BEHAVIOUR OF TOPI IN A SHADELESS ENVIRONMENT

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ABSTRACT

Topi, *Damaliscus korrigum*, when living on shadeless pasture, adopt resting postures and an orientation relative to the sun which minimize their exposure to radiation. Their timing of feeding, and hourly variations in faecal moisture loss, contribute to water conservation.

INTRODUCTION

Topi, *Damaliscus korrigum* Ogilby, are large (100–140 kg) alcelaphine antelope distributed patchily in East Africa in discrete areas. In some cases, such as Rukwa and Alia Bay, each distribution area is inhabited by one population, while in others two or more relatively independent populations can be identified. This latter is true of the topi-occupied area of the Serengeti region of Tanzania and the adjacent Mara region of Kenya, within which region several independent populations exist. This topi-occupied area formerly extended as far as Mount Elgon, but cultivation has obliterated nearly all topi north of the lands of the pastoral Maasai people. A remnant population of a few hundred on ranches in the Endebess area will probably disappear in the next few years as these ranches are taken over for small-scale cultivation.

Within their scatter of distribution areas topi occur from sea level up to an altitude of 1 700 m, and in climates which may be cool and equable, or seasonally very hot and dry, or perennially hot and humid (Table 1). Despite these extremely different climates, one characteristic common to all distribution areas is a type of pasture. In all areas topi have available to them for much of the year medium-length, fairly green, leafy swards of grass. The vegetation types containing the grasses cover a wide range: *Hyphaene* palm woodland, lake shore grasslands, open plains, *Acacia* open woodland, and seasonally waterlogged grasslands ('vleis') in ground-water forest. The species of grasses composing the swards also vary greatly. It seems to be the structure of the sward, rather than its component species, which makes it suitable for topi.

Points of interest about topi emerge from this summary. To enjoy a consistent type of pasture topi are tolerant of a wide range of climatic conditions (temperature, humidity and radiation) in a less wide range of vegetation types. This paper reports a brief investigation of one population for signs of behavioural adaptiveness in the species' environmental relationships.

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TABLE 1

Climatic data from areas where topi occur in Kenya, demonstrating the range of climates they will tolerate.

Station name	*Mean annual rainfall (mm)*	*Days rain*	*Temperature °C*	
			Mean Maximum	*Mean Minimum*
Lokitaung	514	26	32	22
Ileret	307	23	32	22
Endebess	1 053	77	25	11
Aitong (this study)	1 044	98	25	8
Galole	469	63	34	22
Witu	1 094	70	29	24

STUDY AREA, ANIMALS AND METHODS

The only topi in Kenya at the time of the study which were at least partly conserved within a park or reserve were those on the Mara-Loita plains in southern Masailand (Narok district). They form a unit population within the distribution area that extends into the Serengeti National Park and adjoining regions of Tanzania (Maswa and Musoma districts). Their seasonal movements are limited in extent, and largely confined to the Mara Maasai Game Reserve. This population, of about 3 000 animals, was chosen for the field study.

The field work, carried out between August 1972 and January 1973, was based either on a camp on the Talek River or at the Kenya Game Department's Mara Research Station at Olemolepo, near Keekorok. Observational work was carried out from a landrover. Observations on the distribution of topi in relation to habitat were obtained during over 300 km of road patrols, when the location (*e.g.* vegetation type, catena level*), group size and composition, and activity of over 2 000 sighted topi were recorded during 60 field hours. Further activity records were collected during 25 hours of more prolonged, stationary observation of herds. Pasture samples from 30 sites were collected from clipped quadrats (a quarter square metre *i.e.* 50 × 50 cm), weighed immediately in the field, and subsequently oven-dried and reweighed. Leaf table height (*i.e.* the mean height reached by the tallest leaves of all the individual grass plants in a pasture) and density of inflorescence were described for the grass

*The term "catena" refers to the sequence of soil types, from eluvial, through coluvial, to alluvial, that reflects the dynamics of soil formation in terrestrial land systems.

communities at over 200 points on the routes of the road patrols. Faecal samples were collected fresh, immediately upon being voided by the topi, and were weighed immediately in the field before being oven-dried and reweighed.

RESULTS

Distribution

The permanent population of topi (as distinct from the Serengeti topi which seasonally invade part of the Mara Maasai Game Reserve) were found, during the six months' study, to be using a few restricted areas consistently and heavily. Each of these areas consisted of an upper plain or ridge of green grassland, a long slope towards a river, and a low-lying area of flat ground by the river, the whole area being relatively clear of trees. One of these areas of concentrated topi use was chosen for long-term observation. Topi occurred in all seasons in lower numbers scattered throughout the wooded grasslands and degenerated thicket country of the Game Reserve and surrounding country. These scattered, low-density areas showed great seasonal variation in topi occupance, an area generally being abandoned when it was very dry, or when the grass was tall and flowering. In the high density areas, there was a tendency for animals to be found on grassland high on the catena during the rains, moving downhill towards the riverine flats in the dry season.

During road counts vegetation samples were taken from pastures being used by topi, and were compared with samples from pastures not being used by topi. Some results of these comparisons are given in Table 2. Topi were not attracted by a high standing crop of grass (total dry mass/m^2), nor even by a high standing crop of grass leaf; nor could their occurrence be consistently linked with a high leaf+sheath : stem ratio in the grasses. The most reliable guide to the appropriateness of pasture for topi seemed to be its height, especially its leaf table when

TABLE 2

Characteristics of grass swards where topi are present or absent. Mean values are given for samples from 16 sites where topi were present and 14 where they were absent, taken in August 1972.

Topi	*Sward*					
	Green %	*Leaf* %	*Sheath* %	*Stem* %	*Dry crop* g/m^2	*Leaf table* cm
Present	46,3	45,0	32,9	22,1	291	11,6
Absent	43,5	45,5	30,3	24,2	441	38,9* (or 2,7)*

*Leaf table values for pastures where topi were absent fell into two categories, one with tall grass, usually in flower, and one with very short grass.

not in flower. It was noted that at times leaf table alone was enough to distinguish pasture being used by wildebeest *Connochaetes taurinus* (Burchell) and Thomson's gazelle *Gazella thomsoni* Günther from that being used by topi. Further measurements would probably show that the pasture being used by topi is most accurately identified by a combination of height, greenness, and leaf + sheath : stem ratio.

Activity

The records of the activities of all animals noted on road patrols or during special observation periods were combined in hour classes to obtain patterns of diurnal activity. The resulting graphs of activity frequencies (Figure 1) show that daily patterns from August and from November-December are closely similar, although there is a slight indication of more diurnal time spent feeding in the August samples (Figure 2), when daytime temperatures were several degrees lower than in November–December.

It was not always possible to observe whether or not a standing or lying topi was ruminating. In impala, *Aepyceros melampus* Lichtenstein, nearly all standing or lying animals were found to be ruminating (Jarman & Jarman 1973), but occasional checks of resting topi showed that this was not true of this species in these circumstances. Many standing topi, and the majority of those lying down, were not ruminating. This apparent 'waste' of ingestive-digestive time requires closer investigation. Non-rumination while resting was particularly connected with certain postures which are described and discussed below.

The majority of a topi's diurnal feeding time occurs either in the early morning or late afternoon, with a minor early afternoon peak. The resting states, standing and lying, form the inverse of this pattern. The implication is that feeding is suppressed by, and resting stimulated by, the higher temperature and radiation levels between 10h00 and 17h00. This pattern of diurnal feeding in relation to water conservation is discussed below.

Resting postures and orientation

When resting, a topi adopts one of a range of postures. These are listed in Table 3. Once these had been identified, it became possible to record their adoption at different times of the day. It can be seen in Figure 1 that standing was more common in the morning than in the afternoon, while lying reached its peak frequency in the afternoon. An individual topi which stops feeding normally stands for a while before lying down; after a period of lying down, it will stand up and begin feeding without an intervening period standing resting.

Figure 3 illustrates the frequency of the four identifiable lying postures during diurnal hours. The major change is obviously in the proportion of topi which had their heads up, as against the head being in one of the three 'down' postures. Once again these population changes reflect an individual's progression. On first lying down a topi usually has its head up, and may be ruminating. After a while it will adopt one of the head 'down' postures. It does not usually revert to a head-up posture for long before standing up. The period of lying head-up before lowering the head is likely to be longer early in the morning than at mid-day or in the afternoon. Nearly all the topi whose activity was recorded in the Mara were in open grassland, and thus were not using the shade of trees when resting. A few observed in woodland in the

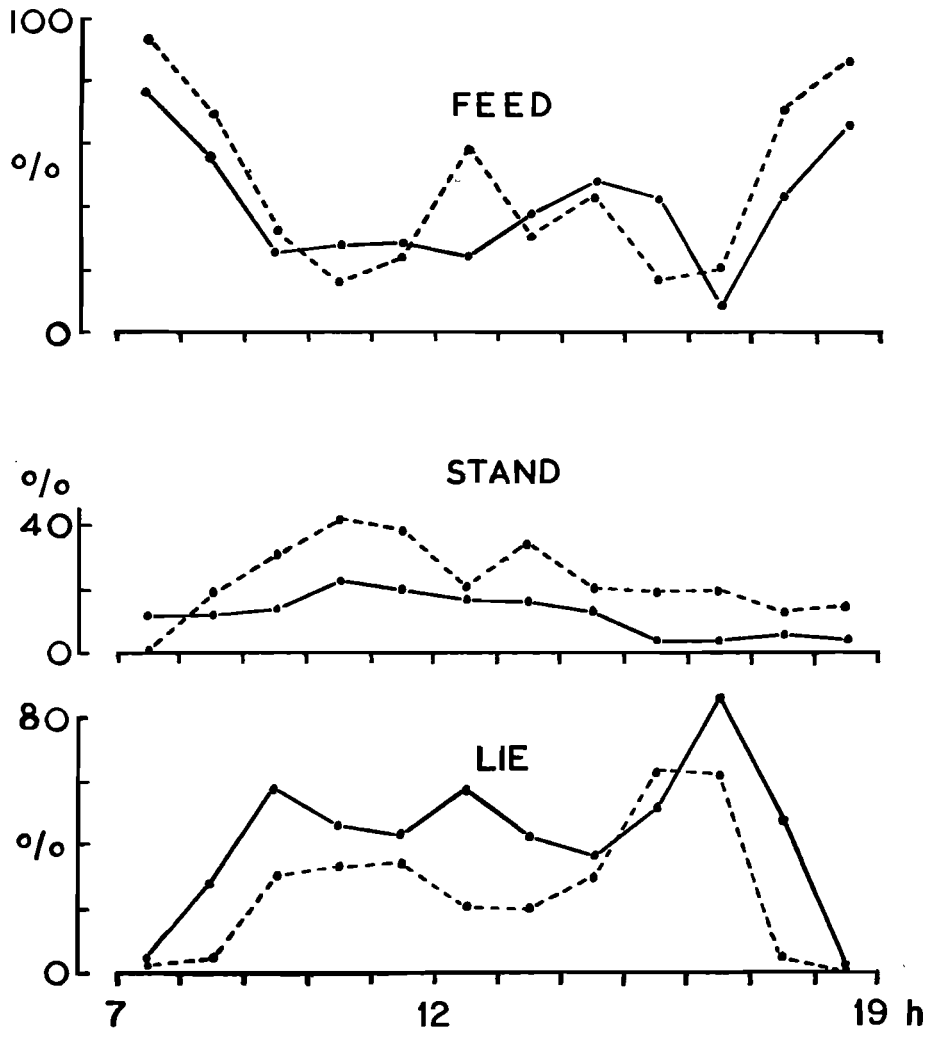

FIGURE 1

The percentage of recorded topi which were feeding, standing or lying down, in hour classes between 07h00 and 19h00. The solid line joins values for November – December, and the dotted line values for August 1972. The sample sizes from which the percentages were derived were as follows:

	Time (hours)											
	07–08	08–09	09–10	10–11	11–12	12–13	13–14	14–15	15–16	16–17	17–18	18–19
August	31	144	107	191	137	29	55	91	101	63	83	21
November – December	604	639	449	494	397	422	484	1 291	436	1 312	430	34

Mara, and many in the woodland parts of the Serengeti National Park, took advantage of the shade of trees when resting, and in these circumstances far fewer animals lay down when resting. From this it appears that lying down, and especially lowering the head, could be associated with resting while exposed to the sun, while standing is more characteristic of resting in shade. Another resting posture, which is characteristic of, but by no means confined to, territorial males, is the 'belvedering' attitude, in which the animal stands with the forequarters raised and the hindquarters lowered. This is exaggerated by standing on a termitarium with the forequarters up the slope. Although this is usually seen with the head held up, the individual may stand in this position with the head forward or lowered.

TABLE 3

Resting postures of topi.

1. Standing, head up.	Muzzle raised; may ruminate in this posture.
2. Standing, head down.	*Either* with neck in normal position angled upwards, but with chin tucked in to neck so that plane of face is angled forward and downwards. *Or* neck angled horizontal or downwards, with face shadowed. No rumination.
3. Lying, head up.	Lying, forelegs under torso, hind legs under abdomen or partly to one side; neck angled upward, muzzle raised. Neck may be at sideways angle to body. May ruminate in this posture.
4. Lying, head forward.	As above, with neck angled upwards, but face tilted forward, chin tucked in and face shadowed. No rumination.
5. Lying, head on ground	Lying as above, but with the neck and chin stretched out along the ground. No rumination.
6. Lying, head to flank.	Lying with the neck turned, horizontal or lower, so that the side of the face rests on the flank, the muzzle in the region of the groin, and the body twisted so the leg on that side is not beneath the abdomen. No rumination.
7. Lying sprawling.	Calves may lie on their sides with all four legs not under the body, the neck and side of the face on the ground.

It was noted that, between 10h00 and 16h00 animals resting, standing or lying, tend to orient themselves so that the spine, or at least the neck, is approximately in line with the sun. This is, of course, not apparent when the sun is at its zenith, and more strongly apparent the less its angle of elevation, except that orientation seems to be unaffected by the sun in the early morning and late afternoon. Figure 4 illustrates the orientation, relative to the sun, of the neck, or neck and spine if in line with each other, of 107 resting topi recorded between 10h00 and 16h00. Of these, 36 held the neck at a noticeable angle to the body when resting;

71 held neck and spine approximately in line. The commonest position was with the head away from the sun, and the neck or neck and spine in line with the sun. Despite possible inaccuracies in estimating relative orientations of neck and sun, these data strongly suggest that topi when resting in the open grasslands of the Mara in the middle of the day did not orient themselves randomly in relation to the sun.

Water balance

During the study, on any day at least some topi were recorded drinking. At dry times of the year probably all animals drank daily, usually around mid-day or early afternoon.

Two facets of daily water balance were revealed by the study. The first was that the moisture content of faeces varies during the day, falling steadily through the day from a high content in the early morning (Figure 5). The decline can be expressed as a regression of faecal moisture $\left(\frac{\text{wet mass} - \text{dry mass}}{\text{dry mass}} \times 100\right)$ content (y) on time of day in hours (x), with the form

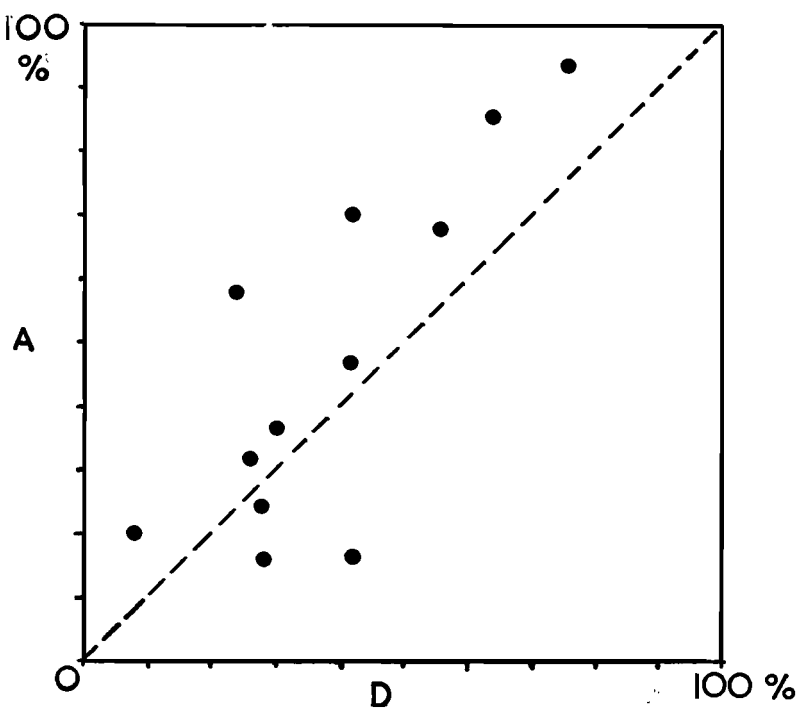

FIGURE 2

A comparison between the percentage of topi feeding in the same hour classes in August (A) and November – December (D). The broken line indicates perfect correspondence. The scatter suggests higher feeding values in August. For sample sizes see legend to Figure 1.

$y = 236{,}9 - 5{,}04x$, which is significant ($p < 0{,}001$).

The second aspect of water balance concerns intake of preformed water in food. It will be seen from Figure 1 that, within the period 07h00 to 19h00, 57 per cent of feeding occurs from 07h00 to 09h00 and 17h00 to 19h00. Measurements of hourly variation in the water content of pasture in the Mara show that moisture content falls steeply from dawn to 09h00, continues to decline until about 14h00 or 15h00, then rises again in the afternoon and evening. So by distributing their feeding time as they do, topi are effectively improving their intake of preformed dietary water, since grass will contain three times as much water in the early morning as at noon.

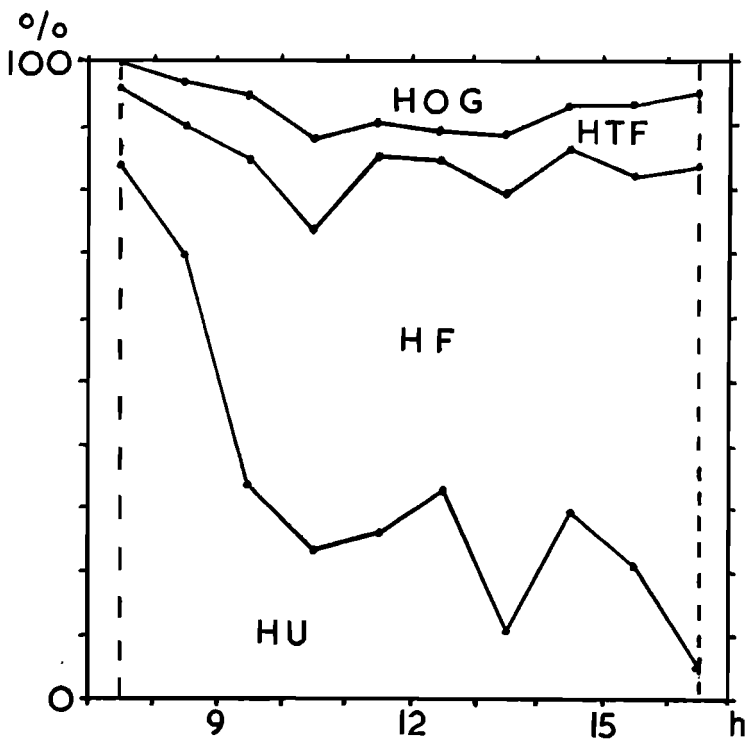

FIGURE 3

The proportions of lying topi in each of four postures in hour classes from 07h00 to 17h00 represented as areas. The sample sizes for each hour class were as follows:

	Time (hours)									
	07–08	08–09	09–10	10–11	11–12	12–13	13–14	14–15	15–16	16–17
N =	25	183	264	229	171	241	210	473	222	1 135

HOG: lying, head on ground. *HTF:* lying, head to flank: *HF:* lying, head forward. *HU:* lying, head up.

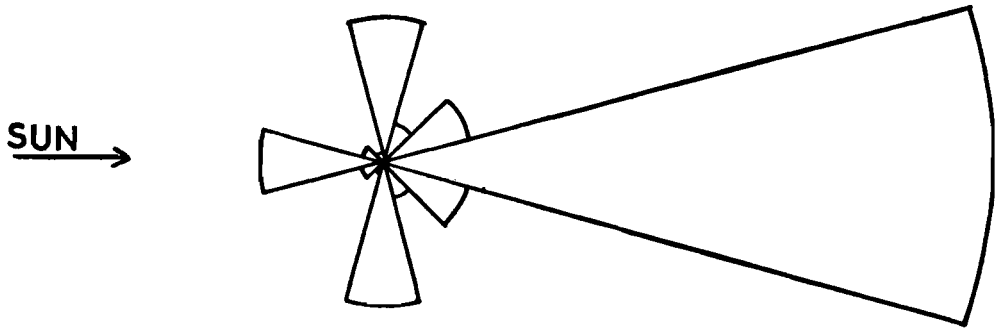

FIGURE 4

Relative frequencies of topi lying with head and neck at different orientations to the direction of the sun. Animals face outwards from the centre of the diagram. Sample size = 107.

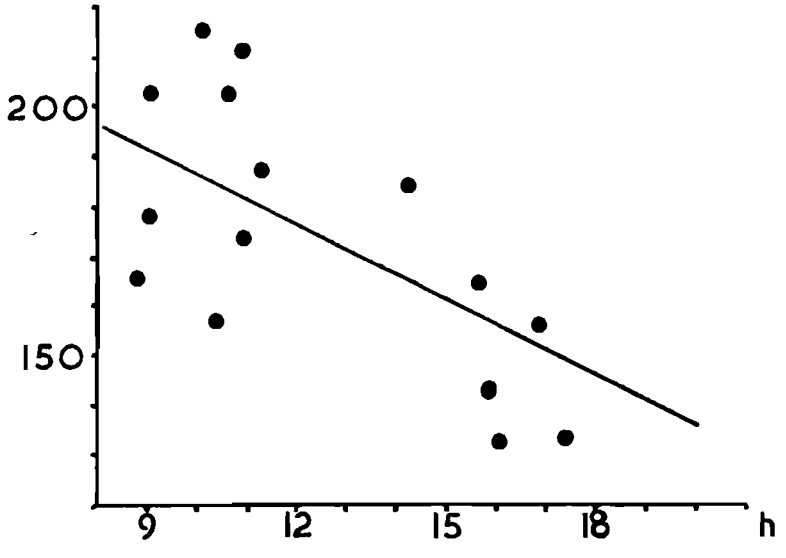

FIGURE 5

Variation in water content of faeces $\left(\frac{\text{water content (grams)}}{\text{dry mass (grams)}} \times 100\right)$ between 08h00 and 18h00. The calculated regression line is shown.

Discussion

From this brief study it appears that topi distribution in the study area is dictated by the animal's feeding style and the pastures most suited to it. Since such pasture is available mainly in treeless grassland (unlike that of some other topi populations), the Mara topi are exposed to high radiant heat loads during the middle of the day. Much of their behaviour could be interpreted as a consequence of this. Thus the metabolically costly process of active feeding is mainly confined to early morning and late afternoon, while the middle of the day is spent resting. The orientation adopted by topi when resting in the open could help to reduce incident radiation. Topi have quite laterally flattened necks and shoulders, and their coat, although dark in colour, is short-haired and shiny, *i.e.* highly reflective. Maintaining the neck in line with, rather than at right-angles to, the sun would minimize the animal's chance of absorbing incident solar radiation in that part of the body. Lying down, rather than standing, would reduce the intake of reflected radiation from the ground. Lying with the head away from the sun in some of the postures adopted ensures that the face and forehead of the animal are in shade. It has been noted elsewhere in East Africa that heat-stressed cattle will strive to keep their heads in the shade (M. D. Gwynne pers. comm.). The topi in nearby wooded areas use the shade of trees to avoid incident radiation, and spend much less time lying down and do not adopt some of the lying postures (postures 4, 5, and 6 of Table 3) at all frequently when resting in shade. The absence of rumination when resting is, at least by contrast with impala and other shade-seeking antelope, peculiar. It could be that when resting in the sun topi are having to reduce heat production to an absolute minimum, and even rumination, which nearly doubles the resting metabolic rate in cattle (Malechek & Smith 1976), must be foregone.

Decrease of faecal moisture throughout the day presumably reflects a form of water conservation through water resorption from the gut, implying that diurnal water intake through food and drinking is not superfluous. The timing of diurnal feeding seems to take maximal advantage of water content of grasses. It would appear that the cost, in terms of lost water, of living on the open grasslands of the Mara must be met by an hourly adjustment of the physiological means of water conservation.

Relatively few antelope species live quite independent of shade. The Mara topi illustrate some of the behavioural and physiological means by which a species which frequently does use shade can adapt itself to a shadeless environment adequately supplied with its other needs, such as food and water.

Summary

1. In the Mara region of Kenya, topi distribution is closely associated with grass sward structure, especially leaf table height. Position on the catena varies seasonally to some extent.
2. Topi feed most actively (diurnally) during early morning and late afternoon. Standing gives way to lying as the resting mode during the intervening hours, and progressively more animals lie 'head down' as the day progresses. Only animals with their heads up ruminate.

3. When resting there is a tendency for the neck, or neck and spine to be oriented in line with the sun, the animal facing away from the sun. Combined with a 'head down' posture, this ensures that the face is always shadowed.
4. Faecal moisture declines throughout the day. Regression of faecal moisture (y) on time of day (x) gives a significant, $p < 0{,}001$, negative slope, $y = 236{,}9 - 5{,}04x$.
5. Times of most intensive feeding correspond with times of highest moisture content of grasses.

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Addendum

Since submitting this manuscript, my attention has been drawn to a detailed report by David (1973) of orientation of bontebok *Damaliscus dorcas dorcas* (Pallas) in relation to the sun. While adopting a typical alcelaphine standing head-forward posture, this species typically oriented head towards the sun, in contrast to the topi which lay with head away from the sun.

Reference

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