

# Behavioural thermoregulation in free-ranging savanna elephants

*(Loxodonta africana)*

By

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# Behavioural thermoregulation in free-ranging savanna elephants

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## ABSTRACT

Savanna elephants currently inhabit some of the hottest environments in Africa. Because of climate change, these environments are likely to get hotter. Due to their large body size and small body surface area to volume ratio, elephants may face difficulties in dissipating heat. Despite this suggestion, we do not understand how elephants in their natural environment respond to present day climatic extremes, which limits our ability to predict how elephants may respond to climate change.

The goal of my study was to quantify behavioural responses of elephants to environmental temperature and to investigate the thermal benefits thereof. In so doing, I aimed to assess the potential consequences of environmental temperature on habitat selection and individual fitness, as well as their ability to adapt to climate change. I used continuous behavioural observations and ambulatory temperature recording devices to quantify and assess daytime behavioural responses to environmental temperature in seven tame, free-ranging savanna elephants in Botswana's Okavango Delta. The elephants were unrestrained and free to roam in their natural environment.

I found that environmental temperature played a significant role in dictating elephant behaviour within a day. At about 30°C, elephants adjusted their behaviour aimed at reducing environmental heat loads and increasing heat dissipation (e.g. shade use, wetting behaviour). I further found that resting increased and feeding decreased with environmental temperature. Age was not a significant factor dictating elephant behaviour. However, the presence of a suckling calf influenced family group behaviour by increasing the probability of shade use and decreasing the probability of walking.

The clear flexible ability of elephants to respond behaviourally to present day environmental temperatures is a promising observation in the face of climate change. However, I suggest

that environmental temperature is likely a key determinant of habitat selection and space use in elephants that may have potential consequences for calf survival, sexual segregation and individual fitness. Further investigation of these consequences is warranted.

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## **DISCLAIMER**

I, Michael Austin Mole declare that the thesis, which I hereby submit for the degree *Magister Scientiae* (Zoology) at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.



Michael Austin Mole

September 2014

## **ETHICAL CLEARANCE**

The procedures used in this thesis were approved by the Animal Use and Care Committee of the University of Pretoria, under the reference EC072-12 on the 8<sup>th</sup> of August 2012.

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## CHAPTER 1. GENERAL INTRODUCTION

### 1.1 BACKGROUND AND RATIONALE

Global temperatures are rising (Salinger 2005; Collins et al. 2013; Coumou et al. 2013; Diffenbaugh and Field 2013). In sub-Saharan Africa, conditions are becoming hotter and for most parts drier (Hulme et al. 2001; New et al. 2006; James and Washington 2013; Nicholson et al. 2013). Climate change will have an effect on biodiversity at all levels, with predicted impacts influencing individuals, populations and ecosystems (Bellard et al. 2012; Gaillard et al. 2013; Willis et al. 2013; Garcia et al. 2014). While in some cases climate change may be beneficial for biodiversity (Walther et al. 2002), the majority of species are likely to be negatively affected. Consequently, there is concern for how species will respond and if they can adapt (Moritz and Agudo 2013; McCain and King 2014).

Maximum surface temperatures are predicted to rise in the next 55 years across southern Africa (Figure 1a). This predicted trend raises concern for savanna elephants, which due to their large body size and small body surface area to volume ratio may face difficulties in dissipating metabolic heat and keeping cool (Schmidt-Nielson 1984; Phillips and Heath 1995; Rowe et al. 2013). Predicted increases of up to 4°C taking place in already extremely hot environments such as northern Botswana (Figure 1b, c) stand to influence at least 130 000 savanna elephants that inhabit that region (Chase 2011). How will these elephants respond to climate change and can they adapt?

A species' phenotypic plasticity or the ability for a species to change physiologically or behaviourally to the environment within a lifetime (Price et al. 2003) ultimately will dictate its ability to persist in a changing environment (Charmantier et al. 2008; Bellard et al. 2012; Moritz and Agudo 2013). Understanding a species' ability to adapt to present day climatic extremes through physiological and behavioural adjustments can give us insights



into how a species may respond and adapt to future climate change. At present, savanna elephants are widely distributed across large parts of southern Africa where thermal conditions vary greatly, implying that they have a broad thermal tolerance (Figure 1b, c). In these areas, air temperatures fluctuate much within and between days (Figure 1b, c). For example, in Kruger National Park, temperatures within a year range from 0-43°C, and within a day as much as 30°C (Figure 1c). In northern Botswana, air temperatures are more extreme, with periods during the year when air temperatures exceed 35°C for up to 8 hours of the day (Figure 1c). Thermoregulatory adjustments, both physiological and behavioural, are likely crucial for elephants to persist in these environments. However, until recently most studies on thermoregulation in elephants were conducted on captive elephants under conditions where they were exposed to moderate environmental temperatures (*see section 1.2 below*). Furthermore, studies on elephant behaviour in direct response to environmental temperature are lacking.

Temperature-induced behavioural adjustments may involve various costs, costs that do not necessarily outweigh the costs of not adjusting, but none-the-less have detrimental effects on an individual's fitness (van Beest et al. 2012; van Beest and Milner 2013). From a broad ecological perspective, environmental temperature can have consequences for how animals use resources across space and time, which may have consequences for individual fitness as a direct effect of trade-offs (du Plessis et al. 2012; van Beest et al. 2012; van Beest and Milner 2013; Long et al. 2014). For example, behaviour employed by an animal for thermoregulation may alter habitat selection and activity patterns, which may decrease feeding time (Belovsky and Slade 1986) or induce trade-offs in forage availability and quality (van Beest et al. 2012; Long et al. 2014). In Alpine ibex (*Capra ibex*) for example, increased environmental temperatures induce altitudinal migration to higher elevations, influencing foraging and movement (Aublet et al. 2009) and in moose (*Alces alces*), the selection of

forested habitats for thermoregulatory reasons can lead to decreased foraging opportunities through reduced forage availability in thermally suitable habitats (van Beest et al. 2012). If individuals are unable to compensate for thermoregulatory costs on foraging, fitness costs may arise (van Beest and Milner 2013).

We know that at a coarse spatial scale, elephants select habitats that are close to water, relatively high in primary productivity, and far from people (Harris et al. 2008; Young et al. 2009; Roeber et al. 2012). However, the influence of climate, particularly at the individual level, has yet to be investigated. Elephants use a landscape in a heterogeneous manner (Duffy et al. 2011). Recognising factors which alter behaviour and consequently spatial use patterns, is important in understanding the impact that elephants may have for other species (Brits et al. 2002; de Beer et al. 2006; Chamailé-Jammes et al. 2007; Guldemond and van Aarde 2008; Vanak et al. 2010) and for the survival of their young (Young and van Aarde 2010). Therefore, it is necessary to further our understanding of the influence of climate on behaviour in elephants.

Temperature effects on behaviour, and consequently related trade-offs and fitness, are likely to rise in the face of climate change (du Plessis et al. 2012; van Beest and Milner 2013). Quantifying behavioural thermoregulation in elephants may greatly enhance our knowledge of how climate change will influence individuals and likely populations.

## **1.2 THERMOREGULATION IN ELEPHANTS**

### **1.2.1 *Heat exchange and thermoregulation***

Studies on the core temperature profiles of captive and semi-captive elephants report that they are homeothermic endotherms able to maintain core temperatures that fluctuate

consistently within a 2°C range over the course of 24 hours, with a mean between 36 and 37°C (Kinahan et al. 2007b; Hidden 2009; Weissenböck et al. 2012). For an animal to maintain thermal homeostasis, a balance must exist between the amount of heat that is gained from metabolic heat production and the environment, and the amount of heat that is lost to the environment (Porter and Gates 1969). If an animal fails to dissipate excess heat to the environment, a rise in core temperature will take place that may be detrimental for an individual.

Heat exchange between an animal and its environment can take place through evaporative and non-evaporative pathways (Porter and Gates 1969; Bligh 1973). Elephants rely on both of these pathways (Williams 1990, Dunkin et al. 2013). Non-evaporative heat flow takes place along a thermal gradient from high to low temperatures via radiation, convection and conduction and is affected by the climatic space (radiation, air temperature, wind speed, air density) an animal finds itself in (Porter and Gates 1969). For heat exchange to take place through non-evaporative pathways, a thermal gradient must exist between the body surface (skin) of an animal and the environment (Porter and Gates 1969). For example, for convective or radiative heat flow to take place from the body to the environment, a temperature difference between skin and surrounding air or radiative temperature must exist (Porter and Gates 1969). It is important to note that radiation may be absorbed from a number of different sources in the environment as direct or reflected radiation (Porter and Gates 1969). If air temperatures are lower than skin temperature, heat will still be gained via radiation if radiant temperatures are higher than skin temperature.

To regulate non-evaporative heat flow with the environment, animals may employ either autonomic or behavioural thermoregulatory responses. (Bligh 1973). However, when air or mean radiant temperatures (from this point referred to as environmental temperatures)

are greater than skin temperature, heat can no longer be lost through non-evaporative pathways and animals become dependent on dissipating heat through evaporation (*discussed in section 1.2.2*).

### **1.2.2 *Autonomic responses***

#### *Vasomotor control*

The control of blood flow to the skin tissue is a common autonomic response in endotherms to increase or decrease non-evaporative heat loss (Bligh 1973). Through vasodilation, increased blood flow to the skin layer increases skin temperature, thus, raising or reducing the thermal gradient between the skin and the environment (Bligh 1973). It is well documented that elephants rely on the control of blood flow to their ears for heat loss (Buss and Estes 1971; Wright 1984; Phillips and Heath 1992; Weissenböck et al. 2010). An elephant's ears are well-equipped organs for thermoregulation as they are highly vascularised and have a large surface area to volume ratio in comparison to the rest of the body (Sikes 1971). By controlling blood flow through the ears, heat can be lost through radiation or convection at low environmental temperatures (Wright 1984; Phillips and Heath 1992). Elephants are also known to increase ear flapping rates in response to a rise in environmental temperature (Buss and Estes 1971, Hidden 2009). Flapping will increase air flow across the ears, which increases convective heat loss and evaporative heat loss. Vasomotor control may not be restricted to the ears; Weissenböck et al. (2010) suggest that blood flow can also be controlled to other parts of the body from which heat can be dissipated.

Vasodilation of blood vessels can increase non-evaporative heat dissipation as long as a thermal gradient between the skin and environment exists. However, savanna elephants inhabit environments where environmental temperatures can exceed 36°C (Figure 1c). If environmental temperatures exceed skin temperature, the animal will gain heat from the

environment (Porter and Gates 1969) and will then have to rely on evaporative heat loss to dissipate metabolic heat and heat gained from the environment by convection and radiation (Bligh 1973).

### *Evaporative cooling*

Evaporation of water from the skin or other body surfaces allows body heat to be dissipated in the absence of a thermal gradient (Bligh 1973). Elephants lack sweat glands and therefore do not sweat (Lillywhite and Stein 1987). However, studies on captive elephants report that they employ evaporative cooling without sweating, through the passive diffusion of water through their skin and through their respiratory tracts (Wright and Luck 1984; Dunkin et al. 2013). An elephant's skin is highly permeable to water (Dunkin 2012) and the rate of cutaneous water loss in elephants may be greater than that of any other large endotherm (Dunkin et al. 2013), with 75-100% of an elephant's heat loss requirements capable of being met through cutaneous and respiratory water loss (Wright and Luck 1984; Dunkin et al. 2013). However, it must be noted that these studies of water loss (Wright and Luck 1984; Dunkin et al. 2013) were conducted in captive conditions at air temperatures below 36°C.

Cutaneous evaporative water loss (CEWL) is an obligatory process ultimately driven by a number of environmental and physiological factors (Dunkin et al. 2013). The rate of CEWL increases with water vapour pressure saturation deficit and with the temperature and hydration of the skin (Dunkin et al. 2013). In extreme hot thermal environments, Dunkin et al. (2013) suggest that elephants may lose up to 100l of water per day through CEWL and respiratory evaporative water loss. CEWL is therefore costly in terms of water loss and relies on the replenishment of body water. If water is not readily available for elephants they may face difficulties in maintaining required rates of CEWL for sufficient heat dissipation.

## *Heat storage*

By storing heat during the day and dissipating it through non-evaporative pathways during cooler environmental temperatures at night, animals can conserve water that would otherwise be lost by serving the needs of evaporative heat loss during high environmental temperatures (Schmidt-Nielson et al. 1957). Such storage of heat results in heterothermy, the variation of core temperature that exceeds the limits of homeothermy (IUPS Thermal Commission 2001). Heterothermy has been suggested to be a crucial thermoregulatory adaptation for the survival of large endotherms inhabiting thermally and water-stressed environments (Mitchell et al. 2002; Mitchell et al. 2009; Hetem et al. 2010; Hetem et al. 2011a; Fuller et al. 2014).

It has been suggested that elephants may too rely on heat storage, and therefore heterothermy, for thermoregulation in hot environments (Elder and Rodgers 1975; Hiley 1975; Weissenböck et al. 2012). Continuous 24-hour recordings of core temperature are required to detect heterothermy in animals. Only three studies have successfully recorded daily core temperature rhythms in elephants, two in savanna elephants (captive, Kinahan et al. 2007b; semi-captive, Hidden 2009) and one in captive Asian elephants (*Elephas maximus*, Weissenböck et al. 2012). During these studies, the elephants maintained a relatively stable core temperature between 36 and 37°C, with a clear 24h core temperature pattern where temperatures increased during the day and decreased at night. Neither Kinahan et al. (2007b) nor Hidden (2009) found evidence to support heterothermy in savanna elephants as fluctuations in daily core temperature were observed (0.8°C, Kinahan et al. 2007b; 1.2°C, Hidden 2009) that were much smaller than those evident in heterothermic mammals (Hetem et al. 2010). Furthermore, core temperatures were independent of environmental temperatures. However, Weissenböck et al. (2012) concluded that Asian elephants do employ

heterothermy based on their findings that Asian elephants in Thailand had a daily core temperature range of 1.15°C (mean) where mean ambient temperatures were ~30°C compared to a range of 0.51°C in Asian elephants located in Germany where mean ambient temperatures were ~21°C. While these findings may imply heterothermy, the studies were conducted on captive zoo elephants from two very different locations with different housing conditions. It remains to be investigated whether elephants in their natural environment under thermally stressed conditions employ heterothermy.

### **1.2.3 Behavioural responses**

With the exception of Hidden (2009) who conducted a study on semi-captive elephants in their natural environment, all other studies on elephant thermoregulation have been conducted on captive elephants, which is a major shortcoming. In captive situations animals are unlikely to employ a full range of behavioural responses due to spatial and resource constraints and therefore are more dependent on autonomic responses to regulate temperature, while free-ranging animals may be less dependent on autonomic responses (Mitchell et al. 2002; Fuller et al. 2004).

In most cases, behavioural thermoregulation is a primary response to unfavourable thermal conditions because it can offset the costs of autonomic thermoregulation and it can be employed for longer durations of time (Bartholomew 1964; Bligh 1973; Hetem et al. 2012). Furthermore, behavioural responses in general are initiated by changes in skin temperature sensed by peripheral thermoreceptors (Roberts 1998), while autonomic responses are initiated more strongly by changes in core temperature sensed by core thermoreceptors (Jessen 1981). As such, because changes in skin temperature take place more rapidly than changes in core temperature, behavioural responses often are initiated before a more costly autonomic response and an autonomic response will thereafter be initiated if a behavioural response is

ineffective in regulating core temperature (Frank 1999, Bulcao et al. 2000; Romanovsky 2007).

The need to maintain thermal comfort, a perceived feeling of comfort within a surrounding thermal environment may also drive behavioural decisions (Gagge et al. 1967; Frank 1999; Bulcao et al. 2000), but these behavioural decisions may not necessarily be a thermoregulatory response but rather a hedonistic response. In humans and likely most mammals, thermal comfort is largely perceived by changes in skin temperature (Frank 1999) and is responsible for initiating a behavioural response that may have thermoregulatory benefits (Gagge et al. 1967; Frank 1999; Bulcao et al. 2000). For animals, we have no way of knowing what they may be feeling in terms of comfort; therefore, caution must be taken when investigating behavioural thermoregulatory responses in animals as any behavioural response to environmental temperature may not be for thermoregulation directly but rather for comfort.

### *Microclimate selection*

A common form of behavioural thermoregulation in large endotherms is the selection of favourable microclimates to reduce heat gain from the environment. Varied vegetation structure and topography within a habitat provides heterogeneous microclimates that an animal can actively occupy to avoid unfavourable macroclimatic conditions (Suggitt et al. 2011). The mobility of most endotherms allows them to select microclimates within a habitat (Porter and Gates 1969). Small endotherms in particular are able to seek refuge underground and in other small microhabitats (Buffenstein 1984; Lagos et al. 1995; Fick et al. 2009). However, large endotherms, particularly elephants, are limited to only a few suitable microclimates which can accommodate their size while at the same time potentially fulfil their thermal requirements. Trees and the shade they provide serve as one such microclimate.



The use of shade in large endotherms is a commonly documented behaviour and is associated with increased environmental temperatures during the heat of the day (Taylor and Lyman 1967; Leuthold 1977; Fuller et al. 1999; Ostrowski et al. 2003; Matson et al. 2005; Hetem et al. 2007; Cain et al. 2008; Hetem et al. 2011a; Hetem et al. 2011b). Trees reduce local solar radiation, alter ground temperature, modify wind, and to some degree alter air temperature and relative humidity levels within and under canopies (Valtorta et al. 1997; Kotzen 2003; Langman et al. 2003; Cain et al. 2008). Both solar and reflected radiation from the ground and other surfaces may be a major source of heat gain for large animals (Bond et al. 1967; Porter and Gates 1969; Kamau and Maloiy 1985; Norris et al. 2010). The reduction of local radiation is therefore a major thermal benefit provided by trees as it reduces the amount of radiant heat load an animal may experience, thus providing reduced heat gain (Kelly et al. 1954; Bond et al. 1967; Blackshaw and Blackshaw 1994; Valtorta et al. 1997).

Radiation is a large source of heat gain in elephants (Hiley 1975), and while to my knowledge the thermoregulatory advantages of shade for elephants have not been investigated, it has been suggested that shade utilisation may be an important behavioural thermoregulatory response in elephants (Sikes 1971; Hiley 1975; Kinahan et al. 2007a). Researchers studying behaviour of elephants in their natural environment have observed shade utilisation taking place during the middle hours of the day (Guy 1976; Leggett 2009). However, these studies did not quantify shade utilisation in direct response to environmental temperature.

Perhaps the most convincing study inferring shade utilisation in direct response to temperature comes from Kinahan et al. (2007a) who recorded spatial use patterns in elephants. At habitat level, Kinahan et al. (2007a) found that elephants selected habitats based on the rate at which ambient temperatures changed, selecting densely covered habitats that

increased in temperature more slowly during the day. Furthermore, several studies have postulated that the selection of dense cover habitat or riverine habitat by elephants may be driven by shade seeking (Buss 1961; Shannon et al. 2009; Roever et al. 2012).

### *Water-related activities*

A number of studies suggest that water-related activities such as mud bathing, swimming and splashing are of thermoregulatory importance for elephants (Wright and Luck 1974; Hiley 1975; Hidden 2009; Dunkin et al. 2013). Like shade utilisation, water-related activities have commonly been observed in elephants in the wild (Jarman 1972; Guy 1976; Leggett 2009), although poorly documented in direct response to environmental temperature.

Mud bathing as a thermoregulatory response has been extensively studied in pigs (Bracke 2011), which like elephants lack operative sweat glands (Ingram 1965). Pigs increase mud bathing behaviour when environmental temperatures increase (Ingram 1965; Huynh et al. 2007, Bracke 2011). Wetting the skin not only provides an immediate cooling effect but also enhances evaporative heat loss, which is particularly effective at high environmental temperatures (Ingram 1965; Gebremedhin and Wu 2001; Huynh et al. 2007). Following mud bathing, mud left on the skin also prolongs evaporative cooling for up to 2h (Ingram 1965).

Similar to studies on pigs, studies conducted on captive savanna elephants found that evaporative heat loss is greatest from wet skin, providing evidence that water-related activities are a thermoregulatory response (Dunkin et al. 2013). Furthermore, the highly wrinkled skin of elephants enhances water retention and the adherence of mud for extended periods of time (Lillywhite and Stein 1987). However, thermoregulation may not be the only reason for mud bathing in animals; other reasons for mud bathing include skin care and health (*see* Bracke 2011).

Other than spraying water or mud on the skin's surface, dust bathing is another behaviour commonly observed in elephants (Leggett 2009). Only one study has ever investigated dust bathing as a potential thermoregulatory response in elephants (Rees 2002). Rees (2002) found that captive Asian elephants increased dust bathing in response to an increase in environmental temperature and suggested that it was a thermoregulatory response. A study on baboons (*Papio hamadryas ursinus*) in the Namib Desert has shown evidence that sand bathing can influence core temperature (Brain and Mitchell 1999). While dust bathing may be a thermoregulatory response for elephants, other reasons for dust bathing such as skin care or protection from insects cannot be ruled out without further investigation (Rees 2002).

#### *Adjustments in activity*

It is important to include behavioural thermoregulation in the context of overall behavioural patterns. A marked decrease in activity (e.g. feeding, walking) often is observed at high environmental temperatures, as documented in a number of large endothermic species (Owen-Smith 1998; Belovsky and Slade 1986; Ostrowski et al. 2003; Maloney et al. 2005; Hetem et al. 2011a; Owen-Smith and Goodall 2014). Active behaviour such as feeding can increase metabolic heat load, as documented in cattle (Mader et al. 2002), likewise in captive elephants during activities such as walking (Rowe et al. 2013). Therefore, it is likely that a decrease in activity can provide a thermoregulatory advantage by reducing metabolic heat load.

Elephants in the wild have been observed to spend less time feeding and more time resting during midday as opposed to the cooler hours of the day (Wyatt and Eltringham 1974; Guy 1976; Shannon et al. 2008; Leggett 2009). Furthermore, periods of resting are often associated with shade utilisation (Leggett 2009). Daily displacement patterns of elephants also indicate that walking takes place more often in the morning and late afternoon hours

(Loarie et al. 2009) with a marked decrease in walking taking place during midday, particularly during the hottest times of the year (Loarie et al. 2009; Leggett 2010).

To compensate for lost time in foraging and reduce the costs of feeding during the heat, some species shift their activity to night time, as observed in the Arabian oryx (*Oryx leucoryx*, Ostrowski et al. 2003; Hetem et al. 2011a) and black wildebeest (Maloney et al. 2005). While there is no direct evidence to indicate that elephants shift activity to night in response to environmental temperature, daily displacement patterns of elephants have shown activity to be greater at night during the hottest times of the year than during the cooler times of the year (Loarie et al. 2009; Leggett 2010).

### **1.3 CONCLUSIONS**

What we know about thermoregulation in elephants mostly stems from studies conducted on captive elephants at relatively mild temperatures. From these studies, we know that at mild environmental temperatures, elephants are likely capable of maintaining thermal homeostasis through non-evaporative heat loss (Williams 1990) but at high environmental temperatures, non-evaporative heat loss becomes impaired through reduced or reversed thermal gradients (Dunkin et al. 2013). While Dunkin et al. (2013) suggest that cutaneous evaporative water loss can fulfil heat loss requirements at high environmental temperatures, we do not know if elephants can be solely dependent on cutaneous evaporative water loss as it entails substantial water loss costs (Dunkin et al. 2013). Furthermore, there is very little evidence indicating that elephants rely on heterothermy (Hidden 2009).

In each of the above studies behavioural thermoregulation was restricted or overlooked (Williams 1990; Hidden 2009; Dunkin et al. 2013). Behavioural thermoregulation is likely a primary response to reduce heat gain and reduce heat loss from the environment

(e.g. shade utilisation) and increase forms of evaporative cooling (e.g. mud bathing), thereby reducing the onset as well as the costs of autonomic responses. Ample evidence from behavioural observations on wild elephants indicates that elephants do adjust behaviour in response to environmental temperature; however, no study to my knowledge has directly quantified elephant behaviour in response to environmental temperature. As a result, the direct (e.g. reduced feeding activity) and indirect consequences (e.g. reduced individual fitness) of temperature-induced behavioural adjustments for elephants are unknown and consequently we lack an understanding of how elephants may respond to future predicted climate change.

#### **1.4 DISSERTATION AIMS**

Ultimately, the goal of my study was to gain a mechanistic understanding of how elephants respond behaviourally to environmental temperature and in doing so, assess and discuss the potential consequences of environmental temperature on elephant behaviour, space use, and individual fitness as well as the ability for elephants to adapt to changes in future climate. To fit this theme, the study was conducted in the Okavango delta located in northern Botswana where ambient temperatures often reach and exceed elephant body core temperature (about 36°C, Figure 1c), a region that is currently inhabited by a large population of savanna elephants (Chase 2011), and a region that is predicted to have an increase of around 4°C in maximum surface temperatures by the year 2070 (Figure 1a).

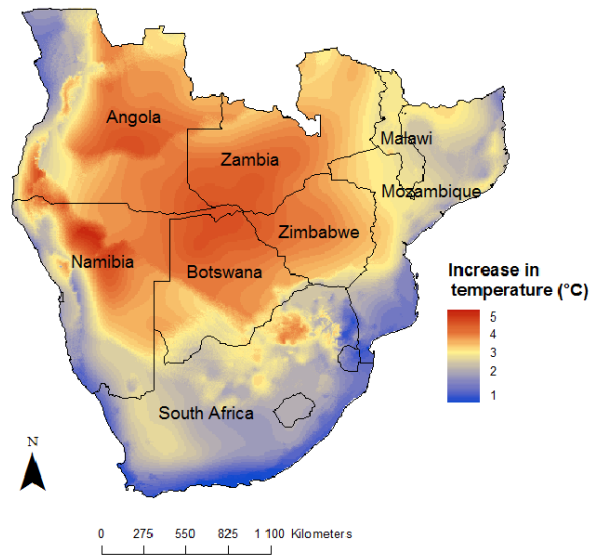
The bulk of my dissertation is contained in two data chapters (Chapter 3 and 4). In Chapter 3, I aimed to quantify behavioural responses of elephants to environmental temperature. I also investigated whether behavioural responses differed over time of day,

between seasons of varying average temperatures, between individuals of different age, and between family groups that differ in demographic structure.

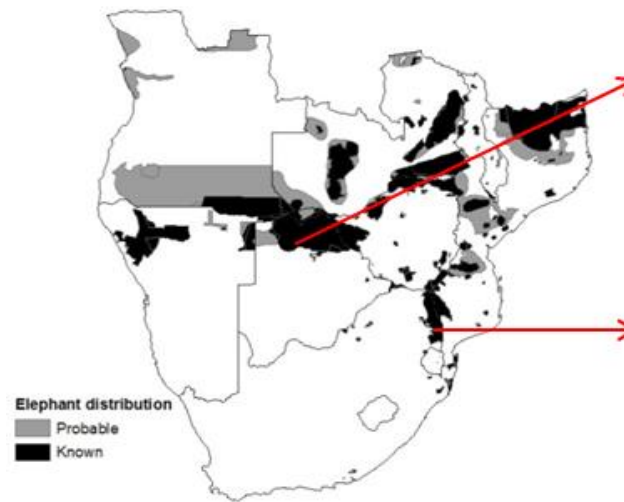
Furthermore, due to limited investigations of behavioural thermoregulation in free-ranging elephants, there is a lack of understanding relating to the thermal benefits that behavioural adjustments such as shade utilisation and water-related activities may provide. Therefore, in Chapter 4 I aimed to investigate the thermal benefits of thermoregulatory behaviour in elephants using ambulatory black mini-globe temperature recording devices (Hetem et al. 2007) placed on the collars of elephants while they traversed in their natural environment, as well as an infrared thermal imaging camera to obtain skin temperature measurements. In this way, the thermal environment the elephants experienced within their habitat and during specific behavioural adjustments was recorded and assessed. From the data obtained from the ambulatory temperature recording devices, I also aimed to identify a critical environmental temperature at which elephants initiate behavioural responses such as shade utilisation and water-related activities (e.g. mud bathing, swimming, splashing).

### 1.5 FIGURE

a. Predicted increase in maximum surface temperatures by 2070



b. Present day elephant distribution



c. Hourly air temperature for the year 2013

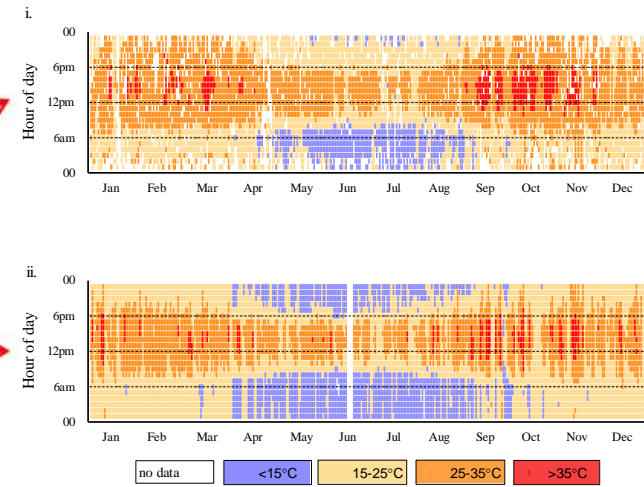


Figure 1.1. a) Predicted increase in maximum surface temperatures across southern Africa by the year 2070 (data source: [www.worldclim.org](http://www.worldclim.org)). b) Known and probable present day savanna elephant distribution across southern Africa (data source: [www.elephantdatabase.org](http://www.elephantdatabase.org)). c) Hourly air temperature for the year 2013 at: i) Maun, bordering the Okavango Delta in Botswana (Botswana Meteorological Services; data source: <http://mesonet.agron.iastate.edu>), and ii) Skukuza, Kruger National Park, South Africa (South African Weather Services; data source: <http://mesonet.agron.iastate.edu>).

## CHAPTER 2. GENERAL MATERIALS AND METHODS

### 2.1 INTRODUCTION

This chapter provides general information regarding the study site and animals. It also provides the methods that were common throughout Chapters 3 and 4, namely: methods followed to record behaviour and prevailing weather conditions. Methods related exclusively to Chapters 3 or 4 are included in the relevant chapters.

### 2.2 STUDY SITE

The study took place in Botswana's Okavango Delta within the vicinity of Abu camp (S19°25'00.3"; E22°35'03.6"), located in block 26 of the Ngamiland district (NG26; Figure 2.1). The Okavango Delta is an inland delta consisting of a wetland approximately 12 000 km<sup>2</sup> in area (McCarthy and Ellery 1998) situated across an alluvial fan up to 40 000 km<sup>2</sup> in size (McCarthy et al. 2003). The NG26 concession (~1853 km<sup>2</sup>) is a photographic non-consumptive wildlife management area used solely for tourist activities, situated in the lower west region of the alluvial fan of the delta (Figure 2.1). This region undergoes seasonal flooding with peak flood levels occurring between May and September, which gradually recede to a low between November and March (McCarthy et al. 2003). Conventionally, the dry season (period of low rainfall) extends from May-October and the wet season from November-April. The present study took place during the dry season during two periods, the hot-dry season in 2012 (September-November) and the cool-flood season in 2013 (May-July). During the entire study period, floodwater was present, although at different flood levels.



The landscape consists of seasonal swamps with associated flood plains and small to large islands (Figure 2.2). Open savanna type habitat with scattered terminalia thicket (*Terminalia sericea*) and mopane woodlands (*Colophospermum mopane*) dominate the islands. Floodplains and islands are lined with strips of riparian vegetation, providing plentiful shade. Large tree species scattered across the islands and within the riparian vegetation include jackalberry (*Diospyros mespiliformis*), sausage tree (*Kigelia africana*), knob thorn (*Acacia nigrescens*), mongostene (*Garcinia livingstonei*), marula (*Schlerocarya birrea*), leadwood (*Combretum imberbe*) and a number of *Ficus* spp.

Monthly air temperatures in the region range between a mean daily minimum of 8°C in June and mean maximum daily temperature of 36°C in October. However, extreme daily temperatures of -3°C and up to 41°C have been recorded in the past (Botswana Meteorological Services, Maun, 2012).

## 2.3 STUDY ANIMALS

A herd of seven tame, semi-captive savanna elephants (*Loxodonta africana*) were used for the present study (Table 2.1, elephant identity and physical characteristics). The elephants belonged to Abu Camp for the purpose of elephant-guest activities and were trained to obey commands from an elephant handler. The herd consisted of three adult females, three weaned calves (one male and two females) and one female suckling calf. The herd furthermore comprised of two family groups (Table 2.1). The two family groups were not closely associated due to unstable social dynamics, spending majority of the day separated. The elephants have been in captivity for majority of their lives. However, over the past few years, previous individuals belonging to this herd have been successfully

reintroduced into the wild and now roam within the concession and the greater Okavango Delta (Evans et al. 2013a; 2013b).

At night the elephants were housed unrestrained in an outdoor boma (50m x 40m enclosure). The boma did not have a shelter for the elephants but there were a number of palm trees within the boma and overhanging branches from trees growing along the outer edges. During the day, the elephants followed a routine that began at sunrise with tourist activities (approximately 2h in duration). The tourist activities consisted of elephant-back safaris or bush walks with guests on foot from the boma to a designated meeting point in the bush. There were at least 12 different meeting points at various locations in the bush, all within a 3km radius of the camp. Following the morning activities, the elephants remained out in the bush and were allowed to roam freely through the bush. Two elephant handlers remained with the elephants keeping an eye on them for safety reasons. During this roaming period, the elephants were free to respond to all environmental conditions and physiological requirements as needed. Furthermore, they were free to interact and socialise with wild elephants. After approximately 16:00 in the afternoon, the elephants were rounded up and moved back to the same meeting point for afternoon tourist activities. The afternoon activities consisted of elephant back safaris or bush walks with guests on foot back to the boma. During the day, the elephants were able to forage for their own food, this was not the case at night and instead the elephants were provided with freshly cut mopani or terminalia foliage in their boma. Water was also available, provided by a trough within the boma.

## 2.4 FIELD PROTOCOL

### 2.4.1 *General*

My study focused on the period during the day, when the elephants roamed freely in the natural environment (~ 09:00-16:00). During this time, one of the elephants was selected as a focal individual and followed on foot. Behavioural observations on the focal individual were then conducted. Concurrently, ambient weather conditions were recorded from a portable weather station located in an open environment within the study area.

### 2.4.2 *Behavioural observations*

The elephants were accustomed to human presence, which enabled a fellow researcher, two elephant handlers and me to follow them on foot in close proximity (~10-50m apart) and observe their behaviour without disturbing them. A continuous sampling approach was used to record predefined behavioural activities of interest, and periods of exposure to sun or shade on a focal individual (Altmann 1974; Lee 1996). I alone recorded behaviour to avoid observer bias. The behavioural ethogram (Table 2.2) was similar to that defined previously by Guy (1976) and Leggett (2009). Start and end times of each activity were recorded so that the proportion and frequency of the behavioural activities could be analysed (Altmann 1974; Lee 1996). The times were rounded off to the nearest minute and a change in behaviour was considered to have taken place only when the proceeding behavioural activity lasted longer than one minute (Guy 1976). In other words, if the elephant was feeding and walked from one shrub to another, walking was considered to have taken place only if the elephant walked for a minute or longer, otherwise it was considered a bout of feeding. All recorded behavioural activities were mutually exclusive except shade utilisation; shade utilisation could occur simultaneously with other recorded

behavioural activities. If the elephants socialised with wild elephant herds, observations continued from the safety of a vehicle or from a distance on foot. During these situations, my ability to distinguish behaviours was not impaired.

### *2.4.3 Prevailing climate*

#### *2.4.3.1 Portable weather station*

During behavioural observations, air temperature (i-Button DS1922L, Maxim Integrated Products, California, USA, resolution = 0.5°C) and black mini-globe temperature was recorded at five-minute intervals from a portable weather station located within the study site, with instruments about 1.8m off the ground. The weather station was placed at the designated meeting point in the bush at the start of each observation day so that it was in proximity (~1 km) to the area the elephants utilised during the day. The weather station was placed in an open habitat where it was exposed throughout the day to direct solar radiation; however, i-Buttons used to record air temperature were artificially shaded to reduce solar radiation effects.

Black miniature globe thermometers were used to measure black mini-globe temperature. Black mini-globes differ from that of the standard black globes in size; the mini-globes are 30mm in diameter as opposed to the standard size of 150mm. Hetem et al. (2007) found that black mini-globe temperatures can be used as an approximation of standard black globe temperatures. The temperature obtained by black globe thermometers is because of two factors, radiant heat and convective heat exchange, the rates of which are influenced by wind and air temperature (Hetem et al. 2007). As such, black globe temperature has been used previously as an indication of environmental temperature

(Dawson et al. 2006; Hetem et al. 2007; Hetem et al. 2011a; Hetem et al. 2011b; Fuller et al. 2014).

The mini-globes were constructed from small 30mm matt black copper spheres and attached to a 3mm steel rod, which in turn was mounted onto a platform on the weather station. Miniature temperature-sensitive data loggers (i-Button DS1922L, Maxim Integrated Products, California, USA) with a resolution of 0.5°C were positioned by silicon at the centre of each mini-globe. All data loggers were calibrated against a certified precision thermometer (Quat 100, Hereus, Hanau, Germany) in an insulated water bath, across a range of 10-50°C.

#### *2.4.3.2 Stationary weather station*

Air temperature, black mini-globe temperature and ground temperature also were recorded at five-minute intervals from a stationary weather station located at the boma during the entire study period. The weather station was exposed to direct sunlight throughout the day. Ground temperatures were recorded from a calibrated i-Button (DS1922L, Maxim Integrated Products, California, USA, resolution = 0.5°C) placed just below the soil's surface (~1 cm) while air temperatures and black mini-globe temperatures were recorded using the same method as that described above for the portable weather station (*see section 2.4.3.1*). Figure 2.3 illustrates the mean hourly temperatures recorded from the stationary weather station during the cool-flood and hot-dry seasons. Temperatures typically peaked between 12:00 and 15:00 during both seasons (Figure 2.3). Table 2.3 is a summary of the daily mean, maximum and minimum temperatures recorded during both the cool-flood and hot-dry seasons. Air temperatures during the entire study period ranged between a minimum of 5.9°C and a maximum of 42.7°C. Daily mean mini-globe, air and ground temperatures were significantly higher during the hot-dry season than

during the cool-flood season ( $p < 0.05$ ; Table 2.3). During the entire study period, rainfall only took place on three separate days, all during the latter half of November.

## 2.5 TABLES AND FIGURES

Table 2.1. Identity, sex, age, family group association and body measures of savanna elephants in the present study.

ID	Elephant name	Sex	Age	Age class	Mass (kg)	Shoulder height (m)	Family Group
Adult female 1	Cathy	Female	47	Adult	3510	2.5	A
Adult female 2 <sup>*</sup>	Shireni	Female	28	Adult	2690	2.4	A
Adult female 3 <sup>♦</sup>	Kitty	Female	18	Adult	2140	2.4	B
Weaned male 1 <sup>*</sup>	Abu	Male	7	Weaned calf	1740	2.2	A
Weaned female 1 <sup>♦</sup>	Lerato	Female	4	Weaned calf	1100	1.9	B
Weaned female 2	Paseka	Female	3	Weaned calf	900	1.6	A
Suckling calf 1 <sup>*</sup>	Warona	Female	1	Suckling calf	320	1.3	A

\*Weaned male 1 and suckling calf 1 are the offspring of adult female 2; <sup>♦</sup>Weaned female 1 is the offspring of adult female 3.

Table 2.2. Ethogram of behaviour recorded as part of the present study.

Behaviour	Description
<b>Walking</b>	Moving at a constant rate from one point to another point.
<b>Resting</b>	Standing or lying down while not engaged in any other behaviour. Includes sleeping.
<b>Feeding</b>	Ingestion and or handling of any plant material that leads to ingestion.
<b>Water-related activities</b>	Any activity associated with water or mud, including dust bathing.
- Drinking	Ingestion of water.
- Wetting	Wetting the body by wallowing in mud or water, spraying mud or water over the body.
- Dust bathing	Throwing of dust over body.
<b>Other</b>	Any unnatural behaviour or behaviour not associated with the above categories or relevant for this study, e.g. social interactions, fighting, playing, nursing.
<b>Shade utilisation</b>	More than 50% of body shaded

*Notes:* Walking, resting, feeding, any water-related activity, and ‘other’ behaviour are mutually exclusive from one another. Shade utilisation can occur simultaneously with any behaviour.



Table 2.3. Summary of temperatures recorded from a stationary weather station located at the elephant boma at Abu camp during the cool-flood and hot-dry season of the present study.

	Cool-flood season (n= 55 days)	Hot-dry season (n= 74 days)	Comparison between seasons (Unpaired t-test)
<b>Air temperature (°C)</b>			
Daily mean ± SD	18.6 ± 2.1	26.2 ± 2.8	$t_{127} = 16.7, p < 0.0001$
Daily mean minimum ± SD	11.7 ± 2.2	18.5 ± 2.7	$t_{127} = 15.1, p < 0.0001$
Daily mean maximum ± SD	28.5 ± 4.4	35.7 ± 3.7	$t_{127} = 10.0, p < 0.0001$
Minimum	5.9	11.9	
Maximum	35.6	42.7	
*Range of temperatures during daytime period of observation	15.1 - 38.1	15.2 - 41.1	
<b>Black mini-globe temperature (°C)</b>			
Daily mean ± SD	20.3 ± 2.6	28.2 ± 3.3	$t_{127} = 14.6, p < 0.0001$
Daily mean minimum ± SD	11.4 ± 2.1	18.1 ± 2.9	$t_{127} = 14.6, p < 0.0001$
Daily mean maximum ± SD	34.7 ± 6.2	42.6 ± 4.6	$t_{127} = 8.4, p < 0.0001$
Minimum	5.3	11.3	
Maximum	41.9	50.1	
*Range of temperatures during daytime period of observation	18.1 - 42.3	19.3 - 47.9	
<b>Ground temperature (°C)</b>			
Daily mean ± SD	20.8 ± 3.0	33.6 ± 4.3	$t_{127} = 17.8, p < 0.0001$
Daily mean minimum ± SD	10.8 ± 1.9	20.9 ± 2.7	$t_{127} = 3.4, p < 0.0001$
Daily mean maximum ± SD	41.0 ± 8.4	56.6 ± 9.5	$t_{127} = 9.1, p < 0.0001$
Minimum	5.5	13.3	
Maximum	48.5	65.9	
*Range of temperatures during daytime period of observation	10.5 - 48.5	22.8 - 65.9	

Notes: SD = standard deviation;

\* Range of temperatures experienced during daytime period of observation represent those temperatures that were recorded when the data was collected during the daytime behavioural observations between ~09:00 and 16:00.

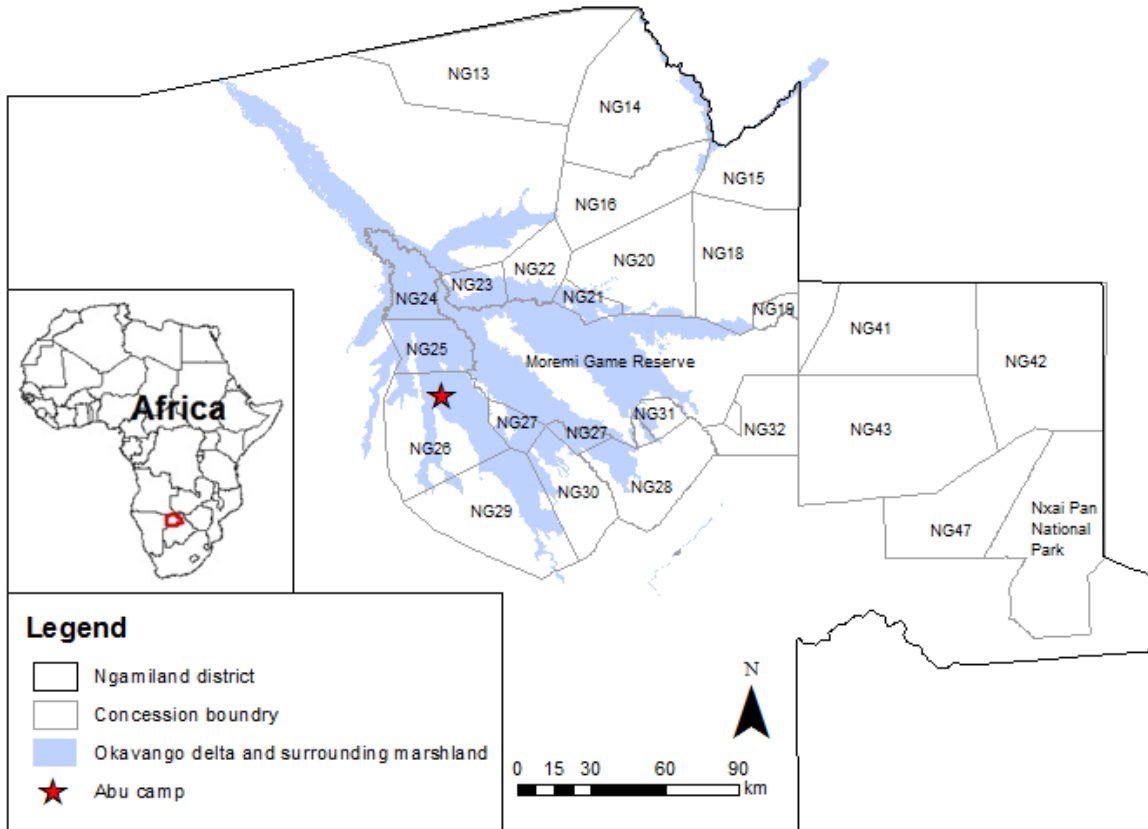


Figure 2.1. Ngamiland district of northern Botswana. The present study took place at Abu camp located in block 26 of the Ngamiland district (NG26), a photographic non-consumptive wildlife management area situated in the lower western region of the Okavango Delta.



Figure 2.2. Aerial photograph illustrating the typical landscape and vegetation structure located within the vicinity of Abu camp in which the present study occurred.

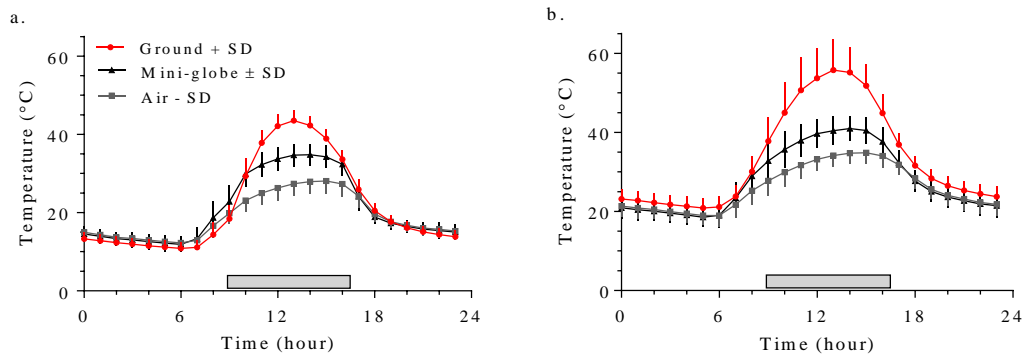


Figure 2.3. Mean hourly temperatures  $\pm$  one standard deviation of the mean (SD) recorded from a stationary weather station located at the elephant boma at Abu camp during the a) cool-flood season (n= 55 days) and b) hot-dry season (n= 74 days). Grey bars illustrate the daytime period during which behavioural observations took place (09:00-16:00).

# **CHAPTER 3. DAYTIME BEHAVIOURAL RESPONSES TO ENVIRONMENTAL TEMPERATURE IN SAVANNA ELEPHANTS (*LOXODONTA AFRICANA*) IN THE OKAVANGO DELTA, BOTSWANA**

## **3.1 INTRODUCTION**

Africa's savanna elephants (*Loxodonta africana*) inhabit landscapes where environmental temperatures vary greatly. Global temperatures also are rising, and conditions in Africa are becoming hotter and drier (Hulme et al. 2001; New et al. 2006; James and Washington 2013; Nicholson et al. 2013). Consequently, the thermoregulatory stressors animals that live here may encounter are likely to increase, with potential consequences for individual fitness and population dynamics (du Plessis et al. 2012; van Beest et al. 2012; van Beest and Milner 2013; Long et al. 2014). Due to their large body size and small surface area to volume ratio, savanna elephants may face difficulties in dissipating heat through non-evaporative means during extreme environmental temperatures (Schmidt-Nielson 1984; Phillips and Heath 1995; Rowe et al. 2013). As of yet, we do not know how elephants respond to and cope with thermally stressful conditions; therefore we do not know what the consequences of climate change may be for elephants.

The adaptive capacity of a species to future climate change may depend largely on its behavioural flexibility (Huey and Tewksbury 2009; Huey et al. 2012; McCain and King 2014). Changes in behaviour are a primary response of animals to buffer themselves against unfavourable weather conditions and maintain thermal balance (Bligh 1973; Kearney et al. 2009; Hetem et al. 2012). Large endotherms typically utilise microclimates, such as those provided by shade, and shift their activity patterns to favourable thermal conditions to thermoregulate (Fuller et al. 1999; Owen-Smith 1998; Aublet et al. 2009; Hetem et al.

2012; Owen-Smith and Goodall 2014). However, there are various costs associated with these temperature-induced behavioural adjustments. For instance, as activity patterns, habitat selection and ultimately spatial use dynamics are altered in response to temperature, feeding activity may decrease (Belovsky and Slade 1986) and trade-offs in forage availability and quality may be encountered (van Beest et al. 2012; Long et al. 2014). Consequently, fitness costs may arise (van Beest and Milner 2013).

Climate as a possible driver of space use in elephants often is overlooked. We know that at a coarse spatial scale, elephants select habitats that are close to water, relatively high in primary productivity, and far from people (Harris et al. 2008; Young et al. 2009; Roever et al. 2012). However, resource use within a landscape depends largely on the physiological requirements and internal state of an individual (Nathan et al. 2008; Jachowski et al. 2013; Long et al. 2014). Within a day, most behavioural decisions made by elephants are likely aimed at acquiring food to maintain their energetic requirements (Owen-Smith 1988). However, the thermal environment may influence these decisions.

Behaviour, such as shade-seeking (Sikes 1971; Kinahan et al. 2007a), changes in intensity of activity (Rowe et al. 2013), and water-related activities (e.g. mud bathing and swimming; Hidden 2009; Wright and Luck 1984; Dunkin et al. 2013) may be employed by elephants to offset costs of autonomic thermoregulation. The use of shade reduces radiant heat loads and thermal stress in large endotherms (Valtorta et al. 1997; Mitlohner et al. 2001; Brown-Brandl et al. 2005; Cain et al. 2008; Hetem et al. 2011a) while metabolic heat production in elephants is reduced during resting with a decrease in activity (Rowe et al. 2013). The use of water also cools the skin directly and may enhance evaporative cooling (Wright and Luck 1984; Gebremedhin and Wu 2001; Dunkin et al. 2013). While these activities for behavioural thermoregulation have been recognised in numerous studies, they

have been poorly quantified in relation to environmental temperature (Wyatt and Eltringham 1974; Guy 1976; Shannon et al. 2008; Leggett 2009).

Heat transfer differs across animals of varying sizes due to differences in surface area to volume ratio and thermal conductance (Peters 1983; Schmidt-Nielson 1984; Porter and Gates 1969; Porter and Kearney 2009), resulting in differences in behavioural activity (Shrestha et al. 2014). Therefore, certain individual characteristics, such as body size must be taken into consideration when investigating animal behaviour. Family group units often consist of adult females with their offspring that typically move and feed together (Buss 1961; Douglas-Hamilton 1972; Moss and Poole 1983). The calves, as smaller individuals, will have higher rates of heat exchange with the environment than older and larger individuals (Peters 1983; Schmidt-Nielson 1984; Porter and Kearney 2009). Therefore, thermal requirements of elephants may vary according to age, altering behaviour between individuals and possibly family groups.

It is of ecological importance to understand how elephants respond behaviourally to environmental temperature. How elephants use space can have ecological consequences for impact on a landscape (Brits et al. 2002; de Beer et al. 2006; Chamailé-Jammes et al. 2007; Guldmond and van Aarde 2008; Vanak et al. 2010), and consequences for survival of young (Young and van Aarde 2010). If environmental temperature drives behaviour in elephants, spatial dynamics may be altered. Furthermore, body size and the daily energetic requirements of elephants may require them to trade-off thermoregulation against foraging, with consequences for individual fitness. Therefore, in this study I asked the following questions: how do elephants respond behaviourally to changes in environmental temperature, and secondly, does the occurrence of specific behaviour differ across time, between seasons, between elephants of different age, and between elephants belonging to

family groups of varying demographic structure? To answer the questions, I set out to quantify daytime behavioural responses to environmental temperature in free-ranging savanna elephants in Botswana's Okavango Delta.

I expected environmental temperature to influence behaviour in elephants. I expected thermoregulatory behaviour (shade utilisation and wetting) and resting to increase with environmental temperature and take place more often during the hottest season. Consequently, I also expected a decrease in feeding and walking activity. Although elephants need to drink to maintain body water reserves for cutaneous evaporative water loss (Dunkin et al. 2013), I did not expect drinking to be dependent on environmental temperature as drinking has no direct thermoregulatory benefit for elephants (Hidden 2009) and water is available and accessible throughout the year in the Okavango Delta. I further predicted that thermoregulatory behaviour and resting would be greater in younger (smaller) individuals, while adults would feed and drink more often and for longer periods. However, because elephants usually move and coordinate activities together in social family groups consisting of one or two related females and their offspring (Buss 1961; Douglas-Hamilton 1972; Moss and Poole 1983), behavioural adjustments may be expressed together as a family group unit in response to the needs of one individual. Therefore, I expected behaviour such as shade utilisation, wetting and resting to be more frequent in family groups with a suckling calf present, but I expected no differences in drinking and feeding between family groups. Lastly, I expected no differences in walking between individuals of different age as walking would likely be expressed as a family group and therefore less frequent in family groups with a suckling calf present.



## 3.2 MATERIALS & METHODS

### *Study area*

See Chapter 2.2 for details

### *Study animals*

See Chapter 2.3 for details

### *Field protocol*

During the day, when the elephants roamed freely in the natural environment (~09:00-16:00), a focal individual was selected and followed in close proximity on foot (~10-50m apart). A continuous focal sampling approach was used to record predefined behavioural activities of interest, and periods of exposure to sun or shade (Altmann 1974; Lee 1996). All recorded behavioural activities were mutually exclusive except shade utilisation; in other words, exposure to shade or sun could occur simultaneously with other recorded behavioural activities. Please see Chapter 2.4 for further details and behavioural ethogram.

### *Climatic conditions*

See Chapter 2.4.3.1 for details

### *Data analysis*

All analyses were carried out in the statistical software R, version 2.15.2 (R Core team 2012). Due to the presence of only one suckling calf, all analyses were conducted with

a dataset excluding data collected for the suckling calf, therefore consisting of only two age classes (weaned calves, and adults).

The proportion of time that elephants spent engaged in a recorded behaviour each day was averaged across all days into activity budgets. Spearman rank correlations were then conducted to visualise general patterns of the daily proportion of time elephants spent engaged in a recorded behaviour as a function of mean daily mini-globe temperature.

Generalised additive models (GAMs) with simple random effects (essentially mixed models) and generalised additive mixed models (GAMMs) were fitted to the data to model the responses of each recorded behaviour to various explanatory variables using the *mgcv* (Wood 2006) and *nlme* (Pinheiro et al. 2013) packages in R. GAMs and GAMMs are nonparametric extensions of generalised linear models and were selected as I had no *a priori* reason for choosing a particular linearized response

A description of all the response and explanatory variables used in the modelling approach can be found in Table 3.1 Air temperature and black mini-globe temperature were strongly correlated (Spearman rank correlation ( $r_s$ ) =0.96). Mini-globe temperature was selected over air temperature because it takes into consideration convective heat loss and radiative heat gain (Hetem et al. 2007), and so gives the best single index of the thermal load experienced by an animal. Furthermore, time of day was included as a potential explanatory variable for all recorded behaviours. The elephants were set in a strict daily routine of morning and late afternoon walks; although they are unrestricted in their movements during the day, years of continuous routines may have resulted in specific behaviour being employed based on time of day. Black mini-globe temperatures were weakly correlated with time of day ( $r_s = 0.43$ , 09:00-16:00).

The recorded behavioural activities of interest were walking, resting, feeding, drinking, wetting, and shade utilisation. The occurrence of each behaviour at every five-minute interval was set as the response variable (Binary 1/0) and the associated black mini-globe temperature, time of day, season, age class, and family group were set as the explanatory variables. In a separate modelling step the duration of time spent in shade per hour was set as the response variable and the explanatory variables were mean black mini-globe temperature, time of day, season, age class, family group and state. State, whether the elephant was wet or dry, was added as an explanatory variable as I hypothesised that elephants that were wet or had employed wetting behaviour within an hour would be less likely to utilise shade.

GAMMs were used to model the response of hourly durations of shade utilisation, while GAMs were used to model the binary responses. GAMs were selected over GAMMs for the binary response models because GAMMs are known to perform poorly with binary data. All models were fitted using a *binomial* family and a *logit* link function. Penalised cubic regression splines were used to represent all the smooth terms in both the GAM and GAMM models (Wood 2006). The restricted maximum likelihood estimation method (REML) was implemented in all the models to produce an unbiased estimation of the variance parameters when the number of fixed parameters in the model increased (Wood 2006). To take into account repeated observations within individuals, individual elephant identity was entered as a random effect structure for the GAMMs (Wood 2006). For each GAM, elephant identity was entered as a simple random effect by treating the random effect as a smooth term (Wood 2008).

Each set of candidate models was formulated using an all subset approach that comprised of various combinations of the explanatory variables. The area under the

receiver operating characteristic curve (ROC) was calculated to assess the accuracy and performance of each GAM (Fielding and Bell 1997). ROC values vary between 0.5 (discriminating power not better than chance) and 1 (perfect discriminating power). Models with ROC values  $\geq 0.7$  were considered to have acceptable discriminating power (Hosmer and Lemeshow 2000). Adjusted  $R^2$  values also were calculated to assess the measure of fit for each GAMM.

For model selection, each candidate mixed model was ranked using Akaike's information criterion (AIC) with the best model having the lowest AIC value (Burnham and Anderson 2002). The strength of support for the best model and alternate best models was assessed using AIC differences ( $\Delta AIC_i$ ) between the approximate best model ( $\Delta AIC_i = 0$ ) and alternate candidate models. Candidate models with  $\Delta AIC_i < 2$  are considered as good as the best model and have substantial support as an alternative best model, models with  $\Delta_i$  in the 2-7 range have some support and should rarely be dismissed (Burnham and Anderson 2002; Burnham et al. 2011). The Akaike weight ( $w_i$ ) for each candidate model was also calculated; this is a normalised likelihood representing the relative strength of support for each candidate model and is essentially the probability that a given model is the best model in a given set of candidate models (Burnham and Anderson 2002). The best model then was plotted and the parameter estimates were assessed. In the event of model uncertainty, the relative importance of each explanatory variable was assessed and ranked by summing the Akaike weights ( $w_i$ ) across all candidate models in which the particular variable appeared. These values ranged between 0 and 1; the larger the value the more important the variable was relative to other variables within the set of candidate models (Burnham and Anderson 2002).

### 3.3 RESULTS

In total, 80 days of behavioural observations were completed, totalling 545 hours (215 hours during the cool-flood season; 331 hours during the hot-dry season). For sampling effort on each individual elephant, please see Appendix I. During the study period, daily mini-globe temperatures ranged from a minimum of  $11.4 \pm 2.1^{\circ}\text{C}$  (mean  $\pm$  standard deviation) to a maximum of  $34.7 \pm 6.2^{\circ}\text{C}$  during the cool-flood season and from a minimum of  $18.1 \pm 2.9^{\circ}\text{C}$  to a maximum of  $42.6 \pm 4.6^{\circ}\text{C}$  during the hot-dry season.

A breakdown of daily behavioural activity patterns is presented in Table 3.2. The data was not normally distributed; therefore, median values are indicated. The elephants spent the majority of the day feeding (85.6%, 80.5%; 88.8% (median, 25<sup>th</sup>; 75<sup>th</sup> percentile)), and very little time engaged in walking, resting, wetting, and drinking. Relatively minor differences in activity patterns were observed between seasons for each behaviour. Dust bathing occurred infrequently and therefore was not included in any of the analyses. The elephants utilised shade for 26.3 % (13.7%; 41.0%) of the day, but more so during the hot-dry season (37.1%, 23.8%; 53.1%) than during the cool-flood season (18.1%, 9.2%; 25.4%).

The time that elephants spent in shade per day increased with mean mini-globe temperature ( $r_s = 0.73$ ;  $p < 0.0001$ ; Figure 3.1a), as did the time spent wetting (through behaviour such as swimming and mud bathing;  $r_s = 0.03$ ;  $p < 0.0001$ ; Figure 3.1b) and resting ( $r_s=0.37$ ;  $p = 0.0008$ ; Figure 3.1c). The time spent feeding per day decreased with mean daily mini-globe temperature ( $r_s= -0.60$ ;  $p < 0.0001$ ; Figure 3.1f), but not the time spent walking which increased significantly, although with a weak correlation ( $r_s = 0.19$ ;  $p = 0.01$ ; Figure 3.1d). Lastly, there was no relationship between the time elephants spent drinking and mean mini-globe temperature ( $r_s = 0.03$ ;  $p = 0.78$ ; Figure 3.1e).

Apparent best and alternate best models ( $\Delta AIC_i < 2$ ) from each set of candidate models (see Appendices II-VIII) suggested some model uncertainty (low Akaike weights for approximate best model), particularly between the binary models for the probability of occurrence of resting, drinking and shade utilisation (Table 3.3). Model interpretation therefore relied mostly on the estimated parameter weights for each set of candidate models (Table 3.4).

Overall, model accuracy and predictability of full models was acceptable for the probability of resting (ROC=0.793) and wetting (ROC=0.757). The full model for the probability of shade utilisation was also acceptable (ROC=0.744), a conclusion supported by a strong fit observed for the full model for the duration of shade utilisation (adjusted  $R^2=0.53$ ). Model accuracy and predictability was relatively poor for the probability of drinking (ROC=0.65), walking (ROC=0.624), and feeding (ROC=0.636), so results for these behavioural activities must be interpreted with caution.

The partial response curves show the relationship of the partial residuals of the response variable and the smoothed explanatory terms in the best approximate models (black mini-globe temperature, Figure 3.2; time of day, Figure 3.3). The response was averaged over the distribution of the values of the other explanatory factors in the best approximate model. Plots were centred to have a mean value of zero along the y-axis and the trends rather than the actual values of the plots describe the responses to the smoothed explanatory variables. Trend lines with 95% confidence intervals above or below the zero mean illustrate a strong trend at that specific interval of the explanatory variable.

### *Shade utilisation*

The probability of shade utilisation occurring and the hourly duration of shade utilisation were best explained by mini-globe temperature and family group (Table 3.4).

Shade utilisation increased with mini-globe temperature with an increased likelihood and duration at temperatures  $> 35^{\circ}\text{C}$  (Figures 3.2a, b). The likelihood of shade utilisation (Estimate =  $0.85 \pm 0.18$ ;  $z = -4.79$ ;  $p < 0.0001$ ) as well as the duration of shade utilisation (Estimate =  $0.85 \pm 0.21$ ;  $t = -3.96$ ;  $p = 0.017$ ) was greater in the family group with a suckling calf present than the family group with no suckling calf present. The duration of time that elephants utilised shade was also dependent on their state (whether they were wet or dry; Table 3.4). For instance elephants that did not partake in wetting activity within an hour utilised shade for longer periods of time, while those that were wet did not utilise shade for extended periods of time (Estimate =  $1.43 \pm 0.12$ ;  $t = -11.96$ ;  $p < 0.0001$ ).

### *Wetting*

The probability of wetting (swimming, mud bathing, spurling water over parts of body) occurring was best explained by mini-globe temperature, time of day, and season (Table 3.4). Wetting incidences increased with mini-globe temperature, with a high likelihood of wetting taking place when temperatures exceeded  $30^{\circ}\text{C}$  (Figure 3.2c). The elephants were also more likely to undertake wetting behaviour during the hot-dry season than during the cool-flood season (Estimate =  $0.68 \pm 0.23$ ;  $z = -2.99$ ;  $p = 0.003$ ). There also was an increased likelihood of wetting taking place around 13:00 (Figure 3.3a).

### *Resting*

Mini-globe temperature was the only factor that explained the probability of the occurrence of resting (Table 3.4), with the probability of resting increasing with mini-globe temperature and an increased likelihood of resting at temperatures greater than  $35^{\circ}\text{C}$  (Figure 3.2d).

### *Drinking*

The probability of drinking was best explained by time of day (Table 3.4). Although, mini-globe temperature was included in the approximate best model (Table 3.3), the parameter weight (Table 3.4) and the partial response curve (Figure 3.2e) for mini-globe temperature imply that the probability of drinking depended more on time of day, with the probability of drinking peaking during the morning hours (Figure 3.3b).

### *Walking*

The probability of walking was best explained by mini-globe temperature, time of day, and family group (Table 3.4). Walking increased with mini-globe temperature, with a higher likelihood of walking at high than low temperatures (Figure 3.2f), but peaking later in the day (Figure 3.3c). The family group with a suckling calf present had a lower likelihood of walking than the family group without a suckling calf present (Estimate =  $-0.47 \pm 0.11$ ;  $z = 4.17$ ;  $p < 0.0001$ ).

### *Feeding*

The probability of feeding was best explained by mini-globe temperature, time of day, and season (Table 3.4). Feeding decreased with mini-globe temperature, and was more likely to take place at temperatures below 30°C than above 30°C (Figure 3.2g). The likelihood of feeding was also less during the hot-dry than cool-flood season (Estimate =  $-0.33 \pm 0.11SE$ ,  $z = -2.97$ ,  $p = 0.003$ ). Although time of day did contribute as an explanatory variable with a high parameter weight (Table 3.4), the partial response curve for time of day (Figure 3.3d) implies a negligible response, with a slight decrease in feeding during midday.



### 3.4 DISCUSSION

In this study, elephants responded behaviourally to high environmental temperatures. As environmental temperature increased, elephants altered their behaviour by utilizing shade, increasing wetting behaviour or increasing resting, either in the shade or in the sun. Increasing environmental temperature also resulted in a decrease in feeding activity and, unexpectedly, an increase in walking. The aforementioned responses have been noted by others (e.g. Wyatt and Eltringham 1974; Guy 1976; Kinahan et al. 2007a; Shannon et al. 2008; Leggett 2009, Dunkin et al. 2013), but none of these studies quantified elephant behaviour in direct response to environmental temperature.

At low environmental temperatures, elephants are likely to optimise nutritional intake. However, as temperatures increase (above ~30°C environmental temperature), the energetic costs of being active (i.e. feeding) in direct sunlight likely increase (Langman et al. 2012; Rowe et al. 2013) and may explain why elephants then decrease feeding, increase resting, seek shade or seek opportunities to wet their skin through mud bathing and swimming. Such behaviour is likely to contribute to thermal comfort and results in thermoregulation (Wright and Luck 1984; Mitlohner et al. 2001; Gebremedhin and Wu 2001; Dunkin et al. 2013; Rowe et al. 2013).

The observed increase in walking with environmental temperature appears at odds with a behavioural response to reduce heat gain. Walking results in increased endogenous heat production and is likely to result in increased thermal stress in elephants at high environmental temperatures (Langman et al. 2012; Rowe et al. 2013). However, elephants typically direct their movements and increase displacement when moving towards resources such as water (Chamaillé-Jammes et al. 2013). By moving towards water or shade during high environmental temperatures, and then mud bathing or resting, the

potential benefits for thermoregulation may outweigh the possible costs of staying where thermal stress is high.

The influence of daily routines enforced by training on the activity patterns of elephants in this study cannot be ruled out, but it was accounted for in the modelling approach by including time of day as an explanatory variable. Specific behavioural activities were dependent on time of day. Drinking in particular was more likely to occur in the morning hours independent of environmental temperature. Elephants are known to drink at any time of day or night, so this result is not unexpected (Wyatt and Eltringham 1974; Guy 1976). Likewise, the increase in walking during the latter part of the day, can probably be attributed partly to instinctive movement towards meeting points for the afternoon tourist activities which begun at around 17:00.

Temperature-induced behavioural adjustments may involve various costs; costs which do not necessarily outweigh the costs of not adjusting, but none-the-less have detrimental effects on an individual's fitness (van Beest et al. 2012; van Beest and Milner 2013). At high environmental temperatures, the prioritisation of activities aimed at heat dissipation may result in a decrease in time available to feed (Belovsky and Slade 1986) or even costly trade-offs in food availability (e.g. van Beest et al. 2012). In my study, elephants spent 60 to 90% of the observation period feeding. This proportion is consistent with previous studies that suggest elephants spend up to 12-16 hours a day feeding (Wyatt and Eltringham 1974; Guy 1976). I suggest that the observed decrease in feeding activity is a repercussion of increased behaviour related to resting, wetting, and walking more often on hotter days and during hotter times of the day, rather than a direct thermoregulatory response of decreased activity (Rowe et al. 2013). Elephants therefore may be vulnerable to thermoregulatory constraints on foraging. How long elephants must feed for to maintain

optimal nutritional intake is unknown, but it is likely dependent on the availability and nutritional quality of forage. To compensate for lost time in feeding elephants may increase foraging efficiency (rate of food intake) or shift feeding activity to cooler times of the day or night (e.g. as noted for other large herbivores; Ostrowski et al. 2003; Hetem et al. 2011a). However, the elephants in this study were unable to shift activity to night, which may explain the lack of daytime resting compared to other studies on elephant behaviour (Guy 1976; Shannon et al. 2008; Leggett 2009). Alternatively, it would be advantageous for elephants to select areas that are thermally beneficial and at the same time high in forage quantity or quality. The elephants in the present study were observed feeding while standing in shade when forage was available. However, if elephants are unable to adjust accordingly to maintain optimal nutritional intake, nutritional requirements may not be met, with possible detrimental consequences for individual fitness.

Shade and water are clearly vital resources for thermoregulation in elephants. On hot days (environmental temperatures  $> 35^{\circ}\text{C}$ ) elephants spent up to 60% of the day in shade. Likewise water-related activity on occasions consisted of up to 10% of the day's activities. The distribution of these resources and the proximity of forage to these resources may influence elephant behaviour at high environmental temperatures. Although water was available throughout the study period, there was a higher probability of wetting during the hot-dry season than during the cool-flood season. In contrast, the probability of shade utilisation and the duration of shade utilisation did not differ between seasons. Environmental temperatures seldom exceeded  $36^{\circ}\text{C}$  in the cool-flood season; therefore, non-evaporative heat loss was conceivably maintained by utilising only shade during the cool-flood season, whereas, increased thermal requirements and environmental temperatures consistently above  $36^{\circ}\text{C}$  during the hot-dry season could have resulted in wetting of the skin more often to enhance evaporative heat loss. In this way, elephants may

have been constrained to forage closer to water during the hot-dry season. During dry and hot periods of the year, elephant distribution is dependent on water availability as elephants tend to forage close to water (de Beer et al. 2006; Chamaillé-Jammes et al. 2007; Harris et al. 2008). Furthermore, elephants often select areas high in primary productivity and high canopy cover (Kinahan et al. 2007a; Smit et al. 2007; Harris et al. 2008; Roever et al. 2012).

Wetting was also more likely to occur during the middle hours of the day. This finding may indicate an anticipatory response to expected high temperatures during the afternoon hours, particularly during the hot-dry season. Furthermore, elephants were less dependent on shade following a wetting event. If foraging was limited to the proximity of water, wetting may result in increased opportunity to forage in otherwise thermally unfavourable habitats, rather than limiting feeding opportunities to habitats of high canopy cover. In this way, both thermal and nutritional requirements may be met. Ultimately, as elephants adjust behaviour aimed at dissipating heat and optimising energy intake, the distribution of not only shade and water, but also forage is key in determining how elephants respond behaviourally and spatially to changes in temperature, as well as the magnitude of trade-offs and costs elephants may face as a result.

Environmental temperature also may influence the behaviour of adult elephants through thermal constraints imposed on calves within a herd. Behaviour did not differ between individuals of different age classes but differed between family groups, with increased shade utilisation and a lower likelihood of walking taking place in the family group with a suckling calf present. Female mammals with offspring often show behavioural adjustments different to those in individuals without offspring that may benefit the survival of their young (Edwards 1983; Bon et al. 1995; Barten et al. 2001). Younger individuals

may be more susceptible to heat gain and thermal stress due to their smaller body surface area to volume ratio (Peters 1983; Schmidt-Nielson 1984; Porter and Kearney 2009). For the well-being of a calf, it is likely that a family group makes behavioural decisions aimed at its thermal and energetic requirements, ultimately driving spatial use patterns of family groups. Breeding herds are known to remain closer to rivers than bulls during dry and hot seasons (Stokke and du Toit 2002), probably for water and shade access (Smit et al. 2007). It is plausible that larger bulls may be more tolerant of thermal stress and less constrained by high environmental temperatures, an aspect worth future investigation. Furthermore, if suckling calves are at a higher risk of thermal stress and family groups do respond spatially to the thermal needs of the calf, thermally and nutritionally stressful conditions may force family groups to move substantial distances between required resources. In this way, calf survival may be at risk.

Behavioural observations on tame semi-captive elephants are not ideal and some unavoidable realities may be seen as a limitation in this study. For example, the elephants were supplemented with food and water throughout the night, which may have resulted in less dependence for food and water during the day. Consequently, more time during the day could have been used for activities such as resting and wetting without a costly decrease in feeding time. Elephants in the wild may be less prone to employ thermoregulatory behaviour if they have not fulfilled their nutritional requirements. Similarly, tourist activities are likely to have an effect on the elephants used in this study. Their morning walks of approximately 2 km likely increases metabolic heat production and as a result, their need to employ thermoregulatory behaviour may be adopted sooner in the day, as opposed to a wild elephant that might be less active in the morning hours. While the above-mentioned realities may be seen as a limitation, the findings of this study are none-the-less valuable in gaining a mechanistic understanding of how elephants respond behaviourally to

environmental temperature. The knowledge obtained from this study can now be used as a platform to postulate validated expectations for how wild elephants may respond to environmental temperature.

In summary, I have shown that environmental temperatures induce fine-scale (within day) behavioural responses in savanna elephants. At high temperatures, fine-scale behaviour appears to be driven by the thermoregulatory requirements of an individual or specific individuals within a herd. In this way, elephants have adapted to cope with extreme environmental temperatures. However, these behavioural responses can have direct consequences for habitat selection and fine-scale spatial use patterns in elephants with indirect implications for individual fitness. As such, environmental temperature is an important factor for elephant ecology and should be included in future studies on the fine-scale spatial ecology of elephants.

Through behaviour, elephants are likely capable of buffering the direct physiological effects of extreme climate. Temperature-dependent behavioural adjustments will only be detrimental for elephants if their ability to behaviourally buffer extreme climates while simultaneously limiting thermoregulatory costs is hampered in any way. Of course, the abundance and distribution of resources such as shade, water and forage is crucial in determining how elephants respond and adapt to changes in temperature, as well as the costs elephants may face as a result. Indirect effects of climate will likely influence vegetation cover and the distribution of water across space (Milly et al. 2005; de Wit and Stankiewics 2006; Scheiter and Higgins 2009). Furthermore, with expanding human densities and settlements, elephant space use may be altered and limited (Hoare and du Toit 1999; Graham et al. 2009; Roever et al. 2012). If elephants are spatially restricted, or lack the resources and opportunities to fulfil basic nutritional and thermal requirements, climate change will have detrimental consequences for elephants.

### 3.5 TABLES AND FIGURES

Table 3.1. Description of response and explanatory variables used in the analytical modelling approach.

Variables	Type	Description
<b>Response variables</b>		
Probability of walking	Binary	<b>1:</b> walking taking place <b>0:</b> no walking taking place
Probability of resting	Binary	<b>1:</b> resting taking place <b>0:</b> no resting taking place
Probability of foraging	Binary	<b>1:</b> foraging taking place <b>0:</b> no foraging taking place
Probability of drinking	Binary	<b>1:</b> ingestion of water took place <b>0:</b> no ingestion of water took place
Probability of wetting	Binary	<b>1:</b> mud bathing/splashing/swimming took place <b>0:</b> no wetting of any sort took place
Probability of shade use	Binary	<b>1:</b> >50% of the body was exposed to shade <b>0:</b> >50% of the body exposed to direct sun
Duration of shade use	Proportional	<b>0-100%:</b> percentage of time spent in the shade per hour
<b>Explanatory variables*</b>		
Tmg	continuous	Black mini-globe temperature measurement (°C), indicator of environmental temperatures
Time of day ( <i>time</i> )	continuous	Each fifth minute interval (Binary models) Hour of day (Duration of shade use models)
Family group ( <i>group</i> )	categorical	<b>A:</b> 5 individuals; 2 adults, 2 weaned calves, 1 suckling calf <b>B:</b> 2 individuals; 1 adult and 1 weaned calf
Age class ( <i>class</i> )	categorical	<b>Adult:</b> Individuals over 11 years old <b>Weaned calf:</b> Individuals 3-7 years old <b>Suckling calf:</b> Individual 3 years and younger (excluded data)
Season	categorical	<b>Hot-dry season:</b> Observations during September to November <b>Cool-flood season:</b> Observations during May to July
State	categorical	<b>Dry:</b> elephant remained dry for entire hour of observation <b>Wet:</b> Wetting took place within the first 45min of the hour

*Notes:* \* names in italics are acronyms or abbreviations used throughout analysis

Table 3.2. Percentage of time per day (median % (25<sup>th</sup>; 75<sup>th</sup> percentiles)) savanna elephants spent engaged in a specific behaviour during the entire study period, the hot-dry season and the cool-flood season.

Behaviour	Entire study Median % (25 <sup>th</sup> ;75 <sup>th</sup> percentile) <i>n</i> =78	Hot-dry season Median % (25 <sup>th</sup> ; 75 <sup>th</sup> percentile) <i>n</i> =46	Cool-flood season Median % (25 <sup>th</sup> ; 75 <sup>th</sup> percentile) <i>n</i> =32
Walking	6.0 (4.7; 7.6)	6.4 (5.2; 8.4)	5.3 (4.5; 6.4)
Resting	0.7 (0; 2.5)	1.2 (0.0; 2.7)	0.1 (0.0; 1.2)
Feeding	85.6 (80.5; 88.8)	81.9 (76.0; 85.9)	88.9 (86.5; 91.2)
Water-related	3.8 (2.4; 5.7)	5.2 (3.3; 6.7)	2.7 (1.7; 4.0)
– Drinking	1.4 (1.0; 1.9)	1.4 (1.0; 2.0)	1.4 (1.0; 1.8)
– Wetting	2.2 (0.7; 3.8)	3.0 (1.4; 5.1)	0.9 (2.2; 3.0)
– Dust bath	0.0 (0.0; 0.2)	0.0 (0.0; 0.3)	0.0 (0.0; 0.2)
Other	1.2 (0.0; 3.2)	1.7 (0.5; 3.8)	0.7 (0.0; 2.0)
Exposure			
– Shade utilisation	26.3 (13.7; 41.0)	37.1 (23.8; 53.1)	18.1 (9.2; 25.4)

*Notes:* data for suckling calf not included. Exposure is not a mutually exclusive behaviour; all other behaviours are mutually exclusive from one another.  
*n*=number of days that full behavioural observations (7h in duration, from 9:00-16:00) took place.



Table 3.3. Summary of selected best and alternative best ( $\Delta AIC_i < 2$ ) generalised additive mixed models from each set of candidate models.

Response	model <sub>i</sub>	K	LogLik	$\Delta AIC_i$	$w_i$	ROC/ $R^2$
Probability of walking	Tmg* + time* + group*	9.5	-1528.09	0.00	0.52	0.622
	Tmg* + time* + group* + season	10.4	-1527.98	1.52	0.24	0.624
Probability of resting <sup>†</sup>	Tmg*	7.5	-557.83	0	0.10	0.788
	Tmg* + class	7.6	-557.85	0.21	0.09	0.789
	Tmg* + group	7.6	-557.81	0.24	0.09	0.788
	Tmg* + time	9.8	-555.69	0.33	0.09	0.793
	Tmg* + group + class	7.7	-557.81	0.43	0.08	0.789
	Tmg* + time + class	9.9	-555.71	0.53	0.08	0.793
	Tmg* + time + group	9.9	-555.67	0.56	0.08	0.793
	Tmg* + time + group + class	10.	-555.66	0.75	0.07	0.794
Probability of drinking	Tmg + time*	4.3	-492.3	0	0.21	0.644
	Tmg + time* + class	5.3	-491.4	0.31	0.18	0.650
	Tmg + time* + season	5.3	-491.8	0.93	0.13	0.645
	Tmg + time* + class + season	6.3	-490.8	0.95	0.13	0.650
	time*	2.0	-495.2	1.23	0.12	0.629
	time* + class	3.0	-494.4	1.51	0.10	0.634
Probability of wetting	Tmg* + time* + season*	15.4	-1066.0	0	0.26	0.757
	Tmg* + time* + group + season*	15.6	-1065.9	0.07	0.25	0.757
	Tmg* + time* + class + season*	15.7	-1065.9	0.15	0.24	0.757
	Tmg* + time* + group + class + season*	15.8	-1065.8	0.25	0.23	0.757
Probability of shade use <sup>†</sup>	Tmg* + group*	9.5	-3459.0	0	0.10	0.743
	Tmg* + group* + class	9.7	-3458.9	0.22	0.09	0.743
	Tmg*	9.9	-3458.8	0.41	0.08	0.743
	Tmg* + class	9.9	-3458.7	0.45	0.08	0.743
	Tmg* + group* + season	10.4	-3458.3	0.51	0.08	0.744
	Tmg* + group* + class + season	10.6	-3458.2	0.73	0.07	0.743
	Tmg* + season	10.8	-3458.1	0.91	0.07	0.743
	Tmg* + class + season	10.9	-3458.0	0.95	0.06	0.743
Probability of feeding	Tmg* + time + season*	12.2	-2794.1	0	0.47	0.636
	Tmg* + time + class + season*	12.4	-2794.0	0.22	0.42	0.636
Duration of shade use	Tmg* + state* + group*	7	-879.7	0.00	0.37	0.54 <sup>#</sup>
	Tmg* + state* + group* + class	8	-879.4	1.39	0.18	0.53 <sup>#</sup>
	Tmg* + state* + group* + season	8	-879.5	1.60	0.17	0.54 <sup>#</sup>

Notes: For each model the number of parameters (K), loglikelihood value (LogLik), difference in AIC between the best fit model and model<sub>i</sub> ( $\Delta AIC_i$ ), Akaike weight ( $w_i$ ), area under receivers operating characteristic curve (ROC), or adjusted coefficient of determination ( $R^2$ ) are shown. Parameters: Tmg = black mini-globe temperature; time = time of day; class= age class; group = family group. \*model parameter coefficient significant ( $p < 0.05$ ); <sup>#</sup>adjusted  $R^2$  values; <sup>†</sup>Only models with  $\Delta AIC < 1$  for particular behaviour shown.

Table 3.4. Summary of the relative importance of each explanatory variable in each set of candidate generalised additive mixed models and area under the receivers operating characteristic curve (ROC) of each full model for each behaviour.

Variable	Probability walking	Probability resting	Probability drinking	Probability wetting	Probability feeding	Probability shade use	Duration shade use
Tmg	<b>1.00</b>	<b>1.00</b>	0.67	<b>1.00</b>	<b>1.00</b>	<b>1.00</b>	<b>1.00</b>
Time of day	<b>0.99</b>	0.44	<b>1.00</b>	<b>1.00</b>	0.92	0.35	0.15
Season	0.31	0.33	0.38	<b>0.98</b>	<b>0.97</b>	0.48	0.30
Family group	<b>0.77</b>	0.47	n/a	0.49	n/a	<b>0.54</b>	<b>0.94</b>
Age class	n/a	0.48	0.48	0.48	0.47	0.48	0.33
State	n/a	n/a	n/a	n/a	n/a	n/a	<b>1.00</b>
ROC	0.624	0.793	0.650	0.757	0.636	0.744	0.530*

*Notes:* The relative importance of each explanatory variable was assessed and ranked by summing the Akaike weights ( $w_i$ ) across all candidate models in which the particular variable appeared. These values range between 0 and 1; the larger the value the more important the variable is relative to other variables within the set of candidate models (Burnham and Anderson 2002). Tmg = black mini-globe temperature.

Variables significant in at least one of the selected best or alternative best models are in bold. Variables not included in the analysis for a particular behaviour are illustrated as n/a.

\*Adjusted  $R^2$  value not ROC value

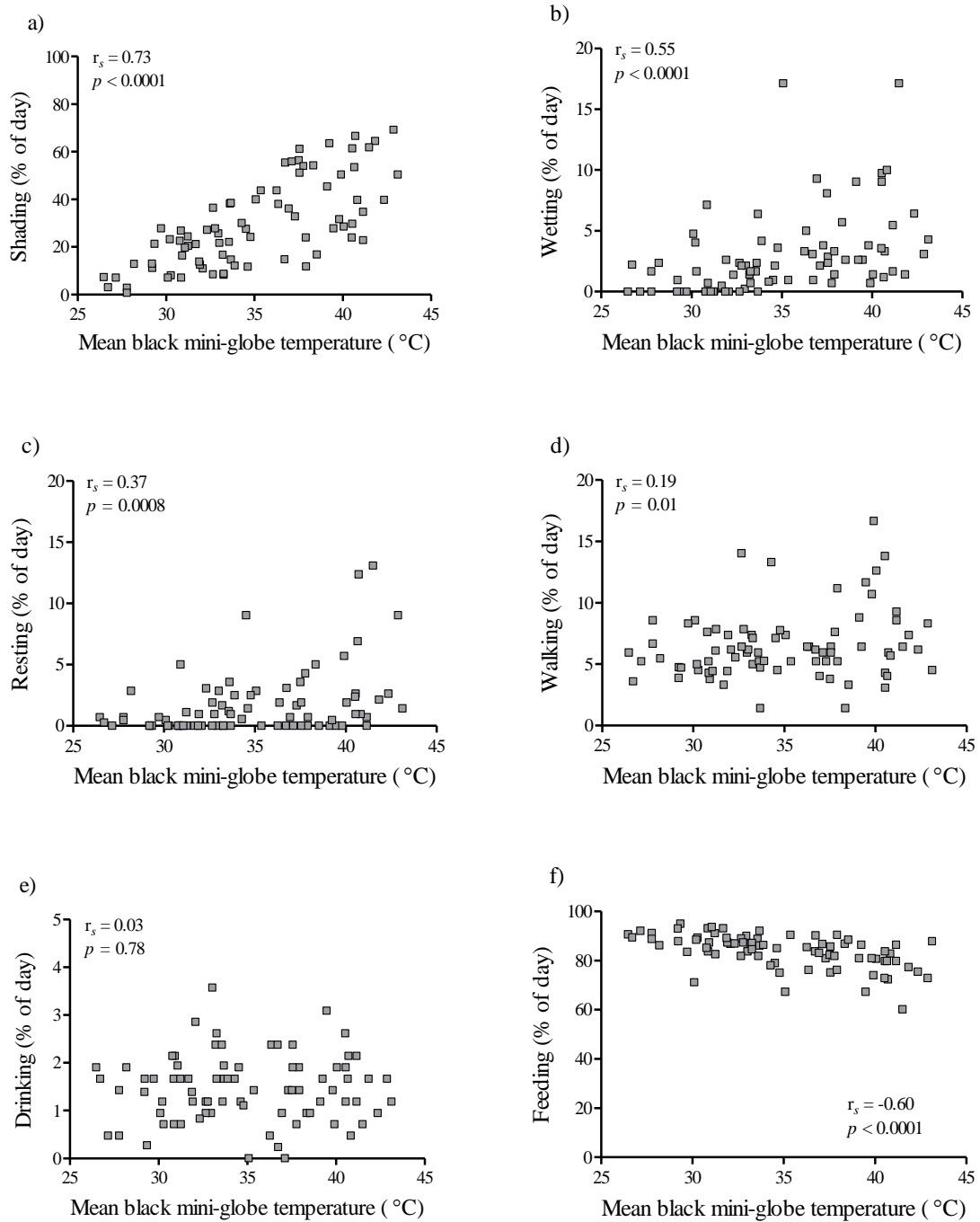


Figure 3.1. Percentage of time between 09:00 and 16:00 ( $n=78$ days) a focal savanna elephant spent (a) in shade, (b) wetting, (c) resting, (d) walking, (e) drinking and (f) feeding as a function of mean daily black mini-globe temperature (°C). Spearman rank correlation ( $r_s$ ) and the significance of correlation ( $p$ ) are illustrated.

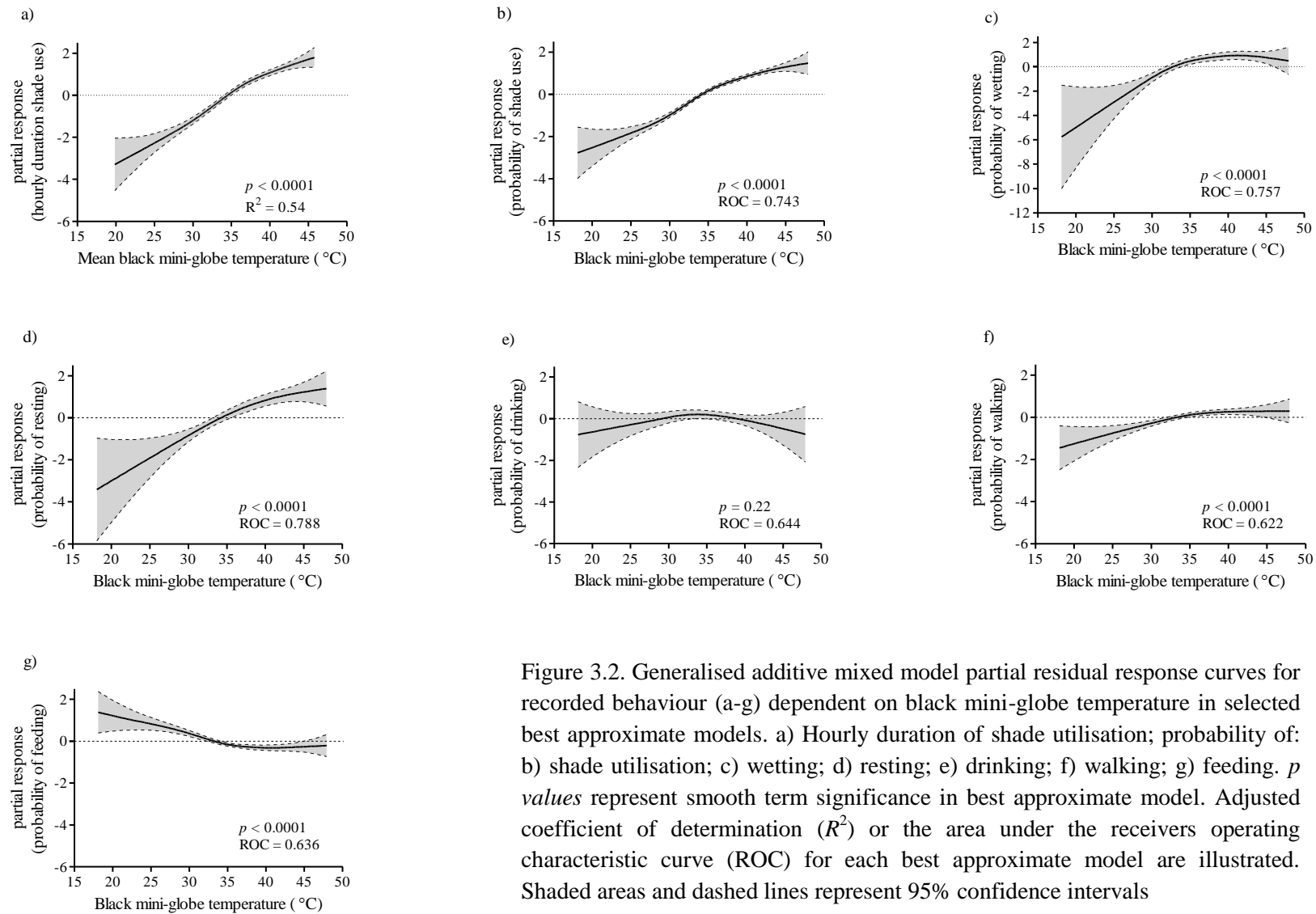


Figure 3.2. Generalised additive mixed model partial residual response curves for recorded behaviour (a-g) dependent on black mini-globe temperature in selected best approximate models. a) Hourly duration of shade utilisation; probability of: b) shade utilisation; c) wetting; d) resting; e) drinking; f) walking; g) feeding.  $p$  values represent smooth term significance in best approximate model. Adjusted coefficient of determination ( $R^2$ ) or the area under the receivers operating characteristic curve (ROC) for each best approximate model are illustrated. Shaded areas and dashed lines represent 95% confidence intervals

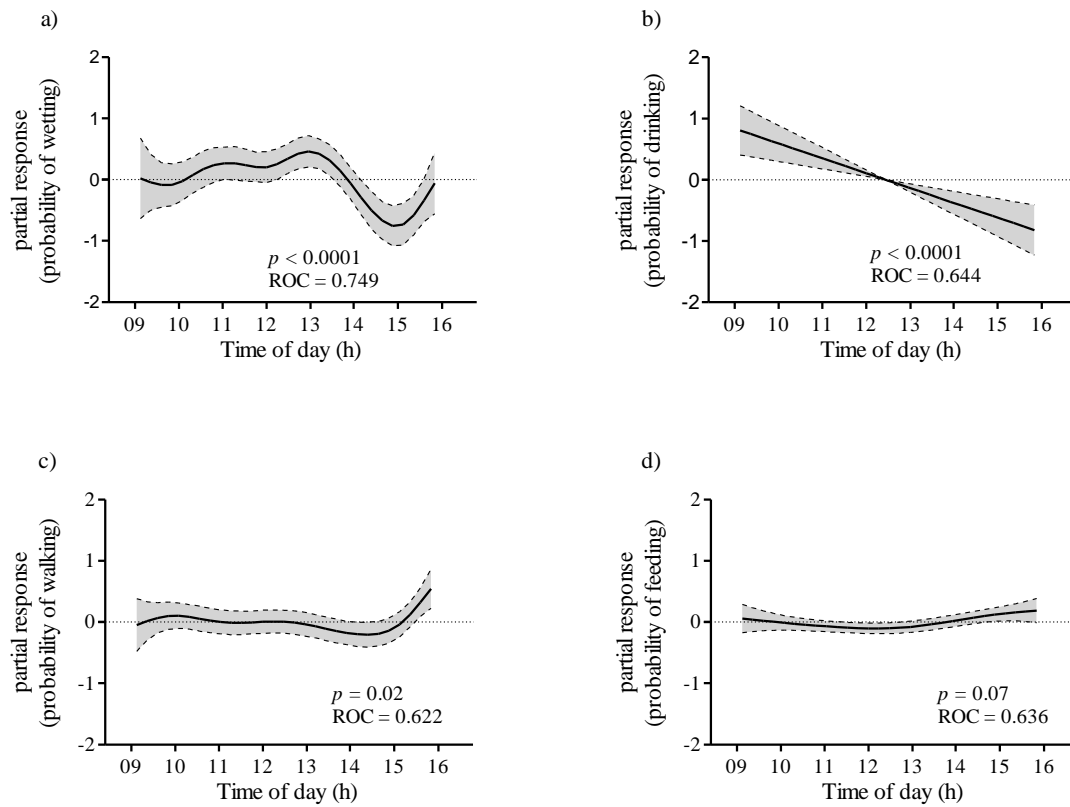


Figure 3.3. Generalised additive mixed model partial residual response curves for recorded behaviour (a-d) dependent on time of day in selected best approximate models. Probability of: a) wetting; b) drinking; c) walking; d) feeding.  $p$  values represent smooth term significance in best approximate model. The area under the receivers operating characteristic curve (ROC) for each best approximate model are illustrated. Shaded areas and dashed lines represent 95% confidence intervals.

## **CHAPTER 4. THERMAL BENEFITS OF SHADE UTILISATION AND WETTING BEHAVIOUR IN SAVANNA ELEPHANTS (*LOXODONTA AFRICANA*)**

### **4.1 INTRODUCTION**

Elephants are large-bodied endotherms with a small body surface area to volume ratio and therefore may face difficulties in dissipating excess metabolic heat (Schmidt-Nielson 1984; Phillips and Heath 1995; Rowe et al. 2013). However, elephants currently inhabit environments where ambient temperatures often exceed core temperatures (Sikes 1971). How do elephants cope in such extreme thermal environments? We know that elephants utilise shade and employ water-related activities (e.g. mud bathing, swimming) when environmental temperatures are high (Chapter 3) but does this behaviour provide the necessary thermal benefits for elephants? And if so, at what environmental temperature do elephants need to begin to employ such behaviour? Answering these questions will strengthen our understanding of the relationship between elephants and climate and allow us to gain insight into how elephants use space at a fine-scale (within a day) across a landscape and when such behavioural adjustments are likely to occur, ultimately allowing us to infer potential physiological and ecological consequences thereof.

Behaviour that alters heat exchange with the environment is likely key for thermoregulation in elephants. In general, heat is conducted to the core or from the core when skin temperature is greater or less than core temperature respectively (Porter and Gates 1969). When environmental temperatures exceed skin temperature, skin temperature will rise, consequently decreasing the thermal gradient between core and skin tissue and the conduction of heat from the core to the skin. If skin temperature exceeds core temperature, heat will be gained from the environment (Porter and Gates 1969). At this point, animals can

no longer rely on non-evaporative heat loss to dissipate heat, instead relying on autonomic responses that increase evaporative heat loss or behavioural adjustments that can vary the rate of heat exchange with the environment or likewise increase evaporative heat loss (Bligh 1973).

In the following study, I aimed to assess the thermal benefits provided by behavioural adjustments of shade utilisation and wetting (mud bathing, swimming, spraying water on the body). I hypothesised that shade utilisation and water-related activities would provide a thermal benefit for elephants. Trees reduce local solar radiation, alter ground temperature, modify wind, and to some degree alter air temperature and relative humidity levels within and under canopies (Valtorta et al. 1997; Kotzen 2003; Cain et al. 2008) while water and mud has a direct cooling effect on a skins surface and can enhance evaporative cooling (Gebremedhin and Wu 2001; Dunkin et al. 2013). Therefore, as elephants begin to employ shade utilisation and water-related activities I expected the environmental heat load that an elephant experiences to be reduced. Secondly, I expected skin temperature to be dependent on the environmental heat load elephants experience within a landscape when elephants adjust their behaviour.

I further aimed to determine a critical environmental temperature (assessed by black mini-globe temperatures) at which shade utilisation and wetting behaviour are employed. I hypothesised that elephants would begin to employ shade utilisation and water-related activities when environmental temperatures began to approach and exceed core temperature. An elephant's core temperature fluctuates between 36°C and 37°C (Benedict and Lee 1938; Buss and Wallner 1965; Kinahan et al. 2007b; Hidden 2009; Rodrigues D'Araujo 2014). To maintain a thermal gradient with the environment I expected that elephants would begin to

adjust their behaviour in the form of seeking shade and water-related activities before environmental temperatures (black mini-globe temperatures) exceed 36°C.

I aimed to test the above expectations with data obtained through the deployment of ambulatory miniature black globe thermometers and infrared thermal images on tame, free-ranging savanna elephants in the Okavango Delta. The use of ambulatory miniature black globe thermometers is a novel, non-invasive method which may be used to record environmental heat loads free-roaming animals experience as behaviour is adjusted (Hetem et al. 2007). Black “mini-globes” differ from that of standard black globes in size; the mini-globes are 30mm in diameter as opposed to the standard size of 150mm. This enables one to place them on the collar of an animal with relative ease and decreases the risk of damage to the instrument itself. The temperature obtained by the globe is not affected by ambient water vapour pressure, but it is affected by radiant heat exchange and convective heat exchange, which is influenced by wind and air temperature (Hetem et al. 2007). As such, black globes take into consideration three of the four factors that influence an animal’s climatic space (radiation, air temperature, wind). This biotelemetry technique has been tested and validated on ungulates (Fuller et al. 1999; Hetem et al. 2007; Hetem et al. 2009; Hetem et al. 2011a; Hetem et al. 2011b; Hetem et al. 2012) but has not been utilised previously on elephants.



## 4.2 MATERIALS & METHODS

### *Study area*

See Chapter 2.2 for details

### *Study animals*

See Chapter 2.3 for details

### *Behavioural observations*

During the day, when the elephants roamed freely in the natural environment (~ 09:00-16:00), a focal individual was selected and followed on foot at a distance of 10-50m away. A continuous focal sampling approach was utilised to record water-related activities of interest (e.g. mud bathing, swimming, spraying water on the skin) and periods of exposure to sun or shade (Altmann 1974; Lee 1996). The ethogram (*see* Chapter 2, Table 2.1) was similar to that defined previously by Guy (1976) and Leggett (2009). Start and end times of each activity were rounded off to the nearest minute and a change in behaviour was considered to have taken place only when the proceeding behavioural activity lasted longer than one minute (Guy 1976). Please see Chapter 2.4 for further details and the behavioural ethogram.

### *Mini-globe temperature measurements*

Mini-globe thermometers were constructed from small 30mm copper spheres spray-painted matt black and attached to a 3mm steel rod mounted onto a collar, which was then placed on the focal elephant during observations. Two different collars were used during the study. The three adult females and the weaned male calf were large enough to accommodate a standard leather elephant collar (African Wildlife Tracking, Pretoria, South Africa; see Appendix IX a). This collar was too large to fit onto the two weaned female calves and

instead they were fitted with a custom-made collar made from a 3 × 150cm nylon strap in which the globe was mounted onto a thin strip of leather (see Appendix IX b). Both collars were weighted to allow the globe to be positioned vertically between the ears and on the neck of the individual. To protect the globes from damage that may have occurred from branches and other elephants, a cage was placed over the globe. The cage comprised of two 4mm diameter brass rods welded together at the centre to form a cross, and bent to form a bell shaped structure where the ends of each rod were attached to the collar.

The mini-globe thermometers placed on the collar of an individual and the temperatures obtained are referred to as collar mini-globe thermometers and temperatures. During observation periods an identical mini-globe with an identical cage placed over it was positioned on a stationary weather station located within the study site about 1.8m (roughly the average shoulder height of all the elephants) off the ground in an open environment exposed to direct sunlight. These mini-globe thermometers and the temperatures obtained are referred to as the weather station mini-globe thermometer and temperature. All mini-globe temperatures were recorded at five-minute intervals by miniature temperature-sensitive data loggers (i-Button DS1922L, Maxim Integrated Products, California, USA), which were positioned by silicone at the centre of each mini-globe, to a resolution of 0.5°C. Data loggers were calibrated against a certified precision thermometer (Quat 100, Hereus, Hanau, Germany) in an insulated water bath, across a range of relevant temperatures.

#### *Skin temperature measurements*

Skin temperature was recorded using a factory calibrated infrared thermal camera (FLIR T640, FLIR Systems Inc., Portland, Oregon, USA, accuracy of 1°C) with a 25° lens and 7.5–13µm spectral range. The camera detects infrared radiation emitted from the surface of an object, which is then converted into a temperature value. Surface temperatures are

depicted in the form of an infrared image (thermograph). To ensure accurate skin temperature recordings I supplied the camera with the following parameters: emissivity=0.98, distance=10m, relative humidity and reflected temperature. Thermographs were obtained on the right and left side (when possible) of the focal individual at 10 minute intervals. Focal individuals were thermographed from an angle perpendicular to its sagittal plane. For a given thermograph, the skin temperature of the individual was calculated using hand-drawn complex polygons of various body parts of the elephant (see Appendix X) in the software package FLIR Reporter Professional 9.0 (FLIR Systems Inc., Portland, Oregon, USA). Mean skin temperature for the entire body was calculated as a weighted average using each body part, based on the number of pixels within each body part.

#### *Data analysis*

Five variables were included in the analysis: 1) periods when an elephant was exposed to sun or shade, and periods of water-related activities, 2) collar mini-globe temperature, 3) weather station mini-globe temperature, 4) difference between concurrently recorded collar and weather station mini-globe temperature (collar minus weather station mini-globe temperature), and 5) mean skin temperature.

The weather station mini-globe recorded temperatures concurrently with the collar mini-globe. The temperatures obtained by the weather station mini-globe indicates the environmental heat load the elephant may have experienced if it were exposed to direct sunlight and in an open environment not sheltered from wind. The temperatures obtained by the collar mini-globe indicated the environmental heat load or environmental temperatures the elephant did experience at a point in time. The weather station mini-globe and the collar mini-globe were both located within the study area and therefore I assumed that both mini-globes at a point in time were exposed to similar wind speeds as well as similar air

temperatures and radiation levels when the collar mini-globe was exposed to direct sunlight and out in the open. Therefore, collar mini-globe temperatures lower than simultaneously recorded weather station mini-globe temperatures (a difference  $< 0^{\circ}\text{C}$ ) resulted from a decrease in radiation, or cooling of the mini-globe taking place from wetting or wind exposure. In other words, the value obtained from the difference between concurrently recorded collar and weather station mini-globe temperatures indicated temperature differences between the environmental heat loads an elephant experienced at a point in time compared to what it would have experienced if it were exposed to direct sunlight and in an open environment.

To assess environmental temperatures experienced by the elephants during shade utilisation and water-related activities, the difference between collar and weather station mini-globe temperatures were plotted over time along with periods of shade utilisation and water-related activities. I then compared median, maximum and minimum values of the difference in collar and weather station mini-globe temperature when the elephant was exposed to direct sun, in shade and when wet. The residuals were not normally distributed; therefore, a non-parametric Kruskal-Wallis ANOVA was run to compare the median difference in mini-globe temperature when elephants were exposed to sun, in shade and when wet.

To model the relationship between skin temperature and the environmental heat load experienced by an elephant, mean skin temperature as a function of collar mini-globe temperature was plotted using a bivariate scatter plot. A generalised linear mixed model (GLMM) using individual elephant as a random effect was then performed to assess the strength of the relationship using the *nlme* package (Pinheiro et al. 2013) in R (R, version 2.15.2; R Core team 2012).

To identify the critical black globe temperature at which the elephants began to seek shade and employ water-related activities, I correlated weather station and collar mini-globe temperatures using linear piecewise regressions with the *segmented* package (Mugge 2008) in R (R, version 2.15.2; R Core team 2012) for each individual elephant. This analytical procedure identifies the most likely point on the x-axis that the pattern can be represented by two linear regressions. I then tested whether the slopes of the two fitted regressions differed significantly from a slope of 1. A slope not significantly different from 1 implies that the individual was conforming to the environment while a slope  $< 1$  implies that an individual was experiencing heat loads cooler than what it would have experienced in an open environment (Hetem et al. 2007). Previous studies using this comparative approach used a simple linear Pearson procedure to deduce the relationship between collar and weather station mini-globe temperature (e.g. Hetem et al. 2007). The intercept of the linear regression with the line of identity (slope of 1) was used as an indicator or threshold temperature at which microclimate selection was initiated. However, a simple linear regression may not accurately identify the threshold temperature because temperatures above and below the threshold will ultimately alter the regression. Considering this, a simple linear regression would most likely overestimate the thermoregulatory ability of elephants at low environmental temperatures. For this reason, I analysed the relationship using a linear piecewise regression and the identified breakpoint was assumed to indicate the temperature at which an individual initiated behavioural thermoregulation (shade use and wetting behaviour).

### 4.3 RESULTS

In total, 77 days of behavioural observations with collar mini-globe temperatures were recorded, totalling 524 hours. During this period, 1050 usable thermal images were captured and analysed. During behavioural observations, weather station mini-globe temperatures ranged from a mean minimum of  $27.9 \pm 5.0^\circ\text{C}$  (mean  $\pm$  standard deviation) to a mean maximum of  $39.7 \pm 4.6^\circ\text{C}$ , with an absolute minimum mini-globe temperature of  $18.1^\circ\text{C}$  and a maximum of  $47.9^\circ\text{C}$  recorded.

Weather station mini-globe temperatures exceeded those on the collar when elephants were in shade or when elephants employed water-related activities (illustrated by a difference of  $< 0^\circ\text{C}$  between collar and weather station mini-globe temperature; Figure 4.1). During relatively hot days (mean daily weather station mini-globe temperature ( $\bar{T}_{\text{mg}}$ )  $> 36^\circ\text{C}$ , e.g. Figure 4.1a, b, c), elephants selected shade, mud-bathed and swam. All these activities induced marked decreases in collar mini-globe temperatures. On relatively cool days ( $\bar{T}_{\text{mg}} < 36^\circ\text{C}$ , e.g. Figure 4.1d, e, f) these activities seldom took place and elephants then stood in the open, exposed to direct sunlight.

Despite a large variation in recorded temperature differences, temperature differences between collar and weather station mini-globe temperatures (collar minus concurrently recorded weather station mini-globe temperature) were mostly below  $0^\circ\text{C}$  when elephants were in the shade or wet (Figure 4.2). The median difference between collar and weather station mini-globe temperature differed significantly from those recorded when the elephants were exposed to sun, in shade and when wet (Kruskal-Wallis  $H_3; 6288=1201; p<0.0001$ ; Figure 4.2). Elephants experienced temperatures up to  $3.5^\circ\text{C}$  (median) lower when in shade than what they would have experienced if exposed to direct sunlight. Likewise, the elephants experienced temperatures up to  $8.5^\circ\text{C}$  lower when wet than what they would have

experienced if dry and exposed to direct sunlight. Differences between collar and weather station mini-globe temperatures were lowest when the elephants were exposed to direct sunlight, with a median difference of  $-0.39^{\circ}\text{C}$ . On occasion, collar mini-globe temperatures were up to  $20^{\circ}\text{C}$  cooler when the elephant was exposed to direct sun or standing in shade; this was as a result of the mini-globe still being wet while the elephant was not employing wetting activity.

A significant linear relationship was evident between mean skin temperature and collar mini-globe temperature ( $y = 0.47x + 18.26$ ;  $t_{1043}=35.7$ ;  $p < 0.0001$ ; Figure 4.3). The model explained 60% of the variation observed in mean skin temperature regardless of whether an elephant was in sun, in shade or wet. Therefore, skin temperature was dependent on environmental heat load.

Elephants selected microclimates and undertook behaviour which resulted in lower environmental heat loads at mini-globe temperatures above  $29.8 \pm 2^{\circ}\text{C}$  (mean identified breakpoint  $\pm$  standard deviation;  $n=6$ ; Figure 4.4). The slope ( $\beta$ ) of the upper breakpoint regression (linear regression lines above the identified breakpoint) for each individual was significantly  $< 1$  ( $p < 0.0001$ ), implying the selection of microclimates or adjustments of behaviour to occupy and achieve lower environmental heat loads. The slopes for the lower breakpoint regressions of adult female 1 and 2 and the weaned male calf were not significantly different from a slope of 1 ( $p > 0.05$ ; Figure 4.4a, b, d), implying that the elephants conformed to the environment and did not occupy microclimates or adjust behaviour to achieve lower environmental heat loads. The slope of the lower breakpoint regression for adult female 3 was only slightly significantly higher than a slope of 1 ( $\beta = 1.06$ ;  $F_{1,434} = 5.07$ ;  $p = 0.02$ ; Figure 4.4c). Lower breakpoint regression slopes for both weaned female calves were significantly  $> 1$  ( $p < 0.001$ ; Figure 4.4e, f), implying the selection of

microclimates or adjustments of behaviour to occupy and achieve lower heat loads at lower environmental temperatures; however, this may be an artefact of few low weather station mini-globe temperature recordings.

#### **4.4 DISCUSSION**

Elephants actively seek shade and employ water-related activities at high environmental temperatures and these behavioural activities occur more often on hotter days (Chapter 3). My results support the notion that this behaviour confers thermal benefits for elephants. By utilising shade, elephants can shelter themselves from high radiative temperatures, consequently reducing radiative heat gain. Furthermore, if air temperature within the shade is less than skin temperature, non-evaporative heat loss can take place, which allows for the regulation of core temperature. Likewise, wetting the skin directly cools skin temperature and likely results in conductive heat loss if elephants are fully wet or submerged in mud or water for extended periods.

For shade utilisation and wetting to provide a thermoregulatory benefit, this behaviour must be beneficial in regulating core temperature. Although the present study does not provide direct evidence of core temperature regulation, core temperatures recorded in the elephants during this study period did not fluctuate beyond a range of 2°C within a day, despite environmental temperatures often exceeding 40°C (Rodrigues D’Araujo 2014). Based on this evidence, I suggest that both shade and water are essential resources for thermoregulation that allow elephants to regulate heat exchange with the environment.

Despite their large size, my results highlight the ability for elephants to utilise resources such as shade and water across space and over time, which allow them to buffer the effects of high environmental temperatures. However, shade alone may not provide an



effective thermoregulatory benefit for elephants at high environmental temperatures. If air temperatures exceed core temperature in the shade, shade utilisation will not increase heat loss, only decrease radiative heat gain, consequently elephants will not be able to lose heat through non-evaporative pathways. During extremely high environmental temperatures, wetting the skin to enhance evaporative cooling and replenishing body water reserves to maintain cutaneous evaporative cooling likely becomes a priority (Dunkin et al. 2013). The need to maintain evaporative cooling may ultimately tether elephants to water sources. During dry and hot periods of the year, elephant distribution is dependent on water availability as elephants tend to forage close to water (de Beer et al. 2006; Chamailé-Jammes et al. 2007; Harris et al. 2008). I suggest thermoregulatory requirements may be a mechanism driving this observed pattern.

Elephants began to employ shade utilisation and wetting behaviour when black mini-globe temperatures were about 30°C. At 30°C, environmental temperatures are not conducive for heat gain as a thermal gradient still exists between the elephant and its environment, favouring non-evaporative heat loss. However, while collar mini-globe temperature takes into account environmental heat load, it does not take into account physiological heat load. Heat storage in deep core tissue may increase in elephants during activities such as feeding and locomotion (Rowe et al. 2013). To dissipate this heat and avoid thermal stress, it would be beneficial for elephants to utilise microclimates such as shade where radiative temperatures are lower and the thermal gradient between their skin and the environment (in this case air temperature) is more conducive for non-evaporative heat loss. As such, behavioural thermoregulation may be initiated at cooler environmental temperatures than expected. An alternative explanation is that perceived rising temperatures on the skin may have induced thermal discomfort, resulting in an anticipatory behavioural response (Frank 1999). It may be energetically too costly for elephants to wait for skin temperature or environmental

temperature to increase to 36°C before behavioural adjustments are initiated. To maintain a level of thermal comfort elephants likely employ an anticipatory behavioural response to ultimately avoid heat gain from the environment. At the same time perceived temperatures on the skin return to a point of comfort.

There are a number of ecologically relative insights that can be gained from the results of this study. Above and below environmental temperatures of 30°C, elephants are likely employing different behaviour aimed at fulfilling different physiological requirements. In this case, the elephants conformed to their thermal environment at relatively cool environmental temperatures (< 30°C), implying that the behavioural decisions made during this period were not thermally motivated. However, as environmental temperature increased (>30°C) the elephants began to adjust their behaviour aimed at decreasing environmental heat load by actively occupying microclimates and employing water-related activities. As such, the elephants were likely in close proximity to shaded habitats and or water. In this way, one would expect fine-scale spatial use patterns to differ above and below approximately 30°C as habitat selection and behaviours are altered. Ultimately, how elephants use space can have consequences for the impact elephants have on a landscape (Brits et al. 2002; de Beer et al. 2006; Chamaillé-Jammes et al. 2007; Guldmond and van Aarde 2008; Vanak et al. 2010) and for the survival of young (Young and van Aarde 2010). Incorporating temperature as a factor driving various space use patterns is therefore crucial in future studies regarding elephant ecology.

Unexpectedly, results obtained for both weaned female calves were different to those observed for the other four adult elephants at low environmental temperatures in that the weaned calves showed a decrease in environmental heat loads at low environmental temperatures, illustrated by a lower breakpoint regression slope > 1. From a statistical perspective, this result may simply be due to few records at low weather station mini-globe

temperatures for the two weaned female calves as weather station mini-globe temperatures below 23°C were not recorded for either of the individuals in comparison to the three adults and weaned male calf. A more analytically correct approach, although impractical at the time, would have been to place collars on all the individuals and record environmental heat loads simultaneously under identical thermal conditions.

From an ecological perspective, it is plausible that the weaned female calves were selecting cooler microclimates and employing water-related activities at low environmental temperatures (~25°C). These behavioural activities were likely not employed as a thermoregulatory response but rather a hedonistic response during social and playing activities. As well as employing shade utilisation and water-related activities at low environmental temperatures, the weaned female calves may have selected or been exposed to microclimates warmer than they would have experienced out in the open at intermediate environmental temperature (~30°C). At times, all of the elephants experienced environmental heat loads greater than what they would have experienced exposed to direct sunlight, particularly at intermediate environmental temperatures. This observation is not unusual and has been recorded previously in studies using ambulatory mini-globe temperature recording devices (e.g. Hetem et al. 2007). I suggest that higher temperatures may have been directly experienced by the elephants through behavioural adjustments of sheltering from wind in which convective heat loss from the globe decreased, or the mini-globe itself may have been heated by radiation emitted or reflected from the elephants body. Although not recorded as a behavioural adjustment, during periods of cool mornings when wind speed was high, I noted that elephants selected for densely vegetated habitats. Interestingly, this behaviour may reflect a thermoregulatory response to reduce convective heat loss by sheltering from the wind. While wind sheltering has not been observed in previous studies in elephants, elephants are known to respond to increased wind during high environmental temperatures by opening

their ears while orientating their body downwind, which likely increases heat loss (Buss and Estes 1971). It must also be noted that the two weaned female calves had a shoulder height of less than 1.9m and were likely more sheltered from wind in dense vegetation than the taller herd members, resulting in warmer collar mini-globe temperatures at low and intermediate weather station mini-globe temperatures.

Ultimately, shade utilisation and water-related activities such as mud bathing and swimming do provide a thermoregulatory benefit for elephants by altering heat exchange with the environment and elephants are more likely to employ such behaviour at environmental temperatures exceeding 30°C. By actively employing these behaviours elephants are able to cope in thermal environments that we may consider extreme. If resources such as shade and water are readily available for elephants to utilise then they will likely be able to buffer the effects of extreme thermal conditions brought about by predicted climate change. However, the ecological consequences thereof need to be investigated further, particularly with regards to fine-scale space use.

## 4.5 FIGURES

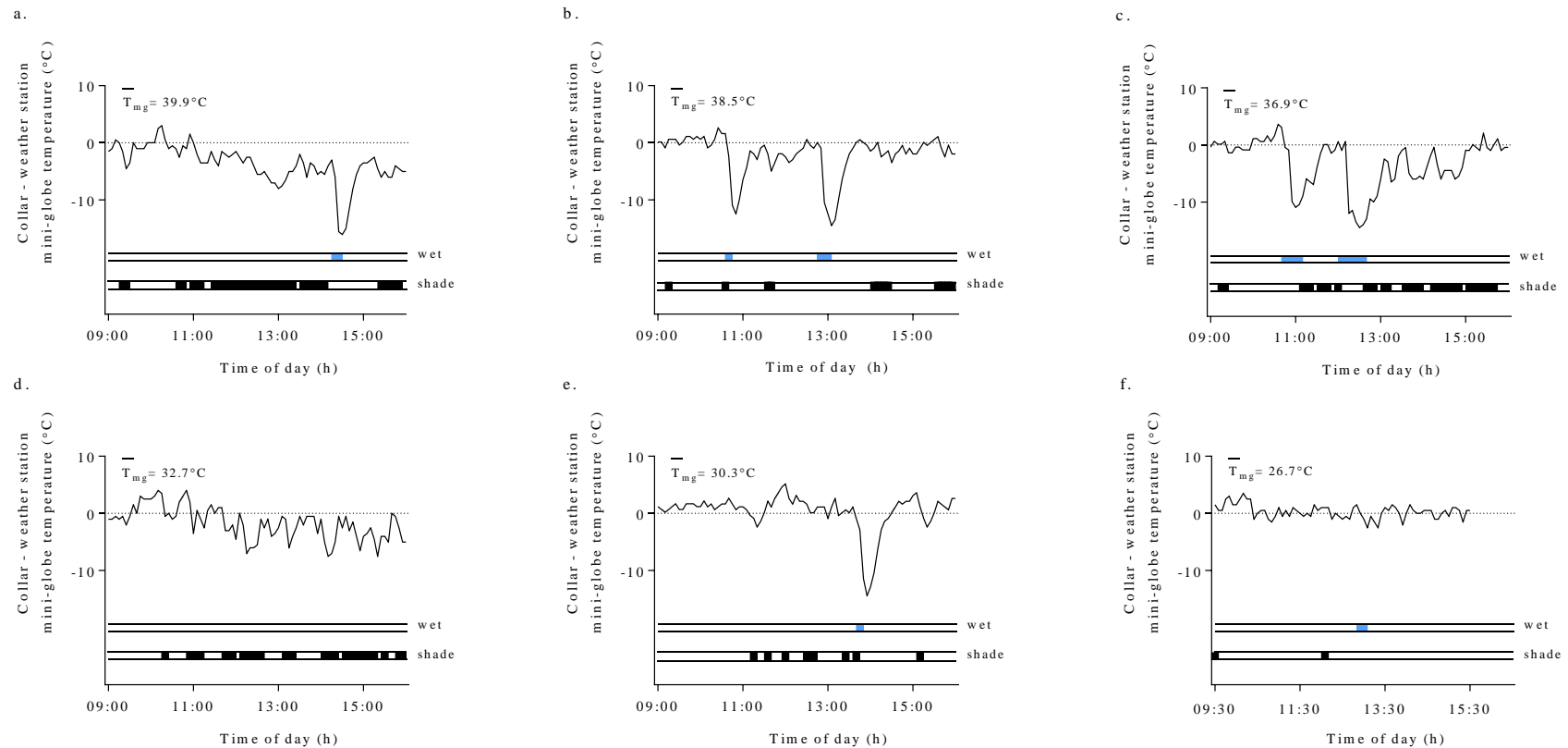


Figure 4.1. Difference between mini-globe temperature experienced by an elephant (collar mini-globe temperature) and the temperature of an identical mini-globe exposed to the sun at a weather station in the study site nearby as a function of time of day for six random days (a-f), together with behavioural observations of shade utilisation (shade= ■) and water-related activities such as mud bathing and swimming (wet= ■). Horizontal dotted lines indicate a  $0^{\circ}\text{C}$  difference between collar and weather station mini-globe temperature. A negative temperature reflects the selection of microclimate conditions or the employment of behaviour that exposes the individual elephant to temperatures that are cooler than what they would experience if dry and exposed to sun.  $\bar{T}_{mg}$  = mean weather station mini-globe temperature during the observation period.

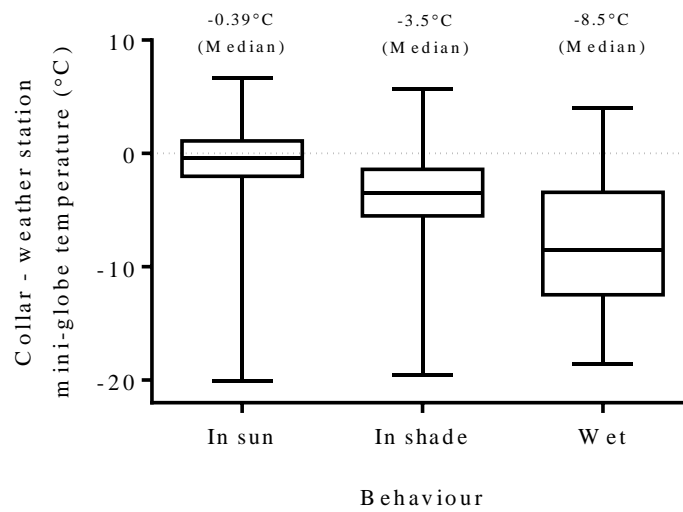


Figure 4.2. Median difference between mini-globe temperature experienced by the elephants (collar mini-globe temperature) under three different behavioural states and the temperature of an identical mini-globe exposed to the sun at a weather station in the study site nearby. Boxes illustrate 25<sup>th</sup> and 75<sup>th</sup> percentiles; bars illustrate minimum and maximum values. Medians differed significantly between behavioural states (Kruskal-Wallis  $H_3$ ;  $6288=1201$ ;  $p<0.0001$ ).

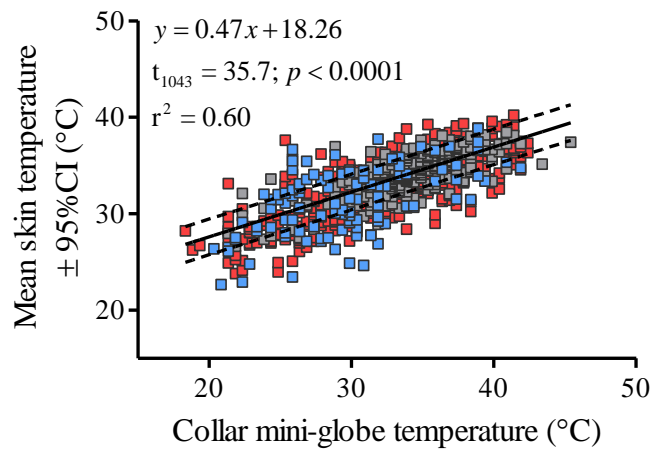


Figure 4.3. Mean skin temperature as a function of collar mini-globe temperature. Collar mini-globes recorded environmental heat loads elephants experienced when the elephant was exposed to direct sun (■, n=646), in shade (■, n=294), and wet (■, n=110). Skin temperature was dependent on the environmental heat load elephants experienced regardless of behavioural state, increasing significantly ( $p < 0.0001$ ) with collar mini-globe temperature. The solid black line is the regression line and the dashed lines are 95% confidence intervals.

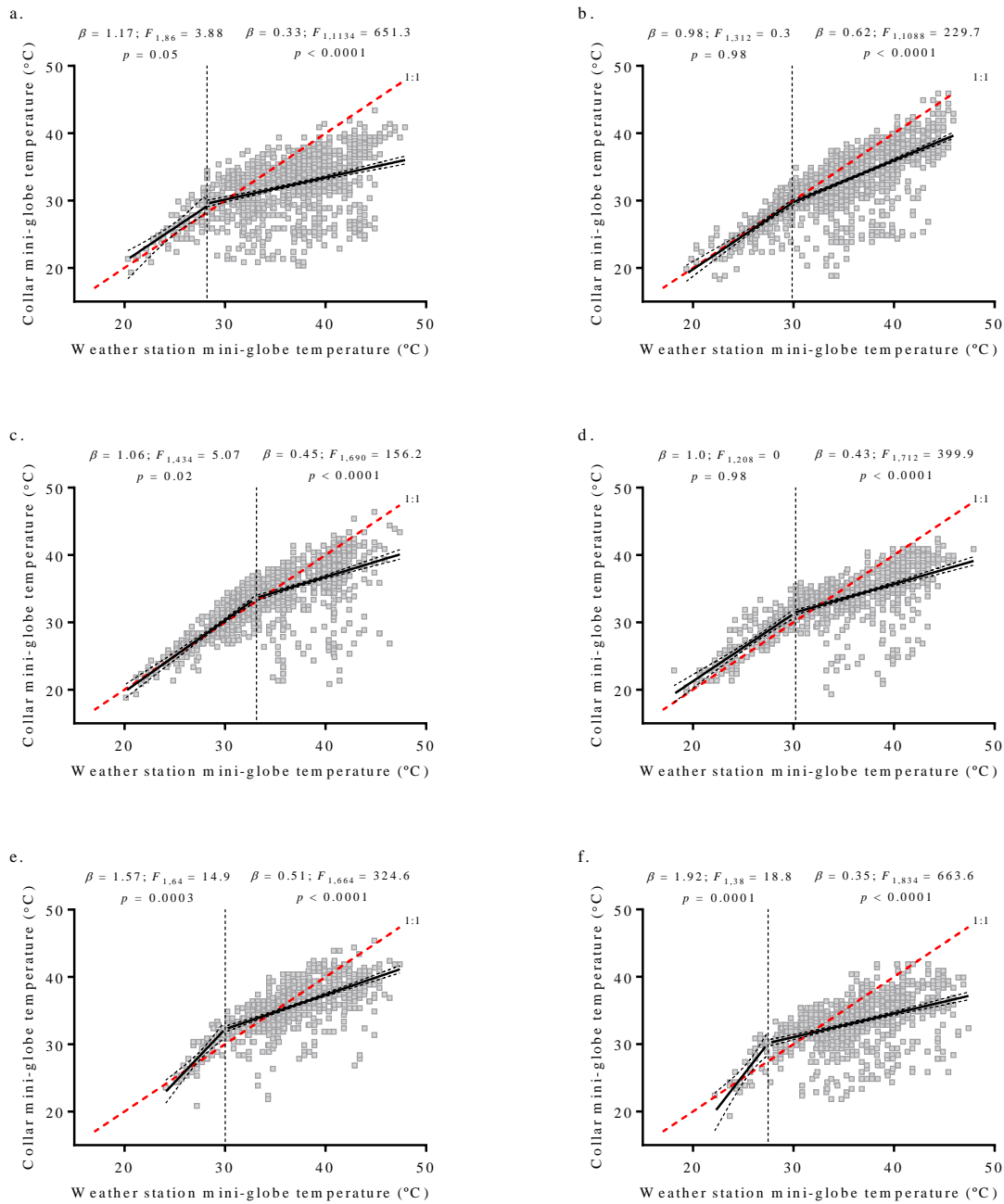


Figure 4.4. Scatter diagram showing the relationship between mini-globe temperature experienced by each individual elephant (collar mini-globe temperature) and mini-globe temperature recorded concurrently at a weather station exposed to direct sunlight in the study site nearby. The vertical dotted line indicates the breakpoints identified by piecewise regression. Slopes ( $\beta$ ) of the linear regression and statistics for the significance of the slope in relation to a slope of 1 before and after the breakpoints are illustrated. The red dashed horizontal lines are lines of identity (slope of 1), solid black lines are the regression lines and the dashed lines are 95% confidence intervals. a) adult female 1; b) adult female 2; c) adult female 3; d) weaned male calf 1; e) weaned female calf 1; f) weaned female calf 2.



## CHAPTER 5. SYNTHESIS

Elephants are keystone species and their presence in savanna ecosystems is crucial (Owen-Smith 1989). They play a key role in shaping savanna vegetation heterogeneity (Guldmond and van Aarde 2008; Kohi et al. 2011; Vanak et al. 2012; Valeix et al. 2011) and the impact they have within a habitat can directly or indirectly influence other species (Pringle 2008; Landman and Kerley 2014). To enhance our ability to conserve this important species in the future and under changing environmental conditions, an understanding of the interaction between elephants and their environment is necessary. In this regard, many previous studies have recognised how elephant behaviour, habitat selection and distribution are affected by surface water distribution (Chamaillé-Jammes et al. 2007; Harris et al. 2008), forage availability (Young et al. 2009), fences (Loarie et al. 2009; Vanak et al. 2010) and humans (Graham et al. 2009; Roever et al. 2012). However, very little attention has been given to climate. The results of my study show that we cannot ignore climate in elephant ecology. Environmental temperature is a significant factor dictating elephant behaviour and is likely a key determinant of habitat selection and space use in elephants. In hot environments, in particular, I suggest that environmental temperature is probably the most influential factor dictating behaviour in elephants and may further be linked to calf survival, sexual segregation and individual fitness.

So what does this finding mean for elephants and climate change? How will elephants respond to climate change and can they adapt? In their review, Bellard et al. (2012) provide an overview for how a species may respond to future climate change. They highlight the importance of phenotypic plasticity, or the ability for a species to change physiologically or behaviourally to the environment across three main axes which function non-exclusively and

at various scales (e.g. within a day or season). These three axes include *spatial changes* e.g. distributional range shifts, microclimate selection; *temporal changes* e.g. shifts in activity, phenology; or *self changes* that involve physiological or behavioural changes unrelated to space and time, that allow a species to cope in unfavourable climatic conditions. Ultimately, failure to respond along one of the above axes will result in extinction for a population or species (Bellard et al. 2012).

In the present study, elephants made use of both *spatial* and *temporal* behavioural adjustments that were of a thermoregulatory benefit during high environmental temperatures. Examples of these adjustments included the selection of shaded microhabitats during the heat of the day and shifts in feeding patterns to the cooler hours of the day. Although not as obvious, *self changes* were also apparent. For example, increased water-related activities may reflect a physiological and behavioural response to maintain body water reserves while simultaneously lower the costs of autonomic responses in keeping cool. Increased water-related activities may also decrease the dependence elephants have on shade, allowing them to fulfil other physiological requirements such as feeding.

I suggest that the *spatial*, *temporal* and *self* behavioural adjustments observed in my study reflect adaptive responses that enable elephants to cope and survive in thermally stressful environments. Furthermore, while not included in this study, core temperature of the elephants was recorded simultaneously with behavioural observations (Rodrigues D'Araujo 2014). There was no evidence from these results to suggest that the elephants were unable to maintain thermal homeostasis, despite environmental temperatures exceeding 40°C. The elephants also did not employ heterothermy (Rodrigues D'Araujo 2014). This result implies that elephants at present can cope in the heat and contradicts previous suggestions that elephants face difficulties in keeping cool due to their large size (Phillips and Heath 1995; Rowe et al. 2013). The clear flexible ability of elephants to respond behaviourally to present

day environmental temperatures in such a diverse manner and their ability to maintain thermal homeostasis is a promising observation in the face of climate change. As long as resources such as shade and water are available for elephants, and their ability to adjust behaviourally is unhindered, then they will likely cope with climate change with no direct consequences of thermal stress.

While increasing temperatures may not directly affect an elephant's ability to keep cool when environmental temperatures exceed those typical of present living conditions, thermally driven behavioural adjustments may have consequences for individual fitness (du Plessis et al. 2012; van Beest et al. 2012; van Beest and Milner 2013; Long et al. 2014). Of particular importance are the costs that temperature-induced shifts in activity and altered habitat selection may have for feeding activities. As activity patterns, habitat selection and ultimately spatial use dynamics are altered in response to environmental temperature, feeding time may decrease (Belovsky and Slade 1986) and trade-offs in forage availability and quality may be encountered (van Beest et al. 2012; Long et al. 2014). If individuals are unable to compensate for these constraints on feeding, fitness costs may arise (van Beest and Milner 2013). How long an elephant needs to feed for to maintain its daily energy requirements is unknown; however, in the wild, elephants spend 12-16 hours per day feeding (Wyatt and Eltringham 1974; Guy 1976). In the present study, behaviour was orientated towards fulfilling thermoregulatory requirements at 30°C (black mini-globe temperature) and above (see Chapter 4). This behaviour included increased shade utilisation, water-related activities and resting. As a result, thermoregulation was prioritised and a trade-off between thermoregulation and energy intake was likely encountered.

To assess the extent to which thermoregulatory behaviour may interrupt or limit feeding activity one only has to look at the amount of time per day which elephants are facing temperatures above 30°C and are likely prioritising behavioural thermoregulation (Figure

5.1). Due to the unavailability of black globe temperature data, air temperature was used (Figure 5.1). At air temperatures of 30°C, black globe or environmental temperatures will be at a minimum of 30°C if there is no radiative heat gain. In most cases however, at air temperatures of 30°C, environmental temperatures will be greater than 30°C. Therefore, the proceeding inferences are likely an underestimate of the amount of time elephants experience environmental temperatures exceeding 30°C. Air temperatures exceed 30°C on days throughout the year in both Kruger National Park and northern Botswana (Figure 5.1a, b). However, the mean percentage (%) of time per day each month that elephants face air temperatures above 30°C in northern Botswana far exceeds the percentage of time per day which elephants experience temperatures above 30°C in Kruger National Park (Figure 5.1c). During the hottest month in Kruger (February), elephants experience temperatures above 30°C on average for only  $21 \pm 11\%$  (mean  $\pm$  SD) of the day, which equates to approximately 5 hours a day. In northern Botswana however, there are five months during the year with averages higher than 21%. In October in particular, elephants experience temperatures above 30°C on average for  $41 \pm 15\%$  of the day, which equates to approximately 10 hours a day (Figure 5.1c). The ultimate question is whether trade-offs experienced during this time have a negative effect on an individual's fitness or not. Without further investigation, we do not know, but the answer will likely depend on a combination between an elephant's ability to compensate for lost feeding time and the availability and distribution of required resources (water, forage, shade) within its surroundings.

In Kruger National Park, conditions during February are suitable for elephants to flourish. February may be the hottest time of the year but it is also very wet (Gertenbach 1980), consequently, plentiful forage and shade is available. As such, elephants are likely able to thermoregulate and maintain water requirements whilst incurring minimal costs on feeding. In contrast, in northern Botswana, it is very dry during October, forage is scarce

(Owen-Smith and Chafota 2012) and water often is limited to the few perennial rivers (Verlinden and Gavor 1998; Stokke and du Toit 2002). In these habitats, I hypothesise that elephants at present are experiencing trade-offs between thermoregulation and energy intake more often than elephants in Kruger National Park. These trade-offs will likely be further compounded by the presence of suckling calves within a herd as elephants may be forced to move long distances between forage and water while simultaneously fulfil thermoregulatory requirements and ensure the survival of their young.

An observation on large endotherms inhabiting hot thermal environments is a shift in feeding activity to night (Ostrowski et al. 2003; Hetem et al. 2011a; Maloney et al. 2005). Recent studies investigating displacement activities in elephants suggest that they are more active at night than during the day during seasons when environmental temperatures are high (Loarie et al. 2009; Leggett 2010). Based on these observations and observations made during this study, I hypothesise that elephants in thermally stressful environments will show increased night activity as a direct consequence of temperature-mediated reductions in daytime feeding activity. Whether or not a shift to night-time activity will compensate for a loss of up to 10 hours of feeding time and the implications this adjustment may have for other activities such as sleeping and socialising remains to be investigated.

While the emphasis of my study was on behavioural thermoregulation, we cannot underestimate the contribution autonomic thermoregulatory responses provide for elephants (see Chapter 1). For example, cutaneous evaporative water loss may allow elephants to dissipate heat while simultaneously fulfilling other physiological requirements. However, cutaneous evaporative water loss results in significant amounts of water loss (Dunkin et al. 2013) and the maintenance of body water reserves may ultimately tether elephants to water sources (Dunkin et al. 2013). In this way, trade-offs between water and forage may be

encountered, particularly during dry and hot conditions. Climate change is likely to intensify this trade-off.

It is clear that while elephants may not struggle to keep cool, increasing temperatures because of climate change may lead to a number of trade-offs and costs which may ultimately be detrimental for individual fitness. These trade-offs cannot be overlooked, particularly when elephants are spatially restricted. Local populations able to expand their range into favourable habitats will be at an advantage, as their ability to adapt and survive in the future with climate change will be improved. However, if elephants are spatially restricted, or lack the resources and opportunities to fulfil basic nutritional and thermal requirements, trade-offs brought about by climate change may increase in magnitude, resulting in detrimental consequences for individual fitness. Space is therefore crucial for elephants in the future of climate change.

In northern Botswana temperatures are extreme (see Chapter 1, Figure 1), yet it is interesting to note that at present an estimated 130 000 savanna elephants inhabit the region (Chase 2011). The large numbers imply that temperature does not or has not played a role in the current distribution of elephants. Elephants are present where there is water, plentiful forage and few people (Harris et al. 2008; Young et al. 2009; Roever et al. 2012), regardless of whether it is hot or cold. Increasing temperatures therefore may not be the immediate concern for elephants but this does not mean that climate change can be ignored.

Without doubt, the greatest concern for elephants is the effect climate change will have on their habitat and consequently the resources they require to survive. Predicted reductions in rainfall and an increase in the frequency of extreme climatic events such as drought within the distributional range of elephants (Collins et al. 2013; Ameca y Juárez et al. 2013), will likely alter local vegetation cover (Scheiter and Higgins 2009; Willis et al. 2013),

and the distribution of surface water (Milly et al. 2005; de Wit and Stankiewics 2006). The reduction of food availability and surface water will have consequences for elephant distribution, reproduction and ultimately survival (Chamaillé-Jammes et al. 2008; Foley et al. 2008; Trimble et al. 2009; Shrader et al. 2010; Young and van Aarde 2010). Furthermore, an elephant's ability to buffer extreme climatic conditions behaviourally without costly trade-offs is likely to be hindered if resources such as shade, water and forage become limited. Climate change in combination with habitat alterations will soon be the primary concern for elephants and when this happens, elephants restricted in space will likely face the full consequences of climate change as their ability to balance nutritional, water and thermoregulatory requirements becomes limited.

### *Moving Forward*

The main objective of this study was to gain a mechanistic understanding of how elephants respond behaviourally to environmental temperature. Behavioural observations on tame semi-captive savanna elephants are not ideal and may be seen as a limitation of this study. However, the elephants I studied were free to respond behaviourally to environmental temperature, as any wild elephant would do. From this perspective, my main objective was achieved. Moving forward however, studies must focus on wild elephants.

From my study, it is clear that climate is likely playing a larger role for elephant ecology than previously recognised. Climate alters behaviour, but its role in altering habitat selection and space use, and consequently the negative effects it may have for local population dynamics directly and indirectly through altered vegetation cover and surface water availability needs further investigation. In the face of climate change there is still a lot that we do not know and it is of critical importance for the conservation of the species that we

fully understand the interaction between elephants and climate and the consequences thereof.

As such, I propose that future studies should focus on answering the following questions:

1. How often and how much do elephants need to eat to maintain energy requirements?
2. How does temperature affect fine-scale habitat selection and space use in elephants and are their consequences on individual fitness?
3. What are the physiological effects of climate on suckling calves?
4. Are there differences between how family groups and adult bulls respond behaviourally to temperature?
5. What is the relationship, if any, between elephant population dynamics and environmental temperature?

To answer the above questions, I propose a comparative investigation between elephant populations along a contrasting thermal gradient, for example between Northern Botswana, Addo Elephant National Park (South Africa) and Kruger National Park (South Africa). These studies should focus on temperature-mediated behavioural adjustments and habitat selection as well as long-term population dynamics. While direct behavioural observations may not be practical, I have shown that ambulatory mini-globe temperature recording devices are a highly valuable and practical tool for future research on elephant ecology. However, I do suggest that the durability of the device is improved. Following this, a number of questions can be addressed, particularly if recorded mini-globe temperatures are combined with concurrently recorded telemetry data.

In conclusion, climate change is a reality and understanding how species will cope with predicted climate change is therefore a priority. We may understand the basic behavioural responses of elephants to environmental temperature but the lack of understanding regarding the consequences of such behaviour for elephants is a concern. We cannot ignore environmental temperature in elephant ecology. As temperatures increase and



habitats become drier, elephants will face a rise in trade-offs and will likely face difficulties in maintaining a balance between nutritional, water and thermoregulatory requirements. Soon climate change in combination with habitat loss will likely become the primary factor dictating elephant distribution across Africa. We must prioritise investigations into the relationship between elephants and climate.

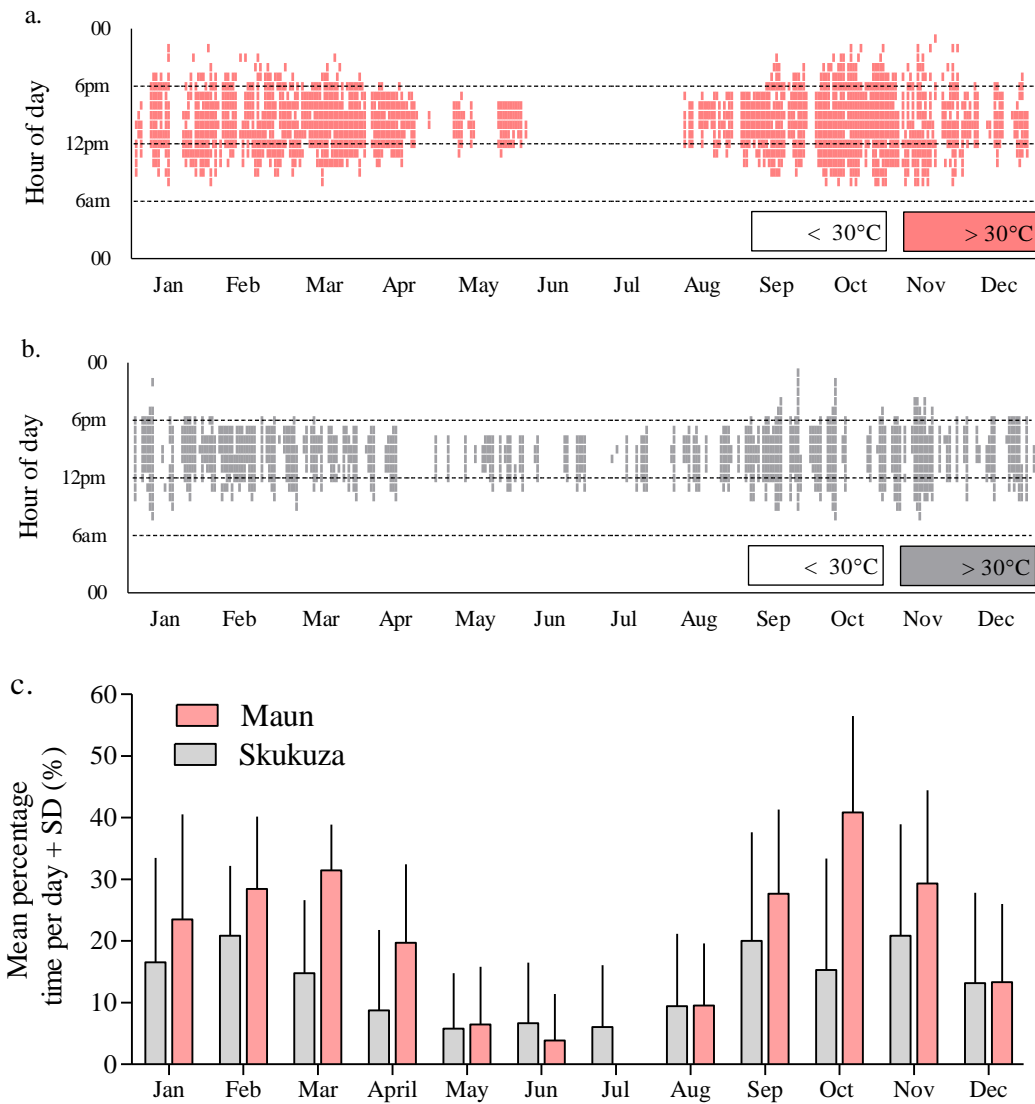


Figure 5.1. Hours during each day of the year 2013 that air temperatures exceeded 30°C for a) Maun, bordering the Okavango Delta in Botswana (Botswana Meteorological Services), and b) Skukuza, Kruger Nation National Park, South Africa (South African Weather Services; data for both stations obtained from [http://mesonet .agron.iastate.edu](http://mesonet.agron.iastate.edu)). c) The mean percentage (%) of time per day + standard deviation (SD) each month that elephants are experiencing air temperatures above 30°C in each location.

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## CHAPTER 7. APPENDICES

Appendix I. Summary of the number of hours that behavioural observations were conducted on an individual elephant in the present study.

	Total no. of days	Total hours sampled	Hours per elephant					
			AF1	AF2	AF3	WM4	WF5	WF6
Hot-dry	48	331	54	90	62	42	42	40
Cool-flood	32	215	41	41	32	35	33	33
<b>Total</b>	<b>80</b>	<b>545</b>	<b>95</b>	<b>131</b>	<b>94</b>	<b>77</b>	<b>75</b>	<b>73</b>

*Notes:* AF= Adult female, WM =Weaned male calf, WF = Weaned female calf.

Appendix II. Summary of candidate generalised additive mixed models for the probability of wetting.

no.	model <sub>i</sub>	K	LogLik	AIC <sub>i</sub>	$\Delta$ AIC <sub>i</sub>	w <sub>i</sub>	ROC
1	Tmg + time + season	15.4	-1066.0	2162.91	0	0.26	0.757
2	Tmg + time + group + season	15.6	-1065.9	2162.98	0.07	0.25	0.757
3	Tmg + time + class + season	15.7	-1065.9	2163.06	0.15	0.24	0.757
4	Tmg + time + group + class + season	15.8	-1065.8	2163.17	0.25	0.23	0.757
5	Tmg + time	14.3	-1071.0	2170.63	7.71	0.01	0.751
6	Tmg + time + group	14.5	-1070.9	2170.73	7.82	0.01	0.751
7	Tmg + time + class	14.7	-1070.7	2170.83	7.91	0.00	0.752
8	Tmg + time + group + class	14.8	-1070.7	2170.96	8.05	0.00	0.752
9	Tmg + + season	9.7	-1085.6	2190.61	27.7	0.00	0.730
10	Tmg + group + season	9.8	-1085.5	2190.69	27.78	0.00	0.730
11	Tmg + class + season	9.9	-1085.5	2190.76	27.84	0.00	0.730
12	Tmg + group + class + season	10.1	-1085.4	2190.87	27.96	0.00	0.730
13	Tmg	8.6	-1092.6	2202.33	39.42	0.00	0.720
14	Tmg + group	8.7	-1092.5	2202.44	39.53	0.00	0.720
15	Tmg + class	8.9	-1092.4	2202.52	39.61	0.00	0.720
16	Tmg + group + class	9.0	-1092.3	2202.66	39.75	0.00	0.720
17	time + season	12.2	-1091.3	2207.06	44.15	0.00	0.736
18	time + group + season	12.4	-1091.2	2207.13	44.22	0.00	0.737
19	time + class + season	12.4	-1091.2	2207.17	44.26	0.00	0.736
20	time + group + class + season	12.5	-1091.1	2207.27	44.36	0.00	0.737
21	season	6.4	-1117.7	2248.36	85.44	0.00	0.699
22	group + season	6.6	-1117.7	2248.43	85.52	0.00	0.700
23	class + season	6.6	-1117.6	2248.47	85.56	0.00	0.700
24	group + class + season	6.7	-1117.6	2248.57	85.66	0.00	0.700
25	time	11.2	-1146.6	2315.48	152.56	0.00	0.662
26	time + group	11.3	-1146.5	2315.57	152.65	0.00	0.663
27	time + class	11.4	-1146.4	2315.64	152.73	0.00	0.662
28	time + group + class	11.6	-1146.3	2315.76	152.84	0.00	0.662
29	group	5.4	-1172.4	2355.57	192.66	0.00	0.600
30	class	5.5	-1172.3	2355.65	192.74	0.00	0.600
31	group + class	5.7	-1172.2	2355.77	192.86	0.00	0.600

Notes: For each model, the model number (no.), number of parameters (K), loglikelihood value (LogLik), Akaike information criteria (AIC<sub>i</sub>), difference in AIC between the best fit model and model<sub>i</sub> ( $\Delta$ AIC<sub>i</sub>), Akaike weight (w<sub>i</sub>), area under receivers operating characteristic curve (ROC) are shown. Parameters: Tmg = black mini-globe temperature; time = time of day; class= age class; group = family group.

Appendix III. Summary of candidate generalised additive mixed models for the probability of shade use.

no.	model <sub>i</sub>	K	LogLik	AIC <sub>i</sub>	ΔAIC <sub>i</sub>	w <sub>i</sub>	ROC
1	Tmg + group	9.5	-3459.0	6936.85	0	0.10	0.743
2	Tmg + group + class	9.7	-3458.9	6937.06	0.22	0.09	0.743
3	Tmg	9.9	-3458.8	6937.26	0.41	0.08	0.743
4	Tmg + class	9.9	-3458.7	6937.3	0.45	0.08	0.743
5	Tmg + group + season	10.4	-3458.3	6937.36	0.51	0.08	0.744
6	Tmg + group + class + season	10.6	-3458.2	6937.57	0.73	0.07	0.743
7	Tmg + season	10.8	-3458.1	6937.76	0.91	0.07	0.743
8	Tmg + class + season	10.9	-3458.0	6937.8	0.95	0.06	0.743
9	Tmg + time + group + season	11.4	-3457.6	6938.12	1.27	0.05	0.744
10	Tmg + time + group + class + season	11.6	-3457.5	6938.33	1.48	0.05	0.744
11	Tmg + time + group	10.5	-3458.8	6938.48	1.63	0.05	0.743
12	Tmg + time + + season	11.8	-3457.4	6938.51	1.66	0.05	0.744
13	Tmg + time + class + season	11.9	-3457.4	6938.54	1.7	0.04	0.743
14	Tmg + time + group + class	10.7	-3458.7	6938.69	1.84	0.04	0.743
15	Tmg + time	10.9	-3458.6	6938.88	2.03	0.04	0.743
16	Tmg + time + class	10.9	-3458.5	6938.92	2.08	0.04	0.743
17	time + group + season	10.7	-3591.2	7203.78	266.93	0.00	0.710
18	time + group + class + season	10.8	-3591.1	7203.88	267.03	0.00	0.710
19	time + season	10.8	-3591.1	7203.93	267.08	0.00	0.710
20	time + class + season	10.9	-3591.1	7203.95	267.11	0.00	0.710
21	group + season	6.8	-3686.4	7386.4	449.56	0.00	0.687
22	group + class + season	6.9	-3686.4	7386.51	449.66	0.00	0.687
23	season	6.9	-3686.4	7386.55	449.7	0.00	0.687
24	class + season	6.9	-3686.4	7386.58	449.73	0.00	0.687
25	time + group	9.3	-3770.3	7559.23	622.39	0.00	0.653
26	time + group + class	9.4	-3770.3	7559.35	622.51	0.00	0.654
27	time	9.5	-3770.2	7559.42	622.57	0.00	0.653
28	time + class	9.5	-3770.2	7559.45	622.61	0.00	0.653
29	group	5.7	-3858.2	7727.77	790.92	0.00	0.618
30	group + class	5.8	-3858.1	7727.89	791.04	0.00	0.618
31	class	5.9	-3858.1	7727.99	791.14	0.00	0.618

Notes: For each model, the model number (no.), number of parameters (K), loglikelihood value (LogLik), Akaike information criteria (AIC<sub>i</sub>), difference in AIC between the best fit model and model<sub>i</sub> (ΔAIC<sub>i</sub>), Akaike weight (w<sub>i</sub>), area under receivers operating characteristic curve (ROC) are shown. Parameters: Tmg = black mini-globe temperature; time = time of day; class= age class; group = family group.

Appendix IV. Summary of candidate generalised additive mixed models for the duration of shade use.

no.	model <sub>i</sub>	K	LogLik	AIC <sub>i</sub>	ΔAIC <sub>i</sub>	w <sub>i</sub>	R <sup>2</sup>
1	Tmg + state + group	7	-879.7	1773.34	0.00	0.37	0.54
2	Tmg + state + group + class	8	-879.4	1774.73	1.39	0.18	0.53
3	Tmg + state + group + season	8	-879.5	1774.94	1.60	0.17	0.54
4	Tmg + state + group + season + class	9	-879.2	1776.48	3.14	0.08	0.53
5	Tmg + time + state + group	9	-879.3	1776.62	3.27	0.07	0.54
6	Tmg + time + state + group + class	10	-879.0	1777.99	4.65	0.04	0.54
7	Tmg + state	6	-883.4	1778.74	5.40	0.02	0.48
8	Tmg + time + state + group + season	10	-879.4	1778.85	5.51	0.02	0.54
9	Tmg + state + season	7	-883.1	1780.25	6.91	0.01	0.47
10	Tmg + time + state + group + season + class	11	-879.2	1780.34	7.00	0.01	0.54
11	Tmg + state + class	7	-883.3	1780.58	7.23	0.01	0.48
12	Tmg + time + state	8	-883.0	1782.07	8.73	0.00	0.48
13	Tmg + state + season + class	8	-883.1	1782.13	8.79	0.00	0.47
14	Tmg + time + state + class	9	-883.0	1783.91	10.57	0.00	0.48
15	Tmg + time + state + season	9	-883.2	1784.31	10.97	0.00	0.47
16	Tmg + time + state + season + class	10	-883.1	1786.17	12.83	0.00	0.47
17	Tmg + group	6	-911.5	1834.99	61.65	0.00	0.37
18	state + time + group + season	8	-909.7	1835.33	61.99	0.00	0.36
19	Tmg + group + class	7	-910.7	1835.48	62.14	0.00	0.37
20	Tmg + group + season	7	-911.6	1837.28	63.94	0.00	0.37
21	time + state + group + season + class	9	-909.7	1837.48	64.14	0.00	0.36
22	Tmg + group + season + class	8	-910.9	1837.74	64.40	0.00	0.37
23	Tmg + time + group	8	-911.5	1839.02	65.68	0.00	0.37
24	state + time + season	7	-912.6	1839.28	65.94	0.00	0.29
25	Tmg + time + group + class	9	-910.7	1839.48	66.14	0.00	0.37
26	Tmg	5	-915.1	1840.25	66.91	0.00	0.30
27	Tmg + time + group + season	9	-911.6	1841.25	67.91	0.00	0.37
28	time + state + season + class	8	-912.7	1841.34	68.00	0.00	0.29
29	Tmg + time + group + season + class	10	-910.8	1841.67	68.33	0.00	0.37
30	Tmg + class	6	-915.0	1841.92	68.58	0.00	0.30
31	Tmg + season	6	-915.3	1842.55	69.21	0.00	0.30
32	Tmg + season + class	7	-915.1	1844.23	70.89	0.00	0.30
33	Tmg + time	7	-915.1	1844.28	70.94	0.00	0.30
34	Tmg + time + class	8	-915.0	1845.95	72.61	0.00	0.30
35	Tmg + time + season	8	-915.3	1846.55	73.21	0.00	0.30
36	Tmg + time + season + class	9	-915.1	1848.23	74.89	0.00	0.30
37	state + group + season	6	-924.8	1861.59	88.25	0.00	0.27
38	state + group + season + class	7	-924.8	1863.67	90.33	0.00	0.27
39	group + time + season	7	-925.0	1863.98	90.64	0.00	0.26
40	state + season	5	-927.4	1864.86	91.52	0.00	0.19
41	time + group + season + class	8	-924.9	1865.83	92.48	0.00	0.26
42	state + season + class	6	-927.4	1866.89	93.55	0.00	0.19

## Summary of candidate models for the duration of shade use continued...

no.	model <sub>i</sub>	K	LogLik	AIC <sub>i</sub>	$\Delta$ AIC <sub>i</sub>	w <sub>i</sub>	R <sup>2</sup>
43	time + season	6	-928.1	1868.10	94.76	0.00	0.18
44	time + season + class	7	-928.0	1870.05	96.71	0.00	0.18
45	state + time + group	7	-929.6	1873.19	99.85	0.00	0.19
46	time + state + group + class	8	-929.5	1875.02	101.68	0.00	0.19
47	time + state	6	-932.2	1876.39	103.05	0.00	0.12
48	time + state + class	7	-932.2	1878.30	104.96	0.00	0.12
49	state + group	5	-934.5	1878.98	105.64	0.00	0.10
50	state + group + class	6	-934.4	1880.89	107.55	0.00	0.10
51	state	4	-936.8	1881.51	108.17	0.00	0.03
52	time + group	6	-935.4	1882.85	109.51	0.00	0.13
53	group + season	5	-936.7	1883.41	110.07	0.00	0.20
54	state + class	5	-936.8	1883.69	110.35	0.00	0.03
55	time + group + class	7	-935.4	1884.81	111.46	0.00	0.13
56	group + season + class	6	-936.6	1885.24	111.90	0.00	0.20
57	time	5	-938.1	1886.15	112.81	0.00	0.06
58	season	5	-939.4	1886.77	113.42	0.00	0.12
59	time + class	6	-938.2	1888.41	115.07	0.00	0.07
60	season + class	5	-939.6	1889.13	115.79	0.00	0.11
61	group	4	-942.2	1892.43	119.09	0.00	0.07
62	group + class	5	-942.2	1894.32	120.98	0.00	0.07
63	class	4	-944.7	1897.41	124.07	0.00	0.00

Notes: For each model the number of parameters (K), loglikelihood value (LogLik), difference in AIC between the best fit model and model<sub>i</sub> ( $\Delta$ AIC<sub>i</sub>), Akaike weight (w<sub>i</sub>), adjusted coefficient of determination (R<sup>2</sup>) are shown. Parameters: Tmg = black mini-globe temperature; time = time of day; class= age class; group = family group.

Appendix V. Summary of candidate generalised additive mixed models for the probability of drinking.

no.	model <sub>i</sub>	K	LogLik	AIC <sub>i</sub>	$\Delta$ AIC <sub>i</sub>	w <sub>i</sub>	ROC
1	Tmg + time	4.3	-492.3	993.23	0	0.21	0.644
2	Tmg + time + class	5.3	-491.4	993.54	0.31	0.18	0.650
3	Tmg + time + season	5.3	-491.8	994.16	0.93	0.13	0.645
4	Tmg + time + class + season	6.3	-490.8	994.18	0.95	0.13	0.650
5	time	2.0	-495.2	994.46	1.23	0.12	0.629
6	time + class	3.0	-494.4	994.75	1.51	0.10	0.634
7	time + season	3.0	-494.9	995.81	2.58	0.06	0.631
8	time + class + season	4.0	-493.9	995.89	2.65	0.06	0.637
9	Tmg	3.1	-500.8	1007.79	14.56	0.00	0.570
10	Tmg + class	4.1	-500.0	1008.17	14.94	0.00	0.585
11	Tmg + season	4.3	-500.4	1009.22	15.99	0.00	0.580
12	Tmg + class + season	5.2	-499.7	1009.78	16.55	0.00	0.591
13	class	2.0	-503.9	1011.88	18.65	0.00	0.554
14	season	2.0	-504.4	1012.88	19.65	0.00	0.551
15	class + season	3.0	-503.5	1013.07	19.84	0.00	0.556

*Notes:* For each model, the model number (no.), number of parameters (K), loglikelihood value (LogLik), Akaike information criteria (AIC<sub>i</sub>), difference in AIC between the best fit model and model<sub>i</sub> ( $\Delta$ AIC<sub>i</sub>), Akaike weight (w<sub>i</sub>), area under receivers operating characteristic curve (ROC) are shown. Parameters: Tmg = black mini-globe temperature; time = time of day; class= age class; group = family group.

Appendix VI. Summary of candidate generalised additive mixed models for the probability of walking.

no.	model <sub>i</sub>	K	LogLik	AIC <sub>i</sub>	ΔAIC <sub>i</sub>	w <sub>i</sub>	ROC
1	Tmg + time + group	9.5	-1528.09	3075.26	0.00	0.52	0.622
2	Tmg + time + group + season	10.4	-1527.98	3076.78	1.52	0.24	0.624
3	Tmg + time	12.0	-1526.86	3077.66	2.40	0.16	0.626
4	Tmg + time + season	13.0	-1526.68	3079.35	4.09	0.07	0.627
5	Tmg + group	4.9	-1536.98	3083.78	8.52	0.01	0.599
6	Tmg + group + season	5.8	-1537.01	3085.69	10.43	0.00	0.599
7	Tmg	7.3	-1535.73	3086.07	10.81	0.00	0.605
8	Tmg + season	8.3	-1535.72	3088.02	12.76	0.00	0.605
9	time + group + season	8.6	-1537.09	3091.34	16.08	0.00	0.600
10	time + + season	10.4	-1536.24	3093.33	18.07	0.00	0.606
11	time + group	6.8	-1541.69	3096.99	21.73	0.00	0.587
12	time	9.4	-1540.5	3099.87	24.61	0.00	0.595
13	group + season	4.0	-1548.12	3104.24	28.98	0.00	0.574
14	season	5.8	-1547.26	3106.17	30.91	0.00	0.577
15	group	2.2	-1552.97	3110.26	35.00	0.00	0.564

*Notes:* For each model, the model number (no.), number of parameters (K), loglikelihood value (LogLik), Akaike information criteria (AIC<sub>i</sub>), difference in AIC between the best fit model and model<sub>i</sub> (ΔAIC<sub>i</sub>), Akaike weight (w<sub>i</sub>), area under receivers operating characteristic curve (ROC) are shown. Parameters: Tmg = black mini-globe temperature; time = time of day; class= age class; group = family group.

Appendix VII. Summary of candidate generalised additive mixed models for the probability of resting.

no.	model <sub>i</sub>	K	LogLik	AIC <sub>i</sub>	$\Delta$ AIC <sub>i</sub>	w <sub>i</sub>	ROC
1	Tmg	7.5	-557.83	1130.65	0	0.10	0.788
2	Tmg + class	7.6	-557.85	1130.86	0.21	0.09	0.789
3	Tmg + group	7.6	-557.81	1130.89	0.24	0.09	0.788
4	Tmg + time	9.8	-555.69	1130.98	0.33	0.09	0.793
5	Tmg + group + class	7.7	-557.81	1131.08	0.43	0.08	0.789
6	Tmg + time + class	9.9	-555.71	1131.18	0.53	0.08	0.793
7	Tmg + time + group	9.9	-555.67	1131.21	0.56	0.08	0.793
8	Tmg + time + group + class	10.	-555.66	1131.40	0.75	0.07	0.794
9	Tmg + season	8.6	-557.33	1131.85	1.2	0.06	0.789
10	Tmg + class + season	8.7	-557.34	1132.05	1.4	0.05	0.790
11	Tmg + group + season	8.7	-557.32	1132.10	1.45	0.05	0.789
12	Tmg + group + class + season	8.8	-557.31	1132.28	1.63	0.04	0.789
13	Tmg + time + season	10.8	-555.56	1132.63	1.98	0.04	0.793
14	Tmg + time + class + season	10.8	-555.59	1132.84	2.19	0.03	0.792
15	Tmg + time + group + season	10.9	-555.54	1132.87	2.21	0.03	0.793
16	Tmg + time + group + class + season	11	-555.54	1133.05	2.4	0.03	0.793
17	time + season	9.5	-566.68	1152.31	21.66	0.00	0.781
18	time + group + season	9.6	-566.67	1152.51	21.86	0.00	0.781
19	time + class + season	9.6	-566.68	1152.53	21.88	0.00	0.781
20	time + group + class + season	9.7	-566.64	1152.71	22.06	0.00	0.781
21	season	6.5	-576.43	1165.81	35.16	0.00	0.752
22	group + season	6.6	-576.42	1166.01	35.36	0.00	0.752
23	class + season	6.6	-576.43	1166.03	35.38	0.00	0.752
24	group + class + season	6.7	-576.4	1166.21	35.56	0.00	0.752
25	time	8.4	-577.86	1172.58	41.93	0.00	0.757
26	time + class	8.5	-577.86	1172.78	42.13	0.00	0.757
27	time + group	8.6	-577.84	1172.79	42.14	0.00	0.757
28	time + group + class	8.7	-577.83	1172.96	42.31	0.00	0.755
29	class	5.6	-587.46	1186.03	55.38	0.00	0.716
30	group	5.6	-587.45	1186.05	55.4	0.00	0.716
31	group + class	5.7	-587.43	1186.23	55.57	0.00	0.716

Notes: For each model, the model number (no.), number of parameters (K), loglikelihood value (LogLik), Akaike information criteria (AIC<sub>i</sub>), difference in AIC between the best fit model and model<sub>i</sub> ( $\Delta$ AIC<sub>i</sub>), Akaike weight (w<sub>i</sub>), area under receivers operating characteristic curve (ROC) are shown. Parameters: Tmg = black mini-globe temperature; time = time of day; class= age class; group = family group.



Appendix VIII. Summary of candidate generalised additive mixed models for the probability of feeding.

no.	model <sub>i</sub>	K	LogLik	AIC <sub>i</sub>	$\Delta$ AIC <sub>i</sub>	w <sub>i</sub>	ROC
1	Tmg + time + season	12.2	-2794.1	5612.69	0	0.47	0.636
2	Tmg + time + class + season	12.4	-2794.0	5612.91	0.22	0.42	0.636
3	Tmg + season	9.7	-2799.0	5617.43	4.74	0.04	0.634
4	Tmg + class + season	9.9	-2798.9	5617.66	4.97	0.04	0.634
5	Tmg + time	10.9	-2799.0	5619.79	7.1	0.01	0.634
6	Tmg + time + class	11.2	-2798.8	5620.01	7.31	0.01	0.634
7	Tmg	8.9	-2804.5	5626.93	14.24	0.00	0.629
8	Tmg + class	9.2	-2804.4	5627.16	14.47	0.00	0.629
9	time + season	9.9	-2814.3	5648.29	35.6	0.00	0.620
10	time + class + season	10.1	-2814.2	5648.51	35.81	0.00	0.620
11	season	6.5	-2829.8	5672.45	59.76	0.00	0.610
12	class + season	6.7	-2829.7	5672.67	59.98	0.00	0.610
13	time	8.8	-2862.0	5741.70	129.01	0.00	0.581
14	time + class	9.0	-2861.9	5741.93	129.24	0.00	0.581
15	class	5.6	-2876.7	5764.46	151.76	0.00	0.559

*Notes:* For each model, the model number (no.), number of parameters (K), loglikelihood value (LogLik), Akaike information criteria (AIC<sub>i</sub>), difference in AIC between the best fit model and model<sub>i</sub> ( $\Delta$ AIC<sub>i</sub>), Akaike weight (w<sub>i</sub>), area under receivers operating characteristic curve (ROC) are shown. Parameters: Tmg = black mini-globe temperature; time = time of day; class= age class; group = family group.

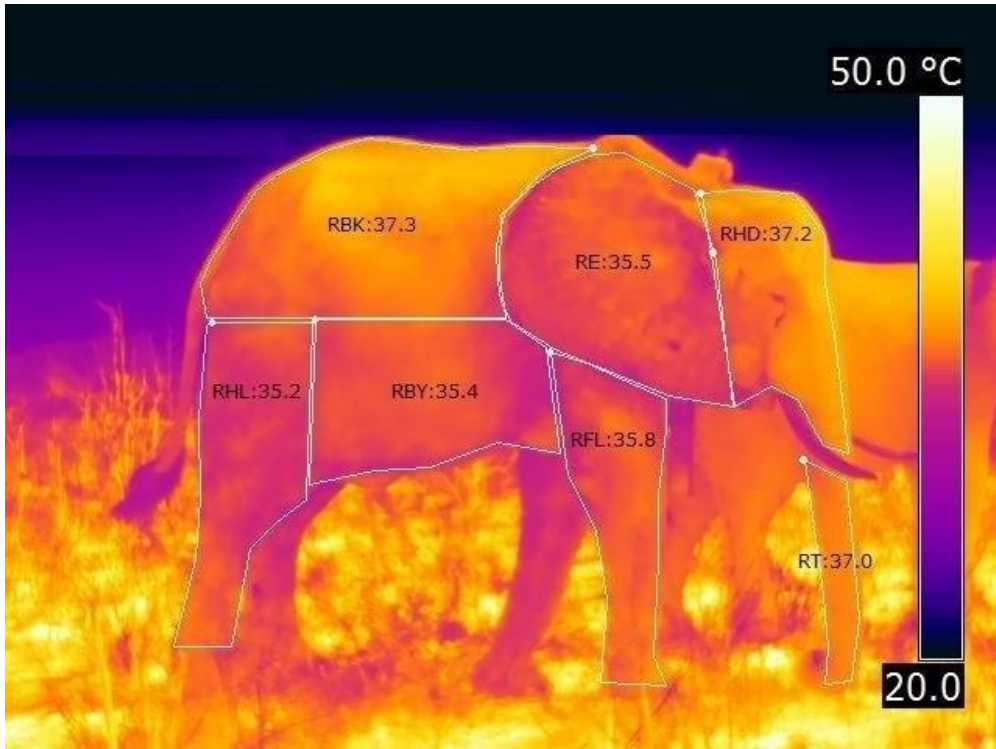
a.



b.



Appendix IX. Collars supporting mini-globe temperature recording devices fitted to the elephants during behavioural observations. a) Standard collar fitted to the three adult females and weaned male calf; b) custom made nylon strap collar fitted to the two weaned female calves.



Appendix X. An example of a thermograph of an elephant in the study, illustrating how each individual's skin surface was separated into predefined parts of the body. An area average is represented for each part of the body. RBK=Right Back, RHL= Right Hindlimb, RFL=Right Forelimb, RBY=Right Belly, RE= Right Ear, RHD=Right Head, RT= Right Trunk.