Aspects of the water economy of Steenbok (*Raphicerus campestris*) in the Namib Desert

by

G. Cloete*

Namib Research Institute
P.O. Box 1204
Walvis Bay 9190

and

O.B. Kok

Department of Zoology
University of the Orange Free State
Bloemfontein 9300

*Present address:
Technikon Witwatersrand
P.O. Box 3293
Johannesburg 2000

ABSTRACT

Behavioural and physiological aspects of the water economy of steenbok (*Raphicerus campestris*) in the Namib Desert were investigated. Field observations indicate that the antelope are normally independent of free water, their main water source being dietary. Daily dietary water intake of captive steenbok was determined as 342,5 ml, while the water turnover rate was calculated as *c.* 135 ml per day. Urine analyses and kidney morphology do not suggest particular adaptation of renal function for desert conditions, while thermoregulatory behaviour appears to play a major role as a water-conserving mechanism.

UITTREKSEL

Fisiologiese en gedragsaspekte van die waterekonomie van steenbokke (*Raphicerus campestris*) in die Namibwoestyn is ondersoek. Veldwaarnemings dui aan dat die bokke normaalweg onafhanklik van vrye water bestaan, hul dieet synde die hoofbron van water. Daaglikse waterinname uit plantvoedsel van steenbokke in gevangenskap is vasgestel op 342,5 ml, terwyl die wateromkeringstempo as *ca.* 135 ml per dag bereken is. Niermorfologie en analise van urine dui nie op 'n spesiale aanpassing van die nierfunksie aan woestyntoestande nie, terwyl termoregulerende gedrag klaarblyklik 'n belangrike rol as 'n waterbehoudende meganisme speel.

CONTENTS

1 INTRODUCTION

Stevenson-Hamilton (1956) mentioned that steenbok have the ability to do without water for long periods. Even in arid areas like the Kalahari they were found up to 17 km from the nearest drinking site (Eloff, 1959). In fact, since they were never recorded anywhere near water, it prompted Eloff (*op. cit.*) to describe the antelope as a true dune animal. It therefore seems plausible that steenbok live independent of surface water as suggested by Dorst and Dandelot (1970) and Zaloumis and Cross (1974). In this study, behavioural and/or physiological means by which this can be accomplished have been investigated.

2 STUDY AREA

2.1 Location

The Central Namib Desert, S.W.A., is bisected by the Kuiseb River which covers a distance of approximately 500 km from its catchment area in the Khomas Hochland to its western delta near Walvis Bay. As a result two main topographical areas can be distinguished, viz. the dune fields to the south and the gravel plains to the north of the river. Although field work was conducted throughout the Namib-Naukluft Park which falls within this area, the main study area was limited to the Kuiseb River Canyon extending from the Namib Research Iunstitute at Gobabeb (23° 34'S; 15° 03'E) upstream for about 47 km to a place called Nareb. As part of a steenbok culling program, field work was also conducted on a farm (Riempie, No. 369) in the

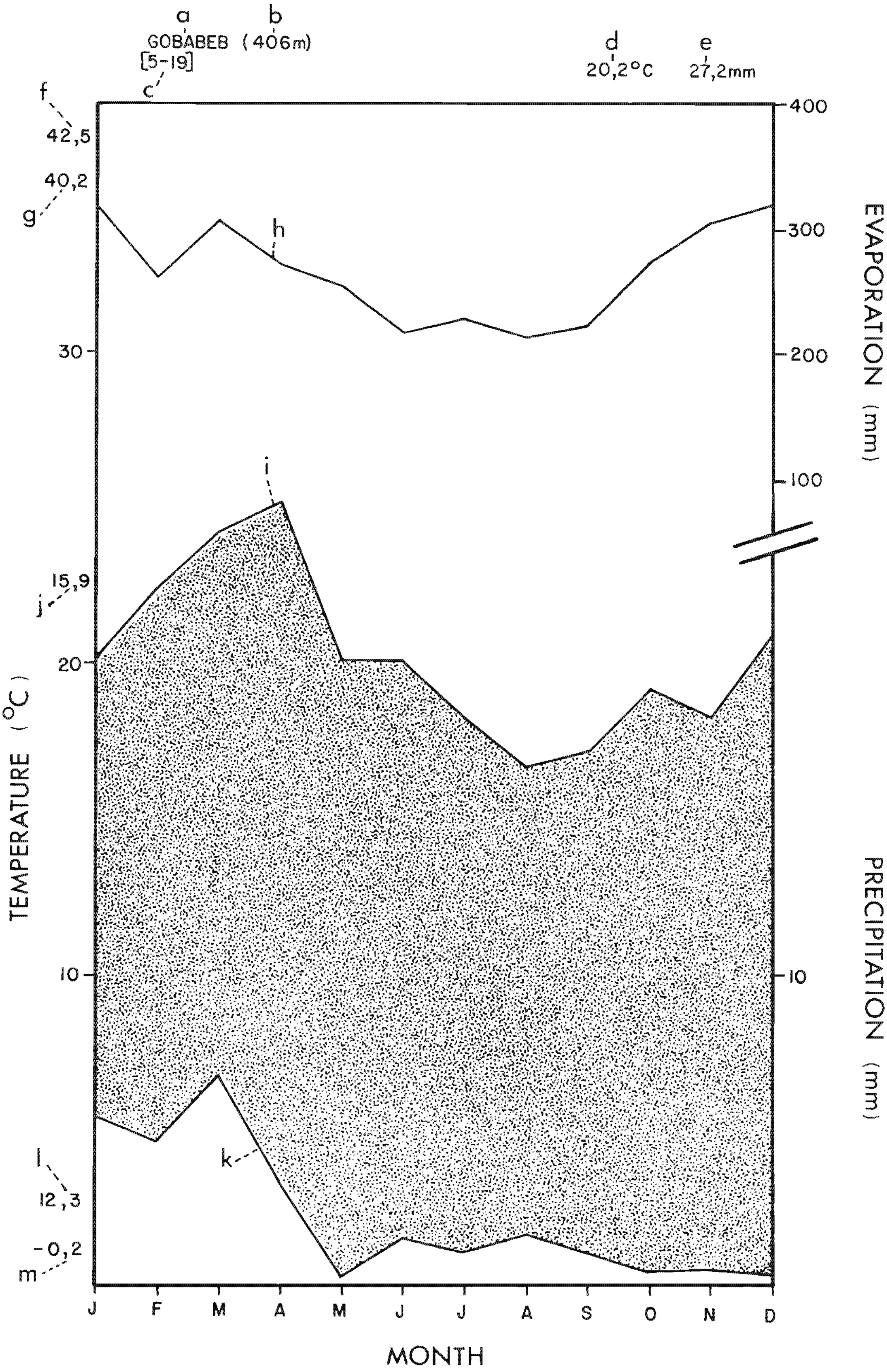

FIGURE 1: Climatogram for Gobabeb (modified from Walter *et al.*, 1975). a, station; b, altitude; c, years of observation (first figure for temperature, second figure for rainfall); d, mean annual temperature; e, mean annual rainfall; f, absolute maximum temperature; g, mean daily maximum temperature for hottest months; h, mean monthly evaporation; i, mean monthly temperature; j, mean daily temperature amplitude; k, mean monthly rainfall; l, mean daily minimum temperature; m, absolute minimum temperature.

Gochas district of the Kalahari Desert during December 1981 and March 1982.

2.2 Climate

Meteorological records, collected since 1962 from the First Order Weather Station at Gobabeb, are summarised in a diagram illustrating the Namib macroclimate (Fig. 1). The climatogram reflects low monthly rainfall and high monthly temperatures which are typical for arid regions. High monthly evaporation figures accentuate the aridity.

As indicated in Figure 2, the main study area is situated within a region that receives an average rainfall of less than 50 mm per year (average of 27,2 mm at Gobabeb). However, advective fog is the major source of precipitation in this area. Such foggy conditions are experienced for about 100 days of the year at Gobabeb, actual precipitation occurring in sixty percent of the cases (Scholz, 1972).

2.3 Vegetation

As a linear oasis in the heart of the Namib Desert, the Kuiseb River supports an extensive growth of trees and other vegetation. Although 19 species of perennial and annual plants were identified during the study, the

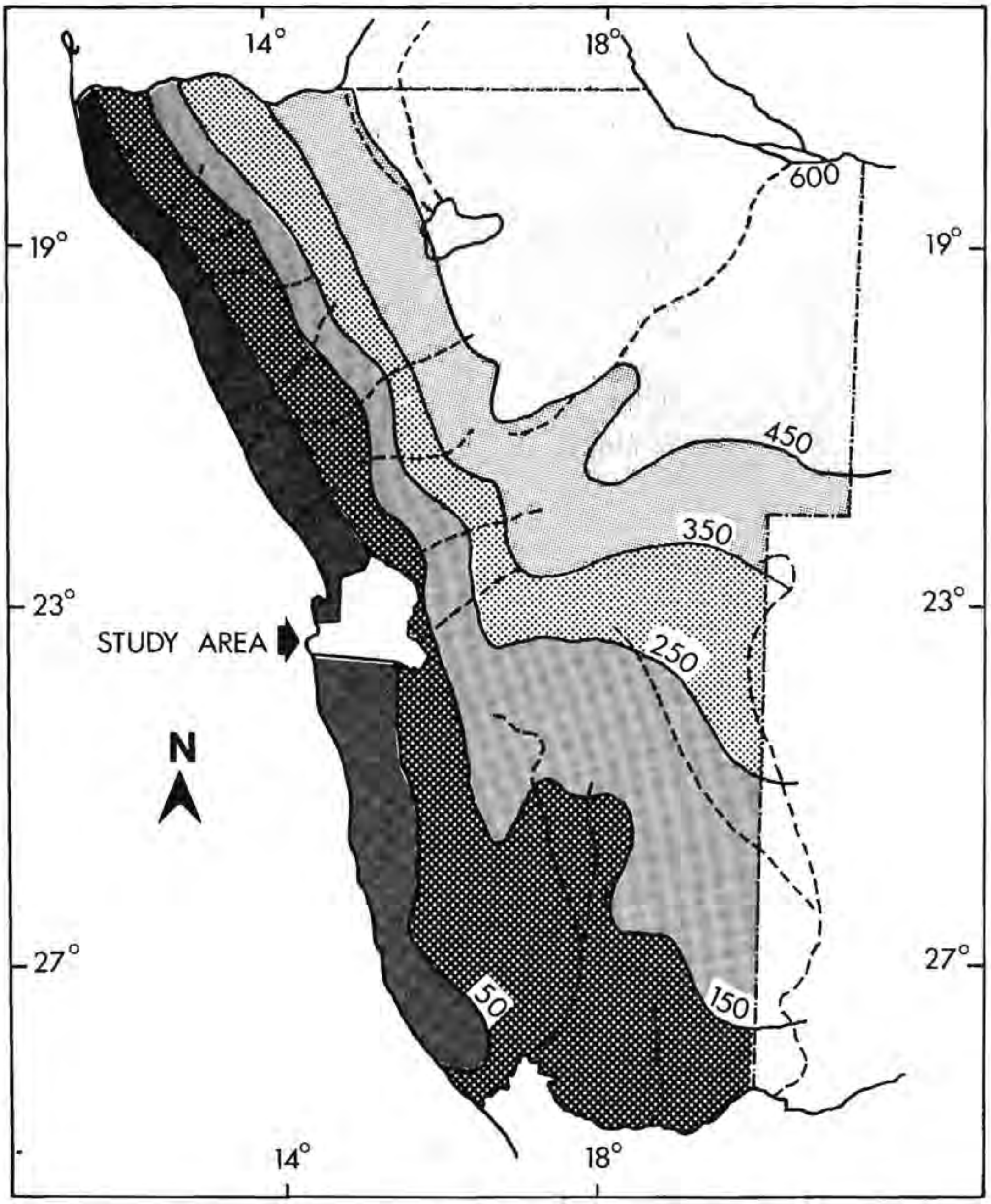

FIGURE 2: Rainfall map for South West Africa (after Stengel, 1966), showing that most of the study area lies in a region that receives less than 50 mm of rain annually.

riverine vegetation is mainly characterised by five tree communities.

2.3.1 *Acacia albida* (Del.)

Well developed *A. albida* communities constitute almost a third of the plants which occur along the Kuiseb River (Seely *et al.*, 1981). The number of ana trees decreases upriver towards Nareb, and disappears at about 68 km upstream from Gobabeb. Trees situated on the river banks and even in the river-bed itself (islands) are generally larger than those farther away from the main stream, reaching heights of 21 m (Theron *et al.*, 1980).

2.3.2 *Acacia erioloba* (E. Meyer)

This community is characteristic of the silt flood plains, but also occurs on the larger islands. It is represented primarily by large, old trees and comprises 10% of the plants in the Kuiseb River Canyon (Seely *et al.*, 1981). Pod production reaches a peak in April and May.

2.3.3 *Euclea pseudebenus* (E. Meyer)

Cape ebony is very sparsely distributed along the river and only occurs sporadically in small clumps. The trees are relatively small and unobtrusive, and comprises *c.* 4% of the total vegetation in the study area. No pods are produced, but the leaves and berries are eaten by game.

2.3.4 *Salvadora persica* (L.)

Although representing 36% of the total plant cover in the Kuiseb River Canyon (Seely *et al.*, 1981), this community is not always present as extensive stands, but forms localised, impenetrable mats. Berries with a high water content which could be used as a dietary source of water by various animals are produced.

2.3.5 *Tamarix usneoides* (E. Meyer)

This community is found in the river-bed, on the flood plains, and also on the outcrops along the Kuiseb River. *T. usneoides* comprises about 20% of the vegetation in the Canyon (Seely *et al.*, 1981).

2.3.6 Other communities

Other trees in the study area include *Ficus cordata* (Thunb.) and *F. sycomorus* (L.) which are occasionally utilised by game. Apart from perennials like *Pechuel-loeschea leubnitziae* (O. Kuntze) and *Pergularia daemia* (Forsk.), ephemerals such as *Berkheya* spp. (Ehrh.), *Flaveria bidentis* (L.), *Forsskaolea candida* (L.) and *Zygophyllum simplex* (L.) are also available as food whenever conditions are favourable, i.e. after annual floods. Of the grass species in the river-bed, *Eragrostis spinosa* (L. fil.) and *Stipagrostis namaquensis* (Nees) form the most important component.

3 METHODS AND MATERIAL

3.1 Censuses

In the period 1980 to 1982, 72 censuses were conducted in the Kuiseb River Canyon, the total distance driven from Gobabeb to Nareb being 47,4 km. Two persons were always counting while travelling at a constant speed of 20 km/h. Including stops to observe steenbok, it normally took about four hours to cover the distance. At least three censuses per month were conducted using the following system: The first census of the month started at 06h00 and the time of arrival back at Gobabeb (zero point) was 14h00. The second census started at 10h00 and was completed by 18h00, while the third census began at 06h00 and ended at 18h00, four hours having been spent at Nareb. In this way the period between 06h00 and 18h00 was effectively covered twice per month. At each sighting the activity of the steenbok, time of day and temperature were recorded. The former was divided into four categories, namely standing (i.e. resting idly or ruminating), walking (directional movement only), browsing (actually collecting food including food-searching movements) and resting (lying down).

3.2 Field observations

Whenever possible, steenbok were followed for continuous periods of up to 12 hours in the field. Following Norton (1981) a one-minute scan method was used to record the instantaneous activity of each individual. The same categories used during the river censuses were applied.

Browsing frequencies (percentage utilisation) for the different plant species were calculated as the total number of feeding records per plant expressed as a percantage of all observations. The cumulative duration of separate bites, defined as the time (using a stopwatch) necessary to collect a mouthful of plant material, was used to determine the actual browsing time per plant. For each plant species the browsing times were combined and expressed as a percentage of all time recordings. Following Kok and Opperman (1980) the relative importance (RI) of food plants was calculated using the equation:

$$RI = \frac{\text{Percentage utilisation} + \text{Percentage duration}}{2}$$

Twenty-four hour observations at various waterholes in the Kuiseb River Canyon and on the gravel plains were also carried out on a monthly basis to determine the extent of surface water usage by steenbok under desert conditions.

3.3 Experimental work

Two steenbok were mesmerised with a 100 watt halogen spotlight by night and captured by hand. They were kept in a small enclosure (3 x 6 x 5 m) at the Namib Research Institute. The enclosure was covered with hession to reduce unnecessary disturbances. Freshly cut leaves and shoots of *Acacia albida,* the main food source of steenbok in the Kuiseb River Canyon, were collected and weighed at 12 hour intervals for two periods of five successive days. In each case, one sample (A) was placed in the shade within the enclosure to reduce the amount of water lost by evaporation, while the other (B) was placed in the shade outside the enclosure. Sample B and the remains of sample A were weighed separately at the end of each 12 hour period. The loss in mass in sample B was calculated as a percentage of the original mass and was used to determine waterloss by evaporation in sample A during the corresponding period. The calculated mass of sample A was subtracted from the original mass of sample A to determine the total mass of plant material consumed. The amount consumed during two consecutive 12 hour periods (day and night) would be the total mass consumed per day (24 hours).

To determine water turnover rate, intramuscular dosages of 20 μ Ci tritiated water (TOH)/kg live weight were administered to the steenbok in captivity, using disposable syringes. Blood samples were taken with sterile Vac-u-Test tubes from the jugular veins, 12 hours after injection and at five day intervals for 20 days thereafter. Calculations are based on the equations as described by Yousef *et al.* (1974):

$$\text{Disappearance rate of TOH (k)} = \frac{\ln Ao - \ln At}{t}$$

where lnAo is the TOH activity from plasma samples at zero time (extrapolated from the curve drawn on semilogarithmic paper) and lnAt is the TOH activity at the end of the period t.

$$\text{Total body water (TBW)} = \frac{100}{\text{TOH activity } (\mu\text{Ci}) \text{ expressed as \% of the dose at zero time.}}$$

For ruminants which have not been fasted beforehand, as in the present case, the obtained value is an overestimation of *c.* 15% (Meissner *et al.,* 1980).

Water turnover rate (WTR) = (k/day) x (TBW)

3.4 Culling data

During a culling program on the farm Riempie, 112 steenbok were shot at night and immediately weighed. Kidneys were removed from 18 specimens, weighed and measured with a pair of callipers. After making a longitudinal section, the cortical and medullary thicknesses were measured at ten intervals along the periphery. Relative medullary thickness was calculated as:

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

where kidney size = $\sqrt[3]{\text{length} \times \text{width} \times \text{depth (mm)}}$
(Sperber, 1944)

Urine samples were removed from 30 bladders with Vac-u-Test tubes and stored at -20°C until later analyses. Osmolalities were determined using an automatic osmometer (Advanced Instruments, model 6731 RAS), while the sodium and potassium content were determined with the aid of a flame photometer (Instrumentation Laboratory, IL 243).

4 RESULTS

4.1 Water intake

During monthly 24-hour periods of observation at various waterholes in the Namib-Naukluft Park, no steenbok in the Kuiseb River Canyon was ever recorded drinking. Steenbok in captivity at the Namib Research Institute likewise made no attempt to drink. When conditions became extreme, however, during the hot summer months prior to the onset of the seasonal rains in January, a few individuals drank occasionally. Eight such incidents were recorded as shown in table 1. The fact that the gravel plains (Ganab) alone are implicated, is also noteworthy. Due to the low vegetation cover as compared to that of the riverine habitat, less shade is available on the gravel plains and could possibly result in concomitant increased rates of water loss. In addition, gemsbok tend to concentrate in the Ganab area with the result that most shrubs and trees show a distinct 1,8 m browse line which prevents the small sized steenbok reaching the relative succulent leaves. According to P.S. Nel (pers. comm.) the average water content of the vegetation associated with the gravel plains and dry washes is also lower than that of the Kuiseb River Canyon.

Water intake can possibly be supplemented by the incidental intake of precipitated fog while feeding during foggy conditions. Fog is, for instance, the major source of water for various invertebrate species in the

TABLE 1: Number of steenbok recorded drinking during monthly 24-hour periods of observation at waterholes in the Namib-Naukluft Park.

Location	Number of Observations	Month	Number of Steenbok	Sex	Time (S.A.S.T.)
Ganab	12	January–September	0		
		October	1	unidentified	06h10
		November	1	male	19h45
		December	1	female	07h30
		December	1	female	19h30
		December	1	female	20h30
		December	1	male	20h45
		December	1	unidentified	20h50
		December	1	female	20h45
Kuiseb River	12	January – December	0		

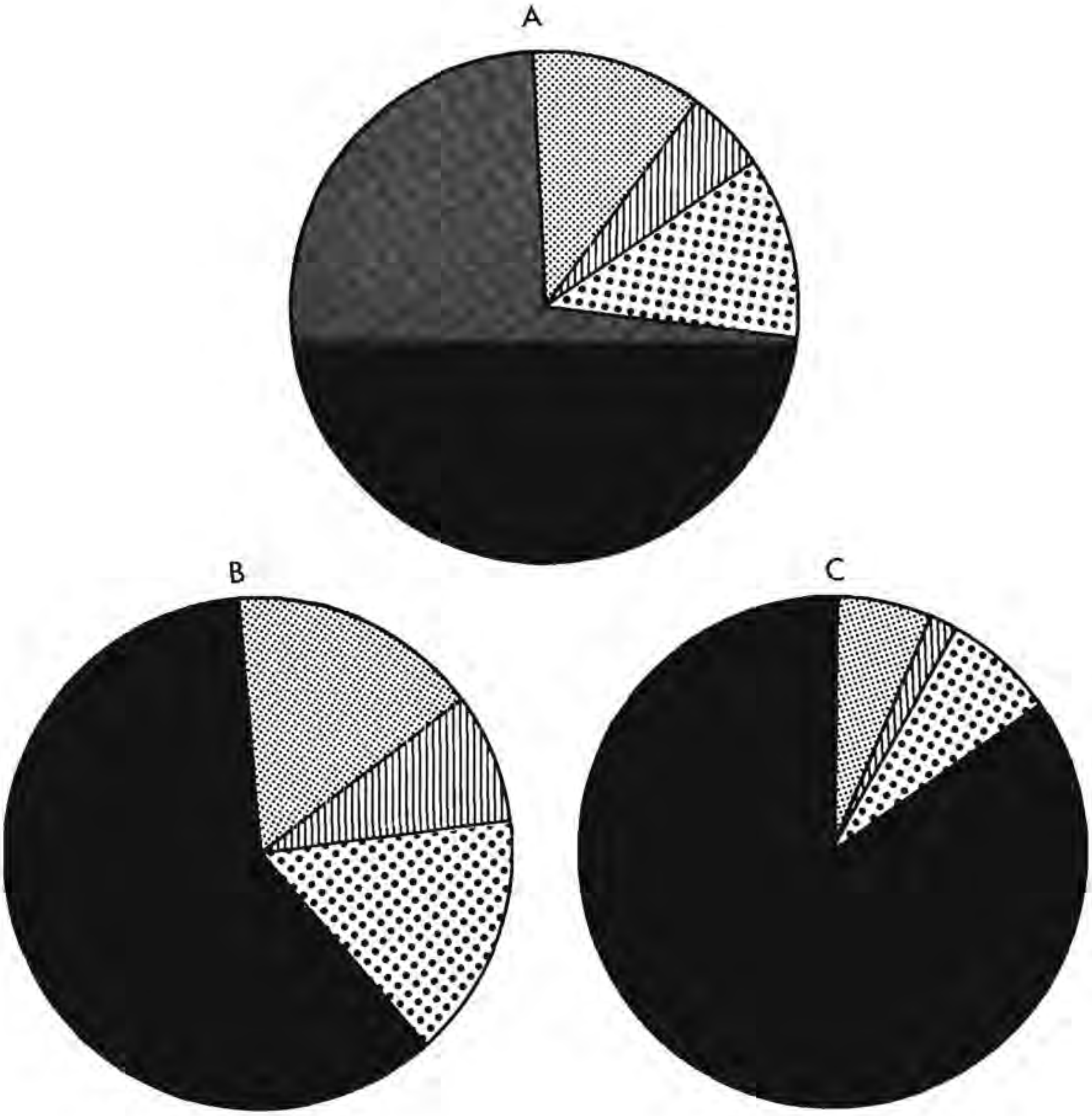

FIGURE 3: Relative importance of plant species in the diet of steenbok in the Kuiseb River Canyon. A, calculated relative importance (% observation + % time ÷ 2); B, utilisation frequency (1636 observations); C, time spent per plant species (9498 computations). Solid araea, *A. albida* leaves and shoots; Coarsely stippled area, dry material such as fallen leaves, pods and bark; Vertically hatched area, *A. erioloba* leaves; Finely stippled area, rest of utilised plant species.

Namib-Naukluft Park (Koch, 1962; Louw, 1972; Seely, 1978 and 1979). As it is, a male steenbok was once observed licking precipitated fog from the leaves of *T. usneoides*. Since the tamarix has the ability to secrete salt through its leaves, it may have been merely a question of incidental water intake while ingesting salt. On another occasion an individual with water condensed on his body was recorded licking himself. Unfortunately, no increase in frequency of such behaviour could be established on foggy days.

4.2 Food preferences

Being predominantly browsers, steenbok subsist on leaves and shoots as well as bark, flowers, fruits, pods and seeds whenever avaialable (Huntley, 1972; Pienaar, 1960; Rautenbach, 1982). Of the 14 different plant species utilised by steenbok in the Kuiseb River Canyon (Cloete, 1983), *A. albida* is by far the most important food plant, both with respect to feeding frequency and time spent per plant (60% and 85% respectively) (Fig. 3). *A. erioloba* and *S. persica* also contribute to the diet, although their Relative Importance values are quite low as compared to that of *A. albida* (5,0 and 3,6 respectively as against 73,0). Since the remaining food plants are only utilised occasionally, their importance can be ignored for all practical purposes. The fact that steenbok ingest such a large amount of dry material (RI = 12,6) is, however, notable.

4.3 Daily consumption of food

Subsequent to a captivity period of 14 days the food consumption by male steenbok averaged 581,50 g per day (Table 2). Due to the superabundance of *A. albida* leaves and shoots in the experimental situation, this may be an inaccurate assessment of requirements under natural conditions. The fact that the heavier individual (B) ingested less food than individual A can probably be attributed to an age difference as external markings and overall appearance indicated that the former individual was relatively old. In fact, it died after about two months in captivity. The mean consumption comprised 2,6% (dry mass) of the mean body mass of the two steenbok involved and supports Owen-Smith's (1979) suggestion that small ruminants take in up to 4% of their live mass daily. No correlation between daily consumption and daily maximum ambient temperatures was found (individual A, r = -0,3532; df = 3 and individual B, r = -0,8317; df = 3). Based on an average water content of 58,9% for *A. albida* leaves and shoots (Cloete, 1983), the dietary intake of captive steenbok was calculated as 342,5 ml/day.

TABLE 2: Daily consumption of *A. albida* leaves and shoots by two separate male steenbok under similar conditions of captivity.

Day	Mass (g)		
	Individual A (9,0 kg)	Individual B (9,4 kg)	Mean
1	739,12	392,21	565,67
2	834,15	580,96	707,56
3	729,21	514,04	621,63
4	747,29	247,62	497,46
5	728,33	302,05	515,19
TOTAL	3 778,10	2 036,88	2 907,51
MEAN	755,62	407,38	581,50
S.D.	± 44,58	± 139,96	± 85,46

4.4 Water turnover rate

Under normal circumstances the water intake of an animal should equal its water loss. Theoretically, after injecting an animal with TOH, the tritium should equilibrate with the animal's body water. The disappearance rate of TOH, namely k, should form a rectilinear curve when TOH concentration per ml plasma is plotted against time on semilogarithmic paper (Yousef, *et al.*, 1974) (Fig. 4). Using the logarithmic values for TOH activity (μ Ci) at zero time (lnAo) and at the end of the experimental period (lnAt), the mean value of k was calculated as 0,021039/day (Table 3). The calculated total body water (TBW) and water turnover rate (WTR) are also represented in the same table.

TABLE 3: Total body water and water turnover rate of steenbok in the Kuiseb River Canyon.

Parameters	Male A	Male B	Mean
Body mass (kg)	9,0	9,4	9,2
Disappearance rate/day (k)	0,020385	0,021692	0,021039
Total body water (ml)	5346,41	7527,97	6437,20
Water turnover rate (ml/day)	108,99	163,30	135,43

As mentioned previously, the dietary water intake of captive steenbok was determined as 342,5 ml/day. When faecal water loss (145 ml/day as calculated from a mean of 49,6% of faecal volume in 12 samples) and daily water requirement (WTR = 135,43 ml/day as corrected for ruminants) are considered, it amounts to a surplus water intake of 62,07 ml/day. It seems reasonable to assume that part of this volume is lost through breathing and the remainder used for cooling. This is in agreement with the finding of Macfarlane and Howard (1972) that water turnover rate does not parallel for flow of energy because water is used also

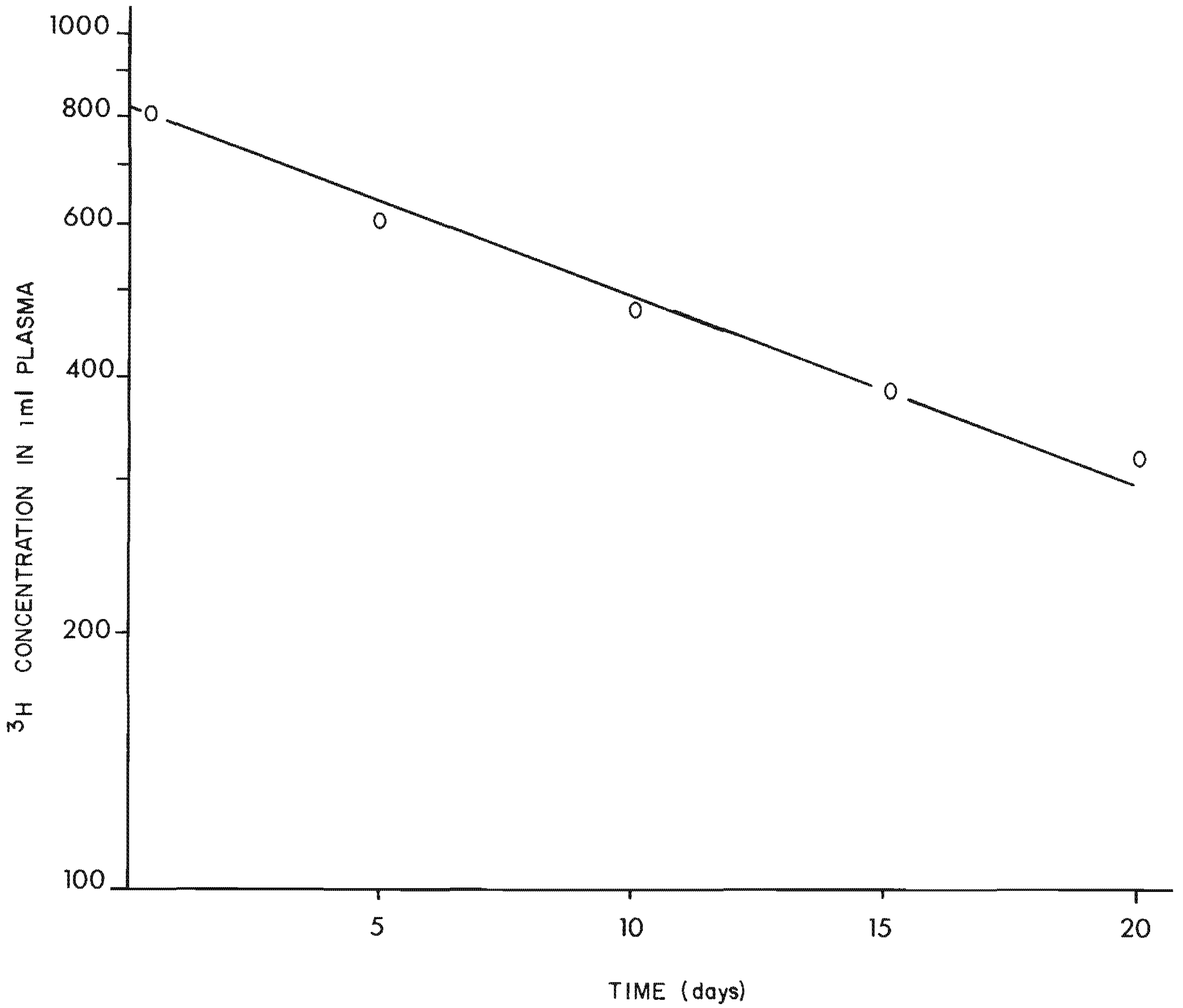

FIGURE 4: Water turnover rate in steenbok over a period of twenty days.

for convection and for evaporative cooling in addition to metabolic uses. By implication then, steenbok not only eat to balance their water budget, but also to balance their energy budget and meet their mineral and vitamin requirements. An excess of water may be taken in involuntarily with the dietary component in the shortest supply.

4.5 Kidney morphology

As studies on experimental subjects indicate that steenbok mainly depend on dietary and metabolic water, it was deemed necessary to determine the renal efficiency of the antelope. This was investigated by measuring the relative medullary thickness of the kidneys as the relative length of the loops of Henlé, which are situated in the medulla, appear to determine the concentration ability of the kidney (Prosser and Brown, 1961). Anatomical evidence obtained from 18 subjects (Table 4) suggest that the level of kidney function of steenbok is well below those of desert-living rodents, and slightly below those of a few other antelope species (Table 5). Such a phenomenon is explicable on the basis that steenbok obtain sufficient water from their diet to support their activity and metabolic functions. Under the special circumstances prevailing in the Namib Desert, steenbok therefore seem to cope without a highly efficient renal function so characteristic of true desert animals.

TABLE 4: Kidney dimensions of steenbok (N = 18).

Parameters	Mean	S.D.	Range
Mass (g)	18,50	± 5,12	12,10 – 30,50
Size (mm)*	28,20	± 2,55	23,80 – 34,40
Medula (%)	62,07	± 11,18	47,57 – 89,34
Cortex (%)	37,93	± 11,18	10,66 – 52,43
Relative medullary thickness	4,61	± 0,96	3,31 – 6,65
Kidney size/body mass × 10^3	3,53	± 0,45	2,90 – 4,41
Kidney mass/ body mass (%)	0,23	± 0,04	0,16 – 0,36
Medullary-cortex ratio	1 : 0,66	± 0,27	

* Calculated as $\sqrt[3]{\text{lenght} \times \text{width} \times \text{depth (mm)}}$

TABLE 5: Relative medullary thickness of the kidneys of various mammals.

Species	Relative medullary thickness
Beaver *(Aplodontia rufa)* [2]	1,30
Man *(Homo sapiens)* [1]	3,00
Steenbok *(Raphicerus campestris)* [5]	4,61
Cat *(Felis domesticus)* [2]	4,80
Wildebeest *(Connochaetes taurinus)* [1]	4,80
Bontebok *(Damaliscus dorcas dorcas)* [1]	4,90
Springbok *(Antidorca marsupialis)* [4]	5,50
Jerboa *(Jaculus jaculus)* [3]	9,30
Gerbil *(Gerbillus gerbillus)* [3]	10,50
Desert Mouse *(Psammomys obesus)* [2]	12,90

Source: 1 – Berry and Louw (1982); 2 – Chew (1965); 3 – Gordon (1972); 4 – Marsh *et al., (1978); 5 – present study*

TABLE 6: Urine analysis of steenbok

Parameters	Number	Mean	S.E.	Range
Osmolality (mOsm/kg)	30	1 787	72	1 160 – 2 650
K^+ (mM)	25	456	27	215 – 800
Na^+ (mM)	30	15	2	1 – 48

Results from the analyses of 30 urine samples (Table 6) likewise indicate that steenbok have a more or less average renal function, 2650 mOsm/kg being the highest osmolality recorded. The respective values obtained for potassium and sodium suggest that the antelope is on a high potassium diet which is typical for herbivores, and that they are husbanding their sodium resources through recycling.

4.6 Thermoregulatory behaviour

Diurnal activity patterns of steenbok in the Kuiseb River Canyon are presented in Figure 5. Mobile activities show distinct peaks in the early morning and late afternoon when the relative humidity is rather high and temperatures relatively low compared with those during midday. This is in general agreement with the findings of Norton (1981), Tilson (1980) and Tinley (1969) on other members of the tribe Neotragini. Obviously, such behaviour is highly advantageous for animals subjected to extreme environmental conditions as is the case in the Namib Desert.

Being small-sized antelope with a relatively high metabolism, steenbok were found to spend a large proportion of the day browsing. On very hot days, however, the animals browsed only little, particularly in the middle of the day. On such occasions they spent most of their time standing idly in the shade, probably as a thermoregulatory mechanism. By contrast, on cooler days the antelope spent much more time feeding and less time standing. In general, steenbok spent considerably more time standing than walking. This can partly be ascribed to the close association between the browsing and standing categories, and partly because steenbok, being highly territorial animals familiar with their surroundings, do not have to spend much time locating suitable food items. The small peaks in the walking category around midday were mostly due to the shifting of resting places, possibly as an antipredator strategy and/or as a means of maximising shade cover.

In contrast with the active categories, periods of inactivity (lying down) show a definite peak around midday and early afternoon when the heat load acting on animals is generally high (Fig. 5). A highly significant positive correlation ($r = 0,84$; $p < 0,01$) was also found between ambient temperature and the percentage time that steenbok spent resting per day. Since resting steenbok make extensive use of available shade (Fig. 6), a positive correlation ($r = 0,83$; $p < 0,05$) could also be demonstrated between temperature and the proportion of daylight hours spent in the shade.

5 DISCUSSION

Since deserts are usually characterised by temperature extremes, a limited water supply and a low density of food resources, it seems logical to assume that ungulates inhabiting such areas should be highly specialised. Morphologically, however, this does not appear

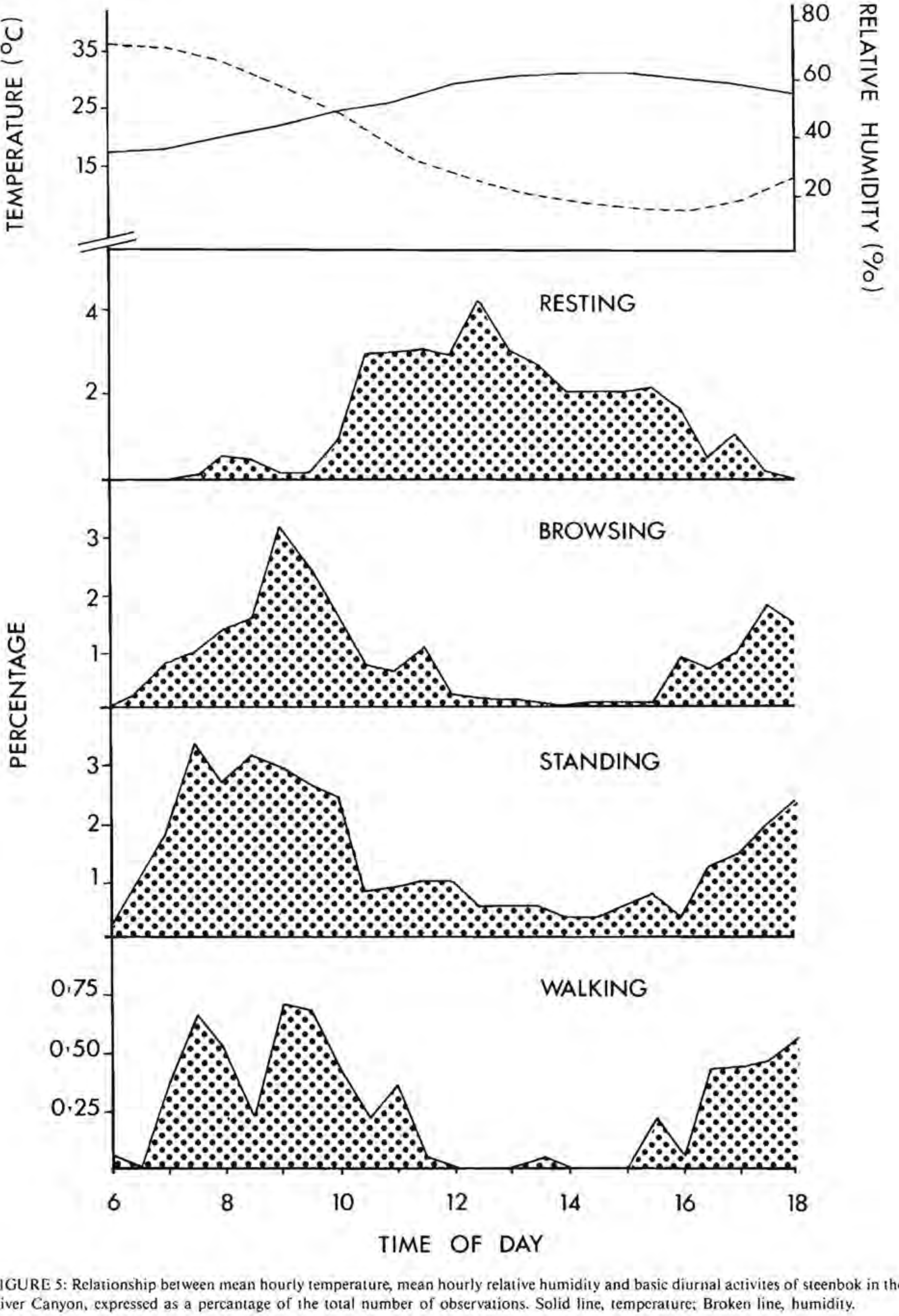

FIGURE 5: Relationship between mean hourly temperature, mean hourly relative humidity and basic diurnal activites of steenbok in the Kuiseb River Canyon, expressed as a percantage of the total number of observations. Solid line, temperature; Broken line, humidity.

to be the case with steenbok. As indicated by their kidney structure and urine analyses, the antelope occupy a relatively low position in terms of the effectiveness of physiological mechanisms for the conservation of water. This suggests that behavioural stratagems are of paramount importance in the steeenbok's survival in hot, arid environments. In part, the ability to survive without drinking water is accomplished by the selec-

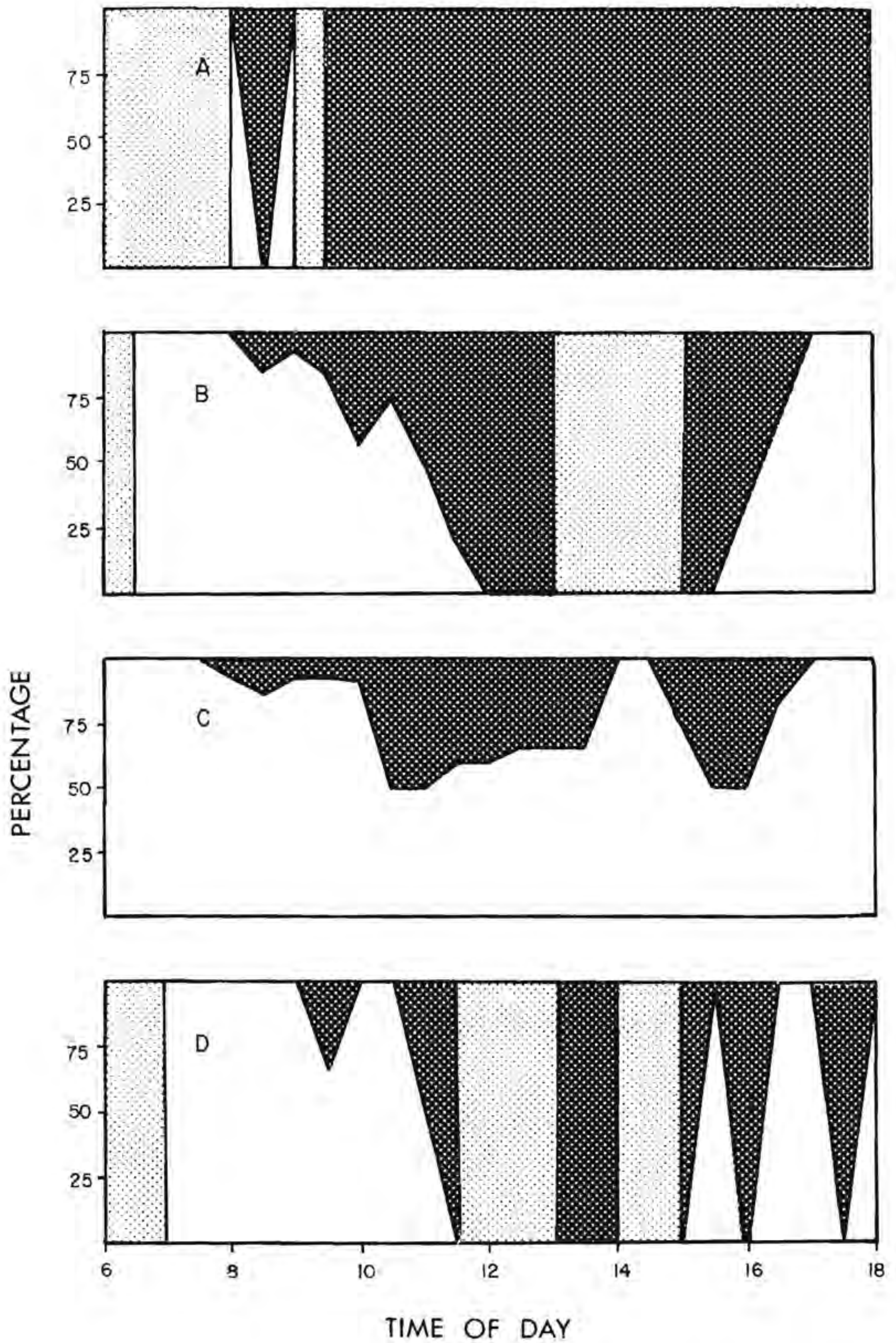

FIGURE 6: Diurnal activities of steenbok associated with direct sunlight (open area) and shade (solid area). A, resting; B, browsing; C, standing; D, walking; Stippled area, no observations.

tion of succulent food. By providing lush vegetation in the heart of the desert, the Kuiseb River plays a significant role, supporting animals which otherwise might suffer to survive in the adjacent desert areas. Other behavioural adaptations include the selection of appropriate microclimates (sun or shade), thereby conserving energy and water reserves, and the restriction of strenuous activities to favourable times (morning and evenings) when solar heat loads are small and surplus metabolic heat can be dispersed most easily without invoking evaporative mechanisms. In final analysis the interaction between ecological and ethological characteristics seems crucial to the well-being of steenbok in the Namib Desert.

6 ACKNOWLEDGEMENTS

Sincere thanks are due to mr. P.S. Swart, Director of the Department of Agriculture and Nature Conservation, and dr. E. Joubert, Assistant-Director, Research, for valuable advice and for permission to conduct the study in the Namib-Naukluft Park. We are especially indebted to prof. G.N. Louw and dr. S. Nicolson, both of the Department of Zoology, U.C.T., for analising blood and urine samples. Dr. M.K. Seely, Director of the Desert Ecological Research Station, and mr. P. Grobler, owner of the farm Riempie, are also gratefully acknowledged for their logistic support.

7 REFERENCES

BERRY, H.H. and LOUW, G.N.
1982: Nutritional measurements in a population of free-ranging wildebeest in the Etosha National Park. *Madoqua*, 13: 101—125.

CHEW, R.M.
1965: Water metabolism of mammals. In: *Physiological mammalogy* II, p 44—178. W. Mayer and R. van Gelder (Eds.). Academic Press, London.

CLOETE, G.
1983: Etho-ecological aspects of the steenbok *(Raphicerus campestris* Thunberg, 1811) in the Namib Desert, South West Africa. M.Sc. thesis, U.O.F.S.

DORST, J. and DANDELOT, P.:
1970: *A field guide to the larger mammals of Africa.* Collins, London.

ELOFF, F.C.
1959: Observations on the migration and habits of the antelope of the Kalahari Gemsbok Park. *Koedoe*, 4: 18—30.

GORDON, M.S.
1972: *Animal physiology: Principles and adaptations.* Macmillan, New York.

HUNTLEY, B.J.
1972: A note on food preferences of a steenbok. *J. Sth. Afr. Wildl. mgmt. Assoc.*, 2: 24—26.

KOCH, C.
1962: The tenebrionidae of southern Africa XXXI. Comprehensive notes on the tenebrionid fauna of the Namib Desert. *Ann. Trans. Mus.*, 24: 61—106.

KOK, O.B. and OPPERMAN, D.P.J.
1980: Voedingsgedrag van kameelperde *Giraffa camelopardalis* in die Willem Pretorius-widltuin, Oranje-Vrystaat. *S. Afr. J. Wildl. Res.*, 10: 45—55.

LEUTHOLD, W.
1977: *African ungulates.* A comparative review of their ethology and behavioural ecology. Springer-Verlag, Berlin.

LOUW, G.N.
1972: The role of advective fog in the water economy of certain Namib Desert animals. *Symp. Zool. Soc. Lond.*, 31: 297—314.

MACFARLANE, W.V. and HOWARD, B.
1972: Comparative water and energy economy of wild and domestic mammals. *Symp. Zool. Soc. Lond.*, 31: 261—296.

MARSH, A.C., LOUW, G. and BERRY, H.H.
1978: Aspects of renal physiology, nutrition and thermoregulation in the ground squirrel *Xerus inauris. Madoqua*, 11: 129—135.

MEISSNER, H.H., VAN STADEN, J.H. and PRETORIUS, E.
1980: *In vivo* estimation of body composition in cattle with tritium and urea dilution. I. Accuracy of prediction equations for the whole body. *S. Afr. J. Anim. Sci.*, 10: 165—173.

NORTON, P.M.
1981: Activity patterns of klipspringers in two areas of the Cape Province. *S. Afr. J. Wildl. Res.*, 11: 126—134.

OWEN-SMITH, N.
1979: Factors influencing the transfer of plant products into large herbivore populations. *CSIR Sav. Symp.*, 31: 1—19.

PIENAAR, U. DE V.
1960: Annual report of the biologist. *Koedoe*, 3: 1—250.

PROSSER, C.L. and BROWN, F.A.
1961: *Comparative animal physiology.* W.B. Saunders Co., London.

RAUTENBACH, I.L.
1982: *Mammals of the Transvaal.* Ecoplan Monograph No. 1, Colbyn, Pretoria.

SCHOLZ, H.
1972: The soils of the central Namib Desert with special consideration of the soils in the vicinity of Gobabeb. *Madoqua*, Ser. II,1: 33—51.

SEELY, M.K.
1978: The Namib Dune Desert: an unusual ecosystem. *J. Arid. Environ.*, 1: 117—128.

SEELY, M.K.
1979: Irregular fog as a water source of Desert Dune beetles. *Oecologica (Berl.)*, 42: 213—227.

SEELY, MARY K., BUSKIRK, W.H., HAMILTON, W.J. and DIXON, J.E.W.
1981: Lower Kuiseb River perennial vegetation survey. *J. S.W.Afr. Scien. Soc.*, 34: 57—86.

SPERBER, I.
1944: Studies on the mammalian kidney. *Zool. Bidr. Uppsala*, 22: 249—431.

STENGEL, H.W.
1966: Vom Regen und vom Regenkarten in Südwest Afrika. *J. S.W. Afr. Scien. Soc.*, 7: 1—8.

STEVENSON-HAMILTON, J.
1957: *Wildlife in South Africa.* Cassel & Co. Ltd., London.

THERON, G.K., VAN ROOYEN, N. and VAN ROOYEN, M.W.
1980: Vegetation of the lower Kuiseb River. *Madoqua*, 11: 327—345.

TILSON, R.L.
1980: Klipspringer (*Oreotragus oreotragus*) social structure and predator avoidance in a desert canyon. *Madoqua*, 11: 304—314.

TINLEY, K.L.
1969: Dikdik *Madoqua kirki* in South West Africa: Notes on distribution, ecology and behaviour. *Madoqua*, 1: 7—73.

WALTER, H., HARNICKELL, E. and MEULLER-DOMBOIS, D.
1975: *Climate-diagram maps of the individual continents and the ecological climate regions of the earth.* Supplement to the vegetation Monographs. Springer-Verlag, Berlin.

YOUSEF, M.K., JOHNSON, H.D., BRADLEY, W.G. and SEIF, S.M.
1974: Tritiated water-turnover rate in rodents: Desert and mountain. *Physiol. Zool.*, 47: 153—162.

ZALOUMIS, E.A. and CROSS, R.
1974: *A field guide to the antelope of Southern Africa.* Natal branch of the Wildl. Soc. of Southern Africa.