$$\frac{\text{medulla thickness (mm)} \cdot 10}{\text{kidney size mm}}$$ (Sperber, 1944)

For comparison with the Kuiseb baboons, the kidneys of 14 baboons (Papio cynocephalus ursinus) (11 adult females and 3 adult males) from the northern Transvaal, South Africa were examined in the identical manner as for the Kuiseb baboons. These baboons formed part of the stock of the Central Animal Service of the Medical School of the University of Witwatersrand and had been in captivity for at least six months before measurements were made on their kidneys.

An ANCOVA (covariate = body mass) was used to compare RMT of the baboons kidneys from the two locations. This procedure was necessary because of the marked sexual dimorphism of baboons and

the fact that only adult male kidneys were collected from the Kuiseb population. To compare adult male kidneys from both populations (n = 3 for both) the Mann-Whitney U test was used.

For predicting maximal urine concentrations (Umax) produced by the baboons' kidneys from the two locations, the following formula was used:

$$\left[\frac{L \times Mb^{-0.188}}{1.54} \right] - 1 \qquad \text{(Greenwald, 1989)}$$

where L = absolute medullary thickness (mm) and Mb = body mass (kg).

This formula, taking absolute medullary thickness and mass specific metabolic rate into consideration, is considerably better at predicting Umax than measured values of RMT (Greenwald, 1989).

Collection and analysis of urine samples

Urine was collected from six adult Kuiseb baboons (four males and two females) on three occasions each: when the baboons were drinking daily, after two days without water and after 12 days without water. I followed the baboons as they climbed a tree and I waited below with a clear plastic sheet to collect their urine. Because the baboons moved around in the tree, I continually had to change position below them. I was usually able to obtain only small quantities (a few drops) of urine. For all the samples analyzed, urine fell straight onto the sheet without touching any

branches or leaves. Any samples possibly contaminated by coming into contact with any object were discarded. Urine on the sheet was transferred to a capillary tube, sealed and stored at -4°C for later analysis. The plastic sheet was cleaned with distilled water and dried before being used again. Urine osmolality was measured by myself using a Wescor 5500 vapour pressure osmometer. Osmolality of each sample was measured in triplicate and mean values determined. Further analysis was precluded by the small samples collected.

Simultaneous plasma and urine samples were obtained from the three adult males killed in dominance fights and the osmolalties determined. Plasma samples were also obtained for the three immobilized baboons (see Chapters 8 and 9) and their respective osmolalities determined.

Faecal water conservation

Three baboons were targeted for faecal collection at the onset of a non-drinking period. The baboons were followed for five days thereafter and, where possible, faecal samples were collected and sealed in glass jars. Samples were also collected from the three baboons after 12 days without water. Only samples that could be obtained within 30 seconds of defecation were collected for further analysis. Samples were stored at -4°C for later moisture content determinations. Water content was determined through mass loss following drying of the homogenized faecal matter at 80°C for four days.

Activity modifications during inter-troop encounters

Interactions between water availability and activity of the Kuiseb baboons are addressed in Chapters 3 and 7. Here I produce evidence for a further interaction between water and activity.

Amongst baboons, inter-troop encounters are associated with increased activity of some kind; the most common of which is the chasing or herding of females by adult males of the same troop (Cheney and Seyfarth, 1977). Chasing behaviour and increased activity increase body temperature (Chapter 8) and probably result in loss of body water through sweating. If there are factors in effect which are inclined to decrease activity amongst baboons, they might influence the inter-troop encounters by decreasing the usual escalated activity and possibly result in body water conservation.

I observed 16 inter-troop encounters between the Lower troop and neighbouring Middle troop (Chapter 1; Hamilton, Buskirk and Buskirk, 1975) over three years. All encounters occurred between the months of October and January when free water was available only at the upriver limits of the Lower troops' range in an area which overlapped with the Middle troops' range (Chapter 1). I was therefore able to assess the periods of water deprivation (in days) that the Lower troop had experienced prior to inter-troop encounters. I related this period of water deprivation to the sequence of events during intertroop encounters to assess whether water availability might affect activity during the encounters.

To record the events during encounters, I positioned myself high on the canyon walls and was able to observe all the baboons and events from beginning to end of an encounter. Any escalated activity amongst the Lower troop baboons (ie, chasing, herding, running, displaying, fighting) was recorded. Circumstances and individuals (identity, rank, oestrus state of females) involved in activities during the encounter were also recorded for Lower troop baboons.

RESULTS

Kidney anatomy and dimensions

For all kidneys analyzed medullary thickness was significantly positively correlated with body mass ($r^2 = 0.7$; $F = 59.1$; $p < 0.001$; d.f. = 15). Kuiseb baboons kidneys had a significantly larger RMT than kidneys from the Transvaal baboons (ANCOVA: covariate = body mass; $F = 11.1$; $p < 0.005$; residual d.f. = 15). Table 10.1 compares renal parameters of the adult male baboon kidneys from both locations and the predicted Umax of the kidneys. Kuiseb baboons appear capable of producing considerably more concentrated urine than the Transvaal baboons.

Renal parameter	Transvaal baboons (n=3)	Kuiseb baboons (n=3)	p
Body mass ($\bar{x}$ ± SD) kg	34.5 ± 2.8	28.2 ± 1.2	<0.03
Medullary thickness ($\bar{x}$ ± SD) mm	17.5 ± 1.5	27.2 ± 1.8	<0.01
Measured RMT ($\bar{x}$ ± SD)	4.4 ± 0.27	5.7 ± 0.2	<0.01
Calculated RMT - 1	4.3 ± 0.6	6.1 ± 0.6	<0.03
Umax from RMT - 1 mosm/kg H_2O	2302.4 ± 304	3180.6 ± 297	<0.03

Table 10.1. Body mass and renal parameters of baboons from the Kuiseb and Transvaal. The use of RMT - 1 for calculating Umax (Greenwald, 1989) is explained in the text. Calculated RMT = (L Mb)/1.54. One RMT unit was subtracted because of Heller and Poulson's (1972) finding that RMT based on kidney mass exceeded RMT based on anatomy by 1.0 units.

The similarity between the measured RMT and the calculated RMT-1 indicated that the calculated value was a valid estimate of RMT if RMT had not been measured. One RMT value was subtracted from the calculated parameter because Heller and Poulson (1972) found that RMT determined by weight exceeded anatomically determined RMT by 1.0 unit.

Urine and plasma osmolality

Table 10.2 shows the changes in urine osmolalities for each of the six baboons during a continuous non-drinking period of 12 days. For all the baboons, the difference between each successive measured urine osmolality was significant (Bonferroni t test; $p < 0.001$).

Baboon I.D.	Urine osmolality (mosm/kg H_2O) days without water		
	0	2	12
Bo	718	1122	1568
Sp	682	1151	1605
Du	812	1129	1999
Gr	724	1133	1451
Gy	737	1023	1496
Ga	786	1109	1516
Mean	743	1111	1601
SD	48	45	203

Table 10.2. Urine osmolalities of urine collected from six Kuiseb R baboons for 0, 2 and 12 days after the baboons had been without water. All urine samples were collected in the same way as described in the text.

The mean osmolality of the plasma samples obtained was 307 ± 38 mosm/kg H O ($\bar{x}$ ± SD; range 301-312; n=6). The urine obtained from the three dead baboons measured 776, 1224 and 1047 mosm/kg H O (1016 ± 225 mosm/kg H O, $\bar{x}$ ± SD), giving urine plasma ratios for the three baboons of 2.5, 3.9 and 3.4 (3.3 ± 1, $\bar{x}$ ± SD) respectively. All three baboons died during a period when water was abundant and the baboons were drinking daily.

Faecal water conservation

On the first day without water, the three baboons faecal water amounted to 481 ± 42 (n = 2), 391 ± 45 (n = 2) and 385 ± 4 (n = 2) g water/100g dry matter, giving a sample mean of 419 ± 54g water/100g dry matter or a mean percentage value of 81 % water. After five days the baboons faecal water contents were 261, 195 and 201 (n = 1 each) g water/100g dry matter respectively, giving a sample mean of 219 ± 36 g water/100g dry matter or a mean percentage value of 69 % water. A regression of faecal water (g water/100g dry matter) against days without water for all samples collected and analyzed over the first five days without water (n=19; one value for each baboon each day) yielded a value of r = -0.77. After 12 days without water the baboons faecal water amounted to 251, 238 and 235 (n = 1 each) g water/100g dry matter respectively thus showing there to be no appreciable change in faecal water content for the samples collected on day five and day 12 without water.

Activity modifications

Inter-troop encounters amongst baboons are usually associated with periods of escalated activity and aggression (Cheney and Seyfarth, 1977). In the Kuiseb, the observed encounters all occurred between 09H00 and 14H00 and neither troop appeared to dominate. The two troops generally approached to within 20 to 50m of each other and on 10/16 of the encounters mingling of troop members occurred. During one of the 16 encounters there

was inter-troop aggression which involved males and females of both troops. However, for the Lower troop, chasing and intra-troop aggression occurred only during 11/16 of the encounters while for the remaining 5/16 no aggression, chasing or escalated activity was observed. In every encounter there was at least one incident of chasing in the Middle troop. There was no significant difference between the incidence of aggression observed for the Lower and Middle troops during encounters (chi-square test with Yates correction, $X = 3.78$, $p > 0.05$). Chases were often spectacular events, especially when a female was chased up a cliff. Males characteristically gave loud double barks while chasing and the concerned female screamed, often urinating as she ran. Other chases consisted of only a brief 10 meter lurch by a male after a female which also sent her off screaming. For all 16 encounters there was at least one oestrus female in the Lower troop, and for the 11 encounters when chasing took place in the Lower troop, an oestrus female was involved in at least one chase. Each female was chased in the 11 encounters and four adult males were responsible for all the chases.

For the 11/16 cases when chasing occurred, the Lower troop had drunk water 0-2 days before the encounter. However, in all five encounters when no chasing or escalated activity occurred, the Lower troop had been without water for 4-9 days, (chi-square test; $p < 0.001$). In four of five encounters where no chasing occurred, the two troops moved towards their own ranges away from the overlap zone, and the Lower troop did not gain access to water for at least one day thereafter.

DISCUSSION

Renal

Relative medullary thickness per se may not be a useful concept in understanding mammalian urine-concentrating ability and perhaps even obscures an understanding of the renal countercurrent multiplier (Greenwald, 1989). Further, RMT is not the parameter to be used when predicting maximum concentrating ability of the mammalian kidney as it bears no relationship to the metabolic (ATP coupled) mechanism that underlies the production of a highly concentrated urine. It is useful, however, when comparing kidney anatomy within or between species. In this regard, and in predicted maximum urine concentration, Kuiseb baboon kidneys were significantly different to those of baboons from the Transvaal.

The predicted Umax values (Table 10.1) for the Kuiseb were much higher than measured urine osmolality (Table 10.2). However, without the knowledge of the plasma osmolality at which urine osmolalities were determined, the true concentrating power of the kidneys cannot be completely evaluated. Where simultaneous urine and plasma osmolalities were measured, the mean urine/plasma (U/P) ratio of 3.3 ± 0.7 is likely to be lower than the maximum U/P ratio possible as the urine osmolalities were considerably lower than those recorded on day 12 in Table 10.2.

If Kuiseb baboon RMT is used as an index of its concentrating ability and compared to other animals, the baboons should be able to produced a U/P ratio of between 8.3 and 8.9 placing them in a urine concentrating class somewhere between a springbok (Hofmeyr and Louw, 1977) and a white rat (Gordon, 1972). If we assume a plasma osmolality of 321 mosm/kg H_2O (the mean value for a water deprived baboon [Zurovsky and Shkolnik, 1982]) for the baboon producing urine of 1999 mosm/kg H_2O concentration (Table 10.2), a U/P ratio of 6.2 would result. The baboons did, however, go for considerably longer periods than 12 days without water (116 days; Brain, unpub. data) and it is possible that they might produce urine of a concentration close to the maximum predicted value (Table 10.1) and then a U/P ratio of around 8.9 could be achieved. However, even a U/P ratio of 6.2 is considerably higher than that achieved by man (Gordon, 1972) or the hamadryas baboon and this ability could be considered as an important adaptation of the Kuiseb baboons to their desert environment.

The origin of the increased RMT in the Kuiseb baboons is speculative but there are various possibilities. Data in Chapter 6 suggest the Kuiseb baboons are genetically no different from further inland baboon populations. One hypothesis is then that Namibian baboons are genetically different from Transvaal baboons. Another possibility is that the increased RMT is an adaptation that develops within the life of each baboon. This idea would mean that the Kuiseb baboons are indeed subject to

continuous water stress, in spite of the moist food available (Chapter 7).

Besides the urine concentrating ability of Kuiseb baboon kidneys, the amount of water required to excrete ingested electrolytes, notably sodium, via the kidneys is likely to be relatively small. Plant foods constituting the major part of the baboons diet have uniformly very low electrolyte concentrations (Chapter 7) and therefore little water would be required for electrolyte excretion.

Faecal water conservation

The moist faeces (70 to 80 per cent) produced by primates under normal conditions potentially enhances the possibility for water conservation through reabsorption of faecal water in the rectum. The 12 per cent decrease in faecal water content recorded for the Kuiseb baboons is similar to that recorded for other medium to large desert mammals (Wilson, 1989). However, the relatively high initial faecal water content for the baboons resulted in no recorded faeces being less than 50 percent water. While faecal water reabsorption no doubt adds to the baboons overall body water conservation, other mammals living alongside the Kuiseb baboons produce faeces under normal conditions with water content lower than the lowest figure recorded for the baboons (Louw and Seely, 1982; Henschel, 1986), and therefore compared to other animals, faecal water loss probably remains a major avenue of body water loss. It is however not clear if Kuiseb baboons were more efficient at water reabsorption from faecal matter than

baboons elsewhere as no comparative results exist for baboons under free-ranging conditions.

Activity modifications

Although periods of 4 to 9 days without water are well within the capacity of the baboons of the Lower troop (Brain, 1988; 1990), the absence of chasing and escalated activity by any individuals of the Lower troop during inter-troop encounters appears related to water deprivation. Water deprivation was found to be associated with shorter distances of daily travel (Chapter 3) and shorter feeding bouts (Chapter 7) for Lower troop baboons and the decreased aggressive behaviour during encounters could be seen as an extension of a behaviourial response to water shortage. The observation that Lower troop baboons did not gain access to water after an encounter may be important here. Body temperature telemetry data (Chapter 8) indicate baboon core body temperature to be rising in the morning so that by 09H00 it is around 38°C and rising. Telemetry also shows that dramatic decreases in body temperature were associated with drinking when evaporative cooling is presumably employed and the amount of water used for evaporative cooling is easily replenished by drinking. Any form of escalated activity may cause core body temperature to rise by as much as 2.3°C in an hour (Chapter 8). Escalated activity, which is usually associated with inter-troop encounters, would probably substantially elevate the baboons' body temperatures. Passive body cooling during the midday period is unlikely and one would expect the baboons to cool themselves through sweating. By

avoiding increased aggression during inter-troop encounters, the baboons are likely to conserve body water. The effect of increased activity on elevating body temperature is also likely to be compounded by the extension of the period of water deprivation.

The finding of decreased activity during encounters being closely linked to periods of water deprivation leads me to suggest that the baboons avoided elevated body temperatures at that time of day, possibly for reasons of body water conservation as access to water after the encounter was not certain. Such an interaction would require that the body fluid system is integrated in some way with the thermoregulatory control system of these animals.

Chapter Eleven

General Conclusions

In this dissertation the eco-physiology of chacma baboons, Papio cynocephalus ursinus, living in the Kuiseb River canyon of the central Namib desert, Namibia was studied. This research has yielded important new information regarding baboon eco-physiology and has identified certain physiological procedures that can be successfully conducted under field conditions on free-ranging baboons.

The demographic structure of a primate population can vary widely under the influence of a number of environmental and social variables that directly affect life history processes, such as birth and death rates (Dunbar, 1988). I have found that for the Kuiseb baboons an unusual, possibly unique, interaction of variables has produced such high mortality among the infants that it is not certain if this baboon troop is self-sustaining. The ectoparasite infestations killing most infants were indicative of unusual environmental conditions. Most important was the occurrence and duration of the short annual floods and the distribution of water after the floods which in turn affected baboon movements. Baboon movement patterns appeared to increase their susceptibility to tick infestation and tick infestation resulted in the death of most infants: a cause and effect relationship not previously recorded for any non-human primates.

The social effects of the high infant mortality appeared to have affected other age/sex groups as well: some high-ranking adult female baboons resorted to fatal infant kidnapping and adult males fought harder to maintain a high rank with reproductive

opportunities. Overall the study was conducted during a period when the baboons' lifestyle was of a destructive nature.

The data regarding the ectoparasite infestations of the baboons and its associated pathology are the first of their kind. Tick infestation of infants' (< 6 months old) muzzles and the subsequent acute inflammation of their muzzles inhibiting the infants from suckling usually caused the death of the infants through starvation and dehydration. New born infants were observed to suckle and maintain health up to the point that they were not able to suckle and died soon afterwards. The infants with inflamed muzzles to which many ticks were attached, showed signs of pain when the mothers teat touched their mouths and were not observed to suckle once their muzzles became inflamed. It therefore seems unlikely that infants died from poor quality or lack of milk production by the mother but rather from a cessation of suckling. In this way, ticks were a major regulating factor within this baboon troop. Ticks infested predominately the ears of all adult and juvenile baboons resulting in chronic inflammation with associated scarring and deformation of the ears. The massive ectoparasite infestations of the Kuiseb baboons were surprising considering the grooming behaviour of the species. However, the near absence of observations of the grooming off of ticks by the Kuiseb baboons suggested that grooming behaviour amongst these baboons was not for hygienic purposes. The aridity of the baboons' habitat also appeared to be responsible for the unusual endoparasite assemblage of these baboons. Protozoans dominated the parasite assemblages of baboon

scats and only three nematode species were found in scat samples of the baboons.

Despite the aridity of the habitat, the baboons appeared to be able to satisfy their water requirements at all times of this study. There was also nothing unusual about the baboons' water flux rates at the time at which I measured them, although conspecific comparisons were not available for animals under free-ranging conditions. The baboons had ready access to plant food of high water content and were able to live without any apparent detrimental physical effect for more than 90 continuous days without drinking. An interesting finding regarding the foods of the baboons was that plant foods had uniformly low electrolyte concentrations. In the desert habitat occupied by the baboons, an important consequence of low electrolyte concentrations ingested by the baboons is that reduced water would be required for their renal excretion.

In terms of water conservation, the kidney anatomy and calculated urine concentrating ability of the Kuiseb baboon kidneys were significantly different from the kidneys of baboons originating from the northern Transvaal, South Africa. The larger RMT and associated maximal urine concentration of the Kuiseb baboons' kidneys indicated a physiological adaptation to the environment. The baboons' ability to reduce their faecal water content (c.a. 12%) at times when free water was not available also indicated them to be adapted to live in an arid environment.

Other significant findings to accrue from this research were those relating to baboon thermoregulation. The patterns of daily body temperature fluctuation related directly to water availability and drinking. Evaporative cooling appeared to be employed with effect only when water was drunk. Within an hour following drinking, the baboons' body temperatures usually dropped by around 2°C. Drinking was timed to occur around the midday period, thus lowering their body temperatures after the mornings activities and causing relatively low body temperatures (37 - 38°C) prior to the initiation of afternoon activities.

There were no dramatic decreases in body temperature during the days when no water was available. Baboon daytime body temperatures fluctuated by as much as 5.3°C when water was not drunk. In the evenings, baboons' body temperatures (often over 40°C) decreased gradually, presumably though passive heat dissipation as the baboons rested below their sleeping cliffs. Some baboons also showered themselves with cool subsurface sand that staggered the rise in their body temperatures, especially during mid-morning periods. The recorded body temperature fluctuations of the baboons indicated a thermolability suggestive of an adaptive heterothermy. An adaptive heterothermy has not been considered for baboons or any other primate before, but all previous results are based on studies of captive or confined animals. The recorded heterothermy further indicates the baboons to be adapted to live in an arid environment.

My study showed the importance of combining behavioural observations with physiological data when studying the natural history of free-ranging animals. For this study of the Kuiseb baboons, the important connection between tick infestations, water use and body temperature of the baboons would not have been obvious without the results obtained from surgically implanted radio-telemeters and the use of labelled water. These procedures were carried out in the Kuiseb River under the most basic of field conditions and with minimal backup. This study therefore emphasised that in any future natural history studies of medium or large mammals in the Namib desert, which are conspicuous through their virtual absence, advanced technology and personal skill should be incorporated to elevate them to the status of eco-physiological studies. Likewise, in future non-human primate studies under natural conditions, physiological data are essential adjuncts to behavioural observations if one is to go beyond merely proving that the animals can survive in their environment, but answer questions of a more profound nature.

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