



**Microclimate mosaic and its influence on behaviour of
free-living African forest elephants
(*Loxodonta africana cyclotis*)**

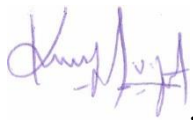
Michael Viyof Kuwong

Dissertation submitted to the Faculty of Health Sciences, University of the Witwatersrand,
Johannesburg, in fulfilment of the requirements for the degree of Master of Science in Medicine.

Johannesburg, 2014

DECLARATION

I, Michael Viyof Kuwong, declare that this dissertation is my own work, with all assistance acknowledged. This dissertation is being submitted for the degree of Master of Science in Medicine at University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other university.



MICHAEL VIYOF KUWONG

06th February 2014

I certify that the procedures used in this dissertation were approved by the Animal Ethics Screening Committee of the University of the Witwatersrand (AESC) clearance number: 2010/50/01

I thank the Brain Function Research Group (BFRG) School of Physiology, University of the Witwatersrand, Johannesburg, the Medical Faculty Research Endowment Fund (MFREF), the National Research Foundation (NRF), South Africa and the North Carolina Zoological Society (NCZ), USA, for their financial support.

ABSTRACT

African elephants are known to survive in habitats with ambient temperatures from below 0°C to about 50°C, implying that they may be exposed to great thermal challenges, especially in hot regions of Africa, where they are common. Thermoregulatory behaviour of the African forest elephant in its natural habitat and the microclimates that it utilizes have not previously been investigated. To understand how such an enormous animal behaves in the hot, humid natural forest environment, I investigated microclimates at forest-savannah interfaces (*bais*) in Lobeke National Park in Cameroon, observed forest elephants' likely thermoregulatory behaviour and correlated the behaviours with environmental microclimatic variables. Portable weather stations equipped with data loggers were deployed at five study sites to record microclimatic variables for three days per site. I used the fixed point sampling method to observe and record behaviours of forest elephants, during the hot, dry season.

Black globe temperature reached an average of about 33°C during the day in the *bais* and decreased to a mean of about 20°C in the night. The day globe temperature often exceeded the body temperature of the elephants, but the vapour pressure of air was lower than that on the elephant's skin. Therefore, at 100% humidity and estimated skin temperature of 35°C, I assume elephants of this study lost heat by evaporation, both under the forest canopy and in the open *bais*. Wind speed in the *bais* was higher than that under the forest canopy, possibly facilitating convective heat loss from the elephants, particularly at night. Ear-flapping rate of the elephants correlated linearly and positively with dry-bulb and globe temperatures. Shade-seeking and dust-bathing only showed weak positive associations both with dry-bulb globe and temperatures. Between 06:00-24:00, elephants that were observed spent a mean of 40% of their time walking,

55% foraging, 7% shade-seeking, 45% ear-flapping, 4% dust-bathing and 9% of time performing water-related activities. The higher number of elephants in the *bais* at night as opposed to the numbers in the *bais* during the day, as revealed by the findings of this study, suggests that the forest elephant may have a more favourable mode of dumping its excess body heat in the open *bais* than under the forest canopy at night. All the *bais* and their vicinity that were investigated in this study were heavily trampled with elephant spoor, because many elephants frequently congregated in the area due to the presence of nutritious herbaceous plants, mineral salts and variations in microclimates in the *bai*-savannah interfaces. The differences in microclimates in the *bais* and their vicinity may play a major role in influencing the forest elephant's thermoregulatory behaviour. To the best of my knowledge, my study suggests for the first time that the forest elephant may use microclimates at the *bai* interface for thermoregulatory needs. However, my study is limited because it was executed for a short duration and over the hot dry season, and factors that may affect elephants such as physiology, the availability and quality of forage and predation risk were not included in this investigation. All these factors may have affected the accuracy of my findings. For these reasons the inferences made in this study on elephant microclimate selection would need further investigation before concrete conclusions are drawn. Expensive research cost, human safety, fear of human presence and hence alteration of elephant behaviour and the obscure nature of the equatorial forest have been recurrent issues hindering the investigation of behaviour of free-living African forest elephants. I suggest that it would be worthwhile investigating the forest elephant's behaviour further by applying GPS/satellite telemetry, real time bio-logging and camera trap techniques, which offer a practical means to carry out an extensive study in the evergreen hot humid equatorial forest of the Congo Basin.

ACKNOWLEDGEMENTS

I am indebted to several people in the BFRG without whom, my research would not have been possible. First to my supervisors, Prof. Duncan Mitchell, Prof. Andrea Fuller and Dr Leith Meyer, for teaching me about research, stimulating me to think critically and to allow me to pursue research of my interest, even when that meant flying to do field work in the jungle of the Congo Basin in Cameroon.

I wish to extend my sincere appreciation to my mentor Dr Michael Loomis of the North Carolina Zoological Society for seeking part of the matching funding for my studies at the University of the Witwatersrand. I am grateful to World Wildlife Fund Cameroon Country Programme Office that facilitated my data collection in Lobeke National Park in Cameroon. I have had the opportunity of collaborating with many colleagues, for whom I have great respect, and I wish to extend my sincere appreciation to all those who have helped me throughout my programme.

I would also like to thank the staff and fellow postgraduate students within the Brain Function Research Group for their advice and support. Finally, I am thankful to my fiancé Irene Mashueabom Gemoh and our daughter Kay Ebude Kuwong for their continuous love and care, my sisters Matilda-Windaline V. Kuwong, Mary N. Kuwong, Lawrence L. Kuwong, my brothers Dr Patrick M. Kuwong and family, Colonel Eric A. Kuwong and family, who supported me financially and emotionally throughout this endeavour, and my friends who helped to maintain a sense of humour and who so often provided a shoulder to lean on in time of unhappiness.

Research for this dissertation was partly funded by the BFRG, the MFREF of the University of the Witwatersrand, NRF of South Africa and NCZS for which I am extremely grateful.

TABLE OF CONTENTS

DECLARATION	i
ABSTRACT.....	ii
ACKNOWLEDGEMENTS.....	iv
LIST OF FIGURES	vii
LIST OF TABLES.....	x
LIST OF ABBREVIATIONS	xi
CHAPTER 1	1
INTRODUCTION.....	1
1.1 African elephants and their thermal niche	2
1.2 Morphological traits of elephants which influence thermoregulation	6
1.3 Autonomic thermoregulation of elephants.....	7
1.4 Behavioural thermoregulation of elephants	9
1.5 Dissertation aims.....	15
CHAPTER 2	17
STUDY SITE	17
2.1 Introduction.....	18
2.2 Study site.....	18
2.2.1 Lobeke National Park	18
2.2.2 Bais and elephant paths.....	23
2.3 Study population	25
2.4 Microclimate assessment	26
A.....	30
2.4.1 Calibration of data logger	32
2.4.2 Procedure for collecting microclimatic data	34
2.5 Procedure for collecting behaviour data	36
2.6 Data analysis	39
2.6.1 Analysis of behaviour data.....	40
2.6.2 Analysis of microclimatic and behaviour data.....	41
CHAPTER 3	42
RESULTS.....	42
3.1 Introduction.....	43
3.2 Microclimate data	43
3.2.1 Black globe temperature	43
3.2.2 Dry-bulb temperature.....	43
3.2.3 Difference between black globe and dry-bulb temperature	46
3.2.4 Vapour pressure of air.....	46
3.2.5 Wind speed.....	49
3.3 Elephant behaviour	57
3.4 Association between microclimate and elephant behaviour at the study sites	69
3.4.1 Walking behaviour.....	69
3.4.2 Foraging behaviour	69
3.4.3 Shade-seeking behaviour	69
3.4.4 Ear flapping behaviour.....	73
3.4.5 Dust-bathing behaviour.....	74
3.4.6 Water-related behaviours	74

CHAPTER 4.....	78
DISCUSSION	78
4.1 Introduction.....	79
4.2. Microclimate mosaic at my study site	79
4.3 Relationship between microclimate mosaic and elephant behaviour	86
4.3.1 Walking behaviour of elephants	86
4.3.2 Foraging behaviour of elephants.....	94
4.3.3 Shade-seeking behaviour of elephants.....	99
4.3.4 Ear-flapping behaviour of elephants.....	105
4.3.5 Dust-bathing behaviour of elephants	106
4.3.6 Water-related activities of elephants.....	107
4.4 Advantages and limitations of this study	113
4.5 Conclusion	116
REFERENCES	122
APPENDICES	134

LIST OF FIGURES

Figure 2.1 Map of Africa, Central Africa and Cameroon showing the location of Lobeke NP in south-east Cameroon.

Figure 2.2 The landscapes of *bais* at the study sites.

Figure 2.3 Elephant east-west direction corridors.

Figure 2.4 The bull tracked near Base de Djembe and a herd of elephants eating, drinking and spilling mud on their bodies in Djaloumbe Bai.

Figure 2.5 White air vane and a tail fin.

Figure 2.6 Two 4-channel data loggers.

Figure 2.7 One example of the linear regression analysis used for the calibration of the Hobo data logger thermometers.

Figure 2.8 Weather stations deployed at noon under closed-forest canopy and in Djanguai Bai.

Figure 3.1 T_g in open *bais* and T_g under forest canopy.

Figure 3.2 T_a in open *bais* and T_a under forest canopy.

Figure 3.3 Differences between T_g and T_a in open *bais* and T_g and T_a under forest canopy at five my study sites.

Figure 3.4 VP in open *bais* and VP under forest canopy.

Figure 3.5 Mean three-day WS in the open *bais* and under forest canopy.

Figure 3.6 Three-day mean T_g , T_a , VP and WS in the *bais* and under forest canopy.

Figure 3.7 Differences of three-day mean T_g and T_a in the *bais* and under forest canopy.

Figure 3.8 Typical mean three-day profile of microclimate variables in the open *bais* and under the forest canopy for Lobeke NP.

Figure 3.9 The linear regression between mean T_g and mean T_a in the open *bais* and mean T_g and T_a profile under the forest canopy.

Figure 3.10 (A) An elephant standing under shade in the Djaloumbe Bai in the afternoon of a sunny day.

Figure 3.11 An elephant cow foraging on abundant foliage along a foraging path at the edge of Base de Djembe.

Figure 3.12 An elephant bull collared with a telemetry collar seen after a dust bath in Base de Djembe.

Figure 3.13 An elephant seen just after walking across Lobeke River during a hot afternoon.

Figure 3.14 Mean percentage of time all elephants monitored in study spent walking and also foraging.

Figure 3.15 Mean percentage of time all elephants monitored in my study, spent shade-seeking, ear-flapping, dust bathing and in water-related activity

Figure 3.16 Mean percentage of time all elephants monitored at different time of the day spent on walking, foraging, shade-seeking, ear-flapping, dusts bathing and in water-related activity

Figure 3.17 Correlation between the mean T_g in open *bais* and the mean percentage time of each hour that the elephants spent walking at the study sites.

Figure 3.18 Association between the mean percent time elephants spent per hour foraging and mean T_g in *bais*.

Figure 3.19 Mean percent time of each hour that the elephants spent seeking shade and mean T_g for that hour plotted as a function of time of the day for all five study sites.

Figure 3.20 Mean percent time of each hour that the elephants spent ear-flapping and the mean T_g for that hour plotted as a function of time of the day for all five study sites.

Figure 3.21 Mean percent time of each hour that the elephants spent dust-bathing and the mean T_g for that hour plotted as a function of time of the day for all five study sites.

Figure 3.22 Association between mean percent time of water related-activities per hour and T_g .

Figure 4.1 Mean percent time of the day that elephants spent walking in Lobeke NP and in Ngorongoro NP.

Figure 4.2 Mean percent time that elephants spent walking within 12-hour day period in Lobeke NP, Lake Manyara NP and Ngorongoro NP.

Figure 4.3 Mean percent time elephants spent walking within 12-hour day period in different studies compared with the walking time of elephants in this study.

Figure 4.4 Mean percent time elephants spent foraging within 12-hour day period in Lobeke NP and in Ngorongoro NP.

Figure 4.5 Mean percent time elephants spent shade-seeking within 12-hour day period during the wet, cold and dry hot seasons in Kunene Region and during the dry season in Lobeke NP.

Figure 4.6 Mean percent time within 12-hour day period that elephants spent shade-seeking in Lobeke NP and in Ngorongoro NP.

Figure 4.7 Mean percent time elephants spent resting within 12-hour day period in different studies compared with the resting activities of the elephants of this study.

Figure 4.8 Mean percent time elephants spent dust-bathing within 12-hour day period during the wet, cold and dry hot seasons in Kunene Region and only during the dry season in Lobeke NP.

Figure 4.9 Mean percent time elephants spent on water-related activities within 12-hour day period in Lobeke NP and in Ngorongoro NP.

Figure 4.10 Mean percent time elephants spent on water-related activities between 07:00-19:00 in different studies compared with the water-related activities of this study.

Figure 4.11 Mean percent time elephants spent on water-related activities between 06:00-24:00 in different studies compared with the water-related activities of this study.

LIST OF TABLES

Table 1.1 Factors that influence evaporation, conduction, convection and radiation between an animal and its environment.

Table 2.1 (A&B). Detailed records of elephants observed in Djaloumbe, Base de Djembe, Djangui, Petite Savane and Bolou Bais during the day and night.

Table 2.2 Dates and sites where weather stations were deployed during study.

Table 2.3 Field data sheet.

Table 3.1 Summary of mean microclimatic variables for all the study sites and the differences between variables in the *bais* and under the forest canopy during day and night.

Table 3.2 Summary of mean WS for all study sites and the differences between WS in the open *bais* and under the forest canopy during the day and night.

Table 3.3 Number of elephants that were identified to have entered each of five *bais* during day and at night during the three-day study at each *bai*.

Figure 4.1 Table of study area, elephant species, climate, seasons and vegetation types

Table 4.2 Summary of foraging data of forest elephants in Lobeke NP and elephants from some other regions in Africa.

Table 5.1 Summarized results of two-way ANOVA of microclimatic variables.

Table 5.2A Summary of the associations between microclimate and elephant behaviour in *bais* for all my study sites

Table 5.2B Summary of the associations between microclimate and elephant behaviour under forest canopy for all my study sites

LIST OF ABBREVIATIONS

NP	National Park
VP	Water vapour pressure of air
T_g	Globe temperature
T_a	Dry-bulb air temperature
WS	Wind speed
RH	Relative humidity
UNDP	United Nation Development Programme
IUCN	International Union for Conservation of Nature
WWF	World Wildlife Fund
WCS	Wildlife Conservation Society

CHAPTER 1

INTRODUCTION

1.1 African elephants and their thermal niche

The African elephant (*Loxodonta africana*) is the largest existing terrestrial mammal and inhabits diverse thermal niches characterised predominantly by high environmental temperature (Spinage, 1968). African elephants currently occur in 37 countries in sub-Saharan Africa. They are known to have become nationally extinct in Burundi in the 1970s, in Gambia in 1913, in Mauritania in the 1980s and in Swaziland in 1920, where they were reintroduced in the 1980s and 1990s (Blanc et al., 2007). The quality of knowledge available on elephant distribution varies considerably across the species' range. While distribution patterns are well understood in most of Eastern, Southern and West Africa, there is little reliable information on elephant distribution for much of Central Africa (Blanc et al., 2007). Little is known about the African forest elephant population. But recent reports reveal that the African forest elephant is under threat of extinction. About 62% of all forest elephants have been killed over the past decade due to mainly poaching to feed Asia's demand for ivory (UNEP et al., 2013) .

African elephants are found in localised regions across the continent from the hot and dry deserts of the Kalahari and Sahara, and the hot and humid jungle of the Congo Basin, to the temperate savannahs and grasslands of eastern and southern Africa (Skinner and Chimimba, 2005). As such the African elephant has developed ways of coping with the diverse environmental conditions it encounters (Skinner and Chimimba, 2005). They are known to survive in habitats with ambient temperatures from a little below 0°C to about 50°C (Sikes, 1971), which shows that they are often under extreme thermal challenge, especially in the typical hot climate in which they normally dwell. This thermal challenge is aggravated by the elephant's small surface area to volume ratio that impairs quick loss of excess body heat (Wright and Luck, 1984), and can be

problematic if an elephant is exposed to heat but could be advantageous in the cold (Taylor, 1970a).

Like all other mammals, the rate at which the elephant exchanges heat with its environment depends on evaporation, radiation, convection and conduction (see summarized information about the four methods of heat transfer and factors that influence the rate of heat transfer in Table 1 (Ingram, 1975; Weissenböck, 2010)). The magnitude of heat transfer by these routes largely depends on the temperature gradient between an elephant's skin and the microclimate of the habitat the elephant is in, the colour of its skin, its body shape, mass, conductance of body tissues and the metabolic heat that the elephant's produces (Willmer et al., 2005). Evaporative cooling may be limited in the natural habitat of the African forest elephant (*Loxodonta africana cyclotis* Matschie), because of the high vapour pressure of the forest.

The nearly hairless body of elephants leaves the animal's skin exposed to radiation and desiccation (Lillywhite and Stein, 1987), but on the other hand, the lack of fur may promote heat loss, via convective and conductive routes. As the temperature gradient between an elephant and its environment diminishes, radiation, convection and conduction become less effective in keeping the elephant cool (Taylor and Lyman, 1967). Thus in circumstances of very small temperature gradients or when air temperature exceeds body temperature, elephants can only effectively dissipate heat by evaporative means (Grenot, 1992; Taylor, 1969).

Much literature exists about the thermal challenges and behavioural thermoregulation of savannah elephants (*Loxodonta africana africana* Matschie) (Kinahan et al., 2007ab) but little

Table 1.1 Factors that influence evaporation, conduction, convection and radiation between an animal and its environment. Sources of information to make Table 1.1: (Ingram, 1975; Weissenböck, 2010)

Mode of transfer	Animal Factors	Environmental Factors
Evaporation	Surface temperature, total percentage wetted area	Humidity Wind speed and direction
	Sites of evaporation	
Conduction	Surface temperature	Surface temperature, thermal conductivity and thermal capacity of the contact material
	Effective surface area	
Convection	Surface temperature	Air temperature; wind speed and direction
	Effective convective area	
	Radius of curvature and surface type	
	Influencing structure like fur or feathers	
Radiation	Mean radiant temperature of surface	Mean radiant temperature, solar radiation and reflectivity of surroundings
	Effective radiating area, reflecting area, reflectivity and emissivity of a surface.	

information exists for forest elephants (UNEP et al., 2013). Elephants in the Congo Basin inhabit the dark canopy, hot and humid forest with average annual environmental temperature ranging between 23°C to 31°C (Nowell, 2005) and a relative humidity of 60% to 90% (WWF, 2006). Therefore, the behaviours of the African forest elephants may be different from that of savannah elephants, due to their structural differences and the different habitats in which these animals inhabit including; forest, arid and semi-arid regions. Both elephant subspecies have massive

bodies that produce large amount of total metabolic heat (McNab, 1983), but because of their relatively smaller surface area to volume ratio, elephants will lose heat, per unit body mass, much slower than will small mammals in the same thermal environment and using the same mechanisms (Williams, 1990). In contrast, the low surface area to mass ratio may be an advantage in that during hot periods an elephant will gain heat from the environment more slowly than an animal of smaller body size (Taylor, 1969). In order to cope with the nutritive requirements of their large bodies African elephants consume about six percent of their body weight daily (Laws, 1970b) and Asian elephants exhibit cathemerality (Van Schaik and Griffiths, 1996) so that they can forage for long periods all day to sustain their needs. Cathemerality is a thermoregulatory behaviour whereby animals reduce their diurnal activities, by resting in a cool environment, and compensate the time lost for activities such as mating, hunting and feeding by increasing their nocturnal activities when it is cool. African elephants devote about three-quarters of their time foraging and spend relatively less time inactive compared to smaller animals (Owen-Smith, 1988). A study of the feeding habits of savannah elephants in Chobe NP in Botswana showed that adult male elephants spend more time foraging than adult females because males are larger than females (Stokke and Du Toit, 2002). Only about 40% of what the elephant eats is digested (Colbert, 1993). The result is that the elephant must eat about 410 kg of food (Cott, 1975) daily in order to maintain its body weight and nutritional needs (Benedict and Lee, 1938).

However, the time elephants spend foraging is influenced by the variation in seasons, the quality and availability of forage and the macroclimate and microclimate which they experience (Kabigumila, 1993a). As the biomass of vegetation (De Beer and Van Aarde, 2008), water supply (Stokke and Du Toit, 2002; Verlinden and Gavor, 1998), climate (Kinahan et al., 2007b)

and absence or presence of humans (Hoare, 1999) differs from place to place and region to region, so do elephants' activity levels and behaviours differ in time and space. Therefore, to have survived so successfully throughout Africa, the African elephant must have evolved and developed morphology, unique behaviours and autonomic mechanisms to effectively avoid deleterious increases in body temperature. (Blanc et al., 2007; Skinner and Chimimba, 2005).

1.2 Morphological traits of elephants which influence thermoregulation

The large size of an elephant poses a problem, because a small surface area limits heat loss, and therefore metabolic heat builds up that may result in an animal overheating (Colbert, 1993). Sparse and uneven hair distribution impairs the insulating capacity of air on the elephant's body surface as compared to other hairy mammals. The combination of thick skin and a thin layer of fat beneath the skin and the low inertia of the elephant's massive body enable it to tolerate cold temperatures (Wright and Luck, 1984). The skin of elephants is sculptured with wrinkles and crevices arranged in a prominent regular pattern. These wrinkles trap moisture and facilitate the movement of fluid over the body surface and enhance cooling by increasing the skin's surface area and decreasing the time it takes for moisture to evaporate (Lillywhite and Stein, 1987). Therefore, wrinkles on elephants' skin facilitate the elephants' body cooling for longer than if they had smooth skin (Smith, 1890). In addition, elephants diffuse water which assists in regulating the body temperature through evaporative cooling (Carrington, 1959). One key organ that elephants use for thermoregulation is their ears. The African elephant's ears have a large surface area-volume ratio as well as a heavily vascularised network of superficial vessels which enables the ear to act as an efficient heat radiator (Wright, 1984). Ear-flapping facilitates heat loss from the large ear surface.

1.3 Autonomic thermoregulation of elephants

An elephant can maintain homeothermy while minimizing energy cost by using different strategies including autonomic thermoregulation. Elephants like all mammals and birds are endotherms and have been reported to use various means of autonomic thermoregulation, which include vasoconstriction or vasodilation (Weissenböck, 2010) and evaporative water loss through their porous skin (Williams, 1990). A 4000 kg elephant needs to maintain a heat loss of about 4.65 kW while moving and feeding (Wright, 1984), and therefore must have an effective mode of controlling heat flow (Phillips and Heath, 1992). Control of the elephant's skin temperature is an extremely important mechanism in thermoregulation (Phillips and Heath, 1995) and the most important thermoregulatory organ is the elephant's ears, which act as "thermal windows". The effect of heat loss or gain at these "thermal windows" is achieved by modifying and controlling blood flow, via vasoconstriction and vasodilation (Sumner et al., 2007). Physiologically, an elephant can increase its heat loss by increasing blood flow to the surface of the body, thus elevating skin temperature, provided that ambient temperature does not exceed the skin temperature. Reports of continuous measurement made on the body temperature of African elephants have shown a high rhythmicity in their body temperatures rhythms with minimum body temperature values occurring early in the morning between 07:00-09:00 and maximum values in the late evening 18:00 (Hidden, 2009) or night at 22:00 (Kinahan et al., 2007a). Autonomic control of vasculature appears to play an important role in regulating elephant body temperature (Wright and Luck, 1984). Small rapid body temperature changes occur as elephants regulate their body temperature within a narrow daily range of about 1°C (Hidden, 2009; Kinahan et al., 2007a). This narrow daily temperature range favours homeostatic processes in the elephant. Although elephants do not pant or sweat, they are still able to dissipate heat through

evaporation of water from their body surface (Williams, 1990). When liquid water evaporates it acquires latent heat from the animal's body to transform from liquid to gaseous state. This heat is absorbed from the skin surface of the elephant and as the gas escapes from the elephant's body surface, the elephant's body temperature is decreased. Evaporative and convective heat loss is increased by flapping the ears (Hiley, 1975). Since elephants do not actively sweat or pant (Lillywhite and Stein, 1987; Spearman, 1970) it has been postulated (Robertshaw, 2006) that they also store heat, particularly, during the day, allowing body temperature to rise and dissipate the heat slowly at night (Hidden, 2009; Weissenböck, 2010) but it is not known if microclimate selection behaviour affects the way forest elephants dissipate their excess body heat.

Temperature gradient, relative humidity and air movement are important environmental factors (Williams, 1990) that influence the elephant's ability to maintain a fairly constant body temperature of about 36°C (Kinahan et al., 2007a). When ambient temperature is less than the temperature of the body surface of an elephant, heat is transferred from the body surface to the environment. When microclimatic temperature exceeds that of body temperature, the ability of an elephant to lose heat is limited and the animal may in fact gain heat (Porter and Gates, 1969). In this scenario, evaporative heat loss becomes the only means by which elephants can dissipate excess body heat (Schmidt-Nielsen, 1997).

The mean skin temperature of the African elephant ranges between 15°C and 35°C (Phillips and Heath, 1992; Williams, 1990) and as ambient dry-bulb air temperature increases, the mean skin temperature also increases (Hidden, 2009). However, as air movement increases, an elephant's evaporative heat loss capacity also increases, and the heat loss capacity is dependent on the

movement of air to displace saturated air just above the damp surface (Gebremedhin and Wu, 2001). The rate of evaporative heat loss also depends on the difference in water vapour pressure between the skin and ambient air. As the gradient between the vapour pressure of air on an animal's body surface and surrounding air increases, so does the animal's evaporative heat loss capacity increase (Cohen et al., 1979). Evaporation stops when these two vapour pressures are equal.

Another important factor that influences thermoregulation is tissue conductance. Conductance refers to the ease of heat flow through body tissue. Tissue conductance decreases with an increase in body size; heat flows quicker through the body of smaller animals than larger ones in the same thermal environment (McNab, 1983). Also the length of time blood takes to circulate through an animal's body increases with increasing body mass (Schmidt-Nielsen, 1984), and the distribution of heat through the body of animals mostly depends on blood circulation (Mitchell et al., 1997). Elephants have amplitudes of daily body temperature fluctuations of only about 1°C (Hidden, 2009). With access to water, they regulate body temperature well during the day and can dissipate this further heat during the more favourable thermal environment of the night (Hidden, 2009; Hiley, 1975; Weissenböck, 2010), thus decreasing the energetic cost of thermoregulation and the need of evaporative cooling (Robertshaw, 2006).

1.4 Behavioural thermoregulation of elephants

Elephant behaviour refers to a specific behavioural response of the elephant to a specific stimulus or group of stimuli. Behaviours that savannah elephants may use for thermoregulation include selecting microclimates (Hiley, 1975). Other behavioural thermoregulatory means include; wallowing in mud, resting, flapping ears, bathing with dust, immersing in water or

spraying water on their bodies (Hidden, 2009; Hiley, 1975; Kabigumila, 1993b; Kalempera, 1987; Leggett, 2008; MCKay, 1973; Scholander, 1955). Microclimate selection behaviour has been poorly studied in elephants. Microclimates are a suite of climatic conditions measured in a localized area near the earth's surface (Geiger, 1965). They are mainly characterised by radiant heat, moisture and wind speed in the local environment that may influence thermoregulatory behaviour of mammals in their habitats. Habitats in terrestrial landscapes are thermally heterogeneous (Li and Reynolds, 1995) because of differences in topography, physical features, slope, gradients of elevation and vegetation types and may constitute a variety of microclimates (Geiger, 1965).

Many studies, as well as anecdotal stories, reveal that elephants flap their ears to keep cool, increasing the rate of ear-flapping as dry-bulb air temperature rises (Hiley, 1975). The rate of ear-flapping has been reported to be positively related to temperature increases but inversely related to wind velocity (Buss and Estes, 1971), because increase wind speed facilitates heat loss through convection. However, semi-tame free-ranging elephants in the Pilanesberg NP (South Africa) flapped their ears irrespective of wind speed (Hidden, 2009) for an unknown reason.

In hot conditions elephants also specifically spray their ears with water (Hiley, 1975). At such times, the ear's large blood vessels make it especially useful as a heat loss organ. Other reports have revealed that another behavioural means by which elephants control their body temperature is frequently wallowing in mud when it is hot, since heat transfer to water is considerably higher than that of air (Scholander, 1955). By rolling on mud or rubbing themselves or immersing themselves in water or spraying themselves with water or mud, elephants lose heat through

evaporation and conduction. On very hot days, when water is lacking, elephants will draw up water from their stomach through their trunks and spray themselves (Hiley, 1975).

Elephant are sometimes found in areas where there is little tree cover or surface water, therefore restricting their behavioural options (Hiley, 1975). Although no thermoregulatory study has been carried out under such conditions, the animal would probably experience thermal and osmoregulatory stress, which if severe enough could adversely affect its survival. Desert-dwelling elephants in Namibia have been reported to have the lowest defecation rate of any elephant studied in Africa. The low defecation rate in the desert dwelling-elephant is because the elephant spends only seven hours of the day foraging and spends the rest of the time avoiding increasing its body temperature, through exposing itself to radiant heat by standing in the shade (Leggett, 2008).

Although elephants do select habitats that offer different microclimates (Hiley, 1975), whether they seek various microclimates for thermoregulatory purposes is not well documented. It has been argued that environmental temperature is a factor that limits landscape choice in the African elephant (Kinahan et al., 2007b) and that elephants select habitats based on their physiological needs (Huey, 1991; Young and Van Aarde, 2010). Elephants seek and stand in the shade, where dry-bulb air and ground temperatures are normally cooler, thereby avoiding long-wave radiant heat load and much of the short-wave radiant heat load from the sun (Hiley, 1975). At midday elephants also decrease their activity, thus minimizing the internal heat production. The decrease in midday activity affects the feeding habits of savannah elephants such that they mostly feed in the morning and early in the evening (Guy, 1976; Hiley, 1977; Kinahan et al., 2007a). Studies in

Tsavo NP (Kenya), Lake Manyara NP (Tanzania) and desert-dwelling elephants in the Kunene Region (Namibia) have shown that savannah elephants reduce their activities during the hottest time of the day, in order to reduce their metabolic heat production (Hiley, 1975; Kalembera, 1987; Leggett, 2008). Little or no research has been done on forest elephants (UNEP et al., 2013). Body temperature measurements have been made only in savannah elephants, albeit in confined habitat. Forest elephants are difficult to study because of the nature of their forest habitat. The effects of microclimates on forest elephants' thermoregulatory behaviour are not known. Assessment of microclimates and their use by forest elephants will provide conservation managers with improved insight into the environmental physiology of African forest elephants, and possibly other large forest mammals, as well as provide valuable information for land-use planning.

Some animals use other strategies in addition to shade-seeking to reduce their exposure to solar radiation and at times to avoid predators. To enable itself to remain more active during the day, giraffe (*Giraffa camelopardalis*) orients the long-axis of its body parallel to the rays of the sun thereby reducing the amount of radiant energy it intercepts (Mitchell and Skinner, 2004). Other large mammals such as the buffalo (*Syncerus caffer*) (Sinclair, 1977) and the Arabian oryx (*Oryx leucoryx*) (Hetem et al., 2010) reduce heat gain by solar radiation by transferring their activity from day to night, when day environmental heat loads increase. Similarly, the black rhinoceros (*Diceros bicornis*) alter their sleep patterns; during the hot period of the day they sleep, but move about and forage in the early morning, late afternoon and at night (Goddard, 1967). Furthermore, a megaherbivore, like the hippopotamus (*Hippopotamus amphibius*) usually comes out to forage on land at night, but spends the day at least partially or fully submerged in water (Luck and

Wright, 1964). The advantage of change of daily activity to the various times of the day is that animals can avoid the adverse effect caused during harsh environment conditions in order to become active only when conditions become favourable. At night, ambient temperature is lower than body temperature of mammals thus allowing passive loss of body heat to the surrounding environment through convection, conduction and radiation. Little or no evidence exists to indicate if the elephant uses these thermoregulatory strategies, that Mitchell et al. (2004), Sinclair (1977), Hetem et al. (2010), Goddard (1967) and Luck & Wright (1964) have described. It has been argued that the principal thermoregulatory mechanism by which elephants cope with warm environments is simple storage of heat during day and cooling during night (Hidden, 2009; Robertshaw, 2006; Weissenböck, 2010), which would be highly efficient in an animal of this size (Elder and Rodgers, 1975; Hiley, 1975).

Many reports have suggested dust-bathing too, in both the African and Asian elephants, is an important behaviour that may have a thermoregulatory function. They argue that dust-bathing protects the skin from the sun (Barnes, 1984; Feldhamer et al., 1999; Haltenorth and Diller, 1980; McKay, 1973; Rees, 2002), but the extent to which dust plays a role in thermoregulation still needs further investigation.

Thermoregulatory behaviours are often favoured over autonomic thermoregulation as less energy and water is required (Jessen, 2001). Because of their size, elephants are limited in the variety of microclimates available to them. Smaller mammals, for example, are able to escape into burrows and crevices, with cool microclimates, while larger mammals, such as the elephants are unable to do so. On the other hand, elephants are able to quickly escape harsh environmental conditions by rapidly traversing large distances (Parker and Robbins, 1985).

While studies on captive elephants have helped us understand their thermoregulation, little information exists on how elephants thermoregulate in the wild and how thermal constraints affect their ecology. Energy and water balance are key determinants for the survival of elephants. Savannah elephants select landscapes based on food and water availability and the thermal characteristics of the environment (Kinahan et al., 2007b). Studies on food (Dublin, 1996; Young and Van Aarde, 2010), water (Stokke and Du Toit, 2002; Verlinden and Gavor, 1998), nutrients (Houston et al., 2001; Ruggiero and Fay, 1994), terrain (De Boer et al., 2000; Nellemann et al., 2002), human settlements (Hoare, 1999), vegetation density (De Beer and Van Aarde, 2008), and ambient environmental temperature (Kinahan et al., 2007b) have aided our understanding of savannah elephant ecology. Young and Van Aarde's (2010) investigation of one of the world's largest populations of savannah elephants in southern Africa, demonstrated that the elephant population regulation is driven by a spatial response to water variability, environmental stochasticity and population density. However, they suggest that further research still needs to be done to identify the demographics and behaviour variables that drive population density.

In the Tembe Elephant Park in Maputoland (South Africa) elephants often seek refuge in thick vegetation, but this behaviour may have deleterious effects on conservation as the vegetation in this park consists of rare endemic sand forests, which due to their unique biology are susceptible to elephant browsing (Mathews et al., 2001). The provision of water points near the Tembe Elephant Park has encouraged elephant population growth and other large herbivores, resulting in them feeding more extensively in these fragile habitats, and as such increasing habitat degeneration and the loss of biodiversity (Shannon et al., 2013) that may exacerbate loss of microclimate useful to elephants in the park.

Biodiversity and habitat loss, poaching and degradation, are worldwide problems. A growing human population and also increase in subsistence farmlands and livestock farming have resulted in a drastic decrease in wildlife habitats and probably also valuable thermoregulatory microclimates available to the African elephant. For example, this is happening in Tsavo NP and its vicinity, where grassland is changing into semi-desert, consequently the trees that provide vital shade and surface water to elephants are disappearing (Hiley, 1975).

African elephants are keystone species. A keystone species is a species that has a disproportionately large effect on its environment relative to its abundance (Paine, 1995). African elephants play a critical role in maintaining the structure of the grassland and forest ecological systems because elephants determine the type and number of other species in an ecosystem (Schulze et al., 1994). Therefore, elephants are key animals that provide ecosystem services. These services ensure the survival of other organisms that are adapted to live with elephants in the same ecosystems. Despite all the research done on the roles African elephants play in ecosystems and how savannah elephants behave and thermoregulate, our understanding of savannah and forest elephants' thermoregulatory behaviour is not complete.

1.5 Dissertation aims

Studies done at boundaries between different types of habitats within landscapes suggest that habitat demarcation cause different sorts of microclimates (Geiger, 1965; Li and Reynolds, 1995; Saunders et al., 1998; Wachob, 1996). There is evidence that ambient temperature is a factor that may limit landscape choice in the African elephant (Kinahan et al., 2007b) but tools to assess the activity and behaviour of free-range savannah African elephants have been limited to observations on a macroclimatic scale within different landscapes. As a consequence,

information on elephant's behaviour at the microclimatic level is lacking, particularly in the forest habitats. Based on the variability of microclimates within landscapes, it has been suggested that savannah elephants (Hiley, 1975) including desert-dwelling elephants use microclimate selection to regulate their body temperature (Leggett, 2008). It is not known whether microclimate selection is a thermoregulatory strategy that forest elephants use when challenged with the typical hot and humid equatorial forest conditions. Therefore, the aim of my study is to find out the following:

- compare the microclimates in *bais* (Savannah-like forest clearings) and in forest canopy areas.
- investigate if forest elephants' activities in the open *bais* and under the forest canopy are influenced by the thermal properties at the *bai* interface.
- determine if observed elephant thermoregulatory behaviours correlate with microclimatic variables.

To answer these questions I used miradows (brown painted chalets) in *bais* to observe elephant behaviour in Lobeke NP, in the Congo Basin region of south-east Cameroon. In chapter two I discuss the methods and procedure used to collect climatic and behavioural data and how I interpreted and analysed the data. In chapter three I summarize and present the data that I collected from forest elephants in five locations in Cameroon. In Chapter four I summarize my findings and the findings of studies in Zimbabwe, Uganda, Cameroon, Namibia and Tanzania and discuss the results in the context of elephant behaviour and thermoregulatory strategies.

CHAPTER 2

STUDY SITE

2.1 Introduction

This chapter aims to describe the study site, the animals studied, the infrastructure, tools and the methods used in this study.

Most of the original data presented in this dissertation were collected during three field trips to Lobeke NP, in south-east Cameroon, between 15 November and 15 December 2010. This period was chosen to carry out the study because it was the hottest season of the year. Lobeke NP was chosen because of the presence of African forest elephant in it and because of the high probability to view and study elephant behaviour in the *bais* that are in the park.

Free-living forest elephants inhabit the dense tropical closed-canopy evergreen forest. For this reason it is difficult, and potentially dangerous, to observe the elephants in their natural habitat. However, *bais* found in these forest habitats are preferred observation sites for elephants and other large mammals, because these animals often visit the *bais* (WWF, 2006). Elephants are usually taller than the vegetation growing in the *bais* and the animals may be viewed easily from a safe distance without the animals being aware of human presence in their vicinity.

2.2 Study site

2.2.1 Lobeke National Park

This study was performed in five *bais* and their vicinities in Lobeke NP namely Djaloumbe, Djangui, Petite Savane, Base de Djembe and Bolou Bais (see Table 2.2). Lobeke NP is situated

Table 2.2 Dates and sites where weather stations were deployed during study

Dates	<i>Bais</i>	Number of days
15 – 18 November 2010	Djaloumbe Bai	3
05 – 08 December 2010	Djangui Bai & Petite Savane	3
10 – 13 December 2010	Bolou Bai & Base de Djembe	3

in the East Province of Cameroon between latitudes N2°05' to N2°30' and longitudes E15°33' to E16°11' (see Figure 2.1), north-west of the Congo Basin. Sunrise was at about 06:00 and sunset 18:00 in Lobeke NP area during the period of this study. The region has a relatively flat relief with occasional hillocks of varying altitudes between 400 m and 700 m above sea level (WWF, 2006).

The park has a surface area of 217,854 ha and shares buffer zones (transition zones) with six community hunting zones surrounding the park (WWF, 2006). The tributaries of River Congo, the Sangha River and Ngoko River, are supplied by many streams that flow through Lobeke region throughout the year. Among the rivers and streams is the Lobeke River that flows and maintain water supply to two of the *bais* (WWF, 2006). *Bais*, as referred to in the local Baka pygmy language, are forest clearings or savannah-like open vegetation sites that occur within the Congo Basin closed-canopy forest (see Figure 2.2). Lobeke forest is made up of typical African tropical closed-canopy dense humid forest-tree-complexes, composed predominantly of three evergreen forest types with vegetation of varying patterns, disseminated unevenly in the region.

Lobeke NP is characterized by a rich variety of habitats, including primary rain forest with a closed-canopy and open-under forest layer (Nzooh Dongmo, 2003). The forest in the Congo Basin is dominated by the densest pattern of *Marantaceae* plant species known to date (Hecketsweiler et al., 1991; Lejoly, 1996). This type of forest harbours one of the largest populations of African forest elephants and it is believed that *bais* and *Marantaceae* plant species are attractive to elephants (Nzooh Dongmo, 2003). Elephants forage on the *Marantaceae* plants and frequent the *bais* to feed on other herbaceous plants (Carroll, 1996; White et al., 1993) and mineral salts too (Turkalo and Fay, 1995; White et al., 1993).

The location of Lobeke NP in the interior of the west coast of Africa means it experiences a more or less monsoon-type climate (Baumann, 2009). Normally, Tropical Easterly winds blow from the Atlantic Ocean, flowing westwards towards South America, but between March and October, some of these winds turn eastwards as they cross the equator and blow towards Africa. The changing of the Tropical Easterlies coming from the North Atlantic determines when areas along the west coast of Africa receive a large amount of rain (Baumann, 2009). As a consequence of the changes in the course of the Tropical Easterlies the wind in West Africa flows in a west-east direction that seems to have some influence on the African forest elephant's movement behaviour on their paths in the forest, in the Central African region (Vanleeuwe and Gautier-Hion, 1998).

The climate of Lobeke region is typically equatorial and is made up of four seasons. Precipitation occurs throughout the year, peaking twice a year to an average precipitation of about 1500 mm per annum, occurring in April and October (Ekobo, 1995; Harrisson and Agland, 1987). The

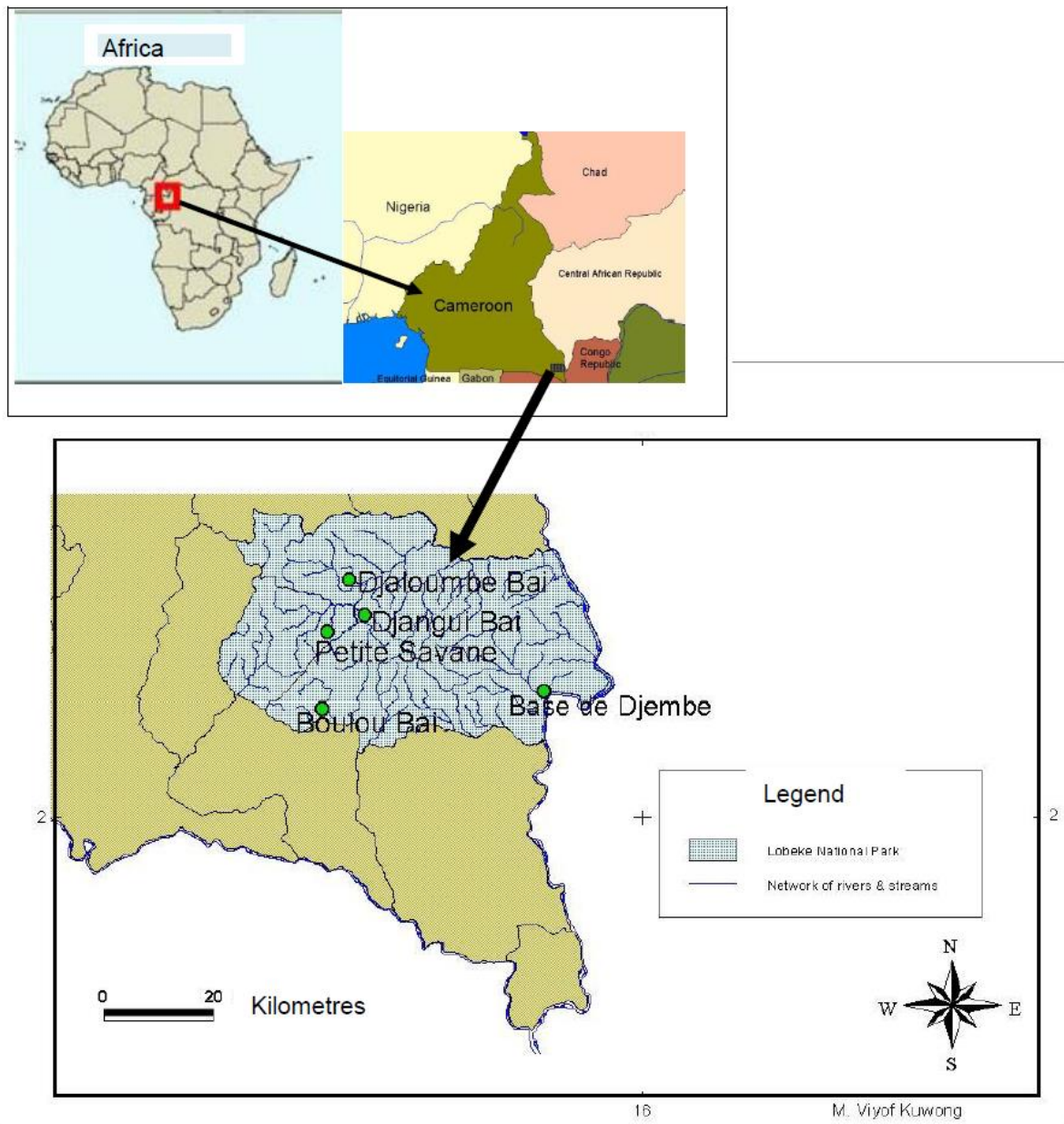


Figure 2.1 Map of Africa, Central Africa and Cameroon showing the location of Lobeke NP in south-east Cameroon. The green circles are the principal clearings or *bais* where this study was carried out. Note the rich network of rivers and streams evenly distributed in the park assuring adequate supply of water to elephants. Layers obtained from WWF to produce map, using Arcview 3.2 GIS ESRI software, USA.



A



B



C



D



E

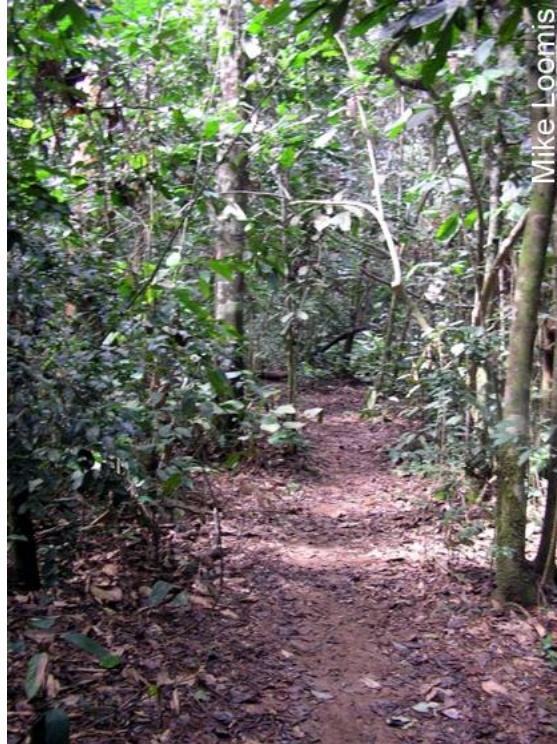
Figure 2.2 The landscapes of *bais* at the study sites. (A) Base de Djembe clearing at the banks of River Sangha, (B) Bolou Bai, (C) Djaloumbe Bai, (D) Djangui Bai early in the morning, (E) Petite Savane.

short wet season (rainy period) is between September to early November while the long wet season is between March and June. The long dry season (period without rain) lasts from November to February and the short dry season lasts from July to August (Ekobo, 1995; Harrison and Agland, 1987). The average dry-bulb air temperature ranges between 23°C and 31°C during the year (Nowell, 2005). Relative humidity of air varies from 60% to 90% (WWF, 2006). The period with the coolest dry-bulb air temperature of the year is during the long wet season while the period with the hottest dry-bulb air temperature of the year is during the dry season.

2.2.2 Bais and elephant paths

Fieldwork to collect microclimate data and explore forest elephant behaviour was done in *bais* and their environs, since *bais* exist in the natural habitat of forest elephants. Also, elephants often visit *bais* (WWF, 2006), *bais* were safe to perform this research and visibility was good. Based on Vanleeuwe and Gautier-Hion's (1998) surveys, a network of three distinct types of elephant paths are found to converge to alleys that open into *bais* (WWF, 2006). Records of high indices of elephant activity have reveal that path alleys near *bais* and *bais* are important forest sites to forest elephants (Vanleeuwe and Gautier-Hion, 1998). As far as I am aware, no study has investigated if path alleys and *bais* play any role on thermoregulation in forest elephants. Based on the sudden change of the vegetation cover in the *bais* and their vicinity, it is likely that microclimatic changes also occur as the vegetation of habitats change in path alleys and their *bais*. These microclimatic changes may affect the changes in the body temperature of forest elephants (due to changes in the effect of radiation, vapour pressure and wind speeds) as

A



B



Figure 2.3 (A) Elephant east-west direction corridors (Boulevards). Paths used by elephants to rapidly link important sites such as *bais* in the forest. (B) A typical elephant alley link near Base de Diembe at midday. The effect of wind and radiation on this paths may play some role in

elephants move across these habitat demarcations. Vanleeuwe and Gautier-Hion's (1998) described elephant paths in the forest, and they distinguished paths based on their direction, length, width, elephant activity and the types of forests that elephants pass through. They called these paths boulevards, foraging paths, and *bai* alleys. Elephant foraging paths mainly run through the medium-density *Marantaceae* forests which provide elephants with both herbaceous foods and tree fruit while boulevards follow a more or less east-west orientation and are used for travelling over long distances (up to 34 km) and for linking up favourite sites. Foraging paths are sinuous and show little consistency in direction. Near *bais*, all these different types of paths ramify into dense networks of *bai* alleys (see Figure 2.3A & B).

Swampy *bais* are mainly covered with forbs and herbaceous plant species. Hard-ground vegetation of *bais* often have grass different from the hard-ground cover vegetation under the forest canopy areas in the vicinity of *bais*, often covered with small trees and shrubs. *Bais* have peculiar climatic conditions; because of the sudden changes in vegetation cover from that of the surrounding forest. As mentioned earlier in this section, these changes affect the intensity of radiation and wind speed of the local environment and the microclimatic changes may be attractive for thermoregulatory purpose to wildlife. The soil composition of *bais* also have natural mineral salts that favours the sprouting of grasses and herbs, contributing to the uniqueness and the complexity of the *bais*, *bai* alleys and their surroundings (WWF, 2006) .

2.3 Study population

Between 15 November and 15 December 2010, I observed forest elephants for a total time of 67.4 hours. Eleven individuals (5 females, 4 males and 2 juveniles) were seen. A total of 429 behaviour observations were made during the day and 425 at night, using the naked eye or 10x50

mm binoculars. Day observations were made between 06:00-18:00 and night observations between 18:00-24:00 (See Table 2.1 & Figure 2.4). Lobeke NP is one of the most-populated forest elephant areas in Central Africa with a density of between 0.81-1.14 individuals per km² (Nzoo Dongmo, 2003; Tutin and Fernandez, 1984; WCS, 1996). During the dry season some elephants traverse the Sangha River through well-defined corridors in to Nuabale-Ndoki NP in the Republic of Congo. More than 2,100 elephants have been identified in the adjacent Dzanga Bai in the Dzanga-Ndoki NP in Central African Republic (Turkalo and Fay, 1995). Based on estimated density of one individual per km², Turkalo and Fay (1995) suggested that the whole elephant population of the Dzanga-Sangha-Ndoki complex may visit the Dzanga Bai. Indirect evidence suggests that forest elephants travel over long distances traversing long forest corridors from *bai* to *bai* (Vanleeuwe and Gautier-Hion, 1998) and other important sites.

2.4 Microclimate assessment

Portable weather stations were used to collect microclimatic data in Djaloumbe, Djanguui, Petite Savane, Bolou and Base de Djembe Bais. A typical weather station consisted of three main components; a white plastic hollow tube on which a vane and a fin are attached (Figure 2.5A), and a black globe (Figure 2.5B) and a data logger (Figure 2.6) protected in a freely ventilated grey plastic box (Figure 2.5A). The fin and hollow tube ensured that the vane always pointed into the prevailing wind, and the white plastic tubing protected the dry-bulb thermometer erected within the tube, from radiation. The sensor of the dry-bulb thermometer was situated at the centre of vane. The vane was attached to the cross-arm at the stand (Figure 2.5B), and the other cross-arm held a globe thermometer, 1.2 m above the ground. The globe thermometer (Vernon, 1930) was a matte black copper 150 mm globe with a temperature-sensitive sensor put in its



A



B



C



D

Figure 2.4 (A) An elephant bull observed near Base de Djembe. (B) A herd of elephants eating, drinking and spilling mud on their bodies in Djaloumbe Bai in Lobeke NP. (C) A herd of five individuals seen early in the morning foraging and drinking water in Djanguai Bai. (D) Solitary bull in Base de Djembe.

Table 2.1 A. Detailed records of elephants observed in Djaloumbe, Base de Djamba, Djangul, Petite Savane and Bolou Bals during the day

Elephant ID & sex	Total hour of observations	Number of elephant observations		Foraging		Drinking hosting or swimming		Playing in mud Wallowing		Dusting		Ear flapping		Shade seeking behaviour		Walking		Standing resting		Lying	
		Possible	Actual	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
E16 ♂ 16 Nov. 2010	5	61	61	45	74	0	0	38	62	0	0	42	91	0	0	46	75	16	26	0	0
E6J1 ♀ 06 Dec. 2010	3.8	46	46	14	30	11	24	35	76	0	0	31	67	0	0	35	76	14	30	0	0
E6J2 ♀ 06 Dec. 2010	3.8	46	46	21	46	10	19	39	85	0	3	35	76	22	48	35	76	13	28	0	0
E6J3 ♂ 06 Dec. 2010	4.3	52	52	25	48	10	19	45	87	17	33	41	79	17	33	39	75	14	27	0	0
E10D ♀ 06 Dec. 2010	4.3	52	52	24	46	15	28	34	65	9	17	40	77	10	19	41	79	13	25	0	0
E6J5 C 06 Dec. 2010	3.8	46	46	19	41	25	54	33	78	0	0	28	61	19	42	34	74	14	30	0	0
E9 PS ♀ 09 Dec. 2010	6	96	83	69	83	0	0	1	1	9	11	68	82	83	100	40	48	42	51	0	0
E14D ♂ 14 Dec. 2010	4	52	43	32	74	0	0	0	0	2	5	32	74	43	100	19	44	16	37	0	0
Grand totals	30.7	451	429	249	58	71	17	225	52	37	3	317	74	194	43	289	67	142	33	0	0

Table 2.1 B. Detailed records of elephants observed in Base de Djembe during the night

Elephant ID & sex	Total hour of observations	Number of elephant observations		Foraging		Drinking hoisting or swimming		Playing in mud Wallowing		Dusting		Ear flapping		Shade seeking behaviour		Walking		Standing resting		Lying	
		Possible	Actual	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
E10 D ♀ 10 Dec. 2010	4	49	49	45	92	0	0	0	0	0	0	41	84	0	0	33	67	16	33	0	0
E10 D ♂ 10 Dec. 2010	3.8	50	46	39	85	0	0	0	0	0	0	35	76	0	0	27	59	16	35	0	0
E 10 DC 10 Dec. 2010	3.9	49	38	34	89	0	0	0	0	0	0	32	84	0	0	27	71	10	26	0	0
E10 D ♀ 11 Dec. 2010	4.3	53	53	48	91	0	0	0	0	0	0	46	86	0	0	39	74	14	26	0	0
E10 D ♂ 11 Dec.2010	6	72	72	39	54	0	0	0	0	0	0	45	63	0	0	57	79	16	22	0	0
E10 D C 11 Dec.2010	4	49	42	40	95	0	0	0	0	0	0	36	86	0	0	30	72	12	29	0	0
E10 D ♀ 12 Dec. 2010	3.3	41	39	37	94	0	0	0	0	0	9	31	79	0	0	25	64	14	36	0	0
E10 D ♂ 10 Dec. 2010	3.8	50	46	39	85	0	0	0	0	0	0	35	76	0	0	27	59	16	35	0	0
E 10 DC 10 Dec. 2010	3.9	49	38	34	89	0	0	0	0	0	0	32	84	0	0	27	71	10	26	0	0
E10 D ♀ 11 Dec. 2010	4.3	53	53	48	91	0	0	0	0	0	0	46	86	0	0	39	74	14	26	0	0
E10 D ♂ 11 Dec.2010	6	72	72	39	54	0	0	0	0	0	0	45	63	0	0	57	79	16	22	0	0
E10 D C 11 Dec.2010	4	49	42	40	95	0	0	0	0	0	0	36	86	0	0	30	72	12	29	0	0
E10 D ♀ 12 Dec. 2010	3.3	41	39	37	94	0	0	0	0	0	9	31	79	0	0	25	64	14	36	0	0
E10 D ♂ 12 Dec. 2010	3.6	49	44	43	98	0	0	0	0	0	0	37	84	0	0	29	66	15	34	0	0
ED 10 C 12 Dec. 2010	3.8	49	42	40	95	0	0	0	0	0	0	31	74	0	0	40	95	18	43	0	0
Mean													79				72		32		
Grand totals	36.7	461	425	365	88	0	0	0	0	0	0	334	79	0	0	307	72	131	31	0	0

Note that 11 Individuals were studied in total and that observations were made more than once on the some Individuals on different instances and locations

♀= Female elephant

♂ = Male elephant

C= Juvenile

A



B



Figure 2.5 (A) White air vane and a tail fin. Also seen is a cable used to connect dry-bulb thermometer to data logger housing. (B) Weather station installed in the field, the vane on left arm of pole and black globe on right arm of pole.



Figure 2.6 Two 4-channel data loggers.

centre. The black globe thermometer provided an integrated measure of the effect of the wind, air temperature and radiation (Vernon, 1930). The dry-bulb thermometer and the globe sensors were connected to a data logger (Hobo®, temp/RH2 ext., Onset Computer Cooperation Massachusetts, USA) and housed below the logger in a naturally-ventilated plastic box. The data logger also measured RH of air via an on-board sensor.

The dry-bulb temperature, relative humidity and globe thermometer, 1.2 m above the ground, were attached on a rotating vane and stand. The data logger logged the variables at five minute intervals. The data logger's memory could store 43,000 data points, so, at a sampling interval of 5 minutes, could log microclimatic data for about 60 days.

2.4.1 Calibration of data logger

I calibrated the data loggers and their sensors using the procedure applied by Hidden (2009). I used a precision thermometer (Quat 100, Heraeus, Hahau, Germany) to calibrate the temperature data loggers connected to sensors in a stirred insulated water bath, across a range of six temperatures between 32°C to 45°C. These temperatures were within the range of the environmental temperature expected to encounter in Lobeke NP during the hot dry season. A linear equation ($y=a+bx$) provided a suitable fit for calibration data from all the data loggers (TableCurve 2D for Windows v3.05, Jandel Scientific, California, USA). The calibration accuracy at the thermometer, as assessed by the standard errors of the fitted lines, was better than 0.1°C. I repeated the calibration procedure at the end of field work and detected no drift exceeding 1°C (i.e. within the temperature range of the amplitude of elephant daily body temperature fluctuation (Hidden, 2009)). Figure 2.8 illustrates an example of a thermometer

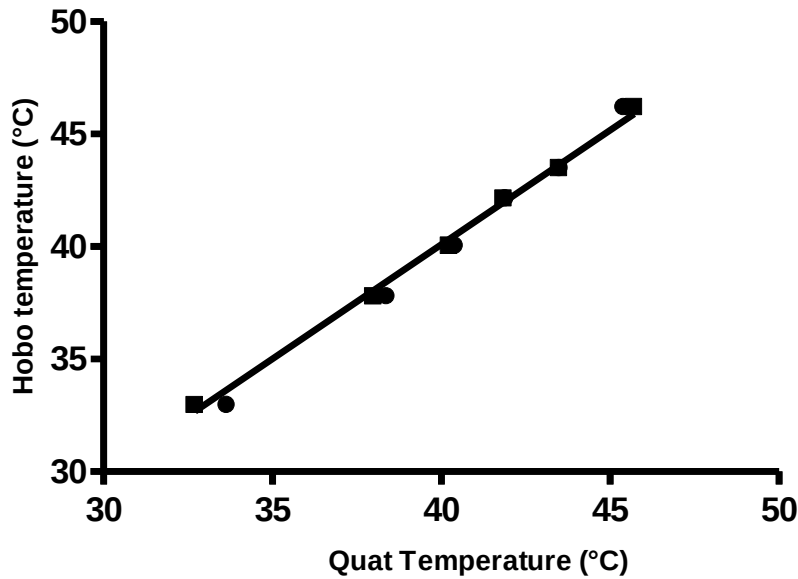


Figure 2.7 One example of the linear regression analysis used for the calibration of the Hobo data logger thermometers that were used for this study, Hobo thermometer (A) temperature = (●) and Hobo thermometer (B) temperature = (■). The linear regression fit to this calibration data was $y=a+bx$; Where ($a=3.9$, $b=0.90$). $r^2=0.99$ Fitted standard error= 0.016°C . This study considered the temperature range within which the normal body temperature of an elephant and also the environmental temperature range that Lobeke NP would be during the dry hot season (20°C to 46°C), before the calibration

calibration done before and after field work. I employed the calibration from the factory for the hygrometer to measure relative humidity.

.4.2 Procedure for collecting microclimatic data

A pair of weather stations was erected at each *bai* (Table 2.2). Using a measuring tape to measure distance, one weather station was erected 100 m away from the open *bai* under the closed forest canopy, and the second weather station was deployed in the open area of the *bai*, such that the weather station was exposed to free air movements and also exposed directly to radiant heat during the day (Figure 2.8). Five *bais* were assessed during this study. The weather stations logged data at each site for three days each. I downloaded information from the data loggers using a personal computer and software (HoboWare, Onset Computer Cooperation Massachusetts, USA). All data were then exported to Excel spread sheets (MS Office, USA) for analysis.

In addition to the microclimate variables measured with weather stations, I measured microclimate wind speed at chosen sites near the weather stations in the *bais* and under the forest canopy, at 30 minute intervals from 06:00-18:00 in all of the study sites. I employed factory calibration for the anemometers. I used a hot-wire anemometer (GGA-65, Alnor Thermo-Anemometer, Finland) and the field assistant in the second group of field workers in this study used a wind vane anemometer (AM-4201 digital Lutron anemometer, USA) to measure and record wind speed (m/s).



A



B



C



D

Figure 2.8 (A) Weather station at noon under closed-forest canopy near Djangui Bai. (B) Weather station at noon in the middle of Djangui Bai. (C) Miradow in Djangui Bai. (D) Side view of closed-canopy forest in Lobeke NP.

2.5 Procedure for collecting behaviour data

I exclusively investigated the behaviour and thermoregulatory strategies of the forest elephant during the field-work of this dissertation. I was assisted by Raul Mambele, an experienced field worker, trained to collect microclimate and elephant behaviour observations for my study. We made observations from 06:00 to 18:00, whenever elephants entered the *bais*. We observed from the miradows, taking precautions not to disturb the animals. Miradows are dull green or brown painted chalets, built on wooden platforms, usually at the forest-savannah borders, with balconies overlooking the *bais*. The colour of the chalet blends with the surrounding environment of the forest, serving as a camouflage. Tourists and researchers use the miradows as shelter and accommodation to observe wildlife safely in the forest vicinity for weeks and even months, without apparent disturbance to animals in their natural environment. On three occasions we observed and recorded data of elephant activity between 18:00 to 24:00 at the banks of the Sangha River in Base de Djembe.

Using the naked eye or 10x50 mm binoculars, we recorded the activity of the eleven elephants seen at five minute intervals. We applied the fixed interval time point sampling method (Guy, 1976; Martin and Bateson, 1986; Wyatt and Eltringham, 1974) to observe elephant behaviour. At times my assistant and I recorded behaviour from different elephants simultaneously using data-recording sheets to record behaviour (Table 2.3). At each five-minute sampling point, we recorded the activity of a focal elephant as one of the behaviour categories previously described in section 2.5. However, I classified the following elephant activities: drinking of water,

swimming, soil eating (geophagy), splashing and smearing of mud on the elephant's body as water-related because water is involved in all the activities.

Since we observed animals from miradours it was difficult to watch nocturnal behaviour of elephants in most of the *bais* at night. However, we observed elephants that visited the Base de Djembe during three consecutive nights between 18:00-24:00. Base de Djembe had security lights that illuminated part of the clearing at night, enough for an observer to see animals at certain locations. Nevertheless, at certain instances throughout this study, the focal animal was obscured by vegetation or darkness, in which case data recording was interrupted. Both of these difficulties were some of the flows in my study.

To overcome some of these difficulties, I also used indices of elephant presence to assess the number of elephants visiting the *bais* and its environs during this study, in order to ascertain elephant presence in the *bais* and its environs at night and in obscure areas of the *bais*. These data were important to assess if elephants were present or absent in the *bais* or under the forest canopy during varying environmental conditions in the course of the 24-hour day period. In many cases indirect methods, such as surveying signs of animals (dung or nests counts) have been used to carryout wildlife surveys in the forest because of the poor visibility and the safety concerns of my field personnel. As such I used indirect methods to estimate the number of elephants entering the *bais*.

I checked whether elephants entered the *bais* in the day or night without being noticed during this study using a topofil. A topofil is a portable instrument made of a small wheel having a

Individual: _____

Date: _____ Locality: _____

Locality:

[illegible]

Ly= lying, St =standing, Wlk= walking, Ru=running, Ho= splashing water, Still= standing still, Pll=parallel, Pplar= perpendicular, Obl=oblique, r=right, l=left

string-pile of sewing thread wound on the wheel that is mounted on an axle. The wheel turns and unwound the thread in the direction of pull. I placed thin sewing threads attached to a topofil, at various entrances of elephant paths into the *bais* along the forest-savannah boundaries. Any elephant or other large animal entering the *bais* would automatically cut and displace the thread with its legs or body towards the direction of motion. I could identify the species subsequently by examining the footprint on the soil. Also, by measuring elephant footprint size, I was able to assess the number of elephants and estimate the time the animals passed through any *bai* entrance. Other supplementary tools that I used to estimate the number of elephants that visited the study sites included number of vocalizations heard at night and number of fresh faecal dropping (fresh faecal < 12 hours old was usually green) identified and the faecal positions noted on the paths and alleys in the vicinity of the *bais*. By measuring the sizes of faecal droppings and foot prints, identifying the shapes and sizes of toe nails, I could estimate the number of elephants. Also the vocal sounds of adults were louder than the vocal sound of calves and juveniles, and these differences were also used to estimate elephant numbers.

2.6 Data analysis

In all statistical analyses throughout this dissertation a p value less than 0.05 was considered significant. I ran two-way ANOVA to assess the differences between the means of the categories of microclimatic data from various weather stations under forest canopy and weather stations from the open *bais*. I also analysed the differences between microclimatic variables in open *bais* and under forest canopy for all the study sites using two-way ANOVA and correlation analysis to assess relationships between microclimatic variables.

Relative humidity data were converted to vapour pressure using a barometric chart (Barenbrug, 1974). To obtain a more accurate microclimate variable for each hour, the mean of five-minute

temperatures and vapour pressures for each hour during a 24-hour time sequence was computed. The mean of the temperatures and vapour pressure for each hour from 06:00 to 18:00 was computed to obtain the mean and standard deviation for globe temperature, the mean and standard deviation for dry-bulb temperature and the mean vapour pressure and standard deviation for each of the sites studied. The standard deviation indicated the how high or low variables were from the mean of the variables. The mean hourly globe temperature, dry-bulb temperature and vapour pressure per site for each day were computed to obtain the mean and standard deviation for three-day microclimatic variables for each study site. To assess if microclimate variables were different between study sites, two-way ANOVA was used to compare the mean microclimatic variables. To assess the 24-hour pattern of the globe temperature (environmental heat load) in open *bais* and the closed-forest canopy at the different study sites, I plotted the mean hourly black globe temperature, dry-bulb temperature and vapour pressure against time of the day for each study site, using GraphPad Prism (Version 4 software, San Diego, CA, USA). In addition to computing the five-minute values of temperature and vapour pressure, I computed the hourly mean wind speed during the day at each study site in the open *bais*, and at each study site under the forest canopy, to obtain a more accurate wind speed for each study site per hour. I plotted graphs of mean wind speed against time of the day for all the study sites.

2.6.1 Analysis of behaviour data

I used data from five-minute observations categorising elephant behaviour to obtain the percentage of the time each of the elephants in this study spent on each activity, at different hours of the day. I then calculated the mean percentage of time spent per hour for each activity by averaging activity times of all elephants that I observed in that specific hour of the 24-hour day. I also calculated the standard deviation of time spent per hour in each activity. I also ran

correlation analyses to compare the mean black globe temperature, dry-bulb temperature and vapour pressure of air for all the study sites with the mean percentages time that all the elephants in this study spent on each activity. This analysis was done in order to ascertain if observed elephant thermoregulatory behaviours correlate with microclimatic variables.

2.6.2 Analysis of microclimatic and behaviour data

The elephant activities such as walking, foraging, shade-seeking, ear-flapping, dust-bathing and water related activities of this study that correlated with black globe temperature, dry-bulb air temperature and water vapour pressure of air were plotted (i.e. behaviour against microclimatic variables). Only the microclimatic profiles that were similar for all the study sites were used to assess effects on elephant behaviour. However, most of my data of elephant activities were obtained mainly in the *bais* and at the edges of the *bais* where elephants were visible and where elephants' indices of presence were seen. I used the indices of elephant presence in this study to assess the number of elephant that entered the *bais* and elephants that were present at the forest canopy at the vicinity of the *bais* in this study. Although no thermoregulatory behaviour could be obtained from the data of elephants' indices of presence, the indices data was important because I used the number of elephants identified to visit the study site at any time of the 24-hour day period to find out if any correlation exist between elephant numbers and microclimate variable of the period of visit.

CHAPTER 3

RESULTS

3.1 Introduction

In this chapter I report the results of the microclimates and the behavioural data of the elephants that I observed at five study sites in Lobeke NP. I obtained microclimate data logged at five minute intervals, for three days each per site, covering 360 hours and total of over 4000 measurements of black globe (T_g), dry-bulb (T_a), vapour pressure of air (VP) and wind speed (WS) variables.

3.2 Microclimate data

3.2.1 Black globe temperature

The T_g in the open *bais* and under the tree canopy is illustrated in Figure 3.1. T_g showed a prominent rhythm, with the profiles on consecutive days being similar, with exceptions on the first day in Djaloumbe and Bolou Bais. T_g peaked between 11:00-13:00, at a maximum temperature that exceeded 40°C in the open *bais* of four of the five sites. Under the tree canopy, maxima were usually below 30°C. Curves of the T_g profiles for the Djangui Bai were different from the other four sites, in that maximum T_g in the open *bais* was close to that under the canopy. Also, the T_g in the *bai* for Djangui was 40°C, unlike that for the other four *bais*. T_g in both the open *bais* and under the tree canopy for all the *bais* declined gradually during the night, reaching a minimum just before dawn.

3.2.2 Dry-bulb temperature

Figure 3.2 illustrates the three-day 24-hour pattern of T_a in the *bais* and under the forest canopy. Early in the morning, at approximately 08:00 the T_a in the open *bais* and under the forest canopy ranged between 15-23°C. As the sun rose in the morning, the T_a also began to rise; steadily increasing to peak at 38°C in the open *bais* and 28°C under the forest canopy, and then gradually

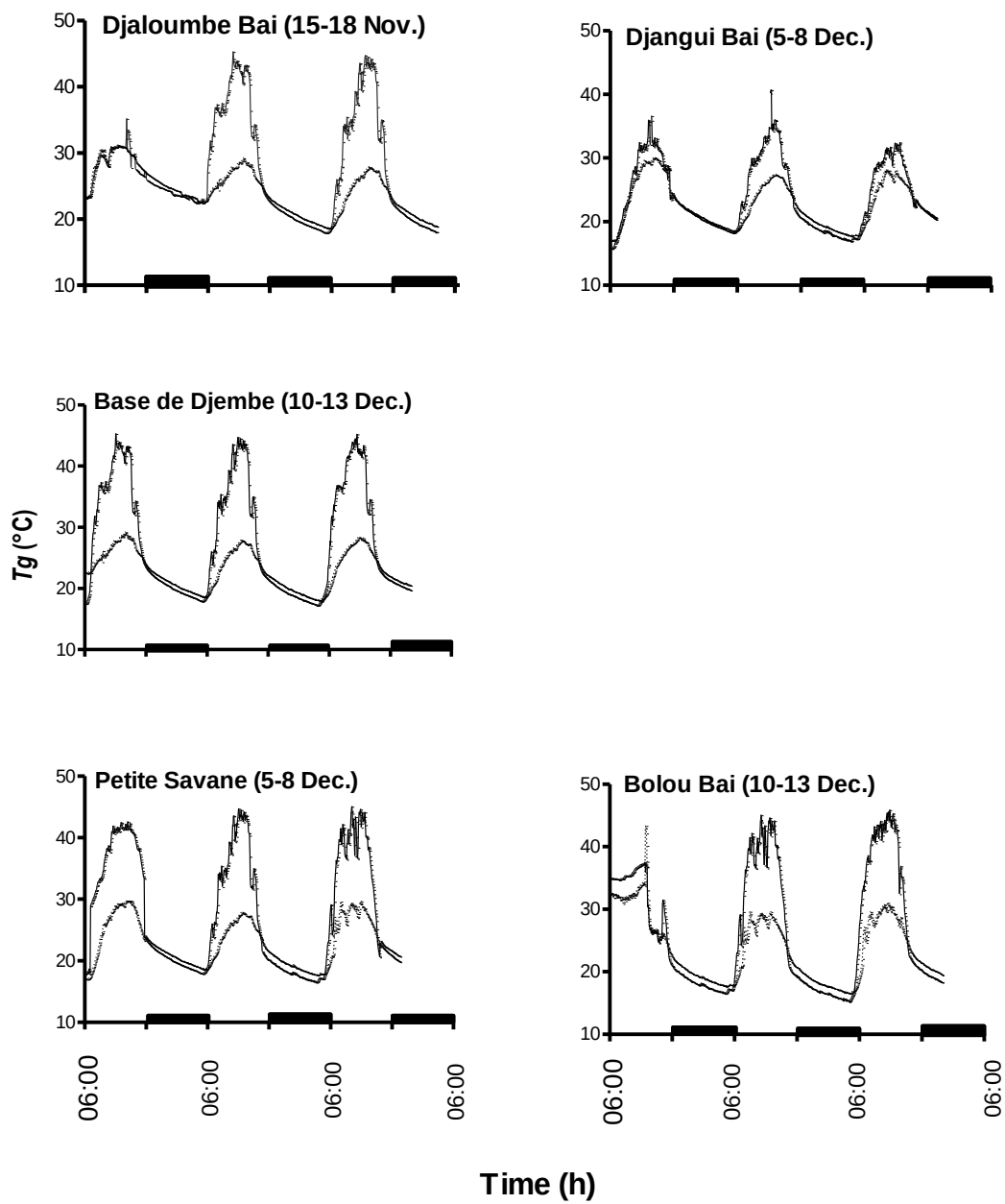


Figure 3.1 T_g in the open *bais* (—), and T_g under the forest canopy (....), at the different study sites in Lobeke NP. The dark bars represent night.

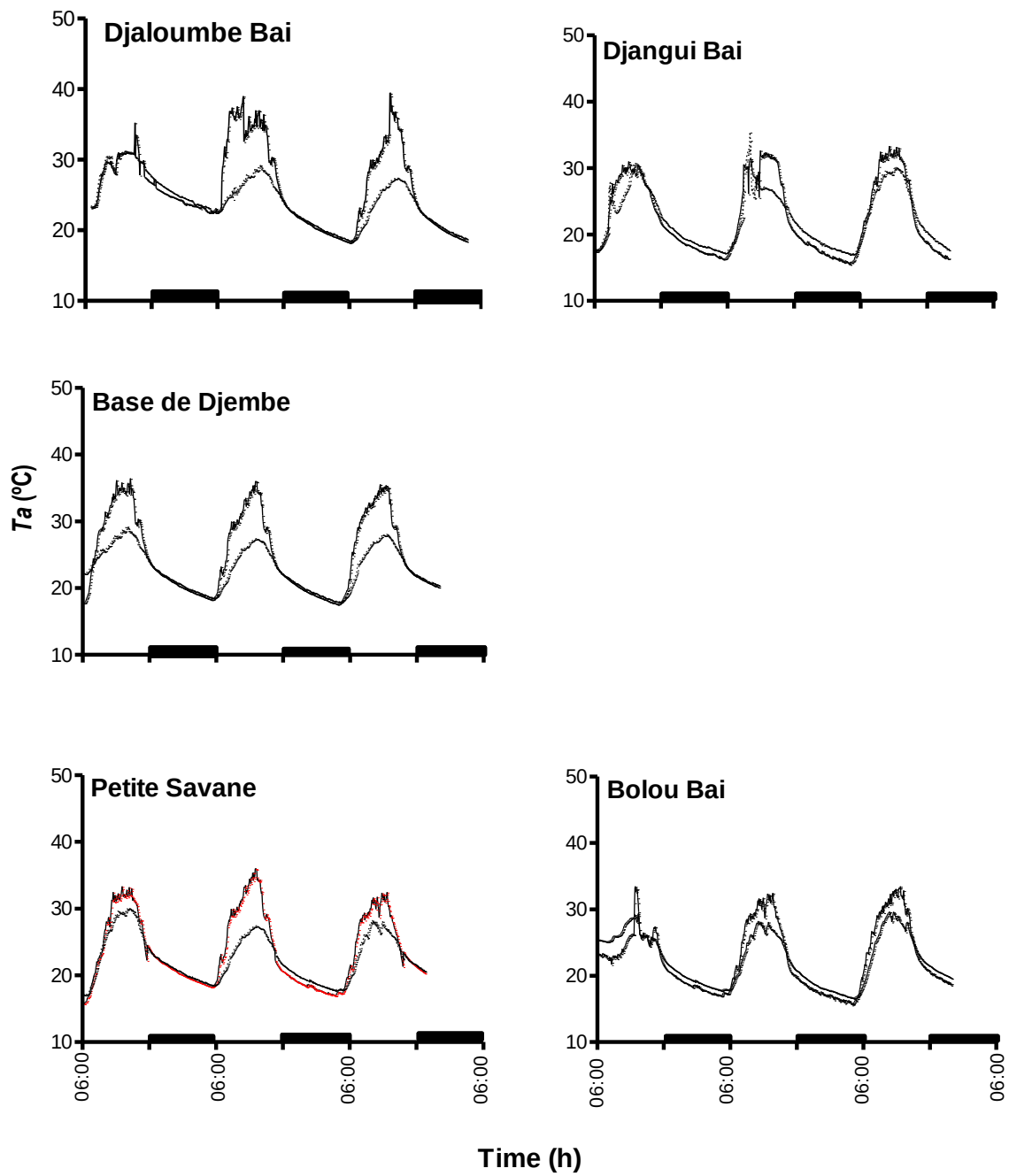


Figure 3.2 T_a in the open *bais* (—), and T_a under the tree canopy (....), at the different study sites in Lobeke NP. The dark bars represent night.

decreasing until sunset. During the night the T_a in the open *bais* and under the forest canopy continued to gradually decrease to just below 19°C just before sunrise.

3.2.3 Difference between black globe and dry-bulb temperature

The temperature difference between T_g and T_a ($T_g - T_a$) in each of the open *bais* is shown in Figure 3.3. Generally, during the day the T_g and T_a increased with the increase in sunlight intensity, and the peak of $T_g - T_a$ occurred at about midday. Between 18:00 and 06:00 $T_g - T_a$ in the *bais* and under the forest canopy was close to zero for all the study sites. However, on the first day of data recording, the patterns of $T_g - T_a$ in Djaloumbe, Petit Savane and Bolou Bais were inconsistent. In the mornings of some days, the $T_g - T_a$ of Djaloumbe, Base de Djembe and Bolou Bais started increased about 15 minutes before 06:00. While the $T_g - T_a$ of the first day of Djaloumbe, Petite Savane and Bolou Bais showed patterns peculiar to $T_g - T_a$ of the rest of the days. $T_g - T_a$ for all the days in Djanguï, day-1 and day-2 of Base de Djembe, day-2 and day-3 of Petite Savane showed $T_g - T_a$ increasing at 06:00.

3.2.4 Vapour pressure of air

Both the VP in the open *bais* and under the forest canopy started to rise at about 8:00 in the morning. Generally, the VP of Djaloumbe, Base de Djembe, Petite Savane and Bolou Bais followed a similar day and night pattern. VP peaks occurred at different times during the day in each of the sites. However, during the first and the second days at Djanguï the VP curve showed a sudden upsurge as high as 3.5 kPa under the forest canopy during the day, but this phenomenon did not occur on the third day. The VP patterns in the open *bais* and under the canopy were fairly similar to each other during the night, but much higher under the forest canopy than in the open *bais* during the day (see in Figure 3.4).

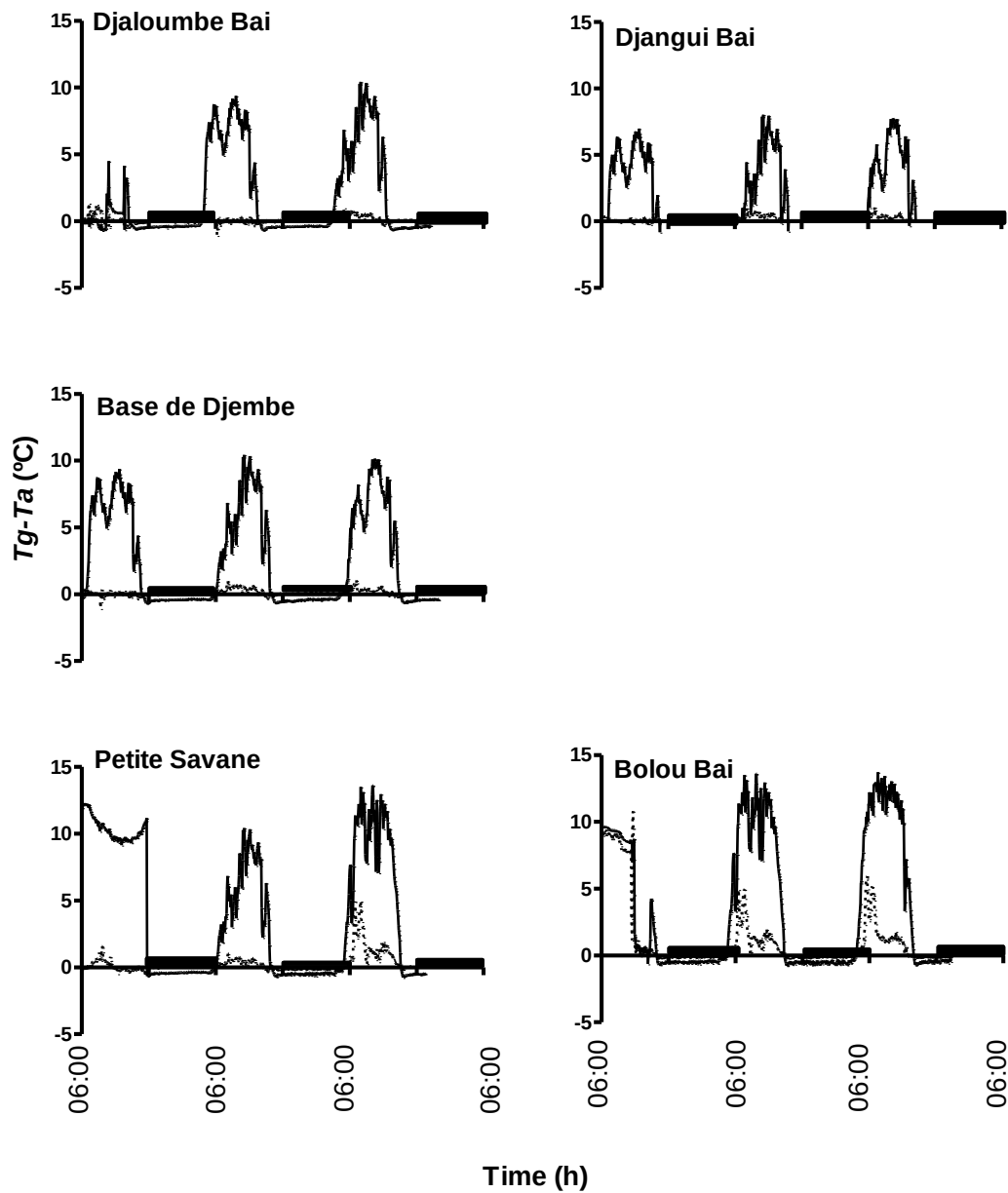


Figure 3.3 Differences between T_g and T_a ($T_g - T_a$) in the open *bai* (—), and under the forest canopy (....), at the different study sites in Lobeke NP. The dark bars represent night.

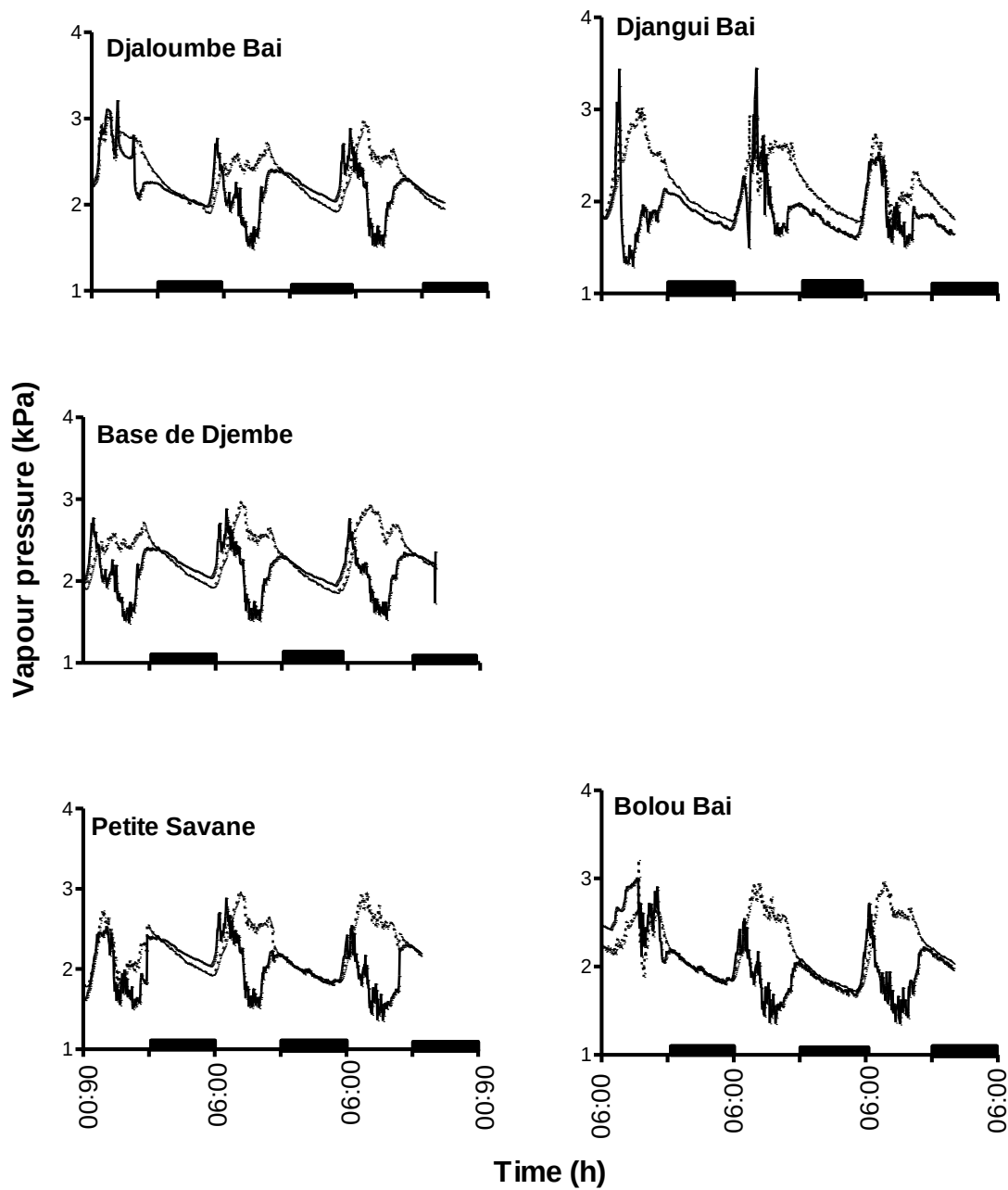


Figure 3.4 VP in the open *bais* (—), and under the forest canopy (....), at the different study sites in the Lobeke NP. The dark bars represent night.

3.2.5 Wind speed

Figure 3.5 illustrates the mean three-day WS profiles for each of the study sites from 06:00-24:00. The WS differed significantly between study sites ($p < 0.05$, $f = 2.68$). There were significant differences between day WS for five of the study sites ($p < 0.01$, $f = 0.74$). WS were generally faster in the open *bais* than under the forest canopy for each of the study sites ($p < 0.05$, $f = 0.740$, during the day; and $p = 0.05$, $f = 2.68$) during the night. WS between day and night differed significantly ($p < 0.05$, $f = 15.2$) (see the summary of statistics in Table 5.1 in the appendix).

Figure 3.6 illustrates the three-day mean T_g , T_a , VP and the WS in the open *bais* and under the forest canopy, during day and night, for each of the study sites. There were no significant differences between the mean T_g and T_a in the open of each *bais* during the day and during the night ($p = 1.10$, $f = 0.03$ for T_g in *bai* and under forest canopy during day; $p = 0.87$, $f = 0.31$ for T_g in *bai* and under forest canopy at night). Also, no significant differences were recorded between T_a in the *bais* and under the canopy and VP in the *bais* and under the forest canopy during the day and night (see stats in Figure 3.6). However, WS was significantly different in the *bai* and under the forest canopy ($p < 0.05$, $f = 7.39$) during the day and $p < 0.05$, $f = 2.68$) during the night. WS in the open *bais* and under the forest canopy were similar for Djaloumbe and Djanguai Bais, but the mean WS in the open *bais* for Base de Djembe, Petite Savane and Bolou Bais were slower than under the forest canopy during the day. At night, the WS in the open *bais* for all the study sites were faster than the speed under the forest canopy. There was no significant difference between the mean $T_g - T_a$ in the open *bais* and under the forest canopy for each of the study sites ($p = 0.10$, $f = 0.16$) during the day. However, there were a significant differences between $T_g - T_g$ during the night ($p < 0.05$, $f = 0.41$) during the night. T_g during the day in the

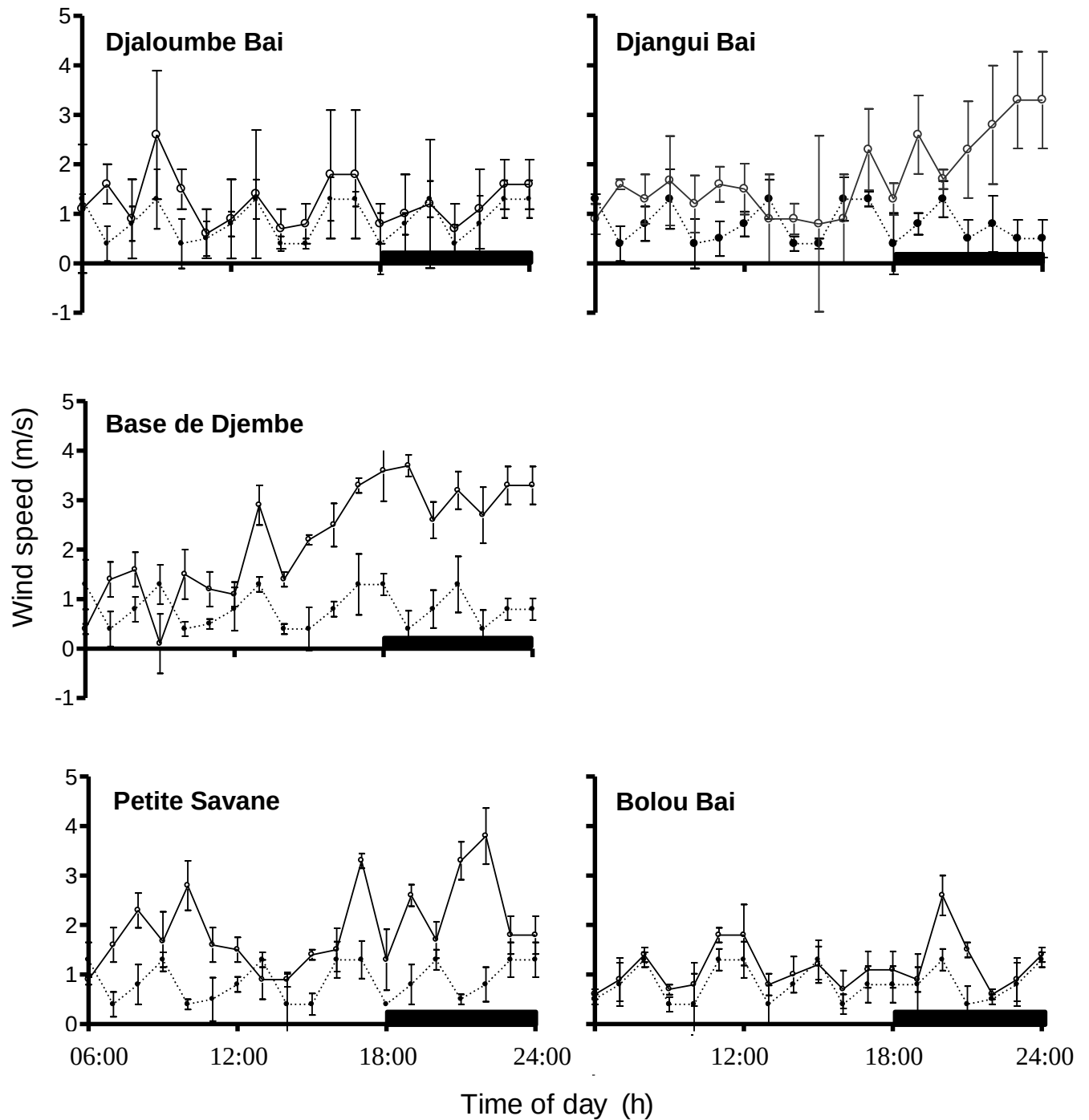


Figure 3.5 Mean three-day (±SD) WS profile in the open *bais* (○) and under the forest canopy (●) for five of the study sites in Lobeke NP between 06:00-24:00. The dark bars represent the night.

open *bais* and under the forest canopy was generally higher in value than *Ta* and as a result *Tg-Ta* had positive values. But at night *Tg-Ta* was significantly different ($p < 0.05$, $f = 0.41$) some being positive in value others being negative (see Figure 3.7). There was no significant difference between the mean *Tgs* for all the study sites. Also, no significant difference was recorded between *Tas*, and *VPs* for all the study sites too ($p = 1.0$, $f = 0.03$ for day *Tg*; $p = 0.98$, $f = 9.01$ for day *Ta*; $p = 0.66$, $f = 0.67$ for day *VP* in the open *bais* and under the forest canopy respectively). Lobeke NP had similar *Tg* and *Ta* and *VP* profiles at all of five study sites but the *WS* profiles were significantly different. Table 3.1 summarises the mean microclimatic profile for Lobeke NP, (*Tg*, *Ta* and *VP* as well as that for *Tg-Ta*, during day and at night). Since *WS* were significantly different in each of my study sites, it was not possible to obtain a profile that pertains broadly to Lobeke area.

Figure 3.8 illustrates the three-day mean *Tg*, *Ta*, *Tg-Ta* and *VP* profiles for all of the study sites in Lobeke NP. Generally, the mean *Tg* profiles in the open *bais* were significantly higher than the *Tg* under the forest canopy between 06:00-24:00 ($p = 0.005$, $f = 4.27$). There was no significant difference between the *Ta* profile in the open *bais* and under the forest canopy during 06:00-24:00 ($p = 0.31$, $f = 2.72$). The profile of *Tg-Ta* in the open *bais* was significantly higher than *Tg-Ta* under the forest canopy ($p < 0.0001$, $f = 11.8$). During similar period, the mean *VP* under the forest canopy was significantly higher than *VP* in the open *bais* ($p < 0.0001$, $f = 1.55$) but no significant correlation was observed between *Tg* and *VP* ($p = 3.33$, $f = 2.83$).

Figure 3.9 illustrates the linear regressions of the variables that correlated with each other following the correlation analysis of the means of the microclimatic variables for all of the study sites. The *Ta* in the *bais* correlated with the *Tg* in the *bais* ($p < 0.05$, $r^2 = 0.94$). Similarly, *Ta* and *Tg*

correlated under the forest canopy ($p<0.05$, $r^2=0.96$). The T_g in the *bais* correlated with the T_g under the forest canopy ($p<0.05$, $r^2=0.86$) and the T_a in *bais* also correlated with the T_a under the forest canopy ($p<0.05$, $r^2=0.93$).

Referring to the values of T_g and T_a VP and WS in Table 3.1, there was no significant difference between the mean T_g in *bais* during the day and night ($p=0.15$, $f=3.81$) or in *bai* and T_g under the forest canopy ($p=0.66$, $f=0.059$). No significant difference was recorded between the T_a during the day and night ($p=0.64$, $f=0.41$) or between the T_a in *bais* and T_a under the forest canopy ($p=0.70$, $f=0.27$). There was no significant difference between VP in the day and VP at night ($p=0.206$, $f=9.00$), or VP in the *bai* and VP under the forest canopy ($p=0.20$, $p=09.0$).

Table 3.1 Summary of mean ($\pm$ SD) microclimatic variables for all the study sites and the differences between the variables in the *bais* and under the forest canopy during day and night.

Microclimatic variables	Day	Night
Mean T_{gb}	32.8 $\pm$ 1.1°C	19.6 $\pm$ 1.2°C
Mean T_{gt}	25.5 $\pm$ 0.8°C	20.5 $\pm$ 1.3°C
$T_{gb}-T_{gt}$	7.30$\pm$0.3°C	-1.1$\pm$0.1°C
Mean T_{ab}	26.9 $\pm$ 1.2°C	19.8 $\pm$ 1.3°C
Mean T_{at}	19.4 $\pm$ 0.8°C	21.2 $\pm$ 0.7°C
$T_{ab}-T_{at}$	7.5$\pm$0.4°C	-2.6$\pm$0.6°C
Mean VP_b	2.10 $\pm$ 0.10 kPa	2.08 $\pm$ 0.11 kPa
Mean VP_t	2.08 $\pm$ 0.10 kPa	2.04 $\pm$ 0.23 kPa
VP_b-VP_t	-0.02$\pm$0.00 kPa	0.04$\pm$0.88 kPa

T_{gb} =globe temperature in *bai*, T_{ab} =Dry-bulb temperature in *bai*, T_{gt} = globe temperature under forest canopy, T_{at} = dry-bulb temperature under forest canopy, VP_b = vapour pressure of air in *bai*, VP_t =vapour pressure of air under forest canopy.

Table 3.2 summaries the mean WS for each of the study sites. The highest mean WS was recorded in the Djangui Bai (3.9 m/s), the least windy conditions occurred in Petite Savane (0.7 m/s). The mean WS profiles for each of the study sites were different from one another. For this reason the profiles did not represent the WS of Lobeke NP and could not be used to assess how WS in the park generally influence the forest elephant's behaviour in the park.

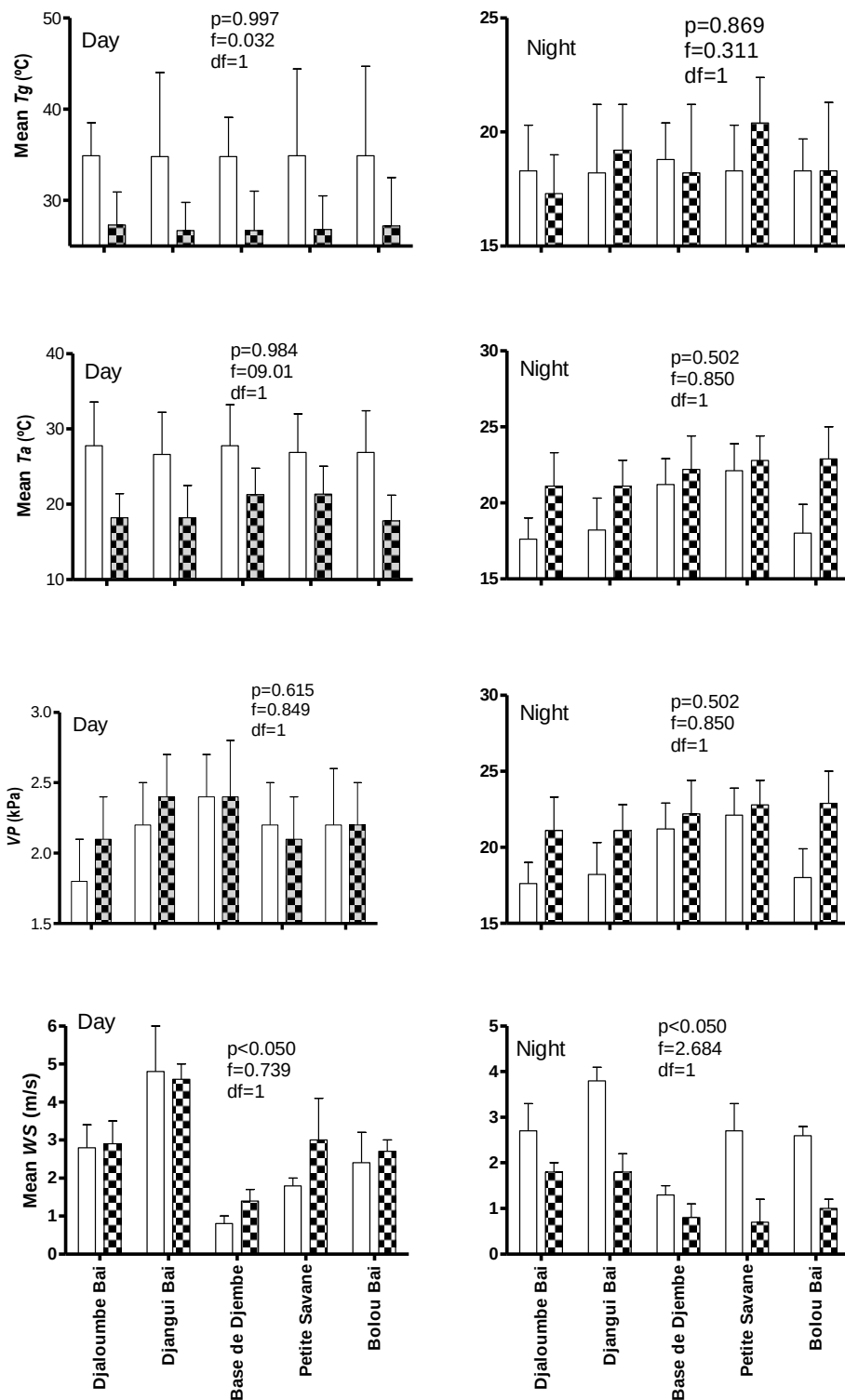


Figure 3.6 Mean T_g , T_a , VP and WS ($\pm$ SD) for three days in the *bais* and under the forest canopy, during the day (06:00-18:00) and the night, for all study sites (18:00-06:00) *bais* in the Lobeke NP. The open bars represent variables in the open *bais* and shaded bars represent variables under the forest canopy.

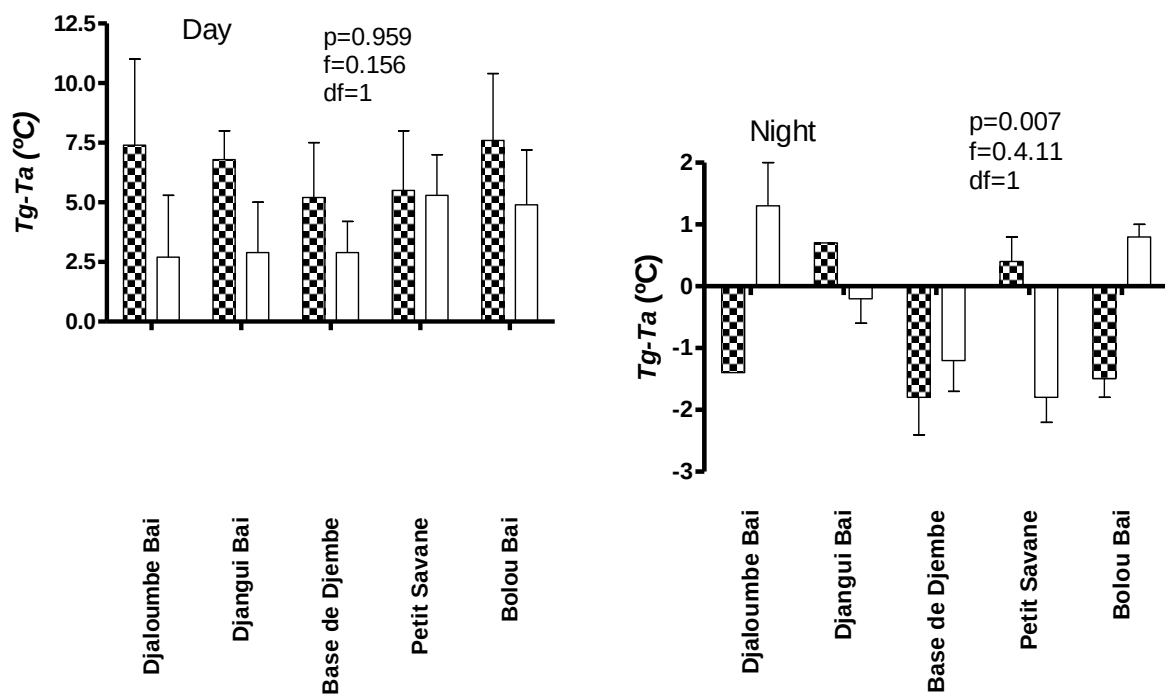


Figure 3.7 Difference of three-day means of T_g and T_a ($T_g - T_a$) in the *bais* and under the forest canopy during the day (06:00-18:00) during night (18:00-06:00) at the different study sites in the Lobeke NP. The open bars represent variables in the open *bais* and shaded bars represent variables under the forest canopy.

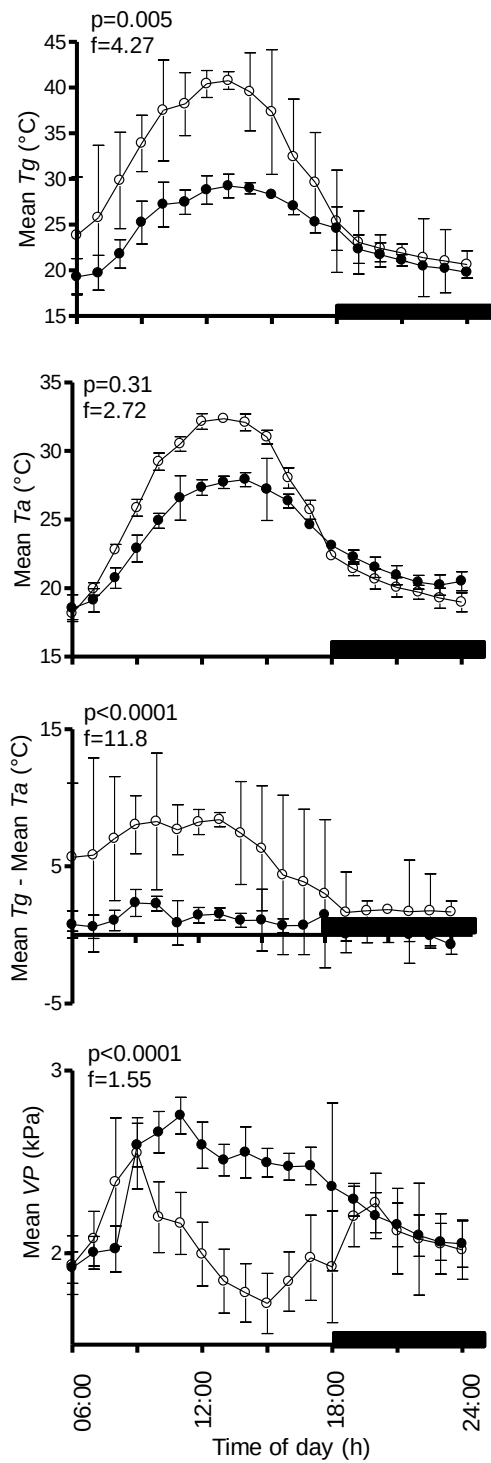


Figure 3.8 Typical mean ($\pm$ SD) three-day profile of microclimate variables in the open *bais* and under the forest canopy for all the study sites in the Lobeke NP between 06:00-24:00. Difference between mean T_g & T_a = mean T_g minus mean T_a . The dark bars = night, -●- = microclimatic variables under the tree canopy, -○- microclimatic variables in the open *bais*.

3.3 Elephant behaviour

Elephant behaviour was recorded for a total time of 64.7 hours. Behaviour data was collected as using fixe interval time point sampling method previously described in section 2.5. Figures 3.10 to 3.13 show some of the elephant behaviours that were observed during this study. These behaviours may influence thermoregulation in elephants. The total number of elephants that were seen and those identified indirectly using elephant indices of presence at each of the study sites, during the day and night is shown in Table 3.3. The data indicated that most of the elephants seen and their indices of present recorded in the *bais* at night (between 18:00-06:00), resulting in a range of 0-22 elephants that entered the open *bais*, and a range of 0-5 elephants that entered the *bais* during the day (between 06:00-18:00). No elephant was seen visiting Djangui Bai during the night and none seen visiting Petite Savane and Bolou Bais during the day.

The mean percentage of time that the elephants were seen spent walking and foraging between 06:00-24:00 is illustrated in Figure 3.14. Only two elephants were observed between 06:00-11:00, at most seven seen between 12:00-15:00, two between 16:00-20:00, none between 18:00-20:00 and three between 20:00-24:00.

Generally the elephants spent a mean time of about 40% walking throughout the day, between 06:00-24:00. They spent less than 25% of their time walking in the morning but, as the morning progressed, their walking activity increased and peaked at about 75% by 10:00. Thereafter, the elephants decreased their walking-time to less than 25% in the late afternoon. However, they spent 55% to 75% of their time between 18:00-24:00 walking. The elephants spent more time feeding in the morning compared to the time they spent walking.

Table 3.2 Summary of mean ($\pm$ SD) *WS* (m/s) for five of the study sites and the differences between mean *WS* in the open *bais* and under the forest canopy for the day and night.

DAY					
Study sites	Djaloumbe Bai	Djangui Bai	Bese de Djembe	Petite Savane	Bolou Bai
<i>WSb</i> in open <i>bai</i>	2.7 $\pm$ 0.3	3.9 $\pm$ 0.4	0.9 $\pm$ 0.7	1.8 $\pm$ 0.5	2.2 $\pm$ 0.5
<i>WS</i> under forest canopy	2.8 $\pm$ 0.2	3.8 $\pm$ 0.4	1.2 $\pm$ 0.6	2.8 $\pm$ 0.6	2.4 $\pm$ 0.4
Difference <i>WS</i> in <i>bai</i> & <i>WS</i> under forest canopy	-0.1$\pm$0.1	0.1$\pm$0.0	-0.3$\pm$0.1	-1.0$\pm$0.1	-0.2$\pm$0.1
NIGHT					
Study sites	Djaloumbe Bai	Djangui Bai	Base de Djembe	Petite Savane	Bolou Bai
<i>WSb</i>	2.8 $\pm$ 0.2	3.8 $\pm$ 1.2	1.2 $\pm$ 0.6	2.8 $\pm$ 0.6	2.4 $\pm$ 0.4
<i>WSt</i>	1.8 $\pm$ 0.3	1.7 $\pm$ 0.4	0.8 $\pm$ 0.5	0.7 $\pm$ 0.3	0.9 $\pm$ 0.6
<i>WSb-WSt</i>	1.0$\pm$0.1	2.1$\pm$0.8	0.4$\pm$0.1	2.1$\pm$0.3	1.5$\pm$0.2
<i>WSb</i> = in open <i>bai</i>					
<i>WSt</i> = under forest canopy					

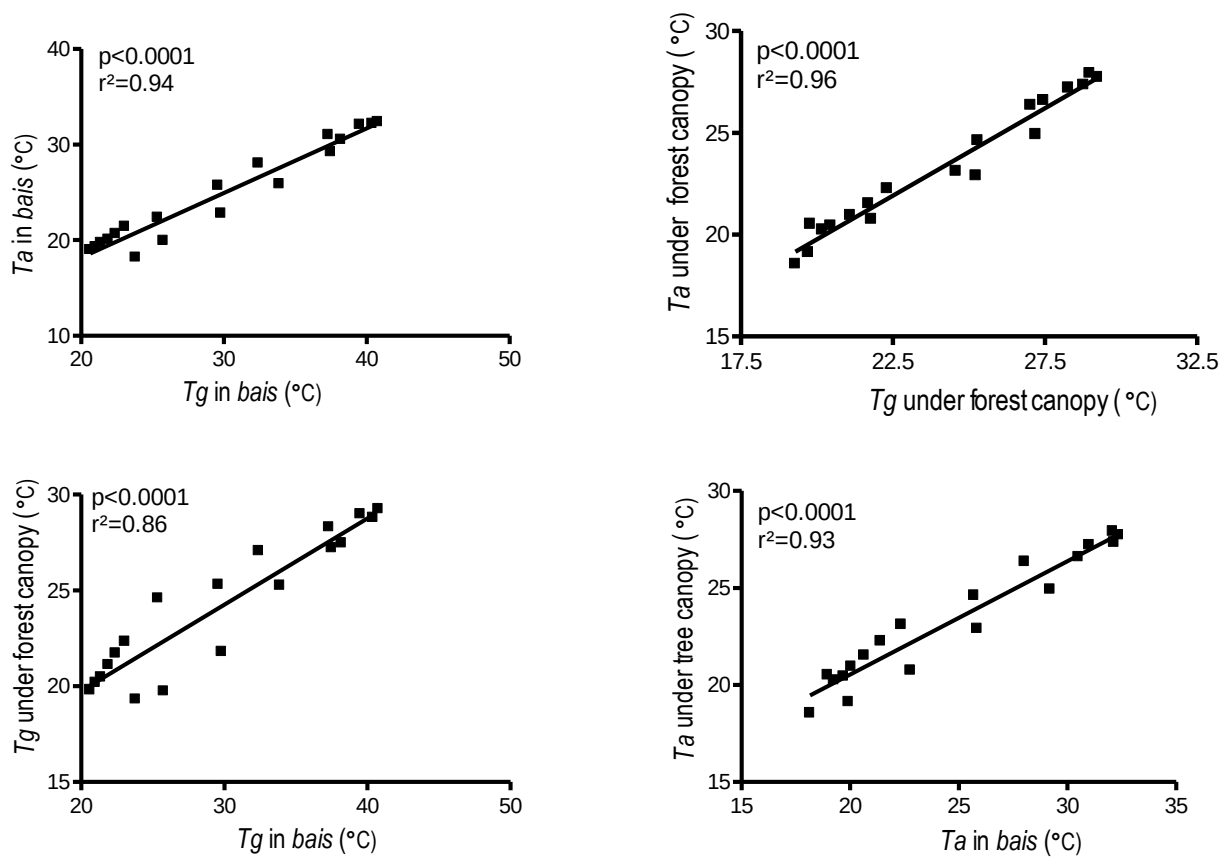


Figure 3.9 Linear regressions between mean Tg and mean Ta in the open *bais* and under the forest canopy (between 06:00-18:00) for all the study sites in Lobeke NP.

A



B



Figure 3.10 (A) An elephant standing under shade in Djaloumbe Bai in the afternoon of a sunny day. (B) The arrow indicates an elephant foraging at midday in the shady area of *Marantaceae* forest thicket near Djaloumbe Bai.

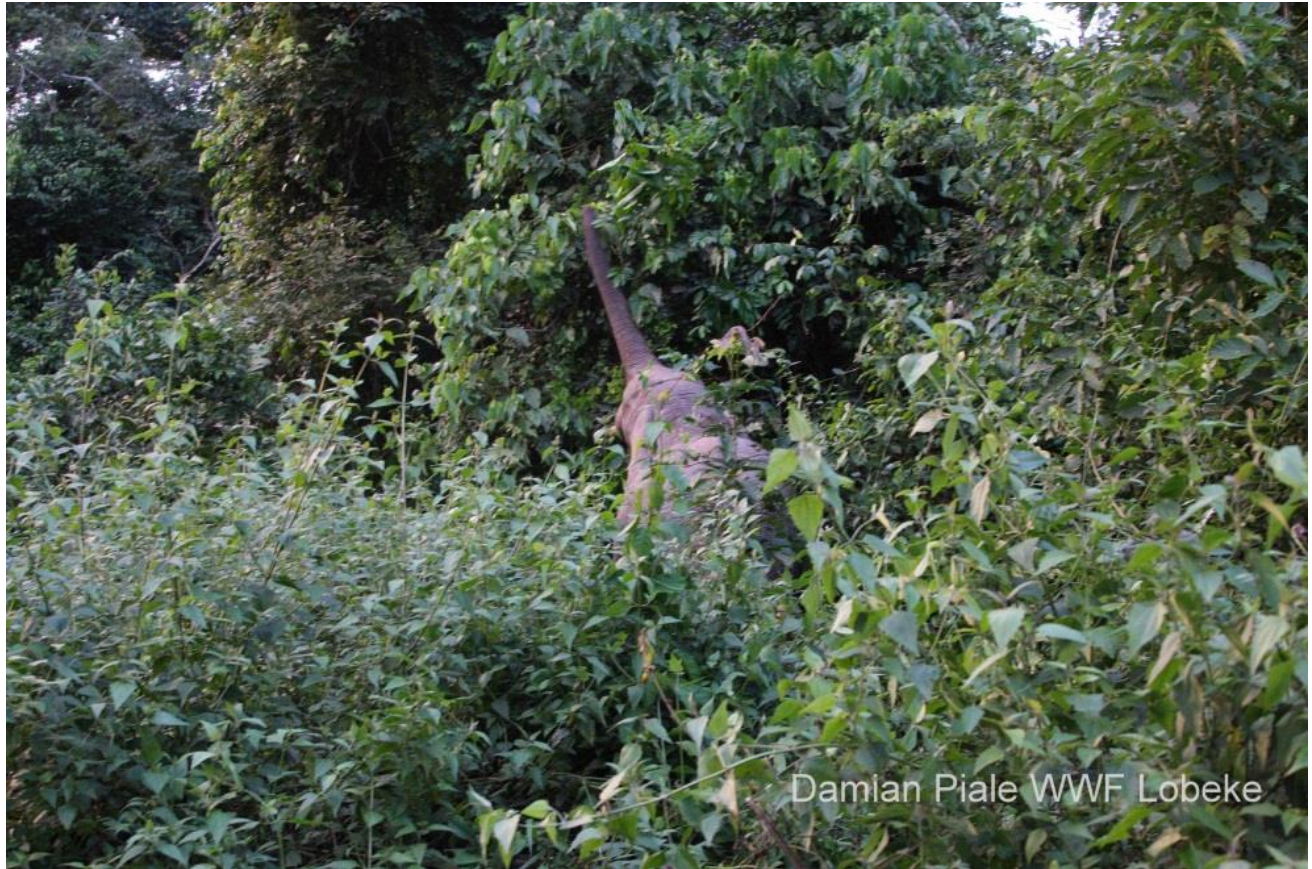


Figure 3.11 A cow elephant foraging in Base de Djembe.

A



B



Figure 3.12 (A) A bull elephant having telemetry collar on its neck. It was seen near base de Djembe, after taking a dust bath such that patches of brown soil were on its body. (B) An elephant bathing its belly with mud (see grey patches of mud on its belly and brown patches of dust on its back from an earlier dust-bath).

A



B



Figure 3.13 (A) An elephant seen just after walking across the Lobeke River during a hot afternoon. See wet portion of the elephant's body below the ears, while the ears and back remained dry, since these portions were not immersed in water (B) Elephant swimming in the Sangha River.

Table 3.3 Estimated number of elephants (using their indices of presence) that were identified to have entered each of the five *bais* during the day and night during the three-day study period at each *bai*.

Time of day	Djaloumbe Bai	Petite Savane	Djangui Bai	Base de Djembe	Bolou Bai
Day	3	0	5	3	0
Night	9	6	0	22	12

Figure 3.15 illustrates the mean percentage of time that observed elephants spent seeking shade, dust-bathing, ear-flapping and performing water-related activities between 06:00-24:00. They started showing shade-seeking activity late in the morning, which progressively increased from about 11:00, peaking at about 50% between 13:00-14:00. Thereafter, their shade-seeking activity continued for about an hour and then stopped or reduced. Dust-bathing occurred between 08:00-12:00 and elephants sprayed dust and dirt on their bodies for between 10-25% of their time. Ear-flapping occurred throughout the day but did so more than 50% of the time between 09:00-12:00. Ear-flapping also occurred frequently at night. Water-related activities were irregular and inconsistent. Elephants in this study were seen performing water-related activities (drink water, bathe with mud or spray body with water) between 08:00-13:00 only, and the total time the elephants spent performing water-related activities between this time was generally less than 25% per session. Base the Djembe is situated at the banks of the Sangha River. All the elephants observed were not seen to drink water or perform any other water-related activity between 18:00-24:00.

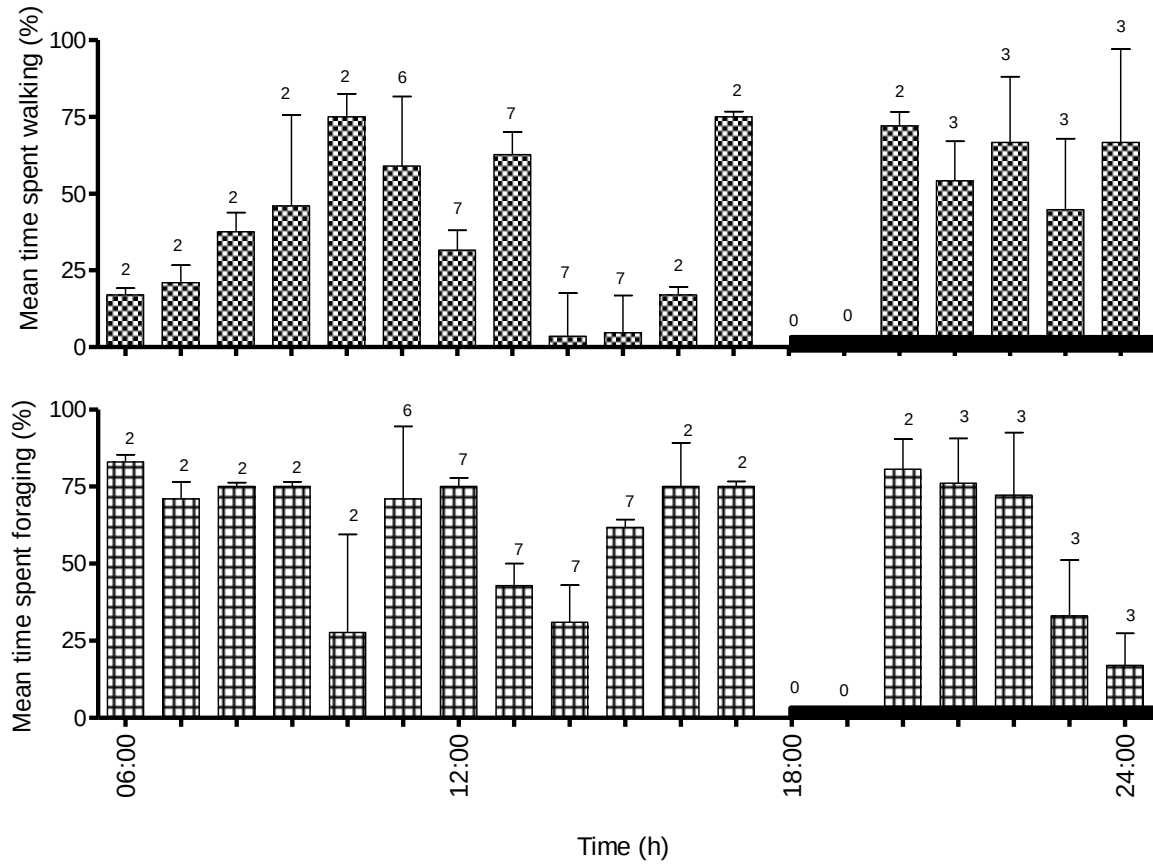


Figure 3.14 Mean (+SD) percentage of time per hour that the elephants observed in the study spent walking (top panel) and foraging (bottom panel) between 06:00-24:00. The number of individuals observed is indicated above the bar for each period. The black bar on the x-axis represents night.

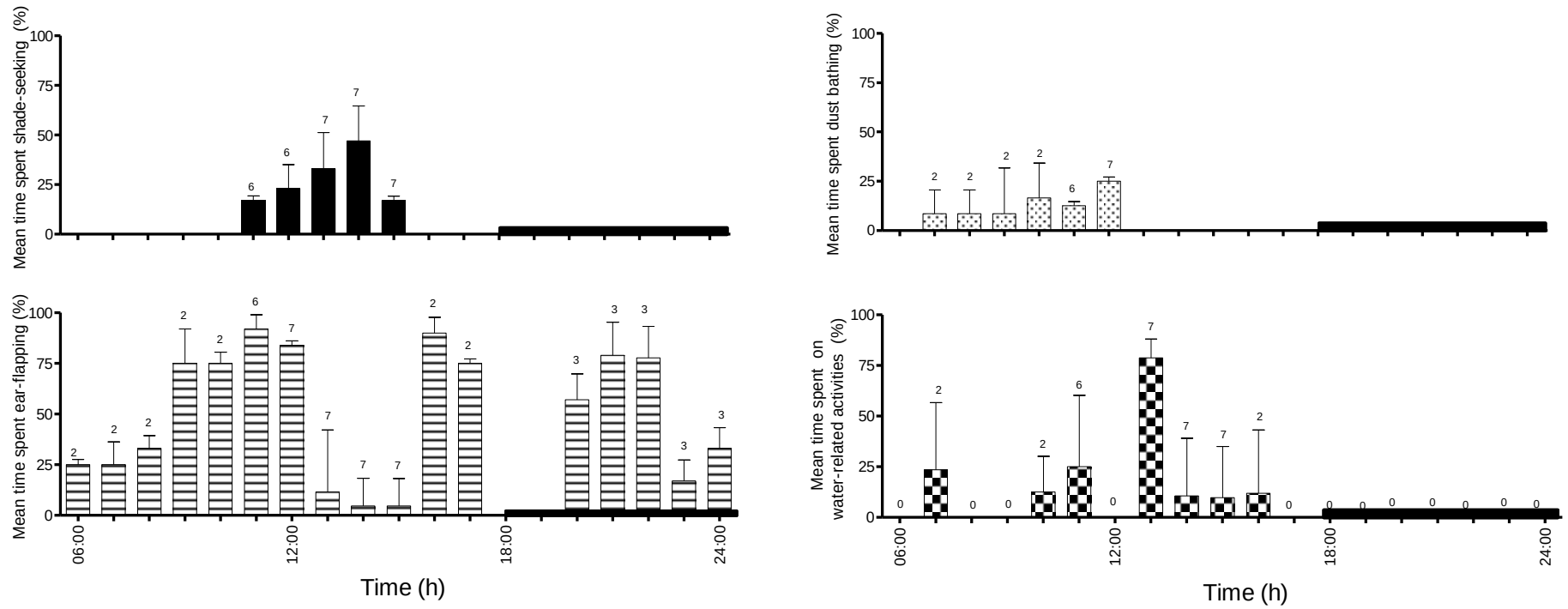


Figure 3.15 Mean (+SD) percentage of time that the elephants observed in the study spent per hour on each activity between 06:00-24:00. The number of individuals observed is indicated above the bar for each time period. The black bar on the x-axis represents night.

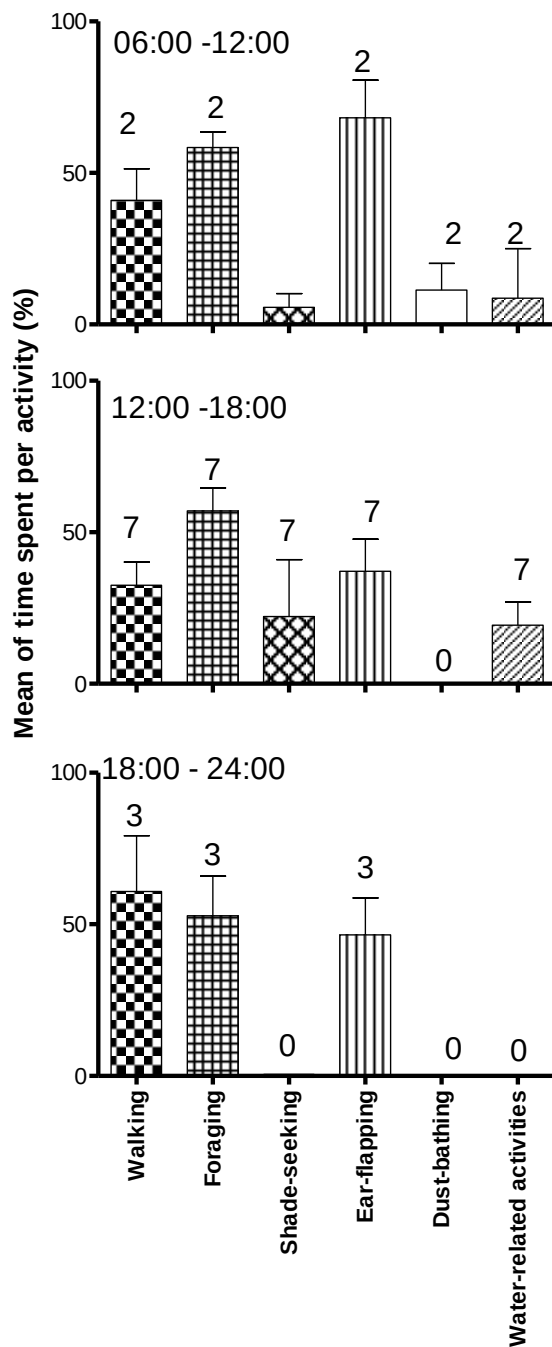


Figure 3.16 Mean ($\pm$ SD) percentage of time that the elephants observed in this study spent on each activity between 06:00-12:00, 12:00-18:00 and 18:00-24:00. The number of individuals observed is indicated above the bar for each time period.

The activities performed by the elephants during all three periods of the day (morning 06:00-12:00, afternoon 12:00-18:00 and night 18:00-24:00) are summarized in Figure 3.16. Walking, foraging, and ear-flapping were the predominant behaviours recorded. Dust-bathing was seen only in the morning, while water-related activities occurred in the morning and afternoon.

3.4 Association between microclimate and elephant behaviour at the study sites

3.4.1 Walking behaviour

There was no significant correlation between the mean *Tg* in the five open *bais* and mean percent time the elephants spent walking ($p=0.33$, $r^2=0.06$, $n=17$) (see Figure 3.17A). Figure 3.17 C illustrates that there is no significant correlation between the mean when the *VP* in the five open *bais* and the mean percent time the elephants spent walking during each hour of the day at the study sites. Similarly, Figure 3.17 C shows that there was no correlation between the time the elephants spent flapping their ears and the time they spent walking.

3.4.2 Foraging behaviour

Figure 3.18A illustrates that there was no association between the mean *Tg* in the open *bais* and the mean time the elephants spent foraging. Foraging behaviour did not show any significant association with *VP* (see Figure 3.18 B). Similarly Figure 3.18 C shows no association between foraging and walking times.

3.4.3 Shade-seeking behaviour

The mean time that the elephants spent seeking-shade as a function of mean *Tg* in the *bais* is illustrated in Figure 3.19A. The elephants in the *bais* started showing shade-seeking activity at

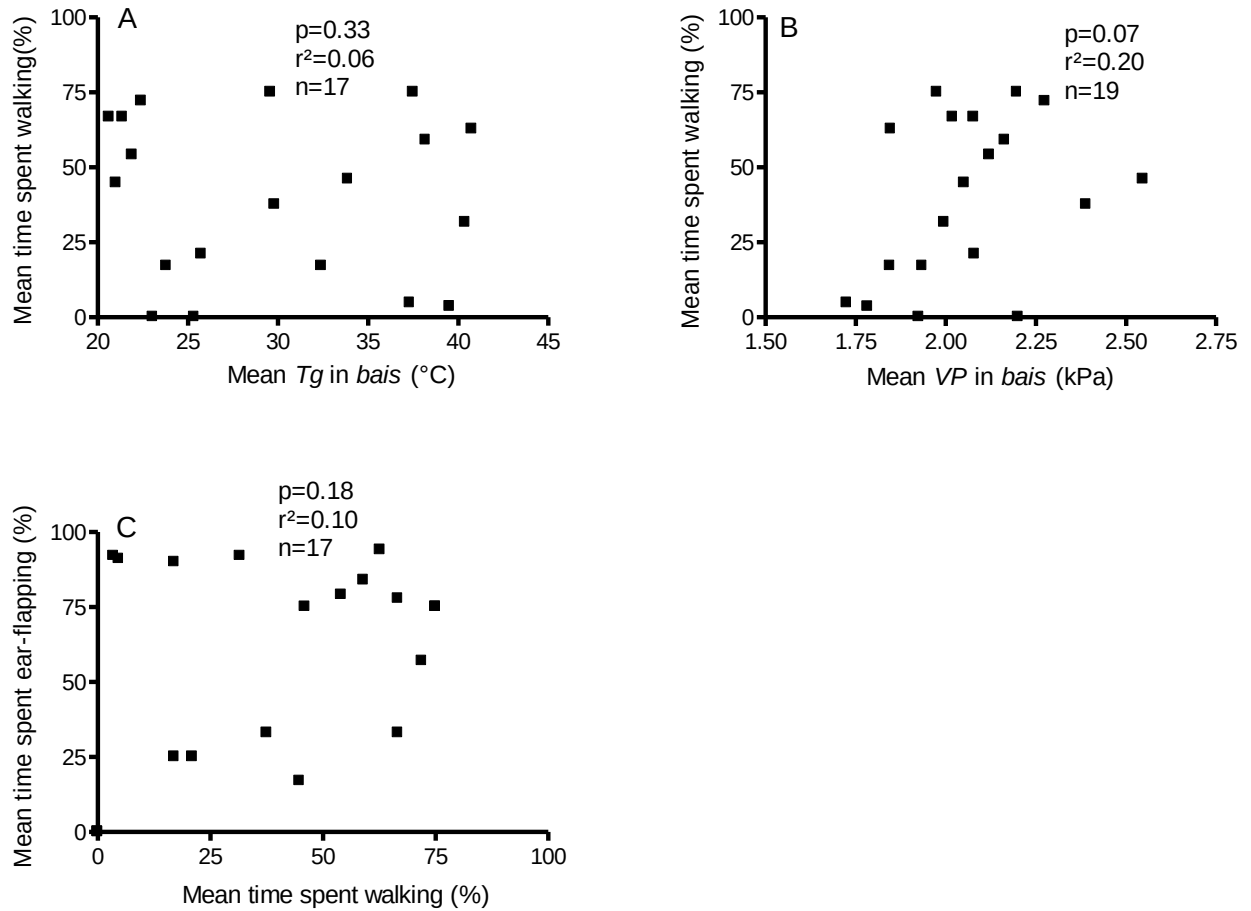


Figure 3.17 (A) Correlation between the mean T_g in open *bais* and the mean percentage time of each hour that the elephants spent walking for all the study sites. **(B)** Correlation between the mean VP in open *bais* and the mean percentage time of each hour that the elephants spent walking for all the study sites. **(C)** Association between the percent time during each hour that elephants of this study spent walking and flapping their ears.

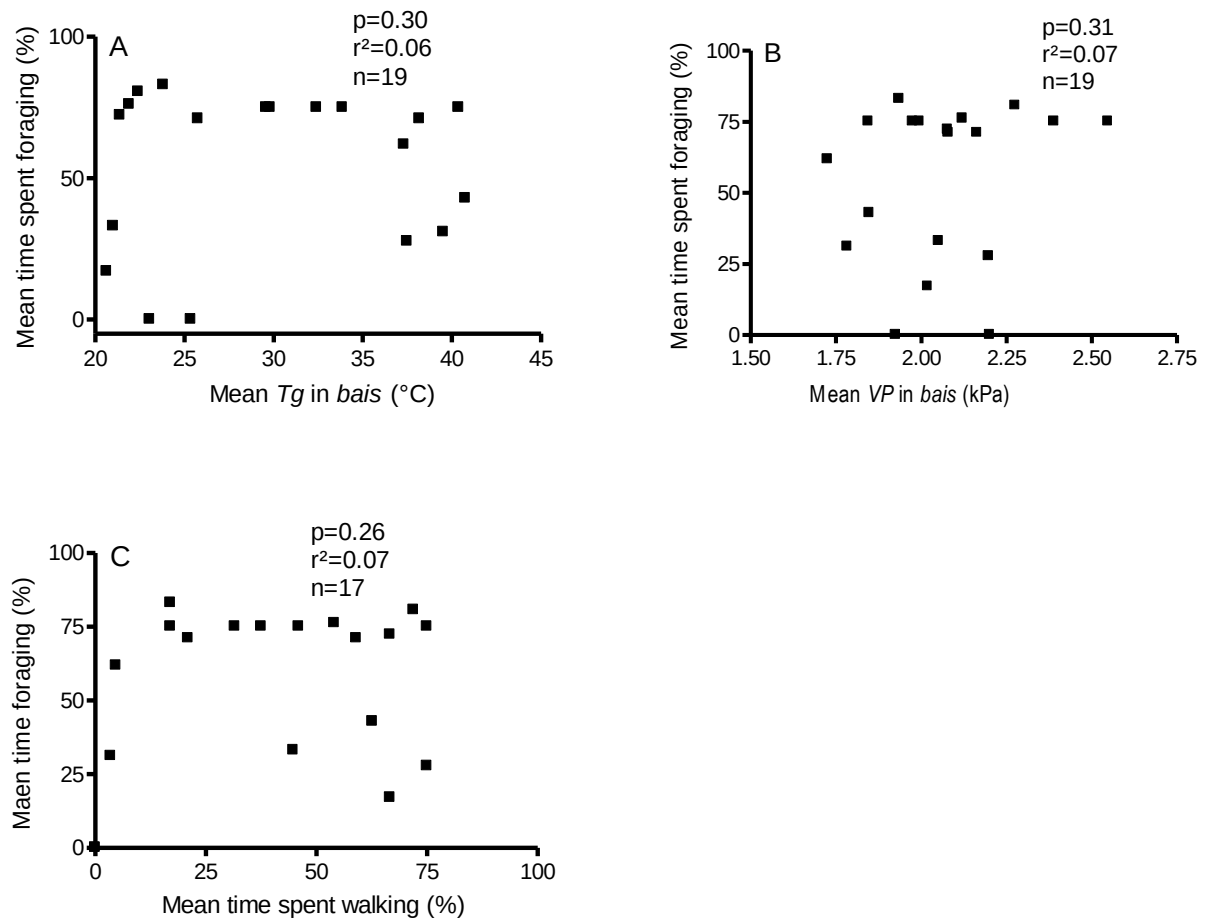


Figure 3.18 (A). Association between the mean percent time elephants spent foraging during each hour and mean T_g for that hour in all the *bais*. (B). Correlation between the mean VP in open *bais* and mean percent time the elephants spent foraging during each hour for all the study sites. (C) Association between the percent time during each hour that all elephants observed spent walking and foraging for all the study sites.

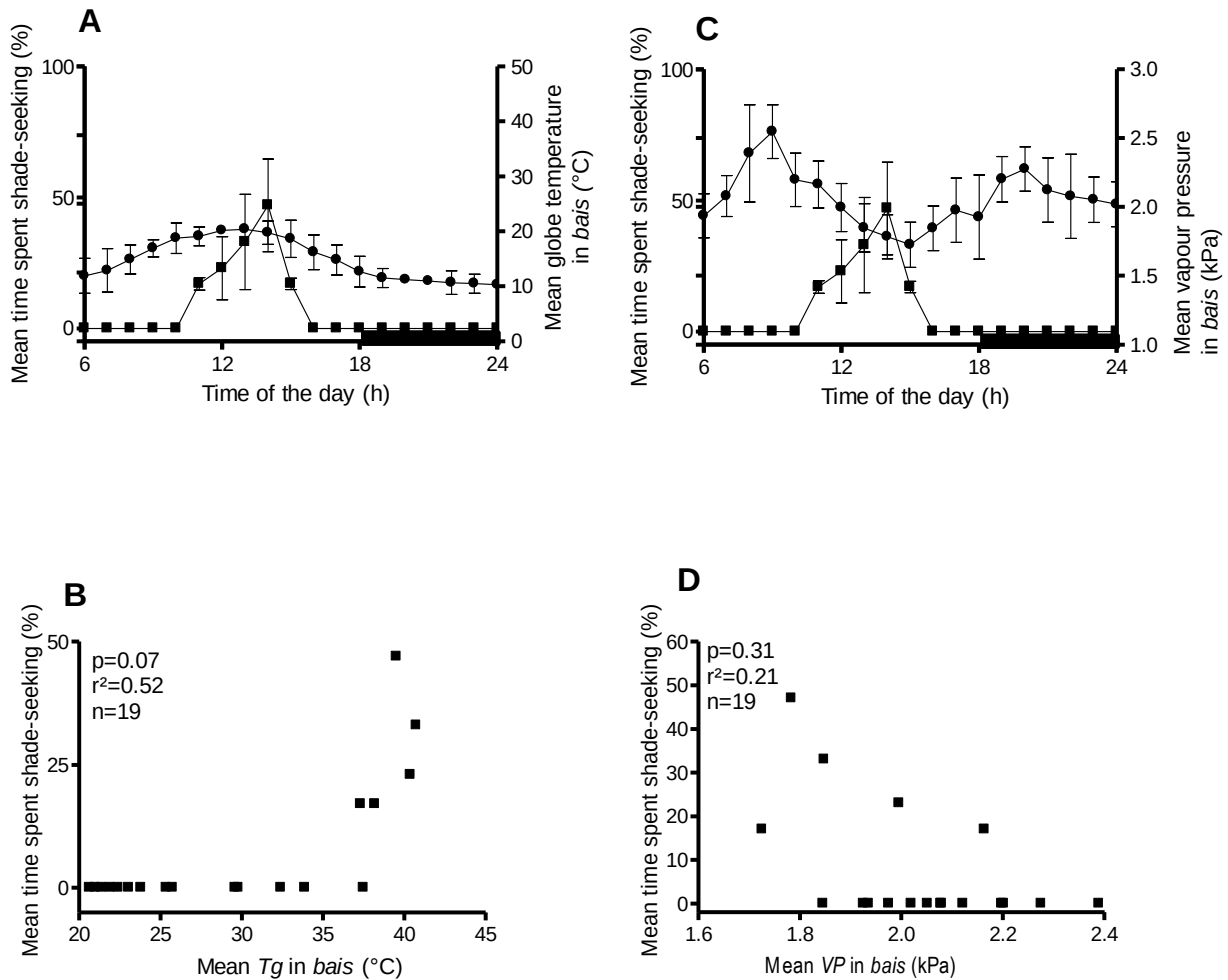


Figure 3.19 (A) Mean ($\pm$ SD) percent time of each hour that the elephants spent seeking shade (-■-, left axis) and mean ($\pm$ SD) *Tg* for that hour (-●-, right axis), plotted as a function of time of the day for all five study sites. The dark bar indicates night. (B). Correlation between mean *Tg* in the open of all the *bais* and mean percent time the elephants spent seeking shade during each hour for all of the study sites. (C) Mean ($\pm$ SD) percent time of each hour that the elephants spent seeking shade (-■-, left axis) and mean ($\pm$ SD) *VP* for that hour (-●-, right axis), plotted as a function of time of the day for all five study sites. The dark bar indicates night. (D) Correlation between mean *VP* in the open *bais* and the mean percent time elephants spent seeking shade during each hour for all the study sites.

about 11:00, when mean T_g in the *bais* was higher than 35°C. Both the shade-seeking activity of the elephants and the T_g increased progressively and peaked between 13:00-14:00. At this point elephants spent about 52% of their time seeking shade. Between 13:00-14:00 the T_g in some of the *bais* was as high as 46°C. There was a weak association between the time elephants spent seeking shade in the *bais* and the T_g ($p=0.07$, $r^2=0.52$). The shade-seeking activity was remarkable high at T_g above 35°C (Figure 3.19B).

The mean time that the elephants spent shade-seeking as a function of mean VP in the *bais* is shown in Figure 3.19 C. At about 10:00 as the mean VP in the *bais* decreased, elephants in the *bais* started seeking-shade more progressively until about 13:00 in the afternoon, and then started reducing their shade-seeking activity until about 16:00. No correlation existed between shade-seeking activity and mean VP in the *bais* (Figure 3.19 D).

3.4.4 Ear flapping behaviour

The percentage time of each hour that the elephant performed ear-flapping and mean T_g for each hour plotted as a function of the time of the day, for all five study sites, is shown in Figure 3.20 A. The elephants flapped their ears all day, progressively increasing the rate of ear-flapping throughout the day. The ear-flapping activity was maintained above 50% until late in the afternoon. There was a significant correlation between the T_g and the percentage time spent ear-flapping per hour ($p<0.01$, $r^2=0.47$, see Figure 3.20 C). Figure 3.20 B illustrates the percentage time of each hour that elephants in this study spent flapping their ears and the mean VP of the air for each hour, plotted as a function of time of the day for all study sites. There was no correlation between VP and the time spent ear-flapping per hour ($p=0.35$, $r^2=0.005$, see Figure 3.20 D), and

no correlation between percentage ear-flapping per hour and foraging ($p=0.08$, $r^2=0.20$, Figure 3.20 E).

3.4.5 Dust-bathing behaviour

The mean time that the elephants spent dust-bathing as a function of mean *Tg* in the *bais* is shown in Figure 3.21 A. Generally the elephants observed in this study bathed with dust between 06:00-13:00. The elephant's dust-bathing behaviour showed a weak association with the mean *Tg* in the *bais* ($p=0.07$, $r^2=0.06$, see Figure 3.21 B). Figure 3.21 C illustrates the mean percentage time the elephants in this study spent dust-bathing per hour as a function of mean *VP* in the *bais*. Figure 3.21 D illustrates that there is no correlation between *Tg* or *VP* and percentage time per hour the elephants spent dust-bathing in the *bais* ($p=0.07$, $r^2=0.6$).

3.4.6 Water-related behaviours

There was no correlation between mean *Tg* and percentage time performing water-related activities per hour in the *bais* (see Figure 3.22 A). Figure 3.22 B illustrates that there is no correlation between the percentage time spent per hour on water-related-activities and the *VP* in the *bais* ($p=0.29$, $r^2=0.13$).

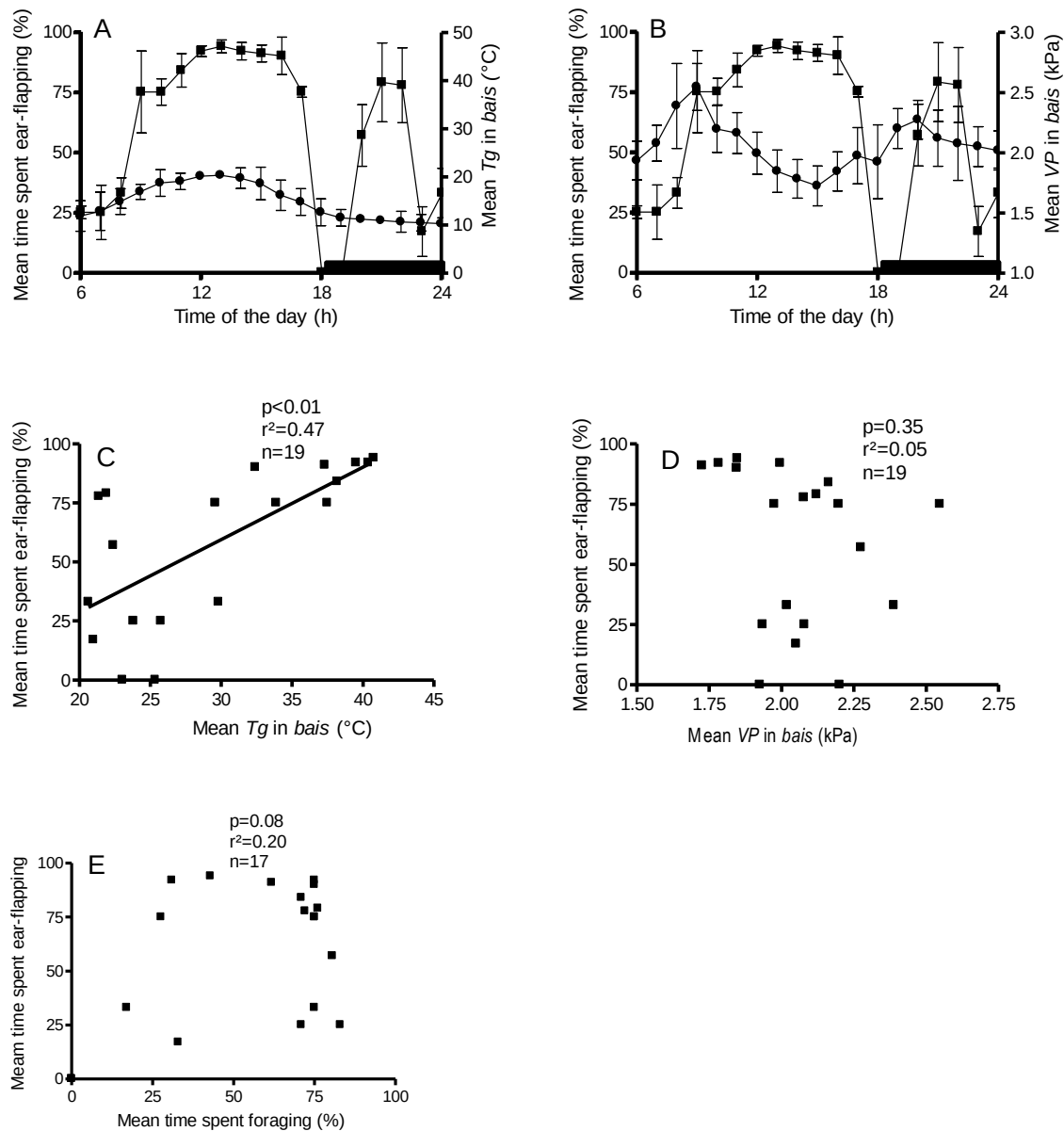


Figure 3.20 (A). Mean ($\pm$ SD) percent time of each hour that the elephants spent ear-flapping (■., left axis) and the mean ($\pm$ SD) Tg for that hour (●., right axis), plotted as a function of time of the day for all five study sites. The dark bar indicates night. **(B).** Correlation between the mean Tg in the open of five *bais* and the mean percent time elephants spent flapping their ears each hour at all the study sites. **(C)** Mean ($\pm$ SD) percent time of each hour that the elephants spent ear-flapping (■., left axis) and mean ($\pm$ SD) VP for that hour (●., right axis), plotted as a function of time of the day for all five study sites. The dark bar indicates night. **(D).** Correlation between the mean VP in the open *bais* and mean percent time the elephants spent flapping their ears each hour for all the study sites. **(E)** Association between foraging and ear-flapping for all of elephants observed in the study.

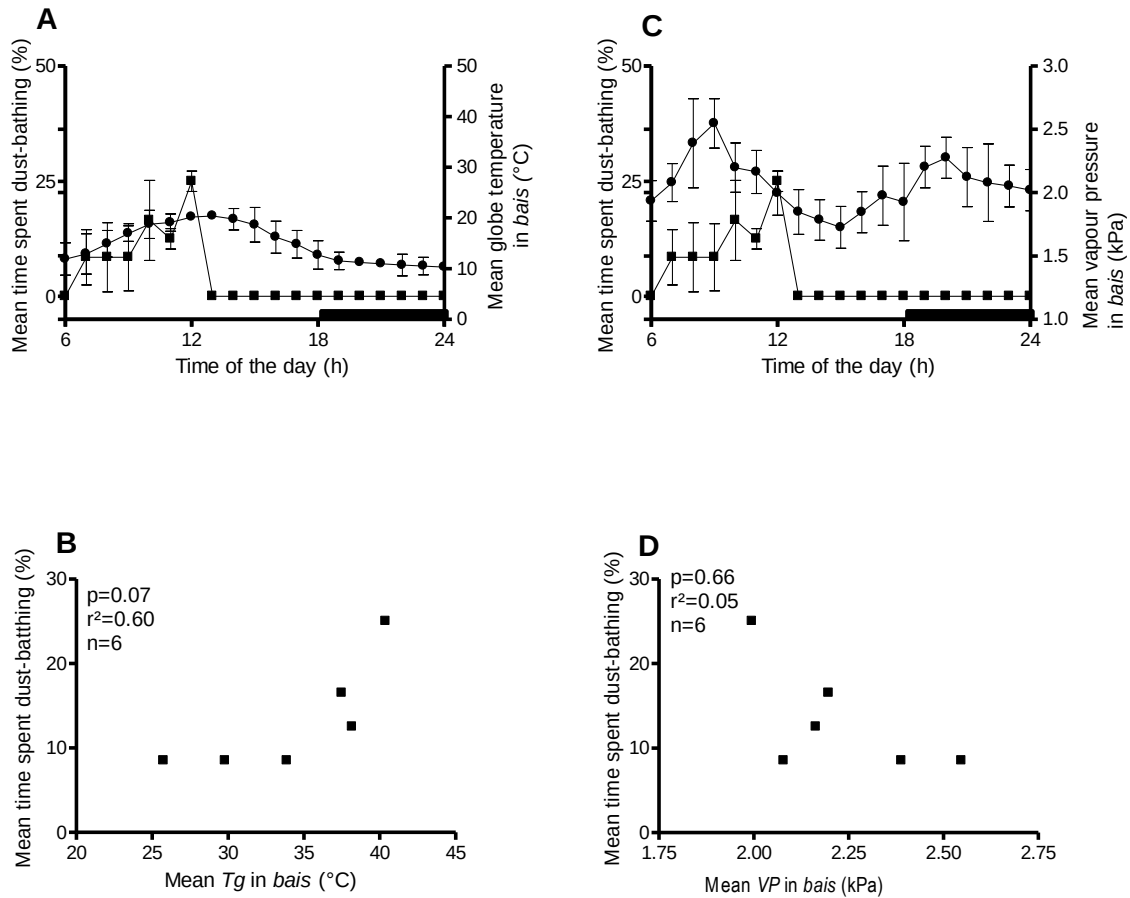


Figure 3.21 (A) Mean ($\pm$ SD) percent time of each hour that elephants spent dust-bathing (—■—, left axis) and the mean ($\pm$ SD) T_g for that hour (—●—, right axis), plotted as a function of time of the day for all five study sites. The dark bar indicates night. (B). Correlation between the mean T_g in the open and under forest canopy and mean percent time the elephants spent dust-bathing during each hour for all the study sites. (C) Mean ($\pm$ SD) percent time of each hour that the elephants spent dust-bathing (—■—, left axis) and mean ($\pm$ SD) VP for that hour (—●—, right axis), plotted as a function of time of the day for all five study sites. The dark bar indicates night. (D). Correlation between mean VP of air in the open and under forest canopy and mean percent time elephants spent dust-bathing during each hour for all the study sites.

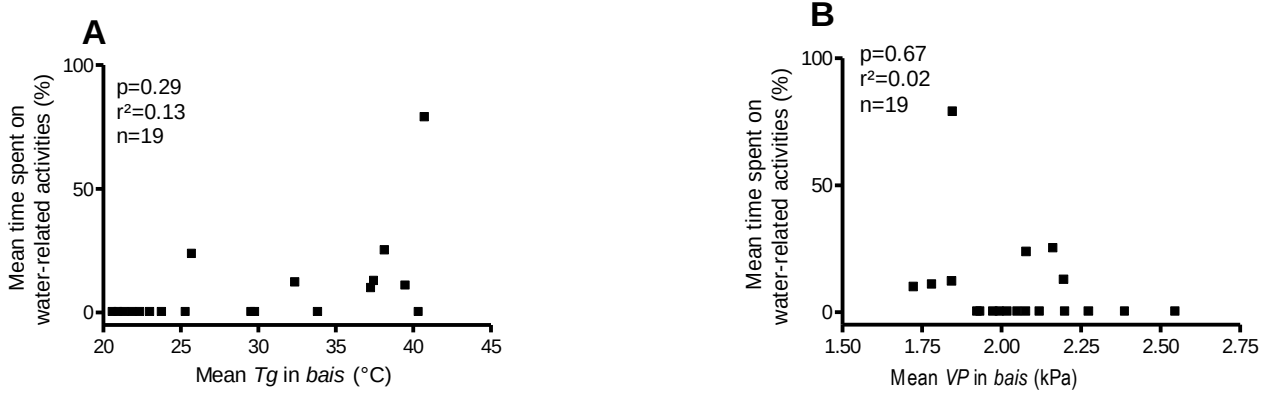


Figure 3.2.2 (A). Association between the percent time elephants performed water-related activities per hour and T_g for that hour for all study sites. **(B)** Correlation between mean VP in the open *bais* and mean percent time the elephants spent on water-related activities during each hour for all the study sites.

CHAPTER 4

DISCUSSION

4.1 Introduction

In this chapter I summarise my findings and discuss my results in the context of elephant behaviour and thermoregulatory strategies in Lobeke NP, Cameroon. I then compare my data on behaviour of African forest elephants to that derived from the works of other elephant studies across Africa. These researchers used either fixed point interval technique (Guy, 1976; Martin and Bateson, 1986; Wyatt and Eltringham, 1974) or continuous survey (Guy, 1976) but data obtained by both techniques could be compared without problems since both types of data are statistically similar as reported by Leggett (2008).

4.2. Microclimate mosaic at my study site

The microclimate available to elephants in Lobeke NP was measured at five sites in the open *bais* and under the forest canopy adjacent to the sites. It was found that the *Tg*, *Ta*, *VP* profiles were similar across all the study sites. There were no significant differences in the *Tg*, *Ta* and *VP* between each of the study sites. No significant difference was recorded between *Tg*, *Ta*, *VP* in the *bais* and under the forest canopy for each of the study sites. However, the *WS* were significantly different between some of the sites. The difference in *WS* was due to variations in vegetation density at each site. The vegetation density affected the ease with which air flowed through the habitat of that site. The discrepancies in the time *Tg-Ta* started increasing in the mornings observed in Djaoumbe and Bolou Bais in Figure 3.3 was due to the height of trees and the difference in tree density per unit space at the eastern edge of both *bais*. Low tree density per unit space in the eastern edge of Base de Djambe, Petit Savane and Djanguai Bais seemed to cover early morning sun rays less than those in Djaloumbe and Bolou Bais as the early morning

sun rays easily penetrated through spaces between tree leaves and branches and heat up the thermometers. As such, the T_g and T_a thermometers reflected higher temperatures in Djaloumbe and Bolou Bais, thus increasing T_g-T_a about 15 minutes earlier than T_g-T_a in Djanguai and Petite Savane. T_g-T_a in in Djanguai and Petite Savane started rising at 06:00. The peculiar T_g-T_a during the first days in Djaloumbe, Petite Savane and Bolou Bais were due to the thermometer stand falling to the ground altering the position of the temperature sensors to give misleading temperature values.

As shown earlier in section 3.2.5, WS in all the study sites were significantly different between open *bais* and under the forest canopy ($p<0.05$, $f=0.74$, during the day and $p<0.01$, $f=2.69$ at night). WS were significantly different between study sites ($p<0.05$, $f=2.68$). WS at Djanguai Bai, Base de Djembe and Petit Savane were the highest, particularly in the late afternoon and at night. Generally, the winds in the open *bais* were higher than those under the forest canopy. The differences in the WS between the open *bais* and under the forest canopy can be explained by the way that air flows through the different vegetation types at the different sites. The less the density of vegetation in any portion of the forest, the faster the wind, due to less resistance to air flow in that portion. On the other hand, the thicker the vegetation-cover, the more the resistance of air flow in that portion, resulting to slow wind. Overall, WS's were relatively low, usually less than 2 m/s and rarely exceeding 4 m/s.

The higher WS in the open *bais* than that under the forest canopy at night seems to attract elephants to visit the *bais*. This may be explained by the higher number of elephants observed or more indices of presence that was recorded in the *bais* than under the forest canopy at night. WS and direction not only certainly contributed to the way the elephants selected the microclimates

of this study, but it also seems that forest elephants use wind directions to identify their orientation in the forest. I observed that elephants entered or left the *bais* mostly following east-west direction. This phenomenon had also been reported on forest elephants by Vanleeuwe & Gautier-Hion (1998).

Vanleeuwe & Gautier-Hion (1998) argued that forest elephants use the direction of the wind to monitor predators before entering the *bais*. The highly developed sense of smell in the elephant (Skinner and Chimimba, 2005) enables them to perceive the direction from which the wind blows toward the elephant's trunk. The wind also enables the elephant to perceive the smell of humans, animals and forage. It is for these reasons that Vanleeuwe and Gautier (1998) speculated that poachers have been using the elephants' alleged monitoring strategies to poach elephants in protected areas in the Congo Basin Forest. Humans remain the number one predator of the African forest elephants in northern Congo (Fay and Agnagna, 1991). Large numbers of carcasses of poached elephants have been discovered at the east-west path entrances to *bais* in Congo Forest, which suggest that the wind direction could be a key factor involved (Vanleeuwe and Gautier-Hion, 1998). However, more studies need to be done since the direction of elephants entering the *bais* and the angle to which they orientate their bodies to the prevailing wind may be thermoregulatory motivated too.

There are also arguments that elephants use long straight paths called "boulevards" to travel long distances in the forest (Vanleeuwe and Gautier-Hion, 1998). These "boulevards" share a more or less common east-west orientation and there are speculations that forest elephants are influenced by the direction of the local prevailing Tropical Easterlies (tropical winds).

Normally the Tropical Easterlies over the Atlantic would be flow westward toward South America, but during the rainy season in the tropics, some of these winds turn eastward as they cross the Equator and head to Africa (Baumann, 2009). The roles that the Tropical Easterlies play on the forest elephant's choice of construction of its paths are still speculations. Whether the direction that elephants construct their paths to enter the *bais*, or the way elephants orientate their bodies at various microclimatic portions of the forest is influenced by thermoregulatory behaviour requirement is unknown. Also the extent to which the Tropical Easterlies may affect the microclimate in both the elephant's paths and *bais* in the tropical forest, are still questions that need more research to find answers.

This study was undertaken during the hot, dry season to assess the microclimates available to forest elephants at this time of the year, when the animals were expected to be under the greatest thermal stress. An average T_g of about 33°C was observed during the day in the *bais*, although maximum T_g usually exceeding 40°C. During the night the mean T_g decreased to a mean of about 20°C. On the hottest day, the T_g and T_a in some of the open *bais* reached 46°C and 35°C, respectively. The lower T_g under the forest canopy during the day is explained by the T_g absorbing less solar radiation under the forest canopy, and long-wave heat from the ground and near-by objects. At night, the mean T_g in the *bais* were about 1°C lower than the mean T_g under the forest canopy, possibly because of the cooling effect of faster WS in the open *bais* than under the forest canopy, or because of greater radiative heat loss to the open sky above the weather station in the open *bais*. In terms of T_g , the open *bais* differed from the forest canopy only during the day. In the day, forest canopy T_g rarely exceeded 30°C, so the forest canopy offered a thermal refuge to the elephants.

The mean T_a in the *bais* in the day was 27°C and under the forest canopy it was 20°C. At night the mean T_a in the *bais* was as low as 20°C, about 3°C less than the T_a under the forest canopy, probably due to the effect of cooling by faster winds (Cohen et al., 1979) in the open *bais* than under the forest canopy. As expected, T_a 's were positively and linearly correlated with T_g 's in this study. Because T_g integrates effects of radiation, T_a and WS into a single index (Vernon, 1930). I therefore used T_g , rather than T_a , to investigate the relationship between microclimate and elephant behaviour.

As mentioned previously in Table 3.1, the mean T_g in the open *bais* and under the forest canopy during the day and night was 32.8°C while during the night the mean T_g falls to 19.6°C, but under the forest canopy during the day, mean T_g was 25.5°C while at night it was 20.5°C. This study suggests that the T_g profiles in all the open *bais* of this study were significantly higher than under the forest canopy during the day and night ($p < 0.05$, $f = 4.27$). The mean VP in the *bais* of this study was 2.10 kPa and 2.08 kPa under the forest canopy during the day. At night the mean VP was 2.08 kPa in the *bais* and 2.04 kPa under the forest canopy. VP profiles in the open *bais* were significantly lower than under the forest canopy for all the study sites both during the day and at night ($p < 0.001$, $f = 1.5$). Implying that at any time of the day, elephants would lose excess body heat through evaporation easier in the *bais* than under the forest canopy at any time of the day. VP occasionally exceeded 3.00 kPa in the open *bais* and under the forest canopy. Therefore, at 100% humidity, the elephants' estimated skin temperature is 35°C (Phillips and Heath, 1992), and the VP on the elephant's skin would be 5.30 kPa. In order for elephants to lose heat through evaporation the VP gradient at their body surface must exceed that of the environment (Cohen et al., 1979). For the Lobeke NP elephants, it is therefore likely that they were able to lose heat by

evaporation both under the forest canopy and in the open *bais*, however, due to the lower *VP* profile in the open *bais* than under the forest canopy during the day and night. Forest elephants would dissipate body heat easier through evaporation in the open *bais* than under the forest canopy, since large *VP* gradient would favour evaporative heat loss. Although there was no wind profile that patterns to all the *bais* or forest canopy, *WS* was generally faster in the open *bais* than under the forest canopy for most of the study sites and *WS* during the day and night differed significantly ($p < 0.05$, $f = 15.2$). But *WS* in open *bais* were significantly faster than under the forest canopy. This implies that fast winds in the *bais* would facilitate heat loss from the body of elephants through convection as wind would continuously displace hot air from the elephant's body surface.

As far as I am aware, this study is the first to investigate microclimates available to forest African elephants in and around *bais*. While there is general macroclimatic data available for forested regions occupied by elephants, there has been no systematic investigation of the microclimates and their influence on the behaviour of the African forest elephants in its natural habitat, particularly in and around the forest-savannah interface (*bais*). However, my study is limited to the hot, dry season, and to only three days of data collection at each of five study sites, November and December and lack of elephant physiology data, because of limited financial resources for this research and field personnel safety concerns. Long-term monitoring of microclimates in forests and forests clearings is important if we wish to understand the environmental stress that the African forest elephants in Lobeke NP and other forest in Africa face, particularly in the face of deforestation and increasingly fragmented habitats (Chen et al., 1995).

The thermal challenges that the savannah elephant faces are likely to be different from elephants in the forest. In the savannahs, temperature extremes during summer (air temperature up to 50°C, (Cole, 1986); and winter *Ta* below 0°C at night (Scholes and Walker, 1993) have been documented. My elephants were exposed to *Ta*'s above 30°C during the day, both inside and outside the forest canopy, but were exposed to moderate *Ta*'s (<25°C) at night. In the Congo Basin, annual *Ta* range between 23°C to 31°C (Nowell, 2005) and RH is as high as 60% to 90% (WWF, 2006), *Ta*'s are unlikely to drop below 0°C currently, so elephants in this habitat are likely to be subjected to less cold stress. Savannah elephants show preference to particular landscapes, for example, during the dry season they may prefer closed woodlands to open areas because the former provides more food. Savannah elephants may also select microclimates in landscapes where the absolute or rate of change in air temperature suits their thermoregulatory needs (Kinahan et al., 2007b). By moving between landscapes with varying microclimates, savannah elephants have the chance to manipulate the rate at which they exchange heat with the environment (Hiley, 1975). Compared to savannahs, the habitat is less heterogeneous in regions where forest elephants are found. Savannah elephants reduce heat load from the sun by seeking shade but may have to move greater distances to find sufficient shade, than forest elephants do. During the cold season, the need for savannah elephants to seek refuge from solar radiation is reduced (Kinahan et al., 2007b).

In comparison to microclimates experienced by savannah elephants (Hiley, 1975) in the hot, dry season, the Lobeke NP elephants faced higher *Tg*, particularly during the day. While *Tg*'s were only slightly lower in open *bais* than under the forest canopy at night, one would predict that the ambient *Tg* and *VP* in the open *bais* may be substantially lower on clear nights (with radiation to

the cold night sky) and higher wind speeds. For this reason, the forest elephant may prefer staying in the open *bais* at night where heat loss by non-evaporative means is facilitated by lower T_g and. However, longer duration of T_g , VP and WS measurements and elephant physiology data are needed to confirm these hypotheses.

4.3 Relationship between microclimate mosaic and elephant behaviour

Vegetation, relief and landforms of the Lobeke NP landscape are heterogeneous, and consequently, radiant heat, VP , WS and wind direction are all expected to be inconsistent within the landscape, resulting in mosaics of varying microclimatic profiles. Changes in environmental variables over the course of the day, and between study sites, combined with the elephant behaviour data that I observed, allowed me to assess the relationship between microclimate and elephant behaviours. As discussed previously in section 2.5, I examined behaviours necessary for thermoregulation such as walking and foraging and behaviours associated with water. I also examined other behaviours that may alter the elephant's thermal physiology such as shade-seeking, ear-flapping and dust-bathing. I compared my data on elephant behaviour to that obtained from other studies, in which similar behaviours have been quantified for forest and savannah elephants. These behaviours include; walking, foraging, ear-flapping, and dust-bathing and behaviours associated with water. Table 4.1 summarises information on the studies that I have used for comparison with my elephants.

4.3.1 Walking behaviour of elephants

Although no elephant was seen between 18:00-20:00 during this study, all the elephants observed in Lobeke NP were walking throughout the day. Early in the morning (06:00) the elephants spent less than 25% of their time walking per hour and progressively increased the

time spent walking to a maximum of about 75% late in the morning (12:00). It is not obvious why these elephants roamed so much, since there is an abundance of forage and water widely distributed in the park. However, based on folklore and anecdotal information it seems that the elephants in Lobeke NP are faced with different choice of what to eat. The Baka Pigmies of Lobeke Region argued that the forest elephants prefer foraging on certain fruits and leaves which are sparsely distributed in the forest (unpublished WWF report). For this reason, elephants may need to move from place to place in search of their preferred food. Also, Vanleeuwe and Gautier-Hion (1998) argued that the forest elephant is under serious threat from humans because of the high demand for ivory and bush-meat. For fear of humans, the forest elephants also may move continuously in the forest (Harris et al., 2008). However, my data showed that during the day elephants continue to move in the shade under the forest canopy most likely because of the continuous cooler diurnal microclimatic mosaic under the forest canopy with less radiant heat than in the *bais*.

The elephants of this study seem to spend more time during a 24-hour day walking than elephants in Namibia, Zimbabwe, Tanzania and Uganda did, despite the abundance of forage and water in Lobeke NP (see Figure 4.1 to 4.3). The savannah elephants of Sengwa Area in Zimbabwe (Guy, 1976), Lake Manyara (Kalemera, 1987), Ngogrongoro NP (Kabigumila, 1993a) in Tanzania, and Queen Elizabeth NP in Uganda (Wyatt and Eltringham, 1974) spent less

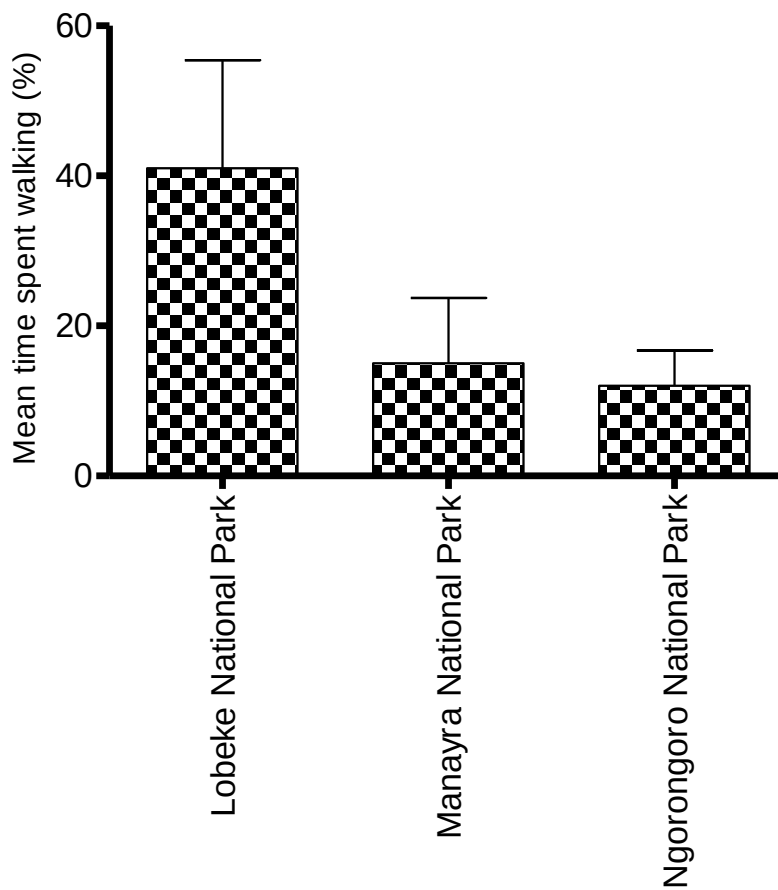


Figure 4.2 Mean percent time ($\pm$ SD) elephants spent walking within 12-hour day period (between 06:00-18:00) in Lobeke NP, Lake Manyara NP and Ngorongoro NP. Data for Lobeke NP was from my study and data for Lake Manyara NP and Ngorongoro NP were derived from Kalembera (1987) p. 260, and Kabigumila (1993a) p.78 respectively.

(<25%) time walking between 06:00-24:00 in comparison to Lobeke NP elephants. Desert-dwelling elephants in Namibia (Leggett, 2008) were closest in terms of time spent walking between 06:00-24:00 (see Figure 4.3). The desert-dwelling elephants of Namibia may spend more time walking than savannah elephants studied in Zimbabwe, Tanzania and Uganda because of less number of trees in the savannahs and fewer shaded microclimate mosaic patches within the diurnal landscape and the scarcity of quality forage and water compared with the other regions. Desert-dwelling elephants need to walk more than the elephants of Zimbabwe, Tanzania and Uganda since they have to traversing a large portion of barren landscapes, in search of forage to cope with their nutritional requirements of their large sizes. Also, since the desert is usually hot during the day, the desert elephants need to walk more in the cooler period of a 24-hour day (see Figure 4.3). The amount of time spent walking may have energetic and thermoregulatory consequences for elephants (Wright, 1984). During resting, elephants generate less heat than when they are exercising through walking, running, playing, fighting or courting. A 4,000 kg elephant, for example, going along with its daily activities needs to maintain a heat loss of 4.65 kW (Wright, 1984). Elephants must also have an effective means of thermoregulation to allow this excess energy to escape as heat. Elephants therefore need to balance costs of walking and other energy-demanding activities with a need to dissipate heat, most likely achieved through seeking cooler microclimates and evaporative heat loss through their skins.

Table 4.1 Table of study area, elephant species, climate, seasons and vegetation types

Study area	Elephant species	No. of elephants or Density of elephants	Climate	Average rainfall (mm/year) or Rainfall range in mm/year	Vegetation type	Season
Lobeke NP	Forest elephants	0.11-1.14 km²	Equatorial	1500	Equatorial forest	Dry season
Santchou Reserve, Cameroon	Forest elephant	0.76 km ²	Equatorial	1750	Montane forest, wet lowland forest & grassland	Dry season Rainy season
Sengwa Area in Zimbabwe	Savannah elephant	8 elephants	Generally equatorial		Mixed woodland, Mopain & Miombo	Three seasons: cold dry
Queen Elizabeth (Ruwenzori) NP, Uganda	Savannah elephant	18 elephants	Generally equatorial	1200	Wide variety of terrain, including volcanic craters, grassy plains & tropical forest	Three seasons: the cold, hot and wet
Manovo-Gounda-St. Floris NP, Central African Republic	Savannah elephant	9 elephants	Semi-humid	900	Seasonally-inundated grasslands in the north, riverine wooded savannah, and gallery forests	Four seasons, two wet & two dry
Lake Manyara, Tanzania	Savannah elephant	1-140 elephants per transect	Warm temperate climate	650	Habitats ranging from the rift wall, ground water forest, acacia woodlands, Open	Warm summers & dry winters

					grasslands, <i>Acacia tortilis</i> woodland	
Ruaha NP	Savannah elephant	4 km ²	Semi-arid	580	<i>Combretum</i> / <i>Terminalia</i> or <i>Commiphora</i> woodland with majestic baobabs found all over the park. Black cotton grassland & Miombo woodland	One wet season, one dry season, hot dry, warm wet
Ngorongoro Crater, Tanzania	Savannah elephant	103 elephants	Semi-humid	400-1200	Grassland & bushland dotted with <i>Euphorbia bussei</i> trees. The crater floor is mostly open grassland with two small wooded areas dominated by <i>Acacia xanthophloea</i>	Rainy season & dry season
Kunene Region, Namibia	Savannah elephant	52 elephants	Semi-arid	50-350	Typically arid	Wet, cold & hot dry season

Sources of data Santchou Reserve (Tchamba and Seme, 1993), Manovo-Gounda- St Floris NP (Ruggiero, 1992), Zengwa Area (Guy, 1976), Ruaha NP (Barnes, 1982a), Ngorongoro NP (Kabigumila, 1993a), Manyara NP (Kalemera, 1987), Kunene Region (Leggett, 2008), Queen Elizabeth NP (Wyatt and Eltringham, 1974) , (Field, 1971) and Lobeke NP (Kuwong,2013).

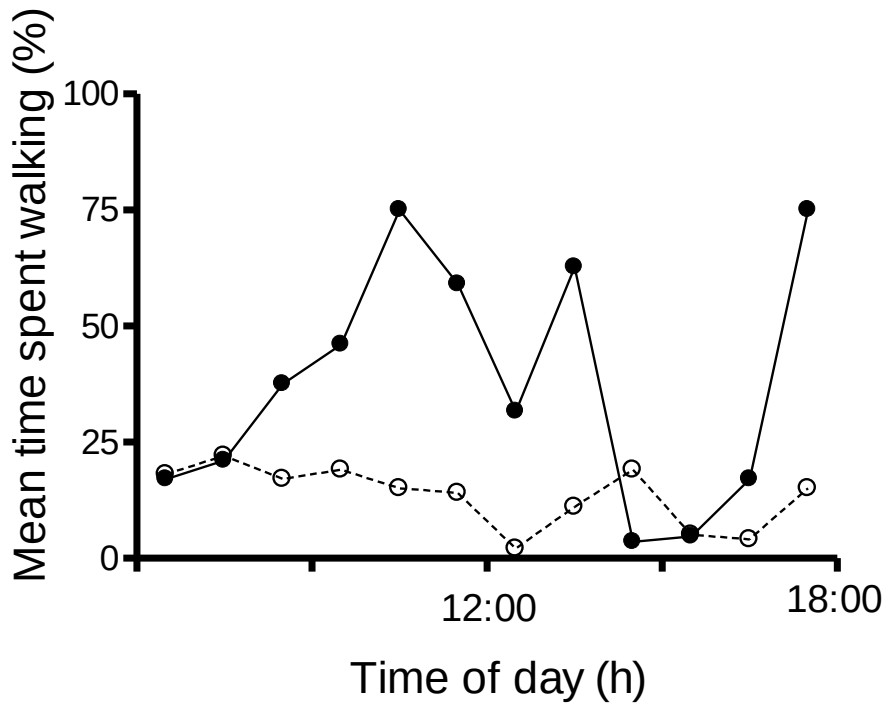


Figure 4.1 Mean percent time elephants spent walking during each hour in Lobeke NP (●) and in Ngorongoro NP (○) between 06:00-18:00. Mean data for Lobeke NP was from my study and the data for Ngorongoro was extracted from Kabigumila (1993a).

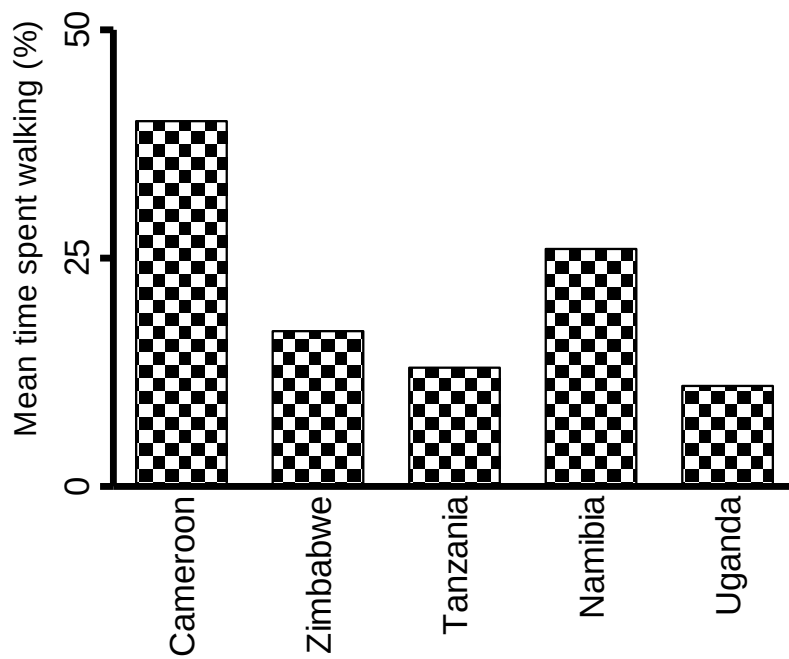


Figure 4.3 Mean percent time that elephants spent walking between 06:00-24:00 in different studies compared with the walking activities of my elephant study in Lobeke NP, Cameroon.

Data from other studies were derived from:

Namibia, Leggett (2008a) p.29 & Barnes (1982a)

Uganda, Wyatt & Eltringham (1974)

Zimbabwe, Guy (1976)

Tanzania, Kabigumila (1993a)

4.3.2 Foraging behaviour of elephants

Lobeke NP elephants fed for about half of their time between 06:00-24:00. Although my study was executed during the hottest and driest season of the year in Lobeke NP (between November and December), the vegetation was still relatively green and wet, compared to the dry seasons in the savannah and semi-arid regions (Leggett, 2008; Ruggiero, 1992). Since elephants have an insatiable appetite for foraging (Benedict, 1936; Lee, 1938; Carrington, 1959; Law, 1970) and because of the elephants' inefficient digestive system (Benedict, 1936), I expected that elephants will continue to forage as much as they can, when forage is abundant. On very hot days in Lobeke NP the forest elephants may continue to forage on abundant foliage along the forage paths and the alleys, while keeping their body cool in the microclimate mosaic under the forest canopy. Consequently, I predicted the forest elephants of my study would have similar time spent foraging compared with the forest elephants of Santchou Reserve and much longer than the savannah elephants. The time that Lobeke elephants spent foraging was higher than the foraging time reported in the arid Kunene Region but much lower than the foraging time the forest elephants of Santchou. Perhaps due to poor visibility in the forest during this study, coupled with the small data size, elephant fright responses to human observers, the sampling method that I used, place, time, and season the season that this research was executed, or a combination of these factors, might have accounted for the differences in my foraging data collected and that of other researchers across. Wyatt and Eltringham (1974), Guys (1976), Leggett (2008), Ruggiero (1992) and all used the focal point sampling method. However, Tchamba and Seme (1993) did not specify the method that they used to collect or analyse the foraging data of their elephants.

The Lobeke NP elephant's foraging time-range falls within the range reported for savannah elephants of Amboseli NP in Kenya (Poole, 1987), Sengwa Area in Zimbabwe (Guy, 1976), Ruaha, Manyara and Mikumi (Barnes 1982a; Barnes 1983), Lake Manyara (Kalemera 1987), Ngorongoro NP (Kabigumila, 1993a) in Tanzania. However, the data of all these studies, including that of this study, were significantly lower than the three-quarters foraging-time per 24-hour day range reported for savannah elephants of North Bunyero and Queen Elizabeth NP's in Uganda (Laws, 1970a), Manovo-Gounda St Floris NP in Central African Republic (Ruggiero, 1992) and forest elephants of Santchou Reserve in Cameroon (Tchamba and Seme, 1993). Among these reports only the data from my study and Santchou Reserve were from the African forest elephant and the rest from savannah elephants. Table 4.2 summarises data obtained at different sites across Africa, in an ascending order of the time elephants spent foraging. The desert-dwelling elephants (also savannah elephants) of Namibia had the least foraging time recorded, while the savannah elephants of Ruaha recorded the most foraging time.

Leggett (2008) argued that the desert-dwelling elephant spends only between 24-29% foraging because of the very hot environment ($>40^{\circ}\text{C}$), few trees, discontinuous cool microclimate mosaics, scarcity of water and little foliage to feed on in the Kunene Region, restricting their behavioural options during a hot day. Kabigumila's (1993a) report showed that high T_a also influences the behaviour of savannah elephants in the Ngorongoro Crater, such that they spend more of their time resting in shade to mitigate the scorching radiant heat during the day. However, Ngorongoro elephants spent more than 50% of their time foraging between 06:00-18:00 (Kabigumila, 1993a). Although Lobeke NP elephants spent more than 60% of their time feeding during the day (06:00-18:00), they reduced their foraging rate to below 40% late in the

Table 4.2 Summary of foraging data of the forest elephants in Lobeke NP compared to elephants from some other regions across Africa during day and night

Elephant species	Mean time spent foraging (h) per day	% of time spent foraging	Research site	Country	Source of data
Savannah elephant	6-7	24-29	Kunene Region	Namibia	Leggett, 2008)
Savannah elephant	7-13	30-55	Amboseli NP	Kenya	Poole, 1987)
Savannah elephant	12-14	36 -57	Sengwa Area	Zimbabwe	(Guy, 1976)
Forest elephant	13	54	Lobeke NP	Cameroon	(Kuwong, 2014)
Savannah elephant	13-15	56-64 (dry season)	Ruaha NP	Tanzania	(Barnes, 1982a)
Savannah elephant	13-20	56-85	Mikumi NP	Tanzania	(Barnes, 1983)
Savannah elephant	14	58 (dry season)	Lake Manyara	Tanzania	(Kalemera, 1987)
Savannah elephant	16-18	67-75	North Bunyero	Uganda	(Laws, 1970a)
Savannah elephant	16-18	67-75	Inadequate information	Inadequate information	(Carrington, 1959)
Savannah elephant	16-18	67-75	Information not specified	Zambia	(Hanks, 1979)
Savannah elephant	17	70	Manovo-Gounda St. Floris NP	Central African Republic	(Ruggiero, 1992)
Savannah elephant	18	75	Queen Elizabeth NP	Uganda	(Wyatt and Eltringham, 1974)
Forest elephant	20	83	Santchou Reserve	Cameroon	(Tchamba and Seme, 1993)
Savannah elephant	20	82-85 (wet season)	Ruaha NP	Tanzania	(Barnes, 1983)

morning and afternoon (between 10:00-11:00 and between 14:00-16:00), the time, which elephant were thought to be resting. The 12-hour day (06:00-18:00) foraging profile for elephants in Lobeke NP and Ngorongoro NP is shown in Figure 4.4.

Elephants spend most of their time feeding in order to cope with the nutritive requirements of their enormous bodies (Benedict et al., 1921) . In the course of the normal day, adult savannah elephants required 160-250 kg of vegetation and up to 160 L of water (Sikes, 1971). As the supplies of these commodities differ in different regions, so do elephants' behaviours tend to differ. Savannah elephants and Asian elephants have been reported to devote about three-quarters of their time to foraging, and spend relatively less time inactive (Owen-Smith, 1988). They are known to have diurnal activity patterns with peak feeding times in the early hours of the morning and afternoon (Guy, 1976; Wyatt and Eltringham, 1974).

However, the time elephants spent foraging may be influenced by variation in the quality and availability of forage (Kabigumila, 1993a; Leggett, 2008) and perhaps the microclimates available to elephants with specific vegetation. Generally, most foraging activity in Lobeke NP took place in the morning and early evening, similar to the behaviour of elephants in Uganda (Wyatt and Eltringham, 1974), Kenya (Hiley, 1975) and South Africa (Hidden, 2009). The elephant has a high heat production per unit of surface area; approximately 2,000 calories per square meter per 24-hours (Benedict and Lee, 1938). This implies that the elephant not only generates energy through metabolism but must also have an effective means of thermoregulation to allow excess energy to escape out as heat. Food availability, the time available to forage, the rate of food collection while foraging and physiological factors such as; the rate of digestion of

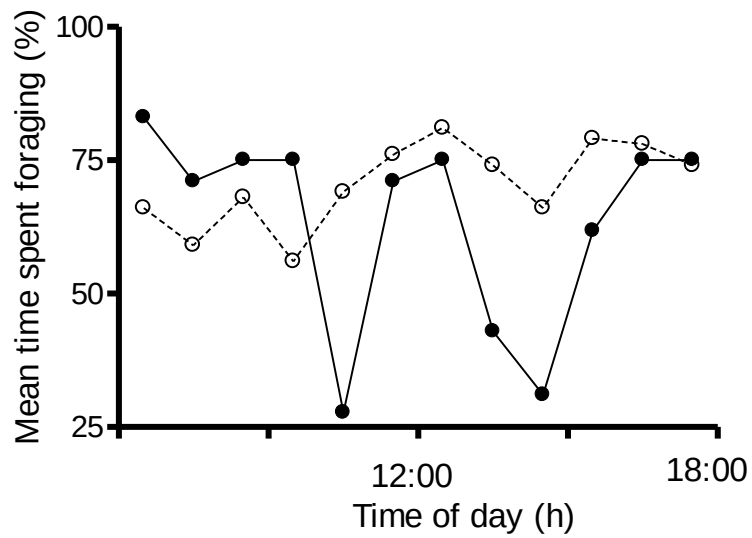


Figure 4.4 Mean time elephants spent foraging in Lobeke National Park (●), and in Ngorongoro National Park (○), between 06:00-18:00. I obtained the data for Lobeke National Park from my study and the data for Ngorongoro Crater were derived from Kabigumila (1993a).

food in an elephant's gut, the ability to assemble and deliver nutrients and oxygen to the tissues and the work capacity of various tissues, dictate the magnitude of energy flow in the elephant (Colbert, 1993).

At midday in Lobeke NP some elephants spent their time in the open *bais* to bathe with mud in the saline marshes, probably to cool their body as well, while the elephants in the foraging paths continued to forage on the foliage. On hot days during the long dry season, Lobeke NP elephants spent their time standing under shade in the *bais* and grazed on grasses, walked or rested under the forest canopy in the hot midday and browsed on trees. The forest elephants did seek shade in the hottest part of the day, all of them foraging under trees until the temperature dropped. Although Lobeke elephants showed evidence of feeding while seeking shade, my results did not reflect the advantage of the continuous cool shady mosaic under the forest canopy, nor on the feeding time that forest elephants may have over savannah elephants during the hot season. The lower than expected foraging time reported for the Lobeke NP elephants also may have resulted from the few elephants seen and the paucity of data collected.

4.3.3 Shade-seeking behaviour of elephants

As shown earlier in my results in Figure 3.21 A, during the day, the shade-seeking activities of the Lobeke NP elephants changed with the T_g in the *bais*. As T_g rose, so did the shade-seeking behaviour of the elephants. However, although my data showed no significant correlation between shade-seeking behaviour and T_g ($p=0.07$, $r^2=0.6$), there appear to be a critical temperature, T_g above 35°C , at which elephants in the *bais* initiated shade-seeking behaviour (see Figure 3.21 B).

The finding of this study suggests that elephants seek microclimates in the forest habitat for thermoregulatory reasons. This finding is similar to those of savannah elephants (Hidden, 2009; Hiley, 1975), implying that shade-seeking and its duration may differ from place to place, because of the variations in environmental temperature during different times of the day, variability in quality and availability of tree-shade, continuity of cool microclimate mosaic, forage and water availability.

Although the hottest day *Tg* in Lobeke NP was as high as 46°C, similar to the temperatures reported in the Kunene Region in Namibia (>45°C) during the hot dry season. The Lobeke NP elephants spent a mean time of only 7% seeking shade in the *bais* and *bai*-alleys and 53% of their time foraging between 06:00-24:00. During the hot dry season in the Kunene Region, the desert-dwelling elephant spent a mean time of about 14% seeking shade and foraged for only 24-29% of total time. The difference in shade-seeking time may be attributed to a hotter microclimate mosaic with fewer trees and patchy shade, combined with scarce forage and water in Kunene Region (Leggett, 2008), compared with that in Lobeke NP. Thus the elephants in Kunene Region may spend much of their time trying to mitigate the effect of the high environmental heat of the day at the expense of energy intake. As a consequence of discontinuous cool microclimate mosaic in the Kunene Region, resulting from the scarce and sparsely distributed tree-shades in the landscape, desert-dwelling elephants spend only between six to seven hours of day feeding, since they spend most of the hot day (at times, >58%) standing under shade (Leggett, 2008). Figure 4.5 illustrates shade-seeking activity of the Lobeke NP elephants compared to shade-seeking activity of the elephants in the Kunene Region. Lobeke

NP data were obtained in the dry season only, while Kunene data were collected year round during the wet, cold and dry hot seasons. Kunene elephants sought shade the most (24%) during the wet season, less (14%) during the hot-dry season and least (3%) during the cold season, suggesting that foraging requirements in the dry season may be traded off with shade use (Leggett, 2008).

The mean time elephants spent shade-seeking in Lobeke NP and in Ngorongoro NP during the day (see Figure 4.6). The habitat of Lobeke NP is closed-canopy evergreen forest while Ngorongoro is grassland and bushland dotted with *Euphorbia bussei* trees. Forest elephants seen in Lobeke NP start exhibiting shade-seeking activity between 10:00-11:00, increased progressively and peaked between 13:00-14:00, and decreased progressively after 15:00. The savannah elephants of Ngorongoro NP spent less than 25% of their time resting or seeking-shade but sought some shade at all times of day (Kabigumila, 1993a).

The Lobeke NP elephants' resting time during the day often coincided with shade-seeking time. They did not rest between 06:00-10:00 and between 20:00-24:00, but rested for about 18% of their time between 10:00-14:00, and 16% of their time between 14:00-18:00. Figure 4.7 illustrates the mean time elephants in Zimbabwe, Tanzania, Namibia, Uganda and this study. The Lobeke NP elephants spent a mean of less than 25% of their total time resting between 06:00-24:00, similar to the resting time reported by Kalembera (1987) and Kabigumila (1993a) for the savannah elephants of Manyara and Ngorongoro in Tanzania, respectively.

Shade-seeking activity did not hinder the feeding habits of the Lobeke NP elephants and probably also the forest elephants in Santchou Reserve, since these elephants can forage under

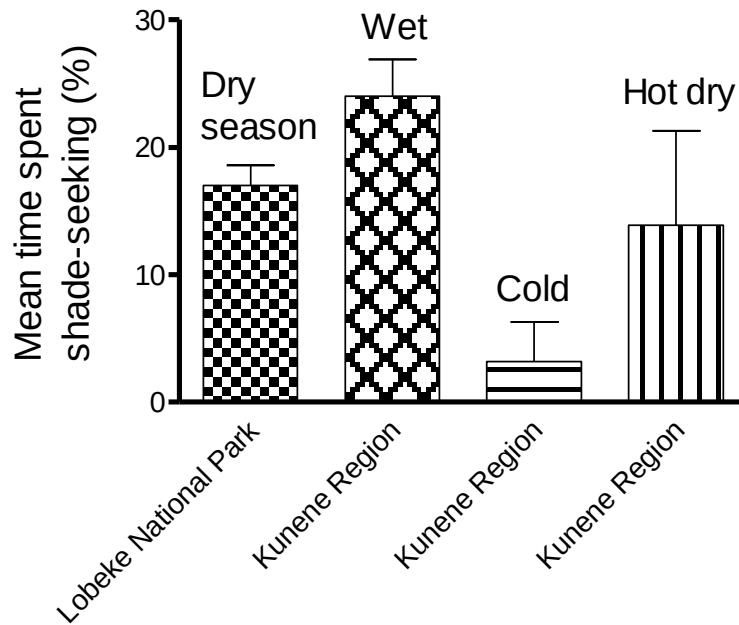


Figure 4.5 Mean percent of time ($\pm$ SD) that elephants spent shade-seeking between 07:00-19:00, the dry season in Lobeke NP and during the wet, cold and dry hot seasons in Kunene Region. Kunene data were derived from Leggett (2008 p.28) and Lobeke NP data were obtained from this study.

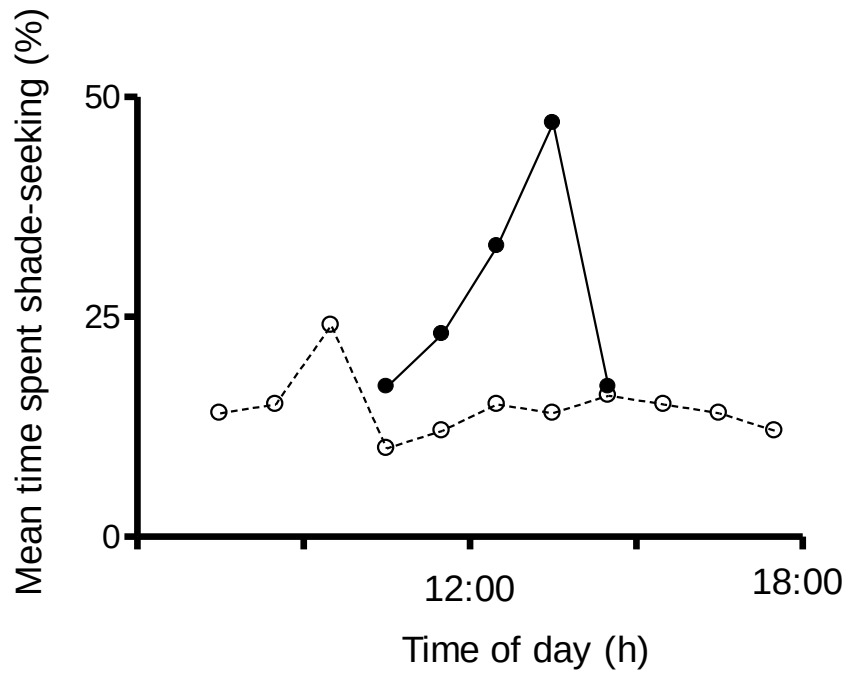


Figure 4.6 Mean percent of time that elephants spent shade-seeking in Lobeke NP (●) and savannah elephants in Ngorongoro NP (○) between 06:00-18:00. Data for Lobeke NP were from this study, the data for the Ngorongoro Crater were extracted from Kabigumila (1993a).

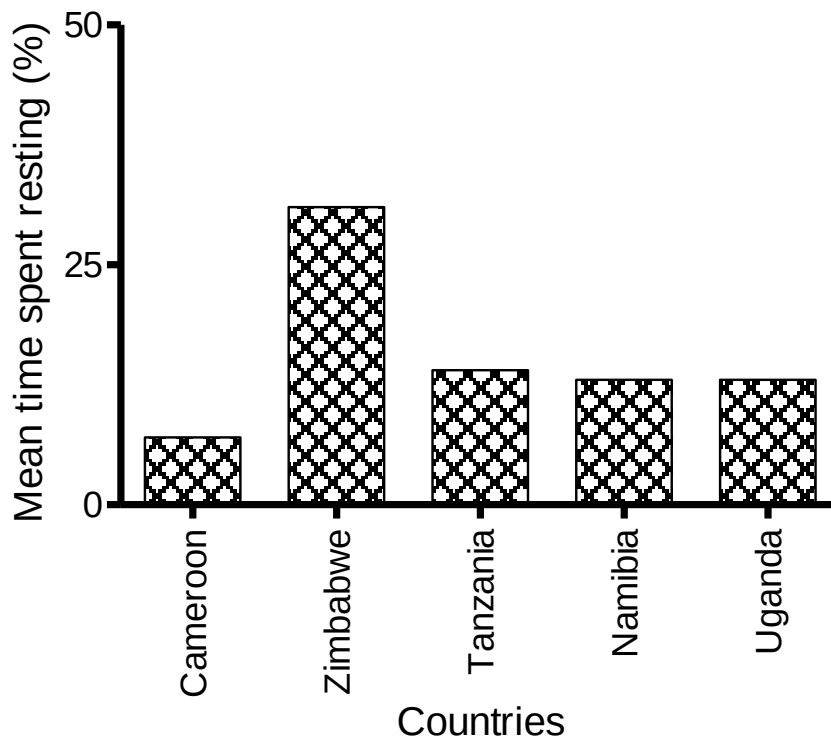


Figure 4.7 Mean percent of time that elephants spent resting between 06:00-24:00 in different studies compared with the resting activities during study in Lobeke NP, Cameroon. Data from other studies were derived from:

Namibia, Legett (2008) p.29 & Barnes (1982a)

Uganda, Wyatt & Eltringham (1974)

Zimbabwe, Guy (1976)

Tanzania, Kabigumila (1993a)

the cool and continuous shady portions under the forest canopy during hot sunny days. The savannah woodland habitats of the Central African Republic, Tanzania, Namibia, Uganda and Zimbabwe may have trees to provide adequate shade, but underneath the trees, forage may be absent or sparsely distributed within the microhabitats.

During the day, most of Lobeke NP elephants were seen in the *bais* only at dawn, dusk or when they were under shade of trees, which implied that the forest elephants were thermally stressed during the dry season when I executed this study. The shaded forest was much cooler (by about 7°C) than the open *bais*. Elephants therefore may have preferred the forest canopy because of a much bigger temperature gradient between the animal's body temperature and the environment facilitating passive cooling of the elephant's body. The forest elephants seen in the open *bais* of Lobeke NP sought shade between 11:00-15:00, while other elephants seen in the park preferred staying in shade under the forest canopy. Although elephants were not seen easily in the forest, their calls could be heard often indicating that they were in the forest portion during hot day.

4.3.4 Ear-flapping behaviour of elephants

This study showed a positive correlation between ear-flapping behaviour and T_g in *bais*, but lacked data under the forest canopy. Unlike, earlier investigators, which considered only the influence of T_g or T_a on ear-flapping, in this study, I assess if ear-flapping correlated with VP and wind variations, to ascertain if these microclimatic variables influenced thermoregulatory behaviour of the forest elephants. VP did not correlation with ear-flapping behaviour of the elephants in this study ($p=0.35$, $r^2=0.05$). As seen earlier, winds in the open *bais* were often faster than wind under the forest canopy. Because fast winds facilitate evaporative heat from the

body surfaces of elephants, evaporative heat loss resulting from the effect of wind is more effective in the open *bais* than under the forest canopy. This effective cooling effect seems to attract more elephants in the *bais* at night than during the day, based on the data previously shown on Table 3.3, indicating the number of elephants that entered each *bai* during the night or day. My result on ear-flapping responses to environmental temperature was similar to that of Buss and Estes (1971), Hidden (2009) and Rowe (1999), which also showed that the ear-flapping rate of elephants increased with an increase in environmental temperature.

According to earlier studies, savannah elephants flap their ears to keep their body cool (Hiley, 1975; Wright and Luck, 1984); and the rate of flapping increase as temperature rises (Buss and Estes, 1971; Hidden, 2009). Studies on savannah elephants have shown that blood leaving the ears is significantly cooler than blood entering the ears, which suggests that the ear radiates heat from the elephant's (Phillips and Heath, 1992). It is likely that flapping the ears facilitates not only convective heat loss from the ear of elephants, but also evaporation of water from the ears. Elephants also may flap ears in response to other factors such as bites of tse-tse (*Glossina spp.*) and horse flies (*Tabanidae spp.*) found in Lobeke NP. The bites of these flies irritate elephants, causing them to shake their body and flap their ears (personal observations). However, the finding of this study showed that ear-flapping increased with *Tg* suggesting that ear-flapping serves to cool the body of forest elephants too.

4.3.5 Dust-bathing behaviour of elephants

No correlation was observed between dust-bathing behaviour and *Tg* under the forest canopy ($p=0.07$, $r^2=0.26$). However, there was a weak positive association between dust-bathing

behaviour and Tg in the *bais* ($p=0.01$, $r^2=0.47$), suggesting that dust-bathing may also be a thermoregulatory behaviour in forest elephants. The elephants in the open *bais* spend more time dust-bathing than those observed under the tree-shades in the *bais* or under the forest canopy. Perhaps this discrepancy in the correlation of environmental heat load and dust-bathing in the *bais* and under the forest canopy could be because few numbers of elephants observed in this study due to the obscure nature of the dense evergreen Equatorial Forest.

As shown in the earlier photographs (Figure 3.12), after elephants dust-bathed in Lobeke NP, a thin film of dust particles stuck on their bodies and they appeared reddish-brown. Reports have suggested dust-bathing is an important thermoregulatory mechanism of savannah and Asian elephants (Barnes, 1984; Feldhamer et al., 1999; Haltenorth and Diller, 1980; MCKay, 1973; Rees, 2002). Dust protects the elephant's skin from the sun or parasites; or a combination of both of these functions in the savannah elephants (Barnes, 1984; Feldhamer et al., 1999; Haltenorth and Diller, 1980; MCKay, 1973; Rees, 2002). It has been argued that the desert-dwelling

elephants in Namibia performed dust-bathing behaviour for thermoregulatory reasons (Leggett, 2008). Although both the forest elephants and desert-dwelling elephants spent less than 25% of the time between 07:00-19:00 dust-bathing, the desert-dwelling elephants performed dust-bathing behaviour less than the Lobeke NP elephants. However, Lobeke NP data was obtained in the dry season only; while desert-dwelling elephant data were collected year round (see Figure 4.8).

4.3.6 Water-related activities of elephants

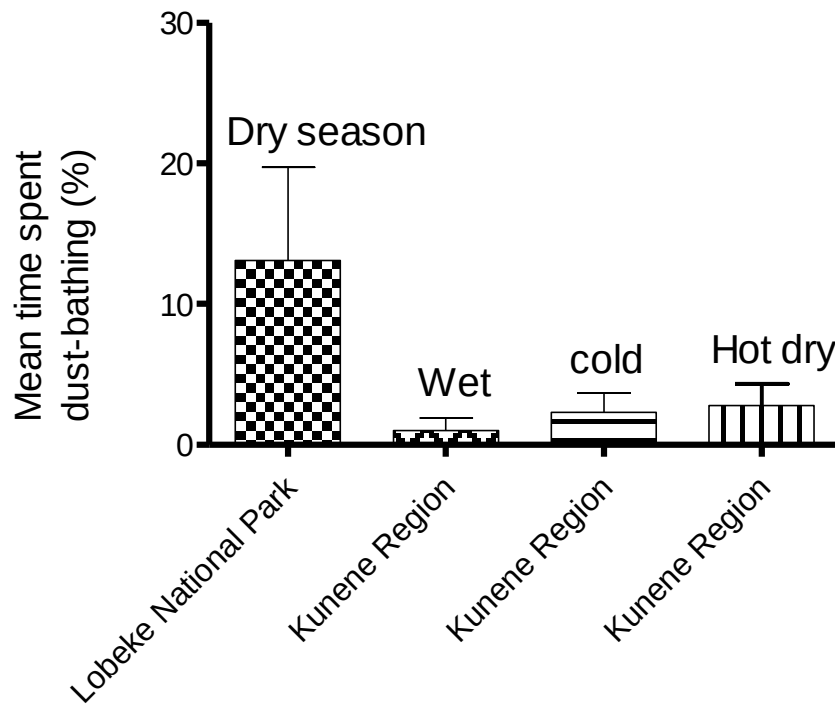


Figure 4.8 Mean percent time ($\pm$ SD) that elephants spent dust-bathing activities between 07:00-19:00, during the dry season in Lobeke NP only, and during the wet, cold and dry hot seasons in Kunene Region. Kunene data was derived from Leggett (2008 p.28) and Lobeke data was obtained from my study.

No significant correlation between *Tg* and water-related activities were observed ($p=0.29$, $r^2=0.13$). Also, there was no association between the amount of time the Lobeke NP elephants spent on water-related activities and ambient *VP* ($p=0.67$, $r^2=0.02$). A similar study in Ngorongoro NP showed that elephants maintained a more or less steady profile of water-related activities, below 10% of total time (Kabigumila, 1993a); see Figure 4.9). Throughout the year, the desert-dwelling elephants performed fewer water-related activities than the Lobeke NP elephants (Figure 4.10). This research was done only during the hot dry season, so that may explain the higher indices of water-related activities in Lobeke NP. However, the abundance of swampy *bais* and water supply in Lobeke NP also may explain why forest elephants' behaviour is different to that of elephants in other regions, even in the hot dry season.

Researchers have argued that dry mud on an Indian or savannah elephant's body serves as a thin protective sheet against solar radiation and also serves as a remedy for parasites similar to dust (Barnes, 1984; Feldhamer et al., 1999; Haltenorth and Diller, 1980; McKay, 1973; Rees, 2002). But it is not known if mud serves the same purpose as in the savannah and Indian elephant. Some researchers have argued that forest elephants visit the *bais* to bathe and eat mud because of the nutritive benefits that forest elephants obtain from the natural mineral salt deposits on the top soils present in *bais* (Turkalo and Kidjo, 1996; White et al., 1993).

Based on other reports on savannah elephants (Hiley, 1975; Leggett, 2008) it also seems likely that water-related activities in forest elephants may be influenced by thermoregulatory needs. All elephants lack sweat glands, thus the main mode of excess body heat loss is through evaporative heat loss through a porous skin (Carrington, 1959). Regular wetting of the skin

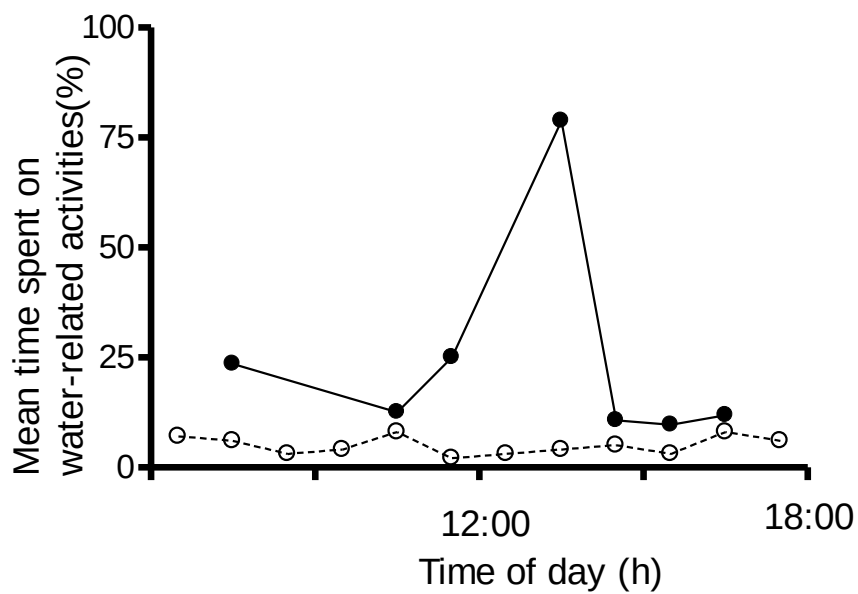


Figure 4.9 Mean percent time that elephants spent on water related activity in Lobeke NP (●) and in Ngorongoro NP (○) between 06:00-18:00. Data for Lobeke NP were from my study and data for Ngorongoro from Kabigumila (1993a).

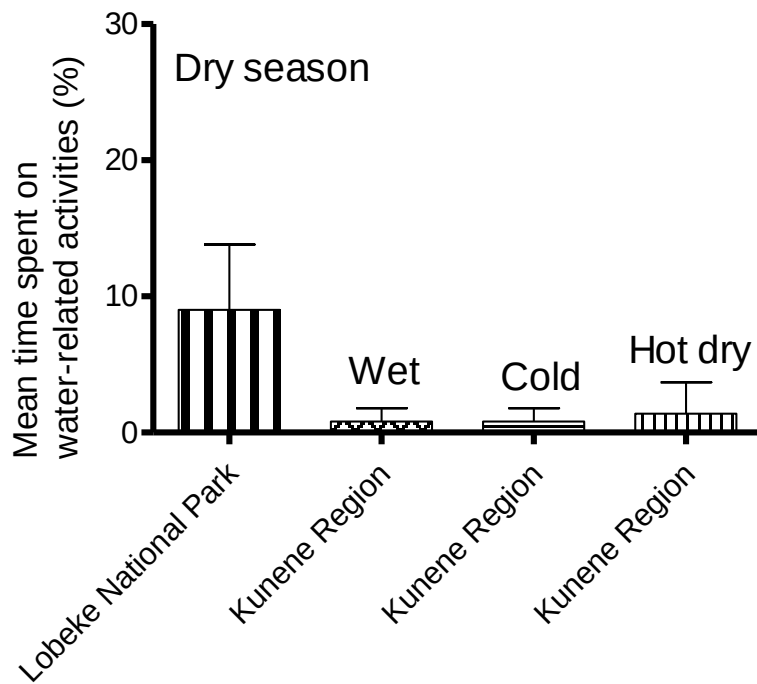


Figure 4.10 Mean time ($\pm$ SD) that elephants spent on water-related activity between 07:00-19:00, during the dry season in Lobeke NP and during the wet, cold and dry hot seasons in Kunene Region. Kunene data was derived from Leggett (2008 p.28) and Lobeke NP data was obtained from my study.

favours continued evaporative heat loss (Lillywhite and Stein, 1987). Lobeke NP elephants may perform water-related activities in order to facilitate evaporative heat loss by maintaining a high diffusion gradient (Taylor and Layman, 1967) between the skin *VP* and the ambient *VP* of Lobeke area. It is likely that African forest elephants would prefer a microclimate that facilitates evaporative heat loss. Although my finding suggest that *VP* in the *bais* were significantly lower than that under the forest canopy during the day and night, forest elephants preferred staying under the forest canopy probably because of the high environmental heat load in the *bais* during the day, although the low *VP* in the *bais* and under the forest canopy would favour evaporative heat loss from the body of an elephant. This behaviour may have accounted for the low number of elephants (0 to 5) that visited the *bais* during the day between 06:00-18:00 and the high number of elephants (0 to 22) that visited the *bais* at night (18:00-06:00). This data was based on the number of elephants seen and their indices of presence recorded in this study. The higher number of elephants that entered Djanguai Bai compared to the other four *bais* could have been because of the lower mean *Tg* recorded at Djanguai Bai during the day. The lower local *Tg* and *Ta* of Djanguai Bai during this study resulted a dusty haze above the Djanguai area, following a violent storm. The dusty haze impaired solar radiant heat from reaching Djanguai Bai thus preventing the area from heating up during the day. Also the elephants were observed to perform more water-related activities than only drinking water. These activities included; eating mud, smearing mud on their body and spraying water on their bodies probably as an alternative means to mitigate heat stress, instead of selecting a favourable microclimate. Reports have shown that the morphology of elephants' skin surface favours the retention of water in the skin crevices (Lillywhite and Stein, 1987). As moisture is retained on elephants' body surface (Lillywhite and Stein, 1987), evaporative heat loss is facilitated and cooling of the body is maintained (Hiley,

1975). In the arid region of Namibia, the day temperatures are high ($>40^{\circ}\text{C}$) and surface water is scarce (Leggett, 2008). As a result, survival is difficult for these animals (Seely, 1978; Viljoen, 1992) because of the extreme high temperatures and dry environment. Water activities of the desert-dwelling elephants between 07:00-19:00 throughout the year were higher than had been reported by any other study (Leggett, 2008) when compared to 24-hour day water-related activities of savannah elephants reported in other studies e.g. Zimbabwe, Tanzania and Uganda (Figure 4.11). This is because the desert-dwelling elephant uses water-related activities as the main way of mitigating heat stress (Leggett, 2008), though, it also exhibits microclimate selection too. Whether the water-related activities of the Lobeke NP elephants were for thermoregulatory reasons, nutrition, anti-parasitic therapy or a combination of all these functions is still not elucidated. More research is required to be able to answer these questions.

4.4 Advantages and limitations of this study

This study was limited because of the problems encountered to obtain Physiological data such as body temperature, rates of evaporative heat loss, respiratory rate and effect of altitude on forest elephants. Also environmental factors that may affect the behaviour of forest elephants such as predation risk, effect of altitude, availability of forage, food quality and quantity, fear for humans and water distribution could not be obtained due to the difficulties previously mentioned including. These include expensive project cost, difficulties surveying the forest elephants' activities in the dense closed-cover tropical forest and personnel safety.

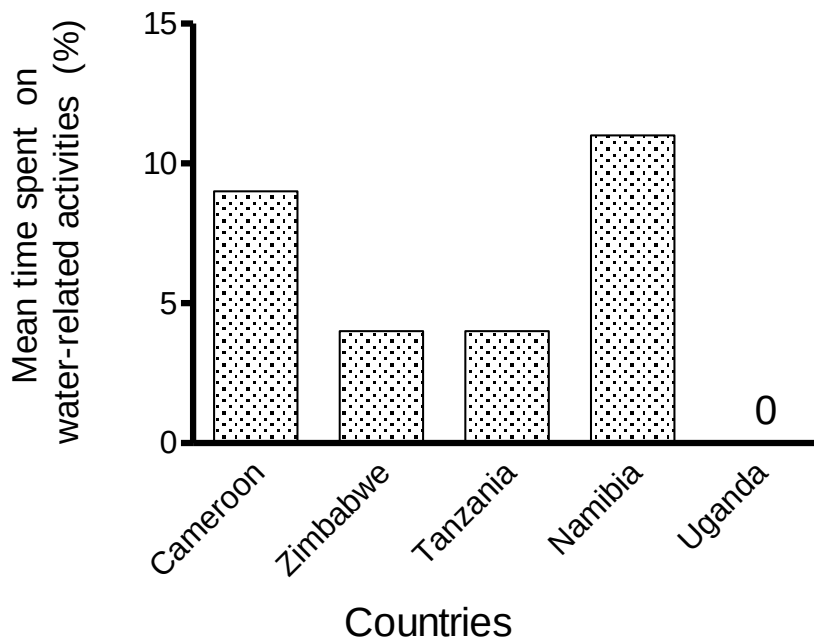


Figure 4.11 Mean percent of time that elephants spent on water-related activities between 06:00-24:00 in different studies compared with the water-related activities of my elephant study in Lobeke NP, Cameroon. Data from other studies were derived from:
Namibia, Legett (2008) p.29 & Barnes (1982a)
Uganda, Wyatt & Eltringham (1974)
Zimbabwe, Guy (1976)
Tanzania, Kabigumila (1993a).

Previous studies have reported data on elephant feeding, resting and walking, and social activities e.g. (Kalemera, 1987; Kabigumila, 1993; Leggett, 2008a), but often omitted activities associated with thermoregulatory processes and microclimatic variables, particularly *VP*, *WS* and *Tg*. I could not compare my data systematically with that of previous studies since most researchers paid less attention to microclimate available to elephants. However, this is the novelty in my study and I recommend that future studies on elephant behaviour should include climatological data in both macroclimatic and microclimatic levels.

The reported methods for analysing elephant behaviour and activity data also have varied significantly throughout the past decade, although most studies have used fixed point interval technique (Guy, 1976; Martin and Bateson, 1986; Wyatt and Eltringham, 1974). I used a five-minute fixed point interval method to recorded elephant behaviour and activity data. Others have used four-minute sampling techniques (Barnes, 1983; Barnes, 1982a). In this method multiple animals were analysed at any one time. Wyatt and Eltringham (1976) collected data at four-minute intervals while Kabigumila (1993a) and Lee (1987) collected theirs at five-minute intervals. Others used a combination of multiple elephant surveys at five-minute intervals and the continuous survey method (Guy, 1976). However, it has been argued that different sampling methods may yield different conclusions, but Leggett (2008) has shown that there are no statistical significant differences between the data obtained by any of these methods, implying that the behaviour data obtained from either fixed sampling or continues sampling techniques would be yield similar results.

This forest elephant activity pattern study was carried out for only 15 days (only three days per study site) during the long dry season, between November and December 2010. No data was gathered during the short dry season, long rainy season or short rainy season. This elephant behaviour survey was done between 06:00-24:00. No survey was done 24:00-06:00. However, unlike previous studies, I did focus on activities such as foraging, ear-flapping, walking, resting, shade-seeking, water-related activities and dust-bathing behaviour, providing novel insight of the forest elephant's thermoregulatory-related behaviour.

As with the majority of behaviour studies on wild megaherbivores, investigating elephant activity is difficult (Harris et al., 2008; Wronski et al., 2006) and I believe it is dangerous and expensive. From personal experience, forest elephants are difficult to observe. For these reasons I used miradows at the edges of *bais*. Unfortunately, the behaviour of only eleven elephants was observed in this study. However, as mentioned previously in the procedure for collecting behaviour section 2.5, supplementary tools such as topofil (a device composed of a thread that may entangle on the leg of an animal and displaces towards the direction of movement of the animal indicating its presence at that place, even if the animal has moved off-sight), elephant vocalizations heard at night, fresh faecal droppings and foot prints identified, proved useful to investigate some of the activities of the forest elephants and to also estimate the number of elephants that visited the study sites.

4.5 Conclusion

This study supported the hypothesis that habitats in the *bais* and in the vicinity of the *bais* differ in microclimates. The data of this study suggested that the differences in the microclimates

appeared to influence elephant behaviours, particularly those likely to be used for thermoregulatory purposes. Ear-flapping behaviour of the African forest elephants correlated positively with T_g and T_a . Very weak positive associations between T_g or T_a , and shade-seeking and dust-bathing were also observed in this study. Based on the weak association between dust-bathing and T_g and suggestions on the thermoregulatory effect of dust-bathing in savannah elephants (Barnes, 1984; Feldhamer et al., 1999; Haltenorth and Diller, 1980; MCKay, 1973; Rees, 2002), dust-bathing behaviour in this study may have been an additional mechanism that forest elephants use to adjust their body heat load. VP did not correlate with thermoregulatory behaviour of elephants in this study. Also, the VP profiles for all the open *bais* in this study were significantly lower than under the forest canopy during the day and at night. This implies that a forest elephant would lose excessive body heat through evaporative heat loss faster in the open *bais* than under the forest canopy. However, WS in open *bais* were significantly higher than WS under the forest canopy during the day and at night. Fast wind facilitates evaporative heat loss (Cohen et al., 1979). Although this study has shown that VP profiles in *bais* and under forest canopy are significantly different during day and at night, forest elephants prefer spending most of their day under the forest canopy and night in the open *bais*. However, based on reports savannah elephants often lose heat through evaporation since VP on their body surface is often higher than ambient VP . It is likely that T_g , VP , WS are the thermoregulatory factors that explain the high number of elephants seen or the indices of forest elephant presence recorded in the *bais* at night and less number of elephants during the day. Forest elephants probably avoid the higher T_g in the *bais* during the day in favour of the cool shade under the forest canopy. Also, during the day forest elephants may stay in the forage paths because of the abundant forage and the advantage of staying in a continuous cool microclimate mosaic during the heat of the day, and

return to the open *bais* at night to utilize the effect of wind to cool their bodies. Although I did not have physiological data for the forest elephants, it seems they are faced with serious thermoregulatory problems during the day because of the high *Tg*. But based on many anatomical similarities between forest elephants and savannah elephants (Skinner and Chimimba, 2005), I assume that the forest elephants in Lobeke NP also dump heat in the same manner described by Hidden (2009), Robertshaw (2006) and Weissenböck (2010); and heat dumping in the park at night is facilitated by the large *VP* and temperature gradients between elephants' bodies and ambient *Tg*, *VP* and fast *WS* in the *bais*.

To the best of my knowledge, this study in the Congo Basin forest suggests, for the first time, that shade-seeking and dust-bathing may be important thermoregulatory mechanisms that forest elephants use when hot, although other researchers have also suggested dust as a natural anti-parasitic agent employed by elephants (Barnes, 1984; Feldhamer et al., 1999; Haltenorth and Diller, 1980; MCKay, 1973; Rees, 2002). Body and skin temperature measurements are required to elucidate if such behaviours do alter body temperature, or if they may be used for thermal comfort, possibly reflected by a reduced skin temperature.

Based on the number of elephants that were observed and the indices of presence recorded, the meadows at all the *bais* and their vicinities investigated in this study were heavily trampled with elephant spoor, faeces and urine. This suggests that *bais* are “hotspots” in the forest frequented by forest elephants and, as elephants move in and out of these areas, the changes in the microclimates affect the elephant's thermoregulatory processes. *Bais* also provide areas for social interactions (Turkalo and Fay, 1995), they are rich places for nutritious herbs (Carroll,

1996; White et al., 1993) and places with mineral salt-licks (Turkalo and Fay, 1995; White et al., 1993).

Although the data obtained in this study are too small to draw up concrete conclusions that may apply generally to the behaviour of forest elephants, the information provides an insight of how African forest elephants behave within the microclimatic mosaics in Lobeke NP, and perhaps across the Congo Basin forest landscapes. Studies on free-living African forest elephants' behaviour in the microclimates anywhere in the Congo Basin Forest had not previously been investigated. Information on variability of microclimate and possible effects for thermoregulatory behaviour of a keystone species such the forest elephant is vital and urgent due the current threats; growth of human population due to reduced child mortality and longer human life span, deforestation, habitat loss, habitat fragmentation, poaching and climatic change (Chivian and Berstein, 2008), and alteration of forest biodiversity (Root and Schneider, 1995). Indeed, according to the IUCN's 2006 Red List, slash-and burn of bushes for crops and livestock is a threat to more than 20% of terrestrial species, including African forest elephants. Elephants are key animal species that always directly or indirectly ensure the survival of organisms living in the same ecosystems with them (Schulze et al., 1994), including humans. Thus human would be in serious trouble surviving, if elephant populations are reduced or if these animals cease to exist. African elephants are under serious threat of extinction because of poaching for ivory and bush meat trade, and have been listed as threatened on the IUCN Red List of Threatened Species (IUCN, 2009).

Humans have already altered to a varying degree nearly half of the earth's land surface (Wilson, 2008) consequently, microclimates have also been altered. In the next thirty years, this number will likely rise to about 70% of the land surface (UNDP, 2002) further threatening the existence of elephants. Presently, home to about half of the world's population, cities are growing by 2% each year on average, so that urban population, according to the United Nation Population Division, will grow to 60% of the world's total by the year 2030, with even greater proportion in the developing world (UNPD, 2005). Also the building of dams, irrigation projects, and other water development activities can disrupt the integrity of landscapes, habitats, macroclimate and microclimates and threaten species. While each of these activities bring great development to humanity, they all come with sufficient cost to species and ecosystems (Wilson, 2008) where elephants and humans coexist. Many scenarios have demonstrated complex relationships by changing land-use and land cover producing unforeseen impacts of both wildlife and human health. Land-use change has been linked with emerging diseases due to conversion of the tropical forest. The IUCN currently lists habitat loss, and therefore, loss of microclimates, as a key contributor to the endangerment of nearly 50% of all threatened species. (Wilson, 2008).

Climate change projections indicate that key portions of the elephants' habitats will become significantly hotter and drier (Root and Schneider, 1995), resulting in poorer foraging conditions and threatening survival of animals (Chivian and Bernstein, 2008). Young and Van Aarde (2010) recently showed that a decrease in the survival rate of young elephants, between four to seven years old, in southern Africa may be associated with changes in vegetation productivity, water availability, ecophysiological variability and drought. Young elephants are particularly vulnerable in hotter and drier environments predicted to occur with climate change and

deforestation thus further aggravating the existence of effective elephant populations and ecosystems.

In order to be able to predict and mitigate adverse effects on elephants, it is imperative to know the role microclimates play in the thermal biology of elephants. Inferences made in this study on the microclimate mosaics that forest elephants select for thermoregulatory reasons would need further investigation before concrete conclusions are drawn. Due to the difficulties, danger and high cost to study mega-herbivores in the wild (Harris et al., 2008; Wronski et al., 2006), I believe it would be worthwhile investigating forest elephants' behaviour by applying GPS/satellite collaring, real time bio-logging and also camera trapping techniques, which may help characterize activity patterns. Both techniques are feasible in the forest, although activity data-loggers require capture of elephants to fit collars. In order to truly know how microclimate mosaics influence the thermoregulatory behaviour of a keystone species such as forest elephants in the evergreen, hot humid equatorial forest of the Congo Basin, extensive studies in all seasons within a wide range of habitats are necessary. This study serves as a starting point. Knowledge of wildlife behaviour in macroclimates and microclimates within a wide range of habitats will contribute to provide more information for the Millennium Ecosystem Assessment, which will provide insights for policy makers to approach development and human and wildlife health at the level of specific health risk factors, climate change, landscape and habitat change, and economies and behaviours.

REFERENCES

- Barenbrug, A. W. T. 1974. Psychrometry and Psychrometric Charts, Cape and Transvaal Printers Ltd. Cape Town 1-59.
- Barnes, R. F. W. 1982a. Elephant feeding behaviour in Ruaha National Park, Tanzania. *African Journal of Ecology*, 20: 123-136.
- Barnes, R. F. W. 1983. Elephant behaviour in a semi-arid environment. *African Journal of Ecology* 21: 185-196.
- Barnes, R. F. W. 1984. Elephants. In: Macdonald, D.W. (Ed.), *Encyclopedia of Mammals*. Andromeda Oxford Ltd., Abingdon.
- Baumann, P. R. 2009. Tropical wet realms of Central Africa, part I Geo/SAT 2 <<http://www.oneonta.edu>> Downloaded 19 January 2012.
- Benedict, F. G., E. L. Fox, and M. L. Baker. 1921. The surface temperature of elephant, rhinoceros and hippopotamus. *African Journal of Physiology* 56: 464-467.
- Benedict, F. G., and R. C. Lee. 1938. Further Observations on the Physiology of the Elephant. *Journal of Mammalogy* 19: 175-194.
- Blanc, J. J. et al. 2007. African Elephant Status Report 2007: an update from the African elephant database. Occasional paper of IUCN Survival Commission Gland, Switzerland, 33.
- Buss, I. O., and J. A. Estes. 1971. The functional significance of movements and positions of the pinnae of the African elephant (*Loxodonta africana*). *Journal of Mammalogy*, 52: 21-27.
- Buss, I. O., and A. Wallner. 1965. Body temperature of the African elephant. *Journal of Mammalogy*, 46: 104-107.

- Carrington, R. 1959. Elephants. A short account of their natural history, evolution and influence on mankind. New York Basic Books, Inc., : 272-280.
- Carroll, R. W. 1996. Status of the lowland gorilla and other wildlife at the Dzanga–Sangha region of south-western Central African Republic Primate Conservation, 7: 38-41.
- Chen, J., J. F. Franklin, and T. A. Spies. 1995. Growing-season microclimatic gradients extending into old-growth Douglas-fir forests from clearcut edges. Ecological Applications, 5: 74-86.
- Chivian, E., and A. Bernstein. 2008. Sustaining Life: How Human's Health Depends on Biodiversity. Oxford University Press, USA
- Cohen, I., G. R. Beaton, and D. Mitchell. 1979. The South African Text Book of Sports Medicine. University of the Witwatersrand, Johannesburg 5-20.
- Colbert, E. H. 1993. Feeding strategies and metabolism in elephants and sauropod dinosaurs. American Journal of Science, 293-A: 7-19.
- Cole, M. M. 1986. The Savannas: Biogeography and Geobotany. Academic Press, London, : 72-78.
- Cott, H. B. 1975. Looking at animals. A zoologist in Africa: New York, Charles Scribner's Sons. 221: 84-86.
- De Beer, Y., and R. J. Van Aarde. 2008. Do landscape heterogeneity and water distribution explains aspects of elephant home range in southern Africa's arid savannas? Journal of Arid Environments, 72: 2017-2025.
- De Boer, W. F., C. P. Ntumi, A. U. Correia, and J. M. Mafuca. 2000. Diet and distribution of elephant in the Maputo Elephant Reserve, Mozambique. African Journal of Ecology, 38: 188-201.

- Dublin, H. T. 1996. Elephants of the Masai Mara, Kenya: seasonal habitat selection and group size patterns. *Pachyderm*, 22: 25-35.
- Ekobo, A. 1995. Conservation of the African forest elephant (*Loxodonta africana cyclotis*) in Lobéké, south-east Cameroon. PhD Thesis, University of Kent.
- Elder, W. H., and D. H. Rodgers. 1975. Body temperature in African elephant as related to ambient temperature. *Mammalia*, 39: 395-399.
- Fay, J. M., and M. Agnagna. 1991. A population survey of forest elephants (*Loxodonta africana cyclotis*) in northern Congo. *African Journal of Ecology*, 29: 177-187.
- Feldhamer, G. A., L. C. Drickamer, S. H. Vessey, and J. F. Merritt. 1999. *Mammalogy. Adaptation, Diversity, and Ecology*. McGraw-Hill, Boston,
- Field, C. R. 1971. Elephant ecology in Queen Elizabeth Natinal Park, Uganda. *African Journal of Ecology* 9: 99-123.
- Gebremedhin, K. G., and B. Wu. 2001. A model of evaporative cooling of wet skin surface and fur layer. *Journal of Thermal Biology* 26: 537-545.
- Geiger, R. 1965. *The Climate Near the Ground*. Cambridge (MA): Harvard University Press: 12-24.
- Goddard, J. 1967. Home range, behaviour, and recruitment rates of two black rhinoceros populations. *African Wildlife Journal* 5: 133-150.
- Grenot, C. J. 1992. Ecophysiological characteristics of large herbivorous mammals in arid Africa and the Middle East *Journal of Arid Environments* 23: 125-155.
- Guy, P. R. 1976. Diurnal activity patterns of elephant in the Sengwa Area, Rhodesia. *African Journal of Ecology* 14: 285-295.

- Haltenorth, T., and H. Diller. 1980. A Field Guide to the Mammals of Africa, including Madagascar. Collins, London: 54- 88.
- Hanks, J. 1979. The Struggle for Survival: The Elephant Problem. Mayflower, New York.
- Harris, G., G. Russell, R. Van Aarde, and S. Pimm. 2008. Rules of habitat use by elephants *Loxodonta africana* in southern Africa: insights for regional management. *Oryx*, 42: 66-75.
- Harrison, M., and P. Agland. 1987. A draft proposal for the designation of three new national forest parks Dja River Films, Ltd.
- Hecketsweiler, P., C. Doumenge, and J. Mokoko Ikonga. 1991. Le Parc National d'Odzala, Congo. IUCN Programme de conservation des forêts, IUCN, Gland, Switzerland.
- Hetem, R. S. et al. 2010. Variation in the daily rhythm of body temperature of free-living Arabian oryx (*Oryx leucoryx*): does water limitation drive heterothermy? *Journal of Comparative Physiology B*. 180: 1111-1119.
- Hidden, P. A. 2009. Thermoregulation in African elephants (*Loxodonta africana*). MSc Dissertation, University of the Witwatersrand, Johannesburg.
- Hiley, P. 1977. The thermoregulatory response of the rhinoceros (*Diceros bicornis* and *Ceratotherium simum*) and the zebra (*Equus burchelli*) to diurnal temperature change. *African Wildlife Journal*, 15: 337.
- Hiley, P. G. 1975. How the elephant keeps its cool. *Natural History*, 84: 34-41.
- Hoare, R. E. 1999. Determinants of human-elephant conflict in land-use mosaic. *Journal of Applied Ecology*, 36: 689-700.

- Houston, D. C., J. D. Gilardi, and A. J. Hall. 2001. Soil consumption by elephants might help minimize the toxic effects of plant secondary compounds in forest browse. *Mammalian Review*, 31.
- Huey, R. B. 1991. Physiological consequences of habitat selection. *The American Naturalist*, 137: 91-115.
- Ingram, D. 1975. Evaporative cooling in the pig. *Nature*, 207: 415-416.
- IUCN. 2009. Red List of Threatened Species. Gland, Switzerland.
- Jessen, C. 2001. Temperature Regulation in Humans and Other Mammals. Berlin, Germany
- Kabigumila, J. 1993a. Diurnal activity of elephants in Ngorongoro Crater, Tanzania. *African Journal of Ecology*, 31: 75-80.
- Kabigumila, J. 1993b. Feeding habits of elephants in Ngorongoro Crater, Tanzania. *African Journal of Ecology*, 31: 156-164.
- Kalemera, M. C. 1987. Dry season diurnal activity of elephants in Lake Manyara National Park, Tanzania. *African Journal of Ecology*, 25: 255-263.
- Kinahan, A. A., R. Inge-moller, P. W. Bateman, A. Kotze, and M. Scantlebury. 2007a. Body temperature daily rhythm adaptations in African savanna elephants (*Loxodonta africana*). *Physiology and Behavior*, 92: 560-565.
- Kinahan, A. A., S. L. Pimm, and R. J. Van Aarde. 2007b. Ambient temperature as a determinant of landscape use in the savanna elephant, *Loxodonta africana*. *Journal of Thermal Biology*, 32: 47-58.
- Kuwong, M. V. 2014. Microclimate mosaic and its influence on behaviour of the free-living African forest elephant (*Loxodonta africana cyclotis*). MSc Dissertation, University of the Witwaterand, Johannesburg.

- Laws, R. M. 1970a. Elephants and habitats in North Bunyoro, Uganda. *African Wildlife Journal*, 8: 163-180.
- Laws, R. M. 1970b. Elephants as agents of habitat and landscape change in East Africa. *Oikos*, 21: 1-15.
- Lee, P. C. 1987. Allomothering among African elephants. *Animal Behavior*, 35: 278-291.
- Leggett, K. E. A. 2008. Diurnal activities of the desert-dwelling elephants in northwestern Namibia. *Pachyderm*, 45 20-33.
- Lejoly, J. 1996. Biodiversité végétale dans le Parc National d'Odzala (Congo). Projet ECOFAC (Conservation et utilisation rationnelle des écosystèmes forestiers en Afrique Centrale) - Composante Congo, AGRECO-CTFT, Bruxelles. 127: 125-128.
- Li, H., and J. F. Reynolds. 1995. On definition and quantification of heterogeneity. *Oikos*, 73: 280- 284.
- Lillywhite, H. B., and B. R. Stein. 1987. Surface sculpturing and water retention of elephant skin. *Journal of Zoology*, 211: 727-734.
- Luck, C. P., and P. G. Wright. 1964. Aspects of the anatomy and physiology of the skin of the hippopotamus (*H. amphibius*). *Experimental Physiology*, 49: 1-14.
- Martin, P. H., and P. Bateson. 1986. *Measuring Behaviour* Cambridge University Press, Cambridge: 193-205
- Mathews, W. S., A. E. Van Wyk, N. Van Rooyen, and G. A. Botha. 2001. Vegetation of the Tembe Elephant Park, Maputaland, South Africa. *African Journal of Botany*, 67: 573–594.
- MCKay, G. M. 1973. Behaviour and ecology of the Asiatic Elephant in southeastern Ceylon. *Smithsonian Contributions to Zoology*, 125: 113-117.

- McNab, B. K. 1983. Energetics, body size and the limits to endothermy. *Journal of Zoology*, 199: 1-29.
- Mitchell, D. et al. 1997. Activity, blood temperature and brain temperature of free-ranging springbok. *Comparative Biochemistry and Physiology B*, 167: 335-343.
- Mitchell, G., and J. D. Skinner. 2004. Giraffe thermoregulation: a review. *Transactions of the Royal Society of South Africa*, 59: 109-118.
- Nellemann, C., R. M. Stein, and L. P. Rutina. 2002. Links between terrain characteristics and forage patterns in elephants (*Loxodonta africana*) in northern Botswana. *Journal of Tropical Ecology*, 18: 835–844.
- Nowell, A. A. 2005. Behavioural development in wild Western lowland gorillas (*Gorilla gorilla gorilla*). PhD Thesis, University of Liverpool.
- Nzoohe Dongmo, Z.-L. 2003. Suivi écologique dans le parc national de Lobéké et sa zone périphérique: Données de base sur la dynamique des populations de grands et moyens mammifères et des activités anthropiques, Rapport, WWF CPO, 220-227.
- Owen-Smith, R. N. 1988. Megaherbivores: The influence of Very Large Body Size on Ecology. Cambridge University Press, Cambridge: 22-48.
- Paine, R. T. 1995. A Conversation on Refining the Concept of Keystone Species. *Conservation Biology*, 9: 962-964.
- Parker, K. L., and C. T. Robbins. 1985. Thermoregulation in ungulates In: *Bioenergetics of wild herbivores*. ed. Hudson R.J. & White R.G. pp. 161-182. CRC Press Inc., Florida.
- Phillips, P. K., and J. E. Heath. 1992. Heat exchange by the pinna of African elephant (*Loxodonta africana*). *Comparative Biochemistry & Physiology*, 4: 693-699.

- Phillips, P. K., and J. E. Heath. 1995. Dependency of surface temperature regulation on body size in terrestrial mammals. *Journal of Thermal Biology*, 20: 281-289.
- Poole, J. H. 1987. Rutting Behaviour in African Elephants: the Phenomenon of Musth. *Behavior*, 102: 283-316.
- Porter, W. P., and D. M. Gates. 1969. Thermodynamic equilibria of animals with the environment. *Ecological Monographs*, 39: 227-244.
- Rees, P. A. 2002. Asian elephants (*Elephas maximus*) dust bathe in response to an increase in environmental temperature. *Journal of Thermal Biology*, 27: 353-358.
- Robertshaw, D. 2006. Mechanisms for control of respiratory evaporative heat loss in panting animals *Journal of Applied Physiology*, 101: 664-668.
- Root, T. L., and S. H. Schneider. 1995. Ecology and climate: research strategies and implications *Science*, 269: 334-341. .
- Rowe, M. F. 1999. Physiological Responses of African elephant to a cold environment: how does the elephant keeps its heat? , Louisiana State University.
- Ruggiero, R. G. 1992. Seasonal forage utilization by elephants in central Africa. *African Journal of Ecology*, 30: 137-148.
- Ruggiero, R. G., and J. M. Fay. 1994. Utilization of Termitarium soils by elephants and its ecological implications. *African Journal of Ecology*, 32.
- Saunders, S. C., J. Chen, T. R. Crow, and K. D. Brososfaske. 1998. Hierarchical relationship between landscape structure and temperature in managed forest landscape. *Landscape Ecology*, 13: 381-395.
- Schmidt-Nielsen, K. 1984. *Scaling: Why is Animal Size so Important?* Cambridge University Press, Cambridge, : 233-243.

- Schmidt-Nielsen, K. 1997. *Animal Physiology: Adaptation and Environment*, 5th edition. Cambridge University Press, Cambridge.
- Scholander, P. F. 1955. Evolution of Climatic Adaptation in Homeotherms. *Evolution*, 9: 15-26.
- Scholes, R. J., and B. H. Walker. 1993. *An African Savanna: Synthesis of the Nylsvley Study*. Cambridge University Press, Cambridge.
- Schulze, E.-D., H. A. Mooney, and W. J. Bond. 1994. Keystone Species. Springer Berlin Heidelberg 99: 237-253.
- Seely, M. K. 1978. The Namib dune desert: an unusual ecosystem. *Journal of Arid Environments*, 1: 117-128.
- Shannon, G., R. L. Mackey, and R. Slotow. 2013. Diet selection and seasonal dietary switch of a large sexually dimorphic herbivore. *Acta Oecologica*, 46: 48-55.
- Sikes, S. K. 1971. *The Natural History of the African elephant*. Weidenfeld and Nicolson, London.
- Sinclair, A. R. E. 1977. *The African Buffalo. A Study of Resource Limitation of Populations*. The University of Chicago Press, Chicago.
- Skinner, J. D., and C. T. Chimimba. 2005. *The Mammals of the Southern African Subregion*. Cambridge University Press, Cape Town, South Africa, .
- Smith, F. 1890. Histology of the Skin of the Elephant. *Journal of Anatomy and Physiology*, 24: 493-503.
- Spearman, R. I. C. 1970. The epidermis and its keratinisation in the African elephant, . *Zoologica Africana*, 5: 327-338.
- Spinage, C. A. 1968. A quantitative study of the daily activity of the Uganda deffassa waterbuck. *African Journal of Ecology*, 6: 89-93.

- Stokke, S., and J. T. Du Toit. 2002. Sexual Segregation in habitat use by elephants in Chobe National Park, Botswana. *African Journal of Ecology*, 40: 360-371.
- Sumner, R., J. Zolova, P. Kunc, I. Knizkova, and H. Burda. 2007. Pattern of surface temperature in two mole-rats (*Bathyergidae*) with different social systems as revealed by IR-thermography. *Physiology of Behaviour*, 92: 526-532.
- Taylor, C. R. 1969. The eland and the oryx. *Scientific American*, 220: 88-97.
- Taylor, C. R. 1970a. Strategies of temperature regulation: effect on evaporation in East African ungulates. *American Journal of Physiology*, 219: 1131 - 1135.
- Taylor, C. R., and C. P. Lyman. 1967. A comparative study of the environmental physiology of an East African antelope, the eland, and the Hereford steer. *Physical Zoology* 40.
- Tchamba, M. N., and P. M. Seme. 1993. Diet and feeding behaviour of the forest elephant in the Santchou Reserve, Cameroon. *African Journal of Ecology*, 31: 165-171.
- Turkalo, A. K., and J. M. Fay. 1995. Studying forest elephants by direct observations: preliminary results from the Dzanga clearing, Central African Republic. *Pachyderm*, 20: 45-54.
- Turkalo, A. K., and F. C. Kidjo. 1996. Le Statut des Éléphants du Parc National d'Odzala. Rapport final. Projet ECOFAC (Conservation et Utilisation Rationnelle des Écosystèmes Forestiers en Afrique Centrale) – Composante Congo. AGRECO-CTFT, Bruxelles: 42
- Tutin, C. E. G., and M. Fernandez. 1984. Nationwide census of gorilla (*Gorilla gorilla gorilla*) and chimpanzee (*Pan troglodytes troglodytes*) in Gabon. *American Journal of Primatology*, 6: 313-336.
- UNDP. 2002. Global Environmental Outlook-3. Earthscan, London.

- UNEP, IUCN, and TRAFFIC. 2013. Elephant in the Dust - The African Elephant Crisis. A Rapid Response Assessment Programme eds. C. Nellemann, R.K. Formo, J. Blanc, D. Skinner, T. Milliken and T.D. Meulenaer. Birkeland Trykkeri AS, Norway United Nation Environment Programme, GRID-Arendal
- UNPD. 2005. World Population Prospects: The 2005 Revision. United Nations. New York.
- Van Schaik, C. P., and M. Griffiths. 1996. Activity Periods of Indonesian Rain Forest Mammals. *Biotropica*, 28: 105-112.
- Vanleeuwe, H., and A. Gautier-Hion. 1998. Forest elephant paths and movements at the Odzala National Park, Congo: the role of clearings and *Marantaceae* forests. *African Journal of Ecology*, 36: 174-182.
- Verlinden, A., and I. K. N. Gavor. 1998. Satellite tracking of elephants in northern Botswana. *African Journal of Ecology*, 36: 105-116.
- Vernon, H. M. 1930. The Measurement of Radiant Heat in Relation to Human Comfort. *Journal of Physiology*, 70: 15-17.
- Viljoen, P. J. 1992. The desert elephants of Namibia In: Elephants: - Majestic Creatures of the Wild. South African Journal of Wildlife Research 131-133.
- Wachob, D. G. 1996. The Effect of Thermal Microclimate on Foraging Site Selection by Wintering Mountain Chickadees. *The Condor*, 98: 114-122.
- WCS. 1996. The Lobéké forest, southeast Cameroon. Summary of Activities Period 1988-1995, WCS, Yaounde, 217-222.
- Weissenböck, N. 2010. Thermoregulation of African (*Loxodonta africana*) and Asian (*Elephas maximus*) elephants: Heterothermy as an adaptation of living in hot climates, PhD Thesis, University of Vienna.

- White, L. J. T., C. E. G. Tutin, and M. Fernandez. 1993. Group composition and diet of forest elephants, *Loxodonta africana cyclotis* Matschie 1900, in the Lopé Reserve, Gabon. *African Journal of Ecology*, 31: 181-199.
- Williams, T. M. 1990. Heat transfer in elephants: thermal partitioning based on skin temperature profiles. *Journal of Zoology*, 222: 235-245.
- Willmer, P., G. Stone, and I. Johnston. 2005. *Environmental Physiology of Animals*, 2nd ed. Blackwell Science Publishing Ltd, Oxford, London.
- Wilson, E. O. 2008. *Sustaining life: How human health depends on biodiversity* Edited by Chivian, E. & Berstein, A. Oxford University Press, New York.
- Wright, P. G. 1984. Why do elephants flap their ears? *South African Journal of Zoology*, 19: 266-269.
- Wright, P. G., and C. P. Luck. 1984. Do elephants need to sweat? *South African Journal of Zoology*, 19: 270-274.
- Wronski, T., A. Apio, and M. Plath. 2006. Activity patterns of bushbuck (*Tragelaphus scriptus*) in Queen Elizabeth National Park. *Behavioural Processes*, 73: 333-341.
- WWF. 2006. Plan d'aménagement du parc national de Lobeke et de sa zone peripherique période d'exécution : 2006-2010, Ministère des Forêts et de la Faune, Cameroun.
- Wyatt, J. R., and S. K. Eltringham, . 1974. The daily activity of the elephant in the Rwenzori National Park, Uganda. *East African Wildlife Journal*, 12: 273-289.
- Young, K. D., and R. J. Van Aarde. 2010. Density as explanatory variable of movements and calf survival in savanna elephants across southern Africa. *Journal of Animal Ecology*, 79: 662-673.

APPENDICES

Table 5.1 Summarized results of two-way ANOVA of microclimatic variables in the open *bais* and under the forest canopy during the day and at night and for all five of my study sites in Lobeke NP, Cameroon.

			Open <i>bais</i> or under tree canopy			
Microclimatic variables			P value	Significance	F	Df
Open <i>bais</i> & under forest canopy	Day	<i>Tg</i>	0.9971	No	0.0329	1
Day & night			0.1038	No	2.771	4
Open <i>bais</i> & under forest canopy	Night	<i>Tg</i>	0.8688	No	0.3112	1
Day & night			0.4530	No	0.5747	4
Open <i>bais</i> & under forest canopy	Day	<i>Ta</i>	0.9844	No	9.008	1
Day & night			0.0046	Yes	9.008	4
Open <i>bais</i> & under forest canopy	Night	<i>Ta</i>	0.5022	No	0.850	1
Day & night			0.1379	No	2.930	4
Open <i>bais</i> & under forest canopy	Day	<i>Tg-Ta</i>	0.9592	No	0.1559	1
Day & night			0.2234	No	1.5290	4
Open <i>bais</i> & under tree canopy	Night	<i>Tg-Ta</i>	0.0070	Yes	4.1110	1
Day & night			0.1192	No	2.5360	4
Open <i>bais</i> & under forest canopy	Day	VP	0.6153	No	0.6720	1
Day & night			0.8492	No	0.0360	4
Open <i>bais</i> & under forest canopy	Night	VP	0.5871	No	0.71430	1

Day & night			0.8963	No	0.01721	4
Open <i>bais</i> & under tree canopy	Day	WS	<0.0001	Yes	0.7390	1
Day & night			3.3306	No	0.9698	4
Open <i>bais</i> & under forest canopy	Night	WS	0.0045	Yes	2.684	1
Day & night			0.0004	Yes	15.23	4

T_g = globe temperature, T_a = dry-bulb air temperature, T_g-T_a = difference in globe and dry-bulb air temperature, VP = water vapour pressure of air, WS =wind speed. $P<0.05$ = significant difference between mean microclimatic variables, F = signifies the effects, Df =degree of freedom.

Table 5.2A Summary of the associations between the mean *Tg*, *Ta* and *VP* of air and the mean time my elephants spent per activity in Lobeke NP, Cameroon.

Activity	<i>Tg</i> in <i>bais</i>	<i>Ta</i> in <i>bais</i>	<i>VP</i> in <i>bais</i>	<i>WS</i> in <i>bais</i>
Walking	n=19 r ² =0.0638 p=0.3282	n=19 r ² =0.0419 p=0.4307	n=19 r ² =0.2011 p=0.0710	n=19 r ² =0.0011 p=0.9017
Foraging	n=19 r ² =0.0628 p=0.3009	n=19 r ² =0.0236 p=0.5560	n=19 r ² =0.0694 p=0.3070	n=19 r ² =0.0475 p=0.4007
Shade-seeking	n=19 r ² =0.5251 p=0.0655	n=19 r ² =0.7667 p=0.0098	n=19 r ² =0.2050 p=0.8155	n=19 r ² =0.0028 p=0.8935
Ear-flapping	n=19 r ² =0.3015 P<0.0125	n=19 r ² =0.6099 p=0.0002	n=19 r ² =0.051 p=0.3501	n=19 r ² =0.0880 p=0.2478
Dust-bathing	n=6 r ² =0.4732 P=0.0154	n=6 r ² =0.6321 p=0.0587	n=6 r ² =0.0510 p=0.6669	n=6 r ² =0.1485 p=0.3932
Water related activity	n=19 r ² =0.1254 p=0.2854	n=19 r ² =0.1164 p=0.3044	n=19 r ² =0.0237 p=0.6326	n=19 r ² =0.0001 p=0.9820

Table 5.2B Summary of the associations between microclimate and elephant behaviour under forest canopy for all my study sites Lobeke NP, Cameroon

Activity	<i>Tg</i> under tree canopy	<i>Ta</i> under tree canopy	<i>VP</i> under tree canopy	<i>WS</i> under tree canopy
Walking	n=5 r ² =0.0285 p=0.5174	n=5 r ² =0.0267 p=0.5308	n=5 r ² =0.0030 p=0.8340	n=5 r ² =0.0050 p=0.7889
Foraging	n=5 r ² =0.0193 p=0.5953	n=5 r ² =0.03048 p=0.50270	n=5 r ² =0.0104 p=0.6975	n=5 r ² =0.0084 p=0.7266
Shade-seeking	n=6 r ² =0.8045 p=0.0154	n=6 r ² =0.7436 p=0.0125	n=6 r ² =0.0194 p=0.7659	n=6 r ² =0.0767 p=0.4385
Ear-flapping	n=5 r ² =0.0116 p=0.6806	n=5 r ² =0.0196 p=0.5919	n=5 r ² =0.0020 p=0.8654	n=5 r ² =0.0020 p=0.8633
Dust-bathing	n=3 r ² =0.2656 p=0.0688	n=3 r ² =0.226 p=0.0657	n=3 r ² =0.2592 p=0.3023	n=3 r ² =0.0291 p=0.7464
Water related activity	n=3 r ² =0.0062 p=0.8106	n=3 r ² =0.0135 p=0.7191	n=3 r ² =0.0045 p=0.8538	n=3 r ² =0.1301 p=0.3059

Tg=globe temperature, *Ta*=dry-bulb temperature, *VP*= water vapour pressure air, *WP*= wind speed (Note wind speed was the only mean microclimate variable that was significantly different study sites).