RESEARCH

Diurnal activities of the desert-dwelling elephants in northwestern Namibia

Keith Leggett

The Namibian Elephant and Giraffe Trust, PO Box 527, Outjo, Namibia; e-mail: keal@iway.na

Abstract

The diurnal activities of desert-dwelling elephants (*Loxodonta africana*) in arid northwestern Namibia were monitored for five years (2002–2006) through the wet, cold dry and hot dry seasons. Desert-dwelling elephant activity changed from year to year and depended on rainfall and flood events. Three methods were used to collect activity data: two involved focal animals where individual elephants were monitored at five-minute intervals or continuously; the third involved a scan method that monitored individuals or groups at two-minute intervals. No statistical difference was observed in the data obtained by each method. Group activities investigated included feeding, water and social activities, resting and walking, while individual activities were further differentiated to include grazing, browsing, debarking, drinking, wallowing, dusting, resting in shade, resting in the open or sun, and the type of social interaction. These activities were analysed on an annual, seasonal and time-of-day basis. Annual variations in observed activities were probably due to variations in annual rainfall. Feeding activities were the major activities of desert-dwelling elephants, being similar throughout the year and occurring mainly during the 0700–1100 h and 1500–1700 h time periods. Similar proportions of time spent feeding (as a percentage) have been reported from several other African elephant populations; however, grazing rather than browsing was the dominant feeding activity. Defecation rates were lower than those reported for any other elephant populations in Africa, reflecting a lower volume of vegetation intake. Walking and social activities were at their maximum during the cold dry season when adult males came into musth and actively pursued receptive females, and declined in the hot dry and wet seasons. These activities were similar to those reported from Zimbabwe and Tanzania. Activities associated with water and resting increased to a maximum during the wet and hot dry seasons during the heat of the day (1100–1500 h). Water activities were higher than had been reported by any other study, while resting activities were lower than studies reported in Zimbabwe but similar to those in Uganda and Tanzania.

Key words: Diurnal activity, desert-dwelling elephants

Résumé

Les activités diurnes des éléphants vivant dans le désert (*Loxodonta africana*, Blumembach, 1797) dans la zone aride du nord-ouest de la Namibie ont été suivies pendant cinq ans (2002-2006) pendant les saisons pluvieuses, les saisons froides et sèches et les saisons chaudes et sèches. L'activité des éléphants vivant dans le désert change d'année en année et dépend des pluies et des inondations. On a utilisé trois méthodes pour rassembler les données de l'activité: deux méthodes se concentraient sur des animaux focaux où les éléphants individuels ont été suivis à 5 minutes d'intervalles ou de façon continue; la troisième méthode impliquait une méthode de scanner qui suivait les individus ou des groupes à 2 minutes d'intervalles. Aucune différence statistique n'a été remarquée dans les données obtenues par chaque méthode. Les activités de groupe enquêtées comprenaient

l'alimentation, l'eau, le repos, la socialisation et la marche, alors que les activités individuelles ont été davantage différenciées pour inclure paître, brouter, écorcer, s'abreuver, se vautrer, s'épousseter, se reposer à l'ombre, se reposer à ciel ouvert ou au soleil, et le type d'interaction sociale. Ces activités ont été analysées sur une base annuelle, saisonnière et journalière. Les variations annuelles dans les activités observées étaient probablement dues aux variations des pluies annuelles. Les activités d'alimentation étaient les activités majeures des éléphants du désert. Elles étaient semblables au cours de l'année et se produisaient principalement dans les périodes entre 07h00 et 11h00 et entre 15h00 et 17h00. Des proportions semblables de temps passé à l'alimentation (en tant que pourcentage) ont été rapportées chez plusieurs autres populations d'éléphants africains; cependant, paître plutôt que brouter était l'activité d'alimentation dominante. Les taux de défécation étaient inférieurs à ceux rapportés pour toutes les autres populations d'éléphants en Afrique, en reflétant un volume inférieur de prise de végétation. La marche et les activités sociales étaient à leur niveau maximum pendant la saison sèche et froide quand les mâles adultes entraient en musth et poursuivaient activement les femelles réceptives et déclinaient pendant les saisons chaudes et sèches et les saisons pluvieuses. Ces activités étaient semblables à celles rapportées au Zimbabwe et en Tanzanie. Les activités associées à l'eau et au repos augmentaient pour atteindre un maximum pendant les saisons pluvieuses et les saisons chaudes et sèches pendant la chaleur du jour (11h00–15h00). Les activités d'eau étaient beaucoup plus élevées que celles qui avaient été rapportées par toute autre étude, alors que les activités de repos étaient inférieures à celles rapportées par les études au Zimbabwe mais semblables à celles en Ouganda et en Tanzanie.

Introduction

The physical challenges facing mammals in an arid environment, particularly during the hot dry season where daily temperatures are high (>40° C) and surface water scarce, make survival difficult (Seely 1978; Viljoen 1992). Smaller mammals seek refuge underground during the hottest periods of the day and feed at night when ambient temperatures are lowest (Skinner and Smithers 1990; Estes 1992). Many species have physiological adaptations to cope with heat regulation and water conservation (Cloete and Kok 1986). Large mammals, because of their size, do not have the same options as smaller mammals, but they show behavioural responses to aid their long-term survival. Many seek to reduce energy-demanding activities (such as walking and feeding) during the heat of the day, conducting these activities in the cooler periods, thus reducing water loss and conserving energy (Mitchell 1977; Fennessy 2004). While many large mammals have 'thermal windows' such as sparsely haired or naked areas to dissipate heat or are able to dump excess heat by convection while lying on shaded ground (Joubert 1974; Fennessy 2004), few have the physiological adaptations of smaller mammals to cope with an arid environment (Cloete and Kok 1986).

A limited number of papers have been published on the ability of elephants to cope with arid environments. Hiley (1975) reported that African elephants in Uganda coped with increased daily temperatures by using mainly adaptive behaviour, such as dusting, bathing, mud-bathing and resting. Physiologically, elephants have a peculiar ability to store up to 10 L of water in a pharyngeal pouch (Shoshani 1998). This water can be extracted by the trunk and used to cool the elephant during the heat of the day (Leggett 2004). In the course of a normal day, adult African elephants require 160–250 kg of vegetation and up to 160 L of water (Sykes 1971). As these two commodities are generally in short supply in an arid area, desert-dwelling elephants tend to have larger seasonal home ranges and drink less often than savannah elephants (Viljoen 1987, 1989; Viljoen and Bothma 1990a; Leggett 2004, 2006b).

The movements and seasonal home ranges of the desert-dwelling elephants in the northwest of Namibia have been studied in detail (Viljoen 1987, 1989b; Viljoen and Bothma 1990a; Lindeque and Lindeque 1991; Leggett et al. 2003; Leggett 2006a). The home ranges of GPS collared adult male elephants in northwest Namibia varied from 2168 to 12,800 km^2, while those of adult female elephants ranged from 871 to 5900 km^2 (Leggett 2006a). The daily movements of these elephants varied from 4 to 38 km in a 12–hour period (Viljoen and Bothma 1990b), while Viljoen (1989a) reported elephant food preferences, habitat selection and influence of annual vegetation.

Studies of elephant activity and behaviour have been well reported in the literature (Wyatt and El-

tringham 1974; Guy 1976; Barnes 1982; Barnes 1983; Moss 1983; Kalemera 1987; Poole 1987; Kabigumila 1993). The majority of reported activity studies are either seasonal (Wyatt and Eltringham 1974) or annual (Guy 1976; Barnes 1983; Kabigumila 1993). There have been a number of long-term behavioural studies published, most dealing with aspects of sexual selection and offspring raising (Moss 1983; Poole 1987; Lee 1987). However, few studies have examined the long-term, day-to-day activities of elephants. None of these studies have reported the activities of elephants in arid environments.

Reported methods for analysing elephant behaviour and activity have varied significantly, though most use a point-sampling technique (also referred to as a scan technique). Barnes (1982; 1983) used a four-minute sampling technique for bull elephants and a five-minute interval for female family units. Multiple elephants were analysed at any one time with this method. Several authors have reported studies that focused on one elephant at a time. Wyatt and Eltringham (1974) used a four-minute interval. While Kabigumila (1993) and Lee (1987) used five-minute intervals, Guy (1976) used continuous survey methods. Kalemera (1987) used a combination of multiple elephant surveys at five-minute intervals and the continuous survey method described by Guy (1976). However, the results obtained from the use of these methods in elephant behavioural research have not been compared and studies based on different methods may yield different conclusions.

The annual variations in water availability and ambient temperatures are significant in an arid area (Jacobson et al. 1995; Leggett et al. 2001). A comprehensive study examining the behaviour of elephants in this environment must be undertaken on a longer time scale to encompass the wider variation in climatic conditions. This paper reports the diurnal activities of desert-dwelling elephants in the arid northwest of Namibia over a five year period (2002–2006), and investigates whether the activities of elephants in this area vary significantly from those of African elephants in more temperate regions. In addition, it compares and contrasts three different methods for recording the activity of groups and individual elephants.

Study area

The research was located in the Kunene Region in northwest Namibia (Fig. 1). The western-flowing ephemeral rivers of northwestern Namibia carry very little surface water. In the last 23 years, the number of days of flooding ('flood' being defined as any time when there is surface water flowing in the river) in the Hoanib River (at the weir near Sesfontein) varied from four days in 1981 to 52 days in 1983, with an average of 17.7 days (Leggett et al. 2001). For most of the year, the water flows below the surface (Jacobson et al. 1995). The 50-year average monthly rainfall and the maximum and minimum temperatures for Sesfontein are shown in Fig. 2. In the arid western areas of Namibia, rainfall is both spatially and temporally variable with up to 90% fluctuation in annual rainfall (Jacobson et al. 1995). Ambient temperatures can vary by up to 10% annually (Jacobson et al. 1995). There are three recognizable seasons in the western section of the Kunene Region which are functional and broadly defined (after Viljoen 1988): wet season (February–May), cold dry season (June –August) and hot dry season (September–January). The wet season commences with the first rains, or, in the arid western region, with the first flood in the ephemeral rivers; the effect of the wet season is felt for up to one month after the last rains or flood (Viljoen 1988; Leggett et al. 2001). There is a steep decreasing rainfall gradient from east to west across the catchment (Fig. 1, Jacobson et al. 1995; Leggett et al. 2001).

The vegetation in northwestern Namibia has been described by a number of authors (Giess 1971; Becker and Jurgens 2000; Leggett et al. 2002). Becker and Jurgens (2000) reported the vegetation gradient from east to west in the northern Kunene Region and identified 45 major plant communities. In addition, they discerned four identifiable main vegetation units:

a) *Colophospermum mopane–Terminalia prunioides–Combretum apiculatum* savannah, which corresponds approximately to the 250–350 mm rainfall zone;
b) *Colophospermum mopane–Terminalia prunioides* savannah, which corresponds approximately to the 150–250 mm rainfall zone;
c) *Colophospermum mopane* savannah and ephemeral grasslands dominated by *Stipagrostis hirtigluma*, which corresponds approximately to the 100–150 mm rainfall zone;
d) more permanent grasslands dominated by *Stipagrostis uniplumis*, which corresponds approximately to the 50–100 mm rainfall zone.

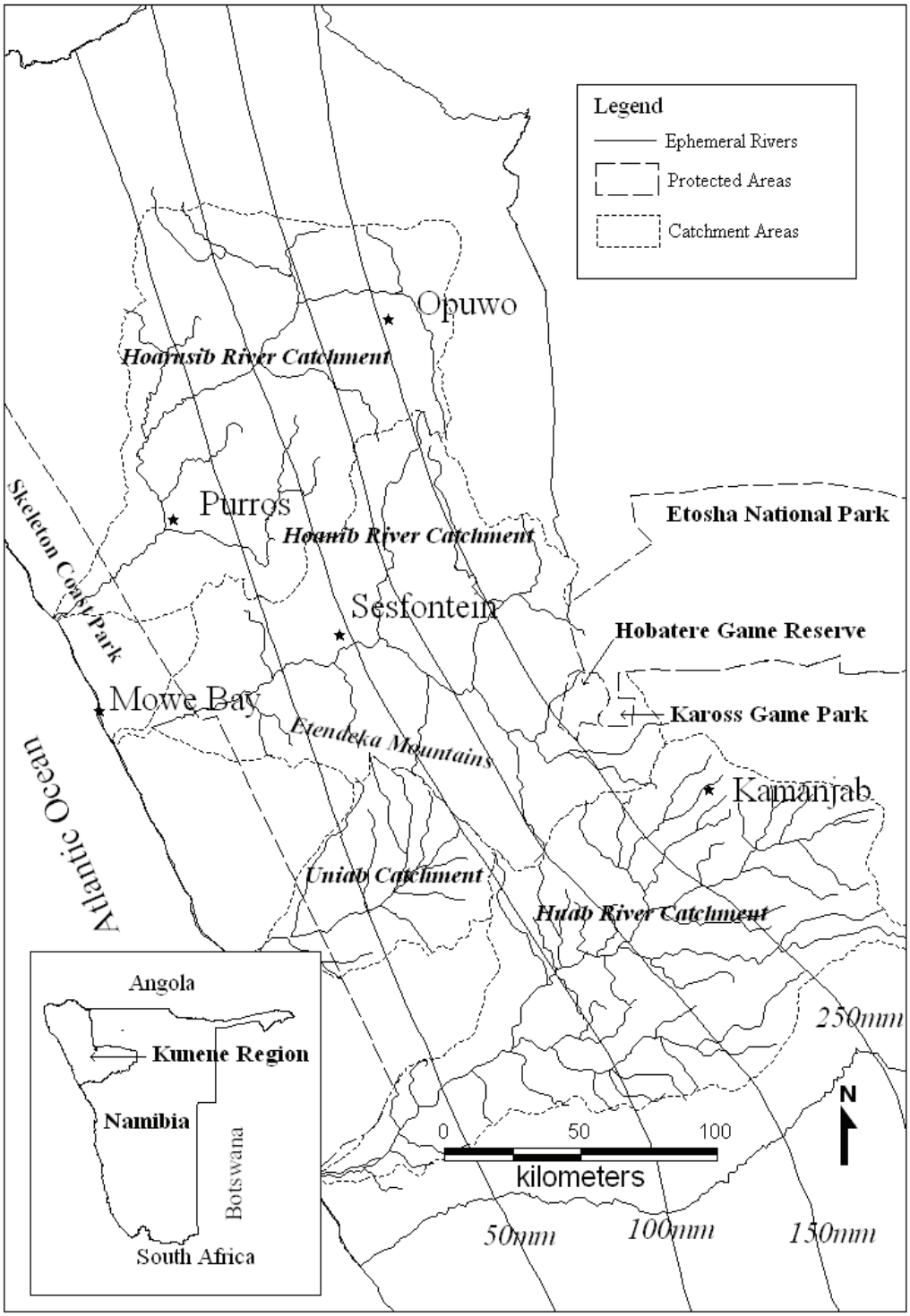


Figure 1. Location of research area in northwest Namibia.

Arid area riverine vegetation, particularly *Faidherbia albida*, *Acacia erioloba* and *Combretum imberbe* trees, dominate the ephemeral rivers (Viljoen and Bothma 1990b; Jacobson et al. 1995; Becker and Jurgens 2000; Fennessy et al. 2001).

The elephant population in the study area has been described in detail by a number of authors (Viljoen 1987, 1988, 1989a, 1989b; Viljoen and Bothma 1990a; Leggett et al. 2003; Leggett 2006a). Initial studies (1981–1984, population ~360) suggested that the population was split into two (Viljoen 1989b), with some possible genetic exchange via a third transitional population (Viljoen 1989a) as no direct contact was observed between the two populations (Viljoen 1989b). With the cessation of civil war (1990), and the advent of community-based conservation initiatives (Leggett et al. 2003), the elephant population has recovered (~760, SSS 1999). Subsequent studies have shown that these populations are not isolated, with movements of adult male elephants from the Etosha National Park into the arid western regions regularly observed (Leggett 2006a).

Near the Hoanib and Hoarusib Rivers, west of the 100 mm rainfall isohyet, there are approximately 36 elephants in seven family units (between three and nine individuals in each), plus up to 16 free-ranging adult males that move into and out of the research area. Only three family units and four to six free-ranging adult males have been observed to move seasonally between the Hoanib and Hoarusib Rivers. This paper focuses on the activities of these 52 elephants.

Materials and Methods

The observations reported in this paper were made between June 2002 and November 2006. During this time, the researchers spent a minimum of 10 days per month in the research area observing elephants and recording detailed information on identification, location (GPS co-ordinates), numbers, activities and behaviour.

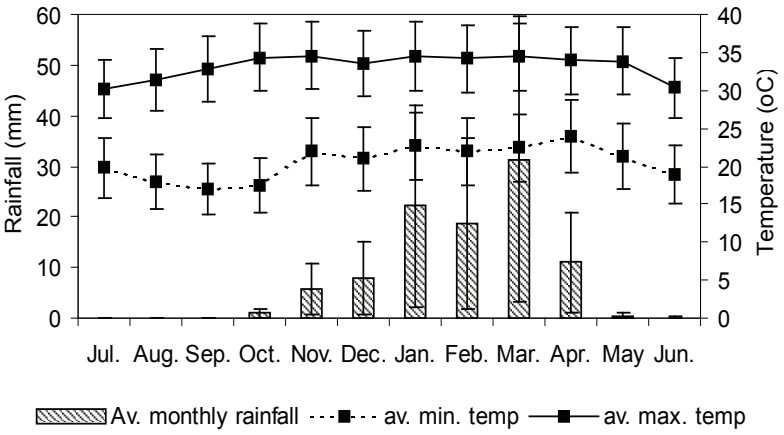
Elephants were individually identified using a combination of photographs and identification sheets. The photographic techniques used were similar to techniques already described by Douglas-Hamilton and Douglas-Hamilton (1975), Moss (1982) and Sukumar (1989). Photographs were taken from the front, left and right side of each individual. In addition, field identification sheets were kept for each individual elephant. When an unknown elephant was identified, it was given a unique nomenclature and, during all subsequent observations, its nomenclature, current elephant-elephant associations and activity were recorded. If an elephant broke a tusk or if any additional ear holes or tears were noted, the relevant identification sheets were updated and changes added to the database.

Three different methods for recording activity were undertaken and compared. All methods used either point sample techniques or focal sample techniques over specified time intervals. When studying elephant groups, a point sample technique similar to that described by Barnes (1982) and Kalemera (1987) was used. All individual activity within the group was recorded at two-minute intervals for up to three hours. The two-minute scan study obtained data only on feeding, water, resting, social and walking activities but did so for all individuals being observed at the time.

The second method used a focal sample technique, where known individuals were observed for a minimum of 30 minutes to a maximum of three hours, data being recorded at five-minute intervals (Kabigumila 1993; Lee 1996). Detailed information on that individual was recorded on a check sheet similar to that described by Lee (1996), and activities were defined in a manner similar to that described by Guy (1976). These were categorized under five main headings and subdivided as follows:

1) Feeding:
    a) grazing
    b) browsing
    c) debarking of trees
2) Activities associated with water (Water Activities):
    a) drinking
    b) wallowing
    c) dust bathing
3) Resting:
    a) standing or sleeping in shade
    b) standing or sleeping in the open or sun
4) Social activities:
    activities include: playing, fighting, communication, aggression, nursing and courtship
5) Walking

The third method, also employed a focal sample technique similar to that described by Guy (1976), focused on an individual, with data recorded continuously for between one and five hours, using the same activity categories as described for the five-minute focal animal study. A change in behaviour was defined as any activity undertaken for longer than one minute. For example, if



Sources:

(a) Ministry of Agriculture, Water and Rural Development, Sesfontein and Windhoek, Namibia

(b) Hoanib River Catchment Study, Desert Research Foundation of Namibia, Windhoek, Namibia

Figure 2. Average monthly rainfall, and maximum and minimum temperatures at Sesfontein, northwest Namibia.

an elephant was walking and stopped to feed for less than a minute, then walked on, the activity would be regarded as 'walking' and not 'walking/feeding'.

At the commencement of the study, it was not clear which activity observational method would be the most appropriate for elephants in arid environments. A study was undertaken to compare the accuracy of the three methods. An adult female was identified and observed for a total of 77.8 hours, with all three methods being used simultaneously to evaluate activity behaviour. In addition, any defecation events observed during the study periods were recorded.

Throughout the study, an effort was made to collect data on all age groups. For the purposes of this study, age groups were defined as follows: juveniles (defined as elephants that had not yet been weaned (0–4 years)), subadults (4–10 years female, 4–14 years male), and adults (>10 years female; >14 years male). During each field trip, attempts were made to collect data on all age groups for every hour between 0700 and 1900 h. However, due to seasonal light availability, this was not possible in all morning and evening time slots.

The first elephant encountered by the researcher at the start of a research day was observed and activities recorded. To avoid biasing the study towards those individuals that were easily found, if the first individual encountered had been observed in the previous month, observations were not undertaken and another elephant sought. Most elephants were initially encountered either in the riverbeds or on the river plains, then followed and observed. Although this might infer a bias towards individuals that reside or traverse these areas, elephants in the study area spend about 85% of their time in these habitats. When undertaking a two-minute scan or a five-minute focal animal study, it was possible to observe up to four different individuals or groups in a day, depending on accessibility. However, the number of studies that could be undertaken was reduced when longer-term studies were conducted. During the wet season, it was difficult to get into the field due to rainfall and flooding in the rivers and so there was generally a shortage of data from this season (Table 1).

Table 1. Number of hours of observation of desert-dwelling elephants, northwestern Namibia 2002–2006

	Observational method			
	2-minute point sample study (hrs)	5-minute focal animal study (hrs)	Continuous focal animal study (hrs)	Total (hrs)
Wet season				
2003		19.7	5.5	23.4
2004		18.3	7.1	25.4
2005	12.1	10.0	9.2	31.3
2006	22.2	15.0	2.5	39.7
Cold dry season				
2002		6.8	38.1	44.9
2003		21.5	30.1	51.6
2004	73.9	22.1	3.8	99.8
2005	63.7	36.0	5.0	104.7
2006	56.1	20.6	18.7	95.4
Hot dry season				
2002		14.3	12.3	26.6
2003		21.2	13.2	34.4
2004		28.3	5.8	34.1
2005	22.1	44.9	12.1	79.1
2006	33.3	27.9	11.7	72.9

The non-parametric Mann-Whitney U-test was used for the statistical analysis of defecation data, while Kraskal Wallis ANOVA was used to analyse annual and seasonal data.

All data presented in Tables 2 and 3 are a combination of the two-minute scan, the five-minute and long-term focal study data sets, while data presented in Table 4 were taken from five-minute focal elephant studies. Annual data sets were combined for the same category of activity and then tested for differences between different activity categories. In the Tables, data are presented as a percentage, with the average (Av.) and standard deviation (±SD) values shown.

Results

Comparison between methods and other areas of Africa

The results obtained from a simultaneous comparison of the three activity methods (the two-minute scan and the five-minute and continuous focal animal techniques) are presented in Table 5. There was no significant difference between the data obtained by any of the methods.

Published data from other researchers elsewhere in Africa are presented in Table 6. While researchers have consistently reported data on feeding, resting and walking, data on social activities and activities associated with water are lacking in two of the studies.

Annual and seasonal variations in activities

The seasonal activity percentages for desert-dwelling elephants in the study period 2002–2006 are presented in Table 2. This Table presents the combined data from all three activity methods. Annual activity data vary from one year to the next and are dependent on rainfall, flood events and variations in ambient temperature.

From the results it can be seen that amount of time spent feeding varied little between the seasons. The small decrease in the level of feeding activity observed during the cold dry season was not significant. Also, there was little significant difference between the seasons in the levels of activities associated with water, with only a small decrease in the level of these activities being observed during the cold dry season. The amount of time spent resting was highest during the wet and hot dry seasons, and decreased during the cold dry season. Again the decrease is not significant. The levels of social and walking activities were observed to increase during the cold dry season, but did not significantly decrease during the wet or hot dry seasons.

Defecation rates

Table 2 also contains the seasonal defecation rates of male and female elephants in the study area. Male elephant defecation rates were significantly greater ($U = 0.00$, $P = 0.0463$) than female rates in

Table 2. Variation in observed annual and seasonal activity of desert-dwelling elephants, northwestern Namibia, 2002–2006

	Wet season					Cold dry season						Hot dry season					
ACTIVITY	2003	2004	2005	2006	Av.	2002	2003	2004	2005	2006	Av.	2002	2003	2004	2005	2006	Av.
	Av. (±SD) %[a]	Av. (±SD) %[a]	Av. (±SD) %[a]	Av. (±SD) %[a]	(±SD) %[a]	Av. (±SD) %[a]	Av. (±SD) %[a]	Av. (±SD) %[a]	Av. (±SD) %[a]	Av. (±SD) %[a]	(±SD) %[a]	Av. (±SD) %[a]	Av. (±SD) %[a]	Av. (±SD) %[a]	Av. (±SD) %[a]	Av. (±SD) %[a]	(±SD) %[a]
Feeding	64.5 (±2.9)	41.8 (±7.9)	45.7 (±6.8)	43.7 (±6.8)	48.9 (±12.8)	46.5 (±20.4)	54.4 (±4.1)	41.8 (±17.1)	38.9 (±25.0)	54.0 (±2.7)	47.1 (±35.7)	46.4 (±0.2)	45.4 (±2.6)	55.7 (±8.5)	45.7 (±19.0)	49.1 (±7.8)	48.4 (±22.4)
Water	11.0 (±10.3)	12.7 (±3.9)	7.0 (±7.6)	12.5 (±5.0)	10.8 (±14.1)	13.4 (±3.4)	6.8 (±3.1)	12.7 (±12.3)	6.3 (±2.8)	10.6 (±12.4)	10.0 (±18.3)	20.3 (±0.8)	8.5 (±3.1)	2.5 (±2.7)	9.6 (±7.0)	12.5 (±12.8)	10.7 (±15.2)
Resting	8.8 (±7.3)	6.9 (±0.4)	19.4 (±6.8)	21.5 (±8.7)	14.1 (±13.2)	11.7 (±14.8)	11.1 (±4.1)	6.9 (±3.1)	12.3 (±7.7)	15.0 (±2.5)	11.4 (±17.6)	14.9 (±1.4)	9.8 (±1.1)	18.2 (±18.2)	12.2 (±9.9)	14.8 (±5.1)	14.0 (±21.4)
Social	1.2 (±0.9)	2.3 (±0.5)	2.8 (±1.6)	1.2 (±1.0)	1.9 (±2.1)	5.6 (±0.7)	1.1 (±0.6)	2.3 (±2.7)	4.2 (±3.3)	2.4 (±0.6)	3.1 (±4.4)	2.4 (±3.3)	0.6 (±0.8)	0.0 (±0.0)	5.1 (±4.9)	2.4 (±0.8)	2.1 (±6.0)
Walking	14.5 (±0.7)	36.3 (±4.9)	25.1 (±9.2)	21.8 (±0.7)	24.4 (±10.5)	22.7 (±9.9)	26.5 (±2.5)	36.3 (±15.7)	38.4 (±18.1)	18.0 (±8.4)	28.4 (±27.4)	16.0 (±1.2)	35.6 (±5.3)	23.7 (±7.0)	27.2 (±3.0)	21.3 (±14.7)	24.8 (±17.4)
Defecations per hour																	
♂						0.53 (±0.26)					0.30 (±0.15)						0.46 (±0.22)
♀						0.21 (±0.10)					0.24 (±0.12)						0.21 (±0.10)

[a] percentage of time

northwestern Namibia. The maximum defecation rates observed in males during the wet and hot dry seasons were 0.48/hr and 0.41/hr, respectively, with minimum rates of 0.32/hr being observed during the cold dry season. Female elephants showed similar defecation rates in all the seasons (0.18–0.25/hr). No significant difference was observed in defecation rates between seasons for either male or female adult elephants.

Age/sex activities

The breakdown of age/sex-related activity is presented in Table 3.

Wet season

With the exception of subadults, whose feeding activity was higher during the wet season, all other ages and both sexes were observed to have similar levels of feeding activity. In comparison to other age/sex classes, adult males spent more time engaged in activities associated with water and resting, and less time engaged in social and walking activities. Adult females and juveniles spent similar amounts of time engaged in activities associated with water and resting, but adult females spent less time engaged in social activities and more time engaged in walking activities (e.g. social; *H=3.74, P=0.30*). Subadults and juveniles showed similar levels of social (associated with play behaviour) and walking activities, but subadults showed decreased levels of the activities associated with water and resting than either adult females or juveniles.

Table 3. Age/sex and seasonal observed activity budgets in desert-dwelling elephants, northwestern Namibia, 2002–2006

	Wet season Av. (±SD) %	Cold dry season Av. (±SD) %	Hot dry season Av. (±SD) %
Adult male			
Feeding	48.5±12.3	55.6±13.9	45.6±11.8
Water	12.7±8.3	5.9±0.4	8.8±3.5
Resting	18.5±10.3	12.9±1.8	16.3±8.6
Social	0.7±1.0	2.7±0.6	1.8±1.9
Walking	19.6±3.5	22.9±0.3	27.5±11.6
Adult Female			
Feeding	45.7±3.9	52.1±3.7	47.1±24.0
Water	11.9±4.2	8.7±0.9	13.1±4.8
Resting	15.1±7.4	10.1±3.8	12.8±13.1
Social	1.4±0.8	1.8±0.8	2.2±1.8
Walking	25.9±10.2	27.3±11.3	24.8±8.8
Subadult			
Feeding	58.2±19.8	53.5±6.2	57.9±30.4
Water	10.4±6.7	8.5±2.2	7.1±7.5
Resting	9.3±11.8	8.2±1.5	16.8±10.0
Social	2.4±2.2	2.5±2.1	2.5±3.5
Walking	19.7±3.6	27.3±2.5	15.7±10.3
Juvenile			
Feeding	42.8±18.6	43.6±13.0	46.2±9.8
Water	10.3±11.2	8.2±2.2	8.0±10.3
Resting	23.7±8.2	10.8±8.8	17.9±7.8
Social	3.3±0.9	4.5±2.9	1.8±1.3
Walking	19.9±20.2	32.9±20.7	26.1±7.0

Cold dry season

All activities—feeding, water, resting, social and walking were at similar levels for all the ages and sexes during this season (e.g. walking; *H=6.37, P=0.09*). However, levels of social activity were observed to increase compared to the wet and hot dry seasons in both adult males and adult females, but remained similar in subadults and juveniles. Adult males (approximately 15% of the adult male population at any one time) were observed to be in musth during this season.

Hot dry season

While adult male and subadult elephants showed similar levels of feeding activity, levels of feeding activity in adult females and juveniles decreased during this season. Adult males, adult females and subadults spent similar amounts of time engaged in water and resting activities, but juveniles showed an increase in the amount of time spent in both activities. Levels of social activity in subadults and juveniles decreased during the hot dry season compared to those observed during the wet and cold dry seasons. Levels of walking activity in adult females and juveniles were greater than those in either adult males or subadults.

Diurnal activities

The breakdown of diurnal activities during the 0700–1100 h, 1100–1500 h and 1500–1900 h time periods is presented in Table 4.

Wet season

There was an observed increase in the amount of time spent feeding during the 0700–1100 h and 1500–1900 h time periods, with a significant decrease (*H=5.69, P<0.05*) in feeding activity and a significant increase in resting activity (*H=8.80, P<0.01*) during the 1100–1500 h time period. Grazing comprised a significantly greater percentage of feeding activities (*H=4.84, P<0.05*) during the

Table 4. Daily and seasonal activity budgets of desert-dwelling elephants, northwestern Namibia, 2002–2005

	Wet season			Cold dry season			Hot dry season		
	0700–1100 Av. (±SD) %[a]	1100–1500 Av. (±SD) %[a]	1500–1900 Av. (±SD) %[a]	0700–1100 Av. (±SD) %[a]	1100–1500 Av. (±SD) %[a]	1500–1900 Av. (±SD) %[a]	0700–1100 Av. (±SD) %[a]	1100–1500 Av. (±SD) %[a]	1500–1900 Av. (±SD) %[a]
Feeding									
(a) Grazing	22.3 (±18.9)	2.5 (±3.1)	5.6 (±10.3)	7.9 (±11.9)	7.0 (±5.7)	4.8 (±10.6)	4.9 (±3.1)	2.0 (±3.9)	8.8 (±12.6)
(b) Browsing	30.7 (±26.5)	20.3 (±20.5)	59.6 (±57.7)	52.2 (±46.2)	33.7 (±31.2)	53.7 (±37.4)	50.7 (±48.1)	32.3 (±23.6)	47.4 (±50.6)
(c) Debarking	0.0 (±0.0)	0.0 (±0.0)	0.0 (±0.0)	0.0 (±0.0)	0.0 (±0.0)	0.0 (±0.0)	0.3 (±0.6)	0.0 (±0.0)	0.18 (±0.5)
Water									
(a) Drinking	3.3 (±3.3)	1.7 (±3.2)	2.8 (±4.4)	3.6 (±6.4)	9.3 (±11.7)	3.8 (±5.5)	3.9 (±5.3)	9.3 (±11.9)	2.4 (±3.5)
(b) Wallowing	0.2 (±0.5)	2.6 (±3.1)	0.5 (±1.3)	0.6 (±1.7)	0.2 (±0.8)	0.2 (±0.9)	0.0 (±0.0)	4.1 (±26.8)	0.2 (±0.5)
(c) Dust bathing	1.7 (±2.4)	0.0 (±0.0)	1.4 (±2.4)	0.8 (±2.1)	3.6 (±5.0)	2.5 (±6.7)	1.8 (±1.3)	4.5 (±2.3)	2.0 (±2.1)
Resting									
(a) Standing in shade	11.4 (±14.3)	57.6 (±48.4)	3.2 (±4.3)	3.2 (±8.9)	22.6 (±16.3)	6.3 (±9.8)	12.4 (±19.0)	21.9 (±32.0)	7.3 (±2.2)
(b) Standing in full sun	0.2 (±0.5)	0.8 (±1.6)	0.0 (±0.0)	0.5 (±3.2)	0.2 (±0.8)	0.0 (±0.0)	2.4 (±1.7)	12.6 (±14.2)	4.4 (±9.0)
Social	0.5 (±1.1)	2.5 (±4.8)	1.9 (±2.1)	1.4 (±2.9)	2.3 (±4.5)	2.3 (±1.5)	1.2 (±1.3)	0.4 (±0.8)	0.6 (±1.0)
Walking	29.7 (±32.5)	11.9 (±15.2)	25.0 (±17.7)	29.8 (±16.9)	21.1 (±24.6)	26.4 (±27.5)	22.4 (±19.6)	13.0 (±4.6)	26.8 (±18.1)

[a] percentage of time

0700–1100 h time period, decreasing throughout the day. While activities associated with water were observed to be similar throughout the day, the amount of time spent wallowing increased during the 1100–1500 h time period. Similarly, levels of social activity were observed to increase during the 1100–1500 h time period. The level of walking activity was at a maximum during the 0700–1100 h and 1500–1900 h time periods and decreased during the 1100–1500 h time period.

Cold dry season

Feeding activity remained at similar levels during the 0700–1100 h and 1500–1900 h time periods, with a decrease observed during the 1100–1500 h time period. Browsing was the dominant form of feeding activity. The level of activities associated with water, particularly drinking, increased during the 1100–1500 h period, and the amount of time spent resting increased significantly ($H=5.91$, $P<0.05$) during this period. Social activities showed a non-significant increase during the 1100–1500 h and 1500–1900 h time periods. The amount of time spent walking was at a similar level throughout the day, with only a small decrease observed during the 1100–1500 h period.

Hot dry season

The level of feeding activity decreased significantly ($H=5.81$, $P<0.05$) during the 1100–1500 h period and an overall decline in the percentage of time spent grazing was observed. Browsing was still the dominant form of feeding activity. Debarking was only observed during this season and then only rarely. The amount of time spent engaged in activities associated with water and resting increased during the 1100–1500 h period, resting activities significantly

Table 5. Comparison among two-minute interval, five-minute interval and continuous survey methods of activities recorded

	Observational method		
Activity	2-minute point sample group study Av. (± Std) %[a]	5-minute focal animal study Av. (± Std) %[a]	Continuous focal animal study Av. (± Std) %[a]
Feeding	52.0±16.5	56.3±9.2	56.0±12.6
Water	5.5±4.9	3.9±1.6	4.3±3.0
Resting	16.2±3.3	17.1±1.1	14.3±1.9
Social	3.7±2.9	2.1±1.8	2.0±1.2
Walking	22.5±5.4	20.7±8.4	23.5±12.8

[a] percentage of time

Table 6. Comparison between African elephant activity data collected by similar methods from other African countries

	Uganda[a]	Zimbabwe[b]			Tanzania[c]		Namibia[d]		
Activity	%	Wet Season Av. (±SD) %	Cold Season Av. (±SD) %	Hot Season Av. (±SD) %	Wet Season %	Hot Season %	Wet Season Av. (±SD) %	Cold dry season Av. (±SD) %	Hot dry season Av. (±SD) %
Feeding	74.2	56.5 (±8.4)	46.9 (±6.9)	36.1 (±5.4)	70.1	66.8	48.9 (±12.8)	47.1 (±35.7)	48.4 (±22.4)
Water		5.1 (±1.2)	3.0 (±0.9)	2.9 (±1.0)	4.0	3.8	10.8 (±14.1)	10.0 (±18.3)	10.7 (±15.2)
Resting	13.2	20.9 (±6.2)	31.4 (±5.3)	42.0 (±7.8)	12.7	16.0	14.1 (±13.2)	11.4 (±17.6)	14.0 (±21.4)
Social		1.0 (±4.9)	0.4 (±0.6)	-			1.9 (±2.1)	3.1 (±4.4)	2.1 (±6.0)
Walking	11.3	16.4 (±3.9)	17.9 (±1.7)	19.0 (±1.8)	13.2	13.3	24.4 (±10.5)	28.4 (±27.4)	24.8 (±17.4)
Other	1.3								
Defecations per hour									
♂		0.65	0.48	0.70	1.32[e]	0.40[e]	0.48 (±0.26)	0.32 (±0.15)	0.41 (±0.22)
♀		0.40	0.33	0.44			0.24 (±0.10)	0.25 (±0.12)	0.18 (±0.10)

[a] Watt & Eltringham (1974)
[b] Guy (1976)
[c] Kabigumila (1993)
[d] This study
[e] Barnes (1982)

(*H=7.42, P<0.05*), with an increase in the amount of time spent resting in full sun during 1100–1500. There was an observed decrease in the amount of walking activity during the 1100–1500 h period. The majority of social activities occurred during the 0700–1100 h period, with a decrease in this type of activity being observed during the 1100–1500 h and 1500–1900 h time periods.

Discussion

Results obtained by different methods

While there was little statistical difference between the three activity study methods, practically, each method had positive and negative aspects. The two-minute studies provided a great deal of data in a relatively short period of time concerning a group of elephants, but yielded no detailed information on individuals. The five-minute focal study provided detailed information on an individual, but tended to be biased towards major activities. This is not surprising as there are fewer data points in any given time period than in either of the other studies, but, over a longer time frame, this bias should be removed. The continuous study again focused on individuals, obtaining continuous data over a longer time period (1–5 hrs). The results obtained from this method were closer in activity percentages to the two-minute study than they were to the five-minute studies. However, monitoring changes in activity was difficult and subjective. In addition, it was much more difficult to obtain data for more than one individual in a day by the continuous survey method, while the two other methods allowed for data collection from multiple individuals in a day. Using only the long-term continuous data collection method could lead to bias in the data towards particular animals unless an effort was made to observe both sexes and all different age groups in any given time period.

The lack of difference between the data obtained from the various sampling methods leads to two further conclusions. Firstly, all previous studies, regardless of the manner of data collection, can be legitimately compared. Secondly, the choice of

method for a particular study can be made according to the constraints of the study itself, rather than being dictated by the methods.

Feeding activities and defecation rates

Annually, the differences observed in types of feeding activity were probably attributable to variations in annual rainfall. In years of above average rainfall, annual grasses and forbs were more abundant, and increased levels of grazing activity were observed. During average or below average rainfall years, browsing dominated. This was completely different from what had been reported in other African countries where seasonally available grazing made up a higher percentage of the diet (Wyatt and Eltringham 1974; Guy 1976; Kabigumila 1993). During the wet season, the percentage of time that desert-dwelling elephants spent in feeding activities was similar to that reported by Guy (1976) for elephants in Zimbabwe, but was lower than that reported for Uganda (Wyatt and Eltringham 1974) and Tanzania (Kabigumila, 1993). Levels of feeding activity decreased slightly during the cold and hot dry seasons with browsing being the dominant feeding activity during these seasons. Elephants sought out fruiting *Acacia erioloba* and *Faidherbia albida* trees during the cold and hot dry seasons respectively (Leggett 2006a). This undoubtedly accounts for the higher levels of feeding activity observed here in the cold and hot dry seasons than those reported in Zimbabwe (Guy, 1976). These levels were however, lower than those reported in Tanzania (Kabigumila 1993). Debarking was only observed during the hot dry season and then only rarely, which was different from the feeding activity reported by Guy (1976) where debarking made up a substantial percentage of feeding activity during the hot dry season.

Male desert-dwelling elephant defecation rates during the wet and hot dry seasons were similar, with a decrease observed during the cold dry season. The low defecation rates during the cold dry season could be due to the adult males being in musth and spending greater amounts of time in socializing and walking activities in search of receptive females. A loss in body condition in musthing males was reported by Poole (1982) and thought to be due to a change in activities. Female desert-dwelling elephants showed similar defecation rates during the wet and cold dry seasons with a slight decrease during the hot dry season when vegetation was scarcer. Guy (1976) reported a similar trend in defecation rates with a cold season low, but his reported defecation rates were higher than those of the desert-dwelling elephants in all seasons. Barnes (1982) reported even higher rates of seasonal defecation for male savannah elephants in Tanzania. This would imply that desert-dwelling elephants, while feeding for a similar proportion of their time as other elephants in Africa, take in a smaller quantity of vegetation.

Water

As with all activities, annual and seasonal variations in activities associated with water were probably attributable to variations in ambient temperature and water availability. During the wet and hot dry seasons, the high daily temperatures resulted in a higher percentage of time being spent on activities associated with water than during the cold dry season. The level of water activities observed was higher than that reported in the rest of Africa (Wyatt and Eltringham 1974; Guy 1976; Kabigumila 1993). The observed increase in wallowing activity during the hottest part of the day (1100–1500 h) was similar to that reported by Guy (1976). In particular, adult females and juveniles spent longer periods engaged in water activities than either adult males or subadult elephants. Water activities were probably used to reduce heat stress associated with higher ambient temperatures. The level of activities associated with water decreased slightly during the cold dry season, but was higher than that reported by Guy (1976), who observed a decrease in the levels of water activities from the wet season to the cold dry and hot dry seasons, and explained that this decrease was due to the lack of available water during the cold dry and hot dry seasons. This was probably not the case in the study area as there was water available in the ephemeral rivers, but it is more likely that the reduced temperatures in the cold dry season did not encourage these activities.

Resting

Levels of resting activity in all seasons were lower than those reported by Guy (1976), but were similar to those reported by Kabigumila (1993) and Wyatt and Eltringham (1974). Desert-dwelling elephants probably reduce their diurnal resting times to allow sufficient time for other activities. During the 1100–1500 h time period of the hot dry season, a greater percentage of time was spent resting by all age/sex groups. This was undoubtedly due to the high ambient temperatures during the heat of the day when elephants rested in the shade of large trees. Juvenile elephants rested more

than any other age group. In response, adult females also increased their rest periods during the hot dry season to protect and assist the juveniles.

Social

During the wet and hot dry seasons, an increase in social activity was observed during the 1100–1500 h time period. This can probably be attributed to the aggregation of elephants under available large shade trees, thus allowing a greater opportunity for interaction. Levels of social activity were higher in all time periods during the cold dry season. This was caused by an increase in adult male musthing and sexual contact with females. Contact mostly took the form of male/female interaction, with males often smelling females' genitalia and laying their trunks along the females' backs. This level of activity varied year to year depending on annual rainfall, and the amount and quality of vegetation consequently available. For example, if insufficient nutritious vegetation was available, it is unlikely that females would have come into season (Moss, 1982), thus reducing sexual activity. Similar behaviour was reported by Guy (1976), albeit during the wet season when he observed heightened sexual activity (males coming into musth, seeking females and then courtship behaviour). Increased play and sparring were also observed between sexes and among age groups during this period. A similar increase in social behaviour by all age groups during periods of increased adult sexual contact was reported by Kabigumila (1993).

Walking

The majority of the walking activity during the wet and hot dry seasons was during the cooler periods (0700–1100 h and 1500–1900 h) of the day. Generally, in the northwestern areas of Namibia, water was available throughout the year at known water sources (Leggett 2006b). The distribution of water throughout the veld generally does not increase greatly in the wet season, as rainfall is temporally and spatially variable, but the ephemeral rivers do flood (i.e. contain surface-flowing water) for varying lengths of time (Leggett et al. 2001). While this provides more water in the riverbeds (Leggett et al. 2001), palatable vegetation may still be quite some distance away, requiring elephants to walk long distances (Viljoen and Bothma, 1990a). Adult females and their dependent offspring were observed to walk further than adult males and subadults. Barnes (1983) reported similar observations, with longer daily movements for females and their dependent offspring in the search for water and forage during the dry season in Tanzania. Further, he reported that the benefits of additional nutrition outweighed a likely increase in juvenile mortality resulting from such high levels of walking activity. In the study area, levels of walking activity remained high during the cold dry season. Although elephants tended to concentrate around known water points during this season (Leggett 2006a), they still needed to walk long distances between water sources and feeding areas. In addition, with increased sexual activity observed during the cold dry season, musth adult males, in particular, tend to undertake almost constant movement searching for receptive females (Leggett 2006a).

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