

## **Climatic influences on the behavioural ecology of Chanler's mountain reedback in Kenya**

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### **Summary**

The effects of rainfall and temperature on the behavioural ecology of Chanler's mountain reedback (*Redunca fulvorufula fulvorufula* Rothschild) were examined on ranchland near Gilgil, Kenya. Ambient temperature was shown to be the proximate determinant of diurnal activity and rumination patterns. Mountain reedback were active during early morning and late afternoon, but rested and abandoned rumination when temperatures peaked at midday. There was close synchrony in levels of activity, rumination and use of cover and shade between males and females. Seasonal variations in time budgets were strongly influenced by rainfall patterns. Analyses revealed a one-month lag between rainfall and both peak grass growth and a decrease in rumination frequency. The proportion of time allocated to feeding decreased one month later, and was coincident with an increase in the proportion of grass in the diet. Reedback may therefore be prevented from exploiting high-quality new grass, possibly by gut-fill or induced imbalances in rumen pH. It is suggested that the unexpectedly high levels of browse in the diet is an adaptive response to low rainfall during the preceding two months.

*Key words:* reedback, *Redunca*, temperature, rainfall, rumination

### **Résumé**

On a examiné les effets des chutes de pluie et de la température sur le comportement du redunca de montagne (*Redunca fulvorufula fulvorufula* Rotschild) dans une région d'élevage près de Gilgil, au Kenya. On a montré que la température ambiante est un facteur déterminant pour l'activité diurne et le schéma alimentaire. Les reduncas de montagne sont actifs en début de matinée et en fin d'après-midi mais se reposent et cessent de ruminer quand la température culmine en milieu de journée. Il y a une synchronisation étroite entre les niveaux d'activité, la rumination et la recherche d'un abri ou d'ombre par les mâles et les femelles. Les variations saisonnières de l'emploi du temps sont fortement influencées par les chutes de pluies. Les analyses révélaient un délai d'un mois entre les chutes de pluie et d'une part, la croissance maximale de l'herbe et d'autre part, une baisse de fréquence de la rumination. La proportion de temps consacré à l'alimentation diminue un mois plus tard et ceci coïncide avec l'augmentation de la proportion d'herbe dans le régime alimentaire. Ainsi les reduncas peuvent être empêchés d'exploiter l'herbe jeune de haute qualité, peut-être par un remplissage des intestins ou par un déséquilibre induit du pH du rumen. On suggère que le taux étonnamment élevé d'aliments broutés dans le régime est une réponse aux faibles chutes de pluie au cours des deux mois précédents.

## Introduction

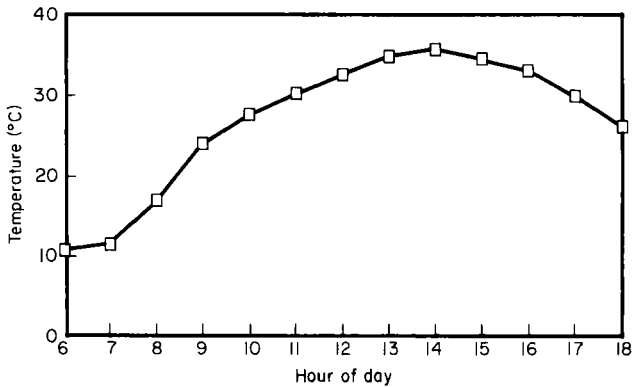
Chanler's mountain reedruck (*Rudunca fulvorufula chanleri* Rothschild) inhabit widely separated hills and mountains from southern Ethiopia to northern Tanzania and eastern Uganda (Haltenorth & Diller, 1980; Kingdon, 1982; East, 1988). Survival over much of its range is threatened by poaching and agricultural encroachment onto mountain slopes (East, 1988), and knowledge of its ecology and habits are needed for effective conservation. In 1975, Hendrichs noted the paucity of available information on this species in comparison to the other members of the Reduncinae, but several recent studies (e.g. Irby, 1977a, 1977b, 1979, 1981, 1982; Mason, 1977; Oliver, Short & Hanks, 1978) have examined various aspects of the species' ecology in some detail.

Irby determined the activity patterns of southern mountain reedruck (*R. f. fulvorufula* Afzelius) in South Africa (Irby 1981), and of Chanler's mountain reedruck in the Horseshoe Crater near Gilgil, in Kenya's Rift Valley (Irby, 1982). He found that both subspecies were generally more active during the early morning and late afternoon, and rested during the middle of the day. This pattern of activity was correlated with a consistent diurnal movement pattern, wherein animals habitually descended slowly from the cone's upper slopes during the morning, occupied the cone floor or slope base during early afternoon, and returned up-slope in the late afternoon. He suggested that temperature was the most likely proximate factor regulating the animals' movements (Irby, 1982).

In this paper we specifically investigate the roles of temperature and rainfall as key determinants of reedruck activity cycles, using data from a field study of reedruck groups on the Eburru Cliffs, near Gilgil, Kenya. The Eburru Cliffs are located approximately 5 km south of Irby's study area in the Horseshoe Crater. The paper also elaborates on Irby's (1982) observations by comparing inter-sexual and seasonal variations in these patterns. Variations in the proportion of dicotyledonous plants included in the diet, rumination frequency, and the use of cover and shade are also examined.

## Methods

The data were collected by RD with the assistance of Patsy Dunbar during a series of field studies in February 1980, January–June 1981 and January–April 1982. Scan samples (Altmann 1974) of all visible animals were made at 10 minute intervals between 0600 h and 1900 h, recording activity category and use of shade and cover. Mountain reedruck were either solitary or occurred in groups of up to eleven individuals, with group sizes of 1–4 being most common (Dunbar & Roberts, unpubl.). As groups do not have great temporal stability (Irby, 1977b; Dunbar & Roberts, unpubl.), each animal within a group was sampled independently. The sex ratio of the population appeared to be female-biased, an observation supported by other studies of mountain reedruck (Irby, 1972; Irby, 1973, 1977b; Mason, 1977). The exact size of the Eburru population was not determined, but samples of the number of individuals that could be observed simultaneously suggest that a minimum of seventeen females, in addition to four resident males, lived on the cliffs. A total of 842 activity records were obtained for males and 3015 for females; juveniles were excluded from the analysis. No attempt is made to



**Fig. 1.** Diurnal variations in ambient temperature at the Eburru Cliffs, Gilgil.

subdivide males by social status. However, the resident males, who could be individually recognized, were intolerant of non-territorial intruders (Dunbar & Roberts, unpubl.; Mason, 1977; Howard, 1986a); consequently non-territorial males were seen only infrequently, and accounted for very few of the activity records for males. Data from males and females are pooled where appropriate. In addition to the day-time activity records, 347 records were obtained during all-night watches. For present purposes, all activity records were classified into one of five behavioural categories: lying, standing, moving, feeding and 'other' (includes social interactions, grooming, defaecation and urination). For certain analyses, the categories of moving, feeding and other were pooled as 'active' animals. When observation conditions allowed, lying and standing animals were also noted as either ruminating or non-ruminating. Whenever the sun shone such that a clear shadow was cast, each individual was recorded as being either in the sun or in shade. Furthermore, each animal was recorded as being either in the open or in cover (with the latter defined as areas in which bushes and shrubs covered at least half the ground surface). An animal could be classed as in the sun and in cover simultaneously.

Diurnal temperature variations (Fig. 1) were recorded at the foot of the cliffs, at ten minute intervals on selected days covering the entire study period. Monthly rainfall data were obtained from the Kekopey Ranch Office weather records. The study periods were timed so as to monitor behaviour towards the end of the long dry period, and the beginning of the rainy season. For the purposes of this paper, we may pool data from January and February into 'dry' months, and from March to June into 'wet' months.

In order to investigate potential food availability, two 900 cm<sup>2</sup> enclosure plots were each clear-cropped at around 14-day intervals. The clippings were oven-dried to constant weight and then weighed (see Table 1).

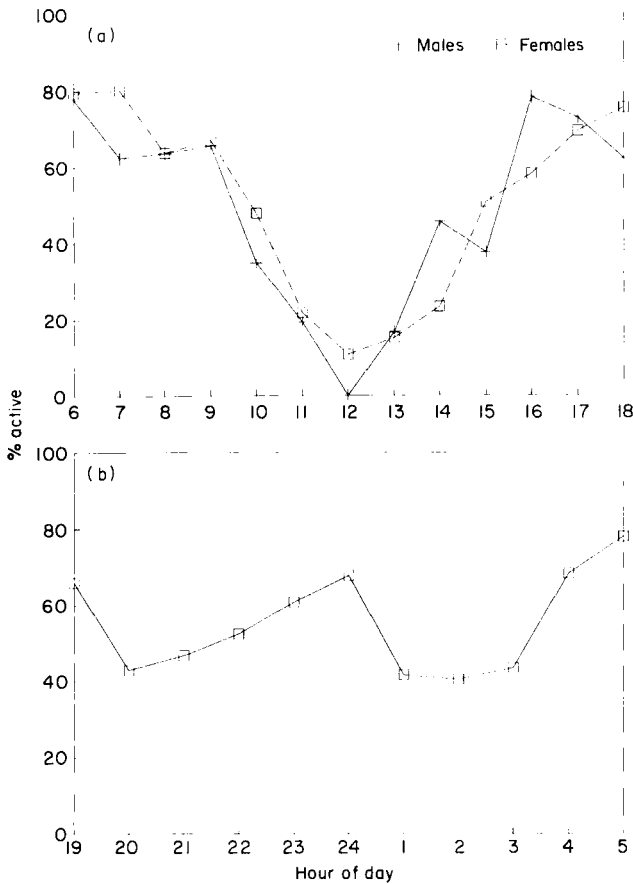
## Results

### *Activity patterns*

Reedbuck groups had a well-defined diurnal cycle of activity (Fig. 2a). Most animals were active throughout early and mid-morning, and in late afternoon, with a distinct resting period around midday. The activity cycles of males and females were closely correlated (Spearman rank correlation,  $r_s = 0.764$ ,  $N = 13$  hours,

**Table 1.** Grass renewal rates on two clear-cropped plots at Gilgil

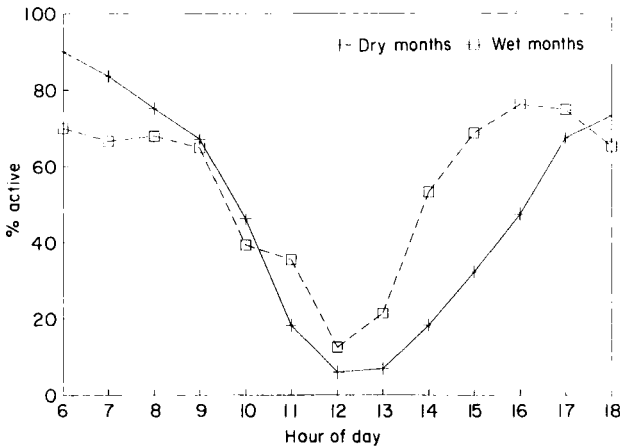
Month	Grass production (g dry wt/m <sup>2</sup> )		
	Plot A	Plot B	Mean
Mar 1981	10.9	—	10.9
Apr 1981	9.4	—	9.4
May 1981	110.4	93.9	102.2
Jun 1981	3.0	24.6	13.8
Feb 1982	0.0	0.0	0.0
Mar 1982	0.3	5.1	2.7

**Fig. 2.** Percentage of animals that were active: (a) during daytime, and (b) during night-time. A three-point running mean was used for the night-time records due to small sample sizes.

$P < 0.005$ , two-tailed). Temperature appears to be an important determinant of reedback activity (see Table 2), but the negative association was significant only in the case of females. This can probably be attributed to the territorial behaviour of the males (Mason, 1977; Dunbar & Roberts, unpubl.), which may oblige males to be active at times when they would otherwise be resting. Reedbucks were also active

**Table 2.** Spearman Rank correlations between temperature and activity and habitat use patterns across hours of the day

	Correlation to mean temperature							
	Cover		Shade		Activity		Rumination	
	Male	Female	Male	Female	Male	Female	Male	Female
$r_s$	+0.68	+0.73	-0.62	-0.45	-0.47	-0.76	-0.62	-0.68
$n$	13	13	11	12	13	13	12	12
$p^1$	<0.02	<0.01	<0.05	NS	NS	<0.005	<0.05	<0.02

<sup>1</sup>Two-tailed.**Fig. 3.** Percentage of animals that were active during wet and dry months.

throughout the night (Fig. 2b), with periodic peaks and troughs in feeding and resting. Activity levels tended to be higher at night than during daylight, with less pronounced resting periods.

A comparison of wet and dry months (Fig. 3) shows that, in dry months, animals were more active between 0600 h and 0900 h (Wilcoxon test,  $P=0.0571$ ), and then became less active than in wet months throughout the afternoon ( $P=0.0754$ ), although there was little difference between 1000 and 1300 h ( $P=0.2429$ ).

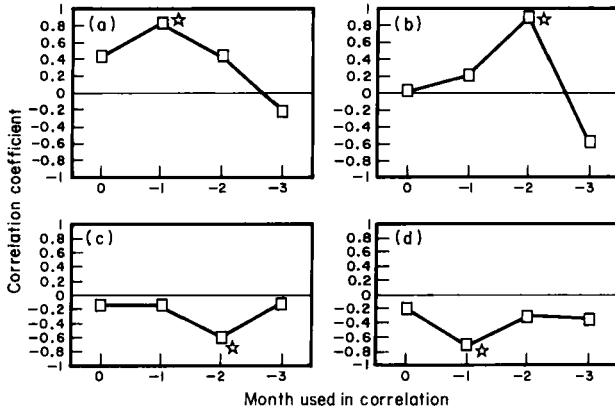
Inter-sexual differences in time budgets across study months were slight (Table 3), as the amounts of time spent feeding (Wilcoxon tests;  $z = -0.11$ ,  $P=0.4602$ ), moving ( $z = 1.29$ ,  $P=0.0985$ ) and standing ( $z = 0.53$ ,  $P=0.2981$ ) by each sex were similar. However, females did appear to lie more often than males ( $z = -1.63$ ,  $P=0.0516$ ).

While temperature is an important influence on diurnal variations in reedduck activity, seasonal variations are perhaps best examined in relation to rainfall: the importance of precipitation in determining seasonal changes in above-ground plant biomass is well-established (Le Houeron & Hoste, 1977; Rutherford, 1980;

**Table 3.** Sex differences in monthly time budgets

Month	Percentage of animals recorded in each activity category											
	Male						Female					
	L	S	M	F	O	n	L	S	M	F	O	n
Feb 1980	28.5	35.9	6.7	28.1	0.9	256	35.5	27.6	7.2	29.6	0.2	583
Jan 1981	—	—	—	—	—	5	13.2	38.3	13.2	35.3	0	68
Feb 1981	20.5	25.5	10.8	43.3	0	157	19.0	28.8	9.6	42.6	0	552
Mar 1981	16.0	26.0	12.0	46.0	0	50	15.8	24.3	7.4	52.6	0	247
Apr 1981	26.4	20.8	9.4	43.4	0	53	30.9	16.3	7.3	44.6	0.9	233
May 1981	6.5	61.3	9.6	22.6	0	31	43.2	36.4	3.0	17.4	0	132
Jun 1981	6.2	50.0	18.8	25.0	0	16	50.8	41.4	2.3	5.5	0	128
Jan 1982	26.0	19.2	4.8	45.2	4.8	104	15.1	20.7	5.6	57.8	0.8	502
Feb 1982	12.9	36.4	6.4	42.1	2.2	140	14.2	28.7	4.3	52.8	0	415
Mar 1982	9.3	16.7	9.5	61.1	3.6	54	16.8	18.9	8.0	56.0	0.3	339
Apr 1982	—	—	—	—	—	5	36.4	18.1	9.1	36.4	0	22

Note: L = lie, S = stand, M = move, F = feed, O = other (including social, territorial, defaecatory behaviour).



**Fig. 4.** Spearman's rank correlations between rainfall in preceding months and (a) grass growth, (b) the proportion of grass in the diet, and the proportions of time spent (c) feeding and (d) ruminating in each month. Asterisks denote significant correlations.

Deshmukh, 1984; McNaughton, 1985), and the increase in forage quality and availability at the onset of the rains will usually result in a reduction in time necessary for feeding (e.g. Irby, 1981). In this study the proportion of time spent feeding was lower between April and June than between January and March (data from Table 3,  $z = -2.42$ ,  $N = 20$ ,  $P < 0.0078$ ). The reduction in feeding time was most closely correlated with rainfall experienced two months previously ( $r_s = -0.59$ ,  $P < 0.05$ ) (Fig. 4c). This response appeared to be more distinct in males than in females (males:  $r_s = -0.69$ ,  $N = 9$ ,  $P < 0.05$ , one-tailed; females:  $r_s = -0.51$ ,  $N = 11$ , NS).

**Table 4.** Monthly feeding records for different food classes in diet

Month	Percentage of records for month							Total ground plus grass	Total records
	Ground vegetation <sup>1</sup>	Grass	Herbs	Bush leaves	Shrub leaves	Soil			
Feb 1980	52.4	40.9	4.1	1.7	0.8	—	93.4	242	
Jan 1981	73.3	26.7	—	—	—	—	100.0	30	
Feb 1981	39.1	40.3	13.5	6.8	—	0.3	79.4	325	
Mar 1981	17.6	65.5	8.5	8.5	—	—	83.0	165	
Apr 1981	15.6	84.4	—	—	—	—	100.0	141	
May 1981	12.9	87.1	—	—	—	—	100.0	31	
Jan 1982	14.9	84.0	0.5	0.5	—	—	98.9	375	
Feb 1982	49.4	49.7	0.6	—	0.3	—	99.1	332	
Mar 1982	18.4	70.1	10.0	0.4	1.1	—	88.5	261	

<sup>1</sup>Observation conditions did not allow observer to distinguish grasses from herbs, but most of the records were probably of grass.

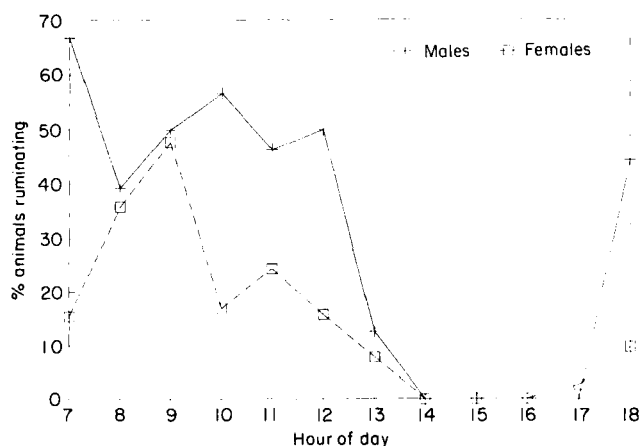
### *Diet*

The proportions of grass, herbs, bush and shrub foliage, and unidentified ground vegetation eaten by mountain reedbeek in each study month are shown in Table 4. Fig. 4a indicates that there is a one-month lag between rainfall and the amount of new grass growth ( $r_s = 0.829$ ,  $P < 0.05$ ), but there is a two-month lag between rainfall and the proportion of grass in the diet (Fig. 4b:  $r_s = 0.894$ ,  $P < 0.05$ ).

### *Rumination*

Patterns of rumination in ungulates are closely correlated with resting periods that occur intermittently during feeding bouts (e.g. Jarman & Jarman, 1973; Norton, 1981; Mloszewski, 1983; Beekman & Prins, 1989), and which often peak around mid-day when animals retire to areas offering suitable shade in order to avoid excessive heat stress (Mitchell, 1977). A large proportion of the mountain reedbeek in this study were observed to ruminate throughout the morning, although the frequency of rumination decreased sharply between 1200 h and 1300 h, and was virtually absent between 1400 h and 1700 h (Fig. 5). Both males and females followed the same diurnal rumination pattern ( $r_s = 0.753$ ,  $N = 12$  hours,  $P < 0.01$ , two-tailed), although a comparison of rumination frequency when at least some animals were ruminating (i.e. excluding 1400–1600 h) reveals that males appear to ruminate more than females (Wilcoxon test,  $z = 2.03$ ,  $m = n = 9$ ,  $P = 0.0217$ ). Contrary to expectation, this diurnal pattern was neither negatively related to feeding periods, nor positively related to the use of cover (Spearman rank correlations, both NS); however, it was associated with the use of shade (males:  $r_s = 0.639$ ,  $P < 0.05$ ; females:  $r_s = 0.682$ ,  $P < 0.02$ , both two-tailed), and was negatively correlated with mean ambient temperature (see Table 2).

The proportion of time spent ruminating was markedly lower in wet months (data from Table 5, sexes pooled) than dry months ( $W_x = 20$ ,  $m = 5$ ,  $n = 8$ ,



**Fig. 5.** Percentage of lying and standing animals that were ruminating during each hour of the day.

**Table 5.** Percentage of animals ruminating in each month (with sample sizes given in parentheses in each case)

	Feb 1980	Feb 1981	Apr 1981	Jan 1982	Feb 1982	Mar 1982	Apr 1982
Males	40.0 (160)	54.8 (31)	—	58.2 (55)	45.3 (64)	0.0 (23)	20.0 (10)
Females	18.3 (328)	36.2 (47)	0.0 (12)	35.7 (252)	32.3 (164)	11.7 (143)	36.8 (19)

$P=0.0148$ ). A similar trend has been demonstrated in African buffalo (*Syncerus caffer* (Sparman)) by Sinclair (1977), in which the ratio of rumination to feeding time was higher in the dry season. Fig. 4d shows that the frequency of rumination was negatively related to the amount of rainfall in the previous month ( $r_s = -0.71$ ,  $P < 0.025$ ).

#### *Use of cover and shade*

As in the diurnal activity cycles, the Eburru mountain reedbeek exhibited a highly distinctive pattern in their use of cover and shade. The proportion of animals in cover increased around midday when temperatures peak, and was negatively correlated with the level of activity (males:  $r_s = -0.676$ ,  $P < 0.02$ ; females:  $r_s = -0.868$ ,  $P < 0.001$ ,  $N = 13$  hours, both two-tailed). Conversely, the number of animals in shade was extremely high in the very early morning, and decreased steadily as the day progressed. Contrary to expectation, this trend was not correlated with the level of activity, nor with the ambient temperature. However, these results might be confounded by the fact that, because of the slope's west-facing aspect, a long shadow was cast during the morning. Males and females were highly synchronized in the use of both cover ( $r_s = 0.830$ ,  $N = 13$  hours,  $P < 0.002$ , two-tailed) and shade ( $r_s = 0.764$ ,  $N = 11$  hours,  $P < 0.01$ , two-tailed).



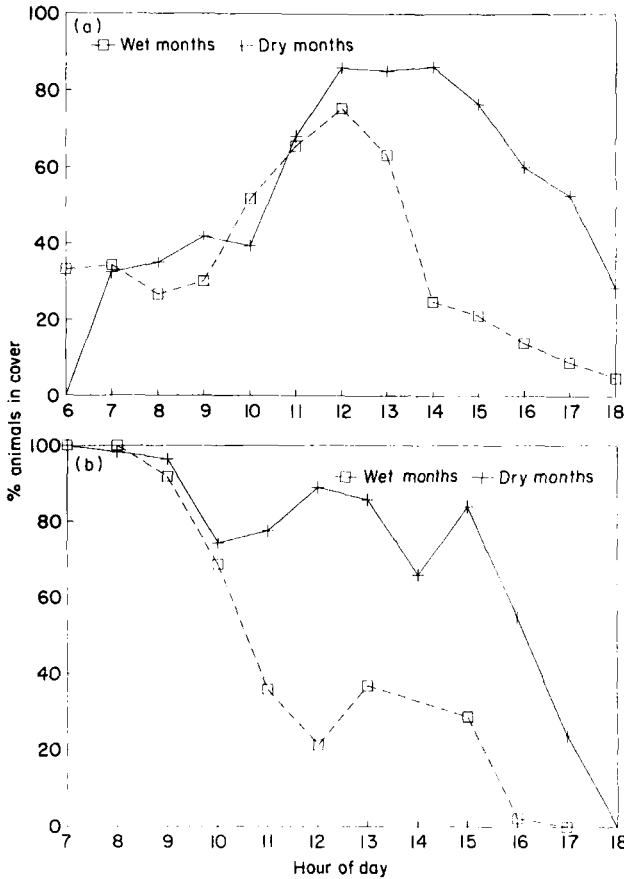


Fig. 6. Percentage of animals (a) in cover and (b) in shade during wet and dry months.

Reedbuck tended to remain within cover and shade (Fig. 6) for longer into the afternoon during the hot dry season months than during the cooler wet season (Wilcoxon tests; cover:  $z = -2.03$ ,  $m = n = 13$  hours,  $P = 0.0212$ ; shade:  $z = -1.02$ ,  $m = 10$ ,  $n = 12$  hours, NS). Although the use of shade by each sex was similar (data from Table 6,  $z = -0.41$ ,  $P = 0.3409$ ), males spent more time in cover than females ( $z = -1.86$ ,  $P = 0.0314$ ). Males' use of cover also appears to be more sensitive to climatic variables than females: they exhibit a stronger positive correlation between cover use and monthly mean maximum temperature (males:  $r_s = +0.77$ ; females:  $r_s = +0.31$ ), and a stronger negative association between cover use and rainfall in the preceding two months (males:  $r_s = -0.62$ ; females:  $r_s = -0.32$ ).

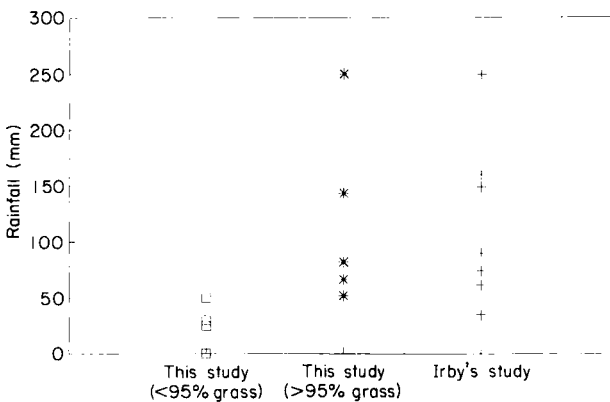
## Discussion

The data presented here quantitatively confirm Irby's (1982) suggestion that mountain reedbuck activity patterns are strongly influenced by diurnal variations in ambient temperature. Both males and females adhere to a regular cycle of elevated activity levels during the early morning and late afternoon, with a distinct resting period around midday when the animals retire into cover. Unlike lesser kudu (*Tragelaphus imberbis* Blyth) however, which spend much of this period ruminating (Mitchell, 1977), reedbuck abandoned rumination completely between 1400 h and

**Table 6.** Monthly variation in the use of cover and shade

Month	Mean max. temp. (°C)	Rainfall <sup>1</sup> (mm)	Use of cover (%)		Use of shade (%)	
			Males	Females	Males	Females
Feb 1980	—	27.1	51.7	57.0	83.8	87.8
Jan 1981	39.0	81.9	—	66.6	—	100.0
Feb 1981	36.5	0.0	52.9	56.2	93.1	94.5
Mar 1981	36.4	29.5	43.8	36.8	92.0	95.3
Apr 1981	33.3	143.4	24.6	29.1	19.2	19.3
May 1981	30.6	249.9	20.0	56.7	—	16.0
Jun 1981	31.0	239.6	26.7	13.4	—	33.3
Jan 1982	35.7	66.4	32.7	33.6	79.8	79.3
Feb 1982	30.6	51.8	32.2	44.0	69.2	81.4
Mar 1982	31.9	15.8	22.6	33.9	69.0	70.6

<sup>1</sup>Total amount of rainfall that fell in the two preceding months.



**Fig. 7.** A comparison of the amounts of rainfall within the previous two months, in relation to differences in dietary composition between Irby's (1977a) study and the present study. Data for this study are separated into months when the reedbeck's diet contained more than, and those when it contained less than, 95% grass.

1600 h. Rumination is an energy-demanding activity, with an increase in heat production at the onset of a rumination bout of between 5 and 17 J/min per kg of body weight (Webster, 1978). It appears that reedbeck may be prevented from ruminating during this period in order to remain within the upper limit of their thermoneutral zone. This is supported by the close correlation between rumination and the use of shade during the day.

The Eburru reedbeck also showed a distinctive diurnal pattern in their use of cover, which was negatively correlated with the level of activity, but positively correlated with ambient temperature. A number of authors have suggested that dependence on cover is a principal part of the reedbeck predator avoidance strategy (e.g. Jungius, 1971; Hendrichs, 1975; Howard, 1986a,b); indeed, some populations appear to completely avoid open areas (Rowe-Rowe, 1983). Reedbeck young are 'hidiers' (Lent, 1974), remaining hidden for longer than most other hiding species (Jungius, 1970). When alarmed, adults may also lie pressed down on the ground in cover until, if the predator approaches too close, they bolt and then hide again (Howard 1986b).

Although the resident populations of most large predators had been eliminated from the surrounding area (Irby, 1972), potential predators observed during the present study included cheetah (*Acinonyx jubatus* (Schreber)), leopard (*Panthera pardus* (L.)), jackals (*Canis* spp.), and striped hyena (*Hyaena hyaena* (L.)); in addition, both martial (*Polemaetus bellicosus* Daudin) and Verreaux's (*Aquila verreauxi* Lesson) eagles were observed harassing adult female reedbuck on cliff faces on separate occasions, apparently with the intention of causing them to fall. On one of these occasions, a martial eagle dived repeatedly onto a reedbuck group lying up on a cliff, and forced the reedbuck to scatter in alarm. An increase in time spent resting (and especially lying down) in response to rising temperatures towards midday, is likely to impose higher risks of predation through reduced vigilance or field of view, and animals should thus retreat into cover at this time.

During the dry season when temperatures are higher, reedbuck remain resting within cover for longer, but compensate with higher activity and feeding levels during the early morning. Males spend more time in cover than females, their cover use being more sensitive to climatic conditions. This is probably explained by the more stringent feeding requirements imposed on females by the energetic costs of reproduction (Clutton-Brock, Guinness & Albon, 1983; Clutton-Brock, Albon & Guinness, 1989; Ginsberg, 1989), causing females to continue feeding at a higher rate for longer into the wet season. Irby (1979) has demonstrated a slight birth peak for reedbuck at Gilgil from March to June.

While temperature is shown to be an important influence on diurnal patterns, seasonal activity variations are strongly related to rainfall, and we demonstrate that observed levels of activity and feeding are lower in the wet season, when forage quality and availability increase. Although increases in grass growth are related to the amount of rainfall in the previous month, the consequent rise in the proportion of grass in the diet, and the corresponding decrease in time spent feeding does not occur until another month later. This suggests that mountain reedbuck persist in selecting a proportion (up to 20.6%) of their diet from available browse items even after the peak in new grass growth, before adopting an exclusive or near-exclusive grass diet in the following month. The implication here is that they may in some way be prevented from exploiting very new grass growth. Such a delay in using high-quality grass might be a product of ruminal fill due to water retention in the coarse structural component of the plant material (cf. Van Soest, 1982). Alternatively, the high soluble carbohydrate content in immature forage may cause a decrease in rumen pH and hence reduced digestion rates (Osbourn *et al.*, 1974, cited in Van Soest, 1982). Both of these will ultimately result in intake limitation. However, the presence of a significant negative correlation between rumination frequency and rainfall in the previous month, which is coincident with peak grass growth, suggests that at least some highly digestible young grass is being ingested at this stage, reducing the need for a high rate of rumination. Thus although gut-fill or reduced digestion rates appear to explain, at least in part, the month's delay before the expected reduction in feeding time, animals may also be attempting to replace depleted fat reserves after the hardships of the dry season (for evidence of poorer body condition at the end of the dry season see Irby (1975), and Stelfox & Hudson (1986)). Higher levels of nutrient intake may also be important at this time of year as a consequence of the increased energetic requirements of gestation and lactation for females (see above). This suggestion is supported by the less distinct feeding

time reduction in response to rainfall in females. This issue clearly requires more detailed investigation.

The proportion of time spent ruminating was significantly lower in wet months than dry months, and was negatively related to the amount of rainfall in the previous month. Rates of rumination tend to increase in proportion to the intake of cell wall in the forage (Van Soest, 1982). The profusion of new growth following the onset of the rains provides a higher leaf/stem ratio, permitting active selection by reed buck of nutritious young leaves (Irby, 1984). McLeod, Kennedy & Minson (1990) have demonstrated a higher voluntary intake of leaf over stem fractions in cattle, which is related to lower proportions of large particles, greater numbers of primary chews, and lower resistance of leaves' large particles during primary mastication. These combined effects result in a 3–5 times greater efficiency of primary mastication and, in addition to decreased particle resistance to degradation during rumination, lower the necessity of a high rumination rate. Thus, as leaf quality and availability increases during the rains, we observe a decrease in the rate of rumination required to achieve maintenance (cf. Van Soest, 1982).

The inclusion of the significant levels of browse in the diet is surprising. Mountain reed buck have been classified as either roughage grazers (on the basis of their rumen morphology: Hofmann & Stewart, 1972) or as selective grazers (Jarman, 1974). Irby (1977a, 1984) analysed diet composition from rumen contents, and demonstrated preferential grazing of both certain grass species and younger, greener leaves. Although there was a rise in stem consumption late in the dry season as the leaf/stem ratio decreased, the proportion of dicots in the diet never rose above 1.1%. Irby (1984) concluded that mountain reed buck do not respond to seasonal variations in nutritive quality by switching from monocots to dicots.

In contrast, the data presented here suggest higher levels of dicot intake than in Irby's study, with a seasonal shift in the proportion of grass in the diet in response to rainfall experienced two months previously. One possible explanation for this contrast might lie in methodological differences: differential digestion rates can bias rumen fragment analysis to underestimate the proportions of highly digestible plant species and parts (Stewart, 1967; Dearden, Pegau & Hansen, 1975). Nonetheless, the technique is still the most accurate of the indirect measures available (Kessler, Kasworm & Hansen, 1981). Alternatively, as our results are based on direct observation, the possibly longer handling time of dicots relative to grasses might overestimate the browse component of the diet. However, neither source of bias is likely to produce quite such disparate proportions of browse between the two studies. One likely explanation for the observed difference is suggested by the presence of a significant positive relationship between the proportion of grasses in the diet and rainfall two months previously. Although in most years reed buck may be able to subsist entirely on monocots, the increase in browse taken during the present study might be an adaptive response to extremely low rainfall. Such a dietary shift towards dicots has been suggested to increase protein intake during the dry season in Grant's (*Gazella granti* Brooke) and Thomson's gazelles (*G. thomsoni* Günther) (Gwynne & Bell, 1968; Spinage, 1980; Stelfox & Hudson, 1986). To test this hypothesis, we compared rainfall recorded at Gilgil during Irby's study (Sept 1971–March 1972) and the present study. We first divided the present study into months in which grass constituted over 95%, and under 95%, of the diet. Then

for each study month we determined the amount of rainfall in the preceding two months (Fig. 7). In those months where grass constituted less than 95% of the diet, there had been significantly less rainfall in the preceding two months than either in months where grasses made up more than 95% of the diet or in Irby's study (Fisher's exact test, *vs* >95% months:  $P=0.014$ ; *vs* Irby's study:  $P=0.024$ ). In contrast, there was no significant difference ( $P=0.568$ , NS) between the amount of rain during Irby's study and study months when reedbuck ate more than 95% grass. This result supports our suggestion and is a cautionary reminder that stochastic climatic variability within a habitat may induce adaptive responses which are detectable only during longer term studies.

### Acknowledgments

The fieldwork in Kenya was supported by an SERC Research grant while RD was in receipt of an SERC Advanced Research Fellowship. CR is currently in receipt of an SERC postgraduate studentship. RD is grateful to the Office of the President of the Republic of Kenya for permission to carry out field research in Kenya, and to the Department of Zoology of the University of Nairobi for sponsoring RD during the study. We are also grateful to Patsy Dunbar for help in data collection, Richard Danzie for permission to work on Kekopey Ranch, and Julie Feaver for help with data analysis. Finally, we thank Louise Barrett, Nilofer Ghaffar and Bettina Grieser for their helpful comments and discussion during the preparation of this manuscript.

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