The relationship between body and environmental temperatures in savanna elephants, *Loxodonta africana*

By

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I dedicate this thesis to my Grandfather, Neville Cufflin.

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ABSTRACT

As a result of climate change, environmental temperatures across southern Africa are predicted to rise by up to 5˚C by 2070. Elephants may be particularly vulnerable to these changes. Their small surface area to mass ratio and lack of sweat glands may impair heat loss. However, it is not known how elephants respond to high environmental temperatures (above 35˚C), limiting our ability to predict the responses of elephants to climate change. My study assessed these responses for the first time. Using an infrared thermal camera and ingestible thermometers, I recorded skin (at 10-minute intervals) and core temperature (at 5-minute intervals) in seven tame, free-ranging elephants. At the same time, I recorded environmental temperature (at 5-minute intervals) using a portable weather station. I expected skin temperature to increase with environmental temperature and to decrease when elephants moved into shade or wet their skin with mud or water. Because of these behavioural changes, I expected that core temperature would not increase with environmental temperature. I expected that if elephants use heterothermy, core temperature range would increase with environmental temperature range and maximum environmental temperature. I also expected that maximum core temperature would increase, and minimum core temperature would decrease with maximum environmental temperature. I found that skin temperature increased with environmental temperature ($P<0.0001$, generalized additive mixed model), and decreased when elephants were in shade ($P<0.0001$) or were wet ($P<0.0001$). Core temperature did not increase with environmental temperature ($P=0.54$), but increased with time of day ($P<0.0001$). Furthermore, core temperature range did not increase with environmental temperature range ($\beta=0.003$, $P=0.83$, generalized linear mixed model) or maximum environmental temperature ($\beta=-0.01$, $P=0.59$). Maximum core temperature did not increase ($\beta=0.01$, $P=0.45$) and minimum core temperature did not decrease ($\beta=0.02$, $P=0.09$) with maximum environmental temperature. I conclude that changes in behaviour, which decrease skin temperature, can assist elephants to maintain homeothermy. My findings show that in the heat, elephants maintain core temperature within a narrow range of 2˚C through behavioural changes, which reduce heat gain. I therefore suggest that elephants will be more likely to cope with the direct effects of climate change than not, provided shade and water are available.

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DISCLAIMER

I, Shaun Rodrigues D’Araujo 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.

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February 2015

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 EC073-12 on the 29th of August 2012.

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CHAPTER 1 – GENERAL INTRODUCTION

1.1. BACKGROUND AND RATIONALE

Evidence suggests that anthropogenic climate change will lead to an increase in the frequency and intensity of warm weather events in the coming decades (Meehl and Tebaldi 2004; Ameca y Juárez *et al*. 2013; Collins *et al*. 2013). The negative effects of these events on species fitness and biodiversity is a concern (Thuiller 2007; Pimm 2009; Bellard *et al*. 2012; Ash *et al*. 2013; Blois *et al*. 2013). To assess the potential responses of species to climate change, a clear understanding of their physiological limits and adaptive capacity is required (Fuller *et al.* 2010; Garcia *et al*. 2012).

In southern Africa, where about two thirds of all savanna elephants (*Loxodonta africana*) live, mean maximum ground surface temperatures are expected to increase by up to 5˚C by 2070 (Figure 1.1). How elephants will respond to these changes lies in the adaptive capacity of the individual, whereby changes in behaviour and physiology may buffer the effects of high environmental temperature (Fuller *et al*. 2010; Bellard *et al*. 2012; McCain and King 2014). Elephants are the largest terrestrial mammals and have a relatively small surface area to mass ratio. As a result, they may face difficulty losing heat when environmental temperature exceeds core body (core) temperature (Benedict *et al.* 1936; Elder and Rodgers 1975; Williams 1990; Phillips and Heath 1995; Kinahan *et al*. 2007a).

While several studies on captive elephants have aided our understanding of elephant thermoregulation (Kinahan *et al*. 2007a; Hidden 2009; Weissenböck *et al.* 2012; Rowe *et al.* 2013), how savanna elephants respond physiologically to environmental temperatures higher than their normal core temperature (~36˚C) is still not known. A clear understanding of these responses is imperative to assess if elephants currently experience heat stress in African savannas, and will provide insight into how elephants may respond to climate change.

1.2. ELEPHANT THERMOREGULATION IN THE LITERATURE

To maintain a relatively constant core temperature (i.e. homeothermy), endotherms need to balance heat gained from metabolic activity and heat gained from the environment, with heat loss to the environment (Porter and Gates 1969; Schmidt-Nielson 1990). The ability of endotherms to lose heat via sensible heat loss (convection, conduction and radiation) is dependent on the magnitude of the temperature gradient between the body surface (skin) and the environment (Porter and Gates 1969). When environmental temperature exceeds skin temperature, heat is transferred from the environment to the individual. Within the individual, if skin temperature exceeds core temperature, heat will be conducted toward the body core (Porter and Gates 1969), increasing core temperature (Mitchell 1977). Conversely, if skin temperature falls below core temperature, heat will be conducted from the core to the skin, decreasing core temperature. Understanding thermoregulation in elephants therefore requires measurements of environmental factors, together with skin and core temperature.

Several studies have investigated thermoregulation in elephants. Initially, core temperature was obtained by inserting a thermometer at arm’s length into the rectum of live (Benedict *et al.* 1921; Benedict and Lee 1936; Benedict and Lee 1938) or recently deceased (Buss and Wallner 1965) elephants. These studies showed that the mean core temperature of elephants was ~36˚C (Table 1.1). However, measurements were discontinuous and no firm conclusions could be drawn about the relationship between core and environmental temperature. Recent advances in biologging (see Cooke *et al.* 2004) have allowed for the continuous recording of 24-hour core temperature (nycthemeral) rhythms of captive and tame elephants (Kinahan *et al.* 2007a; Hidden 2009; Weissenböck *et al.* 2010a; Weissenböck *et al.* 2012). Kinahan *et al.* (2007a) were the first to describe the nycthemeral rhythms of captive savanna elephants. They showed that core temperature increased during the daytime and decreased during the night-time, as it does in other large mammals (Mitchell *et al*. 2002). However, the average 24-hour core temperature range (the difference between minimum and maximum core temperature within a 24-hour period) was only 0.4˚C. Hidden (2009) conducted a similar study on tame, free-ranging elephants and showed a mean 24-hour core temperature range of 1.2˚C. Weissenböck *et al*. (2012) compared core temperatures of two captive Asian elephant populations (*Elephas maximus*) from tropical Thailand and more temperate Germany. They showed a larger mean core temperature range over 24-hours (1.2˚C) in the Thai population than in the German population (0.5˚C) and suggested that this difference provided evidence for heterothermy (discussed further in section 2.1), as an adaptive response to heat, in the Thai population. Despite being conducted on different animals in different localities, the above studies all show low variation (0.4 to 1.2˚C) in core temperature over 24-hours despite large variation in environmental temperature. However, a shortcoming of these studies is that environmental temperatures did not exceed core temperature.

At environmental temperatures below core temperature, mammals are able to regulate heat exchange by altering peripheral blood flow (and hence, skin temperature) in response to changes in environmental temperature (Phillips and Heath 1995). Few studies have recorded skin temperature in elephants (Table 1.2). Williams (1990) recorded skin temperature of two captive elephants to calculate the amount of heat lost via convection and radiation. Weissenböck *et al*. (2010) recorded skin temperature of captive elephants in Vienna Zoo at various air temperatures in an attempt to document the presence of thermal windows (area on the body of an animal where heat loss is most variable). These studies were conducted at low environmental temperatures of 12˚C (Williams 1990) and 10˚C (Weissenböck *et al*. 2010) and as a result, we do not know how elephants regulate skin temperature when environmental temperature exceeds core temperature.

In savannas, environmental temperatures often exceed the normal skin temperature of elephants (Kinahan *et al*. 2007b), impairing sensible heat loss. To cope with heat under these conditions, elephants may employ autonomic responses (discussed in section 2.1). These responses may include increasing blood flow to the peripheries (vasodilation; Williams 1990; Phillips and Heath 1992; Weissenböck *et al.* 2010; Rowe *et al.* 2013), evaporative cooling (Lilywhite and Steyn 1987; Wright and Luck 1984; Dunkin *et al*. 2013) and heat storage (Weissenböck *et al*. 2012). In addition to autonomic responses, elephants may also make use of behavioural responses (discussed in section 2.2) such as shade-seeking (Sukumar 2003; Kinahan *et al*. 2007b), swimming and mud-wallowing (which increases evaporative cooling; Hiley 1975; Dunkin *et al*. 2013) to limit heat gain from the environment and increase heat loss.

2.1 Autonomic responses

Changes in vasomotor tone (*vasodilation and vasoconstriction*)

Dilation of peripheral blood vessels facilitates the redistribution of internal body heat from the core to the skin (Tattersall and Cadena 2010). As a result, the temperature of the peripheral tissues and, subsequently, skin temperature increases above environmental temperature (Rowe *et al*. 2013), facilitating sensible heat loss. Large ranges in skin temperature have been observed in the ears (Benedict *et al.* 1921; Cena and Clark 1973; Williams 1990; Weissenböck *et al.* 2010) and other parts of the body (Weissenböck *et al*. 2010; Rowe *et al*. 2013) in elephants, suggesting that elephants alter vasomotor tone in response to changes in environmental temperature. The ears comprise ~20% of an elephant's total surface area, are highly vascularized (Sikes 1971; Hidden 2009) and are thus well suited for heat loss via vasodilation.

In elephants, ear flap rate increases with environmental temperature (Phillips and Heath 1992; Hidden 2009). At environmental temperatures of ~18˚C, elephants can lose up to 20% to 50% of metabolic heat by flapping their ears (Wright 1984). However, at higher environmental temperatures of ~30˚C, ear flapping may account for less than 8% of total metabolic heat loss (Williams 1990). However, these values were calculated based on captive elephants housed indoors where solar radiation was negligible. In savannas, elephants experience high radiant heat loads due to direct and reflected solar radiation, which may inhibit heat loss despite vasodilation. A recent study (Rowe 2012) suggested that at high environmental temperatures, heat loss through the ears is only effective if elephants limit further heat gain from solar radiation by either seeking shade or through nocturnal activity.

Evaporative cooling

Evaporation from the skin surface is an effective way of losing heat in animals with access to drinking water (Schmidt-Nielson 1990). In most mammals, evaporative cooling may take place by sweating and panting (Willmer *et al*. 2000). However, histological studies have shown that sweat glands are absent in the dermis of elephant skin (Eales 1925; Luck & Wright 1964; Horstmann 1966; Spearman 1970; Smith 1980). Studies later revealed that, despite the absence of sweat glands, transcutaneous water loss in elephants increases as a function of environmental temperature (Wright and Luck 1984; Dunkin *et al*. 2013). Furthermore, Dunkin *et al*. (2013) suggested that evaporative cooling may be the principal autonomic response in elephants, accounting for almost all heat lost at high environmental temperatures.

Evaporative cooling is largely dependent on the availability of water from the environment (Hetem *et al*. 2012). Animals must replenish water lost through evaporative cooling with water obtained from the environment (Cain *et al*. 2006; Molles *et al*. 2008). Elephants apparently drink between ~150 and ~200 litres of water per day (Sikes 1971; Fowler and Mikota 2006) and recent biophysical models (see Dunkin *et al.* 2013) have predicted that elephants inhabiting a hot environment (Okaukuejo in Etosha National Park, Namibia) may incur water debts of up to 100 litres per day. In a more temperate environment (Addo Elephant

Park, Port Elizabeth, South Africa), elephants may incur water debts of up to 22 litres per day. Therefore, in hot environments evaporative water loss may account for 50% to 75% of the 24-hour water requirements of elephants (Dunkin *et al*. 2013). When water is available, elephants may rely on evaporative cooling to thermoregulate. However, in hot, dry environments where water availability is limited, elephants may face risk of dehydration and hyperthermia (a potentially lethal rise in core temperature).

Heterothermy

Heterothermy is characterized by large 24-hour variation in core temperature, corresponding with large variation in environmental temperature. Heterothermy may be an important physiological adaptation in animals inhabiting hot and dry areas, including elephants (Elder and Rodgers 1975; Kinahan *et al*. 2007a; Weissenböck *et al*. 2012). The first study to record this phenomenon was conducted on two sub-adult dromedary camels (*Camelus dromedarius*; Schmidt-Nielson *et al*. 1957). Schmidt-Nielson and colleagues showed that these camels had 24-hour core temperature ranges (the difference between maximum and minimum core temperature within a 24-hour period) of ~2˚C when provided with drinking water. However, when deprived of drinking water, 24-hour core temperature ranges increased up to 6˚C (Schmidt-Nielson *et al*. 1957). The interpretation was that to conserve body water, dehydrated camels stored heat during the day, 'allowing' core temperature to rise, and that during the night this excess heat was lost through non-evaporative means.

Theoretically, although smaller mammals gain heat faster in comparison to larger mammals, they should also dissipate heat faster. In addition, small mammals retreat to cooler microhabitats (e.g. burrows) to prevent further heat gain from solar radiation. Larger mammals, on the other hand, have limited access to cooler microhabitats (Hetem *et al*. 2012; McCain and King 2014). These principles have led to the view that elephants are the most likely of all mammals to employ heterothermy (Benedict *et al*. 1936; Elder and Rodgers 1975; Kinahan *et al*. 2007a; Weissenböck *et al*. 2012). However, studies suggesting heterothermy in elephants have been conducted on captive elephants in atypical environments where environmental temperature did not exceed the normal body temperature of elephants. Furthermore, the criteria supporting heterothermy were not tested (see Mitchell *et al*. 2002; Hetem *et al*. 2012). As a result, conclusions drawn are confusing and it remains unknown whether elephants employ heterothermy as an adaptive response to heat.

2.2. *Behavioural responses*

The opportunity to employ behavioural themoregulation is often limited in captive individuals and, as a result, autonomic responses dominate the literature, particularly in large mammals (Mitchell *et al*. 2002). This gap in our knowledge may result in an incomplete representation of how free-ranging animals respond to changing environmental conditions. In most free-ranging mammals, behavioural thermoregulation is the primary response to reduce heat gain from the environment (Bligh 1973). These behavioural responses occur primarily due to perceived changes in skin temperature (Frank *et al.* 1999), which at some point of intensity becomes a discomfort (Hardy 1971; Bligh 1973; Frank *et al.* 1999; Huizenga *et al*. 2004). Exposure to direct solar radiation may increase skin temperature significantly (Kamau and Maloiy 1985; Phillips and Heath 1995) and cause thermal discomfort. Behavioural responses that decrease environmental heat load and consequently decrease skin temperature may therefore restore thermal comfort (Gagge *et al.* 1967; Porter and Gates 1969; Frank *et al.* 1999) and indirectly prevent an increase in core temperature.

Behavioural thermoregulation has not been documented systematically in elephants. However, during the daytime, elephants have been shown to select areas of high tree canopy cover (Kinahan *et al*. 2007b; Smit *et al*. 2007) and have been observed seeking shade (Sikes

1971; Sukumar 2003). Up to 43% of the heat gained by elephants from their immediate environment is due to direct and solar radiation (Hiley 1975) and, by seeking shade, elephants may limit further heat gain (Bond *et al*. 1967; Porter and Gates 1969). Other large mammals also seek shade (Taylor 1970; Owen-Smith 1988; Fuller *et al*. 1999). White rhinoceros, *Ceratotherium simum*, and Asian buffalo, *Bubalus arnee*, can avoid increases in core temperature of up to 2˚C by standing in shade rather than in sun (Allbrook *et al*. 1958; Moran 1973). Dik-dik, *Rhyncotragus kirki*, can reduce net rate of heat gain up to four times by selecting shade rather than sun (Kamau and Maloiy 1985). Therefore, by moving out of direct solar radiation and into shade, elephants may return a displaced skin temperature to a point of comfort. As a result, there will be no great call upon autonomic responses and elephants can thermoregulate whilst incurring minimal energetic cost, provided air temperature in the shade is below body temperatures. Shade seeking may therefore be one of the primary thermoregulatory responses in elephants, enabling them to cope with high environmental temperatures.

In addition to shade seeking, elephants spend a considerable amount of time wetting their skin surface, swimming and wallowing in mud (Sikes 1971; Hiley 1975). The rate of heat transfer to water and mud is considerably higher than to air (Scholander 1955). A study on evaporative cooling in domestic pigs (*Sus scrofa domesticus*) also showed that the rate of evaporative heat loss increased by up to twenty times by placing mud or water onto the skin (Ingram 1965). However, skin temperature returned to its initial temperature 15 minutes after placing water onto the skin and two hours after placing mud onto the skin. Therefore, by placing water or mud onto the skin, elephants likely can increase evaporative water loss and decrease skin temperature simultaneously.

Most authors of studies on elephant thermoregulation suggest that elephants may have difficulties losing heat, but the results of their studies do not support this notion. It is clear from the literature that captive elephants maintain homeothermy under relatively moderate environmental temperatures. However, this finding may not hold true in savannas, where environmental temperature may exceed core temperature by up to 10˚C (Kinahan *et al*. 2007b). We do not know how wild elephants regulate core temperature and if hyperthermia occurs under these conditions. Without a clear understanding of how elephants respond physiologically to high environmental temperatures at present, predicting how elephants will respond to higher environmental temperatures associated with climate change is near impossible.

1.3. AIM OF THE STUDY

The aim of this study is to assess the physiological consequences of high environmental temperatures for free-ranging elephants in their natural environment. I address this aim in two separate, but cohesive chapters (Chapters 3 and 4). In Chapter 3, I assess the physiological consequences of behavioural thermoregulation (shade utilization and wetting) for free-ranging elephants by quantifying the relationship between body and environmental temperature, to determine whether elephants experience heat stress under extreme environmental temperatures. In Chapter 4, I assess whether elephants employ heterothermy as an adaptation to extreme temperatures by quantifying the relationship between 24-hour core temperature range and environmental temperature range.

Table 1.1. Core temperature indices reported in previous studies on elephant thermoregulation.

Source	Species	Study site	Core temperature (˚C)				
			Measurement	Mean	Max.	Min.	Range
Benedict *et al*. 1921	*L. africana*	New York Zoo, USA	rectal	-	36.7	36.2	-
Benedict & Lee 1936	*E. maximus*	New York, USA	faecal	36.4	36.1	36.6	-
Benedict & Lee 1938	*E.maximus*	New York, USA	urine	-	36.6	36.3	-
Buss & Walner 1965	*L.africana*	Bunyoro, Uganda	rectal	36.4	36.8	36.1	-
Pienaar *et al.* 1966	*L. africana*	Kruger NP, South Africa	rectal	-	37.5	35.3	-
Hiley 1972	*L.africana*	Uganda	rectal		38.4	35.4	-
Elder & Rodgers 1975	*L.africana*	Luangwa Valley, Zambia	muscle	35.1	37.1	33.1	-
Elder & Rodgers 1975	*L.africana*	Kruger NP, South Africa	muscle	35.5	37.2	34.4	-
Kinahan *et al*. 2007a	*L. africana*	Pretoria Zoo, South Africa	GIT	36.2	37.5	35.0	0.4
Hidden 2009	*L.africana*	Letsiteng NR, South Africa	GIT	36.4	37.1	35.8	1.2
Weissenböck *et al*. 2012	*E.maximus*	Munich Zoo, Germany	GIT	36.3	36.6	35.7	0.5
Weissenböck *et al*. 2012	*E.maximus*	Samphran Zoo, Thailand	GIT	36.2	36.9	36.1	1.2
Rowe *et al*. 2013	*E.maximus*	Audubon Zoo, USA	rectal	35.3	-	-	-

GIT = Gastrointestinal tract, NR = Nature reserve, NP = National park

Table 1.2. Skin temperature indices reported in previous studies on elephant thermoregulation.

Source	Species	Study site	Skin temperature (˚C)				
			Method	Mean	Max.	Min.	Range
Benedict *et al*. 1921	*L.africana*	New York Zoo, USA	TC	25.5	28.3	21.4	7.1
Cena & Clark 1973	*L.africana*	Twycross Zoo, England	IRT	-	27.5	24.0	3.5
Williams 1990	*L.africana*	San Diego Zoo, USA	IRT	29.0	34.0	25.0	11.0
Williams 1990	*E.maximus*	San Diego Zoo, USA	IRT	24.0	31.0	22.0	9.0
Weissenböck *et al*. 2010	*L.africana*	Vienna Zoo, Austria	IRT	-	31.0	16.0	15.0
Rowe *et al*. 2013	*E.maximus*	Audubon Zoo, USA	IRT	26.0	39.0	20.5	18.5

TC = Thermocouple, IRT = Infrared thermography

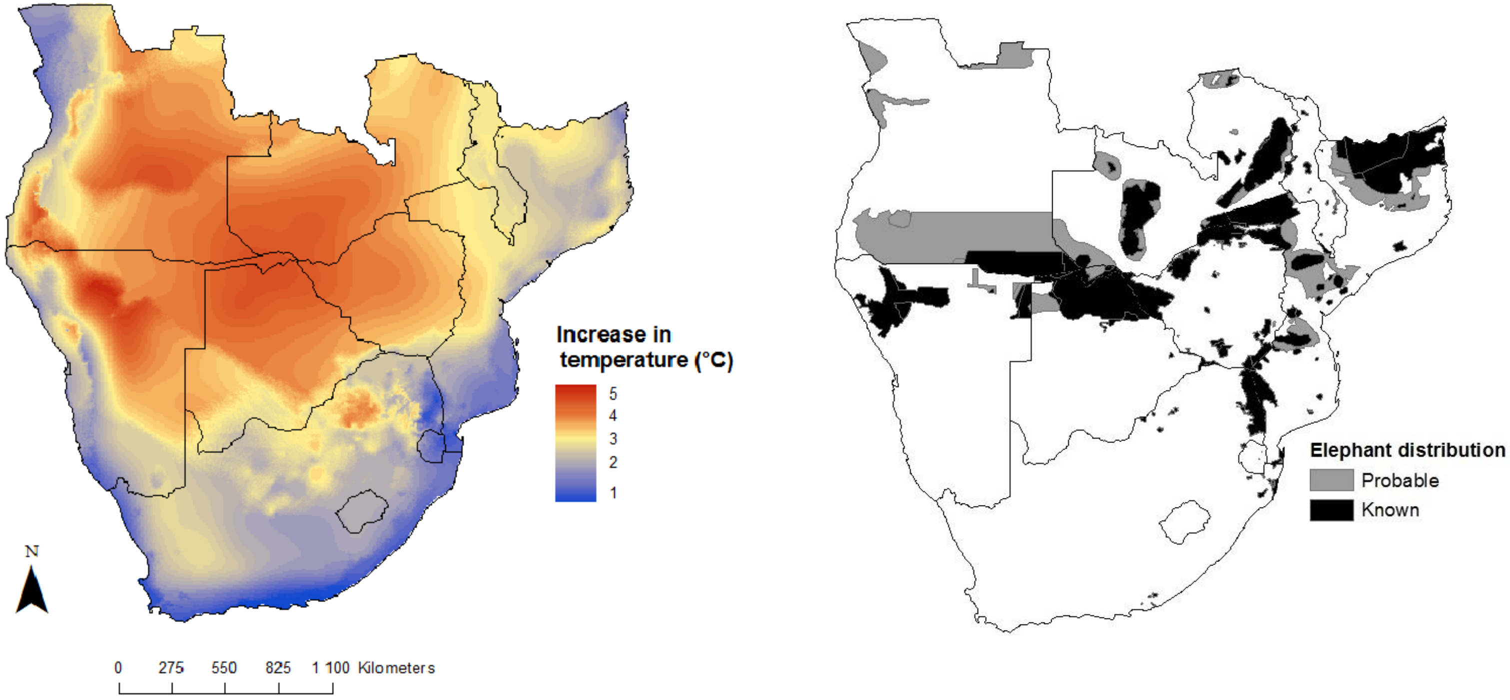

Figure 1.1. a) Predicted increases in mean maximum temperature across southern Africa by the year 2070. Differences were calculated by calculating the difference between current (2014) and future (2070) predicted mean maximum temperatures recorded at a spatial resolution of 5-minutes of a degree of latitude and longitude (data source: http//worldclim.org/CMIP5) and b) the current (2007) distribution of savanna elephants across southern Africa (data source:http://www.elephantdatabase.org/maps/range).

CHAPTER 2 – GENERAL MATERIALS AND METHODS

2.1. INTRODUCTION

In this chapter, I provide information regarding the study site and study animals. I also provide fundamental information regarding the standardization of the procedures used in Chapters 3 and 4, which are not included in those chapters.

2.2. STUDY SITE

This study was conducted in vicinity of Abu Camp (19°10’58.28”S, 23°03’47.01”E), situated in block 26 of the Ngamiland (NG26) district in the Okavango Delta, north west Botswana (Figure 2.1). The Okavango Delta is an alluvial fan that covers 15 000 km^2 and originates from the Okavango river catchment area in Angola (Wolski and Savenije 2005; Evans and Harris 2012). The delta undergoes seasonal flooding between May and September, during which the total area covered by water during the floods extends from 2500–4000 km^2 during March, to 6000–12000 km^2 during August (McCarthy *et al*. 2003). Seasonal flooding does not occur at the same time as the seasonal rains. The dry season (period of low rainfall) typically extends from May to October and the wet season (period of high rainfall) typically extends from November to April (McCarthy *et al*. 2003). This study took place during the dry season, which was subdivided into the hot dry season (September to November) in 2012 and the cool flood season (May to July) in 2013.

The Okavango Delta is characterised by a mosaic of flat, seasonal floodplains and vegetated islands that range from a few square meters to 500 km^2 in size (McCarthy *et al*. 2003). The islands are dominated by open savanna habitat with scattered terminalia (*Terminalia sericea*) and mopane woodlands (*Colophospermum mopane*), while island margins are dominated by narrow riverine forest habitats. Permanently flooded areas are dominated by papyrus (*Cyperus papyrus*); while seasonally flooded areas are dominated by various sedges and grasses.

Annual rainfall is ~460 mm and monthly ambient (air) temperatures range between a mean 24-hour minimum of 8°C in June and a mean 24-hour maximum of 36°C in October. Ambient temperature extremes of -3°C and 46°C have been recorded (Botswana Meteorological Services, 2012).

2.3. STUDY ANIMALS

This study was conducted on a herd of seven tame, free-ranging savanna elephants, *Loxodonta africana*, belonging to Abu Camp. The herd consisted of three adult females, one male weaned calf, two female weaned calves, and one suckling calf (for elephant characteristics see Table 2.1). During the daytime (between 06h00 and 18h00), the elephants roamed freely within the concession within the vicinity of Abu Camp and their movements and behaviour were not constrained in any way. The elephants were able to range freely within the 2338 km^2 concession, however, the elephants did not move further than 15 km away from the fenced enclosures where they were housed at night-time (M. A. Mole, unpublished data). Between 18h00 and 06h00, the elephants were housed together in two outdoor, fenced enclosures at Abu Camp, where they were provided with fresh forage (mainly leaved branches collected locally) and drinking water. The elephants took part in tourist-related activities (elephant back safaris) for the first two hours after being released (06h00 to 08h00) and for the last two hours before returning back to the enclosures (16h00 to 18h00). For safety, two trained elephant handlers were present at all times during field trials. The same elephants were used for the duration of the study.

2.4. CORE TEMPERATURE MEASUREMENTS

Core temperature was recorded using miniature temperature recording data loggers (iButton, Maxim Integrated Products, California, USA). Each data logger contained a silicon chip housing a thermometer and on-board memory, enclosed in a stainless steel casing. Each data logger was 18 mm in diameter with a mass of 3 g and 8192 bytes of memory. At a resolution of 0.06˚C, each data logger was able to record 4096 data points at a sampling interval of five minutes. Data loggers were calibrated against a certified precision thermometer (Quat 100, Hereus, Hanau, Germany) in an insulated water bath across a range of temperatures (between 25˚C and 40˚C, at 5˚C increments). I plotted precision thermometer values as a function of concurrent logger temperature and fitted with a simple linear regression (e.g. Figure 2.2) and substituted the actual temperature recordings into the regression line equation $y = mx + c$. I calculated the calibrated value by solving for y.

I "fed" each data logger to a focal elephant in the form of an ingestible device (Figure 2.3). I attached a brightly-coloured satin ribbon (200 mm in length) to each device to assist passage through the gastrointestinal tract and to aid detection in faeces. Ensuring that the ribbon remained free, I covered each data logger in inert wax (Sasol, South Africa) for waterproofing. When covered in wax, the device was ~25 mm in diameter and weighed ~7 g. Upon feeding a device to a focal elephant I wrapped the ribbon around the device and secured it in place with a small amount of cooking chocolate. The chocolate dissolved following ingestion and prevented the ribbon from irritating the elephant's throat and being expelled (Hidden 2009). I recovered the device in the faeces and downloaded the data post-recovery. Retrieval success and transit times are reported in Table 2.2. The same core temperature data was used in both Chapters 3 and 4.

2.5. SKIN TEMPERATURE MEASUREMENTS

I recorded skin temperature using an infrared thermal camera (FLIR T640, FLIR Systems Inc., Portland, Oregon, USA), which was mounted on a monopod. The camera had a 25˚ lens, with a 7.5–14 µm spectral range and was factory (FLIR Systems Inc., Portland, Oregon, USA) calibrated to record temperature with an accuracy of ± 1.0˚C. The camera detects infrared radiation emitted from the surface of an object, which is converted into a temperature value. These values are depicted in the form of an infrared thermal image (thermograph). Each thermograph is 640 × 480 (307 200) pixels where each pixel represents a temperature value.

The radiation that is detected by the camera originates from three different sources; radiation from the target object, reflected radiation from the object's surroundings and radiation from the surrounding air. Therefore, the camera output can be described as follows:

$$W_{tot} = \varepsilon . \tau . W_{obj} + (1 - \varepsilon) . \tau . W_{amb} + (1 - \tau) . W_{atm}$$

where ε is the emissivity of the target object, τ is the transmittance of the atmosphere, W_{obj} is the amount of radiation emitted from the target object, W_{amb} is the amount of radiation emitted from the object's surroundings and W_{atm} is the amount of radiation present in the surrounding air. To ensure accurate skin temperature recordings I supplied the camera with the following parameters: emissivity=0.98, distance=10 m (unless specified otherwise), air temperature, relative humidity and reflected temperature.

Emmisivity

The amount of radiation emitted from an object comes from two major sources; radiation from the object itself (emissivity, ε) and radiation from the surrounding environment that is reflected off of the object (reflectivity, ρ). This is described as follows:

$$\varepsilon + \rho = 1$$

To calculate the emissivity of elephant skin, I placed an object of known emissivity (black scotch tape, ε=0.95) onto a piece of elephant skin. Both the skin and tape were cooled to the same temperature (5˚C). The emissivity of the camera was adjusted to 0.95 and the surface temperature of the black tape was recorded. I then adjusted the emissivity of the camera until the temperature of the elephant skin was identical to the temperature of the tape. The emissivity at which the skin temperature and the tape temperature were identical represented the emissivity of elephant skin. This value was 0.98, which is similar to the emissivity of human skin. Therefore, 98% of the radiation emitted from elephant skin is radiation from the skin itself and 2% is from reflected radiation. An emissivity of 0.98 was used for elephant skin throughout the study.

Distance

The amount of radiation emitted from the air surrounding the target object is dependent on the volume of air between the object and the observer (Wolfe and Zissis 1989). Therefore, I supplied the camera with the distance between the camera and the focal elephant. I consistently maintained a distance of 10 m to avoid sampling error. Where it was not possible to maintain this distance, I visually estimated the distance and supplied this to the camera.

Air temperature and relative humidity

The amount of radiation emitted from the air surrounding the target object is also dependent on the temperature and water content of the air (Wolfe and Zissis 1989). Therefore, I supplied the camera with ambient temperature and relative humidity that I recorded using a portable psychrometer (ExTech® HD500, Townsend West, Nashua, U.S.A).

Reflected temperature

To account for reflected radiation from the environment, I calculated the reflected temperature by setting emissivity to 1.00 and distance to 0 m, before obtaining a thermal image of a diffuse reflector (Figure 2.4). The diffuse reflector comprised of a wrinkled sheet of aluminium foil placed over a spherical polystyrene ball (250 mm in diameter). Aluminium foil has an emissivity of 0.04. Therefore 99.6% of radiation from the surrounding environment is reflected from the aluminium foil. By setting ε to 1.00, I assumed that all radiation from the surrounding environment was represented by the average temperature of the diffuse reflector. I then substituted this average temperature into the camera parameters before obtaining a thermograph of the focal elephant. This ensured that skin temperature measurements excluded all reflected radiation from the surrounding environment.

I obtained thermographs between 09h00 and 16h00 for a single focal elephant at 10-minute intervals on both sides of the body (left and right), corresponding with core and environmental temperature measurements. Elephants were thermographed from an angle perpendicular to the sagittal plane of the elephant to avoid angle distortion. For a given thermograph, I calculated the mean temperature for each of the seven body areas (Figure 2.5) using hand drawn complex polygons in the software package FLIR Reporter Professional 9.0 (FLIR Systems Inc., Portland, Oregon, USA).

2.6. ENVIRONMENTAL TEMPERATURE MEASUREMENTS

Environmental temperature was recorded using miniature black-globe thermometers (henceforth referred to as mini-globes, see Hetem *et al*. 2007). Each mini-globe consisted of a temperature recording data logger (iButton, Maxim Integrated Products, California, USA; accuracy=0.5˚C) placed in the centre of a hollow copper ball (30 mm diameter) which was spray painted matt black. The mini-globe reached thermal equilibrium when heat gain from radiation was equal to heat loss via convection and conduction. Therefore, the mini-globe increased in temperature when heat gain from solar radiation exceeded heat loss through convection, providing an accurate representation of environmental heat load to which elephants were exposed. A single mini-globe was placed on a portable weather station within close proximity (up to 1 km away) to the herd at all times. All data loggers were calibrated as described in section 2.4.

2.7. AMBIENT TEMPERATURE MEASUREMENTS

Ambient (air) temperature was recorded using miniature data loggers (iButton, Maxim Integrated Products, California, USA; accuracy = 0.5 ˚C). The data logger was artificially shaded from solar radiation and placed on a portable weather station within close proximity (up to 1 km away) to the herd at all times. All data loggers were calibrated as described in section 2.4. Ambient temperature was used as an explanatory variable in Chapter 4, to remain consistent with the literature and compare my findings with those of others.

2.8. BEHAVIOURAL OBSERVATIONS

The elephants were habituated to the presence of humans. As a result, my fellow researcher, two elephant handlers and I were able to observe their behaviour closely (at a distance of ~10–50 m) without disturbing them. All behavioural observations were conducted on foot. Where this was not possible, observations were conducted from a vehicle. Periods of exposure to sun and shade, and predefined relevant activities, particularly when elephants were wet, were documented using a continuous focal sampling approach (Altmann 1973). Exposure to shade was defined as more than 50% of an elephant’s body surface being shaded. Wetting was defined as the wetting of the body surface by swimming, wallowing in mud or spraying mud or water over the body (as described in Mole 2014). For a detailed representation of all behavioural trends recorded in correspondence with the body temperatures in this thesis, please refer to Mole 2014 (unpublished thesis).

Table 2.1. Identity, age, and physical body measures of savanna elephants in the present study.

Elephant	Age (yrs)	Shoulder height (m)	Surface area (m^2)	Mass (kg)
Adult female A	47	2.50	5.43	3510
Adult female B	18	2.36	4.74	2140
Adult female C	28	2.40	5.07	2690
Weaned male	7	2.18	3.96	1740
Weaned female A	4	1.86	2.51	1100
Weaned female B	3	1.64	2.45	900
Suckling female	1	1.34	1.79	320

Note: The elephants were trained to walk onto a large scale (with a precision of ± 100 kg) to determine their mass. Mass was recorded for each elephant in October 2012 and in July 2013 (table values represent mean).

Table 2.2. Summary of the retrieval success of data loggers administered to five elephants and the retention times of these data loggers in the gastrointestinal tract during the two study periods.

	Number of data loggers				Retention time (hours)		
Study period	Administered to elephants	Successfully ingested	Retrieved and functional	Retrieval success (%)	Mean ± SD	Maximum	Minimum
Hot dry	42	38	20	53	52 ± 35	145	21
Cool flood	25	18	12	66	41 ± 20	96	18

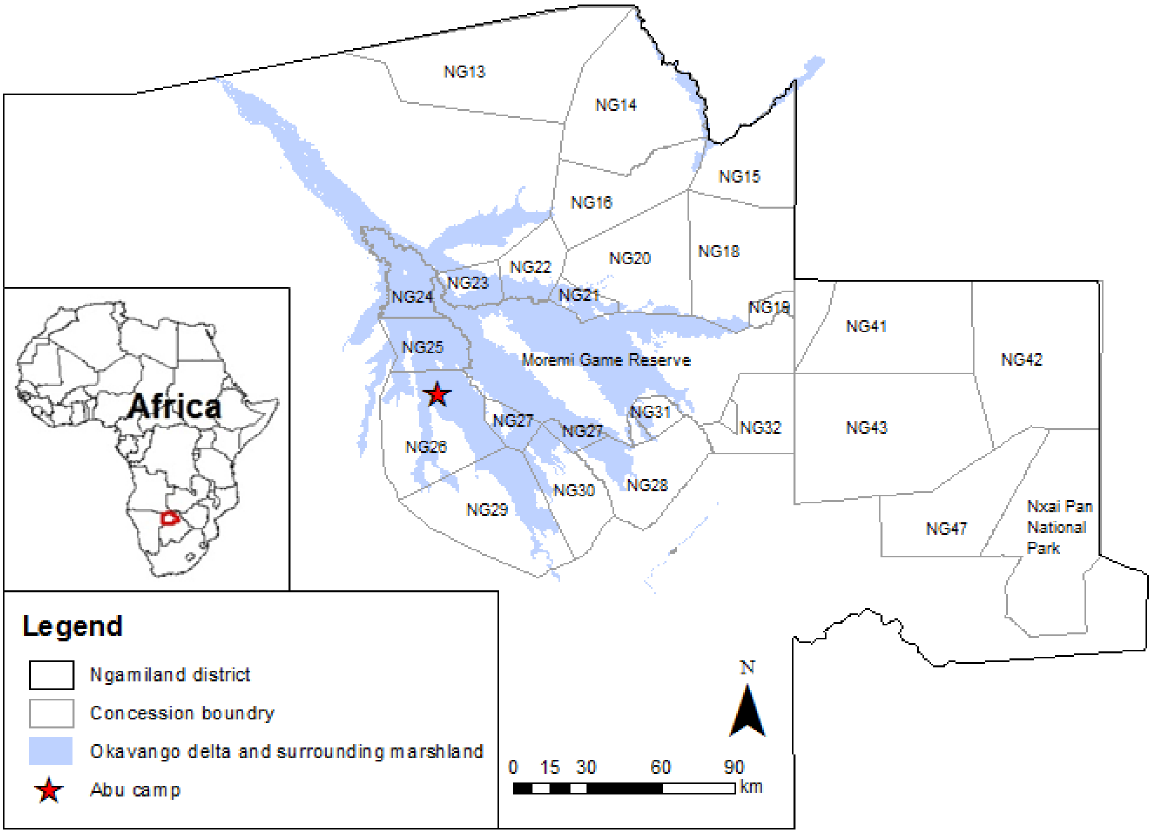

Figure 2.1. Map of the study area in northern Botswana, incorporating the concessions comprising the Ngamiland district. This study took place in the NG26 concession within the vicinity of Abu Camp.

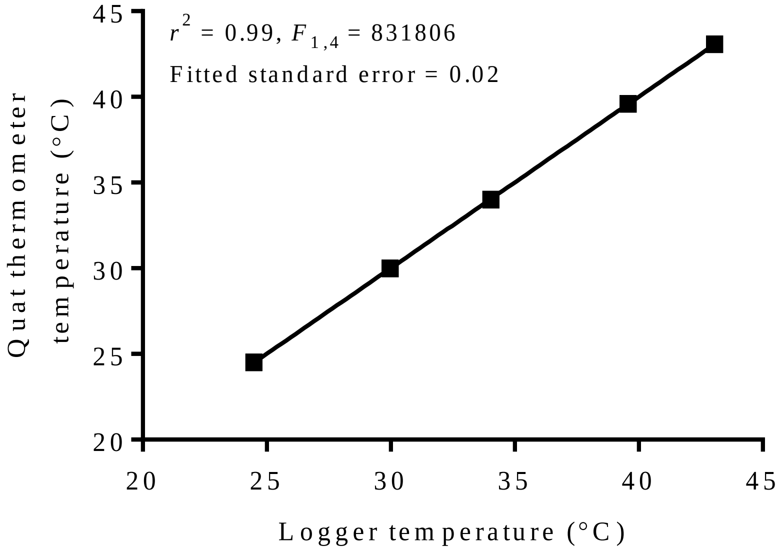

Figure 2.2. An example of a simple linear regression curve used for the calibration of a single data logger.

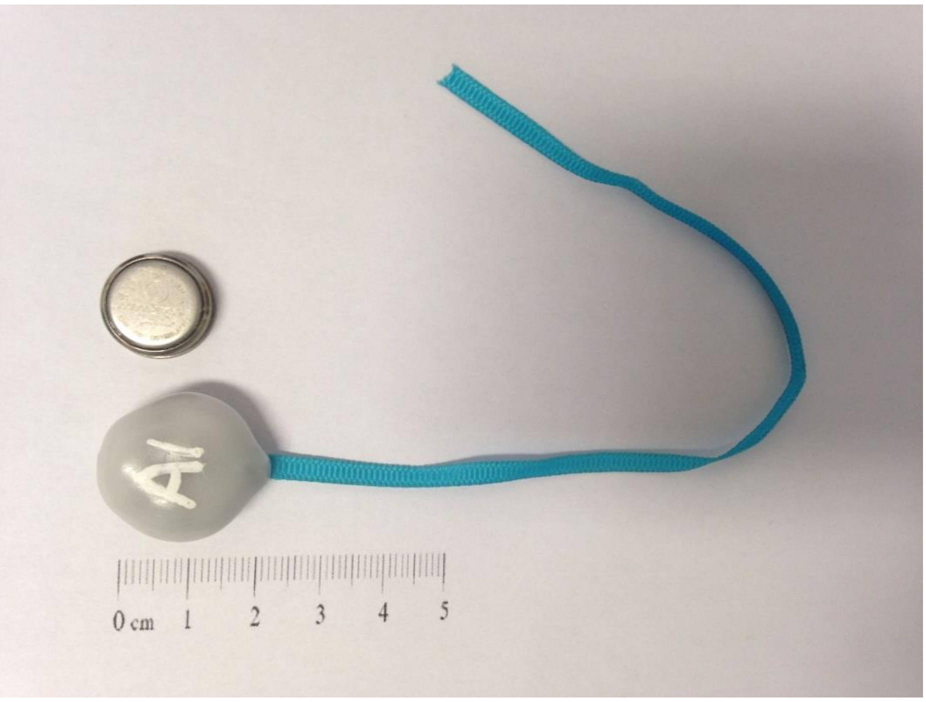

Figure 2.3. Ingestible device used to record elephant core temperature. A hi-resolution iButton (above) was attached to a brightly coloured ribbon and covered in inert wax to form the ingestible device (below, A1). The ingestible device in this photograph is in the final pre-ingestion form. Scale is given in centimetres.

Figure 2.4. Thermograph of a diffuse reflector used to calculate reflected temperature.

Average temperature of the diffuse reflector was calculated using the circle area tool and was substituted into the camera parameters.

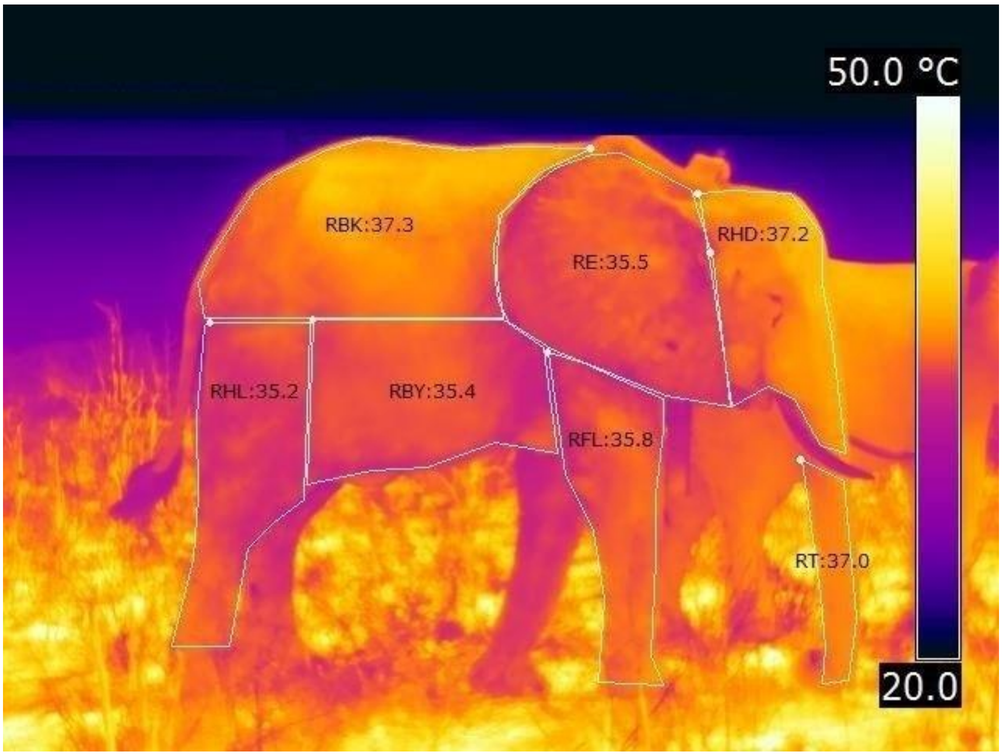

Figure 2.5. A thermograph of Adult female B, illustrating how each elephant's skin surface was separated into predefined parts of the body. An area average is represented for each part of the body. RBK=Right Back, RHL= Right Hindlimb, RFL=Right Forelimb, RBY=Right Belly, RE= Right Ear, RHD=Right Head, RT= Right Trunk.

CHAPTER 3 – THE RELATIONSHIP BETWEEN BODY AND ENVIRONMENTAL TEMPERATURE IN THE SAVANNA ELEPHANT, *LOXODONTA AFRICANA*

3.1. INTRODUCTION

Most large mammals maintain core temperature within a narrow 24-hour range through behavioural and physiological changes (Bligh 1973; Mitchell *et al.* 2002; Fuller *et al.* 2010; Boyles *et al*. 2013). Predicted increases in weather extremes, particularly hotter and drier environments (Parmesan *et al*. 2000; McKechnie and Wolf 2010; Ameca y Juárez *et al*. 2013), may compromise this homeostasis. How savanna elephants (*Loxodonta africana*) will respond to these extremes lies in the behavioural and phenotypic plasticity of the individual (Fuller *et al*. 2010; Kearney 2013; McCain and King 2014). While several studies on captive elephants have aided our understanding of elephant thermoregulation (Kinahan *et al*. 2007a; Hidden 2009; Weissenböck *et al*. 2012; Rowe *et al*. 2013), the physiological responses of elephants to high environmental temperatures (above 35˚C) remain poorly known. A mechanistic understanding of these responses is imperative to assess if elephants experience heat stress in African savannas.

Environmental temperature in savannas typically ranges between 0˚C (Scholes and Walker 1993) and 50˚C (Cole 1986) and levels of solar radiation are high. To regulate core temperature in these conditions, endotherms need to balance heat produced through metabolic activity and gained from the environment, with heat loss to the environment (Porter and Gates 1969). The rate at which an animal gains or loses heat is dependent on the temperature gradient between its skin surface and the environment (Boulant 1991). If environmental temperature exceeds skin temperature, heat is transferred from the environment to the skin, increasing skin temperature. If skin temperature exceeds core temperature, heat is conducted inward toward the body core and core temperature increases (Mitchell 1977; Kamau and Maloiy 1985).

In mammals, changes in skin temperature may lead to the conscious perception of warmth or cold, which at some point of intensity may become a discomfort (Hardy 1971; Bligh 1973; Huizenga *et al*. 2004). Exposure to high environmental temperatures and direct solar radiation may increase skin temperature (Kamau and Maloiy 1985; Phillips and Heath 1995; Rowe *et al*. 2013), causing thermal discomfort and soliciting a behavioural response to reduce skin temperature. Elephants exposed to high environmental temperatures and direct solar radiation may alter their behaviour by selecting cooler microclimates (e.g. shade; Kinahan *et al*. 2007b), decreasing radiant heat gain and skin temperature, preventing an increase in core temperature, which may otherwise have occurred (Gagge *et al*. 1967).

Where resources favouring thermal comfort (e.g. shade, mud and/or water) are not limited, behavioural thermoregulation may be the primary response in elephants to high environmental temperatures. Behavioural responses such as shade-seeking limit heat gain from the environment and could assist elephants in maintaining homeothermy. In marginal habitats, where thermal resources are limited, elephants may rely more on autonomic processes such as evaporative cooling (Wright and Luck 1984; Dunkin *et al*. 2013) and vasodilation (Phillips and Heath 1992; Rowe *et al*. 2013) to lose heat. Evaporative cooling results in the loss of body water (Mitchell *et al*. 2002; Dunkin *et al*. 2013) and during the hot, dry season elephants may face the risk of dehydration-induced hyperthermia if they cannot maintain body water balance through sufficient water intake. As a result, elephants may need to move greater distances to find water, which could compromise individual fitness (Trimble *et al*. 2009; Young and van Aarde 2010). By selecting habitats where suitable shade, forage and water are available, elephants may be able to maintain thermal comfort and regulate core temperature whilst incurring minimal fitness costs.

How elephants utilize space based on their thermal requirements may have consequences at a larger scale, particularly for landscapes (Chamaillé-Jammes *et al*. 2007; Guldemonde and van Aarde 2008) and the survival of young (Young and van Aarde 2010). High levels of solar radiation (resulting in an increase in environmental temperature) may limit elephants to the confinement of shade or within close proximity to water, reducing the amount of time that elephants could spend foraging. Heat stress and dehydration in large herbivores may also decrease appetite and result in a loss of body condition (Kadzere *et al*. 2002), which may affect reproduction in elephants (Moss and Lee 2011). In lactating cattle, high ambient temperatures decrease milk production and slow calf growth (e.g. Kadzere *et al*. 2002). Heat stress may therefore have demographic consequences for elephants. Smaller calves within a family group may also gain heat faster than adult elephants due to their larger surface area to mass ratio. If this is the case, calves could experience heat stress sooner than adults, leading to changes in landscape use and population dynamics in elephants (Mumby *et al*. 2013).

In this study, I aimed to determine whether savanna elephants experience heat stress in savannas by quantifying the relationship between body (skin and core) and environmental temperatures in free-ranging elephants. I tested the working hypothesis that at high environmental temperatures, elephants decrease skin temperature by utilizing shade and/or bathing, subsequently maintaining thermal comfort and homeothermy. In support of this I expected that; (i) an increase in environmental temperature would increase skin temperature, (ii) skin temperature would decrease when elephants utilized shade or bathed and (iii) core temperature would be independent of environmental temperature. Lastly, I expected that suckling and weaned calves would gain heat at a more rapid rate than adults would. As a result, suckling and weaned calves may have higher skin and core temperatures than adults.

3.2. MATERIALS AND METHODS

3.2.1 Study site

Refer to section 2.2 for details of the study site.

3.2.2 Study animals

Refer to section 2.3 for details of the study animals.

3.2.3 Field protocol

It has been shown that tourist related activities do not influence the core temperature of elephants in similar situations (see Hidden 2009), however, to limit the influence that atypical activities may have had on the study, I conducted field trials between 09h00 and 16h00, outside of these activity times. During these field trials the elephants were allowed to range freely within the concession and engage in natural behaviour. A single focal elephant was randomly selected and followed closely on foot. Skin and core temperatures of the focal elephant were recorded at regular intervals, coinciding with environmental temperature recorded on a portable weather station within close proximity to the herd (up to 1 km away). At the same time, continuous behavioural observations were recorded for the same elephant (see Mole 2014) to document periods of exposure to sun and shade, and predefined relevant activities, particularly swimming and bathing in mud or water (henceforth referred to as 'behavioural states').

3.2.3.1 Environmental temperature data

I recorded mini-globe temperature as a proxy for environmental temperature, at five-minute intervals, using a portable weather station, as described in section 2.6.

3.2.3.2 Skin temperature data

I recorded skin temperature at 10-minute intervals using an infrared thermal camera as described in section 2.5.

3.2.3.3 Core temperature data

I recorded core temperature at five-minute using miniature ingestible data loggers as described in section 2.4.

3.2.4 Data analysis

3.2.4.1 Descriptive statistics

To show the mean 24-hour pattern of mini-globe temperature, I calculated the mean environmental temperature for each hourly interval across all days combined and plotted these means from 00h00 to 23h00. This analysis was repeated for both the hot dry season and the cool flood season. For both seasons I calculated the 24-hour mean, mean minimum and mean maximum environmental temperatures. I tested the differences between the 24-hour mean, mean maximum and mean minimum temperatures between the hot dry and cool flood season using unpaired t-tests.

To show the mean 24-hour pattern of core temperature for all elephants, I calculated the mean for each 30-minute interval across all days for each elephant during both the hot dry season and the cool flood season.

To characterize skin and core temperatures I calculated the 7-hour (all data points between 09h00 and 16h00) and 24-hour (all data points between 00h00 and 23h00) mean, daily mean maximum and daily mean minimum skin and core temperatures respectively for each elephant during the hot dry season and the cool flood season. For each elephant, I calculated core temperature range (the difference between the mean minimum and maximum core temperature) for each 24-hour period.

To visualize relationships between skin and mini-globe temperature, and between core and mini-globe temperature, I used non-parametric Spearman's rank correlation (r_s). I used Spearman's rank correlation because my data were not normally distributed. The significance of these correlations were, however, not considered reliable due to my large sample sizes (n>150). I therefore tested the significance of the relationships between body and environmental temperatures using Generalized Additive Mixed Models, which did not assume linearity a priori and took repeated measures into account.

3.2.4.4 Generalized additive mixed models

Generalized additive mixed models (GAMMs) are a form of Generalized Linear Models where the linear predictor is based on a smoothing function (Wood 2006). I used generalized additive mixed models to describe trends in my skin and core temperature data and considered the significance described by GAMMs as an accurate representation of these trends. All analyses were carried out in the statistical software R, version 2.15.2 (R Core team 2012). GAMMs were fitted using the *nlme* (Pinheiro *et al*. 2013) and *mgcv* (Wood 2006) packages. In the models skin or core temperature (recorded between 09h00 and 16h00 at 10 minute intervals) served as the response variables. The explanatory variables were mini-globe temperature, behavioural state and age class as explanatory variable. Elephant was included as a random effect. To account for differences in skin temperature on different parts of the body, I included part of the body as a nested random effect within an elephant. Explanatory variables with a correlation coefficient >0.7 with another explanatory variable were not included in the candidate models. There was no strong correlation between time and mini-globe temperature (r_s=0.32), therefore both were included in the models.

To select the most plausible model I used standard selection criteria (Akaikes Information Criteria, AIC, Burnham and Anderson 2002) to determine which of the explanatory variables best described the variability in my response variables AIC differences (Δ_i) between the approximate best model (Δ_i=0) and alternate candidate models were calculated to assess the strength each candidate model. Candidate models with Δ_i<2 are considered strong and are the best alternative models. Models with Δ_i between 2 and 7 provide some support and should not be dismissed (Burnham and Anderson 2002). When Δ_i was similar between two or more candidate models, there was model uncertainty. To overcome this I first calculated the Akaike weight (w_i), a normalised likelihood representing probability that a given candidate model is the most plausible model (Burnham and Anderson 2002). The relative importance of each explanatory variable was then calculated by summing the w_i of all candidate models each time the explanatory variable of interest appears. More important explanatory variables will be closer to a value of 1 relative to less important explanatory variables, which will be closer to 0. Finally, model assumptions were checked by examining residual diagnostic plots.

3.2.4.5 Generalized linear mixed models

To describe the relationship between mini-globe - skin temperature, I used generalized linear mixed models (GLMMs) using the *nlme* package (Pinheiro *et al*., 2013, in R, version 2.15.2; R Core team, 2012). I included elephant as a random effect to account for repeated measures on each elephant. The difference was positive when mini-globe temperature exceeded skin temperature and negative when skin temperature exceeded mini-globe temperature. Theoretically, when the difference was positive, elephants would gain heat from the environment and when the difference was negative, elephants would lose heat to the environment. To discern the mini-globe temperature that elephants began to gain heat from the environment I solved for x when y=0 using the linear equation $y = mx + c$.

I used similar GLMMs to describe the trend between skin - core temperature and mini-globe temperature. The difference was positive when skin temperature exceeded core temperature and negative when core temperature exceeded skin temperature. Theoretically, when the difference was positive, elephants would gain heat from the periphery to the core and when the difference was negative, elephants would lose heat from the core to the periphery. To discern at which mini-globe temperature elephants began to gain heat toward the core, I solved for x when y=0 using the linear equation $y = mx + c$.

3.3. RESULTS

3.3.1 Environmental temperature

I recorded mini-globe temperature for 64 days during the hot dry season and for 52 days during the cool flood season. During the hot dry season, mini-globe temperature ranged between 11.3˚C and 50.1˚C. During the cool flood season, mini-globe temperature ranged between 5.3˚C and 41.9˚C. Mean maximum mini-globe temperature was significantly ($t_{1,27}$=8.4, P<0.0001) higher during the hot dry season (42.6 ± 4.6˚C) than during the cool flood season (34.7 ± 6.2˚C). Mean minimum mini-globe temperature was significantly ($t_{1,27}$=14.6, P<0.0001) lower during the cool flood season (11.4 ± 2.1˚C) than during the hot dry season (18.1 ± 2.9˚C). Mean mini-globe temperature was significantly ($t_{1,27}$=14.6, P<0.0001) higher during the hot dry season than during the cool flood season (20.3 ± 2.6˚C). During both seasons, mini-globe temperature followed a consistent 24-hour pattern, increasing after sunrise, peaking at about 14h00 and decreasing after sunset (Figure 3.1).

3.3.2 Skin temperature

I recorded skin temperature for 36 days (Adult female A=6 days, Adult female B=6 days, Adult female C=5 days, Weaned female A=3 days, Weaned female B=5 days, Suckling female A=7 days, Weaned male B=4 days) during the hot dry season, and for 28 days (Adult female A=5 days, Adult female B=5 days, Adult female C=3 days, Weaned female A=3 days, Weaned female B=4 days, Suckling female A=4 days, Weaned male B=4 days) during the cool flood season. Skin temperature ranged between a mean minimum of 27.5 ± 3.6˚C and a mean maximum of 40.7 ± 2.9˚C for all elephants (*N*=7) during the hot dry season (mean=34.1 ± 3.0˚C). During the cool flood season, skin temperature ranged between a mean minimum of 20.1 ± 4.4˚C and a mean maximum of 39.1 ± 1.4˚C (mean= 32.2 ± 3.9 ˚C).

There was a moderate positive relationship between skin temperature and mini-globe temperature for all elephants collectively (r_s=0.43, P<0.0001; Figure 3.2). This relationship was similar in all elephants (Appendix II) and across all parts of the body (Appendix III). There was a moderate positive relationship between skin temperature and mini-globe temperature regardless of whether elephants were in sun (r_s=0.56, P<0.0001), shade (r_s=0.57, P<0.0001) or were wet, (r_s=0.48, P<0.0001; but also see Appendix IV).

Of the seven GAMMs, a single model best described the variation in skin temperature with 86% model certainty (w_i=0.86, Table 3.1). Mini-globe temperature, behavioural state and age class were included as potential explanatory variables in this model, which described up to 36% (adjusted R^2=0.36) of the variation in skin temperature. GAMM response plots showed that skin temperature increased significantly as a function of mini-globe temperature (P<0.0001, Figure 3.3a). Skin temperature was significantly lower when elephants utilized shade (P<0.0001) or bathed (P<0.0001) than when elephants were exposed to direct sunlight (Figure 3.3b). Age class was also included in the best-selected model. Although the differences were not statistically significant, suckling (P=0.10) and weaned (P=0.14) calves showed higher skin temperatures than adults (Figure 3.3c).

The difference between mini-globe temperature and skin temperature increased (became more positive) significantly as a function of mini-globe temperature in adults (N=3 elephants, β=0.66, P<0.0001), weaned calves (N=3 elephants, β=0.75, P<0.0001) and in the suckling calf (N=1 elephant, β=0.78, P<0.0001). Mini-globe temperature exceeded skin temperature above a mini-globe temperature of 31.80˚C in adults, 33.75˚C in weaned calves and 34.47˚C in the suckling calf (Figure 3.4).

3.3.3 Core temperature

I recorded 17 days of core temperature for five elephants (Adult female A = 6 days, Adult female B = 2 days, Adult female C = 4 days, Weaned female A = 1 day, Weaned male A = 5 days) during the hot dry season and 8 days of core temperature for two elephants (Adult female A = 3 days, Adult female B = 5 days) during the cool flood season. Core temperature ranged between a mean minimum of 36.0 ± 0.3˚C and a mean maximum 37.1 ± 0.6˚C during the hot dry season and between a mean minimum of 35.9 ± 0.5˚C and a mean maximum of 37.0 ± 0.3˚C during the cool flood season. Mean, minimum and maximum core temperatures differed between elephants (Appendix I) and throughout the day (Figure 3.5). Core temperature followed a consistent 24-hour pattern, increasing during the daytime from approximately 08h00 until approximately 18h00, followed by a decrease during the night. This pattern was consistent in all elephants (Appendix V). The 24-hour mean and mean maximum core temperature range for all elephants (N=5) were 1.20 ± 0.43˚C and 1.46 ± 0.32˚C, respectively, during the hot dry season. During the cool flood season, the 24-hour mean and mean maximum core temperature ranges for all elephants (N=2) were 1.09 ± 0.54˚C and 1.13 ± 0.57˚C respectively.

There was a weak positive relationship between core and mini-globe temperature for all elephants collectively (r_s=0.08, P<0.0001; Figure 3.6). The relationship between core and mini-globe temperature was stronger in weaned calves (weaned female A: r_s=0.23, P<0.0001; weaned male A: r_s=0.36, P<0.0001) in comparison to adults (adult female A: r_s=-0.02, P=0.14; adult female B: r_s=0.13, P<0.0001; adult female C: r_s=-0.16, P<0.0001; see Appendix VI).

Of the 15 GAMMs, two models best described the variation in core temperature with 87% model certainty (combined w_i=0.87, Table 3.2). Mini-globe temperature, time of day and age class were included as potential explanatory variables in the model with the lowest AIC, which described up to 31% (adjusted R^2=0.31) of the variation in core temperature. Mini-globe temperature was included in the most plausible model, but core temperature did not increase significantly as a function of mini-globe temperature (P=0.54, Figure 3.7a). Core temperature did, however, increase significantly (P<0.0001, Figure 3.7b) as a function of time of day (between 09h00 and 16h00). Weaned calves had higher core temperatures than adults did, but this difference was not significant (P=0.08, Figure 3.7c).

The difference between skin and core temperature increased (became more positive) significantly with mini-globe temperature when elephants were in sun (β=0.43, P<0.0001), shade (β=0.33, P<0.0001) or were wet (β=0.53, P<0.0001). Skin temperature exceeded core temperature at mini-globe temperatures above 40.44˚C when elephants were exposed to direct sunlight, above 43.13˚C when elephants were in shade and above 47.58˚C when elephants were wet (Figure 3.8).

3.4. DISCUSSION

Large changes in skin temperature may be perceived by an individual as a discomfort (Hardy 1971; Huizenga *et al*. 2004), soliciting a behavioural response to restore skin temperature to a point of comfort (Bligh 1973; Gagge *et al*. 1967; Huizenga *et al*. 2001). The results from my GAMMs show that elephant skin temperature increased as a function of environmental temperature. At the same time, the probability of elephants utilizing shade and bathing increased as a function of environmental temperature (see Mole 2014). Shade utilization and bathing decreased skin temperature, with bathing possibly facilitating heat loss from the individual to the environment (Bligh 1973; Porter and Gates 1969; Rowe *et al*. 2013). Furthermore, core temperature did not increase as a function of environmental temperature. Therefore, by utilizing shade or bathing in response to increased skin temperature, coupled with autonomic responses, free-ranging elephants regulate core temperature within a narrow 24-hour range.

GLMMs showed that there was no longer a temperature gradient between the environment and the skin at environmental (mini-globe) temperatures of 31.80˚C for adults, 33.75˚C for weaned calves and 34.47˚C for the suckling calf. Theoretically, above these temperatures, sensible heat loss will be impaired and elephants will no longer be able to lose heat through convection, conduction and radiation. Therefore, to lose heat, elephants must make use of either evaporative cooling or behavioural thermoregulation. In this study, elephants began to seek shade and wallow at environmental temperatures of ~30˚C (see Mole 2014). I therefore suggest that when sensible heat loss is impaired, elephants rely largely on shade-seeking and bathing to lose heat and prevent further heat gain. Through these behavioural changes, skin temperature remained below core temperature, and elephants were able to prevent heat internal heat gain. As a result, our elephants could withstand higher environmental temperatures when in shade (43.17˚C) or wet (47.58˚C) before internal heat gain occurs compared to when exposed to direct sunlight (40.44˚C).

Behavioural responses, operating on primarily skin temperature sensitivity alone, may not have been solely responsible for the successful maintenance of core temperature. Although considered separately, behavioural and autonomic thermoregulation are integrated and complementary mechanisms responsible for the maintenance of body temperatures (Bligh

1971). Therefore, autonomic processes which could not be measured in this study, such as transcutaneous water loss (Dunkin *et al*. 2013; Wright and Luck 1984) and vasodilation (Rowe 2013; Williams 1990) may have contributed largely to the maintenance of core temperature. Autonomic processes are, however, energetically costly (Randall *et al*. 2002) and evaporative cooling may result in the loss of body water (Dunkin *et al*. 2013). By utilizing shade or bathing, elephants may delay the activation of autonomic thermoregulatory effectors, greatly extending their tolerance to heat.

The increase in core temperature during daylight hours in all elephants was not dependent on environmental temperature in my GAMMs, but rather on time of day. In mammals, nycthemeral rhythms may be independent of changes in environmental temperature, but are often dependent on day length (Refinetti and Menaker 1992; Benstaali *et al*. 2001). Generally, light induces activity in diurnal mammals, and suppresses activity in nocturnal mammals (Hoole *et al*. 2012). The elephants on which this study was conducted were most active during the daytime, however, activity was limited at night due to confinement to an enclosure. I suggest that the increase in core temperature may be a result of endogenous rhythms, stimulated by light induced activity. Activity patterns in captive and semi-captive elephants are often anthropogenically modified. Therefore, to draw firm conclusions, nycthemeral rhythms of core temperature should be investigated in wild elephants where activity patterns are not limited at night.

Age class was an important factor explaining differences in skin and core temperature. Although the differences were not statistically significant (at α=0.05), suckling and weaned calves showed higher skin temperatures than adults and weaned calves showed higher core temperatures than adults. Higher skin temperatures in suckling and weaned calves, and higher core temperatures in weaned calves suggests that suckling and weaned calves (henceforth, collectively referred to as 'calves') may absorb and transfer more heat to their core than adults do. A faster rate of heat gain may be a potential problem for calves exposed to extreme environmental temperatures, particularly those exposed to direct solar radiation. However, observations on the same elephants, during the same study period, revealed that skin and core temperature in calves remained higher than in adults at night, despite cooler environmental temperatures (Conservation Ecology Research Unit, unpublished data). Based on their larger skin surface area to mass ratio, calves should theoretically have lost heat faster at night, and shown cooler body temperatures than adults. The rate of metabolic heat production, per kilogram of body mass, in other mammals at rest is higher in juveniles than in adults (Laburn *et al*. 2002). To the best of my knowledge, neither the metabolic rate, nor the capacity to lose heat through evaporative cooling in elephant calves has ever been recorded. If calves generate heat at a rapid rate, core temperature will increase, and if evaporative cooling does not decrease skin temperature, skin temperature will increase. Calves may therefore be more susceptible to heat stress than adults and will be more dependent on thermal resources such as shade, mud and water to assist them with thermoregulation.

Studies have shown pronounced differences in elephant space and resource use between bulls and mixed family units (see Ntumi *et al*. 2005; Stokke and Du Toit 2002; Smit *et al*. 2007). Although conducted in different study areas across southern Africa, these studies all show that during the late dry season (September to October), which coincides with the hottest and driest months of the year, mixed family groups congregate closer to permanent water sources and areas of high tree canopy cover than bulls do. The consensus is that differences in energy requirements, mobility and social interactions may account for these sex differences in habitat use (Stokke and Du Toit 2002; Smit *et al*. 2007). Although plausible, I suggest that the thermal limitation imposed by calves may be an additional underlying factor in the sexual segregation of elephants. On average, the first calf will be between 4 and 5 years when the second calf is born (Lee and Moss 2011). Hence, in a family group of 5-10 elephants, calves will most likely be present and within close proximity to their mothers. The thermal requirements of calves may prevent family groups from travelling large distances, away from suitable shade and water. Bulls may therefore have the option to travel further distances to forage, whereas family units with calves at foot may not.

My results show that elephants are not susceptible to heat stress when exposed to high environmental temperatures, provided suitable resources are available for thermoregulation. When shade and water are available, elephants can maintain skin temperature, most likely to maintain thermal comfort reducing heat gain from the environment and maintaining core temperature within narrow limits. Furthermore, I found evidence suggesting that calves could face greater difficulties losing heat than adults may. The activity and movements of family groups may therefore be limited due to the thermal requirements of calves at foot. In marginal habitats where shade and water are scarce, elephants may face greater risk of hyperthermia, although this hypothesis remains to be tested. If elephants in marginal habitats do face greater risk of hyperthermia, individual fitness could be reduced, particularly in adult cows and calves, altering habitat use and demography

Table 3.1. Statistical properties of GAMMs used to describe variation in skin temperature for seven elephants. Elephant was included in the model as a random effect and part of the body was included as a nested random effect within each elephant. Best selected models with an AIC difference (Δ AIC) of less than 2 are highlighted in bold. Parameters that contributed significantly to explaining variation in skin temperature are denoted with an asterix (*).

	Candidate model	K	LogLik	AIC	Δ AIC$_i$	w_i	R^2
1	**mini-globe* + state* + age class**	**10**	**-18526**	**37072**	**0**	**0.86**	**0.36**
2	mini-globe* + state*	8	-18529	37075	3.59	0.14	0.32
3	mini-globe + age class	8	-19019	38053	981.91	0	0.26
4	mini-globe	6	-19022	38057	984.97	0	0.21
5	age class + state	8	-20139	40293	3221.88	0	0.07
6	State	6	-20142	40297	3224.97	0	0.03
7	age class	6	-20263	40539	3467.41	0	0.04

Note: K=number of parameters in model; LogLik= log likelihood; AIC= Akaike's information criterion; Δ AIC$_i$= Difference in AIC between the model and best fitting model; w_i=Akaike weight; R^2=adjusted coefficient of determination.

Table 3.2. Statistical properties of GAMMs used to describe variation in core temperature for five elephants where elephant was included in the model as a random effect. Best selected models with an AIC difference of less than 2 are highlighted in bold. Parameters that contributed significantly in explaining variation in core temperature are denoted with an asterix (*).

	Candidate model	K	LogLik	AIC	Δ AIC$_i$	w_i	R^2
1	**mini-globe + time* + age class**	**8**	**-60.98**	**137.97**	**0.00**	**0.49**	**0.31**
2	**mini-globe + time***	**7**	**-62.25**	**138.49**	**0.52**	**0.38**	**0.18**
3	time* + age class	6	-64.89	141.77	3.80	0.07	0.30
4	Time	5	-66.23	142.46	4.49	0.05	0.17
5	mini-globe + time + age class + state	10	-65.21	150.42	12.46	0.00	0.31
6	mini-globe + time + state	9	-66.49	150.98	13.01	0.00	0.18
7	time + age class + state	8	-69.72	155.45	17.48	0.00	0.30
8	time + state	7	-71.08	156.17	18.20	0.00	0.17
9	mini-globe + age class	6	-112.54	237.08	99.11	0.00	0.19
10	mini-globe + age class + state	6	-112.54	237.08	99.11	0.00	0.19
11	mini-globe	5	-113.77	237.55	99.58	0.00	0.07
12	mini-globe + state	7	-117.47	248.93	110.97	0.00	0.08
13	age class	4	-133.24	274.47	136.51	0.00	0.13
14	age class + state	6	-136.98	285.97	148.00	0.00	0.12
15	State	5	-138.28	286.56	148.59	0.00	-0.01

Note: K=number of parameters in model; LogLik= log likelihood; AIC= Akaike's information criterion; Δ AIC$_i$= Difference in AIC between the model and best fitting model; w_i=Akaike weight; R^2=adjusted coefficient of determination.

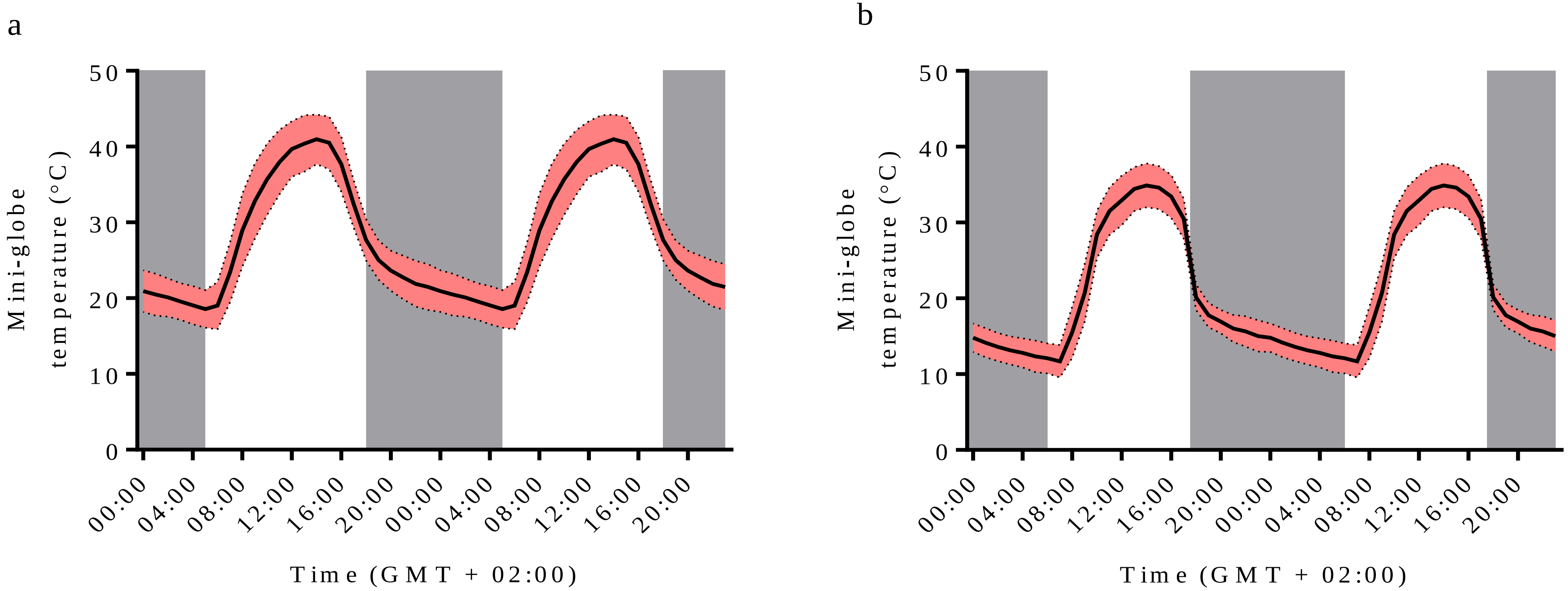

Figure 3.1. A double plot of the mean 24-hour mini-globe temperature (± SD) showing hourly means for a) the hot dry season (*n*=64 days) and b) the cool flood season (*n*=52 days). Standard deviation (pink shaded area) represents variation between days. Shaded columns represent the night-time and unshaded columns represent the daytime.

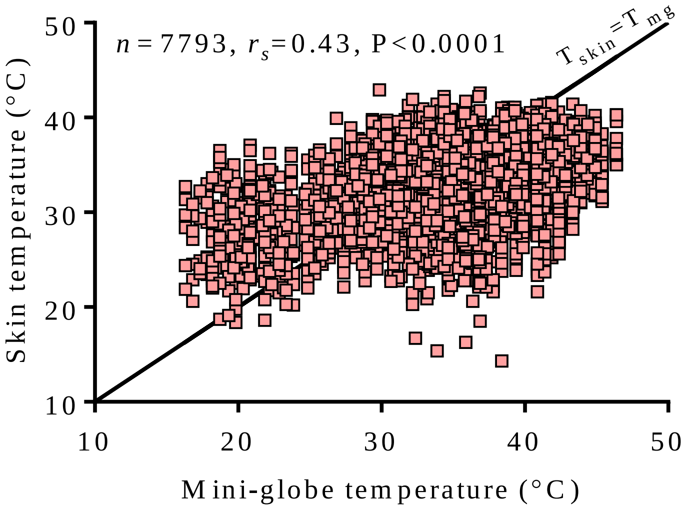

Figure 3.2. Skin temperature as a function of mini-globe temperature for all parts of the body of seven elephants (*n*=7793, r_s=0.43, P<0.0001). The solid line represents a 1:1 ratio where skin temperature (T_{skin}) is equal to mini-globe temperature (T_{mg}).

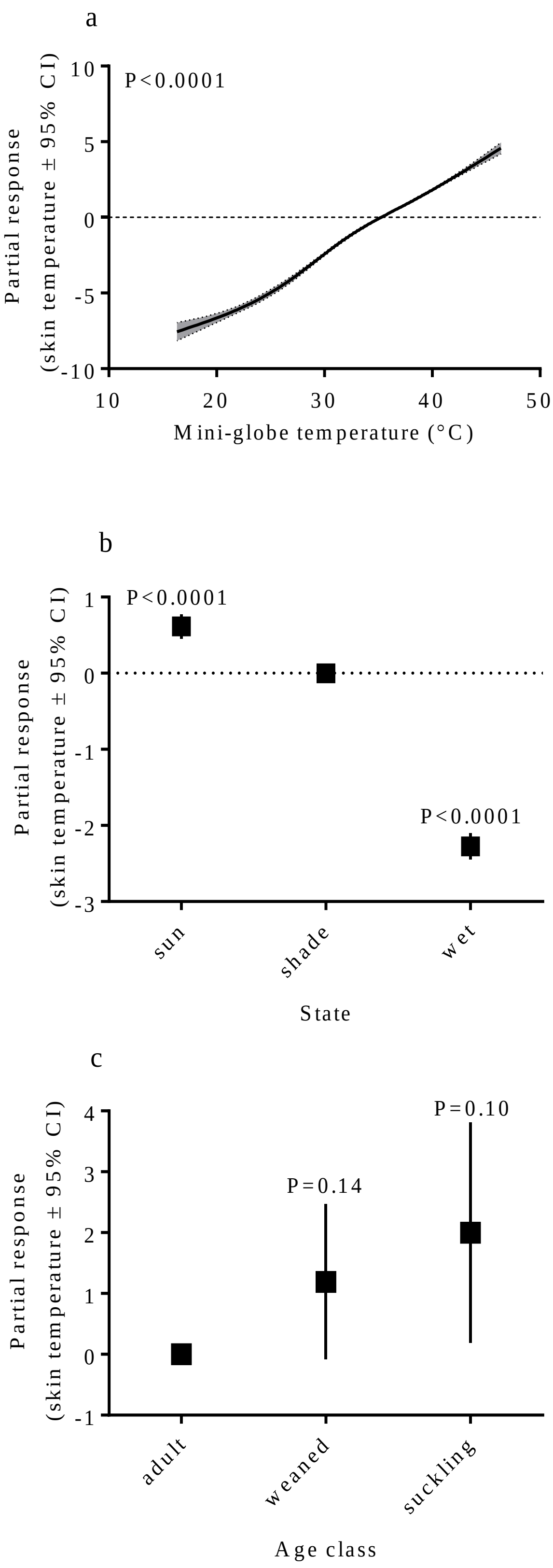

Figure 3.3. GAMM partial response graphs based on residuals from the most plausible model illustrating a) the trend between skin and mini-globe temperature, b) the differences in skin

temperature when elephants were in sun, shade or were wet, and c) the differences in skin temperature between adults, weaned and suckling calves. Shaded areas and error bars represent 95% confidence intervals.

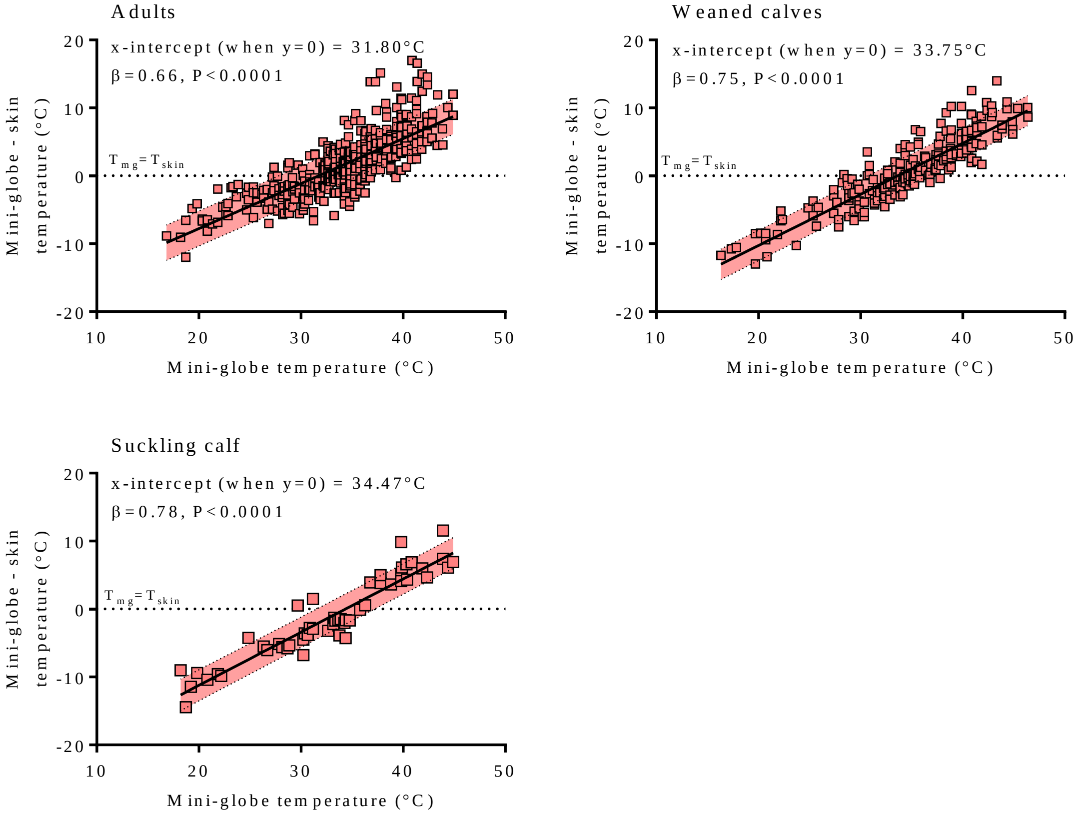

Figure 3.4. Generalized linear mixed models illustrating the difference between mini-globe temperature and skin temperature as a function of mini-globe temperature for all elephants, separated by age class (Adults *N*=3 elephants, Weaned calves *N*=3 elephants, Suckling calf *N*=1 elephant). All points represent elephants exposed to direct sunlight. Error bands represent 95% confidence intervals. The dotted horizontal line represents a difference of zero where mini-globe temperature (T_{mg}) is equal to skin temperature (T_{skin}).

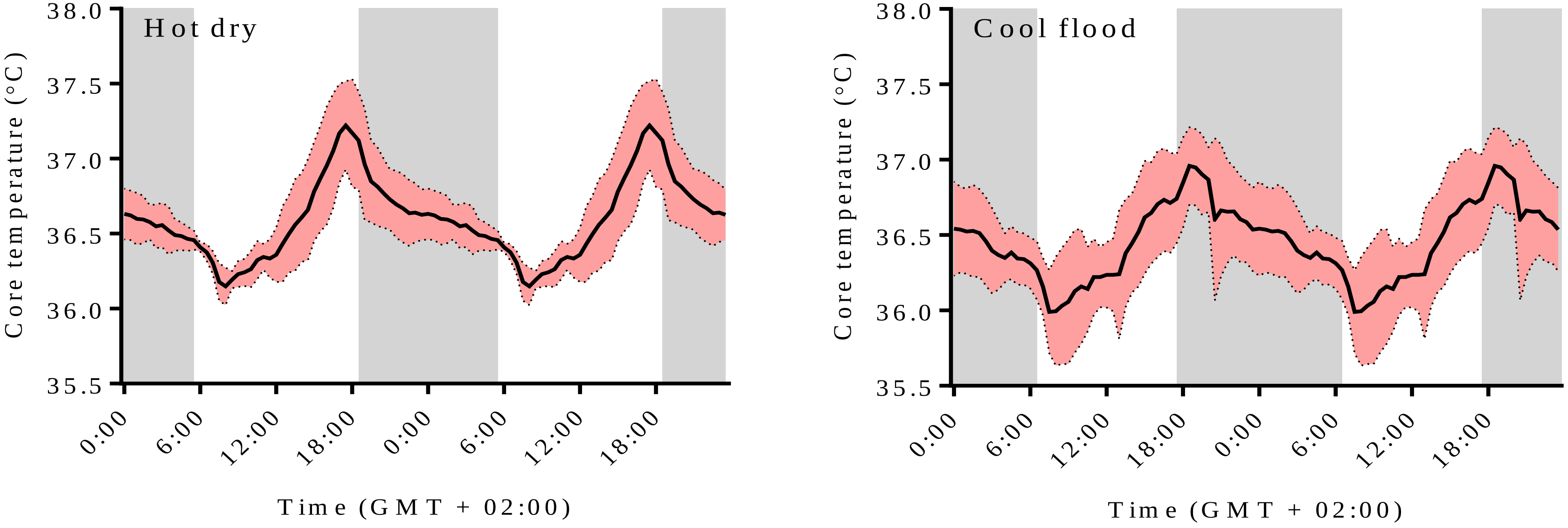

Figure 3.5. Double plots of the mean 24-hour core temperature (± SD), showing half-hourly means for five elephants during the hot dry season and for two elephants during the cool flood season. Standard deviation (pink shaded area) represents the variation between elephants. Grey shaded columns represent night-time and unshaded columns represent the daytime.

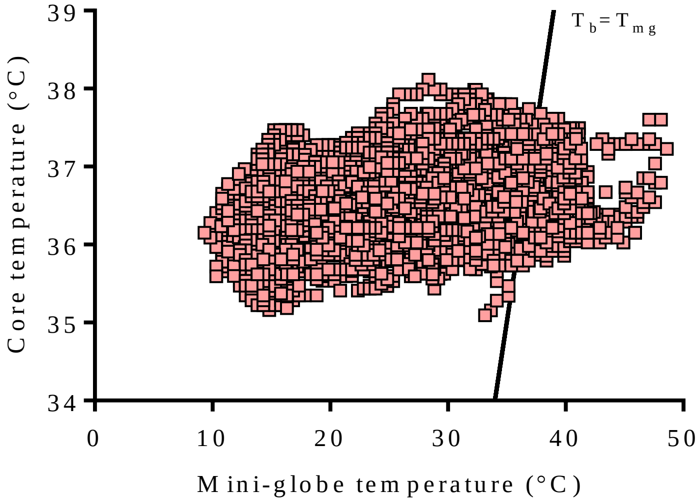

Figure 3.6. Core temperature as a function of mini-globe temperature for five elephants (*n*=11050, r_s=0.08, P<0.0001). The solid line represents a 1:1 ratio where core temperature (T_b) is equal to mini-globe temperature (T_{mg}).

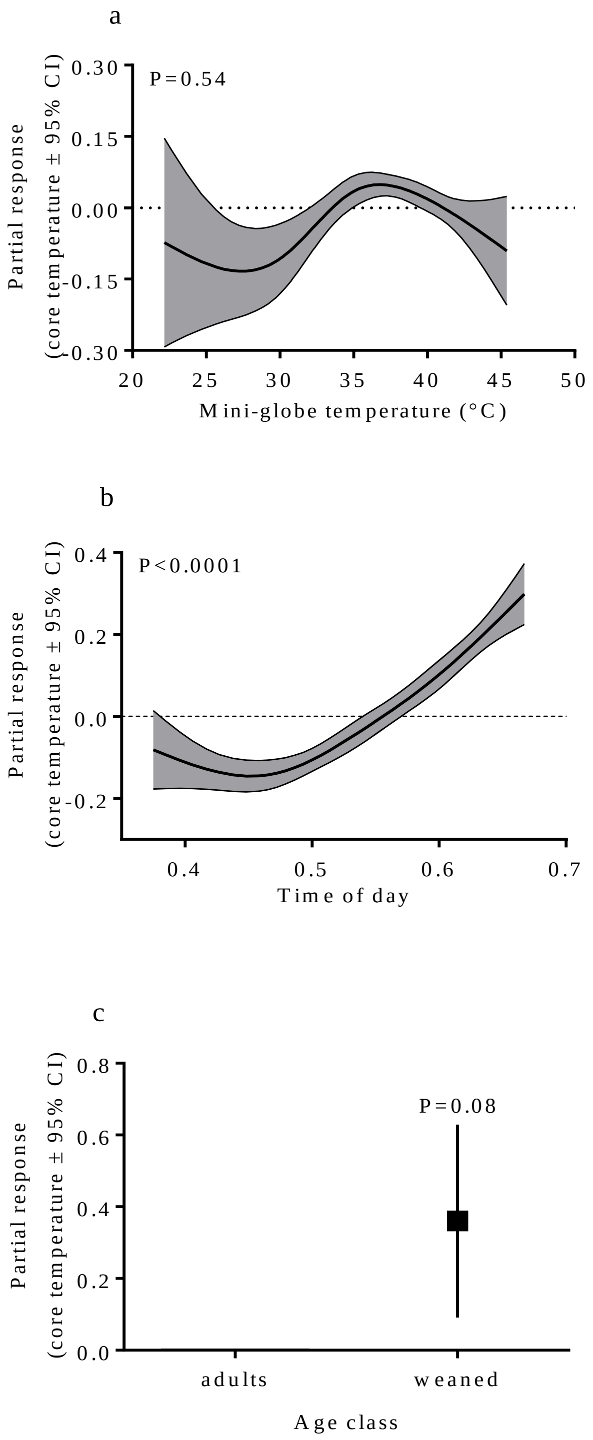

Figure 3.7. GAMM partial response graphs based on residuals from the most plausible model illustrating a) the trend between core and mini-globe temperature, b) the trend between core temperature and time of day, and c) the differences in core temperature between adults and weaned calves. Shaded areas and error bars represent 95% confidence intervals.

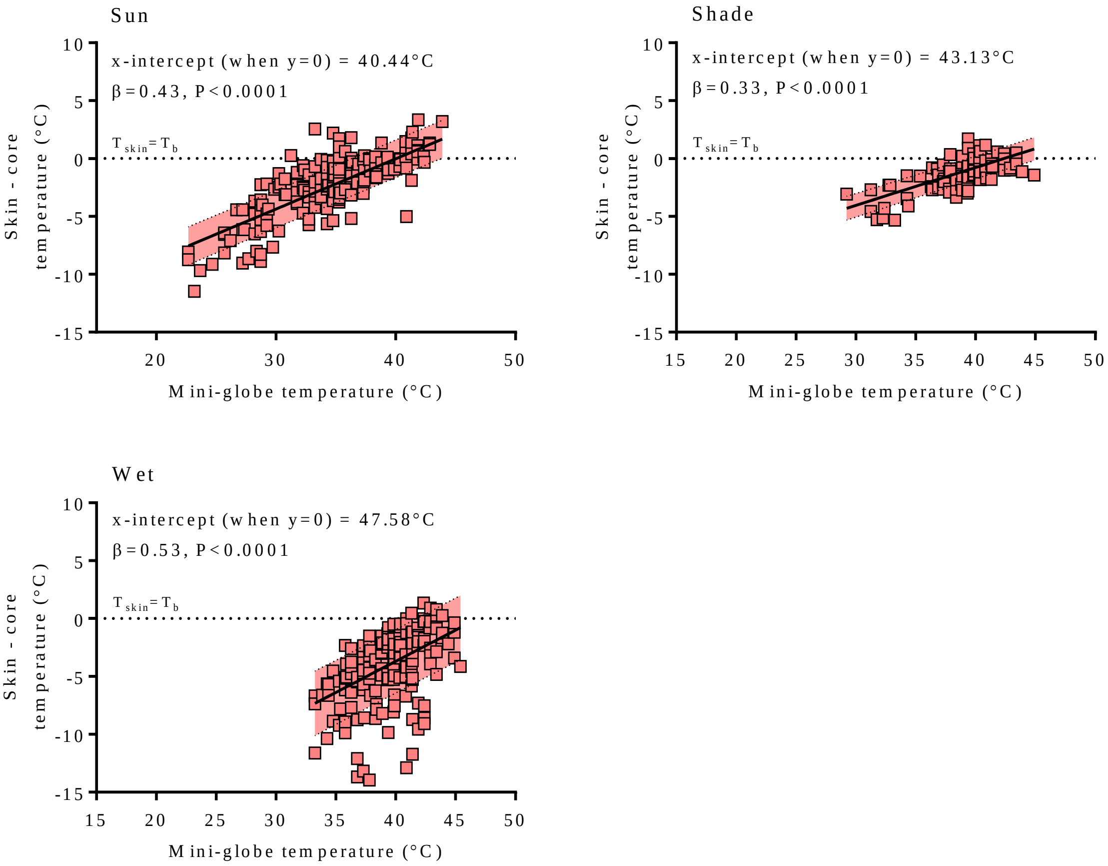

Figure 3.8. Generalized linear mixed models illustrating the difference between skin temperature and core temperature as a function of mini-globe temperature for all elephants (N=7 elephants), separated by behavioural state. Shaded error bands represent 95% confidence intervals. The dotted horizontal line represents a difference of zero where skin temperature (T_{mg}) is equal to core temperature (T_{skin}).

CHAPTER 4 – AFRICA'S SAVANNA ELEPHANTS MAINTAIN HOMEOTHERMY

4.1. INTRODUCTION

Heterothermy is characterized by variation in core temperature corresponding with variation in ambient temperature and has been documented in several endotherms (see McKechnie and Mzilikazi 2011). In hot environments, heterothermy is most likely to occur when ambient temperature exceeds core temperature. Under these conditions, sensible heat loss is impaired and endotherms can dissipate heat only via evaporative cooling (Mitchell *et al*. 2002). However, evaporative cooling may result in a decrease in total body water and dehydration may occur if water availability from the environment is limited (Schmidt-Nielson *et al*. 1957; Fuller *et al*. 2014). In an attempt to conserve body water, endotherms may store heat, allowing core temperature to increase under positive thermal load, reducing the need to lose heat by evaporative cooling (Mitchell *et al*. 2002).

In mammals, total metabolic heat production increases (McNab 1983) and surface area to mass ratio decreases with increasing body size (Schmidt-Nielson 1990). As a result, small mammals alter core temperature through metabolic changes and microhabitat selection with relative ease (Phillips and Heath 1995). Large mammals, however, due to their size and limited access to thermal refuges, may face several difficulties in dissipating excess heat (Phillips and Heath 1995). Heterothermy may therefore be an important physiological adaptation, particularly in large mammals inhabiting hot and dry environments (Schmidt-Nielson *et al*. 1957; Hetem *et al*. 2012; Mitchell *et al*. 2002). The logic is that large mammals have the capacity to absorb excess body heat during the heat of the day, resulting in a consequent rise in core temperature. This heat is dissipated non-evaporatively during the cool of the night, allowing core temperature to fall below normothermic levels, hence decreasing minimum core temperature as maximum ambient temperature increases. However, from published accounts it is not clear whether elephants, the largest extant terrestrial mammals, employ heterothermy.

Recent advances in biologging have allowed continuous recording of the 24-hour core temperature of captive and tamed elephants (Kinahan *et al.* 2007; Hidden 2009; Weissenböck *et al.* 2010; Weissenböck *et al*. 2012). However, the conclusions drawn from these studies are contradictory. Kinahan *et al*. (2007) found no evidence of heterothermy in a captive population of savanna elephants (*Loxodonta africana*) exposed to a mean 24-hour ambient (air) temperature of 21 ˚C. Weissenbock *et al.* (2012) showed that core temperatures of captive Asian elephants (*Elephas maximus*) exposed to a mean ambient temperature of 30 ˚C in tropical Thailand had a higher 24-hour core temperature range (1.2 ˚C) than elephants exposed to a mean ambient temperature of 21 ˚C in temperate Germany (24-hour core temperature range: 0.5 ˚C). They concluded that these differences provided evidence for heterothermy in Asian elephants. However, these studies were conducted on captive elephants that did not have the opportunity to respond behaviourally to changes in ambient temperature and may not reflect on responses to the actual conditions prevailing under natural conditions (Kamau and Maloiy 1985; Mitchell *et al*. 2002). A study conducted on tamed, free-ranging savanna elephants exposed to a mean ambient temperature of 29˚C, showed that core temperature range did not exceed 1.2˚C (Hidden 2009). Furthermore, core temperature range did not increase as a function of ambient temperature, suggesting that free-ranging elephants do not employ heterothermy. Because ambient temperature did not exceed the normal core temperature of elephants (~36˚C), it remains unknown whether elephants employ heterothermy when sensible heat loss is impaired.

Here I test the working hypothesis that free-ranging savanna elephants employ heterothermy in African savannas where ambient temperatures frequently exceed the core temperature of elephants. In support of this working hypothesis I expected an increase in maximum 24-hour core temperature, a decrease in minimum core temperature and an increase in 24-hour core temperature range as ambient temperature increased.

4.2. MATERIALS AND METHODS

The data used in this chapter are the same data used in Chapter 3. The data were however, analysed separately to address the specific working hypotheses of each chapter.

4.2.1 Study site

Refer to section 2.2 for details of the study site.

4.2.2 Study animals

Refer to section 2.3 for details of the study animals. Note that in this chapter, I recorded core temperature in four of the seven elephants (Adult female A, Adult female B, Adult female C and Weaned male A).

4.2.3 Ambient temperature data

Ambient (air) temperature was recorded at five minute intervals as described in section 2.7.

4.2.4 Core temperature data

Core temperature was recorded using miniature ingestible data loggers as described in section 2.4.

4.2.5 Data analysis

For successive 24-hour periods I calculated mean, minimum, maximum and range (difference between the highest and lowest 24-hour core temperatures) of the nycthemeral rhythm of core temperature. To determine whether mean core temperature differed between the two seasons I used unpaired t-tests. I fitted linear mixed-effects models using the *nlme* package (Pinheiro *et* *al*. 2013, in R, version 2.15.2; R Core team 2012) to determine whether 24-hour core temperature range increased significantly as a function of 24-hour ambient temperature range and maximum ambient temperature. An increase was defined as a positive slope that differed significantly ($P \leq 0.05$) from zero. In these models elephant was included as a random effect to account for repeated measures on the same elephants.

I calculated the 24-hour heterothermy index (see Boyles *et al.* 2011) for each elephant using the formula:

$$\mathrm{HI} = \sqrt{\frac{\sum (T_{b-mod} - T_{b-i})^2}{n-1}}$$

where T_{b-mod} is the difference between core temperature at a given time and modal core temperature , T_{b-i} is the core temperature measurement at time i and n is the number of times T_b is sampled. I calculated the 24-hour heterothermy index for each elephant and averaged these to obtain the mean 24-hour heterothermy index for all elephants. The higher the HI metric, the greater the deviation from modal core temperature and the higher the degree of heterothermy.

To determine if large mammals are more likely to employ heterothermy I included the highest maximum 24-hour core temperature ranges recorded for mammals of varying mass, but that inhabit hot environments similar to those inhabited by elephants. Values for elephants were obtained from this study. As an explanatory variable, I obtained the mean mass for each species as reported in each study. Following log transformation to normalize the data, I used simple linear regression to determine if maximum core temperature range increased with increasing body mass. An increase was defined as a positive slope that differed significantly ($P \leq 0.05$) from zero. All results are reported as means ± SD unless stated otherwise.

4.3. RESULTS

4.3.1 Ambient temperature

I recorded ambient temperature for 64 days during the hot dry season and for 52 days during the cool flood season. Mean ambient temperature was higher during the hot dry season (26.2 ± 2.8˚C, mean ± standard deviation) than during the cool flood season (18.6 ± 2.1˚C). Ambient temperature ranged between 11.9˚C (mean minimum = 18.5 ± 2.7˚C) and 42.7˚C (mean maximum = 35.7 ± 3.7˚C) during the hot dry season, and between 5.9˚C (mean minimum = 11.7 ± 2.2˚C) and 35.6˚C (mean maximum = 28.5 ± 4.4˚C) during the cool flood season. Ambient temperature varied with time of day, increasing rapidly after sunrise until midday, and gradually decreased following nightfall during both seasons (Figure 4.1a).

4.3.2 Core temperature

I recorded 17 days of core temperature for four elephants (Adult female A = 6 days, Adult female B = 2 days, Adult female C = 4 days, Weaned male A = 5 days) during the hot dry season and 8 days of core temperature for two elephants (Adult female A = 3 days, Adult female B = 5 days) during the cool flood season. Mean core temperature for 4 elephants was significantly higher (t_{23}= 7.6, P<0.0001) during the hot dry season (36.6 ± 0.2˚C, n = 17 days) than for two elephants during the cool flood season (36.5 ± 0.4˚C, n = 8 days). Core temperature ranged between a mean minimum of 36.0 ± 0.3˚C and a mean maximum 37.1 ± 0.6˚C during the hot dry season and between 35.9 ± 0.5˚C and 37.0 ± 0.3˚C during the cool flood season. There were no differences in mean minimum core temperatures between the hot dry season and the cool flood season (t_{23}=1.72, P=0.09). There were also no differences in mean maximum core temperatures between the two seasons (t_{23}=1.20, P=0.24). Ambient and core temperature followed a similar 24-hour pattern, but core temperature continued to increase despite decreasing ambient temperature after ~1600 hours (Figure 4.1a, b). Mean 24-hour core temperature ranges were similar (t_{23}=0.54, P=0.59) between seasons (1.20 ± 0.43˚C during the hot dry season and 1.09 ± 0.54˚C during the cool flood season). Mean core temperature peaked at ~1800 hours and showed a trough at ~0800 hours during both seasons (Figure 4.1b).

Contrary to my expectations, core temperature range did not increase with ambient temperature range or maximum ambient temperature (Figure. 4.2a, b). Maximum core temperature did not increase and minimum core temperature did not decrease as a function of maximum ambient temperature in any of the elephants (Figure 4.2c, d). The mean 24-hour heterothermy index (HI) for all elephants was 0.35 ± 0.15˚C, which is relatively low on the heterothermy continuum. Furthermore, maximum 24-hour core temperature range of mammals inhabiting hot, dry environments was not a function of body size (β=-0.09, P=0.15; Figure 4.3).

4.4. DISCUSSION

This study is the first to record core temperature range in free-ranging elephants exposed to ambient temperatures that exceeded their normal core temperature. I show that despite large ranges in ambient temperature (of up to 25˚C), free-ranging savanna elephants maintained core temperature within a narrow range. Furthermore, maximum core temperature did not increase, and minimum core temperature did not decrease with maximum ambient temperature, providing evidence that free-ranging savanna elephants do not employ heterothermy.

My findings do not support the literature which suggests that elephants in hot environments employ heterothermy (Elder and Rodgers 1975; Hiley 1975; Weissenböck *et al.* 2012). Their conclusions were based on significantly larger mean 24-hour core temperature ranges in elephants in a more tropical Thailand than in other elephants in more temperate Germany (Weissenböck *et al.* 2012), and a strong correlation between ambient and muscle temperatures (Elder and Rodgers 1975). My results show that the 24-hour mean core temperature range of all elephants was 1.2˚C, which is 0.05˚C higher than the 24-hour mean core temperature range found in captive Asian elephants (Weissenböck *et al*. 2012) and 0.4˚C higher than the 24-hour mean core temperature range recorded in captive savanna elephants (Kinahan *et al*. 2007). Although heterothermy was suggested in the captive population of Asian elephants (Weissenböck *et al*. 2012), the range in 24-hour core temperature did not correlate with the 24-hour range in ambient temperature and does not support the assumptions of heterothermy. Therefore, the inter-population differences in core temperature ranges observed may have been an artefact of different housing conditions, diet or 24-hour activity patterns. Asian elephants may therefore also maintain core temperature within a narrow range despite variability in ambient temperature, although data on Asian elephants requires further testing against the assumptions of heterothermy to draw firm conclusions.

Experimental manipulations have shown that when large mammals become dehydrated, the rate of evaporative water loss is reduced (Finch and Robertshaw 1979). A reduced rate of evaporative water loss is often accompanied by an increase in maximum body temperature during periods of heat exposure, typical of heterothemy (Alamer 2006; Mitchell *et al*. 2009). Admittedly, the elephants in this study were neither water nor food deprived. However, depriving focal animals of water may result in dehydration-induced increases in maximum 24-hour core temperature (Mitchell *et al*. 2002; Fuller *et al*. 2014), without a change in minimum 24-hour core temperature.

I conclude that when opportunities for behavioural thermoregulation are available, free-ranging elephants in optimal habitats do not employ heterothermy, and maintain core temperature within narrow limits, characteristic of homeothermy. Furthermore, elephants represent the upper mass limit in terrestrial mammals and contrary to the general consensus (see Hetem *et al*. 2012), my findings show that large size does not impair thermoregulation and large mammals can maintain homeothermy as efficiently as smaller mammals can.

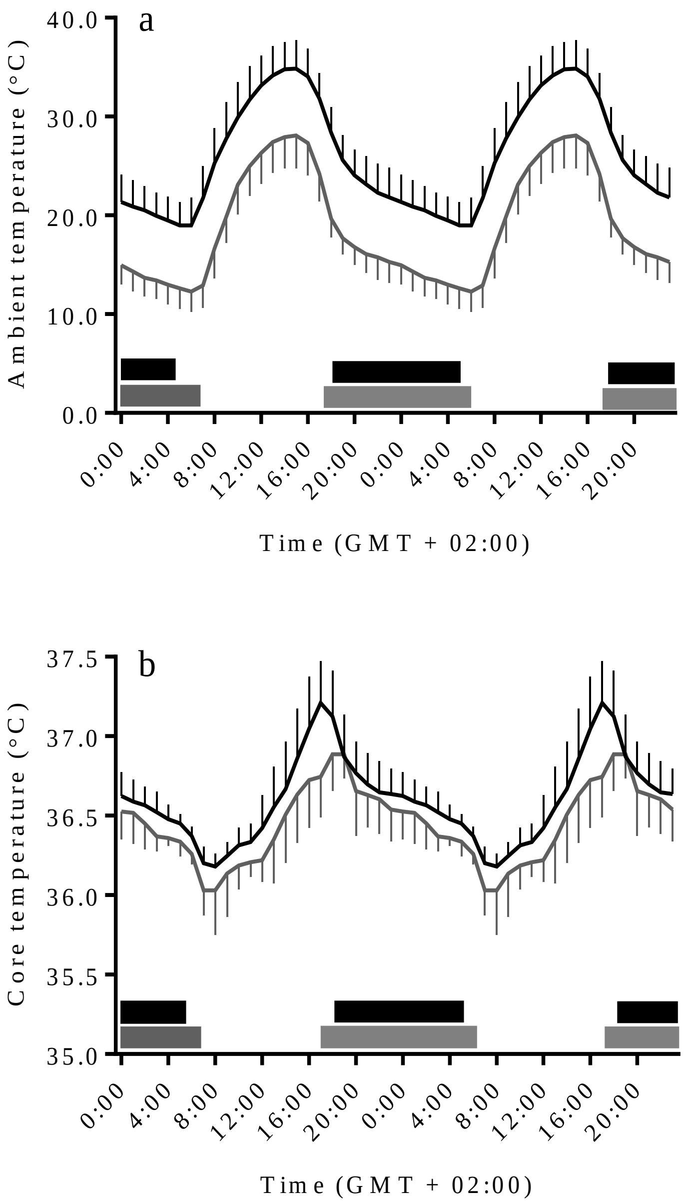

Figure 4.1. Double plots illustrating a) hourly mean ambient temperature (± SD) during the hot dry season (black line; *n*=64 days) and the cool flood season (grey line; *n*=52 days) and b) hourly mean core temperature (± SD) during the hot dry season (black line; *n*=4 elephants) and the cool flood season (grey line; *n*=2 elephants). Black bars represent night-time during the hot dry season and grey bars represent night-time during the cool flood season.

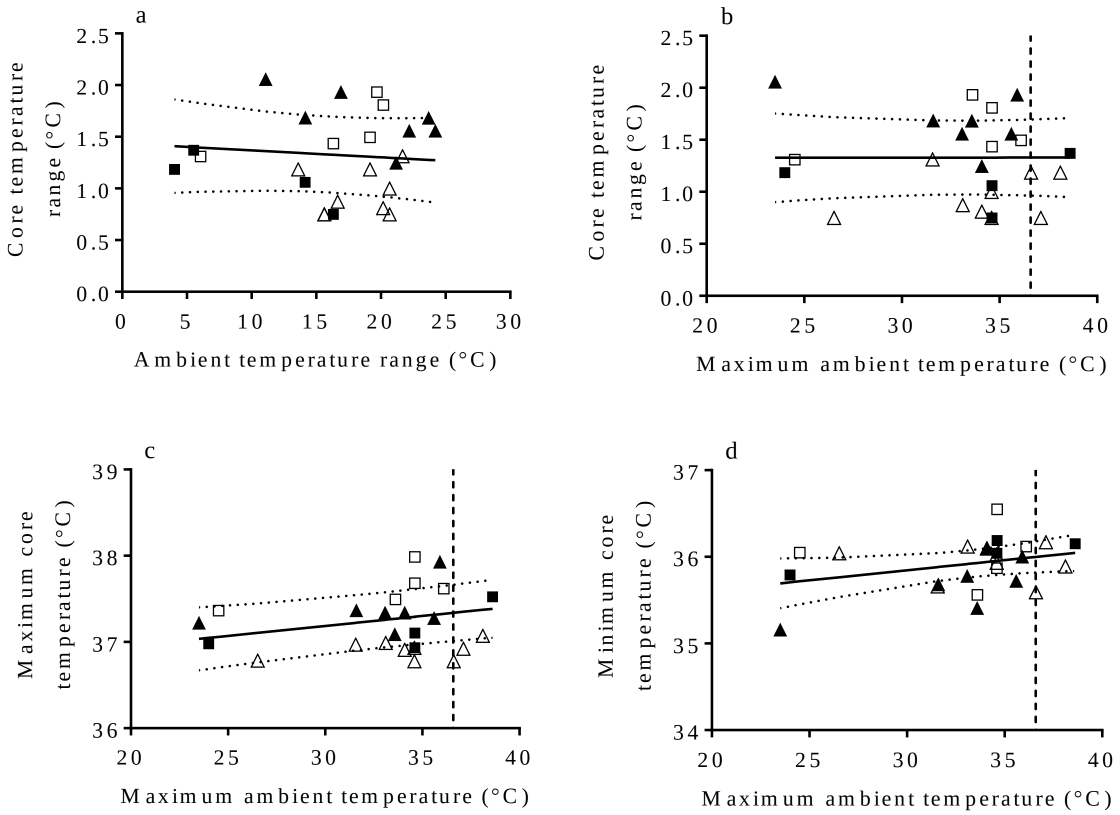

Figure 4.2. The top linear mixed-effects model plots (a and b) show 24-hour core temperature range of four elephants plotted as a function of concurrent 24-hour ambient temperature range (β=-0.01, P=0.56) and maximum ambient temperature (β=0.0001, P=0.99). The middle plots (c and d) show 24-hour maximum (β=0.02, P=0.07) and minimum (β=0.02, P=0.09) core temperature plotted as a function of concurrent maximum 24-hour ambient temperature. Error bands represent 95% confidence intervals. Symbols represent different elephants (unshaded triangles=adult female A, shaded triangles=adult female B, shaded squares=adult female C, unshaded squares=weaned male A). All graphs show 25 days of data.

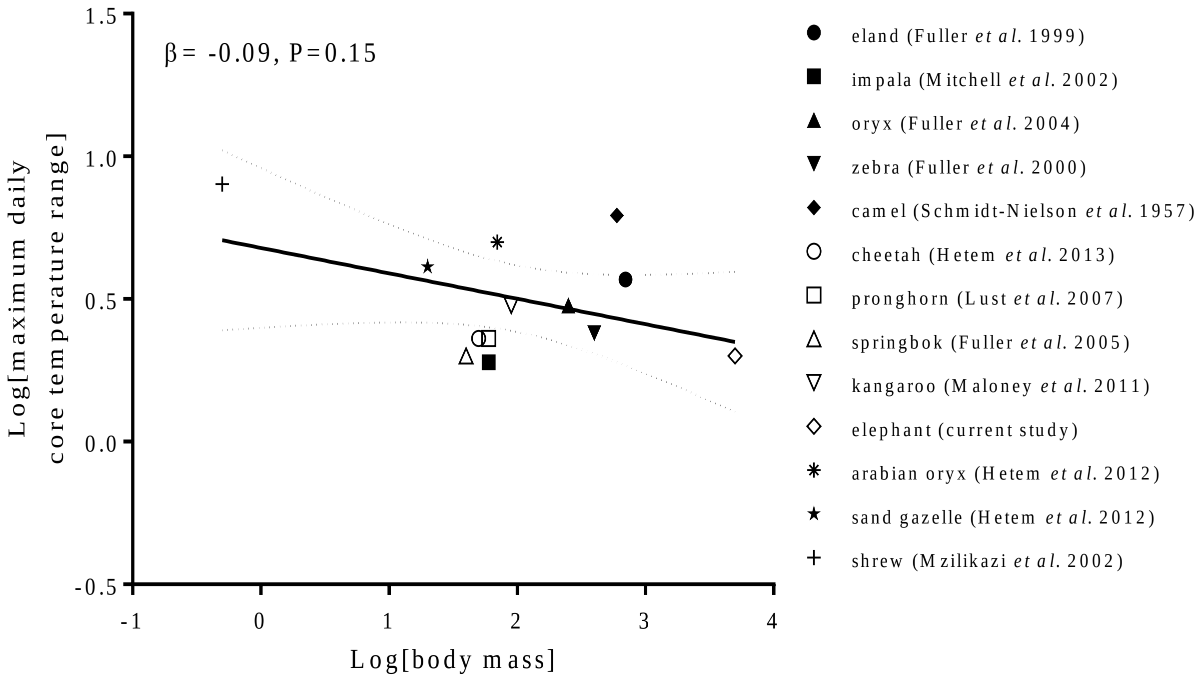

Figure 4.3. Maximum 24-hour core temperature range as a function of body mass for 12 species of mammals inhabiting hot and dry environments similar to elephants (***β***=-0.09, P=0.15). Error bands represent 95% confidence intervals.

CHAPTER 5 - SYNTHESIS

The vulnerability of a species to climate change is dependent on two main factors: the amount of exposure a species may have to adverse conditions, and the physiological limits of the species (Moritz and Agudo 2013). These factors can be mediated by altering activity patterns over time, distribution across space, or by making use of behavioural and physiological plasticity in situ to adapt to climate change (Bellard et al. 2012). The latter is of particular importance as an animal's physiology may play an important role in determining how it interacts with its environment (Hidden 2009).

It has been suggested that elephants may face difficulties losing heat (Benedict *et al*. 1936; Elder and Rodgers 1975; Williams 1990; Phillips and Heath 1995; Kinahan *et al*. 2007a). This raises an important question – how will predicted increases in environmental temperatures affect elephants? To address this question, a mechanistic understanding of how elephants respond physiologically to high environmental temperatures is required (Fuller *et al.* 2010; Garcia *et al*. 2012; McCain and King 2014). However, our knowledge of elephant thermoregulation is based mostly on studies conducted on captive elephants exposed to moderate environmental temperatures (below 35˚C; Kinahan *et al*. 2007a; Wiessenböck *et al*. 2010; Wiessenböck *et al*. 2012; Rowe *et al*. 2013). Therefore, how elephants in their natural environment currently respond to high environmental temperatures has remained unknown, limiting our ability to assess if elephants can adapt to climate change.

My study is the first to assess the physiological responses of free-ranging savanna elephants to currently high environmental temperatures and highlights their dependence on behavioural thermoregulation. I show that when shade and water are available, elephants can maintain homeothermy, even when environmental temperature exceeds body temperatures. At high environmental temperatures, elephants decreased skin temperature and prevented further heat gain by making use of behavioural changes such as shade utilization and bathing (see Chapter 3). Through these behavioural changes, coupled with autonomic mechanisms, elephants were able to maintain core temperature within narrow limits (homeothermy, see Chapter 4). My findings do not support the notion that elephants face difficulties losing heat as has been suggested. I therefore suggest that through adaptive changes in behaviour, which alter their physiology, elephants will likely cope successfully with the direct effects of high environmental temperatures.

Theoretically, elephants should begin to gain heat from the environment when environmental temperature exceeds skin temperature (Porter and Gates 1969; Phillips and Heath 1995). In my study, this took place at environmental temperatures above 31˚C for adult elephants and above 34˚C for calves. However, both adults and calves began to seek shade and bathe at lower environmental temperatures of 30˚C (Mole 2014, unpublished thesis). Increases in skin temperature may therefore initiate a behavioural response before heat gain from the environment even begins. Therefore, where shade and water are available, behavioural thermoregulation may be the primary response to changes in environmental temperature. In this way, elephants may be less dependent on autonomic mechanisms to thermoregulate.

Behavioural responses to high environmental temperatures are not without costs. Elephants must optimize trade-offs between the benefits of high-quality resources and the costs to find them (Harris *et al*. 2008). In optimal habitats, where water is available for drinking and bathing and there is high primary productivity for food and shade, elephants may utilize high-quality resources whilst incurring minimal costs. However, in marginal habitats, where food, water and shade are limited, elephants may need to travel large distances to drink and forage. High environmental temperatures in these habitats may confine elephants to shade or within close proximity to permanent water sources because the costs of thermoregulation may exceed the benefits of foraging. Low-quality forage and heat stress may reduce body condition, particularly in adult cows (as seen in cattle e.g. Kadzere *et al*. 2002). Subsequently, reduced individual fitness may decrease reproductive output, influencing demography.

Calf survival is another factor that may influence elephant demography (Young and van Aarde 2010). During my study, I observed higher skin and core temperature in calves than in adults (see Chapter 3). At the same time, behavioural observations (conducted on the same elephants) revealed that the family group with a suckling calf present utilized shade at lower environmental temperatures than the family group without a suckling calf did (see Mole 2014). High environmental temperatures may therefore have had a greater influence on smaller calves than on larger adults. If calves are more susceptible to heat stress, this may have important implications for the population and may provide an understanding into the mechanisms driving calf mortalities during severe droughts (e.g. Dudley *et al*. 2001; Foley *et al*. 2008). The influence of high environmental temperature on weaned and suckling calves therefore requires further investigation.

Elephants have undergone changes in distribution within Africa over their evolutionary history, which may have resulted from repeated climatic changes at a continental scale (Eggert *et al*. 2002). At present, most elephants occur in conservation areas scattered across southern Africa (van Aarde and Jackson 2007). The amount of space available for elephants in the future may become even more limited because of increasing anthropogenic pressures such as habitat loss, erection of fences and roads (Newmark 2008). Furthermore, predicted changes in rainfall patterns may alter resource (such as shade and water) availability throughout the distribution of elephants in these areas (Hulme et al. 2001; New et al. 2006). Therefore, increasing the amount of space and heterogeneity available for elephants may provide long-term thermal refuges (Moritz and Agudo 2013; Bellard *et al*. 2012) that will enable elephants to naturally adapt to weather extremes. Ensuring connectivity between these areas should therefore be a priority.

LIMITATIONS OF THE STUDY AND FUTURE RESEARCH

Water and shade were present at all times during my study. As a result, I was unable to assess the physiological responses of elephants to high environmental temperatures where water and shade were limited. Therefore, I can only infer that in marginal habitats, elephants may need to rely more on autonomic mechanisms to maintain homeothermy. Where shade is absent, elephants may not be able to limit heat gain from direct solar radiation and where surface water is limited, elephants may be unable to replenish water lost through evaporative cooling. As a result, dehydration-induced hyperthermia could occur. Future research is therefore required to determine the physiological responses of elephants to high environmental temperatures in arid regions. This will greatly improve our understanding of the capacity for elephants to adapt to hotter and drier weather events, which are predicted to increase with climate change.

Due to the techniques used to record skin and core temperature of elephants in this study, recording behaviour and body temperatures in wild elephants was not possible. This study was therefore conducted on tamed elephants, which allowed me to record body temperatures and behaviour whilst on foot, in close proximity to focal elephants at all times. The use of tamed individuals and the observer’s influence on an animal’s behaviour may raise concerns toward the credibility of a study (Guy 1976; Slater 1986). However, during my study elephants were not constrained in any way and were free to range within their natural environment. Furthermore, the elephants were habituated to the presence of human observers. Therefore, I suggest that the influence that an observer may have had on the behaviour of a focal elephant was minimal.

My study provides an understanding of the physiological responses of elephants to high environmental temperatures at the individual level. It therefore serves as the first step toward understanding how environmental temperature may influence elephant spatial use patterns and demographics at a larger scale. Environmental temperature has previously been overlooked in studies on elephant ecology, particularly in resource selection function models based on elephants (e.g. Roever *et al*. 2013). Incorporating environmental temperature as an additional layer into these models may assist in delineating conservation areas whilst incorporating the need for elephants to thermoregulate.

To the best of my knowledge, no studies have investigated the effects of extreme temperatures on the population dynamics of savanna elephants. Although changes in mortality and fecundity are often dependent on a number of factors such as food and water availability (see Gaillard *et al*. 2012; van Beest and Milner 2013), I suggest that maximum and minimum environmental temperatures should be considered as additional factors that may influence population growth rate. Such studies will require long-term data sets which incorporate monthly temperature data and individual life histories.

In conclusion, elephants thermoregulate effectively, provided suitable resources such as shade and water are available. Their marked ability to employ behavioural plasticity in response to high environmental temperatures allows elephants to maintain homeothermy in savannas. However, one of the crucial questions that remains is whether elephants will be able to adapt fast enough to keep up with the rapid rate of climate change. Furthermore, as a result of climate change, elephants are likely to experience changes in vegetation and surface water distribution, which may influence their fitness. Our knowledge of how climate change will affect elephants is therefore not yet complete. Further understanding of how environmental temperature may alter landscape utilization and individual fitness in elephants is still required to assist conservation initiatives in a changing environment.

CHAPTER 6 – REFERENCES

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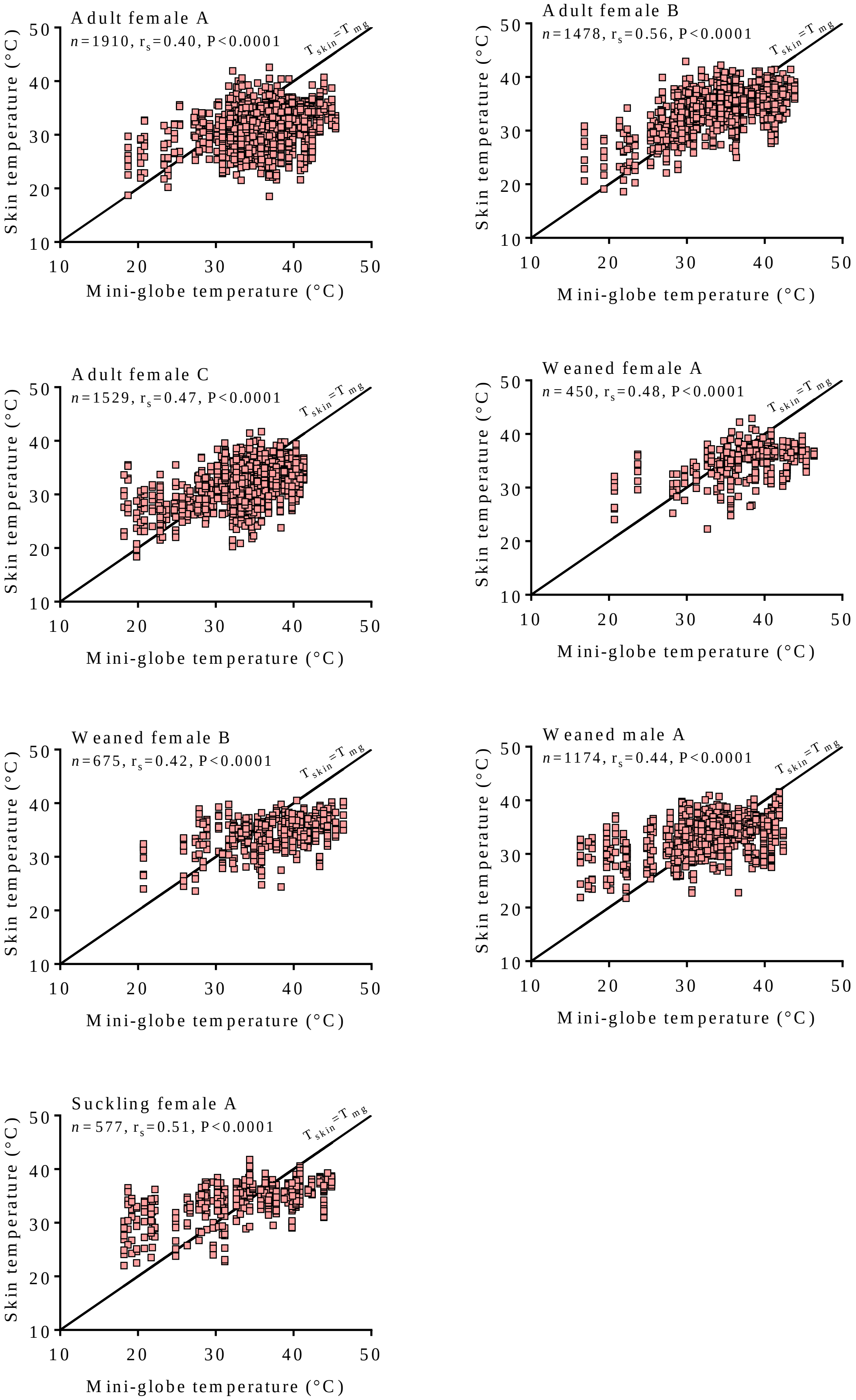
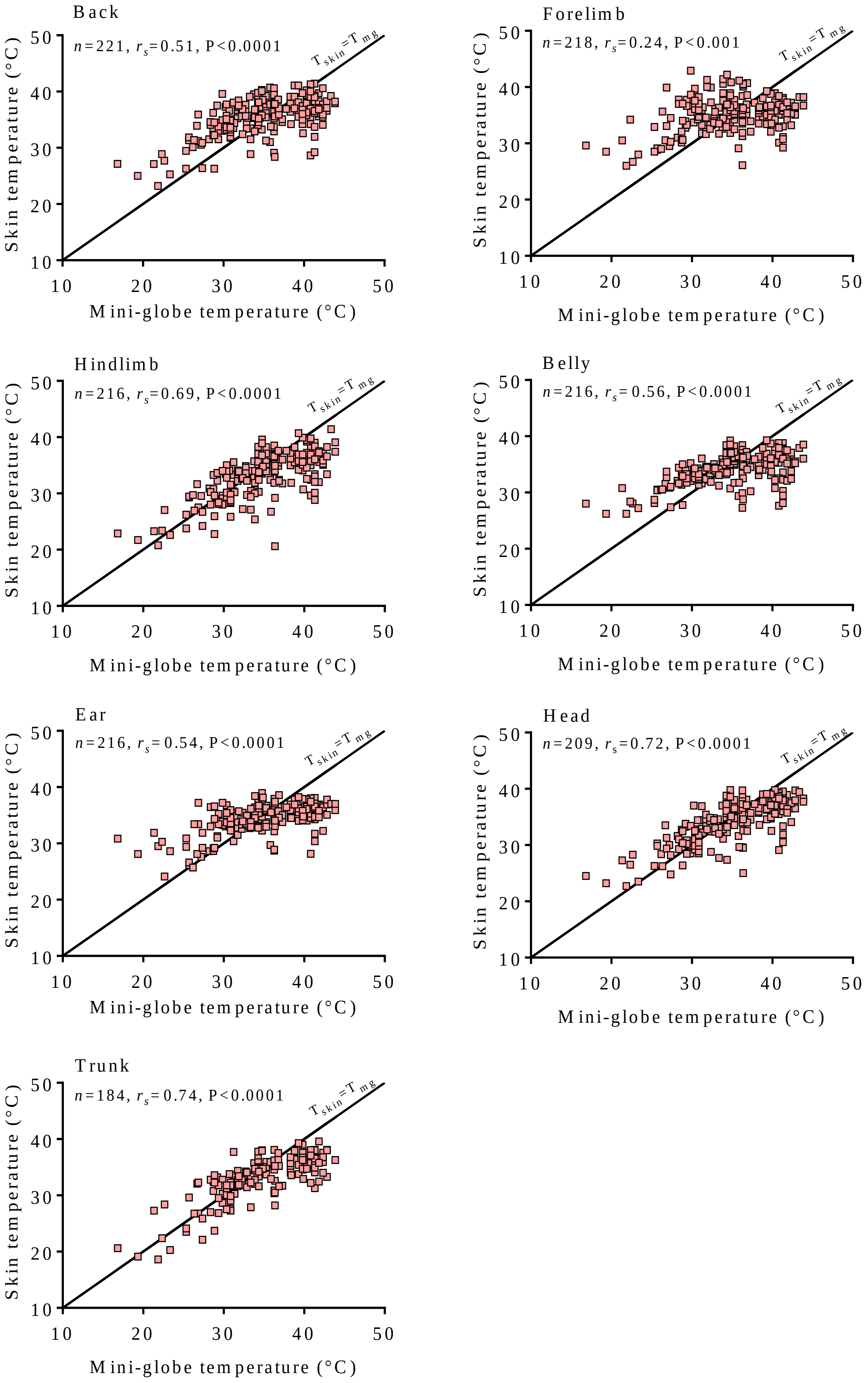
CHAPTER 7 – APPENDICES

Appendix I. Summary of the mean (± SD) core temperature indices for each elephant during the study period.

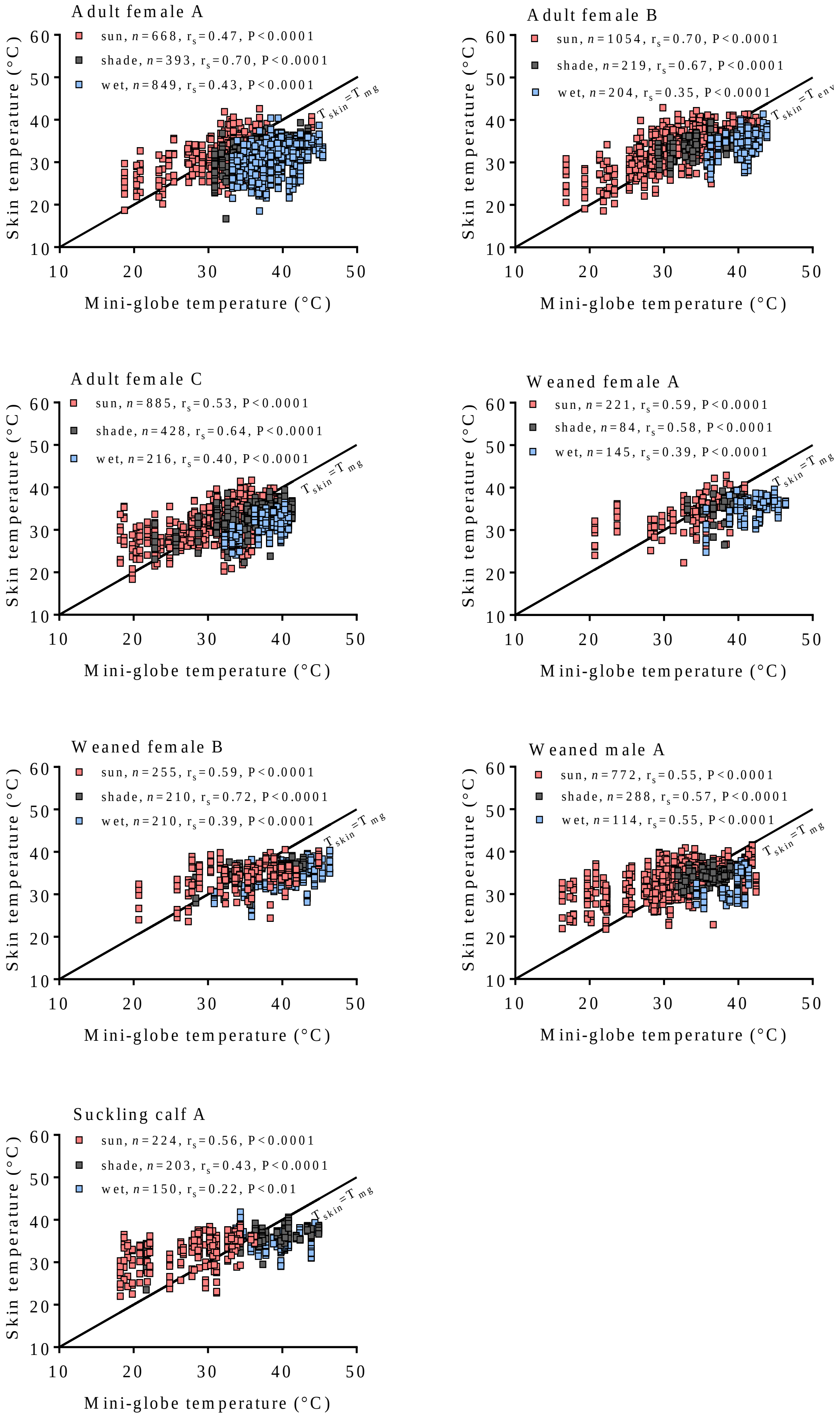
Elephant	*n*	Mean	Maximum	Minimum	Time of maximum	Time of minimum	24-hour range
Adult female A	2222	36.46 ± 0.30	36.85 ± 0.59	36.08 ± 0.32	17:35 ± 1:30	08:15 ± 1:13	0.77 ± 0.85
Adult female B	1564	36.69 ± 0.47	37.39 ± 0.50	36.00 ± 0.47	17:55 ± 1:12	08:50 ± 1:27	1.39 ± 0.78
Adult female C	2152	36.46 ± 0.29	36.01 ± 0.28	36.02 ± 0.20	18:30 ± 1:03	10:00 ± 1:08	1.00 ± 0.20
Weaned male	1713	36.75 ± 0.42	37.47 ± 0.38	36.01 ± 0.38	16:25 ± 2:15	07:55 ± 2:03	1.46 ± 0.32
Weaned female A	377	36.85 ± 0.40	37.76 ± 0.04	36.32 ± 0.04	17:15 ± 1:27	09:25 ± 1:25	1.43 ± 0.01


Adult female A
n=1910, r_s=0.40, P<0.0001
T skin=T mg
Skin temperature (°C)
Mini-globe temperature (°C)
10
20
30
40
50
Adult female B
n=1478, r_s=0.56, P<0.0001
T skin=T mg
Skin temperature (°C)
Mini-globe temperature (°C)
Adult female C
n=1529, r_s=0.47, P<0.0001
T skin=T mg
Skin temperature (°C)
Mini-globe temperature (°C)
Weaned female A
n=450, r_s=0.48, P<0.0001
T skin=T mg
Skin temperature (°C)
Mini-globe temperature (°C)
Weaned female B
n=675, r_s=0.42, P<0.0001
T skin=T mg
Skin temperature (°C)
Mini-globe temperature (°C)
Weaned male A
n=1174, r_s=0.44, P<0.0001
T skin=T mg
Skin temperature (°C)
Mini-globe temperature (°C)
Suckling female A
n=577, r_s=0.51, P<0.0001
T skin=T mg
Skin temperature (°C)
Mini-globe temperature (°C)

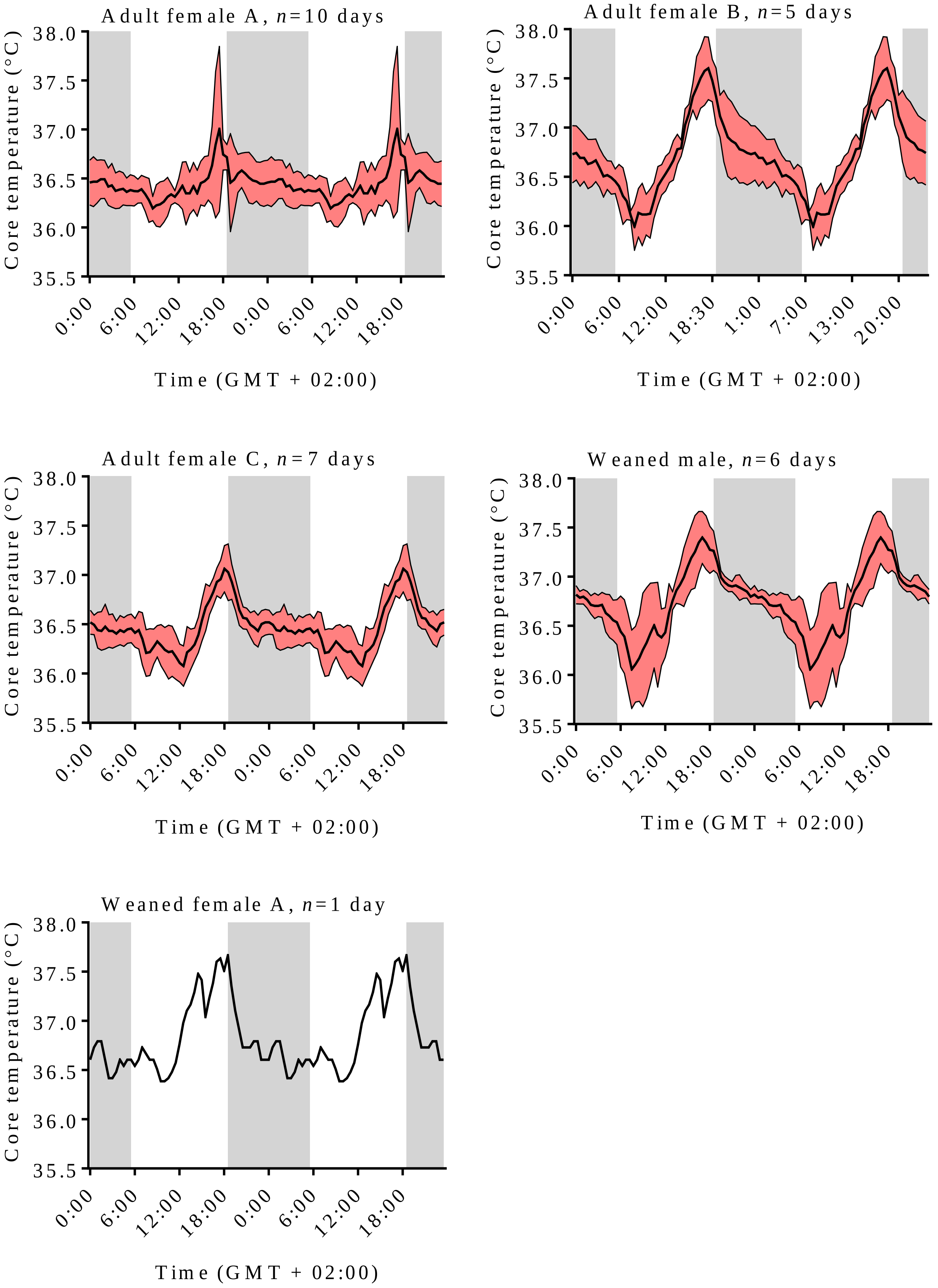
Appendix II. The relationship between skin and mini-globe temperature showing an increasing trend in all elephants. The solid line represents a 1:1 ratio where skin temperature (T_{skin}) is equal to mini-globe temperature (T_{mg}).



Appendix III. The relationship between skin and mini-globe temperature for Adult female B showing an increasing trend in all parts of the body. The solid line represents a 1:1 ratio where skin temperature (T_{skin}) is equal to mini-globe temperature (T_{mg}).


Adult female A
sun, n=668, r_s=0.47, P<0.0001
shade, n=393, r_s=0.70, P<0.0001
wet, n=849, r_s=0.43, P<0.0001
T skin=T mg
Adult female B
sun, n=1054, r_s=0.70, P<0.0001
shade, n=219, r_s=0.67, P<0.0001
wet, n=204, r_s=0.35, P<0.0001
T skin=T env
Adult female C
sun, n=885, r_s=0.53, P<0.0001
shade, n=428, r_s=0.64, P<0.0001
wet, n=216, r_s=0.40, P<0.0001
T skin=T mg
Weaned female A
sun, n=221, r_s=0.59, P<0.0001
shade, n=84, r_s=0.58, P<0.0001
wet, n=145, r_s=0.39, P<0.0001
T skin=T mg
Weaned female B
sun, n=255, r_s=0.59, P<0.0001
shade, n=210, r_s=0.72, P<0.0001
wet, n=210, r_s=0.39, P<0.0001
T skin=T mg
Weaned male A
sun, n=772, r_s=0.55, P<0.0001
shade, n=288, r_s=0.57, P<0.0001
wet, n=114, r_s=0.55, P<0.0001
T skin=T mg
Suckling calf A
sun, n=224, r_s=0.56, P<0.0001
shade, n=203, r_s=0.43, P<0.0001
wet, n=150, r_s=0.22, P<0.01
T skin=T mg
Skin temperature (°C)
10
20
30
40
50
60
Mini-globe temperature (°C)
10
20
30
40
50

Appendix IV. The relationship between skin and mini-globe temperature for when each elephant was in sun, shade or was wet. The solid line represents a 1:1 ratio where skin temperature (T_{skin}) is equal to mini-globe temperature (T_{mg}).



Adult female A, *n*=10 days

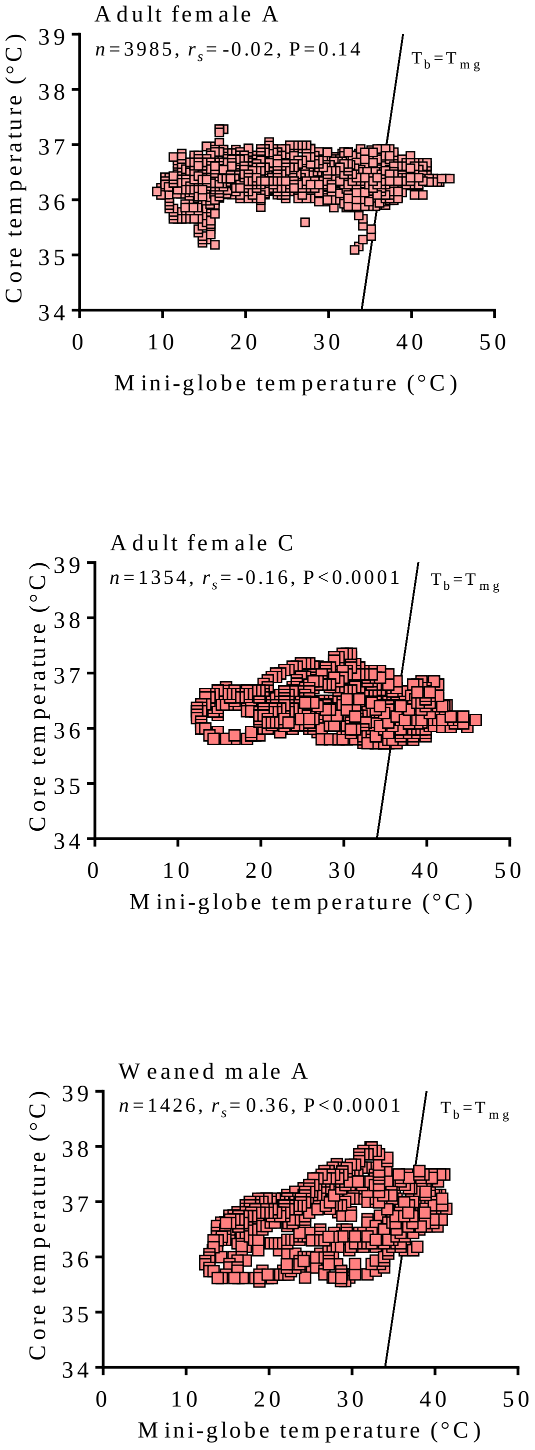
Adult female B, *n*=5 days

Adult female C, *n*=7 days

Weaned male, *n*=6 days

Weaned female A, *n*=1 day

Appendix V. Double plots of the mean 24-hour core temperature (± SD) patterns of each elephant, showing half-hourly means. Standard deviation (pink shaded area) represents the variation between days. Grey shaded columns represent night-time and unshaded columns represent the daytime.



Appendix VI. The relationship between core and mini-globe temperature for each elephant. The solid line represents a 1:1 ratio where skin temperature (T_{skin}) is equal to mini-globe temperature (T_{mg}).