CHAPTER 6. BEHAVIOURAL ECOLOGY

6.1. Introduction

Giraffe occupy a wide range of environments across the African continent. However, the Namib Desert is at their ecological limit. The northern Namib Desert is characterised by extreme climatic conditions, including highly variable and patchy rainfall (<50 mm per annum) and a seasonal temperature range from 0°C to over 40°C (Seely, 1978; Scheepers, 1992). While rainfall is highly variable, precipitation in the form of fog is as much as three times more reliable and is an invaluable water source for flora and fauna (Seely, 1978; 1987). Within the Namib Desert and throughout southern Africa, the behavioural ecology and social organisation of resident ungulates has been linked closely with precipitation and, consequently, with forage quality and quantity (e.g. Underwood, 1982).

The physical challenges of an arid environment, particularly during summer, are characterised by extreme temperatures, while the scarcity or absence of water offers little opportunity for amelioration of these conditions. Smaller mammals in arid areas seek refuge underground during the hottest periods of the day and feed at night when ambient temperatures are lowest (e.g. Skinner & Smithers, 1990). Furthermore, many species have physiological adaptations, such as elaborated renal systems, which aid in heat regulation and water conservation (e.g. Cloete & Kok, 1986). Large mammals in arid areas do not have the same ability to seek out daytime refuges due to their size, but they do show many behavioural responses that aid their long-term survival. One of these is to increase energy consuming activities, such as walking and feeding, during the cooler periods of the day when water loss will be lower, while undertaking energy conserving activities, such as resting, during the hottest periods of the day (Lewis, 1975; Mitchell, 1977). Other activities, such as facing away from the sun, help to reduce heat absorption. In the central Namib, for example, Hartmann's mountain zebra orient their bodies away from the sun while resting or feeding at midday (light to dark ratio 3:1) as opposed to standing broadside at other times (light to dark ratio of the exposed body surface of 1:3) (Joubert, 1974).

Many mammals are able to regulate the rate of heat flow through 'thermal windows', e.g. sparsely haired or naked areas, such as the groin, scrotum and mammary glands. They are also able to dump excess heat by convection while lying on shaded ground, as the relatively cool ground allows for conductive heat flow between the ground and the animal (Schmidt-Nielsen, 1964; Joubert, 1974). The renal efficiency of larger mammals in arid environments is usually less than that of smaller mammals (e.g. Cloete & Kok, 1986), although water loss in faeces is greatly reduced in wild animals in comparison to ill-adapted domestic species such as cattle and sheep (Schmidt-Nielsen, 1964; Joubert, 1974). Across their range, giraffe have been reported to combine both physiological and behavioural adaptations to exploit different environments (Leuthold & Leuthold, 1978; Langman *et al.*, 1979 & 1982; Dagg & Foster, 1982; Pellew, 1984a; Langman, 1982). Examples of these adaptations include biphasic activity behaviour and nasal temporal heat exchange. Investigation of physiological adaptations in giraffe was beyond the scope of this thesis.

6.1.2. Aims

Despite much published work on giraffe behaviour (Innis, 1958; Foster & Dagg, 1972; Leuthold & Leuthold, 1978; Pellew, 1984a; du Toit, 1990a; Skinner & Smithers, 1990; Estes, 1995), investigation of the behaviour of desert-dwelling giraffe in Namibia remains very limited (Scheepers, 1992; Fennessy *et al.*, 2003). The studies reported in this chapter are the first to document the activity budgets of the giraffe of the northern Namib Desert, or of the Namibian giraffe population as a whole. The specific aims were to:

- categorise giraffe behaviours;
- describe overall activity budgets for these behaviours;
- test whether activity budgets vary in relation to ambient temperature;
- compare activity budgets between seasons and between different components of the giraffe population; and
- study flight behaviour and the possible effects of tourist activities.

6.2. Methods and materials

6.2.1. Activity budgets

Giraffe were observed predominantly by vehicle, although sometimes on foot, between sunrise and sunset over a two year period (2002 and 2003). Although the study focussed on the riparian woodlands, giraffe were observed also in the plains, dunes, floodplains and some mountain areas. Observations of behaviour were made in conjunction with the population structure component of the study (see Chapter 4).

Adapting methods used by Norton (1981) and Cloete & Kok (1986), observations of giraffe activity were recorded every minute by scan sampling. By scanning individuals as well as large groups, I endeavoured to obtain a detailed, yet broad, overview of giraffe activity budgets under a range of herd structures. The high intensity observation schedule (every minute) was chosen, even though many studies of giraffe (e.g. Innis, 1958; Leuthold & Leuthold, 1978; Pellew, 1984a; van der Jeugd & Prins, 2000) and other species (e.g. eland—Watson & Owen-Smith, 2000) have used five minute scan sampling (Altmann, 1974). During my preliminary research, the behaviour of giraffe in the study region often changed more frequently than every five minutes. To limit discrepancies and improve standardisation, observations were recorded at the top of every minute (±15 seconds), thus reducing recorder bias and subjective perception of the main activity over a five minute period. Due to the possibility of observing up to ten giraffe at any one time, identifying the sex and age of the giraffe prior to beginning observations was important. Once established, observers were assigned giraffe and a scribe recorded the activities and checked the time to ensure accuracy and efficiency.

The minimum number of monthly observations for giraffe bulls and cows was established at 200 observations for every hour of a 12-hour day (i.e. 7am–7pm). This frequency provided an adequate sample size for analysis. When possible, sampling was undertaken in ‘block’ periods of three to four hours of intensive research at a time during morning, midday and afternoon, and on 10–20 days throughout the month. Spreading observation periods throughout the month limited the potential for temporal confounding, as may happen when all observations are made over a short period. The minimum number of observations was achieved for almost all time periods each month. However, seasonal and daily movements of giraffe, seasonal rainfall and flood events, dense fog, tourist interference and the rugged terrain in the study region, all limited observations on occasions. No systematic observations were made at night.

Activities of adults and subadults were combined for each sex as in previously published studies (Innis, 1958; Leuthold & Leuthold, 1978; Pellew, 1984a; Ginnett & Demment, 1997; van der Jeugd & Prins, 2000), and as suggested from personal observations that indicated little variation in the behaviour of different aged giraffe. Data on juveniles were collected for both sexes and combined.

Observations were recorded predominantly from a vehicle, although giraffe were also tracked on foot and studied from a high elevation vantage point when possible. Based on researcher experience, observations were always undertaken at a distance deemed to have no impact on the giraffe's 'normal' behaviour. This distance varied daily and seasonally depending on environmental factors, such as climatic conditions (wind, fog), topography, herd size, study area, vegetation cover, presence of other vehicles, tourists and other species (domestic and wild). Minolta binoculars, 10x50 and 8x40 magnification, were used to observe giraffe when the animals were too far away to clearly observe with the naked eye.

The behavioural activities of giraffe were divided into 10 distinct categories based on previously published work (Innis, 1958; Leuthold & Leuthold, 1978; Dagg & Foster, 1982; Pellew, 1984a; Le Pendu *et al.,* 2000; van der Jeugd & Prins, 2000) and personal observations of behaviour in the study region. These are listed below:

- Feeding: The giraffe was observed physically eating; this activity included the time spent chewing and swallowing.
- Resting: The giraffe stood, sat or slept in the sun or shade and was neither ruminating nor showing vigilance.
- Ruminating: The giraffe chewed its cud while standing, sitting or walking.
- Walking: The giraffe travelled between forage sources or within the study region (not ruminating).
- Grooming: The giraffe was observed scratching and rubbing itself.

- Sexual behaviour: This activity included flehmen testing, courtship and mounting attempts. Flehmen testing involves the testing of urine (to detect pheromones) to assess a giraffe's reproductive status.
- Excretion: The giraffe was observed defecating or urinating.
- Vigilance: The giraffe focussed on external stimuli such as predators, domestic stock, tourists or other wildlife.
- Interaction: This activity included neck sparring (necking) between males and rubbing or chesting other giraffe.
- Drinking: The giraffe was observed drinking. Due to the apparent independence of giraffe on water in the study region (Scheepers, 1992; Fennessy *et al.*, 2003), every observation of spoor at a water source was noted.

Animals were often observed ruminating in the direct sun or shade. Although ruminating could also be perceived as resting, especially when in the shade, rumination requires energy and was recorded separately. When analysing mean monthly and mean daily activity budgets of giraffe bulls and cows, some activities i.e. interaction, sexual behaviour, excretion and drinking, were combined into 'other' activities. These behaviours comprised a minor percentage of the giraffe's activity budget.

Aside from the standardised collection of activity behaviours, incidental observations of giraffe behaviours were also recorded.

6.2.2. Flight behaviour and impacts of tourism

In the study region, tourism and hunting are two key factors affecting wildlife behaviour. The flight behaviour patterns of giraffe in the Hoanib River study area have been recorded as a potential indicator of the impacts of tourism and, to a lesser degree, hunting, on the population since the late 1980s (Scheepers, 1992).

Flight was defined in the present study as movement away from an observation point due to a direct or indirect stimulus such as vehicles, domestic stock, noise or hunting. Flight distances of giraffe were measured from the initial point of observation to the stopping point, when the animals recommenced 'normal' activity. The flight distances were classified into five distinct categories:

Table 6.1. Flight categories and distances observed for giraffe in the study region

Flight category	Flight distance (m)	Description
1	≤ 10	no significant flight
2	> 10-25	little flight distance
3	> 25-50	medium flight distance
4	> 50-100	large flight distance
5	≥ 100	extreme flight distance

6.2.3. Statistical analysis

A common problem in analysing the results of activity budget studies is that successive observations are necessarily obtained from the same individuals, and these are often pooled before formal analyses are undertaken. The major problem with pooling is that multiple observations of the same individuals are not independent, and inflation of the true sampling size (i.e. the number of individuals observed) by pooling can lead to spuriously significant effects (Machlis *et al*., 1985).

One solution to this problem is to average repeated observations from the same individuals prior to analyses so that n = the number of individuals observed and not the number of measurements. The major disadvantage is that hourly, daily or seasonal comparisons of behaviours are still precluded if data have been collected from the same individuals. In small populations, or situations where individuals cannot be readily identified, multiple observations of the same individuals are likely to be inevitable.

A second possible solution is to use data points from the same individuals that have been shown to be 'independent' in a strictly statistical sense, such as by serial correlogram analysis (Das & Sen, 1995). In practice, this may mean discarding observations taken close together or adopting a minimum time period (one minute in this study, see section 6.2.1) during which any of a defined set of behaviours could be exhibited. Empirical and simulation studies of the effects of data discarding have yielded contradictory results, with some suggesting that even the deletion of >90% of data points will not guarantee statistical independence (e.g. Rooney *et al.*, 1998). Even if some data points are deleted, multiple observations of the same individuals will of course still be biologically dependent and compromise formal statistical comparisons between different times.

A practical resolution of the multiple observation dilemma is to recognise the limitations imposed by non-independent data and seek to employ statistical analyses in an exploratory rather than hypothesis-testing or confirmatory sense (Martin & Bateson, 1993). Here, statistical comparisons can be made of individuals between times and places simply to reveal patterns or changes in behaviours. Because of the constraints inherent in the other approaches to using data from the same individuals, and because I am concerned here with describing patterns of giraffe behaviour, the exploratory approach is preferred.

Chi-squared analyses were used to compare frequencies of each of the categories of behaviour observed and performed by the different population components of giraffe between different hours of the day and between seasons. Where the same data have been compared in more than one analysis (such as in pairwise comparisons between the three seasons), sequential Bonferroni corrections were applied to reduce the risk of committing type-1 errors (Quinn & Keough, 2002). However, probability values adjusted in this way differed little from unadjusted values, so for brevity only the latter have been reported here. Finally, the major activity behaviours of bulls, cows and juveniles were correlated against one another on a minute by minute basis to identify any associations between behaviours.

6.3. Results

In excess of 108 800 individual observations of giraffe were recorded for bulls, cows and juveniles. The activity budget research was undertaken over a total of 1 813 hours, equating to 151 12-hour days and an average of 9 066 individual observations per month. On average 50 hours of actual giraffe observation time was undertaken each month, spread out over 10–20 days per month. Often the 12-hour observations periods would be consecutive.

6.3.1. Activity budgets

A significant difference was observed overall between the diurnal activities of bulls, cows and juveniles (χ^2 =2949.09, d.f.=18, P<0.001; Table 6.2; see Appendix 13). The four dominant activities for all giraffe were feeding, walking, ruminating and resting, which comprised 95% or more of their daily time budgets (Figures 6.1 to 6.5). Differences were detected between these activities for bulls compared to cows (χ^2 =686.18, d.f.=3, P<0.001), with cows spending more of their time feeding (59% vs. 51.1%), as well as resting (14.2% vs. 13%), compared to bulls. Bulls spent more time ruminating than cows (13.1% and 9.1%, respectively), as well as walking (17.4% vs. 15%) and engaged more frequently in interactions (χ^2 =1027.51, d.f.=1, P<0.001).

Table 6.2. Diurnal activity behaviours observed for bull, cow and juvenile giraffe in the study region. Data are expressed as mean percentages of observations.

Activity	Mean (%)		
	Bull (*n*=57 049)	Cow (*n*=39 223)	Juvenile (*n*=12 532)
Feeding	51.1	59.0	51.9
Walking	17.4	15.0	12.9
Resting	13.0	14.2	24.4
Ruminating	13.1	9.1	7.0
Vigilance	1.9	1.5	2.0
Grooming	0.8	0.6	1.1
Interaction	2.1	0.1	0.5
Sexual Behaviour	0.3	<0.1	-
Drinking	0.1	0.3	<0.1
Excretion	<0.1	<0.1	<0.1

Seasonally, bulls spent different amounts of time on different activities (χ^2 =1089.93, d.f.=9, P<0.001). The four dominant activities (feeding, walking, ruminating and resting) accounted for 94–98% of the time budget of bulls in the wet season, 83–98% in the cold-dry season and 88–98% in the hot-dry season (Figure 6.3).

Significant differences were observed in the major activities of bulls between seasons: wet versus cold-dry (χ^2 =142.43, d.f.=3, P<0.001); wet versus hot-dry (χ^2 =156.99, d.f.=3, *P*<0.001); and cold-dry versus hot-dry (χ^2 =295.78, d.f.=3, *P*<0.001) (Figure 6.3). Feeding increased from the wet to the dry seasons (48.07%, 50.13% and 53.2%, wet, cold-dry and hot-dry seasons, respectively). Ruminating was observed less in the hot-dry season (14.7%, 15.25% and 10.75% for wet, cold-dry and hot-dry seasons, respectively), while resting predominated in the wet season (15.4%, 10.56% and 13.92%, wet, cold-dry and hot-dry seasons, respectively). No seasonal difference was observed in walking by bulls. Giraffe bull interactions increased in the cold-dry season (3.41%) compared to the wet (0.79%) and hot-dry seasons (1.33%), although the time spent interacting overall was quite limited.

Giraffe cows spent different amounts of time seasonally in different activities (χ^2 =617.17, d.f.=9, *P*<0.001), with feeding, walking, resting and ruminating predominating (Figure 6.4). These latter activities accounted for 90–100% of the hourly diurnal activities of cows in the wet season, 92–99% in the cold-dry season and 91–99% in the hot-dry season (Figure 6.4). There were significant differences in the time spent by cows in these activities between seasons: wet versus cold-dry (χ^2 =245.85, d.f.=3, *P*<0.001); wet versus hot-dry (χ^2 =64.76, d.f.=3, *P*<0.001); and cold-dry versus hot-dry (χ^2 =460.22, d.f.=3, *P*<0.001). Interestingly, seasonal increases and decreases in different cow activities were different to those of bulls. Feeding increased in the cold-dry season (59.59%, 64.52% and 55.81%, wet, cold-dry and hot-dry seasons, respectively), while ruminating decreased in the wet season (7.96%, 9.23% and 9.67%, wet, cold-dry and hot-dry seasons, respectively). Resting was considerably reduced in the cold-dry season (15.27%, 8.17% and 16.88%, for wet, cold-dry and hot-dry seasons, respectively). Similar to bulls, cows exhibited no seasonal difference in walking activity.

There were significant differences in the frequency of performance of activities by juveniles (χ^2 =877.56, d.f.=9, *P*<0.001), although feeding, walking, resting and ruminating still predominated (Figure 6.5). These four activities accounted for 90–99% of the hourly diurnal activities of juveniles in the wet season, 89–100% in the cold-dry season and 86-99% in the hot-dry season (Figure 6.5). Differences also occurred in the time spent by juveniles in these different activities between seasons: wet versus cold-dry (χ^2 =293.04, d.f.=3, *P*<0.001); wet versus hot-dry (χ^2 =101.63, d.f.=3, *P*<0.001); and cold-dry versus hot-dry (χ^2 =702.13, d.f.=3, *P*<0.001). Feeding increased in the wet season (60.16%, 47.38% and 45.26%, wet, cold-dry and hot-dry seasons, respectively), while resting decreased in the wet season (14.36%, 30.99% and 25.40%, wet, cold-dry and hot-dry seasons, respectively). Little can be inferred from the resting activities due to their age. Similar to bulls and cows, juveniles exhibited no seasonal difference in walking activity.

The diurnal distribution of feeding behaviour of bulls, cows and juveniles was biphasic, with increased feeding occurring post-dawn and again pre-dusk. Fewer feeding activities were observed during the middle of the day, coinciding with increased ambient temperatures and an increase in resting. The pattern of diurnal resting was inversely correlated with feeding by bulls, cows and juveniles (r =-0.92, P<0.001; r =-0.90, P<0.001; r =-0.96, P<0.001, respectively), reaching a peak during midday and early afternoon. Furthermore, the distribution of ruminating was inversely correlated with feeding by bulls, cows and juveniles (r =-0.69, P<0.001; r =-0.72, P<0.001; r =-0.63, P<0.001, respectively), as too was resting to walking (r =-0.77, P<0.001; r =-0.67, P<0.001; r =-0.84, P<0.001, respectively). All other activities, including grooming, vigilance, sexual behaviour, excretion and drinking, were observed infrequently (Figures 6.1 to 6.5).

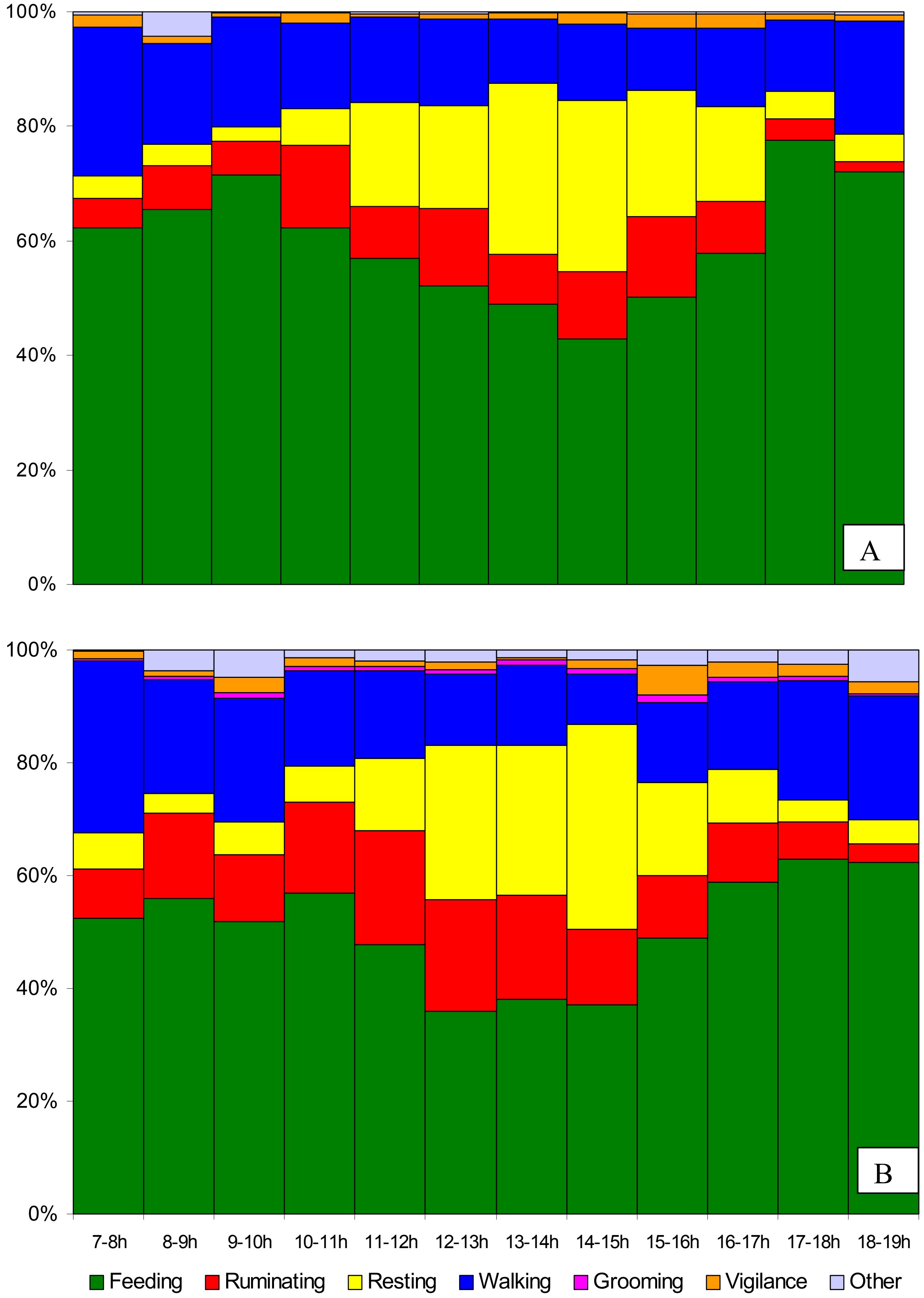

Figure 6.1. Diurnal activity budgets of giraffe expressed as hourly means: (A) cows & (B) bulls.

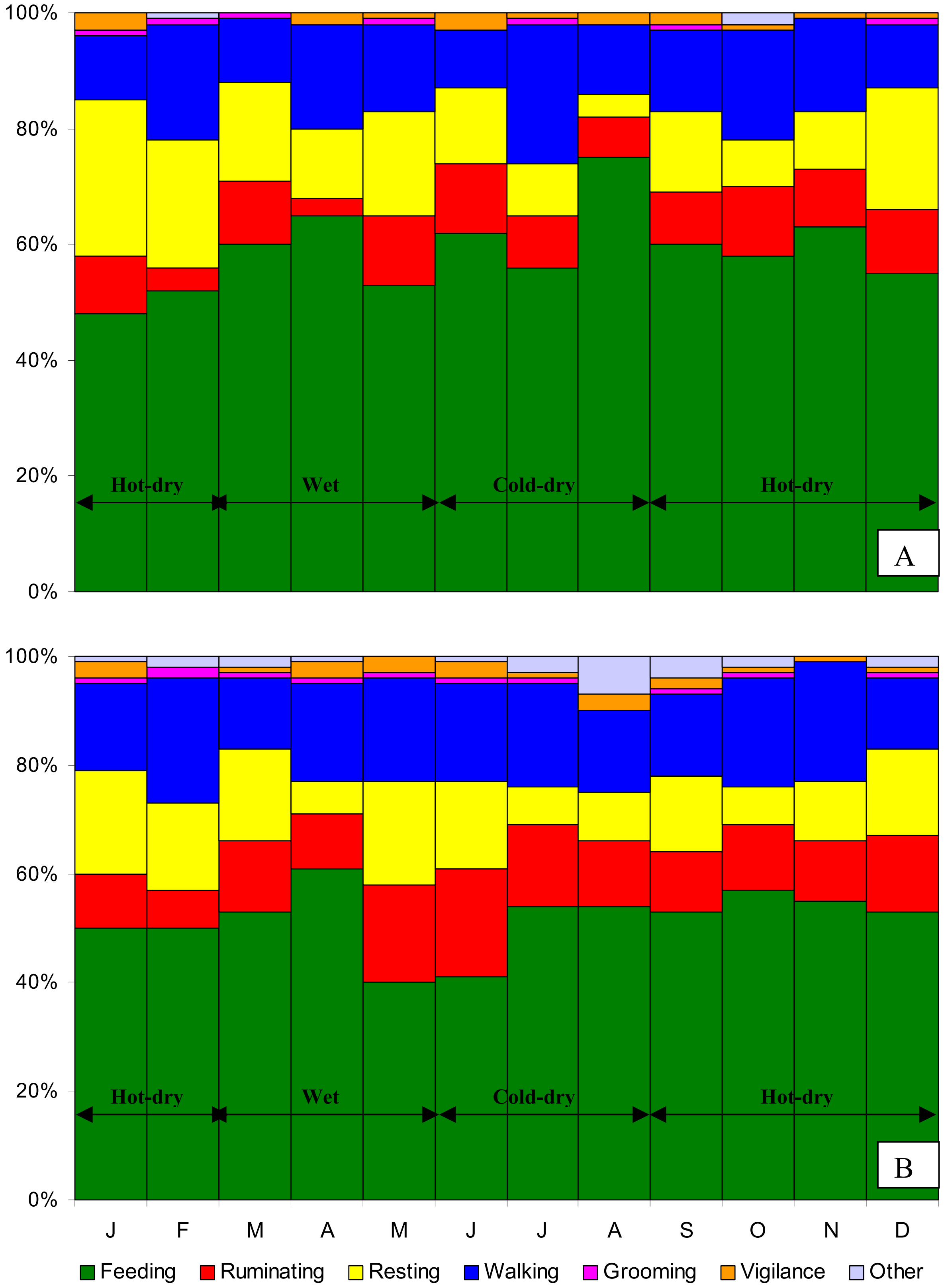

Figure 6.2. Diurnal activity budgets of giraffe expressed as monthly means (seasons highlighted): (A) cows & (B) bulls.

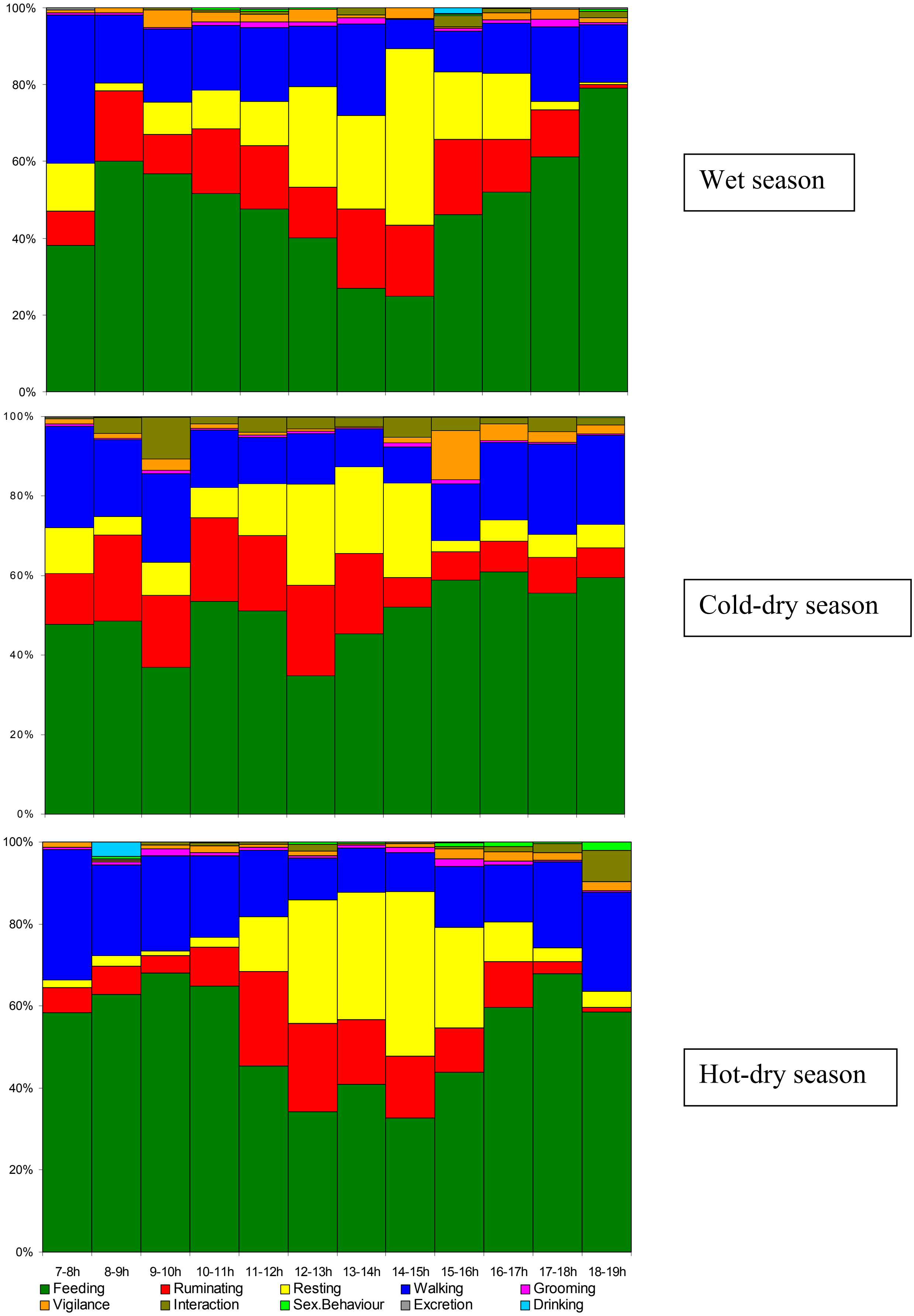

Figure 6.3. Seasonal activity budgets of giraffe bulls in the study region, expressed as hourly means.

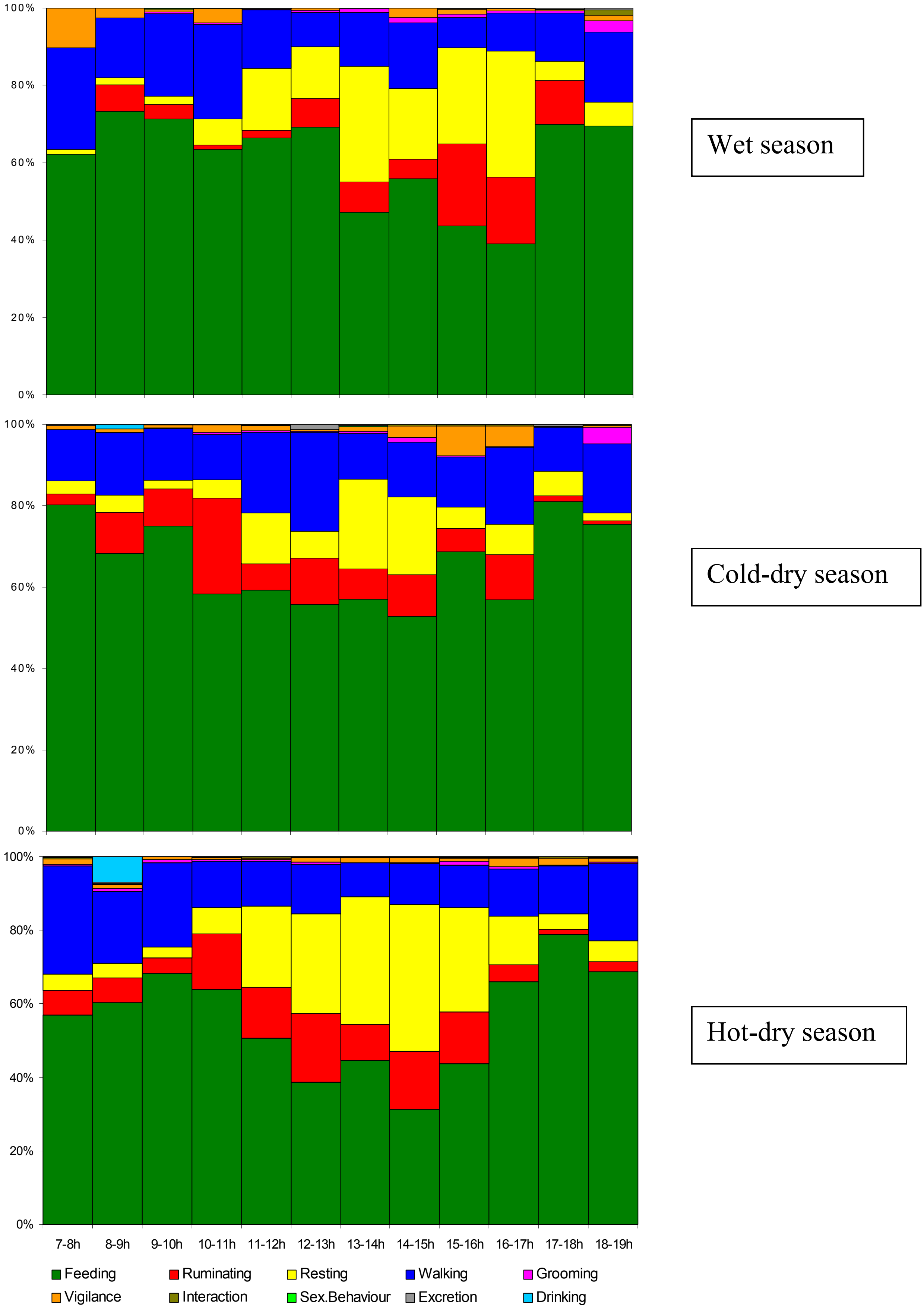

Figure 6.4. Seasonal activity budgets of giraffe cows in the study region, expressed as hourly means.

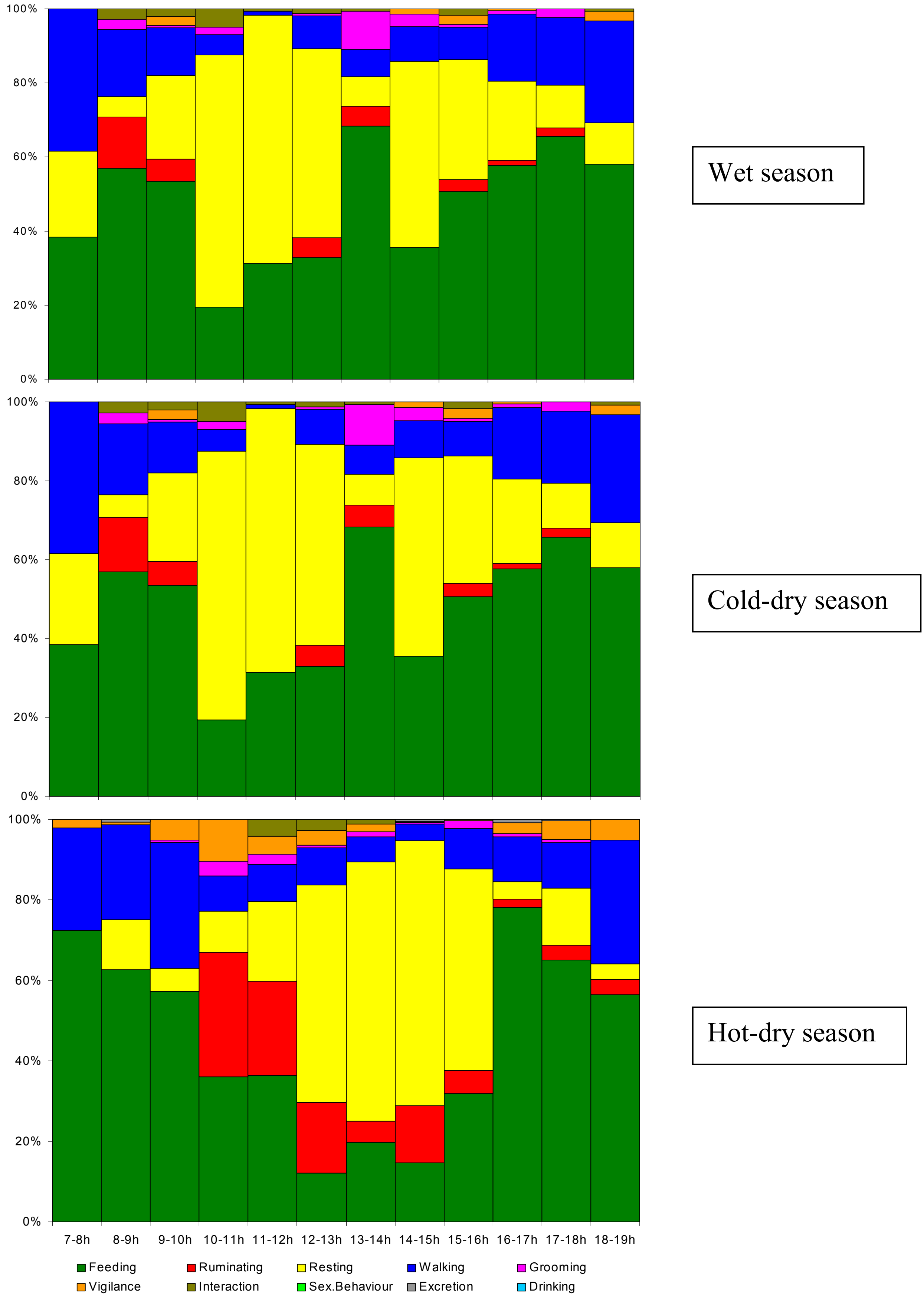

Figure 6.5. Seasonal activity budgets of juvenile giraffe in the study region, expressed as hourly means.

6.3.2. Flight behaviour and impact of tourism

The flight distances observed in this study were markedly less than those previously reported (Scheepers, 1992), averaging 6.7 m over a 12-month period, and ranging from no observed flight to ≤ 25 m (Table 6.3).

Table 6.3. Mean flight distances (m) of giraffe in the Hoanib River study area, 1986–2000.

	Season				
Year	Wet	Cold-dry	Hot-dry	Combined	Source
1986				156 m	Scheepers (1992)
1988				114 m	Scheepers (1992)
2000	6.7 m ±5.5	3.3 m ±4.0	10.0 m ±7.3	6.7 m ±6.0	This study

Seasonal variations in flight distances in this study were not great, although individual giraffe responded differently and contributed to the relatively high observed standard deviations. The marginally increased flight distances observed during the hot-dry season could be attributed to an influx of giraffe into the river systems (Fennessy *et al.,* 2003), coupled with seasonal winds that increase giraffe vigilance, but the high variance does not allow firm conclusions to be drawn.

6.4. Discussion

6.4.1. Activity budgets

Daily and longer term patterns of behaviour appear to reflect responses by giraffe to changing biotic and climatic conditions in the northern Namib Desert. These are discussed below.

6.4.1.1. Feeding

Feeding was the dominant activity of giraffe in the study region, although the proportion of time spent feeding differed significantly between the sexes and seasons. Diurnal feeding behaviour was strongly biphasic, with animals showing strong avoidance of energy consumptive activities such as feeding and walking during the hottest period of the day. Such activities increased in the early morning and late afternoon and correlated with lower ambient temperatures. Energy conserving activities, such as resting, showed a strong inverse correlation with feeding and walking. This activity pattern conforms to the 'heat-load' concept (e.g. Lewis, 1975; Mitchell, 1977; Leuthold & Leuthold, 1978; Pellew, 1984a), where animals maximise heat loss during the day by simply shifting activity. Giraffe across their range show similar biphasic activities (e.g. Leuthold & Leuthold, 1978; Pellew, 1984a) as do other mammals (e.g. elephant—Guy, 1976a; dikdik *Madoqua kirki*—Tinley, 1969; klipspringer *Oreotragus oreotragus*—Norton, 1981; steenbok—Cloete & Kok, 1986; impala—Jarman & Jarman, 1973). Although nocturnal studies were not undertaken during this study, previous studies of giraffe suggest that feeding and walking activities are greatly reduced in the night when ambient temperatures are lowest (Pellew, 1984a).

The feeding behaviour of giraffe cows in the study region can best be explained as an 'energy maximizer' strategy (Schoener, 1971). During the cold-dry season cows increased their time spent feeding, enabling them to increase fat deposition and therefore cope better during the extended dry season. During the hot-dry season forage intake of cows was reduced. Aside from exhibiting increased time feeding during the cold-dry season, the reduction in forage intake in the hot-dry season correlated with a change in dietary intake (see Chapter 7). Seasonal changes in the phenology of woody plants eaten may have enabled cows to obtain their necessary nutrient requirements with reduced forage effort. This ability to reduce the energy consumptive activities at such a critical time of the year should increase the chance of survival.

In contrast, bulls appeared to adopt an 'energy minimizer' strategy (Schoener, 1971) in the study region. A seasonal increase in bull feeding activity was observed from the wet to the hot-dry season, although the increase was not as distinct as that observed for cows. The reduced feeding in the wet season could be attributed to an increase in the nutrient quality of forage (see Chapter 7). The increase in bull feeding activity in the hot-dry season was possibly a result of reduced availability of forage in the canopies; if so, bulls may have been feeding on a wider choice of plants at different heights to maintain their bioenergetic requirements at this time of the year. Similar observations of feeding activities have been reported for giraffe in the Serengeti NP, Tanzania (Pellew, 1984c), Mikumi NP, Tanzania (Ginnett & Demment, 1997), and in Niger (Ciofolo & Le Pendu, 2002).

Maintenance of bioenergetic requirements is dependent on a variety of factors, including the availability, digestibility and quality of forage. Giraffe bulls obtain more nutrients and meet metabolic thresholds from reduced foraging times (e.g. Pellew, 1984c) in part from feeding higher in the canopies than cows (e.g. du Toit, 1990b; Young & Isbell, 1991; Ginnett & Demment, 1997; Woolnough & du Toit, 2001). Bulls feed selectively on new shoots and leaves with higher nutrient levels (e.g. du Toit, 1990b; Pellew, 1984c) or on plants with increased biomass (e.g. Woolnough & du Toit, 2001), which are often out of reach of cows and other herbivores. Similar feeding selection has been reported and correlates with the seasonal nutrient intake and bioenergetic requirements of bulls versus cows (e.g. Pellew, 1984a; Caister *et al*., 2003).

During the wet season, new leaf growth results in higher nutrient levels in some woody plant species (see Chapter 7). These seasonal changes altered forage selection, as well as plant-part selection, by giraffe. For example, pods of *Faidherbia albida* were eaten more often in the hot-dry season. The observed differences between the seasonal feeding pattern of bulls and cows was due to a combination of factors, not the least access to different foliar nutrients and moisture quality, and forage intake rates. Reduced seasonal feeding activity could be expected to limit other energy consuming activities such as walking. However this did not appear to be the case as there were no significant differences in walking activities observed between sexes or seasons.

Although yearly feeding activities varied between bulls (51.1%) and cows (59%), the difference was not as great as reported in other activity studies of giraffe (Leuthold & Leuthold, 1978; Pellew, 1984a; Ciofolo & Le Pendu, 2002). The differences in time spent in diurnal feeding activities between sexes and populations could be attributed to numerous factors, including differences in population structure and density, forage quantity and quality, forage intake rates, habitat use and water availability. For example, van der Jeugd & Prins (2000) postulated that reduced feeding activity by giraffe in Lake Manyara NP, Tanzania (average 35% for bulls and cows), compared to giraffe in the Serengeti NP, Tanzania (55.4% bulls and 72.4% cows: Pellew, 1984a) was due to access to higher quality habitat and/or higher rates of food intake. In Niger, the desert-dwelling giraffe show far greater seasonal variation in feeding activity (Ciofolo & Le Pendu, 2002) than the giraffe in this study. Time spent in feeding activities of giraffe in Niger doubled in the dry season compared to the wet season (46 and 22.8%, respectively), probably due to seasonal shifts in forage quality. Niger's giraffe migrate seasonally between two main habitats, with forage quality being markedly higher in the wet season habitat compared to the dry season habitat (Ciofolo & Le Pendu, 2002; Caister *et al*., 2003).

No similar large-scale seasonal shifts in habitat use were observed during the present study. However, within the Hoanib River study area seasonal changes in the availability of preferred forage may have resulted in dietary shifts (see Chapter 7) and consequent small-scale movements along the riverbed (see Chapter 5). These movements were not as pronounced as in Niger, but are indicative of the different factors that may impact on activity patterns in different areas.

This study could not confirm or refute the suggestion that giraffe do not feed during rain (Dagg & Foster, 1982), but personal observations indicated that windy conditions reduce giraffe feeding activities and increase vigilance. During windy conditions giraffe were observed to seek out sheltered areas away from the main riverbeds. It was unclear whether these activities increased before the onset of windy or other inclement weather conditions, but a distinct decrease in feeding and an increase in vigilance were observed while wind was blowing. Scheepers (1992) observed that flight distances also increased in windy conditions. Further analysis might provide greater insight into the impacts of weather on giraffe behaviour, especially on activity budgets and energy maintenance.

6.4.1.2. Ruminating, resting and vigilance

Time spent ruminating by giraffe was inversely correlated with that spent feeding in both sexes and in juveniles, although not as strongly as the inverse correlation between feeding and resting. Time spent ruminating increased during midday and early afternoon. Giraffe bulls ruminated more often than cows (e.g. Leuthold & Leuthold, 1978; Pellew, 1984a), and less in the hot-dry than the cold-dry season. Increased rumination by bulls is possibly related to their feeding patterns and the ability to extract more nutrients from the food source (E. Cameron personal communication). The large increase in heat-load experienced during the hot-dry season may reduce daily rumination activities (Dagg & Foster, 1982). I could not determine whether rumination increased by night during the hot-dry season, but Dagg & Foster (1982) and Pellew (1984a) reported rumination to be the dominant nocturnal behaviour.

In the Serengeti NP, giraffe ruminated more at midday and in early afternoon, showing a strong inverse correlation with feeding (e.g. Pellew, 1984a). The time spent ruminating by giraffe in my study was less than that reported elsewhere, possibly reflecting an adaptation to conserve energy in the arid environment during the most critical periods of the day. A lack of supportive studies from arid environments limits any strong inference.

Rumination was often associated with vigilance. When vigilant, giraffe focussed their attention in the direction of the stimulus, which was sometimes not obvious to the researcher. Giraffe would begin to ruminate while still being vigilant, although it is unknown whether this was a coincidental activity or nervous behaviour. Similar nervous behaviours associated with vigilance, such as ruminating and self-grooming, have been reported for other African ungulates (e.g. Siegfried, 1980; Mooring & Hart, 1995). Increased vigilance may also help to reduce interactions with predators, other giraffe or competitors, or people.

Throughout the study, giraffe showed varying degrees of vigilance, although this equated to just 1.5% to 2% of the time (bulls, cows and juveniles). Vigilance occurred in response to external stimuli, such as the activities of communal farmers, tourists, light aircraft, domestic stock, other giraffe, birds, elephant, gemsbok, springbok and/or predators. All of these potential conflicts, competitive situations or predatory distractions were common throughout the study region. It is important to note that in the daily activities of the giraffe population in the communal areas of the northern Namib Desert, people, as much as other wildlife, are potential threats, particularly in light of historical poaching activities.

The percentage of daytime activity dedicated to vigilance in the study was not mostly related to dominance, as proposed previously by Young & Isbell (1991). Increased vigilance comes at a cost to foraging time, while conversely it reduces the risk of predation (Siegfried, 1980). Many African ungulate species aggregate in large numbers for protection against predators (e.g. Bertram, 1979; Siegfried, 1980; Underwood, 1982; FitzGibbon, 1989; Mooring & Hart, 1995); however, the giraffe's obvious height advantage reduces such a need. Furthermore, ungulates increase vigilance behaviour during seasonal breeding periods (e.g. Underwood, 1982; Jarman & Jarman, 1973). Giraffe in the study region and other populations across the range showed seasonal peaks in breeding, but these were not as defined as for other ungulates. As a consequence, little seasonal variation in vigilance activity was observed in the study region. Interestingly, time spent in vigilance in the study population was considerably less than that reported for giraffe in East Africa (e.g. Ginnett & Demment, 1997) and in comparison to other African ungulates, such as impala, which spend 22% to 27% of the day being vigilant (e.g. Hunter & Skinner, 1998; Matson, 2003). A low density of predators in the study region (Stander & Hanssen, 2003) might have reduced the need for extensive vigilance activities.

Giraffe preferred resting in the riparian woodlands rather than in open habitats (personal observation). The riparian woodland in the study region has large banks that channel wind along the rivers. Matson (2003) proposed that impala inhabiting semi-arid and desert climates may use particular slope orientations in relation to topography to optimise heat loss, whilst Hudson & White (1985) noted that the lightest of winds could reduce herbivore skin temperatures substantially. Giraffe in the study region appeared to rest in microhabitats, such as under trees within the riparian woodland, allowing shade and wind to optimise heat loss or gain. When observed resting on occasions in the open, giraffe orientated their body away from the sun. This behavioural orientation reduces water loss and is observed in other species in arid environments (e.g. Hartmann's mountain zebra; Joubert, 1974). Such behaviours assist giraffe under extreme thermal conditions.

Diurnal sleeping was not observed commonly during the study, but giraffe of all age and sex classes slept at some point by day. The limited time (<0.1%) spent in diurnal sleep was similar to that reported for giraffe elsewhere (e.g. Leuthold & Leuthold, 1978; Dagg & Foster, 1982; Pellew, 1984a). Although not quantified in the wild, giraffe sleep mostly at night (e.g. Kristal & Noonan, 1979; Dagg & Foster, 1982; Pellew, 1984a; Tobler & Schwierin, 1996). Perhaps too, in the present study, it is possible that giraffe spent some time asleep while sitting or standing, hence resulting in an underestimation of diurnal sleep behaviour.

Giraffe usually sleep when recumbent, lying with the neck bent backwards, head under the rump, on the hind limb or on the ground (e.g. Kristal & Noonan, 1979; Dagg & Foster, 1982; Moss, 1982; Pellew, 1984a; Tobler & Schwierin, 1996). This form of sleep is referred to as 'deep sleep', and giraffe are sometimes presumed to fully rest only in this position. However, based on studies of other ruminants (e.g. Ruckebusch *et al.*, 1974), it seems likely that giraffe can sleep while recumbent with their necks in an upright position (Kristal & Noonan, 1979), or even while standing (Tobler & Schwierin, 1996).

When giraffe were observed sleeping, the episodes were short and fragmented, a result of their inability to rise quickly from the ground and flee as a response to an external stimulus such as predators (e.g. Tobler & Schwierin, 1996). Such vigilance and predator avoidance may encourage giraffe to sleep in a standing position (Tobler & Schwierin, 1996). Whilst standing or sitting, giraffe were often observed motionless, not ruminating and with an upright neck. From these observations, and those of Tobler & Schwierin (1996), it could be inferred that during rest giraffe sleep more often than previously assumed. Increased periods of resting while both recumbent and standing were observed at midday and during early afternoon, and corresponded with higher ambient temperatures. Tobler & Schwierin (1996) further noted brief periods of sleep during rumination. Ruminating was often associated with both standing-resting and recumbence during this study, but no overall correlation was detected.

6.4.1.3. Grooming and social interactions

Grooming, although observed relatively infrequently, consisted of any of the following: tail swotting, shaking, biting or nibbling, scratching the neck, head, back and inside of the ear on tree trunks, branches and rocks, and scratching the underbelly and legs by straddling small bushes and shrubs. No giraffe were observed dusting, wallowing or bathing as has been reported for other mammals (e.g. Clough & Hassam, 1970; Guy, 1976a; Leuthold, 1977b). The rare behaviour of allogrooming was observed just once. The importance of grooming activities for many African animals has been well documented (e.g. warthog *Phacochoerus aethiopicus*—Clough & Hassam, 1970; impala—Jarman & Jarman, 1973; Hart & Hart, 1992; Mooring & Hart, 1995; zebra—Joubert, 1972; waterbuck *Kobus ellipsiprymnus*—Spinage, 1968; elephant—Guy, 1976a; birds—Redpath, 1988; MacLean, 1993).

Grooming in the present study primarily aided in the removal of ectoparasites such as ticks. Giraffe regularly used small shrubs and bushes, such as *Salvadora persica, Pechuel-Loeschea leubnitziae, Tamarix usneoides* and *Colophospermum mopane,* and branches from trees such as *Faidherbia albida, Acacia erioloba* and *A. tortilis,* to scratch themselves. The use of trees and shrubs as grooming 'tools' has been reported (e.g. Dagg & Foster, 1982). It is not clear why giraffe in the study allocated so little time to grooming. It is possible that they are less affected by water-borne parasites due to their limited use of free-water (e.g. Graczyk *et al*., 1997; Wobeser, 2002), or that increased grooming occurs at night.

The need to groom in many species of African mammals has encouraged the occurrence of bird/mammal associations. Specialist ectoparasite gleaners, such as Oxpeckers (*Buphagus* spp.), occupy specific niches with mutual benefit for both bird and mammal. In regions where specialist ectoparasite gleaners do not occur, facultative ectoparasite gleaners have filled the niche in their absence. This evolutionary process is dynamic. In the study region, facultative ectoparasite gleaners, such as Palewinged Starlings (*Onychognathus nabourup*), were observed in association with giraffe (Fennessy, 2003), providing the first recorded observation of any bird/giraffe feeding association from the region (see Appendix 14 for published article on ectoparasite gleaning of giraffe in this study).

Studies of social interactions among giraffe have revealed many similarities, as well as differences, between populations and subspecies (Innis, 1958; Foster, 1966; Foster & Dagg, 1972; Leuthold & Leuthold, 1978; Dagg & Foster, 1982; Pratt & Anderson, 1982; Pellew, 1984a; Young & Isbell, 1991; Ginnett & Demment, 1997; van der Jeugd & Prins, 2000; Bashaw, 2003). Many of the social activities exhibited by giraffe are similar to those reported for other African ungulates, such as impala (Jarman & Jarman, 1973) and gerenuk (*Litocranius walleri*; Leuthold & Leuthold, 1978). In the study region many social interactions among giraffe were observed. Some of these were age or sex dependent, while others were not. Interactions included (see Innis, 1958; Young & Isbell, 1991; Bashaw, 2003):

- greeting or contact interactions, such as naso-frontal greeting (nosing);
- rubbing, sniffing and licking;
- play interactions, such as gambolling;
- neck sparring and kicking;
- affiliative interactions, such as cow-calf bonding, suckling;
- dominance and agonistic interactions, such as neck sparring, avoidance, chesting, bumping; and
- sexual interactions including flehmen testing and mounting.

Affiliative, contact and play interactions appeared to decline in frequency with an increase in age, while agonistic and sexual interactions increased with maturity. These findings appear to reflect that observed elsewhere (e.g. Pratt & Anderson, 1982; Le Pendu *et al.*, 2000).

In Chapter 4 it was inferred that strong inter-individual associations occurred among giraffe in the Khumib River study area; this population was the smallest in the study region. This population appeared to have a matrilineal structure, while strong bull associations were observed in the Hoarusib River population. Social interactions between giraffe in the study region were most conspicuous amongst bulls and cow-calves. Neck sparring (discussed below) was observed more often in the bull-biased Hoarusib River study area. Cow-calf interactions varied in type but were more frequent in the Khumib River compared to the Hoanib River study area. Juvenile giraffe rubbed their neck or head along the flanks, rump or brisket of their mothers for various reasons. Rubbing often appeared to be a precursor to suckling, but it appeared also to reflect nervous behaviour. When giraffe appeared nervous, independent of age and sex, they would often run away immediately from the stimulus, or seek solace in a nearby giraffe, rubbing or chesting them. This behaviour perhaps enticed the other giraffe to move away from the potential conflict, or simply to seek security. Younger giraffe almost always initiated this nervous contact behaviour and were usually ignored by the dominant giraffe shortly after contact.

Interactions, dominance or leadership amongst giraffe cows are little understood, with most research being focussed on bulls and their social hierarchy (Leuthold, 1979; Pratt & Anderson, 1985; Bashaw, 2003). In the published literature, only occasional observations of cow interactions, such as neck rubbing, neck sparring and chesting, have been reported. Leuthold (1979) reported that interactions among cows in the Tsavo NP, Kenya, were rare, with less than observations being made over a seven year study. In contrast, Pratt & Anderson (1985) reported many interactions among giraffe cows in various parks in Tanzania, with over 140 observations in ten months.

In the study region, interactions among cows were common, although not as lengthy or as often as observed for bulls. All forms of interactions, i.e. contact, play, affiliative, agonistic and sexual behaviour, were observed, but at different frequencies. For example, cow-calf interactions were more common than chesting, which was more common than neck sparring between cows.

Cow-calf interactions were dominant, enabling calves to suckle, while at the same time developing a stronger social bond between the two. Juvenile giraffe had the most contact and play interactions of all giraffe age classes. Juvenile giraffe also showed deliberate physical contact and play behaviour with other giraffe, particularly juveniles. Pratt & Anderson (1982) reported similar observations. Interactions such as naso-frontal greeting, rubbing, sniffing, licking, and gambolling were observed most often in the first weeks of life and decreased markedly after one year. There appeared to be no difference in interaction type or frequency by juveniles of each sex.

One interaction of particular interest was the introduction of a newborn giraffe to a herd. The juvenile was led towards the herd, with the mother initially remaining a short distance away. Immediately, one of the juveniles in the herd playfully chased the newborn. Following this, a subadult cow approached and sniffed the newborn, which caused the newborn to run again. This was followed by the first juvenile playfully chasing it again. An adult cow then approached the newborn and sniffed it. A second juvenile approached the newborn and naso-frontal greeted (touched noses) with it. This caused the newborn to run into a nearby shrub, followed by the two juveniles and two sub-adults, all jumping and running. The newborn and its mother stayed with the herd for ten minutes before slowly moving away. Both of the juveniles then joined the newborn and its mother. Eventually, one of the juveniles returned to its initial herd while the mother, newborn and the other juvenile moved up a gorge and out of contact. The strong interest exhibited by giraffe suggests the existence of some social structure within the population, and provides evidence that giraffe have considerable social awareness of other giraffe beyond that expected.

Significantly more interactions were observed among giraffe bulls compared to either cows or juveniles, primarily due to the high frequency of neck sparring events among bulls. Differences in bull interactions between the three study areas were not assessed, however, from personal observations a marked increase in bull interactions occurred in the bull-biased Hoarusib River study area compared to the other study areas. More interactions also occurred among bulls in the cold-dry season compared to either the wet season or hot-dry season. Giraffe calving peaked during the hot-dry season in the study region (see Chapter 4) which correlates with increased conceptions in the cold-dry. Although I did not observe an increase in courting during the cold-dry season, it is expected that increased interactions among bulls in the cold-dry season were related to increased copulation attempts. These are similar observations to those reported by Dagg & Foster (1982). Since bulls do not defend a distinct territory, it may be that year round neck sparring by bulls is a social cohesion behaviour used to establish their status (dominance) in the population and as a form of play (e.g. Coe, 1967; Dagg & Foster, 1987; Simmons & Scheepers, 1996; Bashaw, 2003).

The frequency of neck sparring and dominance-related activities appears to vary between populations, often independently of population structure (e.g. Innis, 1958; Coe, 1967; Leuthold, 1979; Dagg & Foster, 1982; Pratt & Anderson, 1982 & 1985; Le Pendu *et al.*, 2000). In one bull-biased giraffe population neck sparring led to bulls mounting one another, and Innis (1958) postulated that bull-bias may foster homosexual behaviour patterns. Since this initial hypothesis, mounting attempts of bulls on bulls have been observed regularly and are perceived to be associated with attaining or maintaining status in the dominance hierarchy (e.g. Geist, 1966; Coe, 1967; Dagg & Foster, 1982; Pratt & Anderson, 1982 & 1985; Simmons & Scheepers, 1996).

Neck sparring observed in the study region involved bulls almost exclusively. It has been reported that in the wild only bulls are involved in such activities (e.g. Coe, 1967; Dagg & Foster, 1982), but neck sparring by cows has been observed, although rarely (Pratt & Anderson, 1985). The two observed occurrences of neck sparring by cows in my study involved adults. One bout with a juvenile was most likely play behaviour, although distinctive necking actions by both giraffe were observed. The other neck sparring bout was with a subadult bull. During this bout both giraffe returned blows on several occasions, although the contact appeared less intense than that observed in most neck sparring between bulls.

Various age combinations were observed in neck sparring contests between bulls: adult-adult, adult-subadult, and subadult-subadult. Juveniles were also observed neck sparring on a number of occasions, both with other juveniles, subadult bulls or adults, although the latter interaction was not common. On two occasions groups of three giraffe were observed neck sparring with each other at the same time: adult-adult-subadult, and subadult-subadult-juvenile. Each of these neck sparring bouts lasted less than two minutes.

Neck sparring bouts lasted from less than one minute to intermittent bouts of over 50 minutes, each averaging approximately five minutes. During the study the neck sparring did not appear to represent serious fighting (Pratt & Anderson, 1982 & 1985), even though some bouts lasted almost an hour. On numerous occasions mounting or mounting attempts of one bull on another followed neck sparring. More often than not it appeared to be the older or dominant bull mounting the other, as might be expected from dominance hierarchy theory (e.g. Geist, 1966; Coe, 1967; Dagg & Foster, 1982). Mounting did not always involve the extension of the genitalia, although it often resulted in the mounted giraffe walking away from the immediate area. Interestingly, on one occasion a subadult bull was mounted several times by a number of adult and subadult bulls, even though he did not neck spar with them. This bull was probably relatively low in the population social structure.

On a few occasions during the study period, neck sparring bouts were associated with courting. During bouts between bulls where cows were in close proximity, the dominant bull always returned to court the cow following the bout. Dominant bulls, normally larger, with bigger heads and necks, clearly had increased access to oestrous cows (Pratt & Anderson, 1982 & 1985; Simmons & Scheepers, 1996). Furthermore, dominant giraffe bulls within the study region appeared to court oestrous cows for longer periods. The majority of heterosexual sexual interactions were between adult or subadult bulls and adult cows. On numerous occasions older bulls were observed displacing younger bulls, which were courting or seeking the attention of an oestrous cow. On one occasion, however, an adult cow was so insistent to get the attention of the dominant bull that she isolated the bull from the rest of the herd by steering him away. Pratt & Anderson (1985) reported similar displacement behaviour. Giraffe bulls were observed chesting or chasing away other bulls from trees or shrubs on which they foraged. This behaviour was less common than neck sparring. Little correlation between flehmen testing and mating could be established, as flehmen was observed year= round in the study region, although it was more conspicuous in the cold-dry and hot-dry seasons.

Aggression by giraffe in the study region was rare overall, but when observed was due to three possible stimuli: (a) people (tourist, communal farmer or researcher); (b) other giraffe; and (c) other wildlife, including predators. Giraffe exhibited aggression mainly by stamping their front hooves, snorting or growling (see Dagg & Foster, 1982), and also by charging, necking and kicking. However, avoidance (flight) was preferred (as discussed below).

6.4.1.4. Drinking and independence of water

A unique feature of Namibia's desert-dwelling giraffe is their apparent independence of surface water, a testament to their adaptation to the desert environment (e.g. Viljoen, 1981; Scheepers, 1992; Fennessy *et al.*, 2003). Permanent, slightly saline springs occur in all main riverbeds throughout the study region, while water collects temporarily in mountain pools and crevices following seasonal rainfall. Independence of water in giraffe thus appears not to be a result of lack of availability of surface water, as it is widely distributed, if only seasonally, throughout the study region. Furthermore, the desert-dwelling elephant that occupy the northern Namib Desert drink regularly.

As previously proposed (Viljoen, 1981; Hall-Martin *et al.*, 1988; Scheepers, 1990), giraffe in the study region appear to obtain adequate moisture from food. However, this is only possible because of the coastal fog that sometimes blankets the region up to 60 km inland. Precipitation in the dunes and adjacent riparian woodlands is greater than at the coast due to these seasonal fogs that carry about twice as much moisture as rainfall with a third less variability (Robinson & Seely, 1980; Southgate *et al.,* 1996; MWTC, 2000). The fog envelops the trees and provides giraffe with abundant fresh water (see Chapter 7).

In the Hoanib River, fewer than ten observations have been made of giraffe drinking since 1934 (Viljoen, 1981; Scheepers, 1990; Fennessy *et al.*, 2003). One observation, made in the late hot-dry season in 1978, was of a solitary giraffe in poor condition (Viljoen, 1981). In the Hoarusib River study area, giraffe were observed drinking twice and their spoor was observed at a seasonal wetland. These observations were the first of giraffe drinking in this area, although it should be noted that little focussed research had been carried out previously. In the Khumib River, spoor and sightings of a bull at the Sarusas spring, 7 km west of the population's normal range, remain the only known records of giraffe drinking in the area. Up until the installation of artificial water points in the Hoanib River study area in late 2002, no giraffe had been observed drinking during the study period. However, altered drinking behaviour was observed the year after installation; this is discussed in detail below.

Throughout Africa, giraffe have been reported to survive without water for extended periods (e.g. Taylor, 1968; Foster & Dagg, 1972; Dagg & Foster, 1982; Ciofolo & Le Pendu, 2002). Independence of water in other populations has been attributed to the moisture-rich browse on which they feed, predominantly *Acacia* spp. (e.g. Taylor, 1968; Hall-Martin & Basson, 1975; Dagg & Foster, 1982). The desert-dwelling giraffe of Niger also drink rarely, accounting for only 0.03% of all diurnal activities (Ciofolo & Le Pendu, 2002), unlike giraffe in my study population, were assumed to drink at night. Therefore, the independence of water by giraffe in the Namib appears more marked than in populations elsewhere in Africa.

To survive in the arid northern Namib Desert, giraffe and other mammal species have developed a variety of physiological and behavioural adaptations. These serve to minimise water loss, and include selection of cool habitats, an efficient renal system and nasal heat exchange; the latter adaptation occurs in both hot (e.g. kangaroo rat *Dipodomys* spp.—Jackson & Schmidt-Nielsen, 1964; gemsbok—Joubert, 1974; camel *Camelus bactrianus*—Langman *et al*., 1978) and cold desert taxa (e.g. reindeer *Rangifer tarandus*—Langman, 1985).

Steenbok in the Namib Desert also show independence of surface water (Cloete & Kok, 1986; Seely, 1987) and have similar activity budgets and heat-load adaptations to giraffe (Cloete & Kok, 1986). As with giraffe, the renal physiology of steenbok is similar to that of mesic-dwelling relatives (Cloete & Kok, 1986; L. Scheepers & J. Patterson, personal communication), and animals also obtain moisture purely from their predominant food source, *F. albida*. In the central Namib Desert *F. albida* contains about 59% water (Cloete & Kok, 1986). *Faidherbia albida* is also the preferred forage source of giraffe in the study region and presumably contributes to water balance (see Chapter 7).

Respiratory water loss in giraffe is very small. Langman *et al*. (1979) reported that nasal counter-current heat exchange was an important mechanism for water conservation by giraffe in any arid environment. By cooling the exhaled air on the surface of the nasal mucosa, up to three litres of water per day can be conserved (Langman *et al*., 1979), only half of that exhaled at normal body temperature (Langman *et al*., 1982). The mechanism of recovering water from respired air using nasal heat exchange not only reduces water loss, but can have the added benefit of reducing metabolic heat loss, which is important during cool night conditions. Furthermore, the ability of giraffe to minimise water loss has important consequences for their food and water intake (Langman *et al*., 1982). With limited observations of giraffe drinking in the study region, moisture intake in forage and water conservation appear to be major adaptations.

Giraffe also avoid excessive evaporative cooling via panting and sweating to conserve water. Body temperatures can fluctuate between 3° and 10°C over a 24 hour period, which results in storage of large quantities of heat, while allowing for improved water conservation (Langman, 1982). Giraffe are able to heat up slowly throughout the day, allowing for passive heating and cooling for water conservation (Joubert, 1974; Langman, 1982).

In October 2002 the Namibian Ministry of Environment and Tourism (MET) built two artificial water points on the banks of the Hoanib River (one close to the confluence of the Hoanib and Ganamub Rivers, and one at the confluence of the Hoanib and Mudorib Rivers). These water points tap into the artesian water supply of the Hoanib River system and pump fresh, palatable water into purpose-built open waterholes. The water points were constructed primarily to entice elephant away from nearby Sesfontein village and so reduce human-wildlife conflict (H. Kolberg & B. Beytell personal communication). However, this was a politically driven decision and ecological impacts were not considered; no monitoring was established either pre- or post-installation of the artificial water point. In the year following their installation, use of the riparian woodland by elephant shifted away from the Dubis wetland and Sesfontein village and towards the west along the Hoanib River where the water points are located (K. Leggett, unpublished data). As a result, increased resource competition between giraffe and elephant has occurred. Furthermore, lion, leopard and cheetah numbers and residency in the Hoanib River study area have increased (personal observation).

In North America developments such as artificial water points in desert areas have often been detrimental to the long-term success of mammal populations (McQuivey, 1978; Broyles, 1995). Overpopulation, reduction in plant biomass and habitat destruction are all impacts which affect animal behaviour (Broyles, 1995). Food resources near the water points often suffer long-term damage due to increased concentrations of wildlife (e.g. Lange, 1969; Andrew, 1988; Pickup, 1994; Leggett *et al*., 2003b & c).

Since the installation of the artificial water points, particularly at the confluence of the Hoanib and Mudorib Rivers, giraffe have been observed drinking regularly, sometimes on consecutive days. In the short-term, the reliable supply of clean surface water has created a marked impact on giraffe. Giraffe are competing more often with elephant for the available forage and habitat resources surrounding these water points. In the short-term no actual displacement of giraffe has been observed and increased focal research would be required to better understand these impacts. However, a shift in elephant habitat use since the installation of the water points has resulted in short-term impacts on forage (K. Leggett, unpublished data; personal observation). Long-term monitoring of elephant movements, together with a comparative assessment of forage resources along the Hoanib River, would provide insight into impacts on forage and habitat resources along the river. Forage impacts and population dynamics of the dominant tree in the river, *F. albida*, are discussed in Chapter 7. In light of the construction of the artificial water points, this study may also be a valuable tool in assessing the impact of elephant on the area's resources and any impact on giraffe movement and habitat use.

It is concluded that the desert-dwelling giraffe are superbly adapted to life without drinking. However, their activity, habitat use and social interactions may be affected by the installation of the permanent water points and their associated impact.

6.4.2. Flight behaviour and impact of tourism

The impacts of tourism, poaching and human development on giraffe, other wildlife and habitat have been reported (e.g. Babich, 1964; Le Pendu *et al.,* 2000; Warnken & Buckley, 2000). Flight, a reaction of wildlife to external stimuli, such as predators and tourism, can provide some insight into the degree of habituation.

The flight behaviour of giraffe in the Hoanib River study area during this study was very small (<10 m), and significantly less than that reported a decade earlier (Scheepers, 1992). Prior to the 1980s, access of tourists to the Hoanib River and the rest of the study region was limited. Scheepers (1992) commented that uncontrolled public access and increase in tourist numbers from the 1980s onwards would impact on wildlife and the riparian woodlands. Initial assessment of the impact on giraffe and their subsequent flight behaviour in the Hoanib River area in 1986 and again in 1988 suggested a marked decrease in flight distances over this short period (157m (1986) to 114m (1988): Scheepers, 1992). This reduced flight behaviour was attributed to the habituation of giraffe to tourists.

Scheepers (1992) voiced concern about the disturbance that increased tourist numbers would cause, including potential physiological costs, such as heat exhaustion from flight. The reduced flight distances observed in the Hoanib River study area indicate that such physiological costs could now be negligible. However, the time that giraffe allocate to vigilance is of concern. Vigilance reduces time spent in other activities, independent of whether it is energy consumptive or optimising. Natural predators are an inevitable danger for giraffe and will always result in increased vigilance. However, increased tourism, light aircraft and human movement in the study region should be monitored to assess their long-term impact on giraffe and other wildlife. In the Kruger NP, South Africa, every tourist, on average, commits one or more minor offences during their visit (Babich, 1964). Studies have shown that tourism, particularly in developing areas, has the potential to have large negative impacts if not controlled (e.g. Archer & Cooper, 1994; Berle, 1990; Buckley & Pannell, 1990; Opperman & Chon, 1997). In an uncontrolled environment like the Hoanib River, the effects of tourism could be worse and potentially detrimental over time.

Throughout their range giraffe often live in close proximity to people, including communal farmers and tourists. The ability of giraffe to habituate to their changing surrounds has been reported (e.g. Ciofolo, 1995; Caister *et al.*, 2003). However, in the study region and other parts of Africa where giraffe reside on communal lands, giraffe prefer areas away from people, and this reduces potential conflict. The impact on giraffe of the increasingly sedentary lifestyle of communal farmers in the study region is unknown but, with increased tourism and predation, may dramatically alter their behaviour and population status over the longer term.

6.5. Conclusion

Marked differences were observed between the diurnal activity budgets of giraffe bulls, cows and juveniles. Feeding occupied most of the time and, together with walking, resting and ruminating, accounted for at least 95% of all diurnal activities. Giraffe were strongly biphasic, with energy consuming activities such as feeding and walking being reduced during midday and early afternoon when ambient temperatures and heat load were greatest. Energy conserving activities, such as resting, increased during the same period. The dispersal of surplus metabolic heat when temperatures are lower, together with evaporative cooling and water conservation, contributes to the biphasic diurnal activity pattern. Furthermore, behavioural adaptations such as the selection of microclimates offering shade and wind, as well as body orientation, conserve energy and water.

Giraffe cows exhibited an energy ‘maximizer’ strategy while bulls exhibited an energy ‘minimizer’ strategy. Similar behavioural strategies have been reported for other giraffe populations in Africa, although in the study region differences in the activity patterns of cows and bulls were not as marked. This suite of responses is of paramount importance for the survival of giraffe in the arid northern Namib Desert.

Giraffe activities in the study area ranged from being social to solitary. The importance of understanding what giraffe do not do is as important as they do. Social interactions in giraffe are little understood and longer-term research will help to decipher their social bonds and hierarchy. Increased tourism in the study region could be detrimental to giraffe behaviour and ecology if it remains uncontrolled, but further research is required to test this hypothesis.

The independence of giraffe on water in the study region is most likely a result of their daily behavioural strategies, but even more so of their selection of forage (see Chapter 7). In the next chapter the seasonal forage preferences of the desert-dwelling giraffe and the chemical composition of their preferred forage are examined in order to better understand their independence of water intake. The impact of giraffe on forage resources and their potential role as habitat changers are also analysed.