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Time budgets of Waterbuck *(Kobus ellipsiprymnus)* of different age, sex and social status

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Abstract

Daytime budgets of waterbuck *(Kobus ellipsiprymnus)* of different age, sex, and social status were measured at Lake Nakuru National Park, Kenya.

Adult and subadult females spent more time feeding than adult and subadult males. Inside territories, females spent more time feeding than outside of territories. Time spent for agonistic behaviour was highest in young males. Satellite males spent less time for sexual behaviour than territory holders, but more time than bachelor males. Territory holders and satellite males spent the same amounts of time feeding – much more than bachelor males. Because the amount of forage ingested by ruminants is positively correlated with forage quality, this indicates that bachelor males were relegated to nutritionally inferior areas. Time budgets of males and females, site preferences of females, and faecal crude protein content of animals feeding at different sites (Tomlinson 1979) all suggest that territories are high quality feeding areas and that the social system of waterbuck is a resource defence polygyny.

Sex differences in time spent feeding at the same site probably reflect a fundamental difference in the behavioural programming of males and females: females of polygynous species are more likely to be "energy maximisers" than males. Recent evidence points to differences in levels of sexual hormones as a proximate cause of sex differences not only of sexual and agonistic behaviour but also of maintenance behaviour.

Introduction

Regardless of age, sex, or social status, all members of a species have the same amount of time available to spend every day. They can, of course, be expected to spend it on different activities. In polygynous species, adult males will spend time to acquire females, whereas adult females will spend time to produce viable offspring (Schoener 1971; Trivers 1972; Clutton-Brock et al. 1982; Hoffman 1983; Owen Smith 1984). As the amount of time per day is a finite value, spending more time for one activity must mean spending less time for one or several other activities. This study shows how the age classes, sexes, and holders of different social status of a polygynous mammal differ in allotting time to their activities during the day.

Waterbuck *(Kobus ellipsiprymnus)* are antelopes similar in size to red deer; they occur throughout Africa south of the Sahara (Dorst and Dandelot 1970; Haltenorth and Diller 1977). The social structure of waterbuck living in Lake Nakuru National Park, Kenya, has been described previously (Wirtz 1981, 1982). With an average of 30 waterbuck/km^2, Lake Nakuru NP has by far the highest population density recorded for the species. Probably as a consequence of the high population density, only about 7 % of the adult males held a territory during the study period and half of the territory holders tolerated one or several additional adult males, "satellite males", in the territory. Within the territory, satellite males were subdominant to the territory holder and participated in the defence of the territory. About 9 % of the adult males acted as satellite males and the remaining 84 % were bachelor males spending most of their time outside territories. Females moved in herds of changeable size and composition over home ranges encompas-

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sing several territories and non-territorial areas. Most territories were located along the lake shore and along rivers. During the day most females were inside territories (Wirtz 1982).

Material and methods

Study area and recording technique

The study area has been described previously (Wirtz 1982) in a paper that also gives the definitions of the age classes used: adult male, young male, juvenile male, adult female, subadult female, and calf.

Both study years (1978 and 1979) were exceptionally wet years compared to long-term means (Kutilek 1975); see figure 2 in Wirtz (1982) for the monthly rainfall values. Data on time budgets were collected throughout the course of the two study years.

Time budgets of the different age classes, sexes, and social classes (territory holder, satellite male, bachelor male) were measured between 7 am to 7 pm. Groups of animals were observed with binoculars (Leitz Trinovid 10 × 40) from a Land-Rover or from tree hides. Observations were recorded on a tape recorder. The animals were accustomed to cars and during observations would graze as close as 5 m from the Landrover; average observation distance is estimated to be about 50 m. Uninterrupted observations at the same site lasted from one to twelve hours, on average three hours.

Data were collected using the „scan sampling" technique (Rollinson et al. 1956; Altman 1974; Martin and Bateson 1986). The observer would scan the group at regular intervals and record the momentary activity of each animal seen. The proportion of records of a behaviour pattern is an approximation of the proportion of time spent performing this behaviour pattern. Inter-scan interval was five minutes. Large groups sometimes took longer to scan and the inter-scan interval was then set at ten minutes.

All activities were classified into the eleven types described below (see Walther [1958] for a description of behaviour patterns such as Flehmen, and see Tomlinson [1980] for a description of the expressive behaviour of waterbuck in particular):

1. Browsing	Feeding on dicotyledons, such as shrubs or *Acacia* leaves
2. Grazing	Feeding on grasses
3. Standing	Standing on all four legs; part of the time in this position is spent ruminating
4. Lying head up	Lying on the ground with head raised above the ground; part of the time in this position is spent ruminating
5. Lying head down	Lying with the head resting on the ground
6. Walking	Moving forward at slow to moderate speed
7. Running	Trotting or galloping
8. Agonistic	Female butting her head into the flank of another female; male confronting another male with head raised high and horns tipped forward; male approaching another male in submissive low stretch posture with horns tilted backwards; males fighting with interlocked horns; male galloping after another male
9. Sexual	Male sniffing female, rubbing a female with its head, performing Flehmen or Laufschlag, running after a female, attempting to mount or mounting a female, copulating
10. Grooming	Scratching the own body with hoof or horn, licking own body (allogrooming was only observed in mothers grooming their calves; this was recorded as "others")
11. Others	Drinking, defaecating and any other behaviour not mentioned above; also behaviour recorded as "unidentified" when an animal was partially hidden by the vegetation (0.1 % to 1.0 % of all records in the different age classes).

The observations are biased in at least the following ways. Only groups of more than five animals were used for activity records. Among other things, this means that the data for territory holders apply only to territory holders that have females with them and not to territory holders without females. Observations were made only on groups in open grassland, open shrub, and open forest but not on groups in dense shrub and dense forest where animals were difficult to see. Less than 6 % of the waterbuck were recorded in these two types of habitat during counts of habitat utilization (Wirtz and Kaiser 1988). Nevertheless, a slightly higher proportion of "browsing" would probably have been recorded if these two types of habitat had not been ignored. Recording the activity of each animal at the moment it is seen through the binoculars meant that an animal walking a few steps whilst grazing was recorded as "walking" rather than "grazing". Bouts of ruminating are frequently interrupted and animals seen at such moments were then recorded as "standing" or "lying head up" instead of "standing ruminating" or "lying ruminating". We therefore decided not to report values for the two

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incomplete measures of ruminating activity and have included them in "standing" and "lying head up", respectively.

The data presented here describe daytime activity of waterbuck at Lake Nakuru National Park. Waterbuck are also active at night. For technical reasons, only few quantitative observations on nighttime activity could be taken. During several clear nights, approximately 20 hours of observations were made and there was no indication that the major patterns might be different from those recorded during daytime.

Number of observations

A total of 957643 observations were taken between 7:00 h and 19:00 h (observations per hour: 5513, 8630, 8480, 8516, 8305, 7855, 6845, 9048, 9906, 8812, 11422, 2411). The numbers of observations for the different waterbuck classes are given in Tables 1–4. The data for territorial males are from 39 individuals, those for satellite males from 36 individuals. More than 100 different individuals contributed to the observations for adult females and for bachelor males.

Treatment of data and statistical procedure

Numbes of observations were unequally distributed through the course of the day. For instance, relatively more observations were taken during hours when the animals spent most of their time grazing; a daily mean from unweighted data would then result in an overestimate of this activity. For each hour, the number of observations of each activity was expressed as the percentage of all observations during this particular hour; the daytime mean was then calculated from these percentages (cf Figure as an example).

When comparing two different waterbuck classes, their daytime means were reconverted into frequencies of observations on the basis of the total numbers of observations. The proportions of an activity in the total time budget (e.g. number of observations "grazing" versus number of observations of all other activities) were then compared by chi-square test.

When there were fewer than 100 observations for one of the classes compared during one of the hours of the day, this hour was exluded from the comparison.

Daytime budget of the "average waterbuck" was calculated by combining the data for all age classes in the proportions at which they were collected, i.e. by simply summing all observations per hour of all animals, regardless of age, sex, and social status.

The shorter the inter-scan interval, the better the estimate of the true amount of time spent for various activities (Harker et al. 1954). On the other hand, very short observations intervals can result in measuring the same phenomenon repeatedly and producing "dependent data", i.e. an inflated sample size unsuitable for statistical analysis. Scanning a group every five minutes may lead to dependent data for some activities with very long bout lengths. A statistical comparison would then lead to unrealistic levels of significance. To be on the safe side, we here call a difference "significant" only if $p < 0.001$ (chi-square value > 10.83, 1 degree of freedom).

Results

The "average waterbuck"

The "average waterbuck" spent 37 % of its daytime feeding (35.9 % grazing plus 1.1 % browsing), 15.5 % standing, 37.8 % lying, 6.7 % walking and less than 3 % for all other activities (Fig.). The two social behaviour patterns "agonistic" and "sexual" took up only 0.3 % each of the daytime activity of the "average waterbuck". Lying head down also was a comparatively rare behaviour, taking only a few minutes at a time, as is typical for large bovids (Balch 1955).

The Figure shows the distribution of the major (most time consuming) activities throughout the day. There was a morning and an evening peak of the activities grazing and walking and a corresponding midday peak of lying. Solar radiation at Nakuru reaches a maximum at about 13–14 h (Vareschi 1982, Fig. 3a), i.e. the time when the animals spent the highest proportions lying head up (48 %) and lying head down (2.4 %).

The distribution pattern of the activities throughout the course of a day as shown in the Figure was essentially the same for all classes of waterbuck. In the following, we therefore compare only the daily means of animals of different age, sex, and social status.

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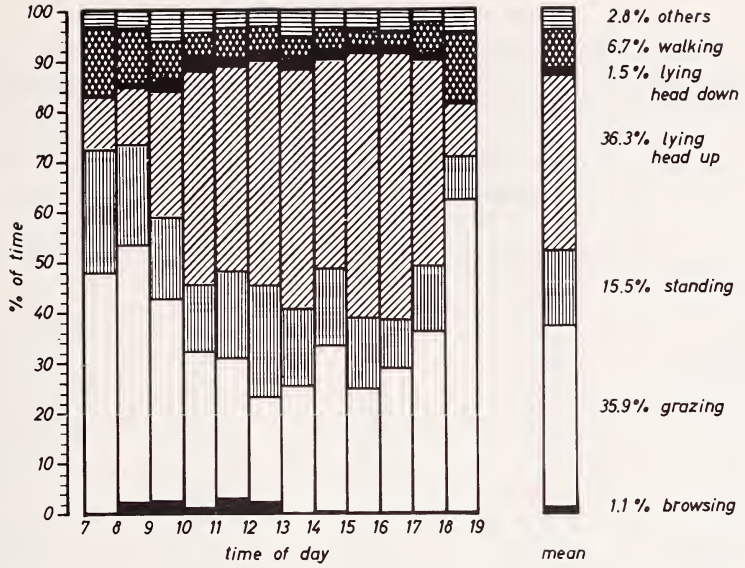

Fig. 1. Distribution of activities of the "average waterbuck" through the course of a day and daily means of the different activities. See text for numbers of observations per hour

Sex differences

Adult male – adult female

Adult males and adult females differed markedly in their time budgets (Table 1). Whereas adult males spent 26.8 percent of their time feeding, adult females spent 39.7 percent – almost 1.5 times as long as males (chi-square 877, $p < 0.00001$). In contrast, adult males spent more time lying than adult females (chi-square 464, $p < 0.00001$). Note that the majority of these adult males are bachelor males and that the time budget of adult males in general is therefore largely determined by the time budget of bachelor males. A comparison of the time budgets of bachelor males, territory holders, and satellite males is given below.

Table 1. **Comparison of time budgets (% of observations) of adult males, adult females, and subadult females (7–19 h)**

	Adult male	Adult female	Subadult female
Browsing	0.4	1.3	1.2
Grazing	26.4	38.4	38.1
Standing	15.1	15.3	15.4
Lying head up	43.0	34.5	31.7
Lying head down	2.2	1.1	1.2
Walking	5.6	6.6	8.0
Running	0.2	0.2	0.2
Agonistic	0.5	0	0.2
Sexual	2.1	0	0
Grooming	4.1	2.3	3.8
Others	0.4	0.3	0.2
n observations	18 844	32 958	14 821

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Juvenile male – subadult female

For juvenile males, we have insufficient data for the time 18 to 19 h. A direct comparison with subadult females is therefore impossible. After truncating the data for subadult females at 18 h, a comparison of juvenile males and subadult females (Table 2) also shows a

Table 2. **Comparison of time budgets (% of observations) of subadult females, juvenile males, young males, and adult males (7–18 h)**

	Subadult female	Juvenile male	Young male	Adult male
Browsing	1.3	0.5	0.6	0.5
Grazing	35.7	27.8	26.3	24.2
Standing	16.1	24.2	20.4	15.5
Lying head up	34.2	29.4	36.7	45.4
Lying head down	1.2	2.9	1.8	2.3
Walking	7.1	8.9	6.3	5.4
Running	0.2	0.3	0.2	0.1
Agonistic	0.1	0.4	1.1	0.5
Sexual	0	0	0.2	1.8
Grooming	3.9	5.3	6.2	4.0
Others	0.2	0.3	0.5	0.3
n observations	14 641	3331	12 708	18 282

large difference in the time spent feeding: whereas juvenile males spent 28.3 % of their time feeding, subadult females spent 37 % (chi-square 89.6, $p < 0.00001$). In contrast, juvenile males spent more time standing than did subadult females (chi-square 122, $p < 0.00001$).

Age differences

Adult female – subadult female

Adult females and subadult females closely resembled each other in the times spent for the different activities (Table 1). There were no obvious age differences in their time budgets. Those activities restricted to sexually mature females (e.g. suckling a calf or licking a calf) were recorded in the category "others" and took up less than one percent of the adult females' time.

Adult male – young male – juvenile male

Young males spent less time lying (38.5 %) than adult males (47.7 %) (Table 2, chi-square 262, $p < 0.00001$). Instead, they stood longer, groomed longer and spent more time in agonistic interactions (chi-square > 36, $p < 0.00001$ in each case). Feeding time of young males (26.9 %) was slightly higher than that of adult males (24.7 %) (chi-square 19.1, $p < 0.0001$).

Juvenile males spent even less time lying (32.3 %) and more time standing than young males (chi-square > 22, $p < 0.00001$ in both cases). They also spent slightly more time feeding than young males, but this difference does not reach the significance level. Juvenile males spent approximately the same amount of time for agonistic behaviour as did adult males (chi-square 0.6), i.e. much less than young males (chi-square 14.1, $p < 0.0002$).

Thus, with increasing age, males tended to spend less time standing and feeding and more time lying; time spent for agonistic interactions was highest for young males.

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Social status

Territory holder – Satellite male – Bachelor male

Table 3 compares the time budgets of territory holders, satellite males and bachelor males. As there were insufficient data for bachelor males from 7 to 8 h and from 18 to 19 h, the data for the other two classes were also reduced to the time span 8 to 18 h.

Table 3. **Comparison of time budgets (% of observations) of territory holders, satellite males, bachelor males, and adult females (8–18 h)**

	Territory holder	Satellite	Bachelor	Adult female inside territory
Browsing	0.4	1.4	0.4	1.3
Grazing	28.1	27.2	19.3	37.3
Standing	14.4	18.1	13.1	14.3
Lying head up	39.9	36.7	49.1	38.5
Lying head down	2.0	1.3	2.6	1.3
Walking	6.5	5.7	4.3	4.4
Running	0.2	0.2	0	0.1
Agonistic	0.7	0.4	0.8	0
Sexual	5.1	3.0	0.5	0
Grooming	2.1	5.6	9.3	2.4
Others	0.6	0.4	0.6	0.4
n observations	2886	2215	11 828	21 808

Territory holders and satellite males spent the same amounts of time feeding (28.5 % and 28.6 %); in contrast, bachelor males spent much less of their time feeding (19.7 %; chi-square > 88, $p < 0.00001$ for both comparisons).

Bachelor males spent more than half (51.7 %) of their daytime hours lying head up or head down. Satellite males and territory holders spent much less time for this type of activity (38 % and 41.9 %; chi-square > 89, $p < 0.00001$ in both cases). Compared to territory holders, satellite males stood longer (chi-square 12.4, $p < 0.0004$) but spent less time lying; however, the latter difference does not reach the predetermined significance level (chi-square 7.7, $p < 0.005$).

Bachelor males spent more time grooming themselves than did satellite males (chi-square 32, $p < 0.00001$), which in turn spent more time grooming themselves than did territory holders (chi-square 43.5, $p < 0.00001$).

Whereas territory holders spent 5.1 % of their time for sexual behaviour, bachelor males spent only a tenth of this time on sexual behaviour (chi-square 354.8, $p < 0.00001$). Satellite males spent less time on sexual behaviour than territory holders, but spent considerably more time on sexual behaviour than did bachelor males (chi-square 13.9, $p < 0.0002$ for comparison with territory holders, chi-square 130.1, $p < 0.00001$ for comparison with bachelor males).

Territory holders with and without Satellite males

Table 4 compares the time budgets of territory holders when a satellite male was present and of territory holders in the absence of a satellite male. Because of insufficient data for the time period of 18 to 19 h in one of the classes, both data sets are truncated at 18 h. Territory holders without satellite males spent more time grazing, less time lying and more time for sexual activities but none of these differences reached the predetermined level of significance ($6.95 >$ chi-square > 6.30, $0.02 > p > 0.005$).

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Table 4. **Comparison of time budgets (% of observations) of territory holders with satellites and territory holders without satellites and of adult females inside territories and adult females outside territories**

	Territory holder with satellite (7–18 h)	Territory holder without satellite (7–18 h)	Adult female inside territory (8–12, 14–16, 17–18 h)	Adult female outside territory (8–12, 14–16, 17–18 h)
Browsing	0.6	0.2	1.4	2.6
Grazing	23.5	27.2	41.1	27.6
Standing	14.2	14.5	13.9	15.8
Lying head up	41.9	37.6	34.4	36.0
Lying head down	2.2	2.0	1.3	1.9
Walking	6.6	5.4	4.9	2.9
Running	0.2	0.2	0.1	1.0
Agonistic	0.6	0.8	0	0
Sexual	6.6	9.2	0	0
Grooming	3.2	2.0	2.5	10.9
Others	0.4	0.4	0.4	1.3
n observations	1548	1548	15 217	1644

Adult females inside territories and outside territories

During the day, most females were inside territories. Even though adult females were the largest class in the population (31 % of the waterbuck seen during monthly road strip counts were adult females, Wirtz and Kaiser 1988), there were insufficient data for the time budgets of adult females outside territories for five of the twelve daytime hours. A comparison between adult females inside territories and adult females outside territories (Table 4) can therefore only be made for the following fragments of a day: 8–12, 14–16, and 17–18 h.

When inside territories, adult females spent much more time grazing (41.1 %) than when outside territories (27.6 %) chi-square = 112, $p < 0.00001$). Outside the territories, adult females spent more time browsing (chi-square = 13.8, $p < 0.0002$) and grooming themselves (chi-square 323, $p < 0.00001$) than inside territories.

Sex differences revisited : adult females – adult males, inside territories

The time budgets of adult females and of adult males were compared in a previous section. However, the two data sets differ not only in the sex of the animals but also in the location where they were taken: the majority of the data for adult males are of bachelor males (i.e. from outside territories), and the majority of the data for adult females are from females inside territories. To eliminate the bias caused by differences in site of observation, the time budget of adult females inside territories has to be compared with that of adult males inside territories. Table 3 shows the time budget of adult females (between 8 and 18 h) in comparison with that of territory holders and satellites.

Inside territories, females still spent much more time feeding than did males (chi-square > 85 in both comparisons, $p < 0.00001$). The sex difference in time spent lying, however, is no longer significant when considering only animals inside territories (chi-square 4.6 in the comparison with territory holders, $p < 0.05$; chi-square 2.6 in the comparison with satellite males, $p < 0.15$). Adult females outside territories and inside territories differed conspicuously from adult males in spending almost no time on agonistic and sexual interactions ($p < 0.00001$ for all comparisons).

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Discussion

An understanding of the nutritional physiology of ruminants is essential for the interpretation of their time budgets. The food intake of ruminants is limited by the time required to process the food in the rumen. They can ingest food only as fast as they can digest it. Better digestible forage moves faster through the digestive system and thus permits the animal to take up more of it. Low digestibility of food cannot be compensated for by a greater food intake – on the contrary, food intake is reduced because the time required for processing is longer. Except for highly digestible food (Ammann et al. 1973), the amount of forage ingested and the time spent feeding are positively correlated with the quality of the forage (Blaxter 1962; Thornton and Minson 1972; Arnold 1985). Waterbuck are "grass and roughage eaters" taking food of comparatively low digestibility requiring relatively long processing times (Hofmann 1973).

The social structure of Lake Nakuru waterbuck

Inside territories, females spent more time feeding than outside territories. This indicates better quality of the forage conditions inside territories. Females are free to move between these areas and the observation that female density is higher inside than outside territories (Wirtz 1982) suggests that territories are superior feeding sites. However, there could also be alternative and additional reasons for the female preference for territories (e.g. more frequent harassment by bachelor males outside territories). Adult males show similar site differences in feeding times: bachelor males spent less time feeding than territory holders and their satellite males. Waterbuck territories usually border on water and, to the human observer, the grass outside territories often appeared to be higher and dryer. Dry grass usually has a higher proportion of lignin and thus a lower digestibility (cf Sinclair 1975), which would cause longer processing times and lower rates of uptake.

Protein content is generally acknowledged as a major determinant of nutritive value of forage for ruminants (Sinclair 1975; Festa-Bianchet 1988 and references therein). Faecal crude protein content is closely correlated with dietary protein and has been used to assess forage quality in studies of domestic cattle (Bredon et al. 1963) and wild ungulates (see references in Festa-Bianchet 1988). In a Rhodesian population of waterbuck, the faeces of territory holders and of adult females had a higher crude protein content than the faeces of bachelor males (Tomlinson 1979). This Rhodesian population of waterbuck had the same social structure as Nakuru waterbuck suggesting that Tomlinson's (1979) results would also apply to Nakuru waterbuck. Site-dependent differences in faecal crude protein of males, site preference of females, site-dependent foraging times of females, and site-dependent foraging times of males all suggest that territories are high quality feeding areas. Bachelor males, being excluded from territories, are probably relegated to inferior feeding areas.

The spatial distribution of resources determines the distribution of receptive females, which in turn determines the distribution of males and hence the nature of the mating system (see Emlen and Oring 1977 for a general discussion and classification of social systems, and Geist 1974 for the relationship of ecology and social evolution of ungulates in particular). Territory holders defend high quality feeding sites preferred by females and mate with the females coming to these areas. In the terminology of Emlen and Oring (1977), the mating system of waterbuck is a "resource defence polygyny". (Unfortunately, in their influential paper on the evolution of mating systems, Emlen and Oring [1977], erroneously refer to waterbuck as an example of "female defence polygyny".)

In contrast to females (see below), the fitness of males of a polygynous species, such as waterbuck, is probably determined by non-foraging activities, in particular efforts to acquire females. Because comparatively little time is spent in aggressive encounters, the sex

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difference in aggressive behaviour, likely to be very important in terms of energy and mortality risk, is only weakly expressed in the time budgets. Territory ownership did not cause a reduction in feeding time. On the contrary, territory owners spent more time feeding, on more nutritious food, than did bachelor males. The costs of territoriality are only weekly expressed in the time budgets by slightly higher percentages of walking and running. The differences in energy budget and risk are probably more important.

Sex differences

Even when feeding at the same site and presumably on forage of the same nutritional value, females spent much more time on energy intake than males – a difference already apparent in subadult animals. With increasing age of males (from juvenile male via young male to adult male), this sex difference in maintenance behaviour became more and more pronounced. Spinage (1968) observed the activity of three individually known adult female waterbuck and two individually known adult males (one of them a territory holder) in the Queen Elizabeth Park, Uganda, for continuous periods of up to three consecutive days. The absolute values of his data are not directly comparable with those of the present study, because an animal walking a few steps from one grazing site to another was recorded as "walking" at Nakuru but recorded as "grazing" by Spinage. Nevertheless, Spinage's data similarly show sex-specific differences in maintenance behaviour: the three females spent more time feeding than the two males.

Female waterbuck are probably "energy maximisers" in the terminology of Schoener (1971), i.e. their fitness is determined mainly by the amount of energy acquired. That females spend more time feeding than males is a general finding for all ungulates studied (cf review by Bunnell and Gillingham 1985) and also for several other animal species (e.g. Hoffman 1983). This difference is probably a fundamental behavioural and physiological difference between the sexes, rather than an epiphenomenon of other factors such as differences in bite size. Jewell (1986) showed that in a feral population of sheep at St. Kilda Island, Scotland, rams spent much less time grazing than ewes. Interestingly, castrated males spent almost as much time grazing (71 %) as females. The likely basis for these differences lies in low testosterone levels of castrated males and the accompanying shift to a female type of maintenance behaviour. The proximate cause for the sex difference not only in aggressive and sexual behaviour but also in maintenance behaviour of ruminants could thus be a difference in levels of sexual hormones.

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Zusammenfassung

Zeitbudgets bei Wasserböcken (Kobus ellipsiprymnus) von unterschiedlichem Alter, Geschlecht und Sozialstatus

Im Nakuru Nationalpark, Kenia, wurde gemessen, wie sich Wasserböcke von unterschiedlichem Alter, Geschlecht und Sozialstatus die Tageszeit einteilten. Weibchen verbrachten mehr Zeit mit Fressen als Männchen und innerhalb von Territorien mehr als außerhalb. Bei jungen Männchen war der Anteil Zeit für kämpferische Interaktionen am höchsten. Satellitenmännchen verbrachten zwar weniger Zeit mit sexuellen Aktivitäten als Territoriumsbesitzer, aber mehr als Junggesellenmännchen. Territoriumsbesitzer und Satellitenmännchen wendeten gleich viel Zeit für Fressen auf – wesentlich mehr als Junggesellenmännchen. Da bei Widerkäuern Nahrungsqualität und Nahrungsaufnahme negativ korrelieren, deutet dies an, daß die Junggesellenmännchen in Gebiete schlechterer Futterquali-

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tät abgedrängt wurden. Sowohl die Zeitbudgets von Männchen und Weibchen, als auch die Ortsbevorzugung der fressenden Weibchen und der Proteingehalt von Kotproben (Tomlinson 1979) deuten an, daß Wasserbock-Territorien Orte hoher Futterqualität sind, und daß das Sozialsystem von Wasserböcken als Fortpflanzungsterritorialität bezeichnet werden kann.

Geschlechtsunterschiede im Zeitaufwand für Nahrungserwerb reflektieren wahrscheinlich fundamentale Unterschiede im Verhaltensprogramm von Männchen und Weibchen: bei polygynen Arten sind Weibchen wahrscheinlicher "Energiemaximierer" als Männchen. Neuere Untersuchungen deuten an, daß unterschiedliche Niveaus von Sexualhormonen der proximale Grund nicht nur von Geschlechtsunterschieden im Sexualverhalten und im kämpferischen Verhalten sind, sondern auch der proximale Grund von Geschlechtsunterschieden im Ernährungsverhalten.

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