CHAPTER 5

ACTIVITY PATTERNS

Introduction

The decline in the quality and quantity of food supplies for herbivores during the prolonged dry season in southern Africa, may increase the reliance of mammalian herbivores on body reserves (Sinclair & Duncan 1972). In addition, this induces alterations in their foraging efficiencies, for example increasing food intake rates (Van Soest 1982), changing habitats and diets (Pennycuick 1975, Sinclair 1983, Hofmann 1989) or increasing overall foraging times (Owen-Smith 1982).

Foraging time is also dependent on body size (with larger herbivores devoting proportionally more of their daily activity to feeding (Demment & Van Soest 1985)), individual and species energy and nutrient requirements, the digestive tract anatomy, the amount of digestible food available, the rate at which it can be ingested (Owen-Smith 1982, Hofmann 1989) and abiotic variables such as ambient temperature and wind (Belovsky & Slade 1986). However, the extent to which mammalian herbivores, and particularly ruminants, can increase their feeding time is limited by the bulk and quality of food in the rumen. The need to grind the food (through rumination) into small enough particles to pass through the fine filtering mechanism in the omasum is constrained by the fibre content of the food (Demment & Van Soest 1985). But the rumen cannot digest indefinite amounts of poor quality food, as with high fibre diets the rumen contents can in fact become impacted, which reduces selective outflow from the rumen and digestibility (Hofmann 1973), hence reducing intake and foraging times (Owen-Smith 1982).

Adjustments in herbivore activity between seasons results in either reduced maintenance costs or increased energy and nutrient intakes. Thus, if the

allocation of time to specific behaviours, such as feeding, is considered an optimization process (Pyke, Pullian & Charnov 1977), alterations in the proportion of time spent in that activity would be expected to vary with seasonal variations in the food quality and availability. The lack of any change in activities between seasons, particularly with respect to feeding times, may indicate the animals to be 'time-limited' owing to inefficient foraging rates (Beckman & Prins 1989). The aim of this chapter is to investigate how the daily and seasonal activity patterns of gemsbok and wildebeest reflect their different abilities to survive in the harsh Kalahari environment.

RESULTS

Diurnal activity patterns

Only the seasonal activities of gemsbok were found to differ significantly (F tests: $P<0.05$) (Table 34). Gemsbok spent proportionately more time walking and involved in social behaviour in the cold-dry season, while in the hot-wet season they undertook more resting behaviour. Time spent feeding was found not to differ between seasons. Gemsbok and wildebeest differed in the proportion of time devoted to feeding, resting and social behaviours. In all seasons gemsbok feeding activity (grazing and browsing combined) was less than that found for wildebeest, while the converse existed for the resting and social behaviours. Gemsbok browsed increasingly from the hot-wet to the hot-dry season.

Diurnal patterns of feeding, resting, trekking and socializing behaviours of both species are illustrated in Figures 30 - 32. Feeding activity by gemsbok was concentrated in the early morning and late afternoon, with a smaller midday feeding session occurring in the cold-dry season. In comparison, wildebeest spent more time feeding during three diurnal feeding sessions in all seasons, with the midday session generally being the smallest one, except during the hot-wet season when it was comparable with the early morning session.

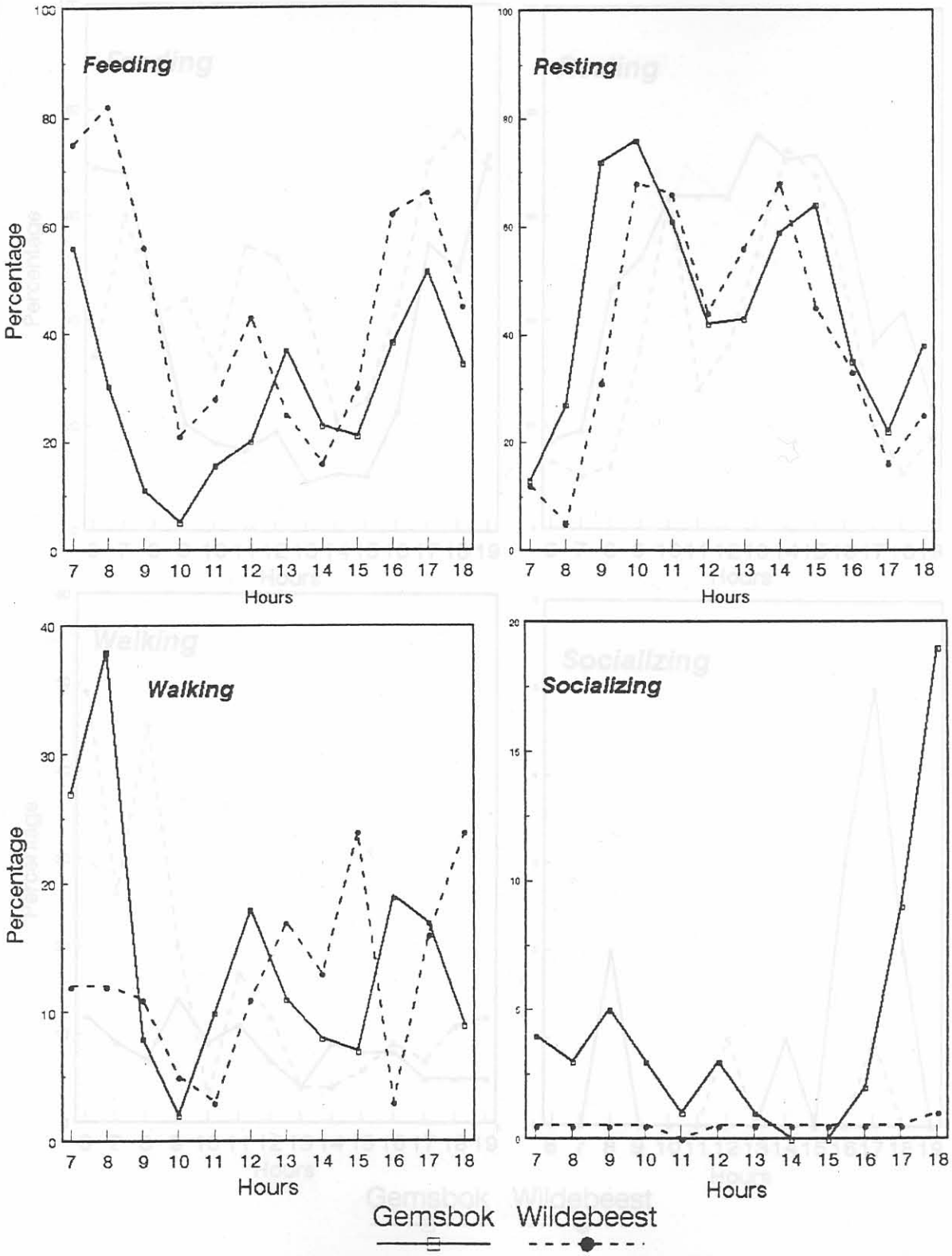

Fig. 30. Diurnal patterns of feeding, resting, walking and social activities of gemsbok and wildebeest in the cold-dry season.

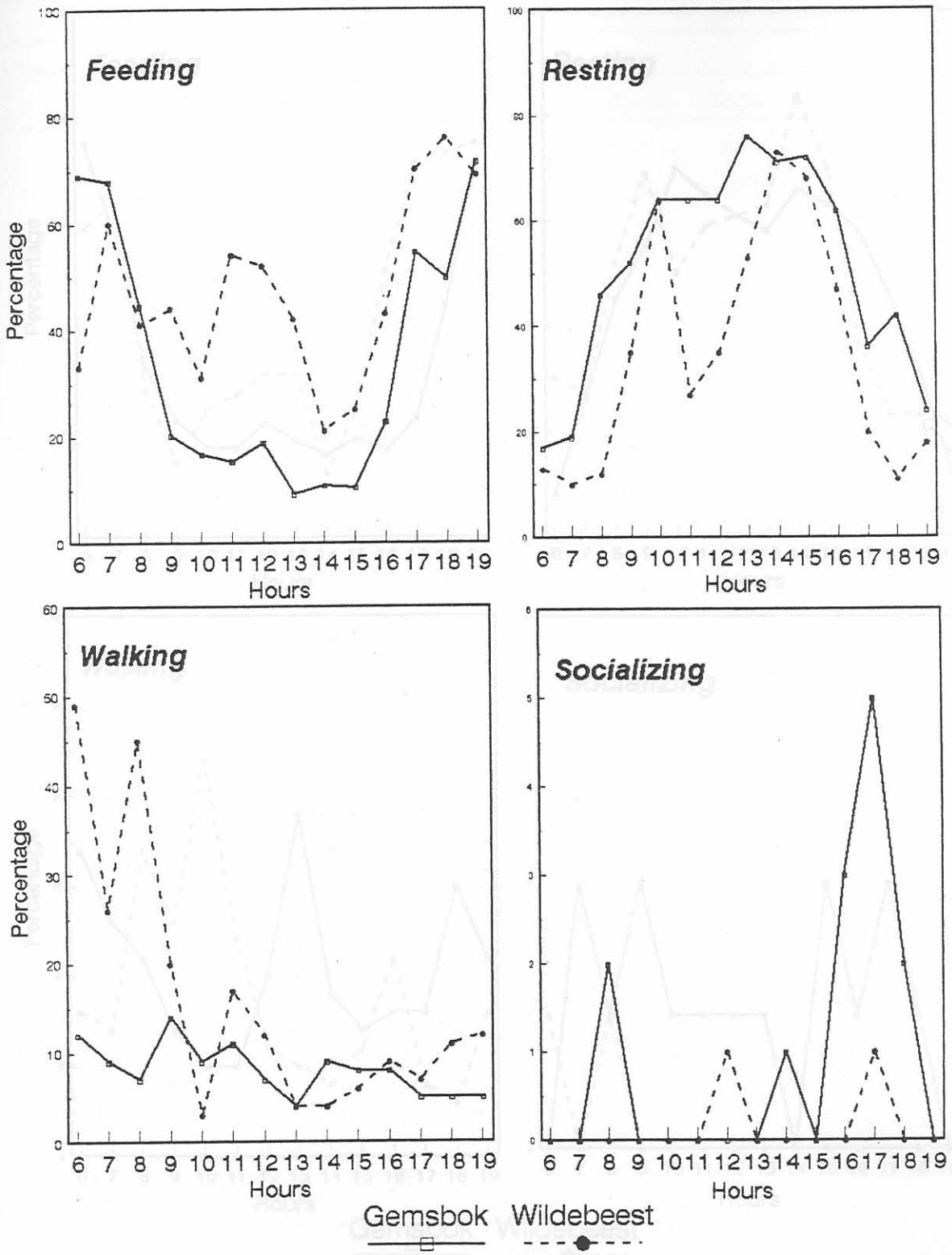

Fig. 31. Diurnal patterns of feeding, resting, walking and social activities of gemsbok and wildebeest in the hot-dry season.

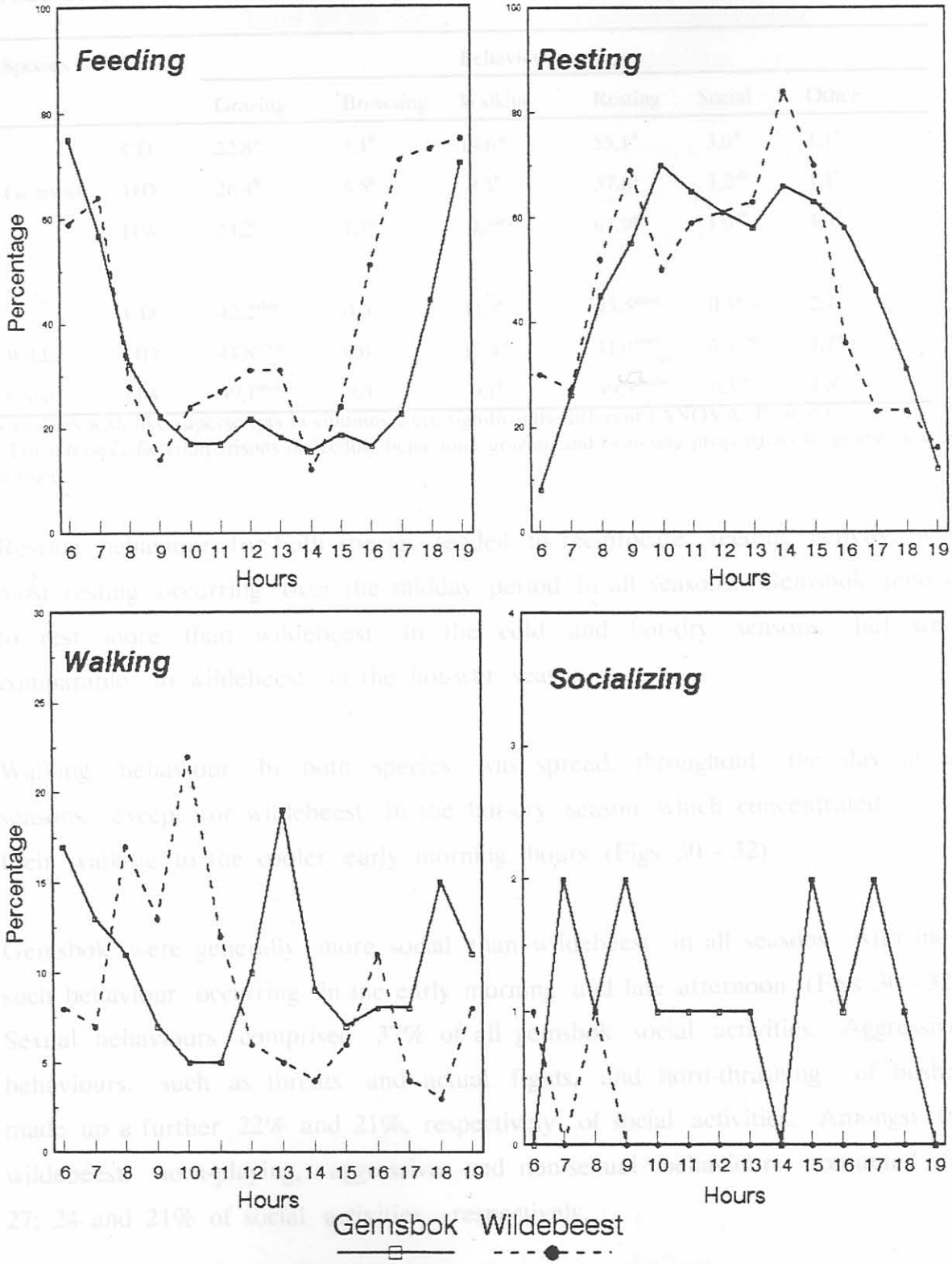

Fig. 32. Diurnal patterns of feeding, resting, walking and social activities of gemsbok and wildebeest in the hot-wet season.

Table 34. Seasonal activity budget (%) of gemsbok and wildebeest. CD=cold-dry; HD=hot-dry; HW = hot-wet. Gemsbok: 4857 scans on 9486 individuals. Wildebeest: 7837 scans on 65800 individuals.

Species	Season	Behaviours					
		Grazing	*Browsing	Walking	Resting	Social	Other
Gemsbok	CD	22.8^{a}	3.4^{b}	14.6^{a}	55.1^{a}	3.0^{a}	1.1^{a}
	HD	26.4^{b}	5.5^{b}	8.1^{b}	57.8^{b}	1.2^{ab}	1.1^{b}
	HW	23.2^{c}	1.7^{a}	9.2^{ac}	61.9^{ab}	1.0^{ab}	3.0^{c}
Wilde-beest	CD	42.2^{abcd}	0.0	11.8^{c}	43.5^{abcd}	0.1^{ac}	2.4^{d}
	HD	44.8^{abce}	0.0	12.4^{d}	41.0^{abce}	0.3^{abd}	1.7^{e}
	HW	39.7^{abd}	0.0	9.1^{e}	49.3^{abcde}	0.3^{abc}	1.8^{f}

Variables with like superscripts in columns were significantly different (ANOVA; $P<0.05$).
* For interspecific comparisons of feeding behaviour, grazing and browsing proportions by gemsbok were lumped.

Resting behaviour for both species tended to reciprocate feeding activity, with most resting occurring over the midday period in all seasons. Gemsbok tended to rest more than wildebeest in the cold and hot-dry seasons, but were comparable to wildebeest in the hot-wet season.

Walking behaviour by both species was spread throughout the day in all seasons, except for wildebeest in the hot-dry season which concentrated their walking to the cooler early morning hours (Figs 30 - 32).

Gemsbok were generally more social than wildebeest in all seasons, with most such behaviour occurring in the early morning and late afternoon (Figs 30 - 32). Sexual behaviours comprised 37% of all gemsbok social activities. Aggressive behaviours, such as threats and actual fights, and horn-thrashing of bushes made up a further 22% and 21%, respectively of social activities. Amongst the wildebeest, horn-playing, aggressive and non-sexual behaviours accounted for 27; 24 and 21% of social activities, respectively.

Relationships between activity and environmental temperature

Positive correlations were found between the proportion of individuals of both species resting, and the ambient and black-bulb temperatures (Table 35). The remaining activities grazing, browsing and walking were found to occur independently of temperature in gemsbok, while wildebeest grazing activity was found to correlate negatively with both temperature variables. Wildebeest walking activity also appeared to be undertaken independently of environmental temperature.

Table 35. Pearson's correlation coefficients (r) between the percentage occurrence of different activities of gemsbok and wildebeest, and ambient and black-bulb temperatures (°C).

Species	Activity	Correlation Coefficient (r)		n
		Ambient Temp. (T_a)	Black-Bulb Temp. (T_{bb})	
Gemsbok	graze	-0.01	-0.06	204
	browse	-0.02	-0.12	85
	rest	0.26*	0.28**	234
	walk	-0.14	-0.10	148
Wildebeest	graze	-0.23**	-0.29**	253
	rest	0.24**	0.30**	260
	walk	-0.13	-0.10	237

* $0.05 > P > 0.01$; ** $0.01 > P > 0.001$.

Use of tree shade

Wildebeest showed a pattern of increasing shade use from the cold-dry to hot-wet seasons, while the gemsbok showed an appreciable decline in the proportion of shade use in the hot-dry period (Table 36). Gemsbok were however, found to make greater ($\chi^2 = 6.2$; $df = 2$; $P < 0.05$) use of shade than wildebeest throughout the year. Both species use of shade increased positively

with increasing temperature, particularly that measured with a black-bulb thermometer (Table 37).

Table 36. Seasonal use (%) of shade per hour by gemsbok and wildebeest. CD = cold-dry; HD = hot-dry; HW = hot-wet.

Species	Season			Test
	CD	HD	HW	
Gemsbok	41.8	30.7	39.6	$\chi^2 = 6.2$; df = 2;
Wildebeest	25.5	30.5	36.8	$P < 0.05$

From Figure 33 it is evident that the use of shade by both species in the cold-dry season was not only limited but restricted predominantly to resting and social behaviours. In the hot-dry season, gemsbok restricted almost all their resting and socializing to within the shade (Fig. 33a), while, although the proportion of resting wildebeest using the shade increased, the majority of animals still rested in the sun (Fig. 33b). In the hot-wet season, the gemsbok showed the same pattern of shade use as found in the hot-dry period, while the proportion of resting wildebeest using shade increased above those in the sun. The greater amount of feeding by gemsbok in the shade than wildebeest, may result from those individuals browsing.

Table 37. Pearson's correlation coefficients (r) between the percentage shade use (per hour) of gemsbok and wildebeest, and ambient and black-bulb temperatures (°C) in the three seasons. CD = cold = dry; HD = hot-dry and HW = hot-wet.

Species	Season	Correlation Coefficient (r)		n
		Ambient Temp. (T_a)	Black-bulb Temp. (T_{bb})	
GEMSBOK	CD	0.94**	0.95**	11
	HD	0.73**	0.72**	12
	HW	0.58*	0.63*	12
WILDEBEEST	CD	0.66*	0.65*	11
	HD	0.64*	0.63*	12
	HW	0.46	0.69**	12

* $0.05 > P > 0.01$; ** $0.01 > P > 0.001$.

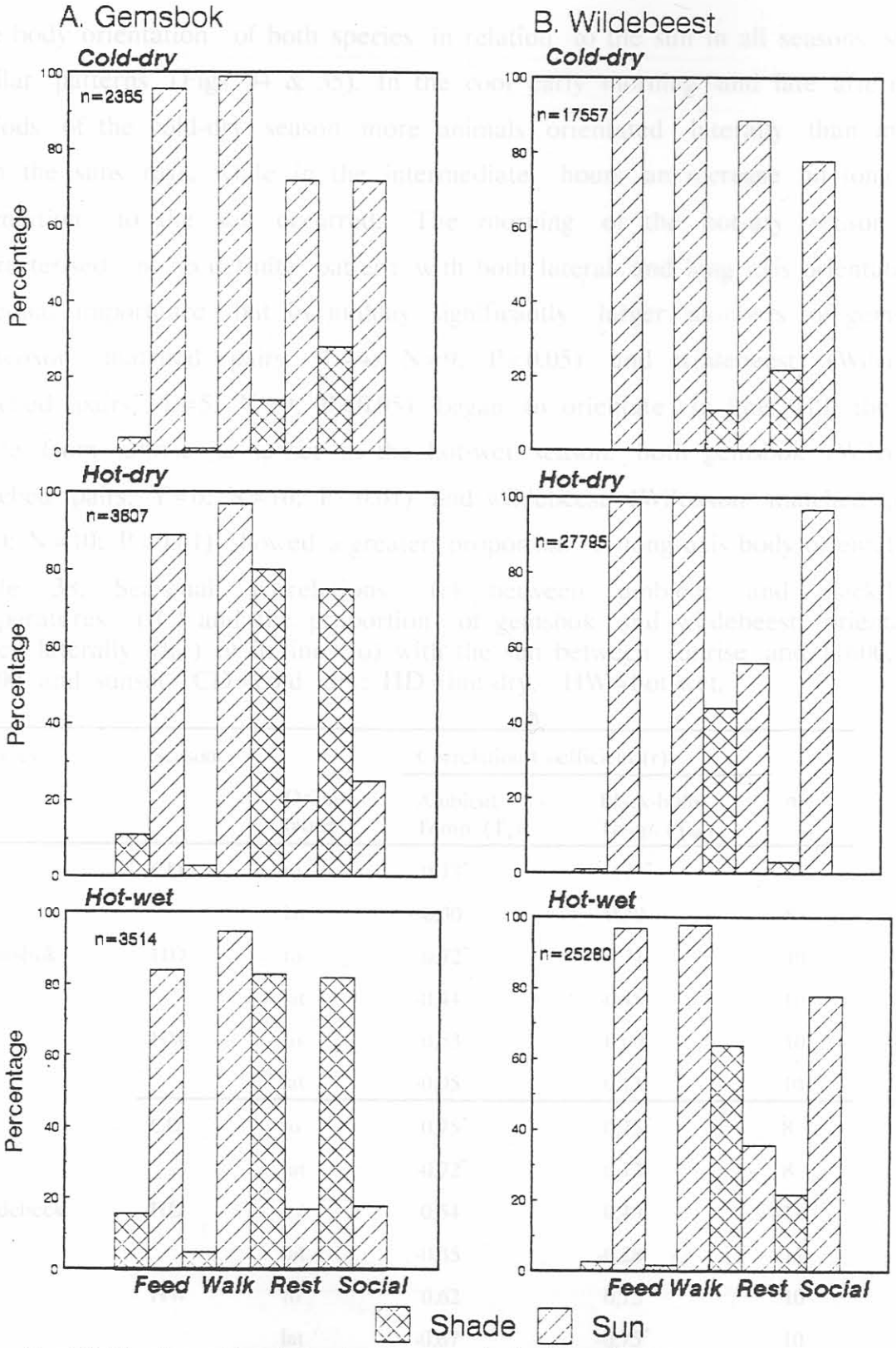

Fig. 33. Shade-seeking behaviour by gemsbok (A) and wildebeest (B) in the three seasons.

Body orientation to the sun and wind

The body orientation of both species in relation to the sun in all seasons shows similar patterns (Figs 34 & 35). In the cool early morning and late afternoon periods of the cold-dry season more animals orientated laterally than in line with the suns rays, while in the intermediate hours an increase in long axis orientation to the sun occurred. The morning of the hot-dry season was characterised by no definite pattern with both lateral and long axis orientations of equal importance but by midday significantly larger numbers of gemsbok (Wilcoxon matched pairs: $T=4$; $N=9$; $P<0.05$) and wildebeest (Wilcoxon matched pairs: $T=5$; $N=9$; $P<0.05$) began to orientate in line with the sun. While from sunrise to sunset in the hot-wet season, both gemsbok (Wilcoxon matched pairs: $T=0$; $N=10$; $P<0.01$) and wildebeest (Wilcoxon matched pairs: $T=0$; $N=10$; $P<0.01$) showed a greater proportion of long axis body orientation.

Table 38. Seasonal correlations (r) between ambient and black-body temperatures (°C) and the proportion of gemsbok and wildebeest orientated either laterally (lat) or in line (to) with the sun between sunrise and 11h00, and 14h00 and sunset. CD=cold dry; HD=hot-dry; HW=hot-wet.

Species	Season	Orientation	Correlation Coefficient (r) Ambient Temp. (T_a)	Black-bulb Temp. (T_{bb})	n
Gemsbok	CD	to	0.73*	0.73*	8
		lat	-0.30	-0.30	8
	HD	to	0.72*	0.71*	10
		lat	-0.44	-0.45	10
	HW	to	0.53	0.69*	10
		lat	-0.05	-0.13	10
Wildebeest	CD	to	0.75*	0.75*	8
		lat	-0.72*	-0.72*	8
	HD	to	0.54	0.49	11
		lat	-0.35	-0.28	11
	HW	to	0.62	0.75*	10
		lat	-0.67*	-0.75*	10

* $0.05>P>0.01$.

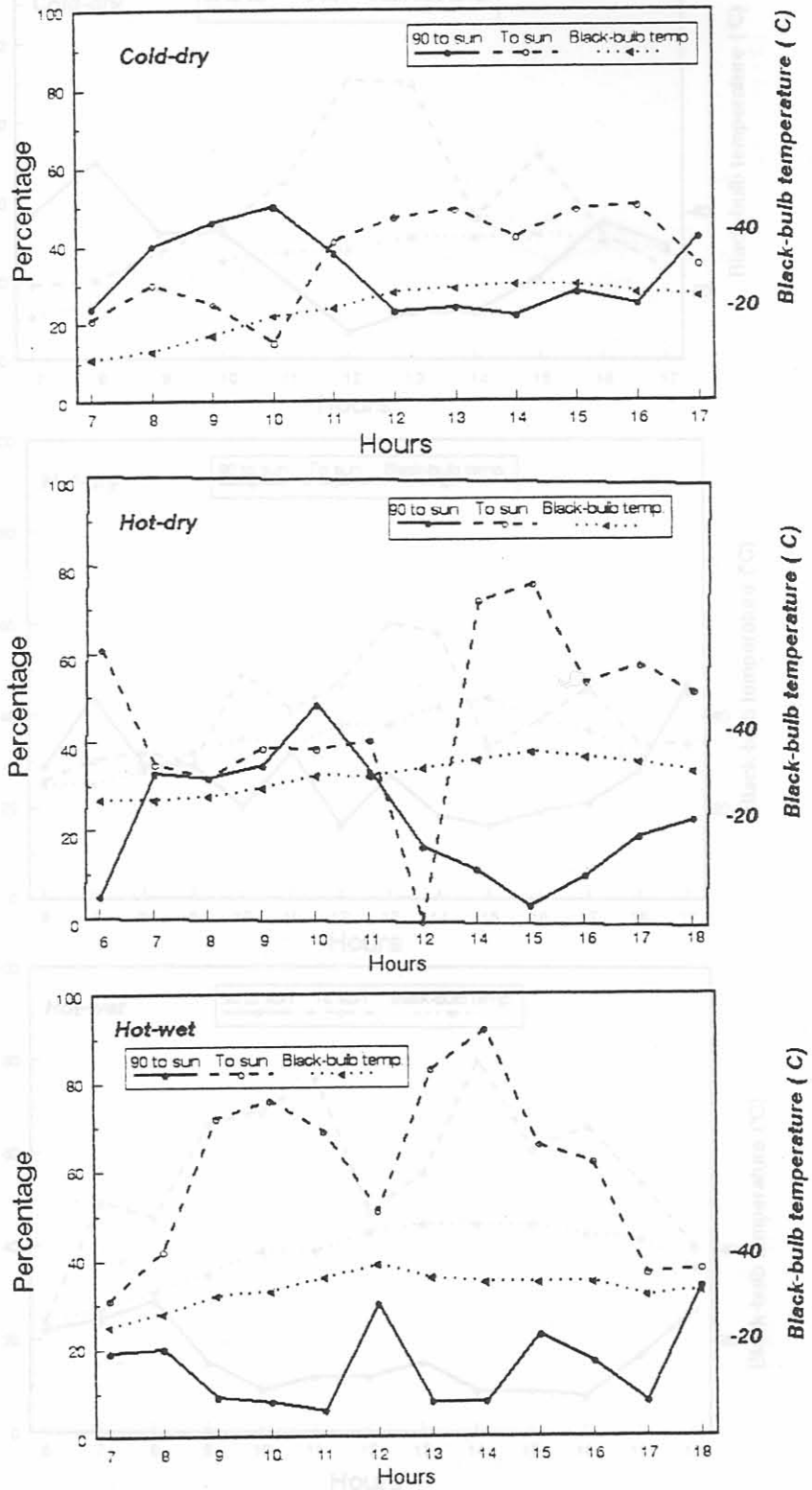

Fig. 34. Orientation of gemsbok to the sun in the three seasons.

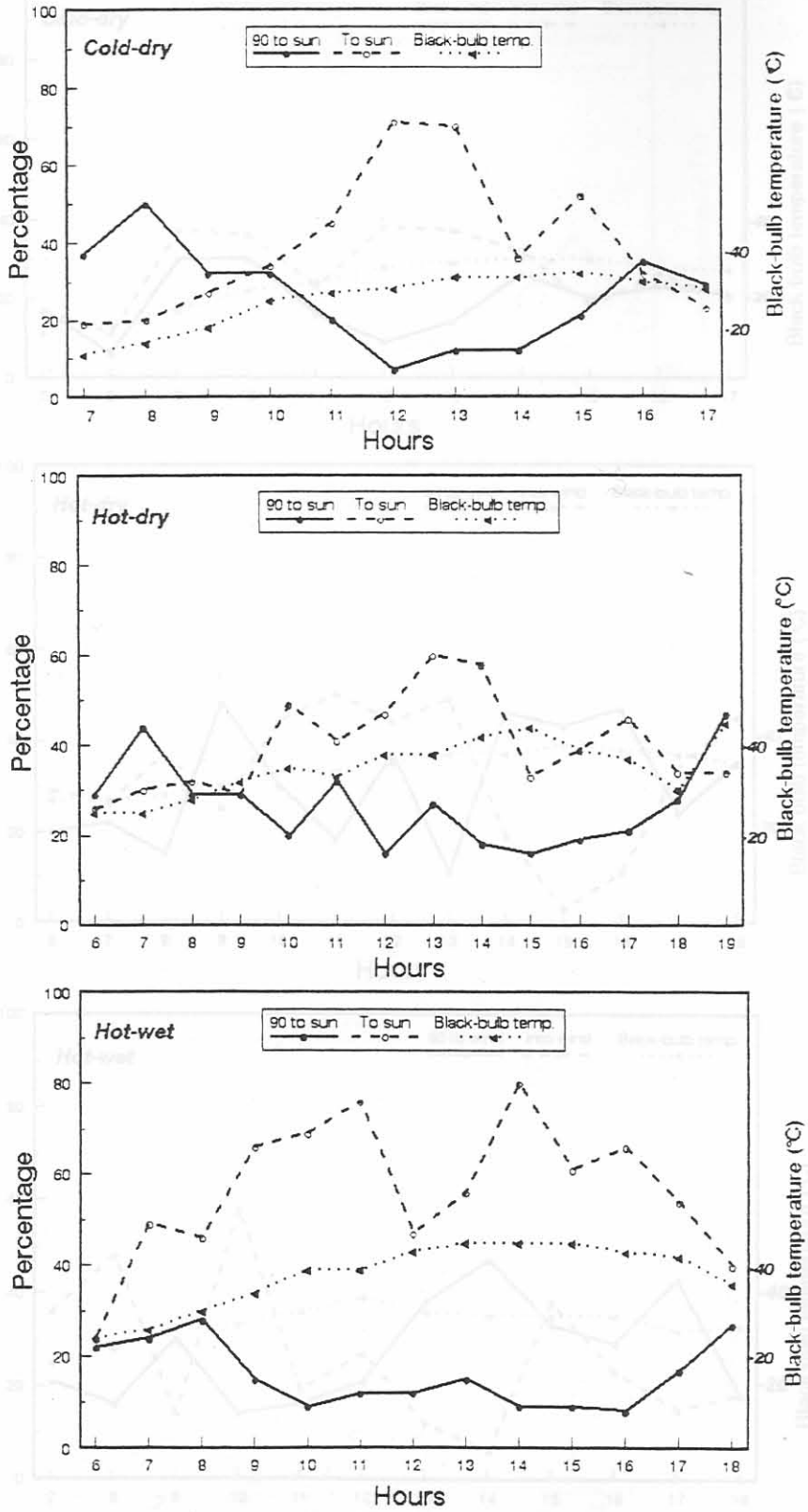

Fig. 35. Orientation of wildebeest to the sun in the three seasons.

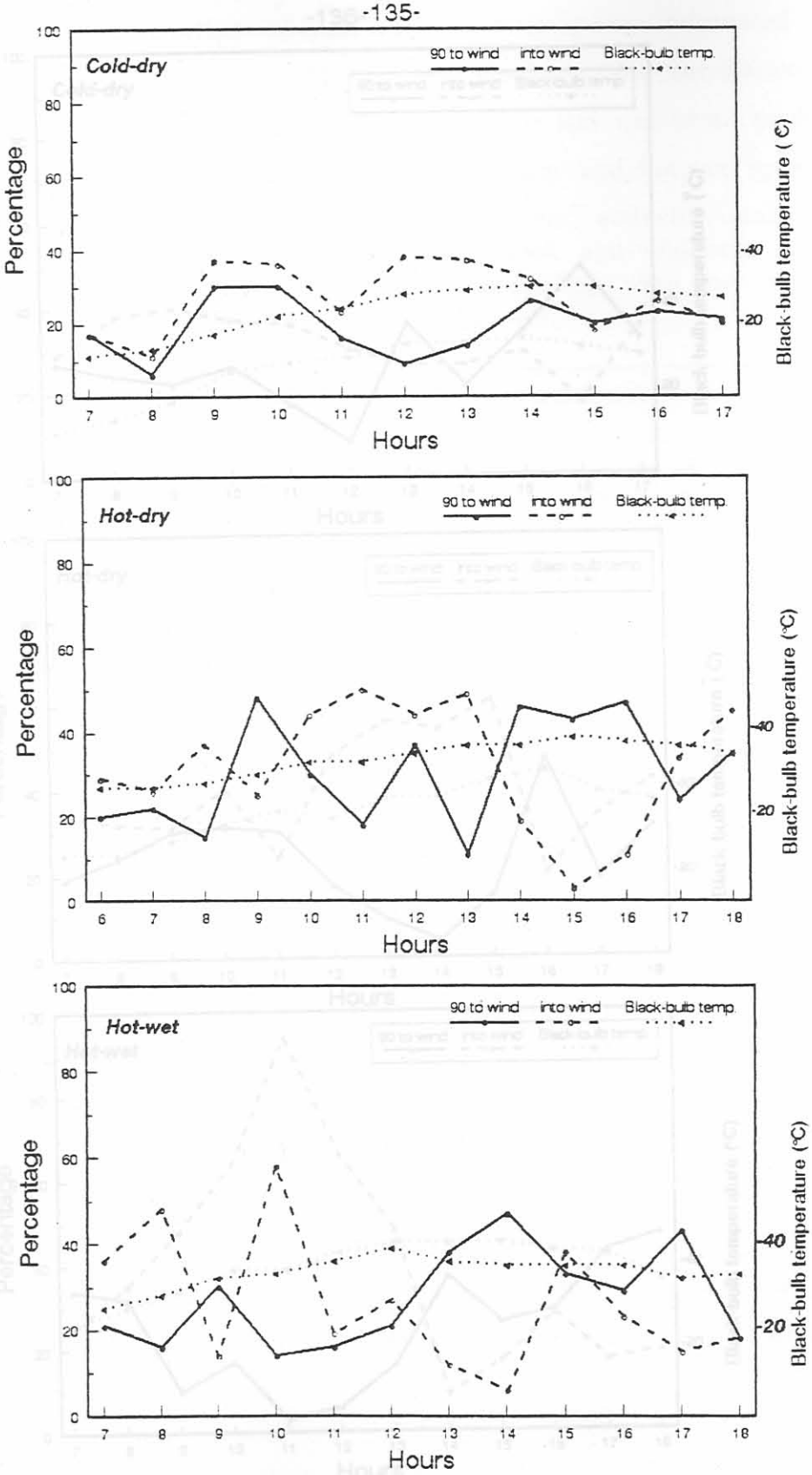

Fig. 36. Orientation of gemsbok to the prevailing wind direction in each season.

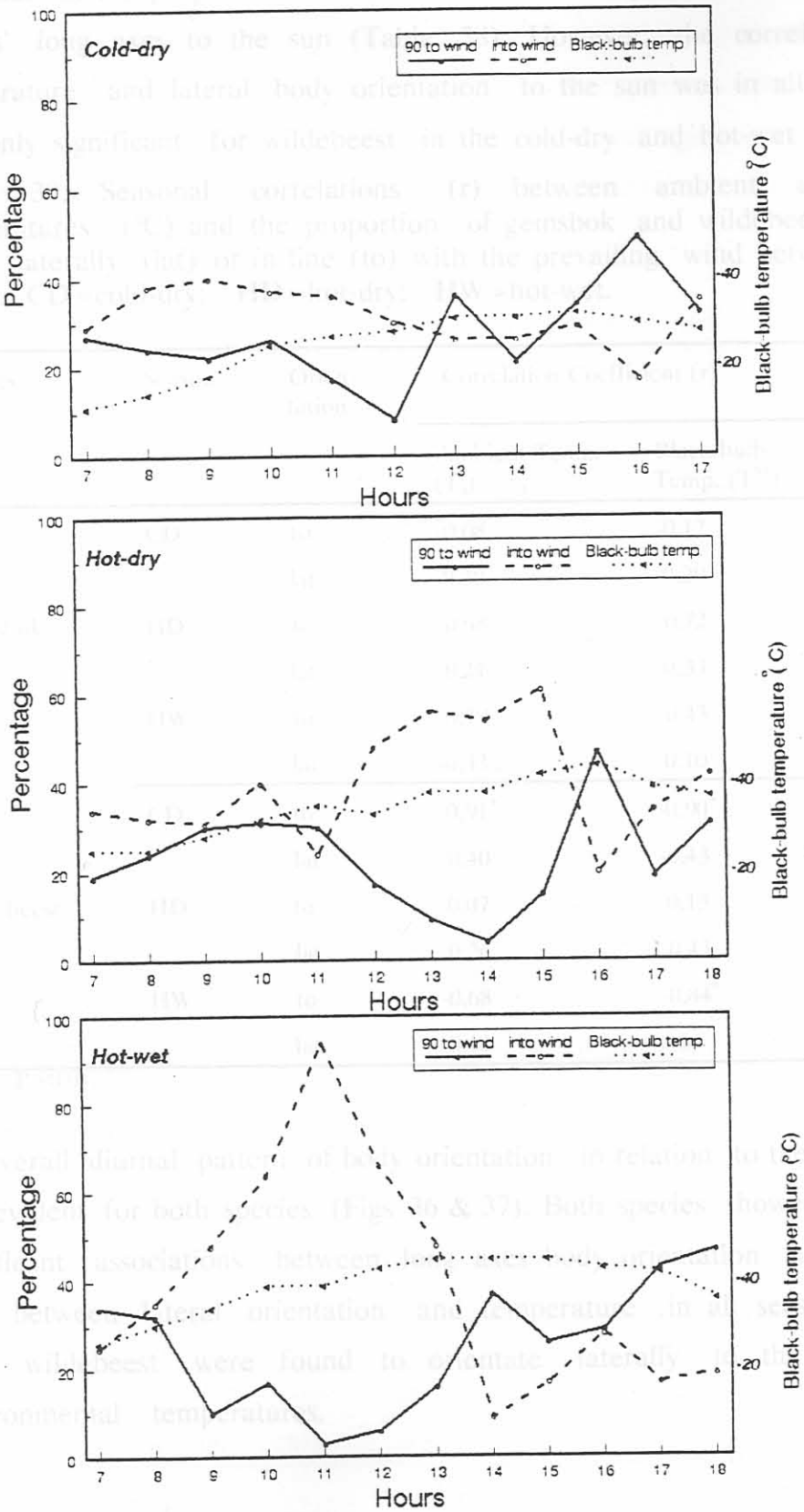

Fig. 37. Orientation of wildebeest to the prevailing wind direction each season.

Increasing ambient and black-bulb temperatures resulted in strong positive increases in the proportion of individuals of both species orientated with their bodies' long axes to the sun (Table 38). However, the correlation between temperature and lateral body orientation to the sun was in all cases negative and only significant for wildebeest in the cold-dry and hot-wet seasons.

Table 39. Seasonal correlations (r) between ambient and black-bulb temperatures (°C) and the proportion of gemsbok and wildebeest orientated either laterally (lat) or in line (to) with the prevailing wind between 10h00 and 15h00. CD = cold-dry; HD = hot-dry; HW = hot-wet.

Species	Season	Orientation	Correlation Coefficient (r)		
			Ambient Temp. (T_a)	Black-bulb Temp. (T^{22})	n
Gemsbok	CD	to	-0.08	-0.12	6
		lat	-0.30	-0.29	6
	HD	to	-0.68	-0.72	6
		lat	0.21	0.33	6
	HW	to	-0.19	-0.43	6
		lat	-0.33	-0.10	6
Wildebeest	CD	to	-0.91*	-0.90*	6
		lat	0.40	-0.43	6
	HD	to	0.07	-0.13	6
		lat	0.26	0.43	6
	HW	to	-0.68	-0.84*	6
		lat	0.46	0.64	6

* 0.05 > P > 0.01.

No overall diurnal pattern of body orientation in relation to the prevailing wind was evident for both species (Figs 36 & 37). Both species showed more frequent significant associations between long axes body orientation and temperature. than between lateral orientation and temperature in all seasons (Table 39). Only wildebeest were found to orientate laterally to the wind at lower environmental temperatures.

Nocturnal activity

No seasonal, nor interspecific differences ($X^2=0.62$; df=2; P>0.05) between the proportions of time spent active in the nocturnal period were detected (Table 40). Furthermore, no differences between the percentage nocturnal and diurnal activity for both gemsbok ($X^2=0.07$; df=2; P>0.05) and wildebeest ($X^2=0.65$; df=2; P>0.05) were found.

Table 40. Percentage of nocturnal period spent active by radio-collared gemsbok and wildebeest. CD=cold-dry; HD=hot-dry; HW=hot-wet; n=number of months sampled.

Species	Seasons					
	CD	n	HD	n	HW	n
Gemsbok	58.5	7	61.3	3	55.9	2
Wildebeest	56.7	7	66.0	3	73.1	2

Nearest neighbour distances

Nearest neighbour distances within foraging groups of gemsbok were found to be significantly greater (F=36.1; df=387 & 2; P<0.01) in the hot-dry season in comparison to the other seasons, while no seasonal differences were detected for wildebeest (Table 41). Significant decreases in the nearest neighbour distances were found with an increase in gemsbok (r=-0.23; n=391; P=0.0001) and wildebeest (r=-0.06; n=2934; P=0.04;) group sizes.

Table 41. Mean (±SD) nearest neighbour distances (m) of gemsbok and wildebeest by season. CD=cold-dry; HD=hot-dry; HW=hot-wet;

Species	Seasons					
	CD		HD		HW	
	Mean	n	Mean	n	Mean	n
Gemsbok	17.3±23.6	165	43.9±65.7	98	22.4±19.4	128
Wildebeest	7.8±14.0	813	6.8±14.6	663	8.4±12.8	753

Although, the nearest neighbour distances for gemsbok differed significantly within different habitat variables such as: habitat ($F=4.32$; $df=369$ & 2; $P=0.014$), grass density ($F=3.21$; $df=369$ & 1; $P=0.02$), ephemeral dicot density ($F=4.00$; $df=369$ & 1; $P=0.005$), browse condition ($F=2.63$; $df=369$ & 3; $P=0.05$) and browse density ($F=3.50$; $df=369$ & 2; $P=0.03$), the only significant correlations (which in all cases were negative) detected between nearest neighbour distances were with grass length, browse condition and browse density (Table 42).

Table 42. Pearson's correlations coefficients (r) of ranked nearest neighbour distances and habitat variables for gemsbok (n=391) and wildebeest (n=2510).

Species	Habitat Variables							
	CN	GC	GD	GL	AC	AD	BC	BD
Gemsbok	0.01	0.03	0.03	-0.16**	-0.18**	-0.22**	-0.03	-0.04
Wildebeest	0.04	-0.01	0.09**	0.04	0.11**	-0.09**	0.01	-0.05

* $0.05>P>0.01$; ** $0.01>P>0.001$.
CN = general condition; GC = grass condition; GD = grass density; GL = grass length; AC = ephemeral dicot condition; AD = ephemeral dicot density; BC = browse condition; BD = browse density.

The wildebeest nearest neighbour distances were also found to differ significantly between habitats ($F=14.7$; $df=1565$ & 3; $P=0.0001$), grass condition ($F=8.43$; $df=1565$ & 3; $P=0.0001$), grass density ($F=8.51$; $df=565$ & 3; $P=0.004$), ephemeral dicot density ($F=8.67$; $df=1565$ & 3; $P=0.003$) and browse density ($F=7.09$; $df=1565$ & 3; $P=0.001$). But unlike the gemsbok, positive correlations were detected between nearest neighbour distances, and grass length and ephemeral dicot conditions (Table 42).

Diurnal and nocturnal foraging distances

Although no significant seasonal differences were found between the distances moved by foraging gemsbok ($F=2.05$; $df=2$ & 23; $P<0.05$) and wildebeest ($F=1.95$; $df=2$ & 20; $P<0.05$), the mean annual distances of wildebeest were greater than those of gemsbok ($t=3.31$; $df=19$; $P<0.01$) (Table 43). Wildebeest

Table 43. Mean (±SD) diurnal and nocturnal foraging distances (km) of gemsbok and wildebeest in the three seasons. CD = cold-dry. HD = hot-dry. HW = hot-wet. Sample size in parentheses.

Species	Diurnal				Nocturnal
	CD	HD	HW	Mean	
Gemsbok	7.2 ± 4.2[a] (6)	4.9 ± 2.8[a] (12)	3.9 ± 2.3[a] (8)	5.1 ± 3.2[a] (26)	3.8 ± 2.6[a] (14)
Wildebeest	6.8 ± 7.2[b] (7)	10.2 ± 4.6[a] (9)	5.2 ± 3.0[b] (7)	7.7 ± 5.4[a] (23)	4.7 ± 2.9[b] (16)

Variables with like superscripts in columns were significantly ($P<0.05$) different using the Student's-t test.

were also found to move more during the day than at night ($t=2.01$; $df=37$; $P<0.05$).

Discussion

Comparison with other studies revealed that the annual mean 42.2 % of the diurnal period devoted to feeding by Kalahari wildebeest was greater than the 25% and 33% found in a population near Pretoria, Transvaal (Ben-Shahar & Fairall 1987) and Etosha National Park (Berry, Siegfried & Crowe 1982) respectively, but was well below the 73% found in the lake Manyara National Park, Tanzania (Beckman & Prins 1989). Beckman & Prins (1989) suggested that the high proportion of diurnal feeding and virtual lack of nocturnal feeding in the Manyara population did not result from a food shortage but rather in response to increased predation at night. Considering their diurnal result in relation to 24h, results in 36.6% of the day being allotted to feeding, which falls in line with that found in the Pretoria and Etosha populations but below that found in the Kalahari. In fact, the estimated total feeding activity of 47% per 24h for the Kalahari population (calculated from the sum of the diurnal feeding proportion and total nocturnal activity (minus 14% for walking, social and other behaviours, assuming similar proportions to the diurnal period)) is 11% above the feeding time predicted from body mass, and corresponds with actual feeding times found for kudu and zebra (Owen-Smith 1988). This suggests a possible

nutrient deficiency for wildebeest in the southern Kalahari, the south-western limit of their range, and an area that they periodically visited as migrants (Mills & Retief 1984b).

On the other hand, gemsbok in the southern Kalahari devoted a much smaller 27.7% of their diurnal period to feeding than the wildebeest, far below the 50.7% found for gemsbok in the Hester Malan Nature Reserve, Namaqualand (Dieckmann 1980). Total feeding time over 24h (similarly calculated as that of the wildebeest above) averaged 37%, and was 88% of that predicted from body mass (Owen-Smith 1988). The high diurnal feeding time of Namaqualand gemsbok probably resulted from the population being confined to atypical habitat, that was only irregularly used by past free-ranging populations, a similar situation to the wildebeest population studied in the KGNP.

The increase in diurnal feeding activity in response to reduced food quality and quantity in the hot-dry season occurred in both species, and appeared to have increased at the expense of walking in gemsbok and resting in wildebeest. During the hot-dry season gemsbok made greater use of browse to supplement their protein intake, much like the fringe-eared oryx in Kenya (Field 1975). This is facilitated by their relatively smaller mouths and more mobile lips than wildebeest (see Chapter 3). Furthermore, the consumption of poorer quality food in both species would have required increased rumination times, which may infringe upon foraging time (Green & Bear 1990). Ruminants normally ruminate while resting, which might explain the increase in gemsbok resting during the hot-dry period. However, the wildebeest did not show the same pattern and did not appear to increase resting during the nocturnal period which suggests that the wildebeest foraging time may have been time-limited during the hot-dry season. The difficulties in maintaining sufficient intake and quality during this period was further reflected in the decline in body conditions of both species (see Chapter 7).

In addition to the supply and quality of food supplies influencing animal behaviour, other factors such as environmental temperatures, solar radiation, wind and availability of drinking water, play an important role especially in arid environments (Finch 1972, Lewis 1977, Hofmeyr 1985). The degree to which behaviour responds to these factors depends upon the morphological and physiological adaptations of the species concerned (Louw & Seely 1982). Comparative physiological studies on oryx and wildebeest have established that the former species is particularly well adapted to surviving in arid environments (Taylor 1968, Taylor 1970, Hofmeyr 1981). The oryx has: adaptive heterothermic capabilities that allow their body temperatures to fluctuate greatly; a carotid rete to cool the brain; controllable sweat glands; plus a relatively thick, light coloured pelage with high reflectance. While the wildebeest differs in having a more limited adaptive heterothermic capability, no sweat glands and a dark pelage with low reflectance. One would therefore expect wildebeest, being less well adapted to hot semi-arid environments as gemsbok, to make extensive use of shade to escape the stresses of high ambient temperatures and solar radiation. However, they showed significantly less use of shade than gemsbok in all seasons which may be an artifact induced by the need to graze for longer periods owing to an inadequate food supply, and/or the available drinking water may have enabled them to easily dissipate the heat load resulting from feeding for longer periods of the day. Within the more mesic central Transvaal, wildebeest were found to respond more readily to heat stress by using shade more often than red hartebeest which associate more with open arid grass plains (Ben-Shahar & Fairall 1987). This appears to further substantiate the reasoning that the permanent wildebeest population in the southern Kalahari were in suboptimal conditions with respect to their food supply, but can maintain their presence because of an optimal water supply. Were this not the case, they would adopt a migratory pattern in search of a more abundant, better quality food supply.

Body orientation in relation to the sun and wind, are also important behaviours reducing heat stress (Louw & Seely 1982). Gemsbok and wildebeest both

showed strong positive correlations between long-axis body orientation in relation to the sun rays and ambient temperatures, as also noted for wildebeest in Etosha (Berry, Siegfried & Crowe 1982). The greater preponderance of this orientation by both species in the hot-wet in comparison to the hot-dry season, probably arises from the higher relative humidity in the former season and hence less effective evaporative cooling mechanisms of sweating and panting. While at low ambient temperatures, the wildebeests' apparent greater use of lateral orientation to the sun probably arises from their black pelage and higher associated absorbance which would reduce energy requirements for maintaining a constant body temperature in cold periods (Hofmeyr 1985).

The importance of wind in thermoregulatory behaviour was less apparent with wildebeest appearing to avoid long axis orientations to the wind at higher temperatures in an attempt to maximize body heat off-loading through convective cooling. But the fact that the wildebeest appeared to make greater use of the wind than gemsbok may stem from their overall greater diurnal activity, associated higher heat loads, as well as the disadvantages of a dark pelage and less efficient adaptive heterothermia.

The thermal problems encountered during the diurnal period, particularly in the hot seasons, may account for the increased nocturnal activity and hence the relatively low day:night foraging ratios of 0,62 and 0,81 for gemsbok and wildebeest respectively, in comparison to that predicted from body mass (Owen-Smith 1988). Belovsky (1986) noted how aspect use by bison (Bison bison) in a prairie environment played an important role in thermoregulation and in activity times. Foraging in the cooler nights in the Kalahari, would be advantageous with respect to conserving body water and energy but disadvantageous with respect to possible greater exposure to predation (Beckman & Prins 1989). The lower day:night foraging ratios for the two species may have arise from the method used in determining nocturnal activity in this study through monitoring pitch modulation of the transmitter. However, limited (four nights of observations between August 1988 and February 1989) nocturnal

activity recorded for one wildebeest and two gemsbok bulls with radio-transmitters fitted with trip switches that pulsed at different rates when the head was lowered more than 45° below the horizontal (similar to that used by Priddel (1986) for kangaroos) revealed that wildebeest and gemsbok bulls were feeding (assumed to be in the head down position) 59% and 41% of the nocturnal period (Knight personal observations). These proportions compared favourably with mean nocturnal feeding activities (calculated from the total nocturnal activity minus the sum of non-feeding diurnal activity proportions, assuming that similar proportions of these activities occurred at night) of 53% and 45% for wildebeest and gemsbok, respectively. Furthermore, given that female ungulates are generally more active than the males (Owen-Smith 1982), would mean that mixed groups of gemsbok and wildebeest tracked at night would have even higher nocturnal activity levels. In Etosha, the nocturnal feeding activity of wildebeest averaged 35% of the night, similar to the diurnal 34% (Berry et al. 1982). It therefore appears that both species are more active at night, probably feeding more than during the day, even though both tended to cover less ground in the night.

The decline in nearest-neighbour distances with increasing group sizes in both gemsbok and wildebeest have been noted in other ungulates and are suggested to arise from a greater ease in foraging away from group members in smaller groups (Clutton-Brock, Albon & Guiness 1982, La Gory 1986). However, other factors such as habitat, food quality and dispersion, visibility, length of feeding time and different species requirements (Lewis 1978, Jarman 1974, Pulliam & Caraco 1984) may account for the gemsbok and wildebeests' nearest neighbour distances correlating with different habitat variables, thus obscuring the possible underlying proximate and ultimate causes of grouping characteristics.

In conclusion, it appears from the activity data that wildebeest in the southern Kalahari are possibly nutrient stressed, as they forage for longer periods than gemsbok. The longer diurnal foraging sessions of wildebeest that exposes them to more dehydrating sun and heat may be facilitated by the availability of

drinking water. On the other hand, gemsbok appear to emphasise inactivity within the shade during the day to avoid heat stress, and more nocturnal feeding to possibly reduce energy and water loss.