THERMOREGULATION IN AFRICAN ELEPHANTS (*LOXODONTA AFRICANA*)

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A dissertation submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfilment of the requirements for the degree of Master of Science.

Johannesburg, 2009

DECLARATION

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

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(PHILIPPA ANN HIDDEN)

……… day of …………………..... 2009

I certify that the procedures used in this dissertation were approved by the Animal Ethics Screening Committee of the University of the Witwatersrand (AESC clearance number: 2006/55/03).

The financial assistance of the National Research Foundation (NRF) towards this research is hereby acknowledged. Opinions expressed, and conclusions arrived at, are those of the author and are not necessarily attributed to the NRF.

PRESENTATIONS

The presentations listed below are offered in support of this dissertation.

Hidden P, Fick L, Mitchell D, Fuller A. The body temperature of African elephants (oral presentation). At the 33rd Conference of the Zoological Society of southern Africa (ZSSA), Potchefstroom, 9-11 July 2007.

Hidden P, Fick L, Mitchell D, Fuller A. The body temperature of African elephants (oral presentation). At the 35th Annual Congress of the Physiology Society of southern Africa (PSSA), Johannesburg, 9-12 September 2007.

Hidden P, Fick L, Mitchell D, Fuller A. Cold ears and hot feet: how African elephants survive the heat (oral presentation). At the Faculty of Health Sciences Research Day and Postgraduate Expo, University of the Witwatersrand Medical School, Johannesburg, 20 August 2008.

ABSTRACT

Elephants have a small surface area to volume ratio, compared to smaller African mammals, and as a result are likely to encounter greater difficulties dissipating excess body heat. Continuous measurements of body temperature have not previously been recorded in unrestrained African elephants living in their natural habitat. Over a series of days during three different climatic periods (cold, warm, and hot) I fed ingestible temperature-sensitive data loggers to four tame adult elephant bulls. Elephant body temperature was recorded at five-minute intervals to determine the 24 h pattern of body temperature as well as the magnitude and frequency of short-term variations in body temperature. I recorded climatic variables and assessed the influence of environmental temperature on elephant body temperature, and I investigated the relationship between elephant body temperature and behaviour also.

Mean body temperature over the study period was about 36.4 ± 0.03°C and mean daily amplitude was about 1.2 ± 0.04°C. Body temperature appeared to be largely independent of environmental (black globe) temperature, which ranged from about -1 to 52°C, and the 24 h pattern of body temperature appeared to be the product of an endogenous rhythm. Large, short-term changes in body temperature (changes of 0.3°C or more, over a five to ten-minute period) occurred on occasion and sometimes were associated with the ingestion of water by the elephants. Swimming and splashing did not consistently result in a decrease in body temperature, and the elephants might have engaged in these behaviours for thermal comfort or pleasure rather than for lowering body temperature. Higher than average body temperatures did not seem to be associated with higher than average flap rates but the rate of ear flapping increased with an increase in environmental temperature. Further investigation of the influence of environmental temperature on the frequency of other thermoregulatory behaviours is needed. Investigation of the 24 h pattern of changes in skin temperature, the interaction of skin temperature with core body temperature, and the role of cutaneous moisture loss, will further complete our understanding of elephant thermoregulation. I conclude that despite their large size, African elephants, with access to water, regulate their body temperatures within narrow limits, with a 24 h pattern similar to that seen in other medium- and large-sized mammals.

DEDICATION

To my brother Brett, who has shown me what it really means to persevere, and who constantly reminds me that what is contained within a person's heart is more important than their ability to achieve that which the world applauds.

ACKNOWLEDGEMENTS

For help on the technical side of things I would like to thank:

Professor James Mercer (Medical Faculty, University of Tromsø, Norway) for making the long trip to South Africa to provide his expert assistance with the infra-red thermography; Rohloff South Africa, for providing the state-of the-art infra-red cameras, and Mr Tjaart Broodryk for giving up his time in order to help us capture the high quality images which we did.

I would like also to formally acknowledge:

The National Research Foundation of South Africa, for the scholarship provided;

Brett, Jala, Pontsho, Lovemore, Clement, Sunny, Elias, Elvis, Joel & Peter at Pilanesberg Elephant Back Safaris for accommodating and assisting this ‘crazy scientist’;

My supervisors, Dr Linda Fick and Professors Andrea Fuller and Duncan Mitchell, for their patient coaching and for giving me the space to explore and to grow;

Rich, for his quiet strength, for being there to share in my mirth as well as my frustration, and for being a consistent voice of encouragement;

My parents, Mike and Angela, for their wholehearted commitment to me, both emotional and financial, for giving ear to my endless ‘updates’ and for helping me to navigate the ‘rough bits’;

God, who I am convinced delights in our exploration of His Creation and without whom I would most surely have lost my sense of humour.

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Chapter 1

Literature review

1.1 Introduction

The African elephant (*Loxodonta africana*) is the largest extant terrestrial mammal, and as such experiences unique thermoregulatory challenges. The elephant's large size influences the rate at which heat is exchanged between its body and the environment, which may in turn affect the elephant's thermoregulatory strategy. It is not fully understood how African elephants regulate their body temperature, and what environmental conditions result in heat stress for an elephant. But an understanding of how elephants respond physiologically to changes in environmental conditions may be crucial to the conservation of the species.

Many conservation scientists recognise the need for an understanding of physiology to understand population dynamics and to assess the efficacy of management strategies (Wikelski & Cooke, 2006). A better understanding of how elephants' physiological requirements affect their use of various habitats may assist the management of wild populations. Also, there is evidence that the African elephant's environment is changing. Conservationists and managers are better equipped to facilitate animals' adaptive responses when there is an understanding of their physiological capacity to adapt to changes in their environment. Of particular importance is the question of how elephants will adjust to the changes in environment brought about by global climate change.

A defence of the global climate change hypothesis does not fall within the realm of this dissertation. Suffice to say that several studies provide compelling evidence of changes not only in temperature but in solar radiation and precipitation also (McCarty, 2001; Hulme, 2005). And researchers have identified the need for a change in conservation approaches as the threat of global climate change becomes more evident and the impact on wildlife becomes more apparent (McCarty, 2001; Hulme, 2005; Thuiller, 2007). Changes in climate have been linked to changes in species distributions (Thuiller et al., 2006), species losses (Erasmus et al., 2002) and population declines (Ogutu & Owen-Smith, 2003). A species' capacity for responses, including changes in physiological responses, should be considered when assessing the potential effects of global climate change on animal populations (Martin & Nagy, 2002).

Africa is becoming hotter and drier (de Wit & Stankiewicz, 2006; New *et al.*, 2006), and an understanding of the thermoregulatory physiology of the elephant will assist efforts to manage and conserve the species. The extinction of the woolly mammoth (*Mammuthus primigenius*) may have been caused by the simultaneous reduction in its geographic range resulting from a change in climate and increased hunting pressure from humans (Nogués-Bravo et al., 2008). Results of a recent study suggest that ambient temperature, possibly through its impact on an elephant's ability to thermoregulate, influences the distribution of elephants within a given area (Kinahan *et al.*, 2007b).

1.2 Environmental effects on body temperature

The elephant is a eutherian (placental) mammal and as such, one would expect it to have a mean body temperature within the range given for that mammalian group (38 ± 2°C; Schmidt-Nielsen, 1997). The body temperature of homeothermic mammals does not remain constant but generally fluctuates by about 1 to 2°C in a fairly regular manner over the course of 24h (Refinetti & Menaker, 1992). Changes in body temperature are related to the balance between the amount of heat gained by the animal, either through metabolic heat production or from the environment, and the amount of heat lost by the animal to its environment (Gordon *et al.*, 1982). If more heat is gained by the animal than is lost, the heat is stored, which results in an increase in body temperature (Mitchell, 1977). Conversely, if more heat is lost than is gained by the animal, the result will be a decrease in body temperature.

Heat exchange between the animal and its environment can take place by radiation, convection and conduction. The magnitude of heat transfer by these routes largely depends on the temperature gradient between the animal's body surface (either fur or skin) and the environment (Boulant, 1991). When environmental temperature is less than the temperature of the body surface, heat is transferred from the body surface to the environment. When environmental temperature exceeds that of body temperature, the ability of an animal to lose heat is restricted by the reduction in the temperature gradient and in fact, heat may be gained by the animal (Porter & Gates, 1969). Under these circumstances, evaporative heat loss becomes the only means by which a terrestrial mammal can dissipate excess body heat, creating the additional challenge of replacing lost body water (Schmidt-Nielsen, 1997). Although evaporative heat loss enables an animal to lose body heat, it is dependent on the movement of air to displace saturated air just above the damp surface (Gebremedhin & Wu, 2001).

Determining the exact amounts of heat transferred between an animal and its environment can be challenging, especially outside of a laboratory setting (Porter & Gates, 1969; Williams, 1990). However, measurements of environmental variables can be used to gain some understanding of the amount of heat to which an animal is subjected in a particular terrestrial environment (the environmental heat load). Such measurements include air temperature and relative humidity, and an index of environmental heat load now commonly used in physiological studies is black globe temperature (Hetem *et al.*, 2007). Black globe temperature is especially useful as it provides an integrated measure of wind speed, radiation and air temperature (Vernon, 1930) and is used to assess the thermal load placed on a variety of species in different habitats (Hetem *et al.*, 2007). Black globe temperature does not incorporate the effects of evaporation, but by including measurements of wet and dry-bulb temperature, one is able to calculate the wet bulb globe temperature (WBGT) which incorporates the contribution of evaporative heat loss (Moran *et al.*, 2001).

1.3 Implications of very large body size for heat exchange dynamics

The surface area available for heat exchange is another important determinant of the magnitude of heat transfer between an animal and its environment; the larger the surface area, the greater the amount of heat which can be lost or gained at the body surface. However, even more important in the exchange of heat is the *ratio* of the body surface area to the mass or volume of the animal's body (Schmidt-Nielsen, 1984).

The area of the body surface relative to an animal's body mass affects the rate at which an animal gains or loses heat. Generally, for animals with a roughly cylindrical body shape, the larger the animal is the smaller is its surface area relative to its body mass, which means that the area available for the exchange of heat with the environment is relatively smaller in a large animal. As a result, one would expect changes in body temperature to occur more slowly in a large animal than in an animal of small body size (Taylor, 1970a). Consequently, the surface area to body mass ratio bears significance when considering the thermoregulation of animals of very large body size.

In addition to the surface area to volume ratio, two other factors, which are involved in heat balance, scale with body mass. The second important factor that scales with body mass is tissue conductance. Conductance describes the ease of heat flow through body tissues and influences the rate of heat loss. Tissue conductance decreases with increasing body size which means that heat flows more quickly through the body of a smaller animal than a larger one (McNab, 1970). Also, the distribution of heat through the body mostly depends on the circulation of blood (Mitchell, 1977) and the length of time taken for blood to circulate an animal's body increases with increasing body mass (Schmidt-Nielsen, 1984). Since blood takes longer to circulate through an elephant's body than it does through a mouse's, heat is transferred more slowly, further contributing to the lower relative value of conductance.

Fortunately, the amount of heat produced per volume of body tissue also decreases with increasing body mass (Schmidt-Nielsen, 1984). However, the magnitude of this decrease is not sufficient to offset the decrease in relative surface area, conductance and blood flow. Since a large animal's ability to dissipate heat is impaired to an extent which is not fully compensated for in a decrease in heat production, to live in hot environments, large endotherms must have effective means of dissipating not only excess metabolic heat but any heat gained from their environment also.

1.4 Thermoregulatory strategies of some large mammals living in Africa

Although often thought of as hot and dry, the African continent is made up of diverse habitats, from the deserts of the Kalahari and Sahara to the equatorial jungles of Central Africa. The mammal species which inhabit these different regions each have different ways of coping with the environmental conditions they encounter, and it is as difficult to generalise about the animals' means of coping as it is to make generalisations regarding the environmental conditions. Historically, elephants had a wide distribution across Africa (African Elephant Specialist Group, 2004), until they were eradicated by poaching in some regions, and elephants appear to survive in a remarkable range of environments (Sikes, 1971). Several other large herbivorous mammals live in Africa and can often be seen in the same habitat as elephants (Skinner & Chimimba, 2005). These animals have in common with the elephant the thermoregulatory concerns resulting from a decreased relative body surface area and must cope with similar environmental challenges. Therefore, in considering thermoregulation in the elephant, it may be helpful to survey the thermoregulatory strategies that these other large herbivorous African mammals employ (elephants' thermoregulatory strategies are discussed in section 1.5).

African mammals of very large body size are sometimes referred to as *megaherbivores* and typically weigh 1000 kg or more (Owen-Smith, 1988). Although the eland (*Tragelaphus oryx*) and African buffalo (*Syncerus caffer)* are not usually included in this category, I have incorporated them in my assessment of thermoregulatory strategies as they are known occasionally to attain masses approaching 1000 kg. Table 1.1 provides a summary of the body masses and body temperatures for seven African megaherbivores (including elephants). Although comprehensive long-term studies of thermoregulation have not been conducted in the majority of African megaherbivores, several studies of both captive and free-living individuals of some species provide some insight into their thermoregulatory strategies. Such studies have revealed the use of behavioural, autonomic and morphological adjustments, which are employed in concert according to the animal's thermoregulatory requirements (Parker & Robbins, 1985).

1.4.1 Behaviour

Terrestrial landscapes are rarely homogenous (Li & Reynolds, 1995) and microhabitats provide a variety of thermal environments. By selecting, or creating, a specific microhabitat, an animal can modify the environmental conditions to which it is exposed (Bartholomew, 1987). Some thermoregulatory behaviours may prevent behaviours such as foraging, but behavioural responses for thermoregulation often are favoured since they usually are less costly than autonomic mechanisms in terms of water and energy savings (Jessen, 2001). However, there are behavioural adjustments which may or may not be available to an animal, depending on its body size. Smaller animals are able to escape to

Table 1.1 The approximate adult body masses and body temperatures of six large African herbivores.

Scientific name	Common English name	Body mass (approximate, kg)			Body temperature (°C)	Site of temperature measurement
		Female	Male			
Tragelaphus oryx	Eland	460	700	(940)†	38.2[a]	Carotid artery
Syncerus caffer	African buffalo	460	600	(860)*	38.7[b]	Muscle
Diceros bicornis	Black rhinoceros	880	850	(1313)*	37.6 - 40.0[b]	Muscle
Giraffa camelopardalis	Giraffe	830	1190		38.5[c]	Multiple
Hippopotamus amphibius	Hippopotamus	1390	1550	(2300) ‡	36.2[d]	Gastrointestinal
Ceratotherium simum	White rhinoceros	1600	2200		33.6 - 37.5[e]	Rectal
Loxodonta africana	African elephant	4000	6000		36.2[f]	Gastrointestinal

All body masses are based on information provided by Skinner & Chimimba (2005); the values indicated in brackets are single measurements recorded for exceptional individuals. † Estes (1999); * Owen-Smith (1988); ‡ Piccione et al. (2005).

If no mean body temperature was provided and could not be calculated from the data reported, the range of values stated by the authors is given. References: [a] Fuller *et al*. (1999), [b] Bligh & Harthoorn (1965), [c] Mitchell & Skinner (2004) [d] Piccione *et al*. (2005), [e] Allbrook *et al*. (1958), [f] Kinahan *et al*. (2007).

burrows, while larger animals have the ability to traverse large distances to quickly escape unfavourable environmental conditions (Parker & Robbins, 1985). But an animal does not always have to travel far; it may move a much smaller distance, perhaps relocating from a position in the full sun to the shade of a tree.

Shade is important as it can enable an animal to endure higher ambient temperatures (Porter & Gates, 1969). African rhinoceros (*Diceros bicornis* and *Ceratotherium simum*) often seek shade during the hottest part of the day (Owen-Smith, 1988) and it has been said that by remaining in the shade throughout the day, a white rhinoceros avoided an increase in rectal temperature of more than 2°C (Allbrook *et al.*, 1958). Eland (*Tragelaphus oryx;* Fuller *et al.*, 1999a) and buffalo (*Syncerus caffer*; Taylor, 1970a) also seek shade during the heat of the day. Indeed, some have claimed that by standing in the shade instead of in the sun, Asian buffalo (*Bubalus arnee*) prevented a rise in body temperature of about 2°C (Moran, 1973 in Sinclair, 1977). Giraffe (*Giraffa camelopardalis*) tend not to seek shade unless ambient temperature is high (34 to 37°C; Mitchell & Skinner, 2004) or when body temperature is increased (~40°C; Langman & Maloiy, 1989). However, giraffe may employ a different strategy to reduce their exposure to solar radiation. By orienting the long-axis of its body parallel to the rays of the sun, a giraffe reduces the amount of solar radiation it intercepts (Mitchell & Skinner, 2004), allowing it to remain more active during the daytime.

An alternative means of reducing heat gain by solar radiation is to change the timing of certain activities. Black rhinoceros generally move about and forage in the early morning, late afternoon and at night, sleeping during the heat of the day (Goddard, 1967) and ambient heat load has been shown to affect the activity pattern of buffalo also (Sinclair, 1977). Not only is radiant heat gain reduced, but metabolic heat gain is reduced during the period when non-evaporative cooling is hampered by unfavourable temperature gradients. Ambient temperature is lower at night, allowing the passive loss of body heat by radiation, convection and conduction. Hippopotamus are mostly active at night when they come on to land to forage but spend most of the day at least partly, if not fully, submerged in water (Luck & Wright, 1964).

Immersion in water may be a very effective behavioural means of increasing heat loss to the environment. When water is available, rhinoceros may lie in pools for several hours, especially during the midday heat in summer (Owen-Smith, 1988). The rate of heat transfer to water is considerably higher than that to air (Scholander, 1955) and submersion appears to be so effective that a hippopotamus may have to leave the water to bask in the sun for short periods when the water is too cool (Noirard *et al.*, 2008). In addition to the loss of heat by conduction, heat is lost by evaporation at the body surface once the animal leaves the water.

Possibly an even more effective means of procuring the benefit of evaporative cooling is mud-wallowing. Dousing a pig's flank with water increased the rate of evaporation at the skin surface twenty-fold; while plastering the skin in mud produced a slightly lower increase, the effect lasted significantly longer (two hours as opposed to fifteen minutes; Ingram, 1965). The sustained elevation in evaporation afforded by the mud enables the animal to leave the source of water, allowing it to engage in other activities (Ingram, 1965) such as foraging (Parker & Robbins, 1985). Rhinoceros wallow in mud, especially in the late afternoon (Goddard, 1967; Owen-Smith, 1988) and it was reported that wallowing resulted in a lower than normal body temperature (Allbrook *et al.*, 1958). Buffalo often wallow during the heat of the day (Sinclair, 1977), while giraffe neither swim nor wallow in mud (Owen-Smith, 1988).

1.4.2 Morphology

The giraffe is unique among the megaherbivores in its unusual morphology, which may not permit swimming and mud-wallowing. The other large African herbivores are best represented geometrically by short cylinders of large diameter, while a giraffe's elongated neck and limbs result in an increase in its surface area to mass ratio, which favours the loss of body heat (Mitchell & Skinner, 2004). Changes in body shape tend to occur only over many generations (Bartholomew, 1964). The most immediate change in morphology is effected by a change in posture to expose more, or less, of the body surface to the sun or wind (Jessen, 2001) and is probably better labelled as a behavioural response. In animals of large abdominal diameter and possessing short, stocky limbs, changes in posture are limited to standing up or lying down.

However, there are aspects of morphology apart from body shape which may also play a role in thermoregulation. The rhinoceros and hippopotamus, together with the elephant, are referred to as pachyderms because of their thick integument. A study of rhinoceros skin found that the dermis of a juvenile individual ranged from a minimum of 18 mm to a maximum of 45 mm (Cave & Allbrook, 1958). Hippopotamus skin (sampled from an adult) showed a similar range, 12 – 35 mm (Luck & Wright, 1964). Investigators have suggested that such a thick skin acts as an efficient barrier to heat loss (Benedict *et al.*, 1921; Cave & Allbrook, 1958) but the amount of heat lost (or gained) through the skin depends on the distribution of blood vessels in the skin. It may also be that, as with the coat of a furred mammal, a pachyderm's outer packaging reduces the amount of heat gained by solar radiation.

The pachyderms are virtually hairless except for a few coarse bristles scattered across portions of the body surface (Benedict *et al.*, 1921; Cave & Allbrook, 1958; Luck & Wright, 1964). Giraffe, buffalo and eland are covered in fur and the importance of a fur coat in achieving heat balance has been demonstrated in eland. An eland's coat reflects about 25% of the solar radiation it intercepts and re-radiates about 69% of the heat it absorbs, significantly reducing heat gain from the environment (Finch, 1972). Giraffe do not posses the light and uniformly-coloured coat of the eland. A giraffe's coat is covered in dark patches which, because darker colours absorb more solar radiation than do lighter ones, could present a thermoregulatory disadvantage. However, for giraffe, keeping warm is often more of a challenge than keeping cool (Mitchell & Skinner, 2004) and the patches may facilitate a mechanism of temperature regulation which enables giraffe to meet this challenge.

1.4.3 Autonomic mechanisms

Often, a morphological trait facilitates an autonomic mechanism. An example is the unique arrangement of blood vessels in the skin under the dark patches of a giraffe's skin (Mitchell & Skinner, 2004). Based on its thermoregulatory requirements, a giraffe may alter the amount of blood flowing through the vessels under these patches. Vasodilation of the vessels in peripheral tissues increases the temperature of the skin by conveying heat from the body core, whereas vasoconstriction reduces the transfer of heat from the core to the periphery (Jessen, 2001). The particular arrangement of vessels in the giraffe's skin enhances this ability, and the greater production of sweat by the skin underlying the darker patches may further facilitate the dissipation of excess body heat by evaporation (Mitchell & Skinner, 2004).

Giraffe (Mitchell & Skinner, 2004), as well as eland (Finch, 1972), buffalo (Robertshaw & Taylor, 1969), rhinoceros (Cave & Allbrook, 1958) and hippopotamus (Luck & Wright, 1959, 1964) all possess sweat glands and appear to rely, to varying extents, on sweating to dissipate excess body heat. However, sweating is not the only form of evaporative cooling. The formation of sweat requires specialised glands which empty their contents onto the skin surface, but water also is lost passively through the skin (Mitchell, 1977). A study of evaporative water loss in hippopotamus showed that a large amount of water is lost transepidermally (Luck & Wright, 1964).

Water is lost from the surfaces of the respiratory tract also. Panting enhances the evaporation of water by increasing air flow over the moist respiratory surfaces and offers several advantages over sweating. By creating its own air movement over these surfaces an animal is less dependent on the presence of wind for evaporative cooling, electrolytes are not lost and a panting animal is able to maintain relatively higher skin temperatures (Taylor, 1977). Sweating cools the skin surface, increasing the temperature gradient between the animal's body surface and the environment which in turn promotes the flow of heat into the animal's body (Taylor, 1977). Eland pant under conditions of heat stress (Taylor & Lyman, 1967). Buffalo also pant, but tend to rely to a greater extent on sweating (Taylor, 1970b), as do rhinoceros (Hiley, 1977). It appears that hippopotamus (Wright, 1987) and giraffe (Langman *et al.*, 1982) do not pant.

Although giraffe do not pant, respiration rate increases with increasing body temperature (Langman *et al.*, 1982). Usually, the air an animal inhales is warmed and becomes saturated with water upon reaching the lungs, and both water and heat are lost from the body when the air is exhaled (Cole, 1953). However, the giraffe exhales air which has been cooled below body temperature and in so doing, recovers precious body water (Langman *et al.*, 1979). Heat from the air leaving the lungs is transferred to blood vessels in the lining of the passages and, as the air is cooled, its capacity to retain water is reduced and the condensed water is recovered (Schmidt-Nielsen *et al.*, 1981). However, the consequence of water recovery in this situation is a decrease in evaporative cooling and retention of body heat, and such a mechanism may be used by the giraffe to conserve heat under conditions of cold stress (Langman *et al.*, 1979). Under conditions of heat stress, the cooling of the respiratory surfaces by incoming air may enable the giraffe to employ another thermoregulatory strategy.

Giraffe, as well as several other large mammals, are able to cool blood on its way to the brain. The cooling of blood is facilitated by a unique arrangement of blood vessels, including the carotid rete and cavernous sinus, which lie at the base of the brain (Baker, 1979). These vessels form a counter-current heat exchanger and blood, cooled as it passes through the nasal mucosae during panting, under certain circumstances, is diverted to the cavernous sinus to cool arterial blood flowing to the brain (Kuhnen, 1997). It was initially thought that this selective cooling of the brain was used to protect the brain against thermal damage when body temperature increased, especially during exercise (Mitchell *et al.*, 2002). However, the evidence collected in support of this theory often was obtained using flawed techniques and the experiments were conducted in animals kept in artificial environments (Mitchell *et al.*, 2002). To my knowledge, no studies of selective brain cooling (SBC) have been conducted in buffalo, rhinoceros or hippopotamus and investigations of SBC in giraffe have proved inconclusive (Mitchell & Skinner, 2004). Eland were one of the earliest wild large species in which SBC was described (Taylor, 1969) but a recent study, in which blood and brain temperatures were continuously recorded, found that eland hardly ever employed SBC in their natural habitat, despite large environmental heat loads (Fuller *et al.*, 1999a). From this and several other studies of SBC, it is now believed that SBC is used to reduce dependence on evaporative cooling when an animal is at rest. When at rest, the animal does not attempt to prevent a rise in body temperature by evaporative cooling, saving body water. However, upon physical exertion or stress, selective cooling of the brain is discontinued, resulting in the activation of evaporative cooling mechanisms to dissipate the heat produced by the increase in activity (Fuller *et al.*, 2004).

Together with SBC, adaptive heterothermy was believed to be crucial to the survival of animals inhabiting hot, dry environments (Mitchell *et al.*, 2002). As environmental heat load increases, instead of defending body temperature using evaporative cooling, an animal stores the heat it gains from the environment, allowing body temperature to increase over the course of the day. In the evening, once environmental temperature no longer exceeds body temperature, the animal dissipates heat non-evaporatively and body temperature slowly decreases to below normal levels through the night (Mitchell *et al.*, 2002). Large animals are well-suited to adaptive heterothermy because of their large thermal inertia (Taylor, 1970a).

Adaptive heterothermy was first suggested by Schmidt-Nielsen and colleagues (1957) as a strategy used by camels to conserve body water and soon researchers were looking for evidence of this autonomic response in large mammals living in Africa. Measurement of the rectal temperature of a white rhinoceros showed an increase in temperature of 3°C between sunrise and sunset when the rhino had been in the sun all day (Allbrook *et al.*, 1958). Shortly after this study, an investigation of the body temperature of the hippopotamus was conducted (Luck & Wright, 1959). Unfortunately, measurements of rectal temperature could be made only once the animals had been shot and only one value could be obtained from each individual. However, measurements were made at different times of day and the authors stated that no “obvious variation” in body temperature with time of day was evident. Later, measurements, including rectal temperature, were made (during the daytime only) in a live hippopotamus, which was restricted to a small enclosure (Wright, 1987). Despite wide fluctuations in environmental heat load (radiant temperature increased from about 20 to 60°C on one of the study days) the hippopotamus’ temperature varied by less than 1°C. Since measurements were discontinuous, no comment can be made about the variation in body temperature over 24 h and no firm conclusions can be drawn regarding the relation of body temperature to environmental heat load. Continuous measurements of body temperature have been made in a hippopotamus but the animal was kept in a laboratory (ambient temperature maintained at 21°C; Piccione *et al.*, 2005). Consequently, no conclusions can be made regarding the use of adaptive heterothermy by hippopotamus and rhinoceros.

Without continuous measurements of body and environmental temperature, it is impossible to determine whether an animal employs adaptive heterothermy (Mitchell *et al.*, 2002). In a study conducted in the 1960’s, which included several species of African mammal, continuous measurements of body temperature were measured in unrestrained, wild animals (Bligh & Harthoorn, 1965) for the first time. The researchers admitted that the site of temperature measurement (an 80 mm-deep incision in the muscle of the neck or back) was not ideal and that there were insufficient data to determine the relationship between body and ambient temperature. However, the data recorded for African buffalo and black rhinoceros revealed that these two species might have relatively labile body temperatures (a range of between 2.0 and 2.8°C over 24 h for the buffalo, and 2.4°C over 12 h for the rhinoceros). However, measurements made in giraffe raised the possibility that they might have a relatively stable body temperature (Bligh & Harthoorn, 1965), that is, the daily amplitude of body temperature was less than 2°C.

However, in a later study of giraffe, continuous measurements of rectal temperature in six captive individuals showed 24 h fluctuations in body temperature of up to 6.2°C (Langman & Maloiy, 1989) and a previous study demonstrated that body temperature was closely related to ambient temperature ($r = 0.8$; Langman *et al.*, 1982). In contrast, other studies have confirmed the stability of giraffe body temperature, and in their review of giraffe thermoregulation Mitchell and Skinner (2004) conclude that there is more evidence in support of giraffe having a stable body temperature than not.

Another animal around which there has been debate regarding the use of adaptive heterothermy is the eland. In 1969, Taylor observed a 24 h body temperature amplitude of 6°C when an eland was exposed to hot (air temperature = 40°C) as opposed to cool (air temperature = 22°C) laboratory conditions, and stated that eland employ adaptive heterothermy in order to conserve body water. Fuller and co-workers (1999a) conducted an investigation of body temperature in free-living eland, recording arterial blood temperature at five-minute intervals over 46 days, and found no evidence of adaptive heterothermy. In addition to having free access to water, the behaviour of the free-living animals was unrestricted, enabling them to make behavioural adjustments to regulate body temperature (Fuller *et al.*, 2004).

1.4.4 A complex interaction of adjustments

There is a complex interaction between morphological traits, and behavioural and autonomic adjustments to changes in environmental conditions and in investigating the thermoregulatory strategy of a species one must keep in mind all three. By using different combinations of adjustments, an animal can maintain homeothermy whilst incurring the minimum cost. For example, by standing in the shade, an eland can reduce the rate of evaporative water loss (Finch, 1972). A rhinoceros, by wallowing in mud, may substantially increase the dissipation of heat by evaporation without an increase in the loss of body water and electrolytes (Taylor, 1977). Often, a morphological trait may facilitate or enhance the effects of a behavioural or autonomic response; the absence of hair on a rhinoceros' body enhances the cooling effect of the evaporation of the mud because the skin itself is cooled (Ingram, 1965).

1.5 Thermoregulation in the African elephant (*Loxodonta africana*)

1.5.1 Classification and general thermoregulatory strategy

There is some debate regarding the classification of species within the genus *Loxodonta*. It is generally accepted that there are two types of elephant in Africa and there appears to be sufficient genetic evidence to classify them as two different species (Skinner & Chimimba, 2005). One is the forest elephant (*Loxodonta cyclotis*) and, as its name suggests, it inhabits the more densely forested regions of Africa. The other species, the savanna elephant

(*Loxodonta africana*), is more often found in open grassland or mixed woodland (Skinner & Chimimba, 2005). Although it is unlikely that there are large differences in the body temperature of the two species, the thermoregulatory strategies they employ may differ due to differences in the habitats which they occupy. It is the regulation of body temperature in the savanna elephant which is considered in this dissertation and any reference to 'African elephants' is to the savanna species.

Human-elephant interactions aside, elephants can be found in a wide range of habitats across Africa south of the Sahara (African Elephant Specialist Group, 2004) and can survive ambient temperatures ranging from below 0°C to nearly 50°C (Sikes, 1971). Cold environments probably do not present a thermoregulatory challenge to elephants because their low surface area to mass ratio favours the conservation of body heat. In a hot environment, however, an inability to dissipate excess body heat may be problematic. But an elephant's low surface area to mass ratio may also be an advantage in that an elephant will gain heat from its environment more slowly than an animal of smaller body size (Taylor, 1970a). Also because of its large size, a large amount of heat is required to raise body temperature (Parker & Robbins, 1985). Nevertheless, any heat which is gained by the body and which cannot be dissipated will result in an increase in body temperature. To have survived so successfully throughout Africa, elephants must be able to avoid deleterious increases in body temperature.

Thermoregulation in the African savanna elephant has been investigated previously. However, not all of the investigations included measurements of body temperature and only one recorded it continuously; Table 1.2 summarises the body temperature values recorded by various investigators. Despite elephants' substantially greater mean body mass (3 700 – 4 000 kg for females and 5 500 – 6 000 kg for males), their body temperature appears to be very similar to that of the other megaherbivores described in Table 1.1.

Because of the elephant's enormous height, it is likely that convection is important for heat loss (Benedict & Lee, 1938). An analysis of heat transfer in elephants demonstrated that almost 90% of an elephant's total heat loss requirements could be met by convective and radiant heat loss (Williams, 1990). However, as one of the authors acknowledged, the study animals were not subjected to conditions typical of their natural habitat (indoor zoo enclosure, air temperature equal to about 13°C). The African savanna does not present conditions conducive to the dissipation of heat by radiation, convection and conduction and heat may often be gained by these routes (Wright & Luck, 1984). Under such conditions, elephants must employ evaporative cooling to lose body heat.

Ultimately, the amount of heat which can be lost by evaporation depends on the water vapour deficit between the body surface and the ambient air. However, there are adjustments which elephants may employ in order to maximise the amount of moisture which is evaporated from various body surfaces. Elephants could employ panting to increase evaporative cooling across the surfaces of the buccal cavity, but it appears that they do not (Robertshaw, 2006); elephants do not breathe through their mouths (Raath,

Table 1.2 Previously reported body temperature of the African elephant.

Study site	Animal status	Body temperature (°C)					Air temperature (°C)	Reference
		mean	min	max	amplitude	site		
Zoo, USA	Tame	-	36.2	36.7	-	rectal	19.5	Benedict *et al*., 1921
Circus, USA	Tame	36.4	36.1	36.6	-	faecal	-	Benedict and Lee, 1938
Circus, USA	Tame	-	36.3	36.6	-	urine	-	Benedict and Lee, 1938
Field, Uganda	Deceased	36.4	36.1	36.8	-	rectal	-	Buss & Wallner, 1965
Field, Uganda	Wild	36.4	36	36.8	-	faecal	-	Buss & Wallner, 1965
Field, Zambia	Immobilised	35.1	33.1	37.1	-	muscle	25.6 - 35.0	Elder & Rodgers, 1975
Paddock, Uganda	Tame	-	35.4	38.4	-	rectal	-	Hiley, 1972
Zoo, South Africa	Tame	36.2	-	-	0.4	GIT	11.2 - 37.7	Kinahan *et al*., 2007*

* Kinahan and colleagues' (2007a) study was not yet published when I started my investigation. The results of that study will be discussed in the context of Chapter 4. GIT = gastrointestinal tract.

1993), so it is not possible for them to employ open-mouth panting. However, although not designed for panting, the elephant's trunk may play an important role in heat loss since it is well vascularised (Benedict, 1936). At typical ventilation rates (about 6 breaths per minute) and an ambient air temperature of 19°C, about 3.4% of the heat produced by basal metabolism was lost from the respiratory tract of an Asian elephant (Benedict, 1936). However, due to the length of the trunk (up to 2 metres; Skinner & Chimimba, 2005) it is likely that some of the heat and water given to the air as it is inhaled is transferred back to the tissues of the trunk as it is exhaled, as happens in the respiratory passages of the camel (Schmidt-Nielsen *et al.*, 1981). Whether or not such cooling of exhaled air has any implication for water saving is not certain since no studies have specifically addressed the issue in elephants. I suspect that the water condenses on the inside of the trunk and drips out when the trunk is held tip-to-ground.

Sweating is another means of evaporative cooling but in spite of early insistence that elephants sweat (Benedict, 1936), several studies have shown that elephants do not possess sweat glands (Spearman, 1970; Lillywhite & Stein, 1987). But that is not to say that no cutaneous moisture loss occurs. Paper impregnated with starch and iodine changed colour, indicating the presence of water, within 20 seconds of being placed onto an elephant's skin (compared to 60 seconds when placed onto a cow, a sweating animal; Hiley, 1972). Quantification of cutaneous moisture loss at several sites across an elephant's body revealed losses of 2500 $ml.h^{-1}$ (across the elephant's entire body surface which measured $11m^2$), equivalent to 400 $ml.h^{-1}$ in an adult man (Wright & Luck, 1984). The investigators determined that up to 75% of an elephant's heat loss requirements could be met by the evaporation of moisture from the skin surface (Wright & Luck, 1984). However, elephants may not have any control over the amount of moisture lost from the surface since cutaneous moisture loss did not vary under different ambient conditions (Hiley, 1972). But the amount of moisture lost through the skin is not independent of environmental conditions. For example, the rate of cutaneous moisture loss depends on wind movement (Gebremedhin & Wu, 2001) and an elephant may adjust the amount of wind to which it is exposed by choosing an appropriate location.

Cutaneous moisture loss also depends on the temperature of the skin (Wright & Luck, 1984) as well as its state of hydration. Elephant skin is 30 to 40 mm thick (Skinner & Chimimba, 2005) and large losses of water through the skin may seem surprising. However, as long as an elephant's skin remains sufficiently hydrated, water moves easily through it (Wright & Luck, 1984). One of the ways in which an elephant keeps its skin moist is by swimming, and by wallowing in mud. The wrinkles in an elephant's skin improve the retention of water; the smaller crevices behave like capillaries, enhancing the distribution of water through the skin, and the larger folds increase the adherence of mud (Lillywhite & Stein, 1987). By comparing the water and mud retention properties of elephant skin with those of a flat surface, investigators found that the wrinkles increased the amount of water retained by 4.5 to 10 times and prolonged the drying time of mud by up to 7 hours. Also, the wrinkles reduced the extent to which the mud split and cracked, ensuring a more continuous sheet of moisture protection (Lillywhite & Stein, 1987).

Swimming and wallowing may reduce an elephant's reliance on body water for evaporative cooling, but these activities still require the availability of surface water. Elephants are highly dependent on water (Skinner & Chimimba, 2005); they may drink more than 100 l per day, and if surface water is not available, elephants will dig for it (Sikes, 1971). Elephants are known, under hot conditions, to regurgitate water from their stomachs to spray over their bodies (Sikes, 1971; Leggett, 2004).

Elephants' dependence on drinking water may partly be explained by an inability to reduce excretory water losses. A 70 kg human produces about 1.5 l of urine per day, and if urine production scaled proportionately with mass, a 4000 kg elephant should produce about 85 l per day. But records show that an elephant produces up to only 50 l of urine per day (Benedict, 1936), considerably less than the volume which could be expected for an animal of that size. However, measurements of the specific gravity of elephant urine suggest an inability to concentrate urine; the specific gravity of the urine produced by an Asian elephant ranged from 1.004 to 1.033 (Benedict, 1936). Admittedly, the elephant had free access to water and was not exposed to heat stress, but based on the structure of elephants' kidneys, it seems probable that African elephants are incapable of concentrating their urine to the same extent as some other mammals (Maluf, 1995).

If it is the case that an elephant is unable to reduce excretory water loss, as some other mammals do, cannot regulate cutaneous moisture loss, which results in substantial losses of body water, and does not recover water from exhaled air, how does it survive high ambient temperatures when water is scarce? Several investigators of elephant thermoregulation have suggested that elephants employ adaptive heterothermy as a solution (Elder & Rodgers, 1975; Hiley, 1975; Wright & Luck, 1984). Certainly, an elephant's large body size enables it to store heat, but the extremes of body temperature associated with this response have not been observed in elephants; the 24 h pattern of elephant body temperature has not been sufficiently investigated for researchers to be able to state whether elephants employ heterothermy or not. It has also been suggested that elephants employ selective brain cooling (Hiley, 1975). Elephants may possess a carotid rete (Shoshani *et al.*, 2006) but no measurements of brain or blood temperature have been made in elephants. To establish whether or not elephants use selective brain cooling and adaptive heterothermy, continuous measurements of body temperatures, including brain and arterial blood temperatures, would have to be made in individuals subjected to significant heat and water stress and which have access to the full suite of behavioural and autonomic adjustments available to them in their natural environment (Fuller *et al.*, 2004).

Elephants living in their natural environment may also rely on behavioural adjustments to regulate their body temperature. Like the majority of other African megaherbivores, elephants are generally less active during the hottest portion of the day (Sikes, 1971; Hiley, 1975), and shade-seeking behaviour may be especially important for elephants. One author claimed that elephants suffer from dehydration and sunstroke if exposed to solar radiation for extended periods of time (Sikes, 1971) but no supporting evidence was provided. Direct and reflected solar radiation may account for 43% of the heat gained by an elephant from its environment (Hiley, 1972). Therefore, shade cover could markedly decrease an elephant’s heat gain from its environment and since elephants are browsers, they have the advantage of being able to continue foraging whilst remaining in the shade.

Elephants might also avoid unfavourable environmental conditions by migrating, since elephants can cover large distances if required (Viljoen & Bothma, 1990). Movement may also be determined by ambient conditions on a daily basis; when given the option, elephants may spend their daylight hours in the cool of forest habitat and move onto the savannas to feed over night and in the cool of early morning and late evening (Sikes, 1971). A study of habitat selection suggested that an elephant chooses a habitat based on its thermal characteristics and the elephant’s thermoregulatory requirements (Kinahan *et al.*, 2007b).

1.5.2 The ears as a thermoregulatory organ

Calculation of the surface area to mass ratio in a 1422 kg hippopotamus produced a value of 0.007 (Luck & Wright, 1964). Body surface area scales with body mass to the power of -0.33 (Schmidt-Nielsen, 1984) therefore, the surface area to mass ratio of a 3500 kg elephant should be 0.005. However, I found that the African elephant has a surface area to mass ratio of about 0.007 (I calculated a range of 0.0062 – 0.0076 using measurements made by Hiley, 1972; Williams, 1990; and Wright, 1984, on elephants ranging in mass from 300 – 4 200 kg). An explanation of how an elephant, which may be up to four times larger in mass than a hippopotamus, can have a surface area to mass ratio so similar to that of the smaller animal, I believe lies in differences in morphology. Elephants possess an anatomical feature which none of the other large African mammals do - their enormous ears.

The pinna (outer ear) of an adult bull elephant may reach 2 metres in height and about 1 m in width, and weighs about 20 kg (Skinner & Chimimba, 2005). Both sides of both pinnae represent about 20% of the total body surface area (Hiley, 1972; Wright & Luck, 1984) and I believe that an elephant's surface area to mass ratio is increased as a result of its ears. However, I am not aware of measurements which would allow for the calculation of the ratio in the any of the megaherbivores apart from hippopotamus and therefore, it is only tentatively that I suggest that an elephant's pinnae may be a significant adaptation which compensates for its increase in body mass, enabling it to overcome the accompanying thermoregulatory challenges. It is quite plausible that the pinnae play an important role in thermoregulation, given that the ratio of their mass to their surface area is high and that the pinnae have an extensive vascular network (Wright, 1984), most visible on the posterior surface.

In his authoritative work on elephant physiology, Benedict (1936) recognised the potential role that the pinnae could play in thermoregulation. However, he firmly dismissed the notion that elephants would need a special mechanism for heat loss, stating that ear flapping and changes in blood supply to the pinnae were the result of a nervous reflex, prompted by excitement of the elephants by people. Two later studies established that the pinnae do in fact play a significant role in elephant thermoregulation.

First, Wright (1984) determined the rate of blood flow through the ears and the difference in temperature between blood entering and leaving the ear. Blood flow through the ear reached 12 $l.min^{-1}$ at times, a supply which exceeded the metabolic requirements of the tissues (Wright, 1984), and with an arterio-venous temperature difference of 2 to 3°C, the ears acted as very effective heat exchangers (between 14 to 66% of the estimated metabolic heat production was lost through the ears). A second study, using infrared thermography to record changes in blood flow, created a model of heat transfer which predicted heat losses, from both surfaces of both pinnae, of up to 91% of metabolic heat production (wind speed = $5m.s^{-1}$, air temperature = 20°C; Phillips & Heath, 1992). Both studies demonstrated a variability of blood flow through the pinnae, and suggested that the flow of blood could be regulated according to the thermal requirement of the animal. Observations made by others confirmed the variability of blood flow under different conditions; in cold conditions the vessels of the pinnae generally were constricted (Sikes, 1971; Cena & Clark, 1973; Hiley, 1975), while in hot conditions the vessels were greatly distended (Sikes, 1971; Hiley, 1975).

Also, there appears to be a difference in temperature between the anterior and posterior surfaces of the pinnae. One study found that at midday, the difference in temperature between the two surfaces of the pinnae was 5 to 6°C (Hiley, 1972). Another study made similar observations but found that the difference was always less than 1°C (Phillips & Heath, 1992). Irrespective of the magnitude of the difference, my interpretation of a lower skin temperature on the posterior surface of the pinnae is that evaporation from this surface was higher (as also noted by Sikes, 1971). Wright and Luck (1984) demonstrated that cutaneous moisture loss was greatest from the posterior surface of the ear (their reported measurements as follows: shoulder: 143 $g.m^{-2}.h^{-1}$; anterior ear: 185 ± 48 $g.m^{-2}.h^{-1}$; flank: 192 ± 75 $g.m^{-2}.h^{-1}$; posterior ear: 493 ± 247 $g.m^{-2}.h^{-1}$). However, a study by Hiley (1972) showed that cutaneous moisture loss was not greater from the ear than elsewhere on the body and did not change with variation in ambient conditions.

It remains to be established how the rate of cutaneous moisture loss varies under different environmental heat loads, but air movement is known to be an important factor. Increased wind speed significantly increased the heat lost from the pinnae by convection (Phillips & Heath, 1992) and increased the heat lost by evaporation also (Wright & Luck, 1984). An elephant may exploit windy conditions by holding its pinnae perpendicular to its body, exposing the posterior surface to the movement of air (Buss & Estes, 1971). But an elephant need not rely on wind to increase evaporative heat loss. By flapping its pinnae, an elephant may greatly increase the cooling of blood passing through these tissues as the posterior surface of the outer ear is exposed to air movements (Sikes, 1971). Ear flapping also produces substantial movements of air, which may increase evaporative cooling from the rest of the body surface (Wright, 1984).

1.5.3 Limitations of investigations of thermoregulation in the African elephant

As with the majority of studies of thermoregulation in the other megaherbivores, measurements of body temperature in studies of thermoregulation in elephants have been discontinuous[1]. Consequently, the nychthemeral rhythm of body temperature could not be

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[1] The study by Kinahan and colleagues (2007a) had not yet been published when I started my investigation.

determined, including defining characteristics such as the daily amplitude and the timing of the minimum and maximum temperatures. Crucial to ascertaining whether or not elephants employ adaptive heterothermy, the relationship between ambient temperature and elephant body temperature could not be established either. Most of the studies reporting thermoregulatory mechanisms or behaviour in elephants did not include measurements of body temperature and therefore did not reveal the animals' thermal status. Although suggestions have been made concerning the relationship between behaviour such as ear flapping and environmental heat load, none of the previous studies investigated the relationship between body temperature and behaviours considered to be of key thermoregulatory importance.

Furthermore, many of the investigations were conducted either in animals confined to small enclosures, or living in habitats which were quite different to their natural environment (that is, zoos or circuses). Those studies which were conducted on animals living in their natural environment employed study animals that were anaesthetised, or the animals were shot and only single measurements were made on the dead animals.

The complexity of an animal's needs and its interactions with its environment make it important to investigate thermoregulation in the context of the animal's natural environment as well as in the laboratory. Experiments conducted in restrained animals, or in a laboratory environment, may reveal important information regarding a species' thermoregulatory physiology, but the way in which an animal's behavioural responses modify heat exchange can be investigated properly only in its natural environment (Jessen *et al.*, 1994; Mitchell *et al.*, 1997; Fuller *et al.*, 1999a). It is difficult to replicate natural conditions in a laboratory or other artificial environment (Finch, 1972) and an animal kept in a constructed environment does not have access to the full suite of responses to changes in environmental heat load it would otherwise have (Fuller *et al.*, 2004). Animals prevented from employing behavioural means of thermoregulation are forced to employ autonomic mechanisms, providing a distorted picture of thermoregulation (Mitchell *et al.*, 2002). Therefore, conclusions regarding the thermoregulatory strategy employed by a species must be made using data recorded in individuals living, unrestrained, in their natural habitat (Fuller *et al.*, 1999a).

1.6 Body temperature measurement in free-living animals

Historically, it was challenging, if not impossible, to make repeated measurements of body temperature in free-living individuals without influencing their natural behaviour. In the 1960's and 70's, researchers recognised the need for continuous measurements of body temperature in unrestrained animals and made the first attempts at radiotelemetry. A fine temperature-sensitive probe, connected to a transmitting unit attached to a harness worn by the animal, was inserted into the muscle of the neck. In this manner continuous measurements of body temperature were recorded for unrestrained sheep over the course of a year (Bligh *et al.*, 1965) and for several African mammals for 12 to 54 hours (Bligh & Harthoorn, 1965). However, the insertion of a probe into an incision made in muscle tissue would not provide accurate measurements of core body temperature and this technique is not optimal for the welfare of the animal concerned. Radiotelemetry later was used to record continuous measurements of rectal temperature in giraffe (Langman & Maloiy, 1989), but changes in the temperature of the rectum occur more slowly than did changes in the temperature of arterial blood (Brengelmann, 1987). Also, slippage of a rectal probe often results in the loss, or inaccuracy, of data points (McKenzie & Osgood, 2004).

The improvement of surgical techniques, and the development of implantable devices, enabled the surgical implantation of temperature-sensitive equipment, allowing the measurement of internal body temperature. Today, radiotelemetry is recognised as a powerful tool for investigating the physiology of free-living animals (Cooke *et al.*, 2004) and telemeters have been used to continuously record body temperature in free-living ungulates (Ostrowski *et al.*, 2003). A temperature sensor is implanted surgically at the site of measurement and may transmit the data to a unit fitted to a collar worn by the study animal. The data then are transmitted to a receiving unit (either hand-held, or satellite-based). Radiotelemetry systems which transmit data to a satellite eliminate the influence of human presence but are prohibitively expensive. The receiving unit on the harness or collar may be equipped with some data storage capacity as is the case with telemetry systems designed for use in humans (Byrne *et al.*, 2006) thereby reducing the need to constantly download data from the unit on the collar. However, the collar and receiving unit are generally quite bulky and may increase the risk of predation (Fuller *et al.*, 1999a). Also, since some of the equipment is attached externally, it is vulnerable to damage (Schoenig *et al.*, 2004).

Implantable data loggers provide an alternative means of obtaining continuous measurements of internal body temperature and do not require the attachment of any external equipment to the study subject (Fuller *et al.*, 1999b). Data loggers have the capacity to store data, eliminating the problems associated with the transmission of data using radio frequencies. However, the logger must be retrieved from the animal in order for the recorded data to be downloaded. Data loggers have been used in studies of thermoregulation in free-living eutherian mammals such as zebra (*Equus burchelli*; Fuller *et al.*, 2000), eland (*Tragelaphus oryx*; Fuller *et al.*, 1999a), oryx (*Oryx gazelle*; Maloney *et al.*, 2002), Arabian sand gazelle (*Gazella subgutturosa marica*; Ostrowski & Williams, 2006) and black-tailed prairie dogs (*Cynomys ludovicianus*; Lehmer *et al.*, 2003). Typically, when data loggers are used to continuously record internal body temperature, the logger is covered in biologically inert wax to prevent irritation of tissues and then is implanted surgically at the desired site of temperature measurement. The data logger is explanted surgically at the end of the study period, meaning that direct human contact for the purposes of temperature measurement is reduced to two occasions. However, surgery is not always possible or desirable and in such cases, alternative sites of body temperature measurement must be considered.

The site of body temperature measurement will depend on the question being asked. There has been disagreement concerning the site which best represents “core” body temperature, but right atrial, or pulmonary artery temperature is considered to provide the best indication of thermal status (Brengelmann, 1987). However, the techniques used to measure right atrial or pulmonary artery temperature are especially invasive, and temperatures recorded at other sites in the body may provide acceptable approximations of core temperature. A more complete discussion of the site of body temperature measurement in the context of this dissertation is given in Chapter 3.

1.7 Dissertation aims

Continuous measurements of body temperature have not been made in unrestrained African elephants, living in their natural habitat, under a variety of climatic conditions. Therefore, the primary aim of this dissertation was to describe the 24 h pattern of body temperature in African savanna elephants using continuous measurements of body temperature. I also investigated the relationship between selected behaviours and body temperature and addressed the influence of environmental temperature on elephant body temperature.

Data loggers have not ever been implanted in elephants and such surgery would have presented several risks. Also, the study animals were "working" elephants, so surgery was not possible. Therefore, I had to employ a non-invasive technique to continuously measure body temperature. The ingestion of temperature-sensitive devices by the elephants provided an alternative since the animals were tame and suitably trained; this technique was used by Kinahan and colleagues (2007) in their study of elephant body temperature, and by Toscano (2001) in his study of transport stress in circus elephants. The adaptation and usefulness of the technique are discussed in Chapter 3. The measurements of elephant body temperature recorded using ingestible data loggers, and the effect of environmental heat load on body temperature, are described in Chapter 4.

Another aspect of elephant thermoregulation which has not received sufficient attention is the relationship between thermoregulatory behaviour and body temperature in elephants. An advantage of conducting the investigation in tame elephants was that I could observe their behaviour without influencing it. Elephants in the wild avoid contact with people whenever possible (Harris *et al.*, 2008), making them difficult to observe. The tame study animals were allowed to move around in a large area of their natural habitat for most of the day, and during these times their behaviour was not restricted. The relationship between selected behaviours and body temperature are considered in Chapter 5.

During the course of my study, a preliminary investigation of elephant skin temperature was conducted over a 24 h period, using infrared thermography. However, insufficient data were recorded for any conclusions concerning elephant skin temperature to be drawn and therefore, the results of this preliminary investigation will not be discussed further in the context of this dissertation.

Chapter 2

General materials and methods

2.1 Introduction

This chapter aims to provide the general information regarding the site where the study was conducted, the study animals, and study methods, which is common to the following three chapters. Additional information will be presented in the chapter to which it is most relevant.

All data reported in this dissertation were collected during several field trips conducted between July 2006 and November 2007.

2.2 Study site

The study was conducted on Letsatsing Game Reserve (25°20’31”S, 27°07’25”E), a private reserve in the North West Province of South Africa, an area in which elephants occur naturally. The reserve is about 800 ha in size and its northern and eastern boundaries border the Pilanesberg National Park. A perennial stream runs through the reserve and a ground water pump supplies a small dam. Mean annual rainfall is about 500 – 600 mm, the greatest proportion of precipitation falling during the summer months (October to March). The months from October through to March are generally the hottest, with an ambient temperature range of about 16 to 32°C. June, July and August are the coldest months when the ambient temperature ranges from about 3 to 26°C (data supplied by the South African Weather Service, 2007).

The vegetation is classified as sourveld (Acocks, 1988) with a mix of woodlands, acacia thickets and grasslands. The Letsatsing Reserve is home to several herbivores such as white rhinoceros, giraffe, kudu, wildebeest, warthog, impala, as well as a variety of birds and other small animals.

2.3 Study animals

Four young adult African elephant bulls (*Loxodonta africana*), belonging to Pilanesberg Elephant Back Safaris, were used in this study (Figure 2.1). Table 2.1 provides measurements of the animals' physical traits. The elephants were tame and were trained to obey voice commands, enabling me to work closely with them and to observe them without influencing their behaviour. Trained and experienced elephant handlers were always present to assist. The elephants were engaged in tourist-related activities, or activities promoting public awareness of elephant conservation, for a portion of each day. The duration of each activity was limited to a maximum of 90 minutes. The total time allowed for these activities was limited to a maximum of 300 minutes over the course of the day (although, in reality, the total was about 210 minutes or less). The elephants spent the remainder of the daytime moving freely through the reserve. Fresh water and browse were available to the elephants and additional food was supplied as needed. For reasons of safety, the elephants were housed, individually, in open-air stables at night (from just after sunset until shortly before sunrise); the elephants had room to lie down in their stables and were able to turn around with room to spare. The same animals were used throughout the investigation and they remained at the field site for the duration of the study.

Figure 2.1 Upper panel: one of the tame elephant bulls living in Letsatsing Game Reserve, during the day. Lower panel: the elephants waiting to be led out of their stables in the morning. The elephants spent the night (from around sunset to sunrise) in the stables.

Table 2.1 Summary of the study animals' physical measurements during the study (information supplied by Pilanesberg Elephant Back Safaris).

Elephant	Age (yrs)	Shoulder height (m)	Estimated mass (kg)
Elephant 1	21	2.9	3700
Elephant 2	22	3.0	4000
Elephant 3	22	2.8	4300
Elephant 4	23	2.8	4000

2.4 Temperature data loggers

Miniature temperature-sensitive data loggers (i-Button DS1922L, Maxim Integrated Products, California, USA) were used to record body temperature. A silicone chip containing the temperature sensor and onboard memory was housed in a sturdy stainless steel case which had an external diameter of 16 mm and a mass of 3 g. The data loggers had 8192 bytes of memory and could store 4096 data points at a resolution of 0.06°C. At a sampling interval of five minutes, as used in this study, up to 341 hours (about two weeks) of data could be logged by a single logger. The data loggers were launched and downloaded using a personal computer and appropriate software (1-wire Viewer, Dallas Maxim, California, USA), and data were exported to a spreadsheet application (Microsoft Excel) for analysis. Chapter 3 describes how these data loggers were used to record elephant body temperature.

All data loggers were calibrated against a certified precision thermometer (Quat 100, Heraeus, Hanau, Germany) in a stirred, insulated water bath, across a range of temperatures (six temperatures between 30 and 40 °C). A simple linear equation ($y = mx + c$) provided a suitable fit for all data loggers (TableCurve 2D for Windows v3.05, Jandel Scientific, California, USA). The fit of the line to the calibration data for each logger was assessed by examining the r-squared value and the fitted standard error (a measure of the deviation of the points from the fitted line). The mean fitted standard error was 0.02 ± 0.01 and all r-squared values were very close to 1.0 (none less than 0.99). Several data loggers were re-calibrated after use (about 18 months after the beginning of the study) to check for deviations in the calibration. No change in the relationship between the temperature recorded by the data loggers and the precision thermometer occurred. Figure 2.2 illustrates results of the calibration process for a single logger.

The fit of the calibration data to the line used to describe the relationship between the precision thermometer and data logger temperatures (the fitted standard error) was less than the resolution of the logger. Thus, the data loggers provided spot measurements of temperature accurate to 0.06 °C.

2.5 Climatic data

Air temperature and black globe temperature were recorded every half-hour using a portable weather station (Hobo Weather Station, Onset Computer Corporation, Massachusetts, USA) erected at the field site. Measurements of black globe temperature were recorded using a thermistor positioned within the centre of a hollow copper globe (150 mm diameter) which was painted matte black. Black globe temperature provides an integrated measure of air temperature, radiant temperature, and the cooling effect of wind. Solar radiation ($W.m^{-1}$) and wind speed ($m.s^{-1}$) also were recorded separately by the weather station every 30 minutes.

Figure 2.3 shows the mean, mean maximum and mean minimum air and black globe temperature for each month of the study period. The study period was divided into three climatic ‘periods’ based on the environmental temperature: July and August were grouped

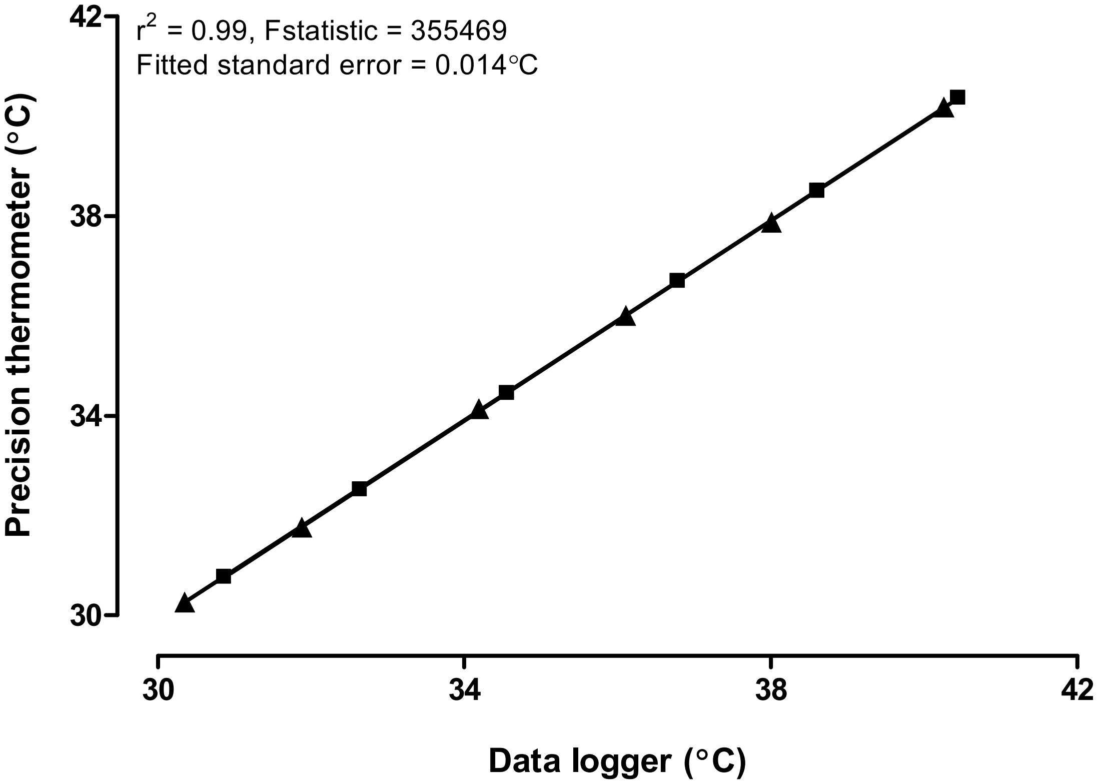

Figure 2.2 An example of the linear regression analysis used for the calibration of a data logger. The linear equation fitted to the calibration data was y = mx + c (for this logger, m = 0.1 and c = 0.18). The points showing the first calibration are indicated by squares and the points illustrating the second calibration are indicated by triangles.

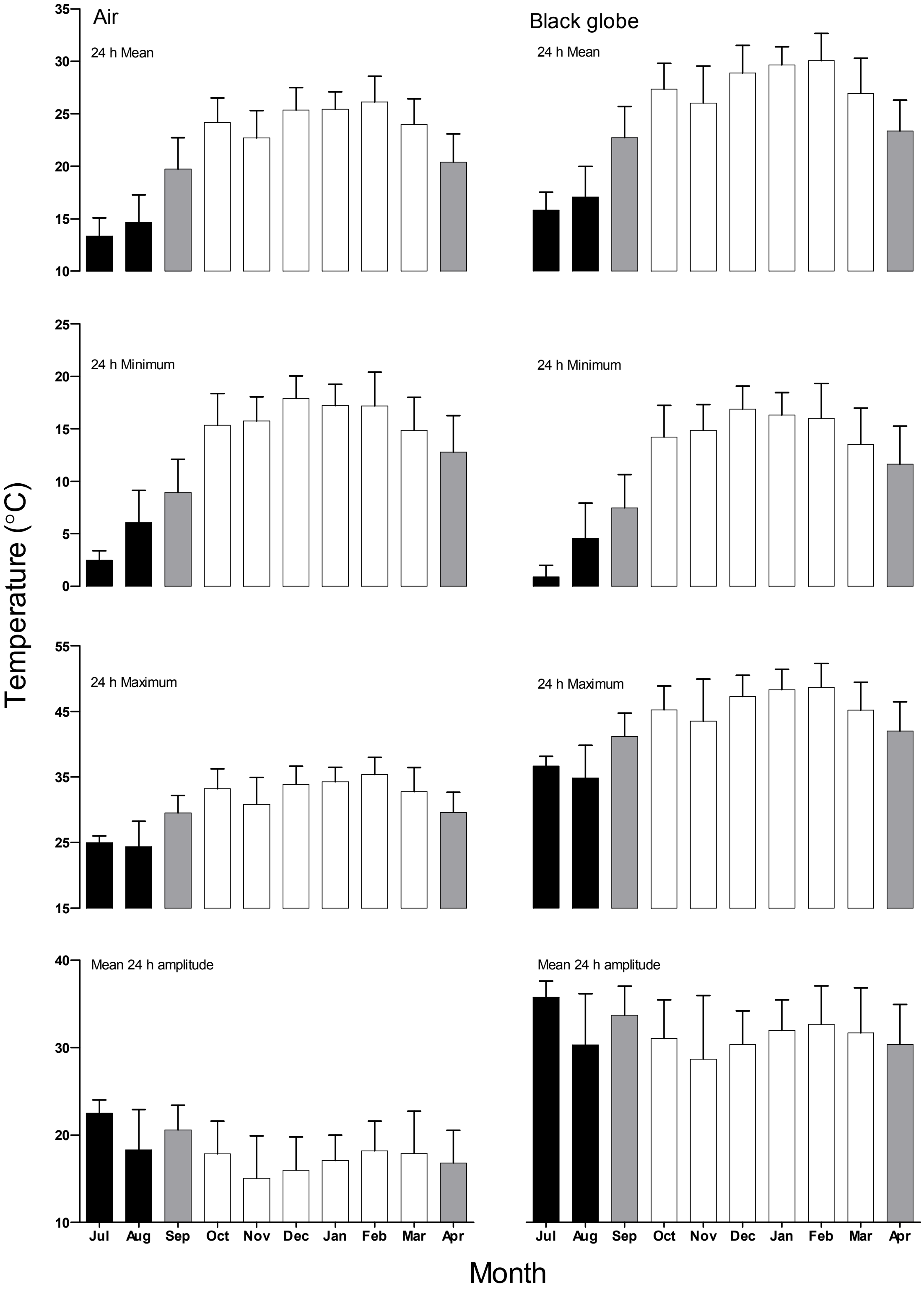

Figure 2.3 Mean daily, mean daily maximum, mean daily minimum and mean daily amplitude (+SD) air temperatures (left panels) and black globe temperatures (right panels) for each month during the study. The cold period is indicated by the solid black bars, the warm period by the grey bars and the hot period by the white bars.

to form the ‘cold’ period as the temperatures were similarly low; September and April were grouped to form the ‘warm’ period as the temperatures were similarly mild; and October, November, December, January and March were grouped together to form the ‘hot’ period as the temperatures were similarly high. The mean, mean minimum and mean maximum were calculated for each climatic period by averaging the mean values of the months included in each period. The mean air and black globe temperatures recorded during each climatic period are given in Table 2.2, as are the mean times of sunrise and sunset for each climatic period. Note that the standard deviations for the times of sunrise and sunset are greater for the hot and warm periods than for the cold period due to the larger number of months included in these two climatic periods.

2.6 Data analysis

In all statistical analyses throughout this dissertation, a p value less than 0.05 was considered significant. If differences between variables were contextually (biologically) insignificant, no statistical test was used (for example, the difference in mean body temperature between elephants, see Chapter 4).

Table 2.2 Mean (± SD) air and black globe temperatures, recorded at the field site, for each of the climatic periods. Times of sunrise and sunset are given as mean ± SD also.

Climatic period	**Mean air temperature (°C)**	**Mean black globe temperature (°C)**	**Time of sunrise**	**Time of sunset**
Cold	14.0 ± 1.0	16.4 ± 0.9	6:40 ± 11	17:50 ± 8
Warm	20.0 ± 0.6	22.9 ± 0.6	6:15 ± 21	18:00 ± 30
Hot	24.6 ± 1.2	28.1 ± 1.6	5:50 ± 39	18:50 ± 33

Chapter 3

A non-invasive technique for measuring the body temperature of tame African elephants

3.1 Introduction

In situations when surgery is not desirable or possible, as was the case in my study, ingestible temperature-sensitive devices provide an attractive alternative to implanted devices for measuring internal body temperature. Ingestible telemeters are one such device. The ingested telemeter measures temperature as it transits the gastrointestinal tract and transmits data to a receiving unit which is either worn by, or kept in close proximity to, the study subject. A variety of ingestible telemeters have been validated against traditionally-accepted measurements of core body temperature in humans. Ten of twelve validation studies concluded that ingestible telemeters provide acceptable measurements of core temperature in humans (Byrne & Lim, 2007). Ingestible telemeters also have been validated for use in animals including swine (Brown-Brandl *et al.*, 2003), cattle (Prendiville *et al.*, 2002) and horses (Green *et al.*, 2005). Investigators who have designed ambulatory systems for monitoring animal health have included ingestible telemeters as the sole source of body temperature data (Nagl *et al.*, 2003; Schoenig *et al.*, 2004). Ingestible telemeters have been used also to study the body temperature of unrestrained dolphins (Mackay, 1964) and elephant seals (McGinnis & Southworth, 1967).

However, there are disadvantages to using ingestible telemeters to record body temperature data; up to 25% of the data set can be corrupted or lost (Byrne & Lim, 2007). Data can be lost when the receiver unit passes out of the range of the telemeter's signal (McKenzie & Osgood, 2004), or as a result of interference from other radio signals (Green *et al.*, 2008). Attaching the receiving unit to a collar or harness placed on the animal reduces the loss of data points, but because the equipment is external, it remains vulnerable to damage. One of the key challenges encountered by researchers designing the ambulatory systems for animals was damage to the receiving unit. Animals living outdoors may immerse themselves in water or bathe in mud, and equipment may be crushed when an animal lies down (Schoenig *et al.*, 2004). Also, the harness may snare, posing a risk to both the animal and the equipment.

In contrast to telemeters, data loggers are self-contained as the sensor and receiving unit are usually housed within the same unit. Once a data logger has been ingested by the study animal, the data it records as it transits the gastrointestinal tract are stored and then downloaded once the logger has been retrieved. Since the logger stores the data, no external equipment needs to be attached to the animal. However, ingestible data loggers have disadvantages also; data can be obtained only once the logger has been retrieved and retrieval of devices can be challenging, even when the study animals are confined to relatively small spaces. As with telemeters, damage to devices during transit may result in the loss of data points. Also, the device must be small enough that it will not become lodged in the oesophagus of the animal which is required to swallow it, but not so small that it can become lodged within the gastrointestinal tract. To date, data loggers have not been designed to be ingested, and may require additional protective coverings to prevent damage during transit through the gastrointestinal tract.

Miniature data loggers have previously been fed to tigers (*Panthera tigris*; Nevill & Friend, 2003), hippopotamus (*Hippopotamus amphibious*; Piccione *et al.*, 2005), as well as to

Asian elephants (*Elephas maximus*; Toscano, 2001) and African elephants (Kinahan *et al.*, 2007a), to record internal body temperature. However, the study animals were either confined to small spaces (Nevill & Friend, 2003), or the investigators experienced high loss of (Toscano, 2001), or damage to (Kinahan *et al.*, 2007a), the ingested loggers. No study has used ingestible data loggers to record body temperature in semi-free living animals.

The aims of this chapter are to:

1. describe the development of the technique which I used to record the internal body temperature of tame, African elephants (*Loxodonta africana*) living in their natural environment.
2. provide an assessment of the ease of ingestion, gut transit times and rates of retrieval of miniature temperature-sensitive data loggers fed to tame elephants.
3. provide a preliminary evaluation of gastrointestinal temperature as a measure of elephant body core temperature.

3.2 Materials and methods

3.2.1 Study site and animals

Refer to Chapter 2 for details of study site and animals.

3.2.2 Experimental procedure

To record measurements of internal body temperature, data loggers (i-Button DS1922L, Maxim Integrated Products, California, USA) were given to the elephants to swallow (described below). In a pilot study I found that loggers inserted into an item of food (such as an apple), were likely to be chewed and damaged. Placing the data logger by hand towards the back of the tongue and supplying a constant stream of water from a hosepipe proved to be the most effective means of getting the elephants to swallow a data logger without damage to the outer protective casing. Therefore, I administered all loggers to elephants with water.

Data loggers were recovered from the faeces. I, or an assistant, followed the elephants during the day and attempted to check all faeces passed by the subject animals by pulling all faecal material apart. All faeces passed overnight in the stables were inspected also.

Several designs of ingestible device were used to record elephant body temperature. It was initially thought that the transit times would be predictable and so that the data loggers would be retrieved easily from the faeces. This proved not to be the case and I therefore explored two ways of locating the logger in the faeces. For the first, the loggers were packaged with a tracking transmitter. For the second, a brightly-coloured ribbon was attached to the logger.

3.2.3 Devices to measure body temperature

Device A (logger)

A data logger (16 mm diameter), not covered in wax (Fig. 3.1 A), was given to an elephant to swallow and a second logger of the same design was given about six hours later. Faeces were sifted carefully and then checked using a hand-held metal detector. I tested this technique on one elephant but abandoned this approach when I realised that the chances of retrieving the loggers were low.

Device B (logger + transmitter)

A small tracking transmitter (Datamet, Potchefstroom, South Africa) was packaged with a data logger (Fig. 3.1 B1). The transmitter measured about 30 x 15 mm and was powered by a 3V lithium watch battery (CR1225, Renata, Switzerland). The devices were wrapped in electrical adhesive sealing tape, and then covered in waterproof wax (Sasol, South Africa) to prevent damage to the electronics and to avoid physical damage to the tissues within the

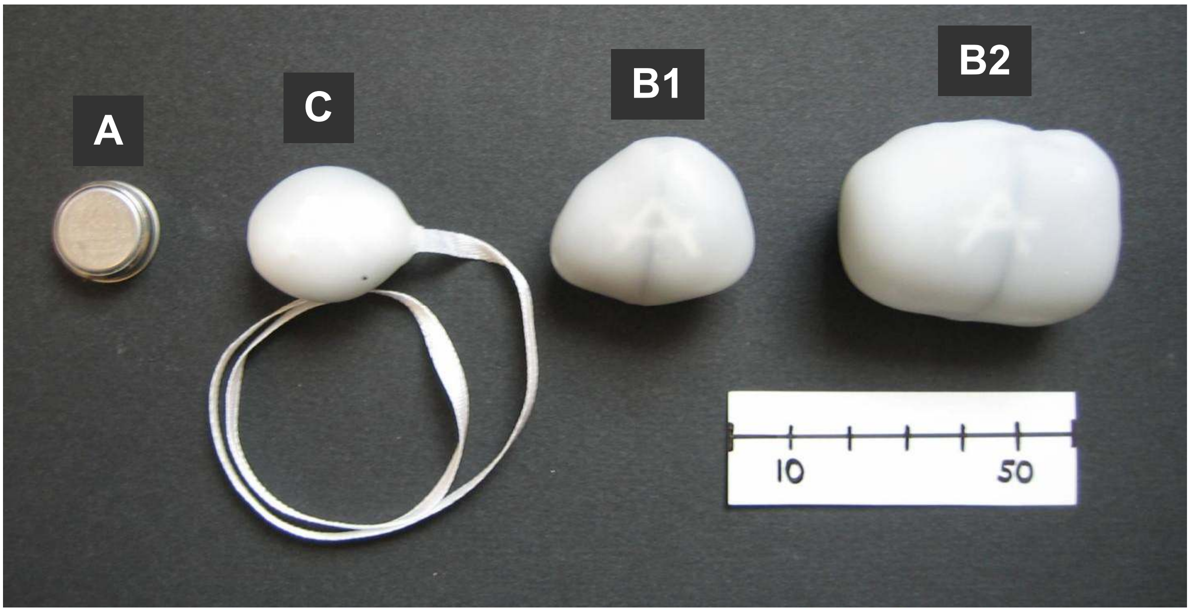

Figure 3.1 The four types of ingestible device used to record elephant body temperature (in final pre-ingestion form). A (Device A): a data logger, which was fed to the elephants without any protective covering; C (Device C): a single data logger, covered in wax, with a length of satin ribbon attached; B1 and B2 (Device B): a single data logger packaged with a tracking transmitter and covered in wax. The scale is given in millimetres.

elephant's gastrointestinal tract. The final dimensions of this combination were 26 x 30 mm. The final mass of the device was about 13 g.

A second data logger and transmitter combination (Fig. 3.1 B2) was tested using a transmitter with greater signal strength. The transmitter measured about 11 mm x 25 mm (Africa Wildlife Tracking, Pretoria, South Africa) and was powered by a 3.6V lithium-thionyl chloride battery (LS 14250, Saft, Bagnolet, France). The tracking transmitter and its battery were covered in dental acrylic and the devices were then packaged together as described above. The final dimensions of this combination were 21 x 45 x 29 mm, with a final mass of about 30 g.

A wide-range VHF receiver (New Concept AR8000, AOR Ltd, Derbyshire, UK) and Yagi H-bar antenna (RA-14K, Telonics, Arizona, USA) were used to detect the signal and determine whether the devices were in the elephant faeces or in the gastrointestinal tract.

Device C (logger + ribbon)

To aid detection of the data logger in the faeces, a 350 mm length of brightly-coloured satin ribbon was attached to a data logger (Fig. 3.1 C). Leaving the ribbon free, the data logger then was covered in wax. The device had a final diameter of 25 mm and a mass of about 7 g. Once the wax had hardened, the ribbon was wound around the device and baking-chocolate was used to hold the ribbon in place. In this way the ribbon would not irritate the elephant’s throat during ingestion, but would free itself as the chocolate melted in the gastrointestinal tract.

3.2.4 Thermal inertia of devices

To determine whether the size of the device and the wax coating influenced the response time of the data loggers to changes in temperature, the time constants were determined. One of each of the devices was left in a large volume of water (19.5°C) overnight. The following morning, the devices were dropped into an insulated, stirred water bath, set at 37.1°C, for thirty minutes. Data loggers recorded temperature every thirty seconds.

3.2.5 Differences in temperature along the gastrointestinal tract

To investigate whether the temperature differed at various locations along the gastrointestinal tract, two devices (both Device C) were given to one of the elephants five hours apart from each other. The interval between the ingestion of the two devices was based on an estimate of the time taken for previous devices, of the same design, to exit the stomach.

3.3 Data analysis

3.3.1 Stabilisation of logger temperature within the gastrointestinal tract

The length of time taken for the temperature of the devices to stabilise within the gastrointestinal tract was determined. The temperature was considered to be stable when the logger had recorded three consecutive temperatures (that is, over a period equal to 15 minutes) which did not differ from each other by more than 0.2°C. Also, the recorded temperatures had to lie within the range of body temperatures previously reported for elephants. The influence of the size of the device on the time taken for the recorded temperature to stabilise was assessed using a Student's unpaired t-test with Welch correction.

3.3.2 Differences in temperature along the gastrointestinal tract

The null hypothesis was that the gastrointestinal tract is isothermal (differences in temperature between regions of the gastrointestinal tract not exceeding 0.1°C). I have used the Bland-Altman method (Bland & Altman, 1986) to assess whether the measurements recorded by the two data loggers ingested by an elephant five hours apart support the null hypothesis. The difference in the temperatures recorded by the two devices was determined for each five-minute measurement (from the point that the two devices had stabilised). The mean difference (*bias*) and 95% limits of agreement were then calculated. Using values deemed to be acceptable by other researchers assessing sites of body temperature measurement (Gant *et al.*, 2006; Byrne & Lim, 2007; Casa *et al.*, 2007; Eigenberg *et al.*, 2008) as a guide, I decided that a bias greater than 0.15°C would not be acceptable.

3.4 Results

3.4.1 Ingestion, retrieval and transit times of devices

Table 3.1 provides a summary of the devices swallowed by the elephants and retrieved from the faeces. The bare data loggers and the loggers with ribbon were swallowed easily by the elephants, but neither of the bare data loggers were found. The loggers with ribbon attached were easy to find in the faeces, the bright colour of the ribbon aiding the retrieval.

The elephants often chewed and expelled the data logger and transmitter combination. For those logger plus transmitter combinations which were swallowed by elephants, a signal from the smaller transmitter could be detected when the radio receiver was held next to the elephant's abdomen, but the signal was intermittent. The batteries used to power these small transmitters failed after about ten days. The first device of this design which was swallowed by an elephant was retrieved after about five days and failure of the battery, therefore, was not a problem. However, the three other devices of this design which were swallowed by elephants were not expelled before their batteries had run flat. The elephants' faeces were searched for about two weeks after the signal from the transmitter had disappeared, but only one of these devices was found. To improve the strength of signal transmission, a different transmitter was used and to extend the length of time that the

Table 3.1 Summary of the number of devices fed to, swallowed by, and retrieved from the four elephants. The transit times of the retrieved data loggers are given as medians (±SD), except for Device A (none retrieved).

Thermometric device	Number of thermometric devices:			Transit time (h)
	Fed to elephants	Successfully swallowed	Retrieved	
A (Logger)	2	2	0	*
B (Logger + transmitter)	12	7	3	500 ± 240
C (Logger + ribbon)	12	11	9	40 ± 36

* devices not recovered after 52 hours.

transmitter would emit a signal, a larger battery was used (hereafter referred to as "large transmitter"). Attached to the new battery, the transmitter emitted a signal which could be detected by the receiver up to twenty meters away from the elephant. However, because of the increase in size, only two of these larger devices were ingested.

The median gut transit times for the devices are given in Table 3.1. An estimate of minimum transit time is given for the two bare data loggers since neither of the loggers were found. All except one of the loggers which had ribbon attached and which were swallowed were retrieved and the transit time ranged from 18 to 127 hours, while the range for the three data logger and transmitter combinations was markedly wider, one device taking 94 hours and the two others taking approximately 504 hours. One of the logger and transmitter combinations (large transmitter) remained in the elephant's gastrointestinal tract for at least four months, at which point the signal from the transmitter was lost and the device was not retrieved. A test device kept in the laboratory continued to transmit a signal after five months of continuous use.

None of the elephants experienced adverse side-effects or exhibited any signs of distress or discomfort after ingesting any of the devices (even after four months, in the case of the device mentioned above). None of the devices which were retrieved showed any signs of external damage. All data loggers were successfully downloaded and no data points were missing from the data set.

3.4.2 Thermal inertia of devices

The results of the thermal lag experiment are illustrated in Figure 3.2. The bare logger (Device A) was the first of the devices to reach bath temperature (3.5 minutes), the logger with ribbon attached (Device C) was the next to reach the correct bath temperature (14.0 minutes), followed by the logger and large transmitter combination (20.5 minutes). Once the data loggers had attained bath temperature, the recorded temperature did not change.

3.4.3 Stabilisation of logger temperature within the gastrointestinal tract

The mean (±SD) temperature recorded by loggers in Device B ($n = 3$) and Device C ($n = 9$) during the 480 minutes after ingestion are shown in Figure 3.3. For 90 to 375 minutes after swallowing, the recorded temperature fluctuated quite widely. The temperatures recorded by the logger in Device B ranged from a mean minimum of 26.8 ± 3.2°C to a mean maximum of 36.5 ± 0.2°C. The temperatures recorded by the logger in Device C ranged from a mean minimum of 23.1 ± 6.5°C to a mean maximum of 36.5 ± 0.4°C. Device B took an average of 123 ± 33 minutes to stabilise while the smaller Device C took an average of 234 ± 99 minutes, a difference which was statistically significant ($t = 2.8$, $p = 0.02$). The temperature of all data loggers stabilised within 360 minutes.

3.4.4 Differences in temperature along the gastrointestinal tract

An elephant was given two devices (both Device C: logger + ribbon), about five hours

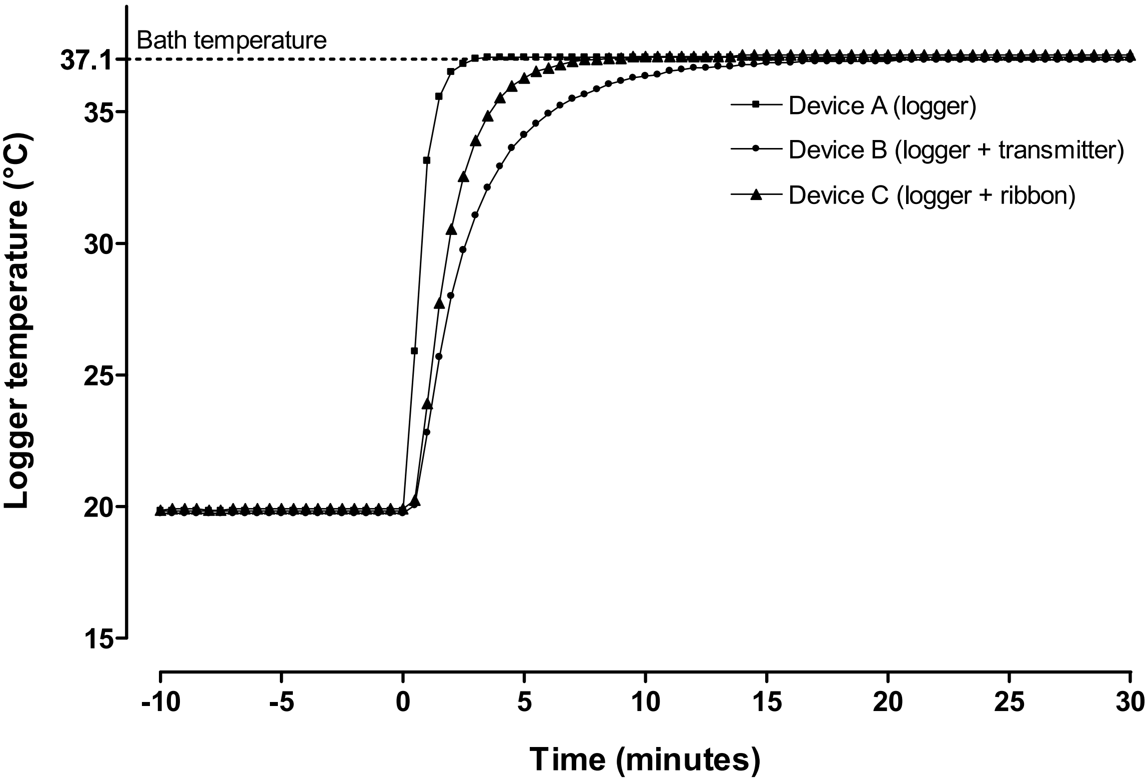

Figure 3.2 The length of time taken for each of three types of device to reach 37.1°C in an insulated water bath. Time zero represents the time of first immersion in the bath.

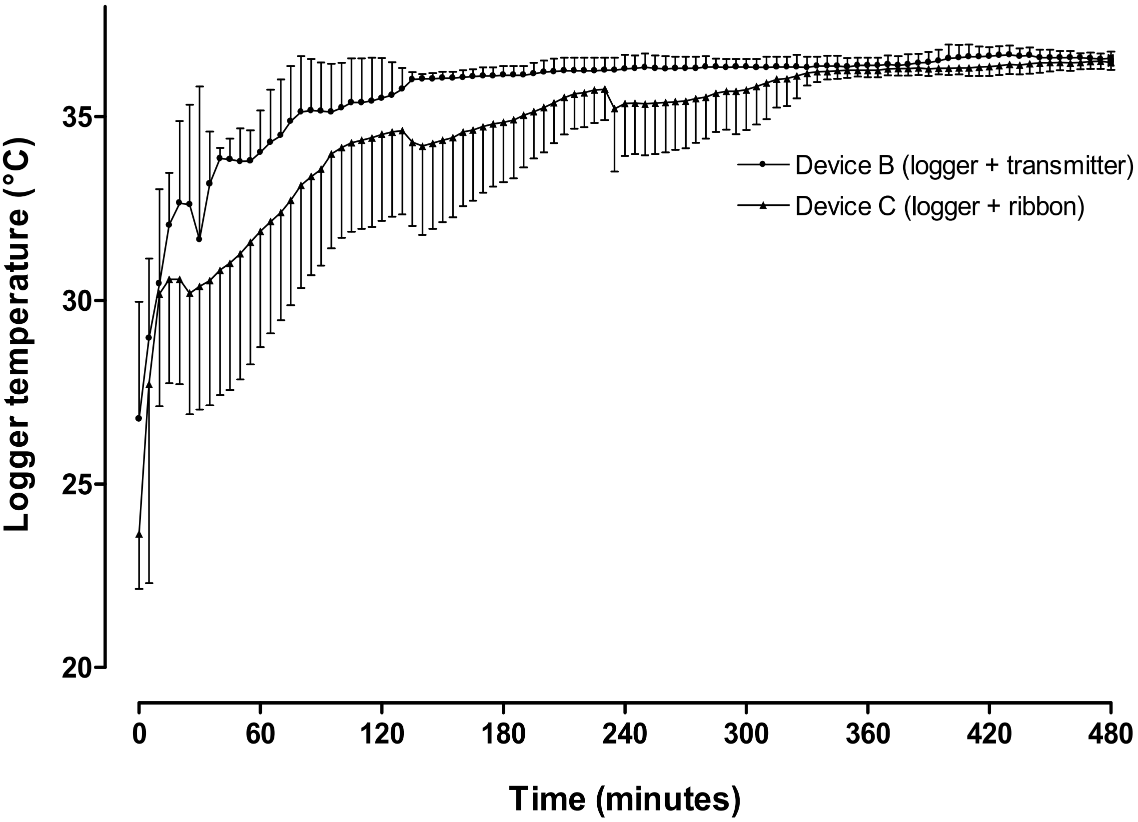

Figure 3.3 Mean (±SD) temperature recorded by Devices B and C during the first 480 minutes after ingestion (Device B: n = 3; Device C: n = 9).

apart, in order to record simultaneous measurements of temperature at different points along the gastrointestinal tract. The data (post-calibration) recorded by the loggers in these two devices are illustrated in Figure 3.4. The large decrease in temperature recorded by the first logger at about 13:00 was caused by the ingestion of water, which I observed, since the device had most likely not yet exited the elephant's stomach. Both loggers were found together in the faeces, 19.5 hours (first logger) and 14.5 hours (second logger) after ingestion. From the time the second logger had stabilised (about 19:20) until both loggers were expelled, 101 simultaneous data points were recorded (illustrated in the lower panel of the figure). The first logger tended to record a slightly higher temperature than the second; the bias was 0.10°C and the 95% limits of agreement were -0.06°C and 0.26°C.

The absolute differences in temperature recorded by the two loggers were grouped into classes (the width of the classes was determined by the accuracy of the data logger; that is, 0.06°C). More than two-thirds (69%) of the differences were less than 0.12°C (and were less than 0.15°C, the maximum acceptable difference stated in section 3.3.2). Almost all (98%) of the differences were less than 0.24°C. The largest difference between the temperatures was 0.29°C but was represented by only two points (indicating a period of ten minutes).

I then compared the temperatures recorded by the two data loggers by standardising the time of their passage through the gastrointestinal tract (Figure 3.5). The fit between the traces was not improved, indicating that their rates of passage along the gastrointestinal tract differed.

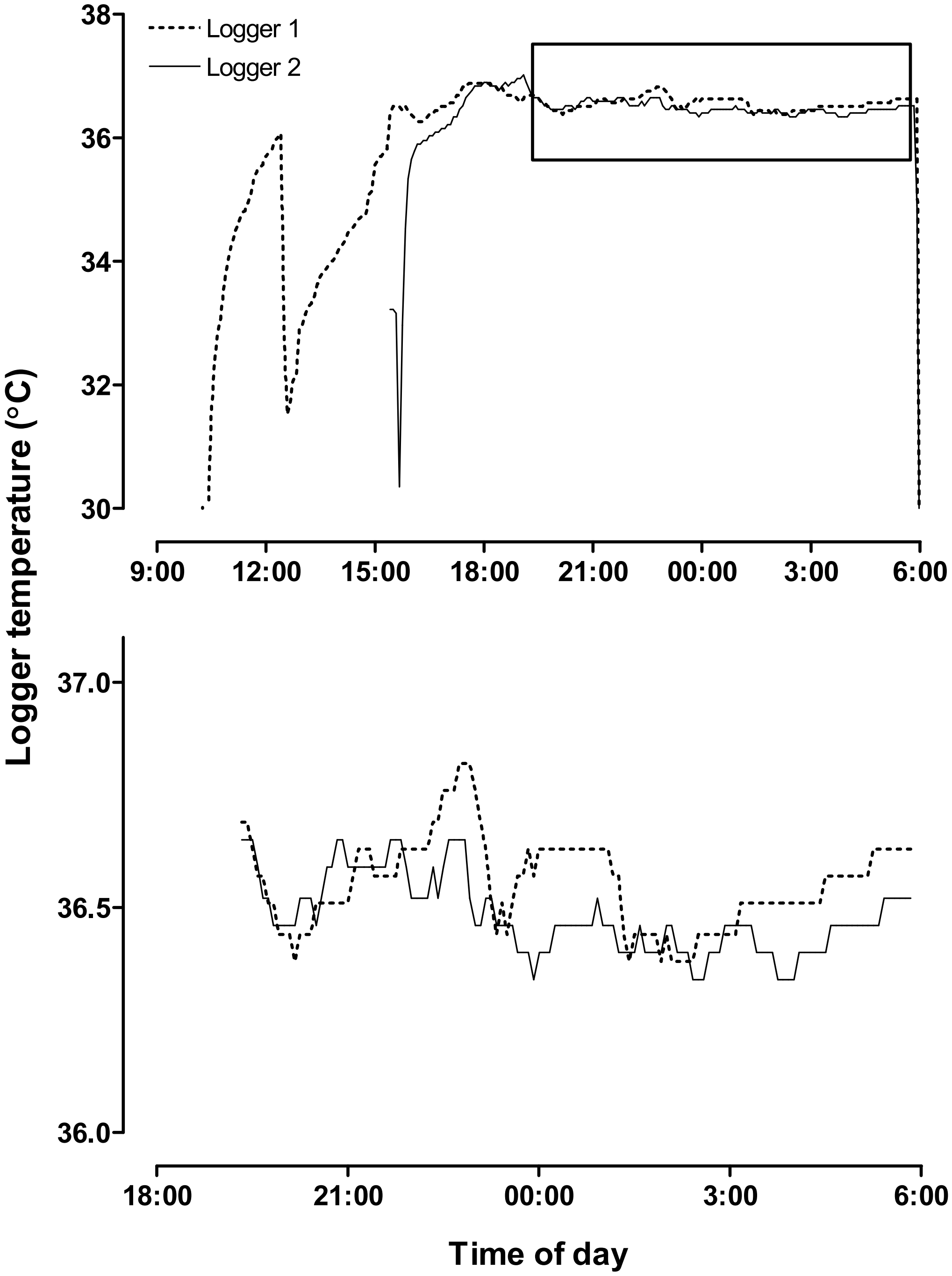

Figure 3.4 The temperatures recorded by two loggers (both Device C) given to an elephant five hours apart, from the time of ingestion of the first device until expulsion of both from the gastrointestinal tract (upper panel). An enlargement of the portion demarcated by the rectangle is given in the lower panel and shows the temperatures recorded by the two loggers from the time the second logger had stabilised until immediately before the loggers were expelled.

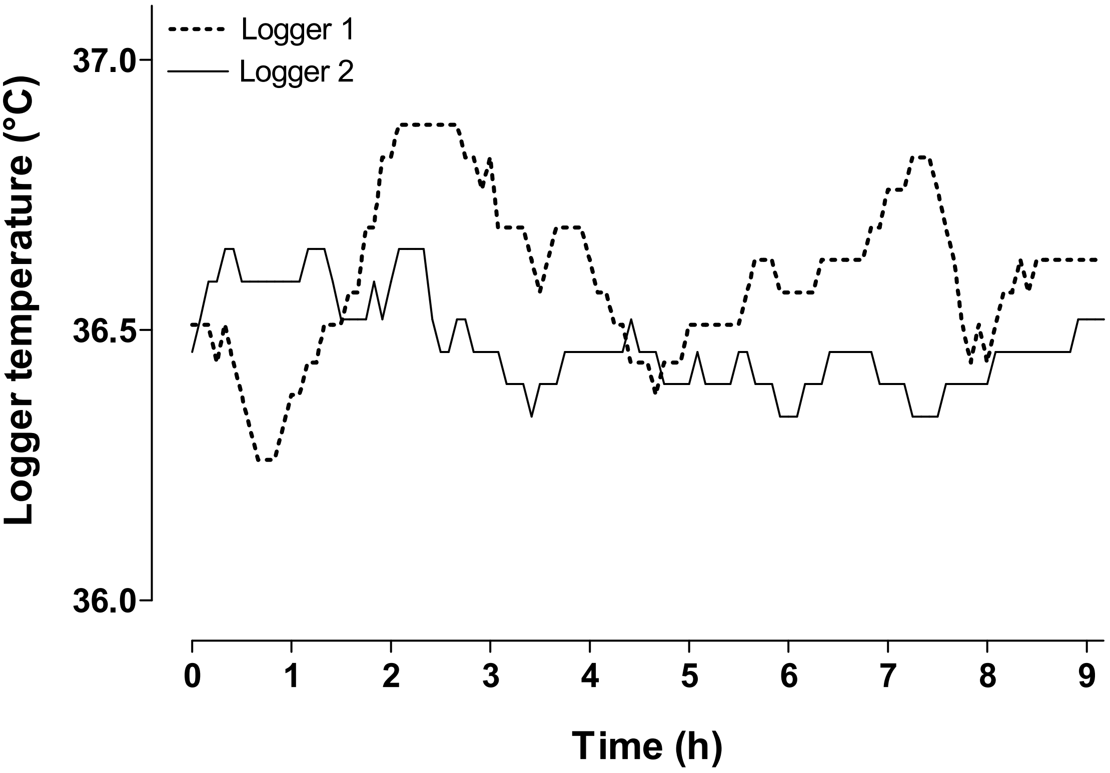

Figure 3.5 Temperatures recorded by the two data loggers ingested five hours apart by an elephant, with the time standardised. If the two loggers transited the gastrointestinal tract at the same speed, then both loggers would have been at about the same position in the gastrointestinal tract at each point in time.

To assess whether the recorded temperature of an ingested device changed in a systematic manner over the course of several days, thirteen consecutive days of body temperature data (recorded in an elephant by a single device) were plotted on the same set of axes (Figure 3.6). The differences in body temperature between days were mostly small (mean standard deviation of temperature across days = 0.14°C) and the daily 24 h pattern was consistent despite wide changes in ambient temperature (black globe temperature exhibited a mean daily amplitude of about 30°C during this period). The patterns of elephant body temperature, and the influence of environmental temperature on body temperature, are discussed in greater detail in Chapter 4. There was no systematic increase or decrease in temperature across days. The greatest variability occurred between 6:00 and 7:00, which was likely to have been the consequence of differences in behaviour. The sources of variability of elephant body temperature are addressed in Chapters 4 and 5.

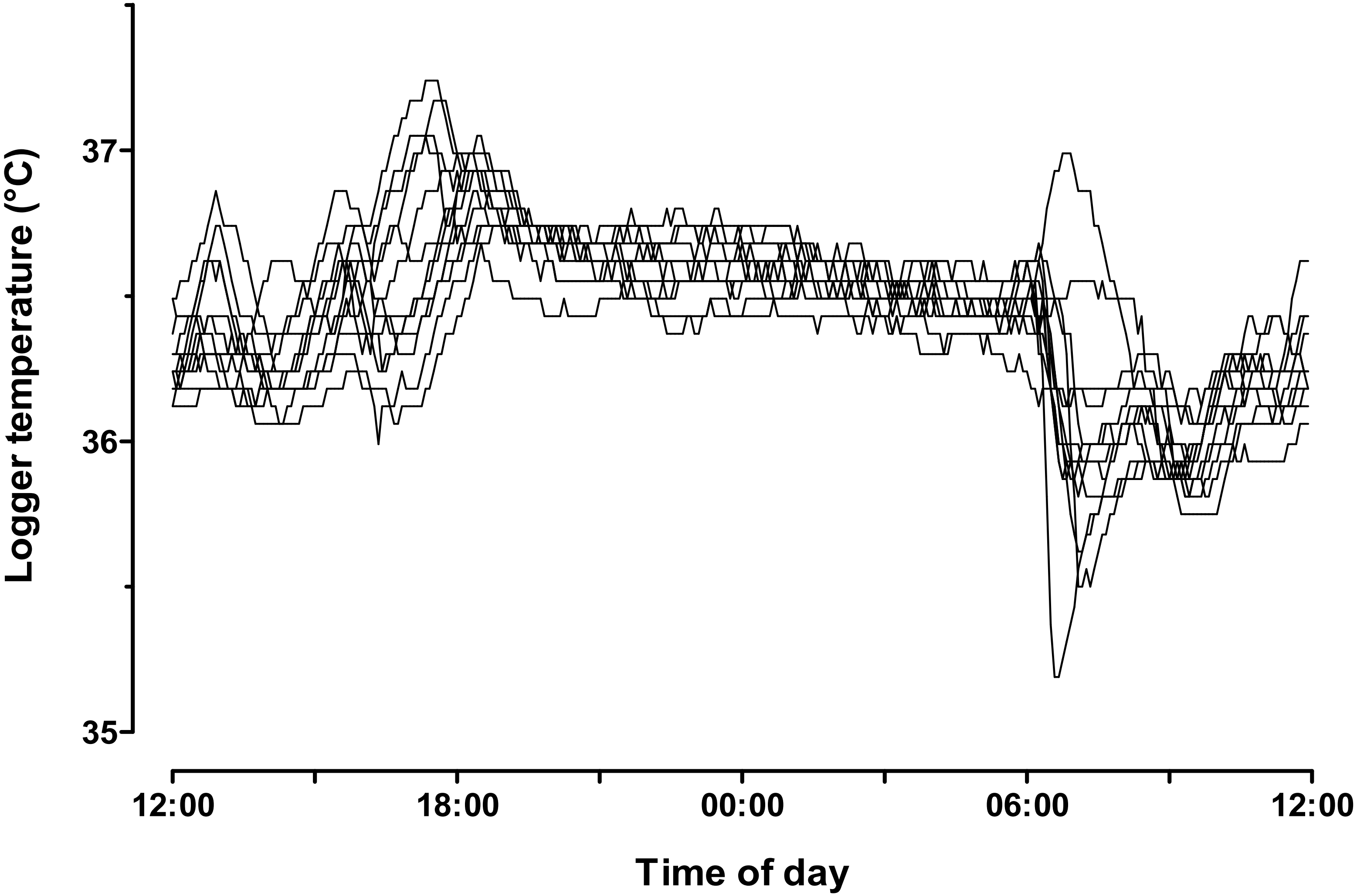

Figure 3.6 Body temperature of a single elephant, recorded in the gastrointestinal tract by a single data logger, over thirteen consecutive days. Each line represents a single day (24 h), starting and ending at 12:00 (midday).

3.5 Discussion

The aim of this chapter was to report the investigation of the use of ingestible data loggers to record continuous measurements of body temperature in tame, semi free-living African elephants. I tested four different designs of ingestible device on four elephants and found that the size of an ingestible device is one of its most important characteristics. The size of a device affects the ease with which an animal can swallow it, the transit time through the gastrointestinal tract, and the ease of retrieval. The most successful design involved securing a length of ribbon to a data logger covered in wax. This device was small and was swallowed easily by the elephants, but was relatively easy to locate in the faeces because of the ribbon. However, the ribbon decreased the transit time, relative to the large devices, reducing the number of data points recorded by a single logger. Despite a greater thermal inertia, the larger devices stabilised faster in an elephant's gastrointestinal tract than the smaller ones, but this may be due to the small number of large devices tested. Once the temperature of any of the ingested devices had stabilised, the logger reliably recorded body temperature, without the loss of data points and within the range of body temperatures previously reported for elephants. The position of a logger along the gastrointestinal tract did not significantly influence the temperature recorded and did not result in a difference in the 24 h pattern of elephant body temperature.

The acceptability of measurements made in the gastrointestinal tract was a concern. I did not compare gastrointestinal temperature with any traditionally-accepted measurements of core body temperature such as arterial blood temperature and, therefore, I cannot conclude whether it is an acceptable substitute for such measurements of body temperature in elephants. However, I found no systematic bias in temperature along the gastrointestinal tract; neither in temperatures recorded by two loggers simultaneously, nor in temperatures recorded by a single data logger on consecutive days. Therefore, I concluded that the repeatability of measurements made in the gastrointestinal tract were acceptable.

One of the more immediate concerns arising from the use of gastrointestinal temperature was the recovery of ingested devices. Elephants defecate roughly every hour and produce large amounts of faeces, making the search for devices a time-consuming process. In their study of the body temperature of zoo elephants, Kinahan and colleagues (2007a) sewed miniature loggers into a pocket of rip-stop nylon. They then attached a 300 mm “strand of trailing material” to the pocket to aid retrieval, a technique which proved very successful. By a process of trial and error I independently arrived at a similar solution and found that the attachment of a length of brightly-coloured satin ribbon greatly improved the chances of retrieval. One of the key differences between Kinahan and colleagues’ study and mine is that I worked with animals not confined to a small enclosure. I might not have witnessed every defecation by the instrumented animals, especially when the herd was out browsing in the reserve, which may explain why not all of the devices were found.

I had hoped that the inclusion of a tracking transmitter would reduce the number of devices lost. The transmitter enabled me to determine whether the ingested device had been expelled by the elephant or not; if a signal could no longer be detected from within the animal, I could return to the area in which the animals had been and try to locate the device on the ground. However, even with the aid of a tracking transmitter, there were occasions when checking the faeces passed by the elephants was not possible. For example, the elephants would sometimes go swimming in the dam and would defecate in the water. I was unable to search the dam for any of the devices, either by hand or by using the radio receiver. The tracking transmitter therefore did not guarantee retrieval and, due to the resultant increase in size, the elephants were less willing to swallow the devices.

For any of the devices to be of value they had to be ingested easily and without damage. The larger devices usually were chewed, even when placed at the back of the tongue and administered with a constant stream of water. Kinahan and colleagues (2007a) inserted their loggers into apples which then were placed into the elephants' mouths. The elephants with which I worked tended to chew devices placed into an item of food, but swallowed the smaller devices when they were placed at the back of the tongue and given with water. The best technique of "feeding" a device to a study animal will depend largely on the training the animals have received as well as the training and experience of the animals' handlers. Generally, wild animals cannot be handled without sedation. Due to the relatively short transit times of devices, animals may need to be instrumented repeatedly and, therefore, wild animals may need to be repeatedly captured and sedated. For this reason it is unlikely that ingestible data loggers could be used in wild animals, unless one can find a way of persuading the animal to ingest the loggers without one having to handle it.

Unpredictable transit times also may complicate the use of ingestible data loggers. If the researcher is unable to anticipate the time of expulsion, the retrieval of devices is less likely. A tracking transmitter may aid the location of an ingested device, but transit times may remain unpredictable. Although one of the transmitter and logger combinations that I retrieved transited the gastrointestinal tract in five days, the other two devices only were expelled after about three weeks (one of these devices included the larger battery, and the other included the smaller battery). One of the transmitter and logger combinations (with the larger battery) remained in the gastrointestinal tract for at least four months, revealing another disadvantage resulting from the increase in size. Removing the transmitter and attaching a length of ribbon markedly reduced the mean gut transit time of the device. Kinahan and colleagues (2007a) and Toscano (2001) both used very similar devices to my small device and made similar observations regarding the gut transit time. Toscano, however, experienced a much wider range of transit time (12 hours to 4 months) and more than half (about 68 out of 109 loggers fed to elephants) of his loggers never were found. He suggested that the longer transit times were due to retention of the logger in the caecum or the rectum. Toscano attached a 150 mm length of nylon ribbon which he embedded in a layer of epoxy covering the data logger. Longer pieces of ribbon, such as those used by Kinahan and colleagues (2007a) and me, probably became entangled in the fibrous food matter consumed by the elephants. As a result, the ribbon reduced the risk of the device becoming lodged in the gastrointestinal tract and in so doing, reduced the transit time. By reducing the transit time, the ribbon increased the chances of retrieval of the device, as there were fewer occasions that the dropping of faeces could be missed by the observer.

Although a long piece of ribbon increases the chances of retrieval of a device, shorter transit times reduce the amount of data collected by a single data logger. If, for the purpose of an investigation, data must be recorded for longer periods of time, several devices would have to be administered to study animals at regular intervals (Toscano, 2001; Green *et al.*, 2008). The ingestion of several devices by a study animal affords the added advantage of an increased chance of at least some of the devices being retrieved.

Kinahan and colleagues (2007a) experienced similar rates of retrieval of devices to those I observed with my study animals. Kinahan *et al.* fed 40 loggers to four zoo elephants and 38 were retrieved. However, the data from 32 of these loggers could not be downloaded despite there being no signs of external damage. Water may have entered the casing and damaged the electronics, as the nylon Kinahan *et al.* used may not have been waterproof. The gastrointestinal tract presents a harsh environment and an ingestible device must be able to withstand immersion in various gastrointestinal fluids. Except for the first two data loggers given to an elephant, I coated all of my devices in several layers of wax. Of the 12 devices which I retrieved from the elephants, none of the data loggers were damaged and none of the data were corrupted.

The only data which could not be used were the data recorded during the initial stabilisation period. For about the first six hours after ingestion, the data loggers recorded large fluctuations in temperature and these temperatures cannot be considered to represent true body temperature. Following this period the loggers were less sensitive to changes in temperature caused by the ingestion of food or water and I assume that at this point the devices had exited the stomach. In their study, Kinahan and colleagues (2007a) concluded that the data loggers remained in the stomach for an average of four and a half hours (with a range of two to nine hours). Data from a number of studies using ingestible telemeters in humans suggest a six-hour stabilisation period (Byrne & Lim, 2007). I am confident that the initial period required for the devices to stabilise in the gastrointestinal tract was not due to an insulating effect of the wax coating, or anything else affecting thermal inertia, since the devices I used displayed time constants well within six hours, including Device B (logger plus transmitter) which took the longest time to reach the correct bath temperature. When ingested by the elephants, Device B stabilised sooner than the smaller Device C but it may be that too few of the large devices were assessed (and that the test lacked statistical power). Alternatively, although I cannot be certain, the difference in time taken to stabilise might have been due to slower passage of Device C through the stomach. The average decrease in temperature recorded by Device C around 240 minutes was not observed for all devices of this design. A skew in the data was caused by one logger in particular which recorded a large decrease in temperature resulting from the ingestion of water by the elephant around that time. Once stabilised, the temperatures recorded by all the devices used showed a consistent pattern of elephant body temperature.

The pattern of body temperature recorded for the elephants appeared to be consistent across days and between elephants regardless of the type of device used. However, it was still possible that differences in temperature along the gastrointestinal tract could account for some of the variability in the body temperature data. In a study conducted in dogs, differences in temperature of up to 0.3°C were shown to exist between some regions of the gastrointestinal tract (Durotoye & Grayson, 1971). In humans, no consistent differences along the gastrointestinal tract have been observed, but the need for further investigation has been identified (Byrne & Lim, 2007). To investigate the possibility of differences along the gastrointestinal tract of my study animals, I gave two devices, several hours apart, to an elephant to swallow. To assess whether the differences in the temperatures recorded by the two loggers were acceptable or not I used, as a guide, the criteria for agreement between sites of temperature measurement stated by several other investigators. In a review of studies validating the use of ingestible telemeters in humans, the authors determined that the mean difference (bias) between measurements made in the gastrointestinal tract and other sites such as the rectum or oesophagus should not exceed 0.1°C and that the 95% limits of agreement should be no greater than 0.4°C (Byrne & Lim, 2007). In a review of similar work conducted in swine and cattle, the authors referred to "precision measurements" as having an accuracy of at least 0.1°C (Eigenberg *et al.*, 2008). On the basis of these and other studies, I decided that the mean difference between the temperatures recorded by the two loggers should not exceed 0.15°C. The majority of the differences between the simultaneously recorded gastrointestinal temperatures were less than 0.15°C, and I concluded that the mean difference of 0.1°C observed in my study was acceptably small, as were the 95 % limits of agreement.

Since the two devices were expelled by the elephant simultaneously, the second logger given to the elephant must have caught up with the first somewhere along the gastrointestinal tract, but it is not clear when this occurred. It may be that the first data logger had not yet exited the stomach when the second was given to the elephant. It is also possible that the first data logger was retained in the rectum and the second logger caught up with it there. It seems that the two loggers did not transit the gastrointestinal tract at the same speed since when the data were adjusted for the time difference, the fit between the two temperature curves was not improved. Had the two loggers travelled at the same speed, they would have passed through similar points along the gastrointestinal tract at each point in time, and should have recorded similar temperatures. However, this was not the case. The phenomenon of differential transit would be worth exploring further, but is beyond the scope of my dissertation.

I am unable to draw a firm conclusion from the data recorded simultaneously by two data loggers, but the data obtained over thirteen consecutive days offers further support for the consistency of temperature along the gastrointestinal tract. Bacteria within the gastrointestinal tract produce heat by fermentation, especially in the caecum and large intestine (Benedict, 1936; van Hoven *et al.*, 1981), and one might expect an increase in the temperature recorded by a logger as it enters these regions. However, I observed no systematic increase or decrease in temperatures recorded a week apart, although the device would most likely have been in quite different regions of the intestinal tract.

The consistency of the pattern of elephant body temperature supports the repeatability of measurements of temperature made in the gastrointestinal tract, but the question of whether the gastrointestinal tract can be considered to be an acceptable site for the measurement of core body temperature remains. In dogs the gastrointestinal tract produces a large amount of metabolic heat and its temperature may exceed that of aortic blood (Durotoye & Grayson, 1971). An investigation of core temperature measurement in horses concluded that gastrointestinal temperature was an acceptable site for core temperature measurement

(Green *et al.*, 2005), and validation studies conducted in swine (Brown-Brandl *et al.*, 2003) and cattle (Prendiville *et al.*, 2002) have drawn similar conclusions. However, comparisons were made with measurements made in the rectum or jugular vein, not in the oesophagus or pulmonary artery, the two sites considered to most accurately represent "core" body temperature (Brengelmann, 1987).

In their review, Byrne and Lim (2007) cited six studies conducted in humans which compared intestinal temperature with oesophageal and rectal temperature. Five of these studies concluded that intestinal temperature was a suitable measure of core temperature. Intestinal temperature tended to be slightly higher than oesophageal temperature and did not respond as quickly to changes in core body temperature but responded faster than did rectal temperature. Consequently, the reviewers concluded that intestinal temperature may be as good as, if not better than, rectal temperature as a measure of core body temperature (Byrne & Lim, 2007). It is unlikely that there is a difference in temperature across the gastrointestinal wall, and therefore, gastrointestinal and abdominal temperature would be virtually the same.

Abdominal temperature has been used often as a measure of core temperature in studies of free-living animals (Craighead *et al.*, 1976; Sargeant *et al.*, 1994; Fuller *et al.*, 2005; Ostrowski & Williams, 2006; Hetem *et al.*, 2008). However, abdominal temperature recorded in a large mammal, the eland (*Tragelaphus oryx*), differed from arterial blood temperature by as much as 1°C at times, and also was more variable (Fuller *et al.*, 1999a). Therefore, although it is widely used as a measure of core temperature, one must bear in mind when using abdominal temperature the fact that it is not a perfect substitute for measurements of core temperature such as arterial blood temperature in animals of very large body size. Whether or not abdominal temperature is an acceptable alternative to arterial blood temperature as a measure of core temperature in animals of elephantine proportions remains to be established.

Chapter 4

The body temperature of African elephants

4.1 Introduction

Due to a small surface area to volume ratio, large animals have a large thermal inertia, and one expects that the amplitude of body temperature variation is reduced as a result (Aschoff, 1982; Mortola & Lanthier, 2004). Since the African elephant is the largest extant terrestrial mammal, the variations of its body temperature are of interest. To understand how elephant body temperature varies over the course of 24 h, continuous measurements of body temperature are required, preferably in individuals that are living in their natural habitat and that are free to employ natural thermoregulatory behaviour (Fuller *et al.*, 1999a).

An understanding of what “normal” body temperature is, and of the factors influencing the variations of body temperature is important, as the rhythm of body temperature is known to affect several key biological functions, including reproduction (Refinetti & Menaker, 1992). Also, an understanding of how an animal regulates its body temperature, and hence its thermoregulatory requirements, is important in understanding the animal’s use of its habitat. An animal’s thermoregulatory demands may affect the animal’s ability to engage in other behaviour such as foraging and it is crucial that conservationists incorporate knowledge of such needs when making management decisions.

There is some understanding of elephant thermoregulation, but several of the studies conducted on African elephants previously did not include measurements of body temperature. Measurements of temperature which have been made mostly were discontinuous, and were recorded in elephants not living in their natural habitat. Continuous measurements of body temperature have not been made in unrestrained elephants living in Africa until recently, and those that have been made have been restricted to zoo elephants over a limited range of environmental conditions (Kinahan *et al.*, 2007a). Also, the short-term variations in body temperature were not assessed, and there were insufficient data to determine the relationship between body temperature and environmental temperature.

By measuring body temperature in elephants living in their natural habitat, with minimal restrictions on their natural behaviour during the day, I aimed to:

1. describe the 24 h pattern of body temperature of African elephants using the mean, minimum, maximum and amplitude, and to assess the magnitude and frequency of short-term variations in body temperature.
2. assess the influence of environmental temperature on elephant body temperature.

4.2 Materials and methods

4.2.1 Study site and animals

Refer to Chapter 2 for details of study site and animals.

4.2.2 Climatic data

Refer to Chapter 2 for details of how climatic data were recorded. The study period was divided into three climatic periods, namely cold, warm, and hot (see section 2.5).

4.2.3 Body temperature measurement

Data loggers were programmed to record body temperature at five-minute intervals at a resolution of 0.06°C. Loggers were given to the elephants to swallow and once a logger was ingested successfully, no further loggers were offered to that individual. I attempted to instrument two animals during each period of data collection, but my attempts were not always successful. Also, an attempt was made to inspect all faeces from about 12 hours after the ingestion of loggers, but there were occasions when it was not possible to check the faeces and some of the data loggers were lost over the duration of the study (refer to Chapter 3 for further detail regarding the use of data loggers to record elephant body temperature). Loggers were fed to, and retrieved from, elephants in each of the three climatic periods. For a summary of the number of data loggers fed to elephants, as well as the number successfully ingested by and retrieved from each elephant, during each of the climatic periods, see Table 4.1.

4.3 Data analysis

4.3.1 Climatic data

To assess differences in the 24 h pattern of environmental heat load between the three climatic periods, mean black globe temperatures were plotted against time of day for each period. I used only black globe temperatures recorded on days when body temperature was recorded.

4.3.2 Body temperature data

Description of body temperature

A total of 26 data loggers was given to elephants to swallow; 20 were ingested and 12 were retrieved (Table 4.1). Not all four elephants were given data loggers in all three climatic periods. Body temperature data were recorded for all four elephants during the longer hot period. However, due to a transit time of less than 20 hours for the loggers fed to Elephant 3, data were incomplete for this animal during the hot period.

Table 4.1 Summary of the number of data loggers, of all designs, fed to, ingested by, and retrieved from each elephant during each climatic period (cold, warm and hot) of the study.

Elephant	**Cold**			**Warm**			**Hot**		
	Given	**Swallowed**	**Retrieved**	**Given**	**Swallowed**	**Retrieved**	**Given**	**Swallowed**	**Retrieved**
Ele 1	-	-	-	-	-	-	5	5	2
Ele 2	3	1	1	-	-	-	2	2	1
Ele 3	4	3	1	2	2	2	5	2	2
Ele 4	-	-	-	1	1	1	4	4	2
Total	7	4	**2**	3	3	**3**	16	13	**7**

Each set of body temperature data was inspected and data recorded prior to logger stabilisation were excluded (as described in Chapter 3). Consecutively recorded days of data were sorted into 24 h periods, to avoid bias resulting from a greater number of data points recorded at a particular time of day. I used 24 h periods from 12:00 to 12:00 in order to maximise the use of data, since data loggers were usually ingested early in the morning.

All data points contained within all 24 h periods were used to construct a frequency distribution of body temperature for each elephant. The width of the classes was determined by the calibrated accuracy of the data logger (0.06°C). The frequency of body temperature values in each class then were expressed as a percentage of the total number of values recorded for each elephant.

To characterise the body temperature of each elephant, the 24 h mean, as well as the mean daily minimum, mean daily maximum and mean daily amplitude of body temperature were calculated for each elephant for each climatic period. The time at which the minimum and maximum temperature occurred each day was determined and the mean calculated for each elephant for each period. The mean body temperature indices (mean, minimum, maximum and amplitude) then were calculated for each elephant across climatic periods. The number of days of data recorded for each climatic period differed and to avoid a bias toward any particular climatic period, a weighted mean was calculated using the following formula:

$$\text{Weighted mean} = \frac{(\sum x/SE^2)}{(\sum 1/SE^2)}$$

The standard errors of the weighted means (SEM) also were calculated, using the following formula:

$$\text{SEM of weighted mean} = \left| \frac{\Sigma(1/SE^2)x^2 - (\Sigma(1/SE^2)x)^2/\Sigma(1/SE^2)}{(n\text{-}1)\ \Sigma(1/SE^2)} \right|^{0.5}$$

To determine the mean 24 h pattern of body temperature for each elephant, half-hourly means were calculated for each day recorded for each elephant and the mean for each 30-minute interval was calculated across all days recorded for each elephant. These mean values then were plotted against the mid-point of each 30-minute period to provide a mean 24 h trace of body temperature for each elephant (note that the standard deviations represent the variation between days, not within each 30-minute period). The data were plotted from 00:00 to 23:55.

From each elephant's curve, the 30-minute mean value for each time point was used to calculate the mean body temperature pattern for the four elephants (n = 4, standard deviations represent the variation between elephants at each 30-minute interval). The trace was then double-plotted.

Relationship between environmental and body temperatures

To assess whether there was a difference in elephant body temperature across the three climatic periods, the data recorded for all elephants in each climatic period were combined and a weighted mean, together with the standard error, was calculated for each of the body temperature indices (mean, minimum, maximum and amplitude) using the equations given previously.

To determine whether elephant body temperature was related to daily environmental heat load, daily mean body temperature data were plotted against the corresponding daily mean black globe temperature. The 24 h minimum, maximum and amplitude of the two variables also were plotted against each other; 24 h periods were started at 00:00 and ended at 23:55 so that daytime periods would not be divided in half. I had a sufficient number of 24 h periods to conduct correlation analyses for Elephant 4 only (hot period data only, n = 12 days). All plots were analysed using Pearson's product-moment correlation. The same process was repeated for the analysis of the relationship between elephant body temperature and air temperature.

To determine whether elephant body temperature was related to black globe temperature over the course of a 24 h period, all body temperature data recorded on the hour or half-hour, including the data not included in complete 24 h periods, were matched to the corresponding black globe temperature and the two values plotted against each other. A separate plot was constructed for each elephant. All plots were analysed using Pearson's product-moment correlation. An analysis of the relationship between elephant body temperature and air temperature was conducted in the same way.

Short-term changes in body temperature

The short-term changes in elephant body temperature were assessed by calculating the change in temperature from one five-minute record to the next. I wanted to assess the relative proportions of short-term changes and, since large changes were not evenly distributed across 24 h, only data from complete 24 h periods were used to avoid bias. The changes were calculated and then grouped into classes (0.06°C wide) for each elephant. The number of values in each class then was calculated as a percentage of the total number of changes determined for each elephant to provide an understanding of the relative occurrence of changes of differing magnitude. Changes over ten-minute intervals were assessed in a similar manner.

4.4 Results

4.4.1 Climatic data

Figure 4.1 illustrates the average 24 h pattern of black globe temperature for each of the three climatic periods (cold: n = 9 days; warm: n = 4 days; hot: n = 23 days). During the hot period environmental heat load began to rise from fairly early in the morning, steadily increased until around midday, and gradually decreased until the late afternoon, from which time the environmental heat load rapidly decreased. In the warm and cold periods the environmental heat load peaked at about the same time of day as in the hot period. However, in the cold and warm periods the heat load tended to start increasing later in the morning and began to decrease earlier in the afternoon than during the hot period. The differences in black globe temperature between the hot and cold periods ranged from about 9 to 20°C. The range of globe temperature during the cold period was -1 to 39°C, and during the hot period was 12 to 52°C.

4.4.2 Body temperature data

The frequency distributions for the body temperature data for each elephant are shown in Figure 4.2. I fitted Gaussian curves, using curve-fitting software (TableCurve 2D for Windows, v3.05), to each of the distributions and found that the fit was good for the data recorded for each elephant (all r-squared values were greater than 0.9). I concluded therefore that the data were normally distributed. The absolute minimum that I observed

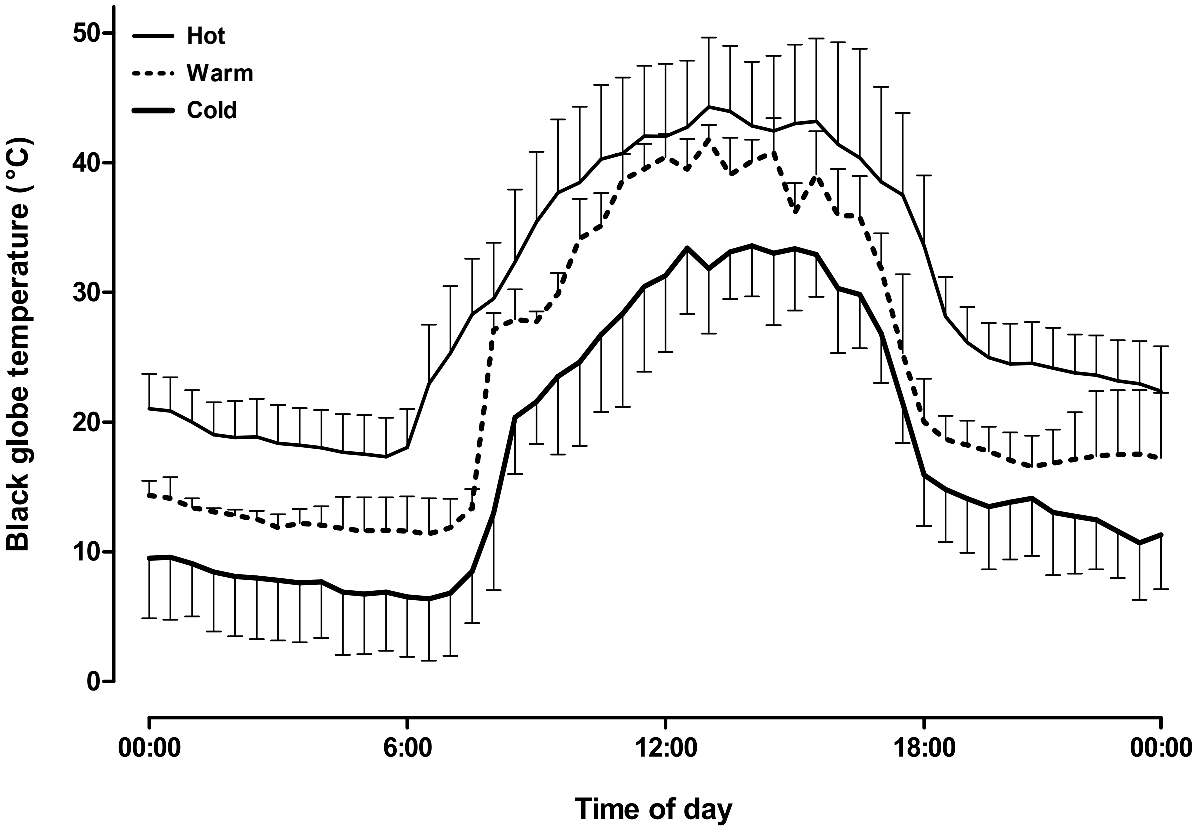

Figure 4.1 Mean 24 h trace of black globe temperature for days when body temperature data were recorded during the hot, warm and cold periods. Cold period: n = 9 days, warm: n = 4 days, hot: n = 23 days. Error bars represent one SD.

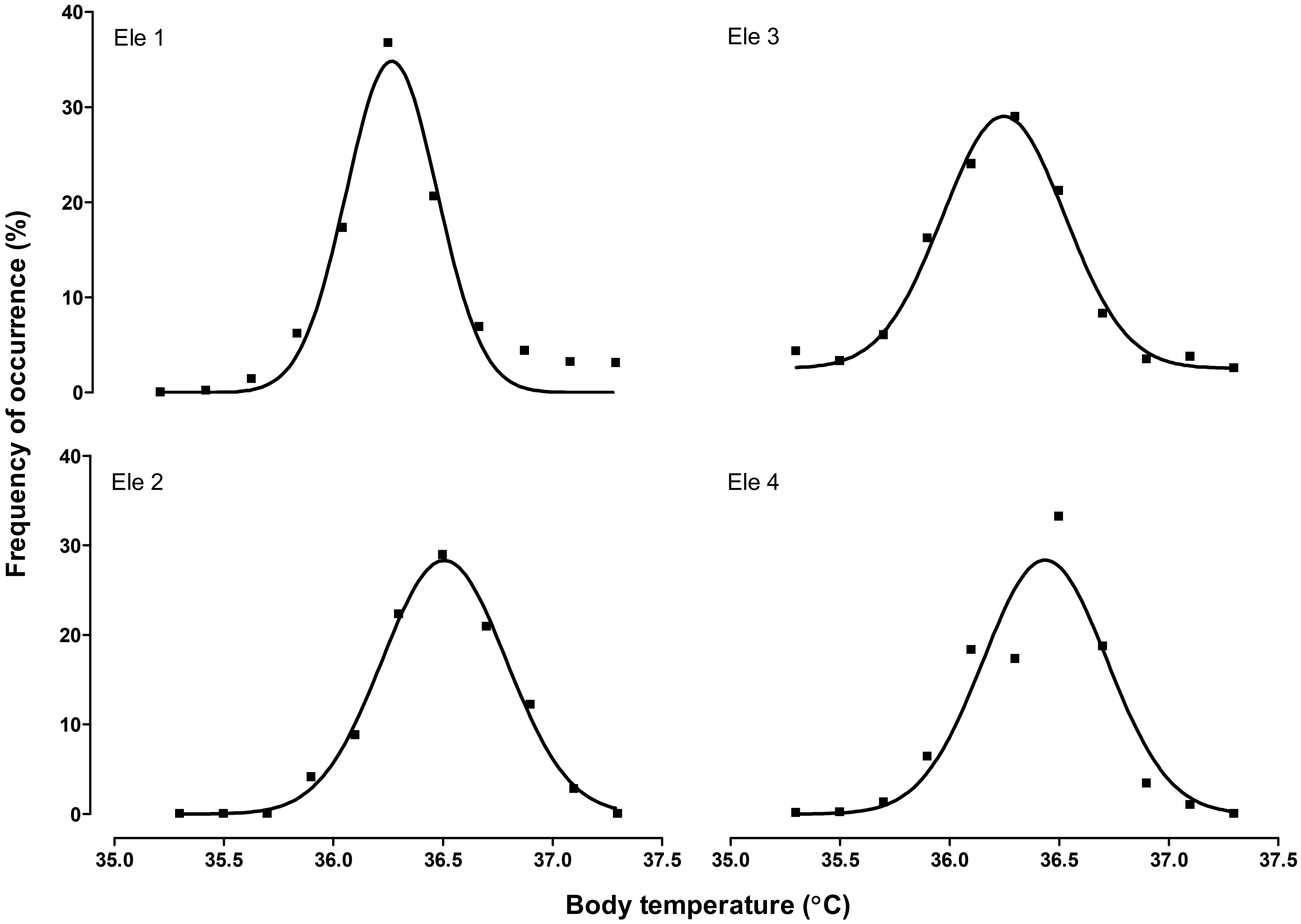

Figure 4.2 Frequency distribution of all body temperatures recorded, at five-minute intervals, for each elephant. Elephant 1: n = 1441 (hot period only), Elephant 2: n = 2377 (hot and cold periods), Elephant 3: n = 864 (warm and cold periods) and Elephant 4: n = 4320 (hot and warm periods). Gaussian curves, fitted to the distributions, demonstrated a good fit (all r-squared values were greater than 0.9).

was 35.2°C, and the absolute maximum was 37.4°C. Body temperature exhibited a mean of 36.3°C for Elephant 1 and Elephant 3, and 36.5°C for Elephant 2 and Elephant 4.

The mean 24 h pattern of body temperature for each of the four elephants is shown in Figure 4.3. Body temperature generally was less variable during the night time than during the day time and the general pattern of body temperature over a 24 h period was consistent between elephants. The minimum body temperature generally occurred between 7:00 and 9:30 and the maximum around 18:00. The time at which the minimum body temperature occurred usually did not coincide with the time of sunrise; sometimes the minimum occurred thirty minutes after sunrise and on other occasions occurred more than three hours after, regardless of climatic period.

The time at which maximum body temperature occurred seemed to be close to the time of sunset (within 15 minutes) in the cold and warm periods, but not in the hot period when it often occurred an hour or more before sunset and then again several hours later (occasionally, the maximum occurred again between 21:00 and 22:00). The timing of the minimum and maximum temperatures did not differ markedly between elephants (Table 4.2). The mean body temperature indices (mean, mean minimum, mean maximum and mean amplitude) recorded for each elephant, in each of the climatic periods, are summarised in Table 4.2.

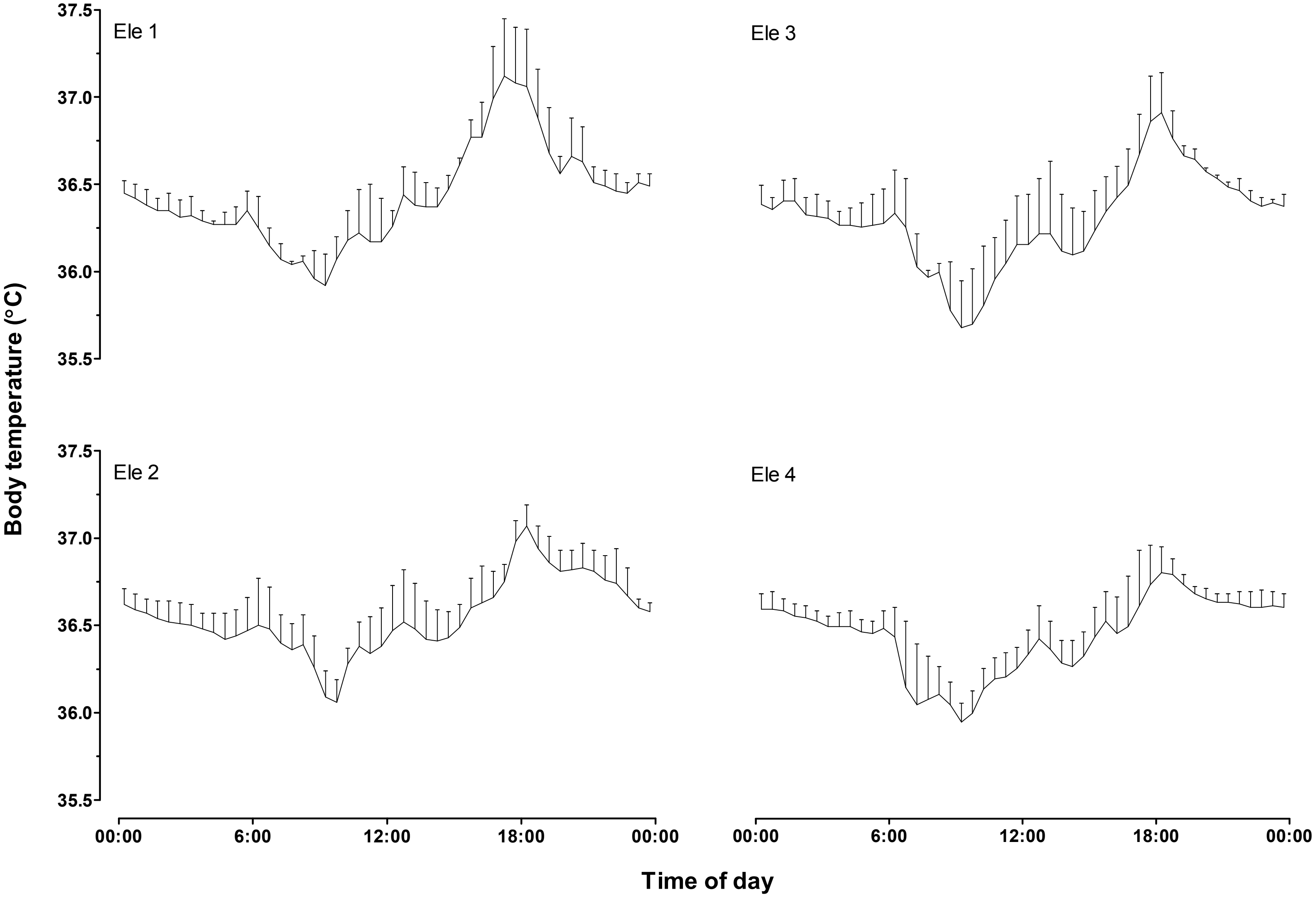

Figure 4.3 Mean 24 h pattern of body temperature for each elephant, showing half-hourly means (24 h periods start at 00:00). Data for all climatic periods were combined. Elephant 1: n = 4 days, Elephant 2: n = 7 days, Elephant 3: n = 3 days, Elephant 4: n = 13 days. Error bars show one SD and represent the variation between days, not within 30-minute periods.

Table 4.2 Summary of the mean (±SD) body temperature indices for complete days for each elephant during each climatic period.

Elephant		Period			
		Cold	Warm	Hot	
Elephant 1	Mean			36.43 ± 0.06	
	Minimum			35.88 ± 0.15	
	Maximum			37.27 ± 0.14	
	Amplitude			1.39 ± 0.22	
	Time of min			08:01 ± 01:30	
	Time of max			18:08 ± 01:19	
	24 h periods			5	
Elephant 2	Mean	36.52 ± 0.04		36.63 ± 0.00	
	Minimum	35.95 ± 0.08		35.87 ± 0.00	
	Maximum	37.15 ± 0.08		37.11 ± 0.09	
	Amplitude	1.20 ± 0.09		1.24 ± 0.09	
	Time of min	10:01 ± 01:10		09:20 ± 00:14	
	Time of max	18:03 ± 00:07		18:23 ± 00:11	
	24 h periods	4		2	
Elephant 3	Mean	36.17	36.34 ± 0.01		
	Minimum	35.29	35.75 ± 0.09		
	Maximum	36.73	36.99 ± 0.26		
	Amplitude	1.44	1.24 ± 0.18		
	Time of min	08:50	09:33 ± 00:39		
	Time of max	17:55	18:03 ± 00:04		
	24 h periods	1	2		
Elephant 4	Mean		36.49	36.44 ± 0.04	36.55*
	Minimum		35.81	35.77 ± 0.23	35.93
	Maximum		36.86	36.96 ± 0.15	37.11
	Amplitude		1.06	1.19 ± 0.24	1.18
	Time of min		06:50	08:05 ± 01:09	09:35
	Time of max		18:05	17:08 ± 03:10	18:20
	24 h periods		1	13	1

* Data were recorded for Elephant 4 on two separate occasions during the hot period.

Differences between individual elephants

Body temperature data were recorded simultaneously for two elephants for one or more 24 h periods on three occasions: Elephant 2 and 4 (hot), Elephant 3 and 4 (warm), and Elephant 1 and 3 (hot). The traces of body temperature recorded simultaneously in these elephants are shown in Figure 4.4 (24 h periods beginning at 12:00 to maximise the number of simultaneously recorded data points). The differences in body temperature between elephants were small and the changes in body temperature generally occurred in the same direction. (Note that less than 24 h of temperature data were recorded for Elephant 3 during the Hot period and therefore, these data were not included in the summary in Table 4.2). No simultaneous measurements of elephant body temperature were recorded during the cold period.

To further assess differences in temperature between elephants, I grouped the data recorded during all climatic periods for each elephant and calculated the weighted means for the body temperature indices (summarised in Table 4.3). All four elephants had very similar body temperature values and as the differences were not biologically relevant, no statistical analysis was used. Figure 4.5 illustrates the double-plot of the mean 24 h pattern of body temperature, using half-hourly means, for the four elephants.

I used the weighted means calculated for the body temperature indices for each elephant to calculate a grand weighted mean (± weighted SD) for each of the body temperature indices (n = 4). Weighted mean body temperature was 36.4 ± 0.04°C, weighted mean minimum

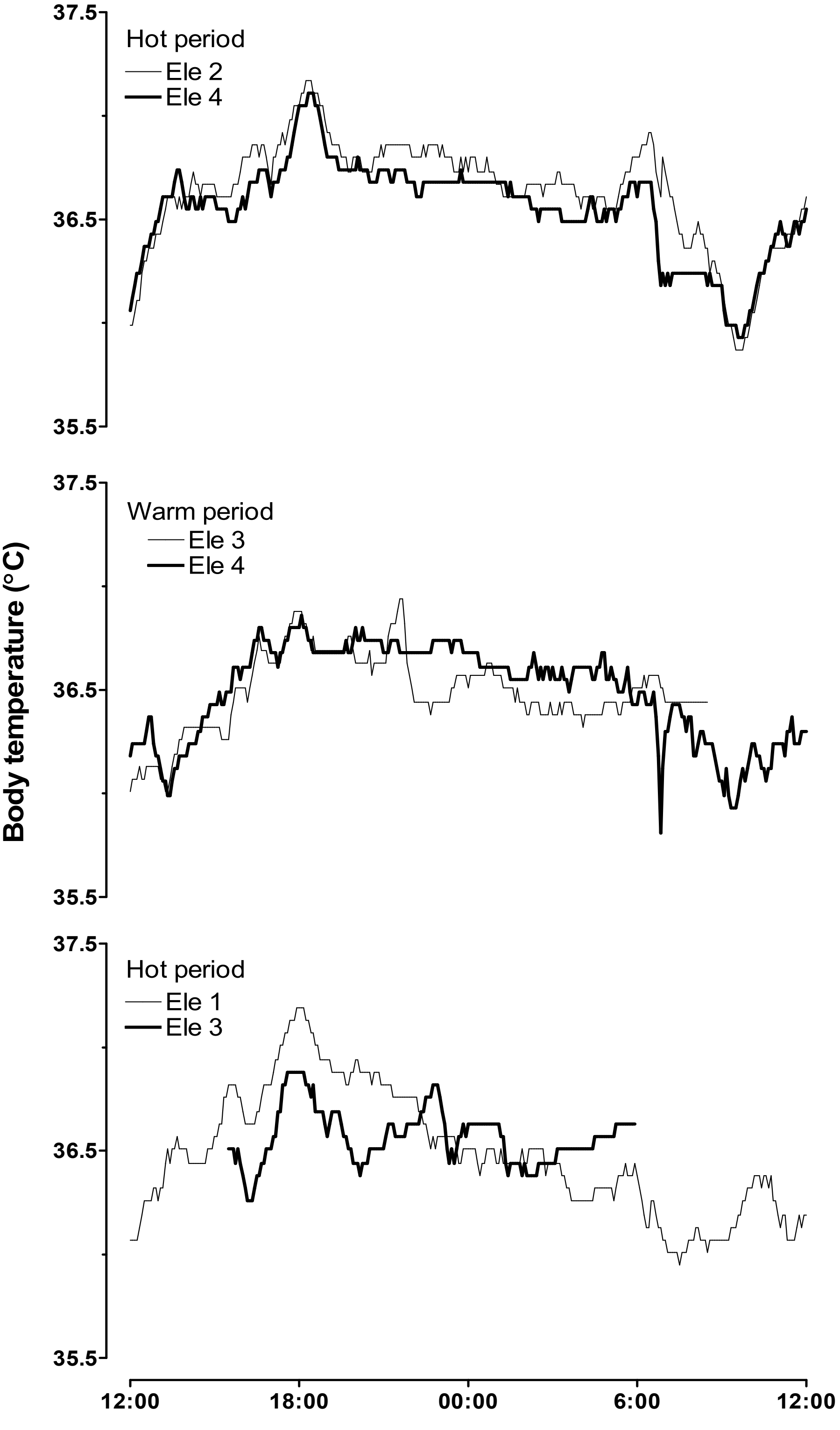

Figure 4.4 Simultaneously recorded body temperatures, logged at five-minute intervals, in three pairs of elephants on three different occasions.

Table 4.3 Summary of the weighted means (± weighted SEM) of body temperature indices for each elephant (data recorded during different climatic periods combined).

	Ele 1	**Ele 2**	**Ele 3**	**Ele 4**
Mean	36.43	36.52 ± 0.03	36.34 ± 0.02	36.45 ± 0.004
Minimum	35.88	35.94 ± 0.02	35.62 ± 0.20	35.78 ± 0.02
Maximum	37.27	37.14 ± 0.02	36.79 ± 0.11	36.95 ± 0.04
Amplitude	1.39	1.22 ± 0.02	1.36 ± 0.10	1.16 ± 0.07
24 h periods	5	6	3	15

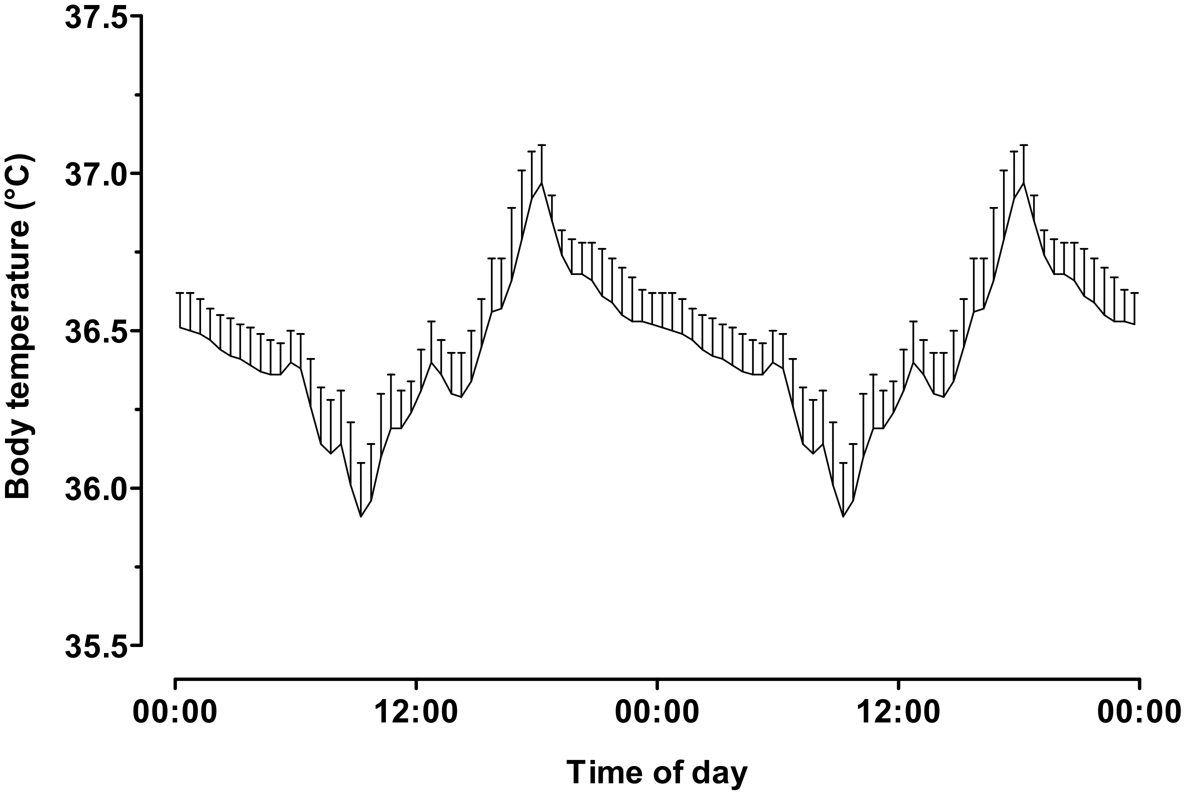

Figure 4.5 A double plot of the mean 24 h trace of body temperature for all four elephants, showing half-hourly means. Error bars show one SD and represent the variation between elephants (n = 4).

temperature was 35.8 ± 0.03°C, weighted mean maximum temperature was 37.1 ± 0.05°C, and weighted mean amplitude was 1.2 ± 0.03°C.

Relationship between environmental and body temperatures

To inspect how body temperature might vary with environmental heat load, I plotted 24 h traces of body temperature with the corresponding trace of black globe temperature for several days for different elephants. Figure 4.6 illustrates two of these traces, recorded for the same elephant during two different climatic periods (Elephant 2, one day recorded during the cold period and one day recorded during the hot period).

On both the cooler and the hotter day, Elephant 2's body temperature continued to decrease in the morning despite a large increase in environmental heat load. In the afternoon, body temperature continued to rise for some time after the environmental heat load had begun to decrease and remained above the minimum body temperature throughout the night, when environmental heat load was at its lowest. The overnight body temperatures for the hotter day were only slightly greater than they were on the cooler day despite the environmental heat load being about 10 to 13°C lower (overnight) on the cooler day. The general pattern of body temperature over the 24 h was not different between the two days.

The means of the body temperature indices recorded for the elephants did not seem to differ between climatic periods either (Table 4.2), and there was no consistent pattern in the differences in the timing of the maximum and minimum. To further assess whether there

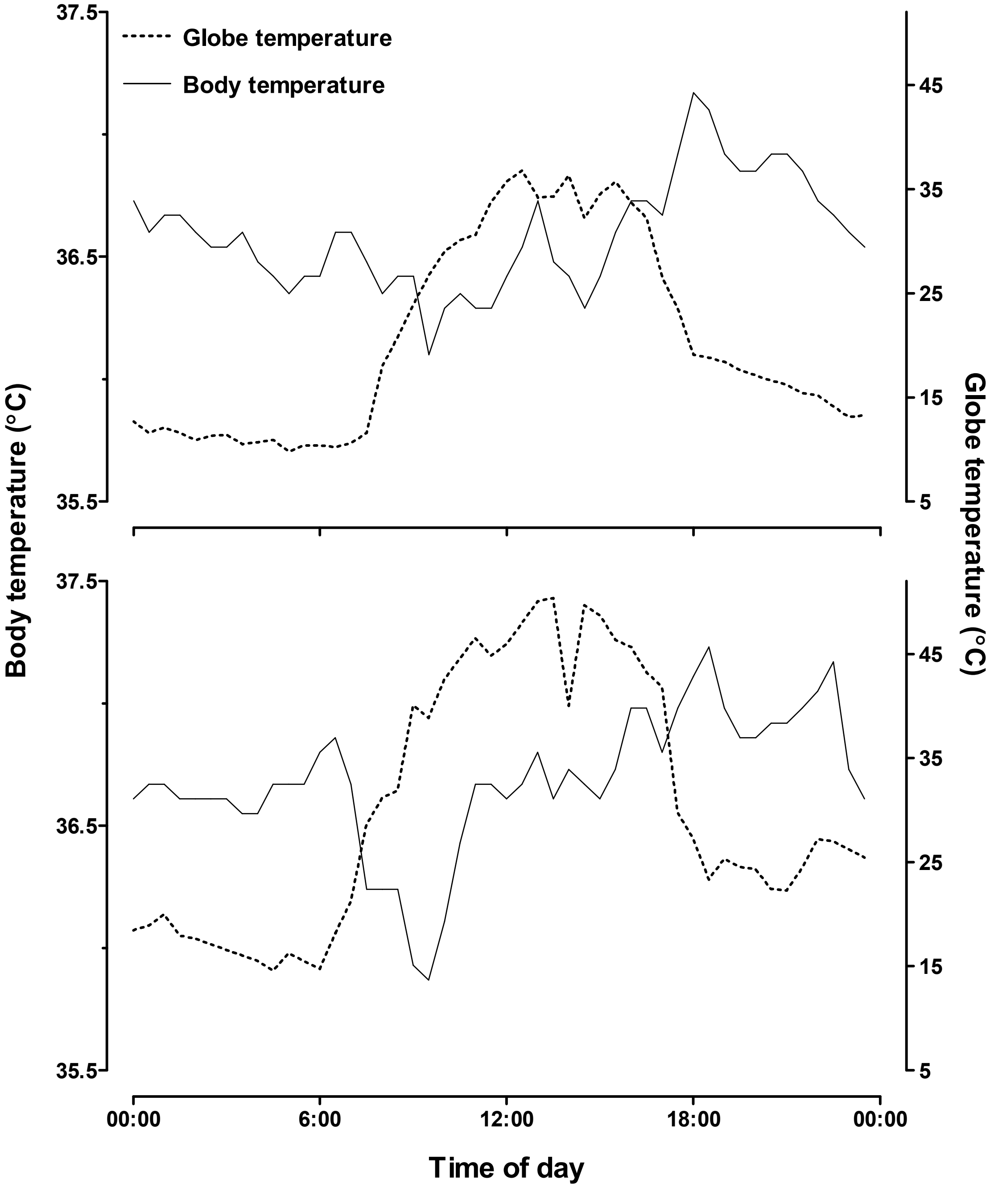

Figure 4.6 Trace of body temperature (Elephant 2) and the corresponding black globe temperature over 24 hours during the cold period (top panel) and during the hot period (bottom panel).

might be a trend for differences in the mean body temperature indices between the three climatic periods, I combined the data recorded for all elephants in each climatic period and calculated the weighted means for each of the body temperature indices (summarised in Table 4.4). The body temperature indices differed little between climatic periods; the differences in temperature were considered biologically insignificant and therefore no statistical analysis was used.

Mean daily body temperature as well as the 24 h minimum, maximum and amplitude for Elephant 4 over twelve consecutive days during the hot period are plotted against the corresponding mean black globe temperature values in Figure 4.7. Based on the r values, the association between elephant body temperature and black globe temperature was not strong, and only the association between the 24 h amplitudes of body temperature and black globe temperature was statistically significant.

Mean daily body temperature as well as the 24 h minimum, maximum and amplitude for Elephant 4 over twelve consecutive days during the hot period are plotted against the corresponding mean air temperature values in Figure 4.8. The r values indicated that the association between the variables was not strong, and none of the associations were statistically significant.

All body temperatures recorded on the hour or half-hour, were plotted against the corresponding black globe temperature for each elephant (Figure 4.9). The Pearson's correlation analysis revealed that there was a significant association between the two

Table 4.4 Summary of the weighted means (± weighted SEM) for body temperature indices during each climatic period (data recorded for different elephants combined).

	Cold	**Warm**	**Hot**
Mean	36.50 ± 0.07	36.34 ± 0.02	36.45 ± 0.31
Minimum	35.86 ± 0.23	35.76 ± 0.03	35.82 ± 0.06
Maximum	37.09 ± 0.15	36.89 ± 0.13	37.07 ± 0.09
Amplitude	1.25 ± 0.10	1.13 ± 0.09	1.25 ± 0.05
No. of elephants	2	2	3

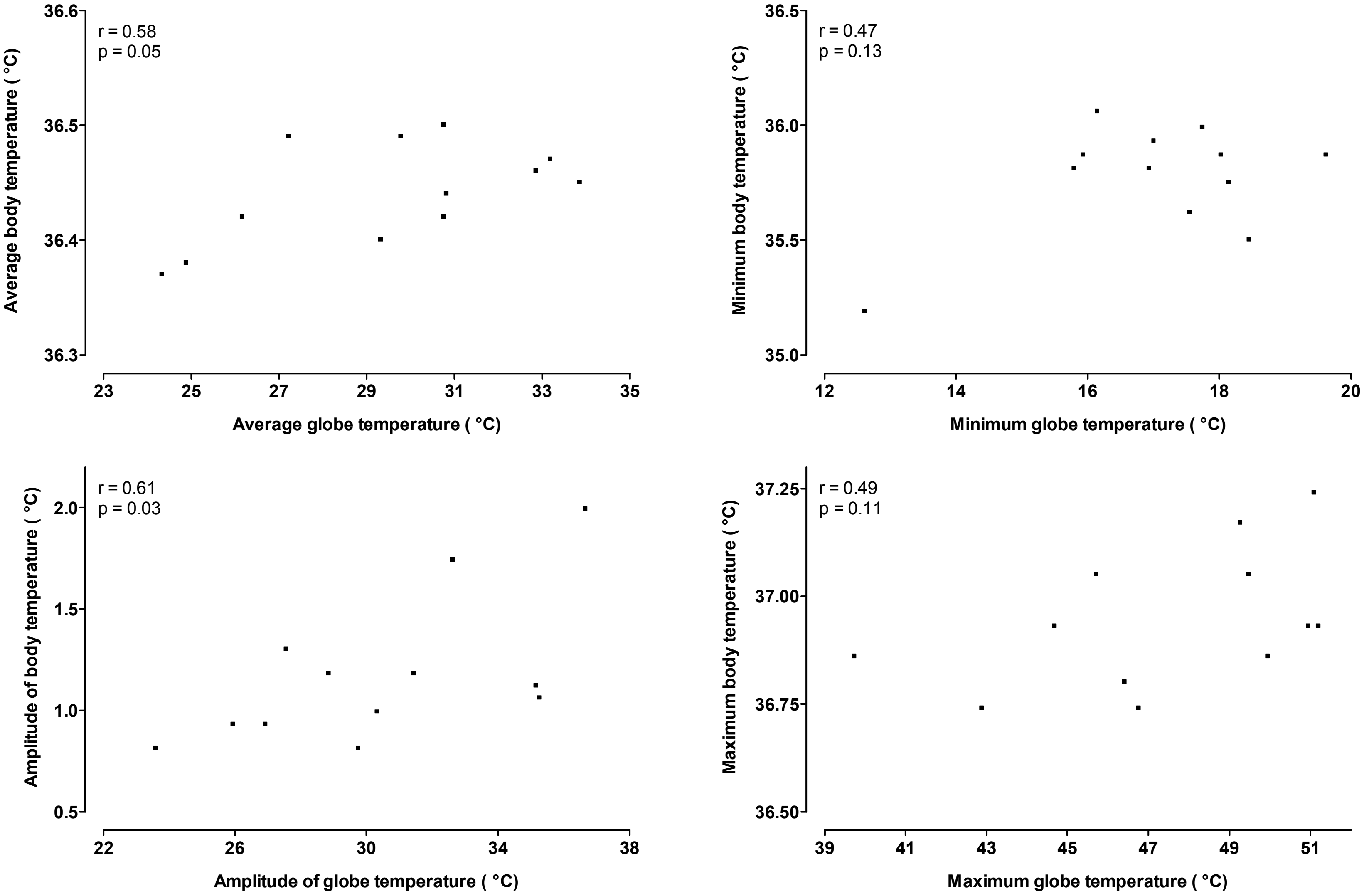

Figure 4.7 Body temperature variables against the corresponding black globe temperature variables (24 h mean, amplitude, minimum and maximum). Values determined for complete 24 h periods only, 24 h periods from 00:00 to 23:55. Sufficient data were recorded only for Elephant 4, and only during the hot period (n = 12 days).

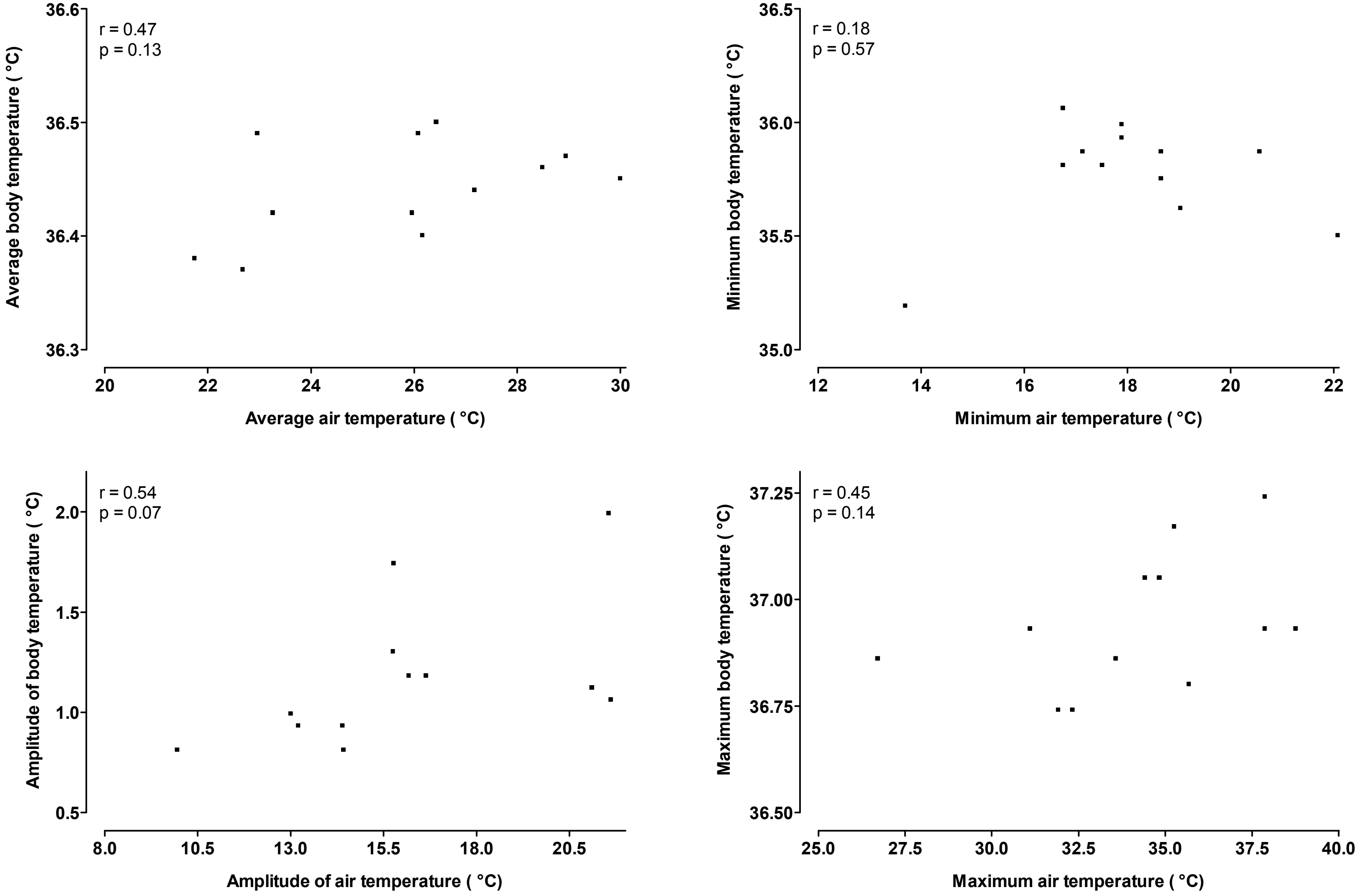

Figure 4.8 Body temperature variables against the corresponding air temperature variables (24 h mean, amplitude, minimum and maximum). Values determined for complete 24 h periods only, 24 h periods from 00:00 to 23:55. Sufficient data were recorded only for Elephant 4, and only during the hot period (n = 12 days).

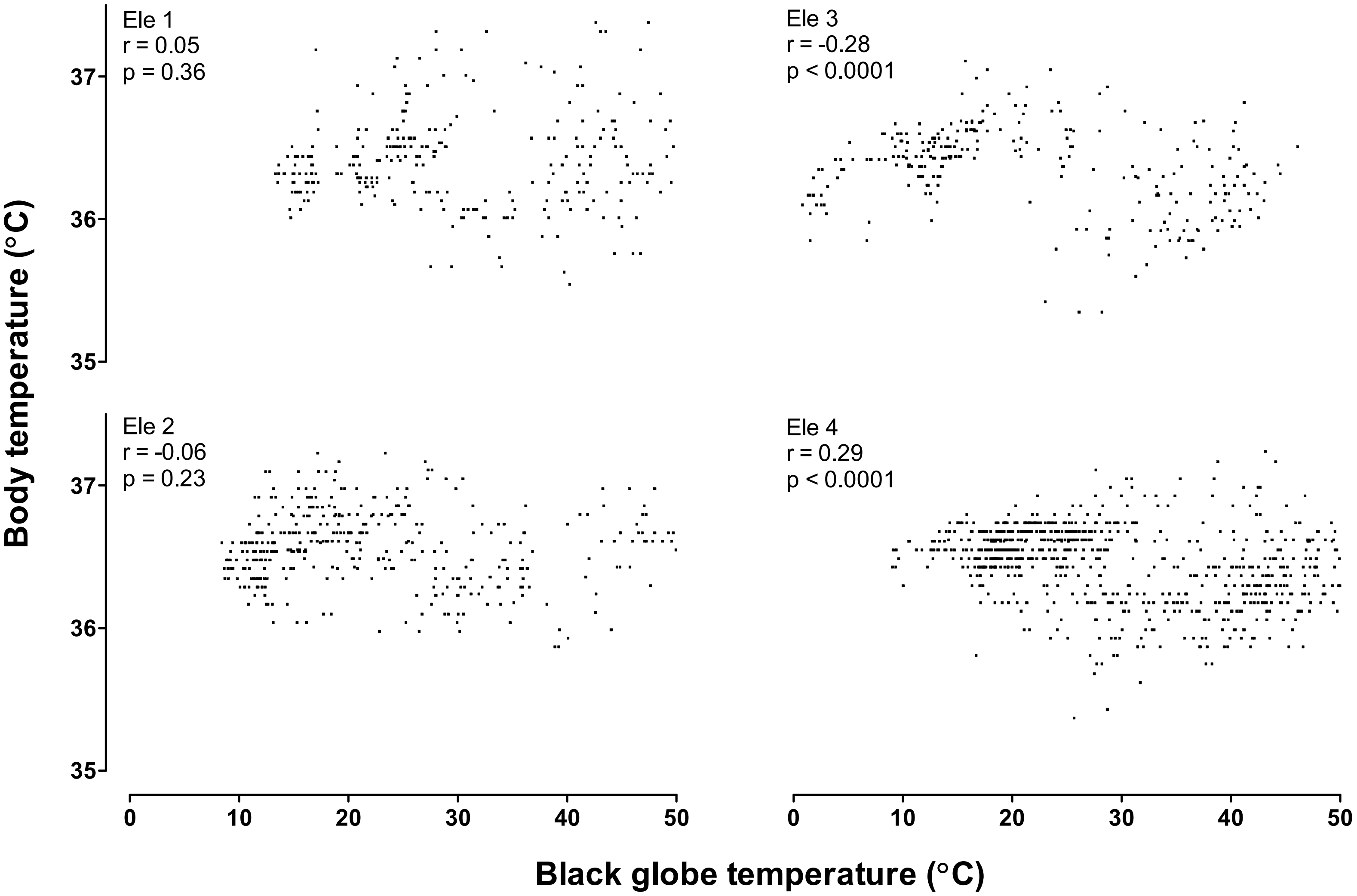

Figure 4.9 All body temperatures, recorded for each elephant on the hour or half-hour, plotted against the corresponding black globe temperature, for each elephant. Elephant 1: n = 278; Elephant 2: n = 390; Elephant 3: n = 275; Elephant 4: n = 770.

variables for Elephant 3 and Elephant 4, but the r values were both less than 0.3. There was no relationship between body temperature and environmental heat load for Elephant 1 and Elephant 2.

All body temperatures recorded on the hour or half-hour, were plotted against the corresponding air temperature for each elephant (Figure 4.10). The Pearson's correlation analysis revealed that there was a significant association between air temperature and elephant body temperature for Elephants 1 and 2, but not for Elephants 3 and 4. Despite the statistical significance of the relationship between the two variables for Elephants 1 and 2, the r values were both small, indicating that the association between the variables was weak.

Short-term changes in body temperature

Changes in elephant body temperature from one five-minute measurement to the next ranged from -0.44 to 0.25°C. In more than half (56 to 69%) of all successive five-minute periods, for all four elephants, there was no change in body temperature. In 30 to 40% of all cases, the change in temperature was greater than 0.0°C but less than 0.07°C. Combined, changes less than 0.07°C accounted for 96 to 99% of all changes. Changes equal to or greater than 0.07°C, but less than 0.25°C, occurred 1 to 4% of the time. Large changes in body temperature were rare; changes greater than 0.24°C occurred on only 8 occasions and in only two elephants (out of a total of 8129 changes calculated for all four elephants). Large decreases were more abundant than large increases. Changes equal to or greater than

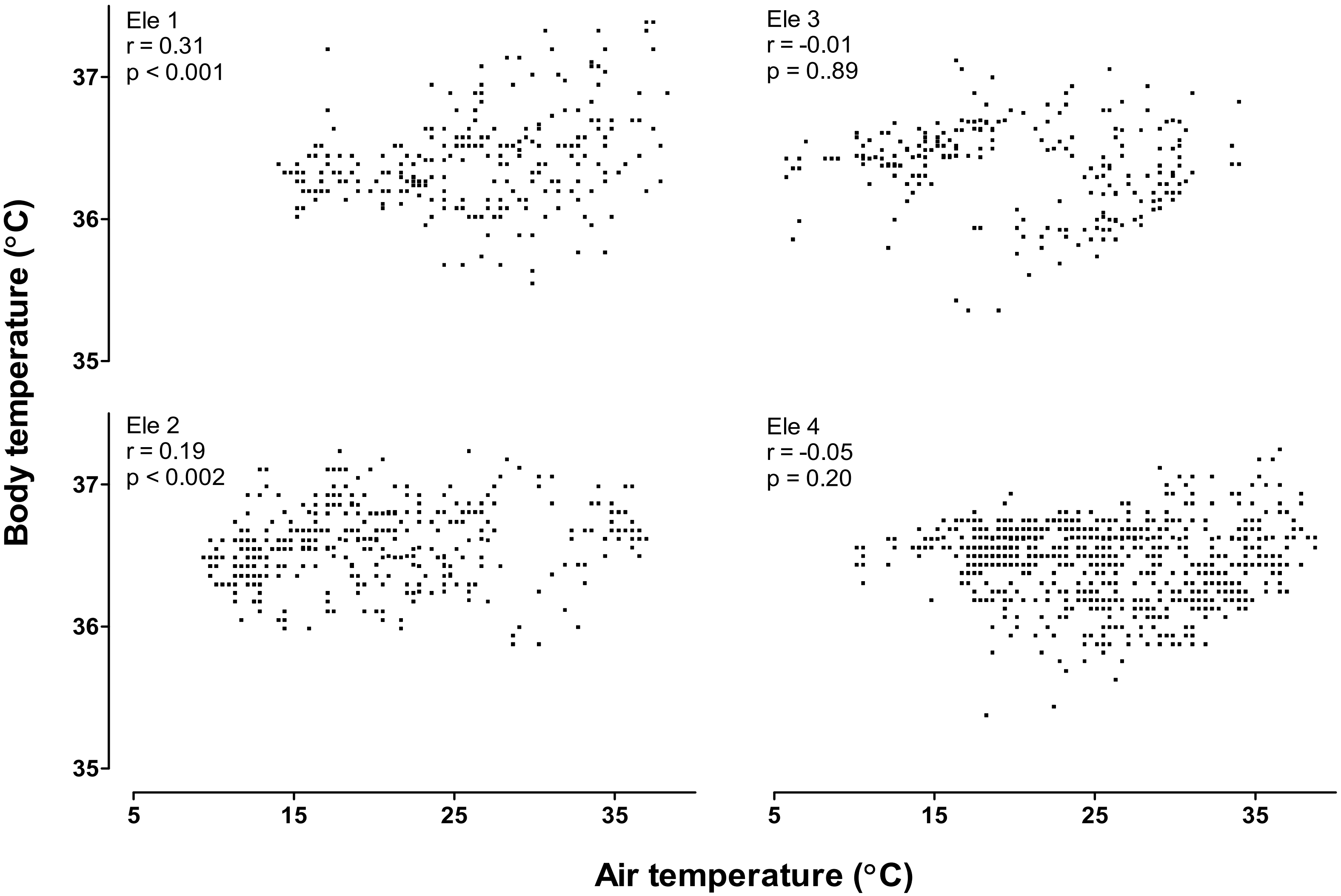

Figure 4.10 All body temperatures, recorded for each elephant on the hour or half-hour, plotted against the corresponding air temperature, for each elephant. Elephant 1: n = 278; Elephant 2: n = 390; Elephant 3: n = 275; Elephant 4: n = 770.

0.12°C tended to occur between 6:00 and 9:00, although changes of around 0.12°C also were observed at other times during the day and occasionally late at night. The greatest proportion of instances of ‘no change’ occurred overnight, especially between 22:00 and 5:00.

The changes in body temperature occurring over ten-minute intervals exhibited a greater range (-0.87 to 0.37°C) than did the changes over five-minute intervals, but the general trends were similar. In 41 to 54% of all instances, there was no change in body temperature, while in 40 to 44% of cases the change was greater than 0.0°C but less than 0.07°C. Combined, changes less than 0.07°C accounted for 85 to 93% of all changes. The proportion of changes between 0.07 and 0.24°C ranged from 6 to 15% between elephants. The number of changes greater than 0.24°C was 15 (out of a total of 3741). For two of the elephants there were more large decreases than increases but for the other two elephants the proportion of large increases increased, and was similar to the proportion of decreases. The role of behaviour in effecting these rapid changes in body temperature is explored in the following chapter.

4.5 Discussion

I have reported continuous measurements of body temperature for African savanna elephants living semi-free in their natural habitat. The body temperatures of four young adult elephant bulls were recorded at five-minute intervals at an accuracy of 0.06°C, on several occasions and under a variety of environmental heat loads. The grand weighted mean of body temperature was 36.4 ± 0.04°C, mean minimum was 35.8 ± 0.03°C, mean maximum was 37.1 ± 0.05°C and the mean amplitude was 1.2 ± 0.03°C. Elephant body temperature exhibited a consistent 24 h pattern, with the minimum occurring in the morning (usually between 6:00 and 9:30, not coinciding with sunrise) and the maximum occurring in the evening (usually around 18:00, closer to sunset in the cold and warm periods than in the hot period). The variation in environmental temperature over a 24 h period was not a major contributor to the variation in body temperature. Short-term variations in body temperature were mostly small (that is, less than 0.07°C), but substantial, rapid changes occurred on occasion. Changes of 0.12°C or greater tended to occur during the day, while body temperature was generally more stable during the night.

It is possible that some of the rapid decreases in body temperature which I observed were experimental artefacts. The position of the data logger within an elephant's gastrointestinal tract may have influenced the logger's sensitivity to the ingestion of water by the elephant. Such drinking-related decreases in body temperature have been recorded in Asian elephants (Toscano, 2001). Ingestion of water influenced the temperature recorded by data loggers which were surgically implanted in the abdomens of study animals (Fuller *et al.*, 2005) and the ingestion of water also was reported to have affected temperatures recorded in the carotid artery of springbok (Mitchell *et al.*, 1997). However, until it is established whether the ingestion of water influences the temperature of the recording device or the temperature of body tissues, one must bear such drinking-related changes in temperature in mind when interpreting body temperature data. Fortunately, since I was often present to observe behaviour during the day, I was able to make a note of several drinking events. The effect of the ingestion of water on body temperature is further examined in Chapter 5.

The elephants I studied had access to water during the day and it is likely that they were never water-stressed (that is, subject to dehydration). Adaptive heterothermy is supposed to confer the advantage of water-saving under conditions of heat and water-stress, and since the study animals were never deprived of water, I can draw no firm conclusions regarding the use of adaptive heterothermy by African elephants in general. The question of whether African elephants use adaptive heterothermy or not would best be investigated in free-living individuals exposed to water and heat stress, an undertaking which would present several challenges.

Recording the body temperature of tame, semi free-living elephants was not without challenges. The technique of body temperature measurement that I used never had been employed in elephants given the freedom to move through their natural habitat. Consequently, the technique required considerable testing and development, and the sample size was reduced as a result. It is a weakness of my study that not all four elephants were instrumented during all three climatic periods and that there were not more measurements made in two or three elephants simultaneously. It is also unfortunate that I recorded no body temperature data for any female elephants. There was a female in the herd living on Letsatsing, but she was pregnant during the study period and was therefore excluded from the investigation.

Despite the limitations of the data, my investigation represents the most thorough documentation of the body temperature of African elephants to date, and the elephants were semi-free living. Many of the early studies were conducted on elephants living in captivity in America and investigators relied on only a few measurements from each of their study animals. When possible, measurements were made in the rectum, but the temperature of freshly-passed urine or faeces was considered to be an acceptable, and more practical, substitute (Benedict & Lee, 1936; Buss & Wallner, 1965). From many measurements of urine temperatures on several elephants, the conclusion was reached that the mean body temperature of elephants was 35.9°C and that body temperature should not vary considerably from this value (Benedict & Lee, 1936). This mean value is slightly lower than that which I observed, most likely due to a difference in the technique of temperature measurement. An even lower mean body temperature (35.1°C) was observed by another team of investigators (Elder & Rodgers, 1975), who also noted a wide range of body temperature (35.1 to 37.2°C). However, temperature was measured in the muscle of the rump, a peripheral tissue which probably did not accurately reflect core body temperature.

Although the muscle of the rump may not have been the ideal site of measurement, the investigators, observing that the lowest temperature recorded occurred at 8:00, were sure that elephant body temperature varied over the course of the day (Elder & Rodgers, 1975). However, they found no convincing evidence of a variation in body temperature with time of day. In a different study of elephant body temperature, the investigator found an increase in rectal temperature over the course of the day, but measurements were made at only three times of day (7:00, 12:00 and 18:00; Hiley, 1972). It was only very recently that continuous measurements of internal body temperature were made in elephants with the aim of describing the pattern of elephant body temperature (Kinahan *et al.*, 2007a).

Kinahan and her colleagues (2007a) used a technique to measure body temperature similar to the one that I used, which allows for a more complete comparison of results. However, two of the three animals they studied were female and the results were not expressed for each elephant individually. The researchers mentioned that the bull's temperature was slightly lower than the females' and since there has been no detailed comparison of the difference in body temperature between male and female elephants, I have compared the results cautiously. The mean body temperature which Kinahan and colleagues reported (36.2 ± 0.49°C) was very similar to that which I observed, while the amplitude they reported was slightly smaller (0.8°C, no SD given). The investigators observed a regular pattern of body temperature, noting that body temperature increased steadily during the day and decreased throughout the night. However, Kinahan and colleagues (2007a) stated that further investigation was required to establish whether the pattern represented a truly endogenous rhythm. I observed the same consistency in the 24 h pattern of body temperature, across elephants and across days, and found the same patterns of increase and decrease, with body temperature tending to be higher at night than during the day. Although a controlled study in a laboratory (that is, without zeitgebers) is required to determine the true rhythm of body temperature (Refinetti & Menaker, 1992), from the data recorded by Kinahan and colleagues (2007a) and myself, elephants appear to have a well-regulated, endogenous rhythm of body temperature. One difference between the results of our studies is that I found that the maximum body temperature occurred in the early evening (around 18:00) while Kinahan and colleagues found that the maximum usually occurred around 22:00. Kinahan and colleagues recorded body temperature every 30 minutes and may have missed earlier instances of maximum temperature values, as I occasionally observed a second appearance of the maximum later in the night (around 22:00). Also, the elephants studied by Kinahan and colleagues were living in a zoo, a less complex physical environment than was experienced by the elephants I studied. It is also possible that external factors influencing the 24 h pattern of body temperature were involved and that these differed between the two studies.

Whether the 24 h rhythm of elephant body temperature is significantly influenced by the environmental heat load is a matter of debate. A study conducted in wild elephants stated that there was no relationship between environmental (air) and body temperature (Buss & Wallner, 1965), but no supporting data were supplied. A later study, also conducted in free-living elephants, found a significant linear relationship ($p < 0.001$) between air temperature and body temperature, but measurements were made in chemically-immobilised individuals and only one or two measurements were recorded for each elephant (Elder & Rodgers, 1975). At the end of their study, Kinahan and colleagues (2007a) concluded that further data needed to be collected to understand the relationship between environmental temperature and body temperature.

I explored the influence of environmental temperature on elephant body temperature by using an index of environmental heat load (black globe temperature). For two of the four elephants, body temperature was not significantly influenced by environmental heat load over the course of 24 hours. For the other two elephants, the influence of environmental heat load was significant, but the r values showed that the association between environmental temperature and elephant body temperature was weak. The same was true of the analysis of the association between air temperature and elephant body temperature. Furthermore, the changes in body temperature were out of phase with changes in environmental temperature. Although body temperature decreased throughout the night, one would expect it to have decreased to a greater extent, had it been more dependent on environmental heat load.

The comparison of body temperatures between days is another means of assessing the effect of environmental heat load on body temperature, and I made use of this comparison also. Analysis of body temperature recorded over 13 consecutive days revealed no relationship between 24 h mean, 24 h minimum, 24 h maximum or the 24 h amplitude of black globe and body temperature. The relationship between mean elephant body temperature and mean black globe temperature narrowly missed statistical significance and it may be that, when explored in a greater number of elephants, the relationship will be statistically significant. Further evidence for the independence of body temperature from environmental temperature was found in the body temperature data which were grouped according to climatic period; no seasonal shift occurred in any of the body temperature indices which I calculated, despite large shifts in the environmental heat load between the climatic periods. The 24 h minimum of black globe temperature occasionally was close to 20°C higher during the hot period than during the cold period, and maximum black globe temperature was greater during the hot period than during the cold period by around 20°C.

I acknowledge that the number of days of body temperature data recorded in the cold and warm periods was small, and that with an increase in sample size, differences in body temperature between seasons may become apparent. Also, it is possible that the differences between body temperatures in different climatic periods will be greater if the differences in environmental heat load were larger, or if the elephants were deprived of water, but from the results of my study it seems that environmental temperature exerts little influence on body temperature. Similarly, Toscano (2001) noted that there was no difference in the mean body temperature of Asian elephants between cold and hot seasons. The independence of body temperature from environmental heat load has been demonstrated in several other African mammals also (Jessen *et al.*, 1994; Mitchell *et al.*, 1997; Fuller *et al.*, 2000; Maloney *et al.*, 2002; Fuller *et al.*, 2005). The implication of the independence of body temperature is that the elephants I studied did not employ adaptive heterothermy, even though their thermal inertia would make it an attractive strategy. Further evidence of the absence of adaptive heterothermy in the elephants studied was the relatively narrow amplitude of body temperature.

It has been hypothesised that large mammals do not experience large 24 h amplitudes of body temperature because of the large thermal inertia of their bodies (Aschoff, 1982). Indeed, a survey of the body temperature of 57 eutherian mammal species showed that animals weighing 1000 g or less tended to have amplitudes of body temperature around 2°C, while animals weighing over 100 kg had amplitudes of around 0.5°C (Mortola & Lanthier, 2004). However, the animals included in that study, by design, were not exposed to wide ranges of environmental temperature and were not studied in their natural environments.

Studies of several African mammals provide values which were recorded in free-living individuals and allow for the comparison not only of amplitude, but of body temperature in general. Free-living zebra (*Equus burchelli*; Fuller *et al.*, 2000), oryx (*Oryx gazelle*; Maloney *et al.*, 2002) and eland (*Tragelaphus oryx*; Fuller *et al.*, 1999a) all had mean amplitudes of around 2°C. Wildebeest (*Connochaetes gnu*; Jessen *et al.*, 1994) and springbok (*Antidorcas marsupialis*; Mitchell *et al.*, 1997) had mean amplitudes of about 1°C, despite their smaller body size and exposure to wide ranges of environmental temperature. The mean body temperatures reported for these ungulates were all slightly higher (mean body temperature of 38 to 39°C) than the mean temperature I observed for the elephants. No equivalent studies of body temperature have been conducted on any of the African megaherbivores. Only discontinuous measurements of body temperature have been recorded for the rhinoceros, and only during the daytime, with the conclusion that the mean rectal temperature of captive rhinoceros increased from 36.9°C at 7:00 to 37.9°C by 18:00 (Hiley, 1977). Continuous measurements of body temperature in captive or restrained hippopotamus and giraffe indicated that hippopotamus have both a similar mean temperature and 24 h amplitude to elephants (Wright, 1987), while giraffe have a slightly higher mean and possibly a greater amplitude also (Mitchell & Skinner, 2004).

There appears to be no clear relationship between mean body temperature and body size in mammals (Schmidt-Nielsen, 1984). And, from the data recorded in free-living animals of varying body size, it seems that the mean daily amplitude of body temperature is not affected by body size to the extent once thought. But apart from the variation in body temperature over a 24 h period, there are changes in body temperature which occur over shorter lengths of time (Mitchell *et al.*, 1997). These short-term variations could be affected by a greater thermal inertia, evident in smaller magnitudes and frequency of occurrence. My study represents the first assessment of short-term variations in the body temperature of African elephants. I observed that, for about 50% of the time, there was no change in elephant body temperature at either the five, or ten-minute, time scale. In contrast, "no change" in body temperature represented only 26% of the differences between consecutive body temperatures recorded at 12-minute intervals in free-living springbok (Mitchell *et al.*, 1997). I observed changes larger than 0.25°C , over a ten-minute period, in about 0.4 % of cases, compared to about 15% of cases in springbok (Mitchell *et al.*, 1997). An elephant may be more than 100 times the mass of a springbok and based on the increase in thermal inertia which should accompany this increase in size, an elephant should only experience changes larger than 0.25°C in about 0.1% of cases. Therefore, although I observed a decrease in the frequency of rapid temperature changes, body temperature did not exhibit the anticipated consequences of an increased thermal inertia.

Since the accuracy of the loggers I used to record body temperature was 0.06°C and the average difference in temperature along the gastrointestinal tract was 0.10°C (see Chapter 3), only changes of 0.10°C or greater should be considered to be ‘real’ changes in body temperature. Changes in temperature greater than 0.10°C usually occurred during the day and may have been related to activity, as seen in springbok (Mitchell *et al.*, 1997). Further investigation of the effect of various behaviours on body temperature during the day is provided in Chapter 5. The large changes in temperature may also have been caused by the ingestion of water. However, changes of 0.12°C occasionally occurred at night when the elephants did not have access to drinking water. Alternatively, the rapid decreases at night might have been the result of the dissipation of large amounts of body heat, favoured by a decrease in the environmental heat load and an increase in the temperature gradient between the elephant’s body and the environment (Mitchell *et al.*, 1997). Peripheral vasodilation, especially of vessels underlying the skin, may have enhanced heat loss at this time of day.

It is known that the flow of blood through an elephant’s skin is variable, especially the flow of blood through the pinnae (Wright, 1984; Phillips & Heath, 1992). Vasodilation in the skin, caused by a sudden increase in solar radiation shortly after sunrise, may result in the cooling of blood passing through cold peripheral tissues, thereby producing a reduction in core temperature (Schmidt-Nielsen *et al.*, 1957), but it is unlikely that this was the case with the elephants I studied. Often the morning decrease in body temperature occurred before the animals were subjected to solar radiation, and may have been due to the sudden increase in activity when the animals left their stables. Similar decreases in body temperature have been attributed to increases in early-morning activity in free-living eland (Fuller *et al.*, 1999a); as the animal begins to move, there is an increase in the flow of blood through the muscles, which have become cold overnight due to the animal's inactivity, and because of low environmental temperatures. Warm blood from the animal's core is then cooled as it passes through the muscles and on returning to the tissues in the core, produces a decrease in core temperature (Fuller *et al.*, 1999a).

Decreases of 0.10°C or more occurred more frequently than increases of 0.10°C or more and therefore it seems that an elephant can lose heat more rapidly than it can gain it. Also when the time interval was extended from five to ten minutes, the proportion of increases increased, relative to the number of decreases, which suggests that increases in body temperature occurred more slowly then did large decreases. Such rapid losses of heat may be important in driving the rhythm of body temperature in large mammals, which appear to promote heat loss more actively than smaller mammals during certain phases of the body temperature rhythm (Mortola & Lanthier, 2004). Furthermore, the role of the skin in effecting these losses seems to be crucial to thermoregulation in animals of large body size and, therefore, the regulation of the temperature of the skin is especially important in determining body temperature and its 24 h rhythm (Phillips & Heath, 1995; Piccione *et al.*, 2005). Indeed, it has been suggested that an inability to regulate its surface temperature, due to its thick coat, may have resulted in the woolly mammoth's (*Mammuthus primigenius*) inability to adjust to a changing climate (Phillips & Heath, 1995).

Cutaneous moisture loss also may play a role in effecting changes in skin temperature in elephants and I attempted to assess cutaneous moisture loss using several designs of absorbent patches. None of the techniques were successful, but it seemed that the greatest amount of moisture was lost from the back of the ears (compared to the flank and leg), reflecting the results observed by Wright and Luck (1984) in an immobilised elephant. I also attempted to address differences in cutaneous moisture loss under different environmental conditions but was unsuccessful. Previous measurements, made on a juvenile elephant, showed that there was no variation in cutaneous moisture loss with varying environmental temperature (Hiley, 1972). However, I believe that the variations in cutaneous moisture loss require further investigation, and that simultaneous measurements of skin and core temperatures should be made.

Chapter 5

Interaction between behaviour and elephant body temperature

5.1 Introduction

In Chapter 1, I highlighted the importance of behaviour to the process of thermoregulation and pointed out that the direct effects of behaviour on the body temperature of elephants have not previously been explored. I observed substantial, rapid changes in elephant temperature (sometimes as large as 0.44°C in five minutes) and wondered whether certain behaviours might be responsible for these changes.

Drinking has been linked to changes in recorded body temperature (Mitchell *et al.*, 1997; Fuller *et al.*, 2005), and water-related activities such as swimming and splashing are considered to be of thermoregulatory importance in elephants (Hiley, 1975) and other African herbivores of large body size (Allbrook *et al.*, 1958; Luck & Wright, 1964; Sinclair, 1977). Unique to elephants, ear flapping has been given particular attention as an important thermoregulatory behaviour (Buss & Estes, 1971; Wright, 1984). However, many assumptions regarding the thermoregulatory role of such behaviours have been made, since continuous measurements of body temperature (before, during and after the activity) together with observations of behaviour have not been made.

It is difficult to assess the interaction between behaviour and body temperature, especially in animals living in their natural environment (Hetem *et al.*, 2007) and I did not conduct a complete survey of the effect of all behaviour on elephant body temperature. I focused my investigation on a few behaviours that I believed might influence elephant body temperature, and posed the following questions:

1. What effect did drinking, splashing and swimming have on elephant body temperature?
2. Was there any interaction between ear flapping and elephant body temperature, and if so what was it? And what was the influence of environmental heat load on the frequency of ear flapping?
3. How did the periods of increased activity (the rides given to tourists) affect elephant body temperature?

5.2 Materials and methods

5.2.1 Study site and animals

Refer to Chapter 2 for details of study site and animals.

5.2.2 Climatic data

Refer to Chapter 2 for details of how climatic data were recorded.

5.2.3 Body temperature measurement

Refer to Chapters 3 and 4 for details of body temperature measurement.

5.2.4 Observations of behaviour

Observations of elephant behaviour were conducted during the day from the time the elephants exited their stables in the morning (just before sunrise; between 5:30 and 6:45) until the animals returned to their stables in the evening (around sunset; about 18:00). No observations were made overnight. Focal sampling was employed and although records of the general behaviour of the herd were made, detailed observations were recorded only for individuals whose temperatures were being measured. Behaviour was recorded every five minutes while the elephants were engaged in natural behaviour. Observations of general behaviour were made during the times when the elephants were engaged in tourist-related activities. Generally, elephants were engaged in natural behaviour from the time the animals left their stables until about 8:30; from 10:00 to 13:00; 14:00 to 15:30; and from about 17:30 until they returned to their stables.

Water-related activities

During the daytime, the elephants had access to a large dam in which they splashed and swam, and from which they often drank. The elephants were also hosed down occasionally (that is, before a ride, if they had become especially dirty) and would drink from the hose also. Drinking, swimming and splashing were recorded whenever they occurred during periods of observation. Water often was available to the elephants during tourist-related activities and if the study animals drank or splashed themselves with water during these times, a record was made. Neither the length of time spent drinking, nor the volume of water ingested, were determined.

The temperature of the water of the dam was recorded at 15-minute intervals during the hot and warm periods with a miniature temperature-sensitive data logger (StowAway Tidbit, Onset Computer Corporation, Pocasset, Mass., USA) placed near the edge of the water at a depth of about 200 mm. The data logger was calibrated against a certified precision thermometer in an insulated hot water bath.

Periods of increased elephant activity

The elephants generally provided two 60-minute rides to tourists each day, typically one in the morning (8:30 – 9:30) and one in the afternoon (16:00 – 17:00). A guide, on foot, would lead the herd on a "safari" through the reserve at a brisk pace (about 6 $km.h^{-1}$); this appeared to be a comfortable pace for the elephants which were not forced to move any faster. These rides represented the longest periods of activity, of the greatest intensity, in which the elephants engaged during my observations.

Ear-flapping behaviour

An "ear flap" was defined as a distinct forward and backward motion of the pinna, as described by Buss and Estes (1971). Ear flapping (presence or absence) was recorded at five-minute intervals during periods of observation. If an elephant flapped its ears more than three times within a five-minute period, it was recorded as having been engaged in ear-flapping behaviour. Ear flap rate was determined by counting the number of ear flaps during one minute. Flap rate data were recorded intermittently during the warm and hot periods, except for two dedicated days during the hot period when flap rate data were recorded for all four elephants, at 30-minute intervals, between 6:00 and 18:00. Flap rate data were not recorded during the cold period because the elephants only occasionally engaged in ear-flapping behaviour in this period.

5.3 Data analysis

5.3.1 Water-related activities and elephant body temperature

To assess the effect of drinking on body temperature, a thermal response index for each drinking event was calculated; the body temperatures recorded at each five-minute interval during the 60 minutes from the start of a drinking event were subtracted from the corresponding mean body temperature calculated for the elephant concerned (the mean temperatures illustrated in Figure 4.3). These differences then were averaged to produce a mean difference over the 60-minute period. The mean difference for all drinking events (for all elephants) which occurred during the morning (before 12:00, when body temperature was low or was decreasing) was then calculated. The mean difference for all drinking events which occurred in the afternoon (after 12:00, when body temperature was high or decreasing) was calculated separately. Only temperature data recorded after the logger had exited the stomach were used.

To assess the effect of swimming on body temperature, temperatures recorded during the 120 minutes from the time the elephant entered the water were subtracted from the mean body temperature (over 120 minutes at the corresponding time of day). These differences then were averaged to produce a mean difference over the 120-minute period. The mean difference for all swimming events which occurred during the morning was calculated, as was the mean difference for all swimming events which occurred in the afternoon. I was unable to determine whether the elephants drank whilst swimming.

The assessment of the effect of splashing on body temperature was conducted as for the assessment of the effect of swimming. If the elephant drank whilst splashing, the event was not included in the analysis.

The duration of individual drinking, swimming and splashing events ranged widely, and I did not determine the exact lengths of time that elephants were engaged in these activities. Also, I did not analyse the influence of environmental heat load on the frequency of swimming and splashing behaviour, since these behaviours were restricted during the times when the elephants were interacting with tourists. However, I made general observations concerning the frequency with which these behaviours occurred in the different climatic periods.

5.3.2 Periods of increased activity and elephant body temperature

The changes in elephant body temperature during rides (60 minutes), and for 60 minutes after a ride had finished, were assessed. Rides conducted in the morning and afternoon were considered separately. No comparison to the mean body temperatures for the corresponding time of day was made since there was only a single day on which no rides were conducted.

5.3.3 Ear-flapping behaviour

I used the flap rate data recorded at 30-minute intervals over the two days in the hot period to construct a frequency distribution of flap rate for each elephant. The first category was designated zero (no ear flaps during one minute). Thereafter, categories spanned five flaps per minute (starting at one flap per minute). The number of flap rates which occurred in each class was then determined as a percentage of the total number of flap rates recorded for each elephant. The percentages calculated for each class for each elephant were averaged to produce a mean value for each class which was representative of the four elephants.

If an elephant was wet or engaged in a water-related activity, the ear-flapping data recorded during that time were not included in the analyses described below.

Relationship between climatic variables and ear flapping

Every flap rate recorded during the study was matched to the corresponding black globe and air temperature, as well as the corresponding value for solar radiation. If the flap rate was not recorded on the hour or half-hour, the nearest value recorded for the environmental variable was used. If a flap rate was recorded on the 15th or 45th minute of the hour, it was excluded, since the weather station only recorded the environmental variables every 30 minutes. Plots of the paired values were constructed for each elephant and the nature and strength of the association between the two variables was assessed using Pearson's correlation analysis.

The values of solar radiation and black globe temperature recorded by the weather station, which was positioned so that it was always in full sun, may have differed substantially from values which would have been recorded by the same instruments positioned in the shade. Therefore, for the analysis of the relationship between ear flapping and solar radiation, any ear-flapping behaviour recorded whilst the elephant was in the shade was excluded. The same condition was applied to data used in the analysis of the relationship between ear flapping and black globe temperature.

The ranges of air and black globe temperatures over which flap rates were recorded were subsequently divided into 2°C classes. All flap rates recorded at the temperatures within each class were averaged, producing a mean flap rate for each class of temperature for each elephant. The mean and standard deviation were then calculated for each class using the values calculated for each of the four elephants. The equation which best described the relationship between the mean flap rate and each of the two temperature variables was determined using curve-fitting software (TableCurve 2D for Windows, v3.05).

The effect of an elephant's exposure to shade and sun on ear-flapping behaviour also was assessed. For all observations of the presence or absence of ear flapping, I noted whether an elephant was in the sun or in the shade. A contingency table was constructed for each elephant, and the association between "flapping" and "not flapping", and exposure to sun or shade, was assessed using Fisher's Exact tests. If the sun was obscured by cloud, or if the sun was not shining directly on the elephant at the time (due to the topography of the land), the data point was excluded. The analysis was conducted using data recorded at all black globe temperatures and was then repeated using observations made when the black globe temperature was above 30°C.

Relationship between elephant body temperature and ear flapping

All flap rates recorded for each elephant while it was exposed to sun were matched with the corresponding body temperature. A plot of the paired values was constructed for each elephant and the relationship between the variables was assessed.

Twenty-minute bouts of “flapping” and “not flapping” behaviour were identified; I considered twenty minutes a sufficient amount of time for body temperature changes to be measured, if they occurred. If the sun was obscured by cloud, or was not shining directly on the elephant, the data were excluded from the analysis. The body temperature recorded at the beginning of the bout was subtracted from the value recorded at the end of the 20-minute period to determine whether body temperature was stable, or had decreased or increased during the 20-minute period. A contingency table was constructed for each elephant and the association between “flapping” or “not flapping”, and change in body temperature, was assessed using Fisher’s Exact tests.

5.4 Results

5.4.1 Water-related activities and elephant body temperature

Temperature of the water in the dam

During the hot period, the mean temperature of the water in the dam ranged from 25 to 30°C, and during the warm period ranged from 19 to 25°C.

Drinking

The mean body temperatures recorded during all drinking events which I observed are illustrated, for each elephant, in Figure 5.1. The ten minutes prior to drinking, as well as the 60 minutes following drinking are shown. In the morning, drinking often was associated with a decrease in elephant body temperature, but temperature during drinking did not always reach the 24 h minimum body temperature. The decrease in body temperature was not evident in the traces of temperature during afternoon drinks.

The mean difference, for all four elephants, between the temperatures recorded during the 60 minutes following drinking and the mean body temperatures for the corresponding time of day was 0.0 ± 0.2°C during the morning and 0.1 ± 0.2°C in the afternoon. No consistent pattern in the difference was observed; there were occasions when body temperature was higher than average during drinking, and occasions when body temperature was lower than

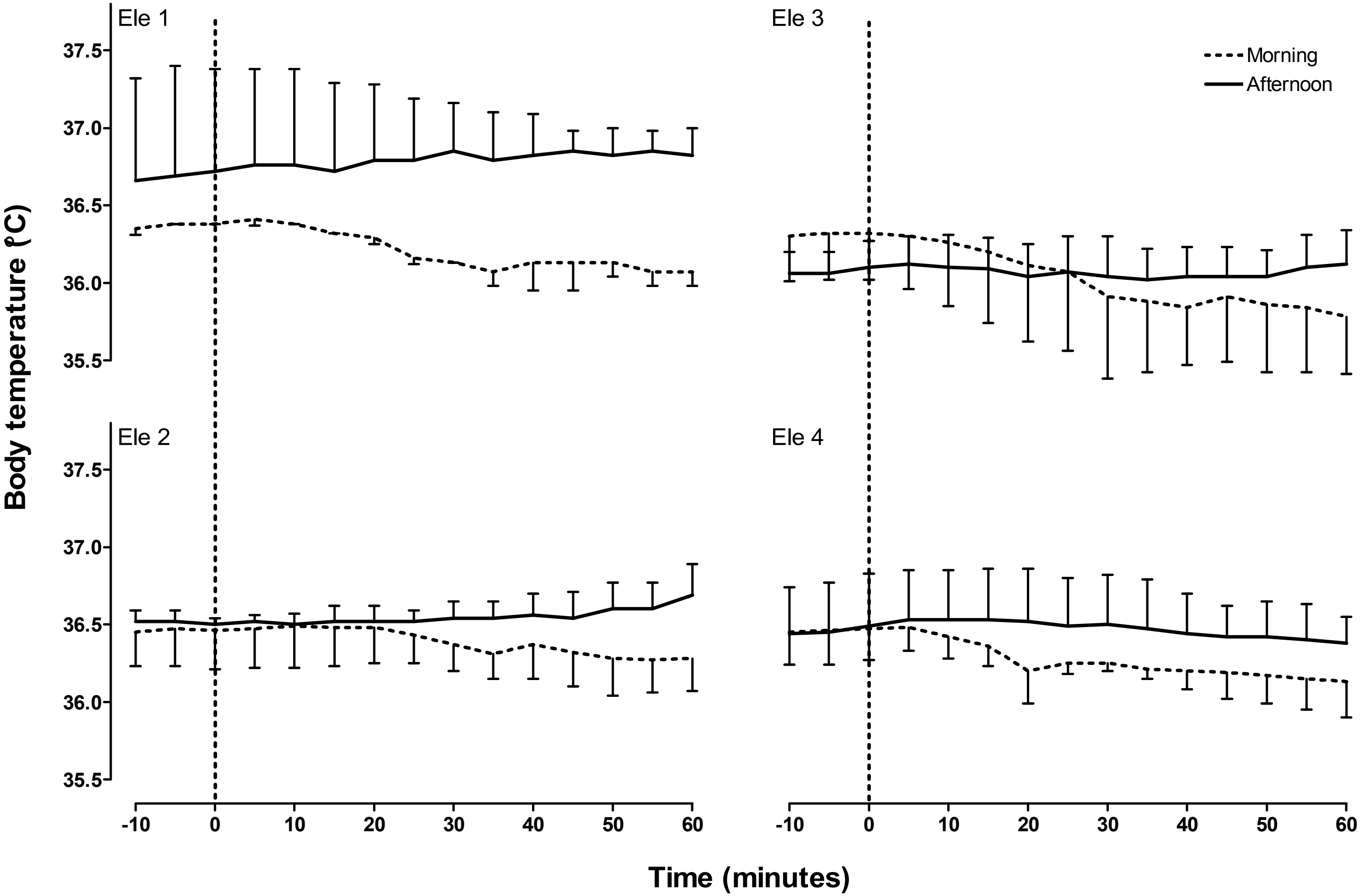

Figure 5.1 Elephant body temperature from 10 minutes prior to drinking and for 60 minutes following (drinking event started at t = 0). The solid lines represent the mean temperature recorded for all afternoon drinking events for each elephant (n = 2, 3, 4 and 5), and the dashed lines represent the mean temperatures recorded for all morning drinking events (n = 2, 6, 3 and 6). Error bars represent one SD. Only temperature data recorded after the logger had exited the stomach were used.

average during drinking, in both the morning and afternoon.

Swimming

The elephants had the opportunity to swim during all three climatic periods and I observed two of the animals swimming in the early morning during the warm period. However, neither of these elephants were instrumented with body temperature data loggers. Body temperatures were recorded for two of the four elephants during swimming in the hot period only (Elephant 1: n = 3, Elephant 4: n = 4). Body temperatures recorded for 10 minutes before the elephants entered the water, until 120 minutes after, are shown in Figure 5.2. On only one occasion did swimming take place in the early morning (Elephant 4, around 6:30), and a marked decrease in body temperature was observed. Elephant 1 swam around 10:30, after the minimum body temperature had occurred and no decrease in body temperature was observed. In the afternoon, that is, after 12:00 midday, body temperature tended to increase during the first 30 to 60 minutes during swimming, and thereafter to decrease (or to show no further change). The elephants did not swim when body temperature was at its highest (refer to the frequency distributions of body temperature inserted in Figure 5.2).

When compared to mean body temperature (over a 120-minute period at the corresponding time of day), body temperature during swimming was higher throughout the 120-minute period. The mean difference between temperatures recorded during swimming in the

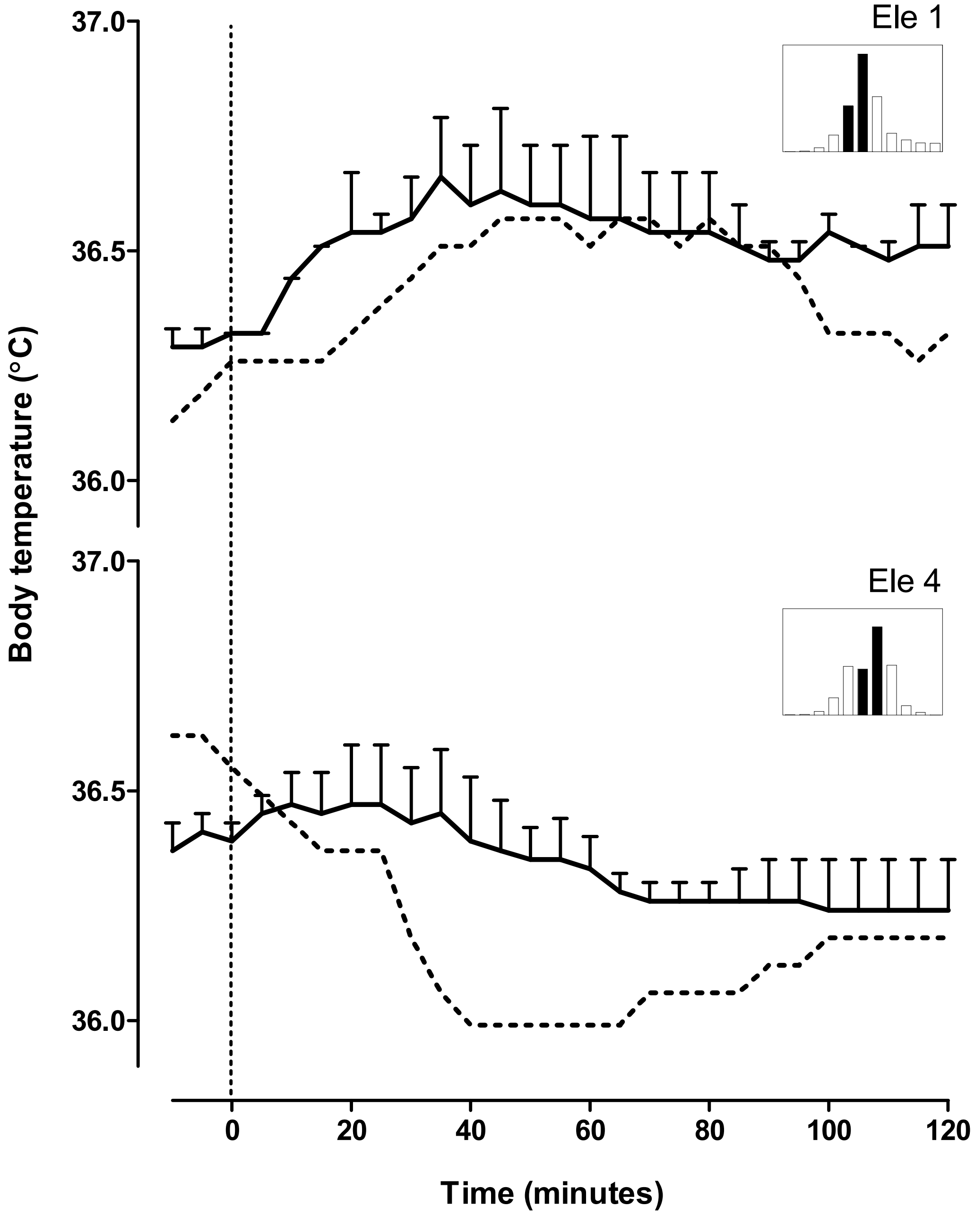

Figure 5.2 Elephant body temperature from 10 minutes prior to swimming and for 120 minutes following, for Elephant 1 (top panel) and Elephant 4 (lower panel). The solid lines represent the mean temperatures recorded for three afternoon swimming events for each elephant, and the dashed lines represent the temperatures recorded for the single morning swimming event recorded for each elephant. Error bars represent one SD. The inserts illustrate the frequency distributions of body temperature and the solid bars indicate the temperature at which the elephant tended to swim.

afternoon and mean body temperature for the corresponding period of time was -0.1 ± 0.1°C.

Body temperature during the swimming events recorded in the morning was, on average, 0.06°C higher than the mean body temperature for the corresponding time of day.

Splashing

I recorded ten splashing events (excluding those when the elephant ingested water at the same time) for the four elephants across the three climatic periods. The body temperatures recorded for 10 minutes before splashing until 120 minutes after, for these ten events, are illustrated in Figure 5.3. The mean difference between temperatures recorded during the 120 minutes from the start of splashing and mean body temperature during the corresponding time of day was -0.2 ± 0.2°C in the morning, and 0.0 ± 0.1°C in the afternoon. The elephants did not splash themselves when body temperature was at, or close to, its maximum (refer to the frequency distributions inserted for each elephant in Figure 5.3).

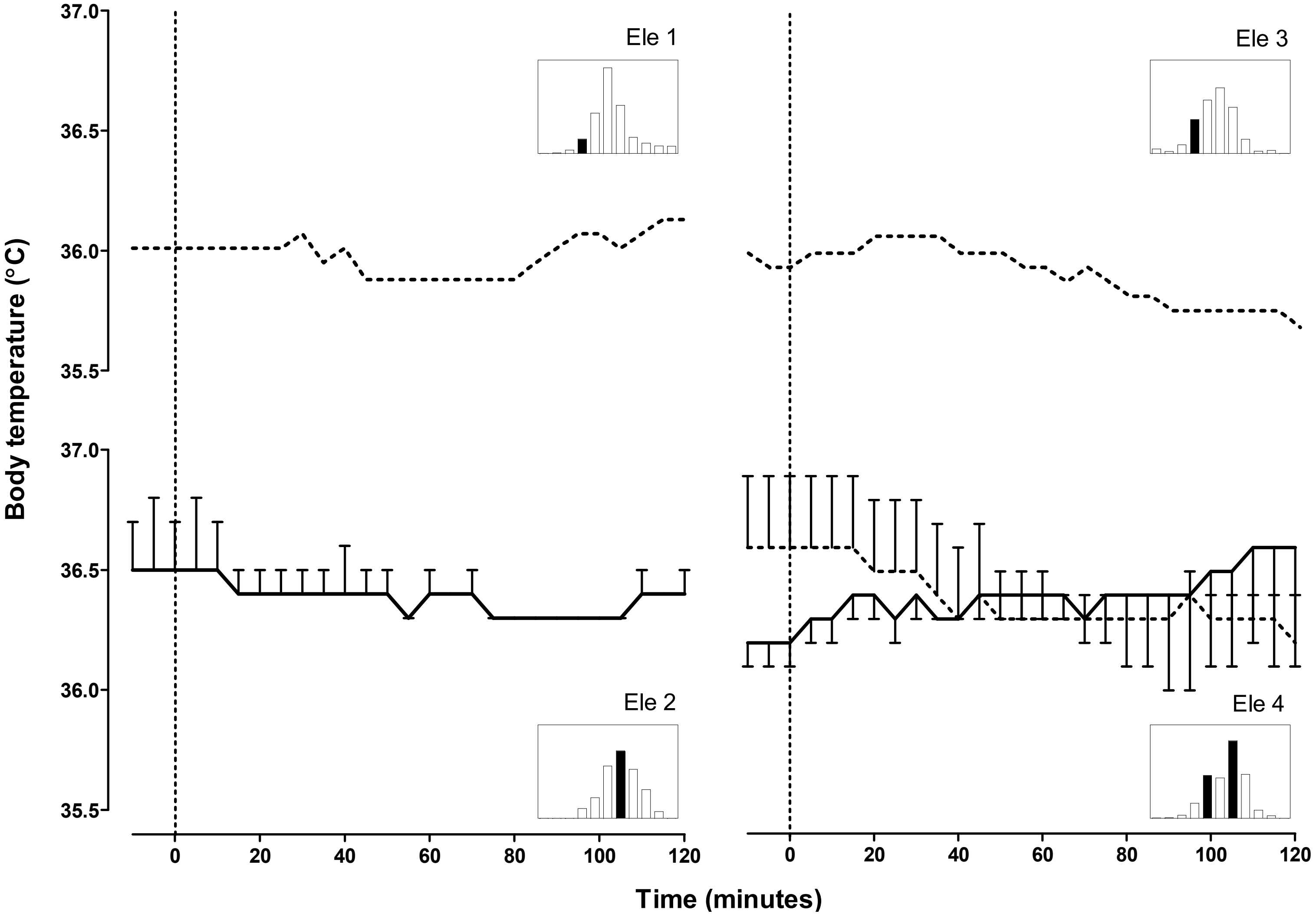

Figure 5.3 Elephant body temperature from 10 minutes prior to splashing and for 120 minutes following. The solid lines represent the mean temperatures recorded for afternoon splashing events for each elephant (n = 0, 2, 0, 2), and the dashed lines represent the mean temperatures recorded for morning splashing events (n = 1, 0, 1, 4). Error bars represent one SD. The inserts illustrate the frequency distributions of body temperature and the solid bars indicate the temperature at which the elephant tended to splash themselves.

5.4.2 Periods of increased activity and elephant body temperature

The changes in elephant body temperature during rides (60 minutes), as well as the changes in temperature during the following 60 minutes, are shown for each elephant in Figure 5.4. During the morning rides, body temperature appeared to be stable throughout the 120 minute period, while during the afternoon, body temperature appeared to increase slightly. I found a mean decrease in body temperature of 0.2 ± 0.03°C over the course of morning rides (60 minutes); and a mean increase of 0.1 ± 0.2°C over the course of afternoon rides.

There was only one day when no rides were conducted. Therefore, the changes in body temperature during rides could not be compared with changes in temperature (at the same time of day) when the elephants were not engaged in increased levels of activity. The mean body temperature pattern over 24 h (for all the elephants) is illustrated in Figure 5.5, which also indicates the periods during which the animals were engaged in rides. Despite the increase in physical activity, elephant body temperature decreased during the morning ride, and the increase in body temperature during the afternoon ride did not appear to occur more rapidly than it did at other times of the day.

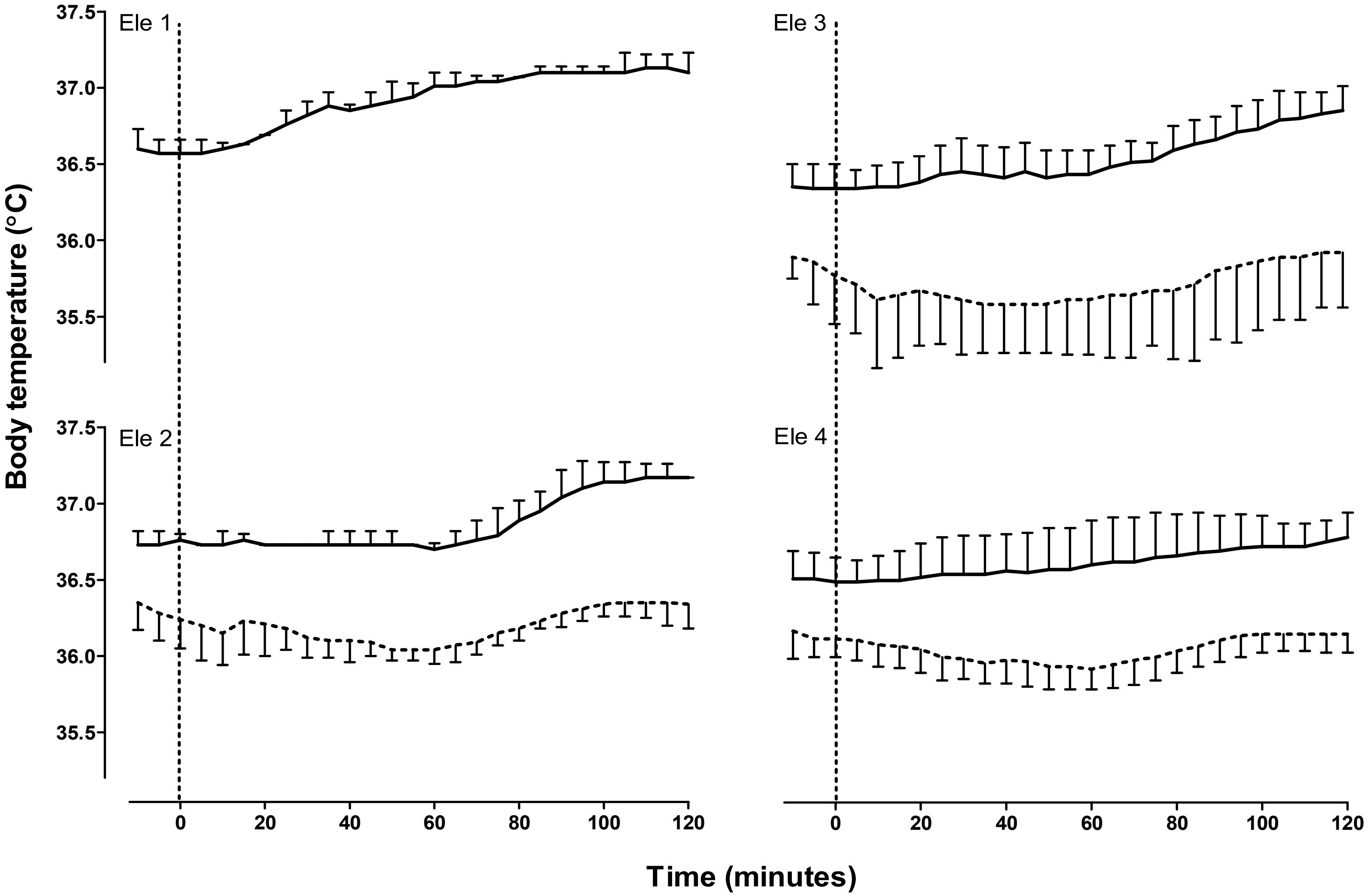

Figure 5.4 Elephant body temperature from 10 minutes prior to rides and for 120 minutes following the start of rides. The solid lines represent the mean temperatures recorded for afternoon rides for each elephant (n = 2, 2, 4, 9), and the dashed lines represent the mean temperatures recorded for morning rides (n = 0, 4, 2, 7). Error bars represent one SD.

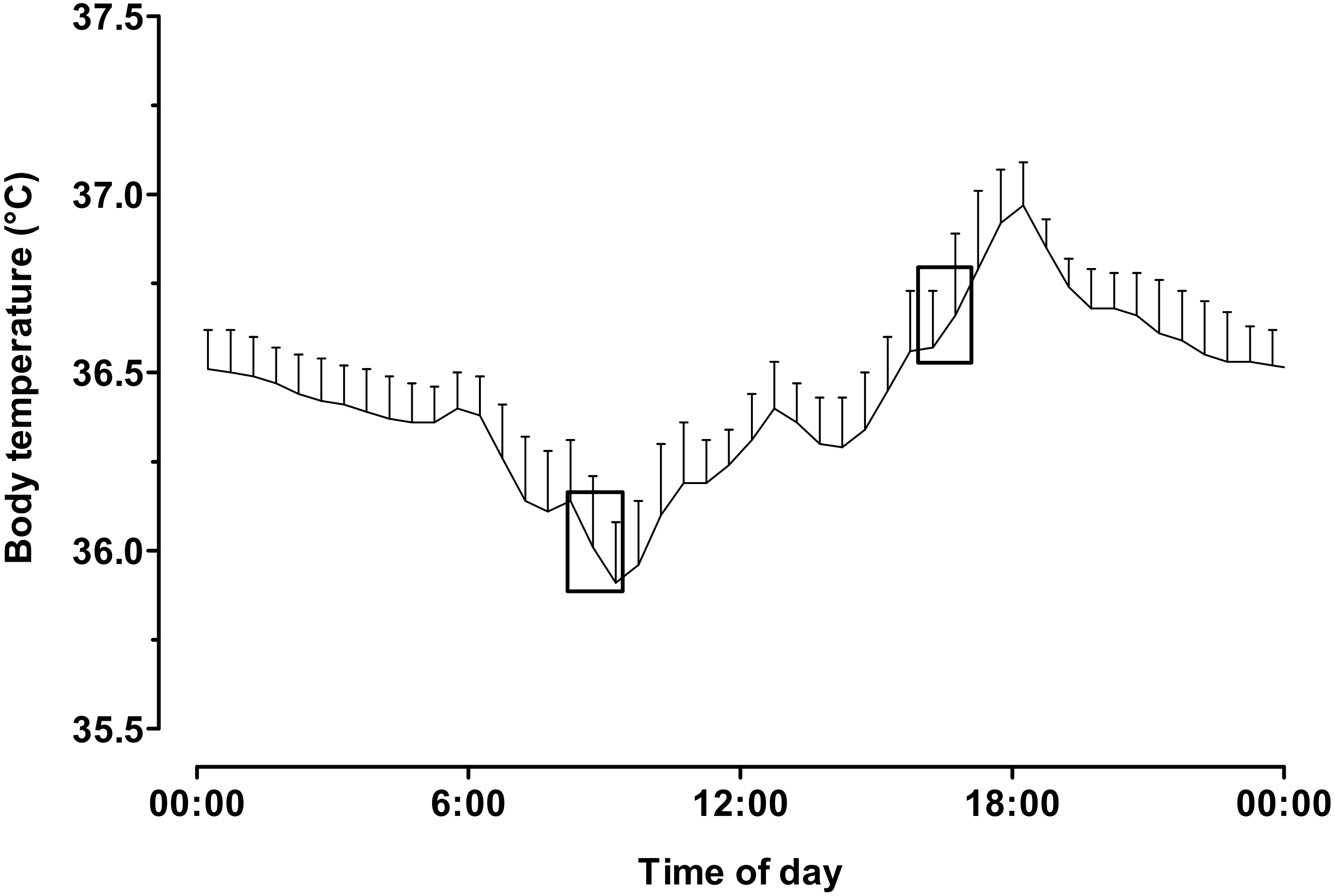

Figure 5.5 Plot of mean elephant body temperature over 24 h. Body temperature was averaged over 30-minute intervals and the average of the four elephants calculated for each interval. The rectangles represent the morning and afternoon rides given to tourists. Error bars represent one SD.

5.4.3 Ear-flapping behaviour

The frequency distribution of flap rate data recorded at 30-minute intervals for the four elephants over two days during the hot period is shown in Figure 5.6. “No ear-flapping” (flap rate equal to zero) was observed 20% of the time, and flap rates of between one and five per minute were the most frequently observed (24%). Low flap rates were observed more often than high ones.

Relationship between climatic variables and ear flapping

The plots of air temperature against flap rate are given in Figure 5.7. At air temperatures below 20°C the elephants usually flapped their ears less than ten times per minute. At air temperatures between 25 and 40°C, flap rate tended to be higher, but there was much variability in the flap rates at higher air temperatures. I found that there was a statistically significant association between air temperature and flap rate for all four elephants, however, the r values showed that the association was not strong. The flap rate data recorded over two days in the hot period, and averaged for all four elephants (mean flap rate for each 2°C class of air temperature), are illustrated in Figure 5.8. The curve which best fit these data was $y = a + bx^c$ (where $a = -3.968$, $b = 0.034$ and $c = 1.829$) and the association between the two variables was statistically significant. The r-squared value showed that this mathematical relationship between the variables was very strong.

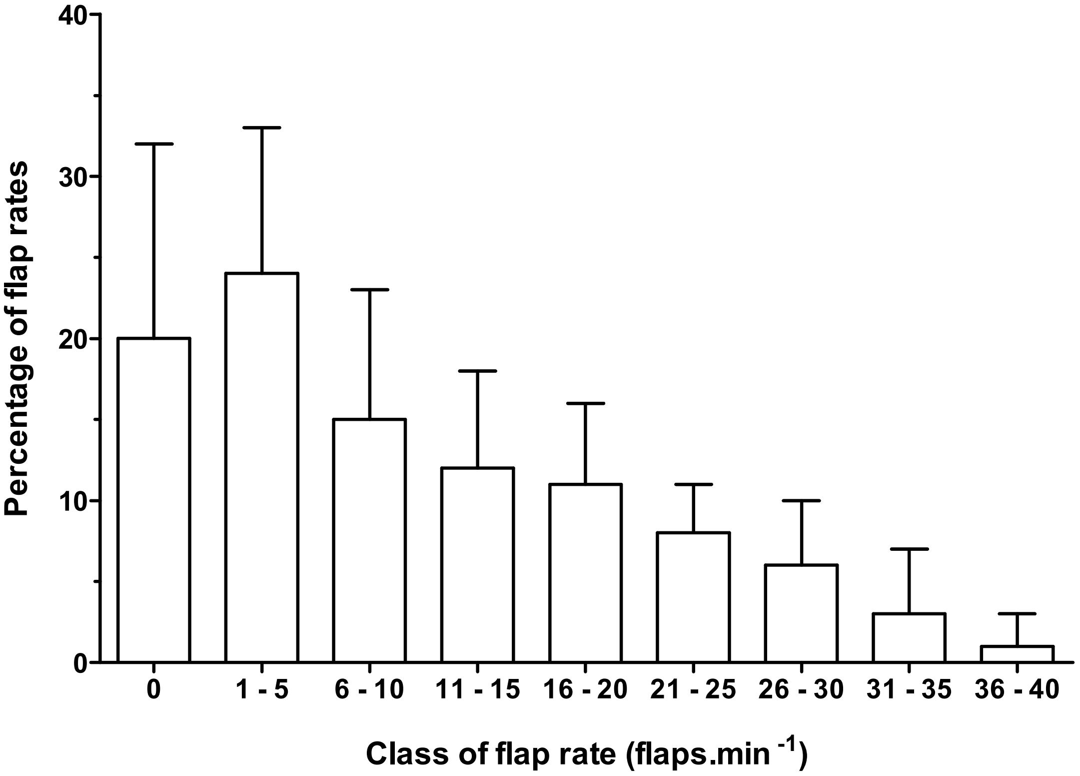

Figure 5.6 Frequency distribution of flap rates for four elephants (mean + SD). Flap rates were recorded every 30 minutes from 6:00 to 18:00 on two days during the hot period. For each elephant, the frequency of flap rates within each class was calculated as a percentage of the total flap rates recorded over the two days. The percentage for each class was then averaged across the four elephants to produce a mean percentage for each class of flap rate.

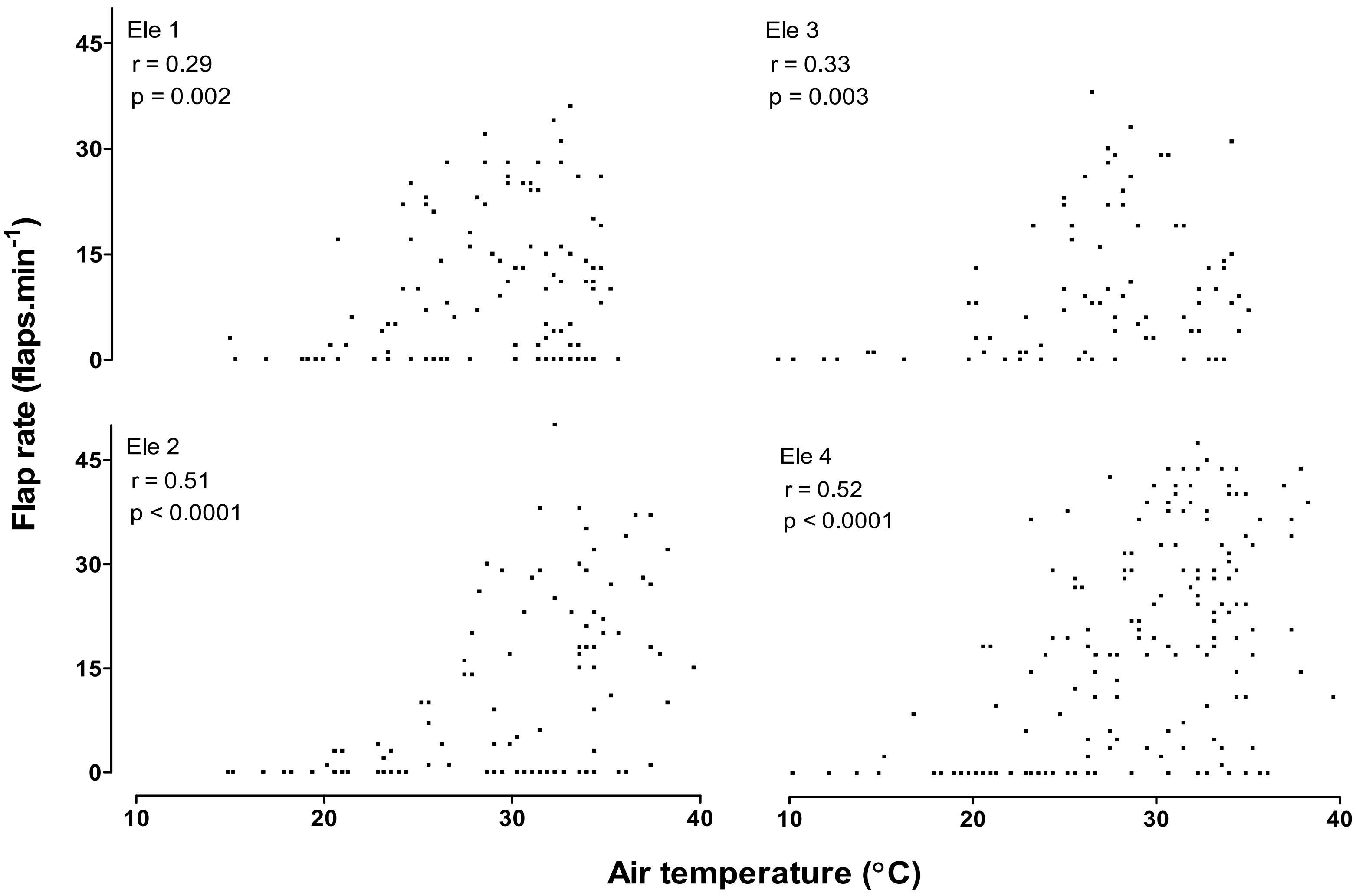

Figure 5.7 Rate of ear flapping plotted against the corresponding air temperature, for each elephant. Data for Elephants 1 and 2 were recorded during the hot period and for Elephants 3 and 4 during the hot and warm periods (n = 111, 97, 80, 181 pairs). Flap rates recorded when an elephant was wet or engaged in water-related activities were excluded.

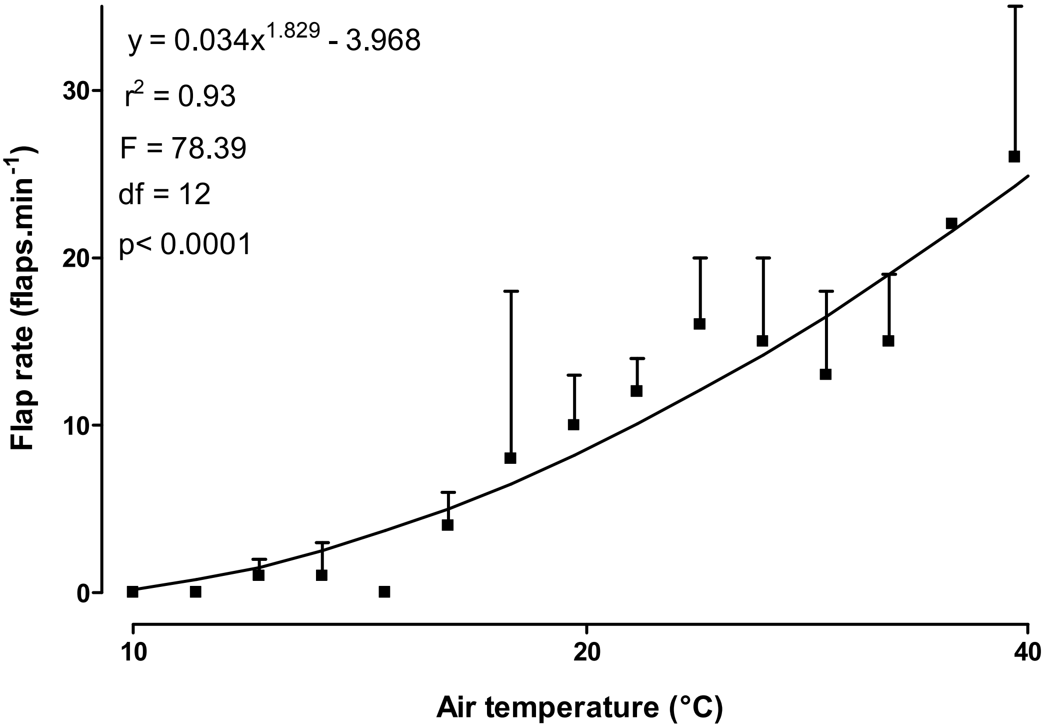

Figure 5.8 Mean flap rate (+SD) for each 2°C class of air temperature. Mean flap rate was calculated for each class for each elephant and the average across elephants was then calculated for each class. Flap rates were recorded every 30 minutes for each of the four elephants from 6:00 until 18:00 for two days during the hot period.

Figure 5.9 shows the plot of black globe temperatures against flap rates for each elephant. At black globe temperatures below 25°C, the elephants tended not to flap their ears. At temperatures above 25°C, the elephants tended to flap their ears at a faster rate, but there was a high degree of variability in the flap rate at globe temperatures above 25°C. I found that there was a significant association between globe temperature and flap rate for all four elephants, however, the r values showed that the relationship was not strong. The flap rate data recorded over two days in the hot period and averaged for all four elephants (mean flap rate for each 2°C class of black globe temperature) are illustrated in Figure 5.10. The simple equation which best fit the averaged data was $y = mx + c$ (where $m = 0.868$ and $c = -1.737$), but the fit of the curve was not nearly as good as it was for air temperature, as indicated by the r-squared value, however, the relationship was statistically significant.

To assess the relationship between the intensity of solar radiation and flap rate, scatter plots of the two variables were constructed for each elephant (n = Elephant 1: 100, Elephant 2: 81, Elephant 3: 38, and Elephant 4: 128). Data were recorded during the hot period only due to a malfunction of the solar radiation sensor during the warm period. No relationship was evident between the intensity of solar radiation and flap rate.

For the observations of the presence or absence of ear flapping, the Fisher's Exact tests showed that standing in the sun or in the shade had no effect on ear-flapping behaviour, except for Elephant 2 (p values: Elephant 1: 1.0, Elephant 2: 0.003, Elephant 3: 0.18, Elephant 4: 0.26). There was no association between the variables for any of the elephants

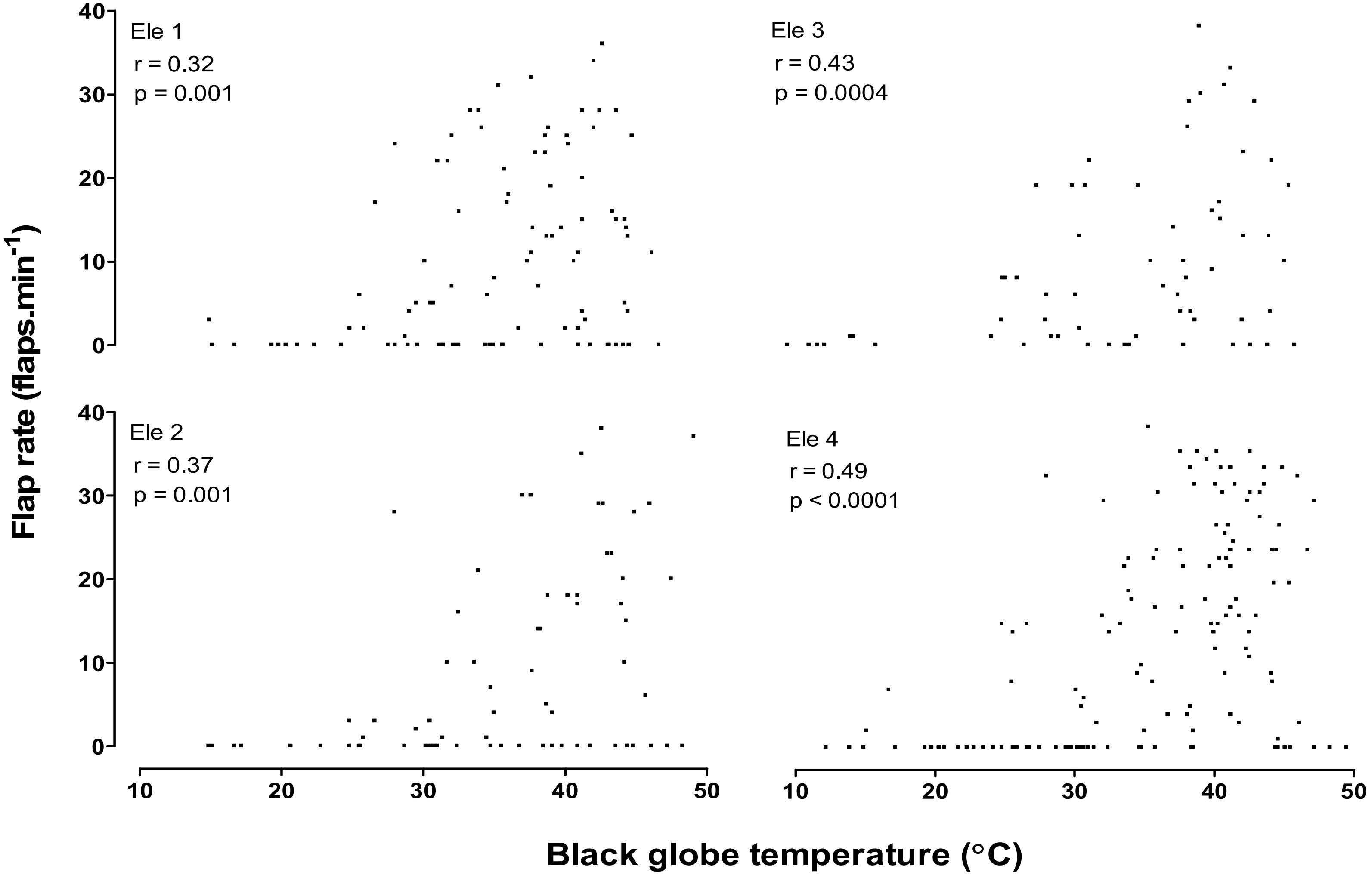

Figure 5.9 Rate of ear flapping plotted against the corresponding black globe temperature, for each elephant. Data for Elephants 1 and 2 were recorded during the hot period and for Elephants 3 and 4 during the hot and warm periods (n = 99, 76, 64, 143). Flap rates recorded when an elephant was wet or engaged in water-related activities were excluded. The curve which best fit the data for all elephants was $y = mx + c$.

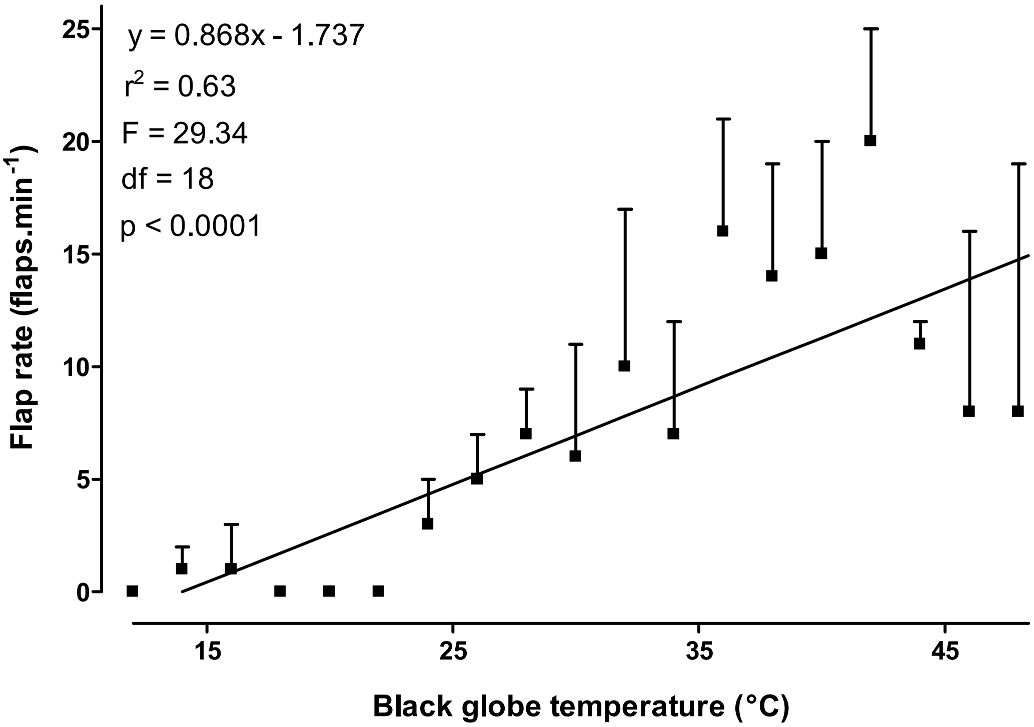

Figure 5.10 Mean flap rate (+SD) for each 2°C class of black globe temperature. Mean flap rate was calculated for each class for each elephant and the average across elephants was then calculated for each class. Flap rates were recorded every 30 minutes for each of the four elephants from 6:00 until 18:00 for two days during the hot period.

when the analysis was repeated for observations made at globe temperatures above 30°C (p values: Elephant 1: 0.42, Elephant 2: 0.16, Elephant 3: 1.0, Elephant 4: 0.66).

Relationship between elephant body temperature and ear flapping

Figure 5.11 shows the traces of Elephant 4's body temperature, from 6:00 to 18:00, on two days during the hot period. Indicated on the graph by horizontal lines are periods when I observed the elephant to be "flapping" or "not flapping" his ears. Body temperature appeared to be unaffected by ear flapping, even when the elephant flapped its ears continuously for 80 to 95 minutes, and ear flapping was not initiated when body temperature was high. The results of the Fisher's Exact tests showed that there was no effect of "flapping" or "not flapping" on body temperature over a period of 20 minutes, except for Elephant 4 (p values: Elephant 2: 0.63, Elephant 3: 1.0, Elephant 4: 0.04). An insufficient number of observations, to be able to conduct this analysis, were made for Elephant 1. On several occasions body temperature either increased, or did not change, during bouts of continuous ear-flapping behaviour.

Body temperatures and the corresponding flap rate (when recorded) were plotted against each other for Elephants 1, 3 and 4 (Figure 5.12); insufficient data were recorded for Elephant 2. No relationship between these two variables was evident in the scatter plots and therefore no further statistical analysis was conducted.

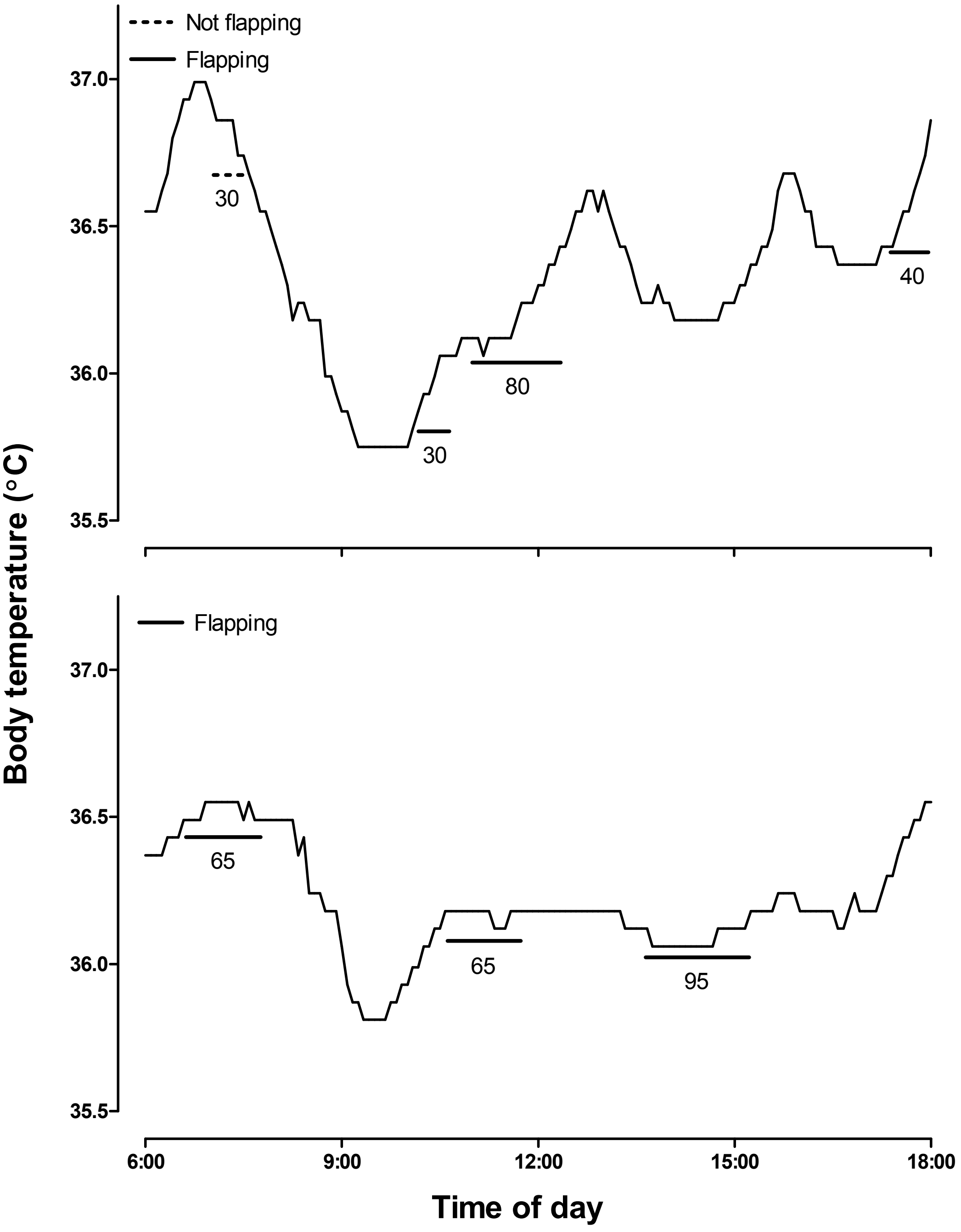

Figure 5.11 Body temperatures recorded during the day for Elephant 4 on two days during the hot period. Periods of "flapping" are indicated by solid horizontal lines and periods of "not flapping" by broken horizontal lines. The length of time (in minutes) spent engaged in the behaviour is given by the number below the line.

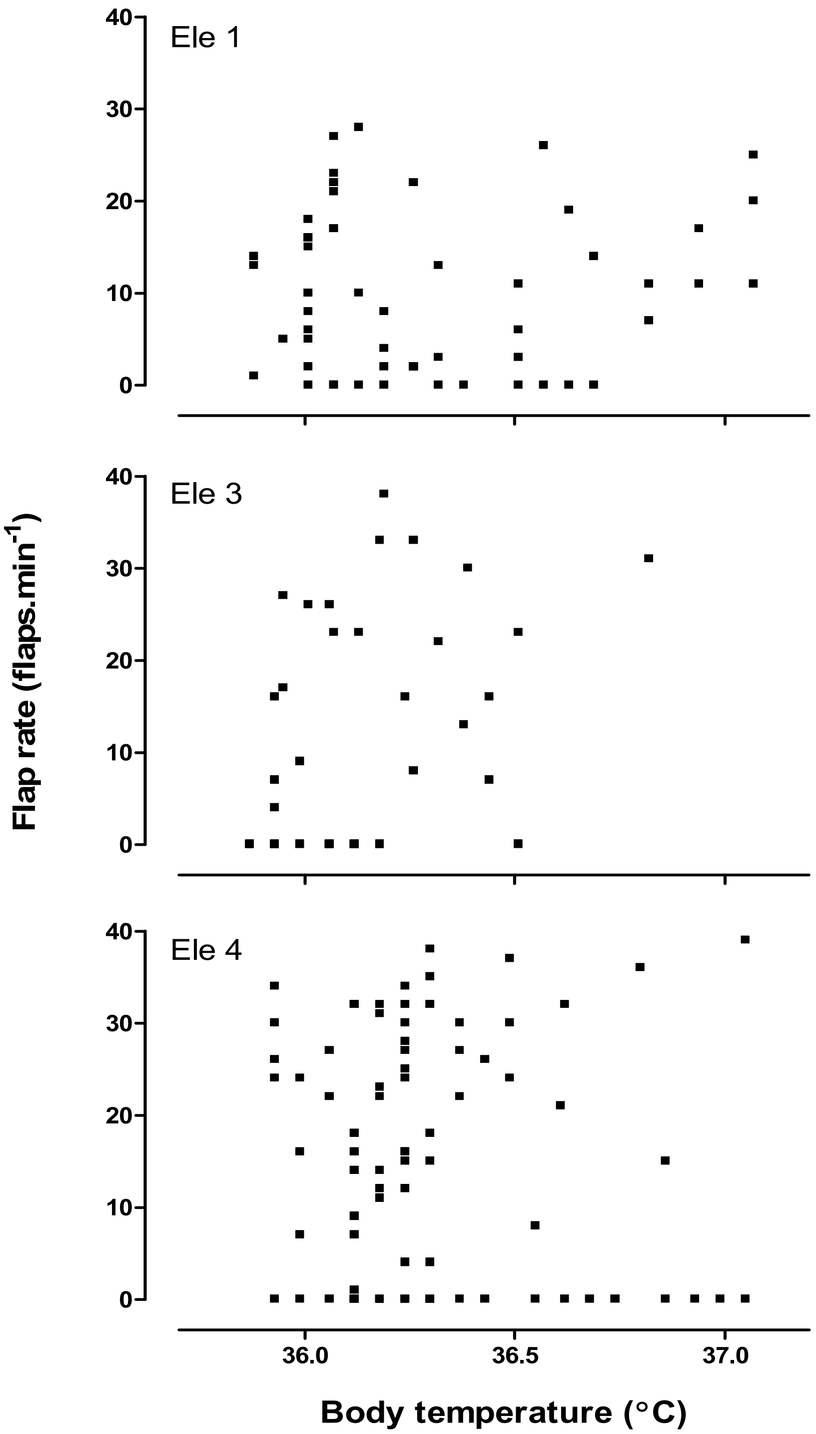

Figure 5.12 Rate of ear flapping plotted against the corresponding body temperature for three elephants. Data were recorded during the hot period for Elephant 1 (n = 61), and during the hot and warm periods for Elephant 3 (n = 37) and 4 (n = 88). Insufficient data were recorded for Elephant 2. Flap rates recorded when the elephants were wet or engaged in water-related activities, or when the elephants were in the shade, were excluded.

5.5 Discussion

To my knowledge, my study is the first to investigate, in African elephants in their natural environment, the relationship between elephant body temperature and behaviours considered to be of thermoregulatory importance. I found that drinking was not always followed by a decrease in body temperature. Swimming and splashing also did not consistently result in substantial decreases in elephant body temperature. Drinking, swimming and splashing were not prompted by higher than average body temperatures which, together with the absence of a decrease in body temperature, suggests that these behaviours were not employed for the regulation of core temperature. Swimming and splashing may be hedonistic (that is, simply for pleasure), rather than for effecting a reduction in body temperature. Alternatively, swimming and splashing may be anticipatory that is, triggered by skin temperature and effective in attenuating a rise in internal body temperature which is expected to occur. However, I did not assess the attenuation of a rise in body temperature by swimming and splashing. Ear flapping also may reduce the rate at which body temperature increases, a hypothesis which could be tested probably only by preventing flapping. I found that an increase in elephant body temperature did not prompt an increase in the frequency of ear flapping, and that continuous flapping of the ears did not reduce internal body temperature. Environmental temperature influenced the rate of ear flapping, but it appeared to be air temperature rather than environmental heat load, as reflected in black globe temperature, that influenced the frequency of ear flapping.

In much the same way that traditionally-accepted thermoregulatory behaviours did not influence elephant body temperature, increased activity did not. In my study, I found that prolonged periods (lasting about 60 minutes) of increased activity did not produce an increase in body temperature. I did not assess the influence of increased activity on the rate of ear flapping.

The activity in which an elephant was engaged immediately prior to measurements of flap rate may have influenced the magnitude of flap rate, which is why I excluded any flap rates recorded when the elephant was wet or engaged in water-related activities from the analyses. Periods of increased activity also may have influenced the rate of ear flapping, but I did not record flap rates before and after the rides on a sufficient number of occasions to determine the influence of increased activity on ear flapping. However, the rides did not incur increased energy expenditure anything close to the maximum for the elephants, as the pace at which the elephants walked was relatively slow (6km.h^{-1}). Elephants do not often run due to the strain that high speeds place on the bones of their legs (Langman *et al.*, 1995), but have been reported to be able to move at speeds of 22 km.h^{-1} or more (Hutchinson *et al.*, 2003), which is more than three times the pace at which my study animals moved during rides. I was unable to compare the pattern of body temperature during and after rides with body temperatures recorded, at the same time of day, when the elephants were not providing rides to tourists. It may be that the pattern of body temperature was influenced to some extent by the rides, but since elephant body temperature increased by less than 0.1°C on average during rides in the afternoon, and decreased during rides in the morning, this level of physical activity did not appear to have a large influence on elephant body temperature.

Because the elephants I studied were engaged in tourist-related activities for portions of the day, some of their natural behaviour (such as swimming, but not ear flapping) was restricted at certain times of day. Therefore, I was unable to assess the influence of environmental heat load on the frequency of occurrence of these behaviours. Since the elephants were housed in stables overnight, their behaviour was restricted during this time also. However, the elephants had access to their full suite of natural behaviour during parts of the day and I was able to assess the effects of certain behaviours, such as drinking and swimming, on body temperature during these times. It is possible that the magnitude of the effect of drinking on body temperature was dependent on the volume of water ingested, but I did not attempt to estimate these volumes. Also, the position of the temperature-sensitive device in the gastrointestinal tract might have influenced the magnitude of the decrease in body temperature associated with drinking, but it was impossible to determine where devices were situated within the gastrointestinal tract.

The influence of the position of the device in the gastrointestinal tract on the sensitivity of the device to the ingestion of water was not clear. Temperature-sensitive devices that had been ingested four and six hours before drinking events recorded smaller decreases in body temperature (0.0 and 0.06°C) after the ingestion of water than a device which had been in the gastrointestinal tract for three days (1.2°C). Also, it would be a mistake to assume that all rapid decreases in temperature reflected drinking, as I observed changes of up to 0.3°C overnight when the elephants had no access to water. Since the largest difference in the temperatures recorded by two devices in the gastrointestinal tract was 0.3°C (see Chapter 3), it is possible that such changes in body temperature were due to a rapid shift in the position of the device along the tract.

However, decreases in body temperature greater than 0.3°C occasionally were recorded during the day (usually in the morning) and these always coincided with drinking events; on one occasion elephant body temperature decreased by 0.44°C in five minutes after the elephant had ingested water (even though the temperature-sensitive device had been ingested three days prior to the drinking event). Similar drinking-related decreases of recorded temperature have been reported for other animals (Mitchell *et al.*, 1997; Fuller *et al.*, 2005). Elephants consume large quantities of water at times (Sikes, 1971) and if the water is below body temperature, some heat will be drawn from the body, most immediately from the tissues of the gastrointestinal tract. When an elephant drank cold water (8 to 12°C) under cool ambient conditions (about 12°C), it shivered (Benedict, 1936), so I believe that is quite plausible that the ingestion of water, which is at a temperature lower than that of an elephant's body, does indeed influence the thermal status of the animal.

I did not quantify the water ingested by the elephants, and therefore could not calculate the influence of the ingestion of a known volume of water on elephant body temperature. However, using calorimetry, I calculated the quantity of water that Elephant 4 would have had to have ingested in order to produce the 0.7ºC decrease in body temperature which I observed on one occasion when he drank (this was the largest drop in body temperature that I recorded, and took place over 70 minutes. The temperature of the water was 25ºC). I found that Elephant 4 would have had to drink about 260 l of water[2], which I know was not the case as he drank only momentarily. The decrease in body temperature which accompanied the ingestion of water may have been the consequence of a physiological reaction, such as a change in the distribution of blood in the body, but does not appear to have been a direct result of cooling of body tissues by the ingested water. The results of the analysis of the effect of other drinking events on body temperature further supported the observation that drinking exerted a limited influence on elephant core body temperature.

The internal body temperature of the elephants I studied sometimes was lower than average after drinking, but there were several occasions when body temperature was higher than average. The mean difference between the temperatures recorded after drinking and mean body temperature was small (0.0°C in the morning when body temperature usually was decreasing, and 0.1°C in the afternoon when body temperature was usually increasing). Therefore, although drinking was followed by decreases in body temperature on occasion, it did not consistently result in a reduction in elephant body temperature. However, drinking may be followed by a decrease in body temperature if an elephant is dehydrated and drinks a very large quantity of water.

It was surprising that swimming also did not consistently result in a decrease in elephant body temperature. Wallowing in water is considered an important thermoregulatory behaviour in other large African herbivores (Noirard *et al.*, 2008), and has been reported to

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[2] Refer to Appendix A for details of this calculation.

reduce rectal temperature below average in rhinoceros (Allbrook *et al.*, 1958) and hippopotamus (Luck & Wright, 1959). Body temperature tended to increase slightly while the elephant was immersed and for a short while after the elephant had left the water. This increase in body temperature may have resulted from vasoconstriction of the vessels in the skin, caused by the sudden exposure of the warm skin to the cooler water (water was usually about 6°C lower than internal body temperature, except in the early morning when it was 12°C lower). Body temperature decreased substantially during Elephant 4's morning swim (the only early morning swimming event I observed, but elephant body temperature normally decreased at this time of the day. Also, body temperature throughout this morning swim was higher than the average temperature recorded for Elephant 4 at this time of day. Elephant 1 also swam in the morning, but the swim took place later in the morning (around 10:30) which was after the minimum body temperature occurred. Body temperature did not decrease at all during Elephant 1's morning swim. It is also interesting that the elephants did not swim when internal body temperature was higher than average (that is, when the elephants might have felt hot). Although the elephants could not swim during the rides, they had the opportunity to swim once the tourist-related activities ended (for example, after the afternoon rides, the elephants were free to swim in the dam had they chosen to do so).

The same was true of splashing; the elephants did not splash themselves when internal body temperature was high, in spite of the opportunity to do so. As with swimming, splashing produced no consistent decrease in elephant body temperature. In the morning, elephant body temperature was higher after an elephant had splashed itself with water than mean body temperature for the corresponding time of day. In the afternoon, it seems that splashing had no effect on body temperature. Kinahan and colleagues (2007a) found no significant differences in the mean body temperature, or the amplitude of body temperature, between days when elephants were sprayed with water by the investigators and days when they were not sprayed, a result which they attributed to the large amount of variation between the elephants. However, it seems that the splashing of water may indeed produce no decrease in elephant body temperature. Swimming and splashing may be more for enjoyment, or may be prompted by increases in skin temperature. By responding to increases in environmental temperature, sensed by an increase in skin temperature, elephants may avoid an increase in core temperature. I observed that the elephants swam and splashed themselves more frequently during the hot period than during the cold and warm periods. However, the interaction of environmental heat load, behaviour and skin temperature requires further investigation.

Swimming and splashing did not produce a consistent decrease in internal body temperature, but was this true of ear flapping? Ear flapping has been suggested as being important in elephant thermoregulation, especially since the ears are said to be used as “thermal windows” (Phillips & Heath, 1992). I therefore assessed the effect of continuous ear flapping on internal body temperature, and found that there was no decrease in body temperature even after 95 minutes of ear flapping. On many occasions, body temperature increased despite prolonged periods of continuous ear flapping. I found also that higher than average body temperatures did not result in higher than average flap rates, so the elephants did not flap their ears more frequently in response to an increase in internal body temperature.

However, the frequency of ear flapping must have been influenced by other factors, since ear flapping was not an “on” or “off” response; there were occasions when the elephants flapped their ears more frequently, and times when the elephants flapped their ears less frequently. Previous investigators have described an increase in flap rate with increasing ambient temperature (Buss & Estes, 1971), which I also observed. I found that ear flapping tended to occur less frequently during the cool of the morning than during the heat of the day, and occurred less frequently during the cold period than during the hot and warm periods. Unlike earlier investigators, who considered only the influence of air temperature on ear flapping, I used black globe temperature to assess the influence of environmental heat load (including the influence of solar radiation and wind speed) also.

I found that flap rate increased exponentially with increasing air temperature, and the variation in air temperature accounted for 93% of the variation in flap rate. Flap rate also increased with increasing black globe temperature, but the relationship between flap rate and black globe temperature was different. At very high black globe temperatures (about 45°C) flap rates were lower than flap rates at globe temperatures of around 40°C and there was a high degree of variability in the flap rate at high black globe temperatures. Consequently, changes in black globe temperature accounted for only 63% of the variation in ear flap rate. Since wind speed and solar radiation are included in the black globe temperature, I concluded that these two factors might also influence the rate of ear flapping.

I examined the influence of solar radiation on ear flapping and found that the rate of ear flapping was not dependent on the intensity of solar radiation. Exposure to the sun did not always result in ear flapping and the elephants often flapped their ears when standing in the shade, probably in response to air temperature. Therefore, I concluded that solar radiation exerted no noticeable influence on the frequency of ear flapping, and I subsequently considered the influence of wind speed.

I was unable to assess the influence of wind speed on flap rate since the wind speed values recorded by the weather station did not always accurately reflect the conditions to which the elephants were subjected, due to the topography of the landscape. However, other investigations have shown that increased wind speeds produce a decrease in the rate of ear flapping, and at high winds speeds elephants often stop flapping their ears and instead hold their ears perpendicular to their bodies, allowing the wind to blow onto either the anterior or posterior surface of the pinnae (Buss & Estes, 1971). Therefore, it seems that wind probably influenced the rate of ear flapping also.

What I can conclude from the results of my investigation is that the rate of ear flapping changes in response to changes in climatic variables, one of which is most certainly air temperature. Air temperature and wind speed may influence skin temperature, which may in turn influence elephants' use of thermoregulatory behaviours such as ear flapping. The issue of why flap rate is better predicted by air temperature than by black globe temperature remains to be resolved. The inclusion of solar radiation in black globe temperature, and the fact that solar radiation does not influence the rate of ear flapping, may partly explain the deterioration of the relationship between black globe temperature and flap rate.

Another factor which may have influenced the rate of ear flapping was the level of the elephants' physical exertion; perhaps an increase in the rate of ear flapping would, under these circumstances, assist the dissipation of excess body heat. Increased activity increases metabolic heat production and, if the heat produced by the body's tissues is not dissipated, results in an increase in body temperature (Gordon *et al.*, 1982). An activity-related increase in body temperature was reported for Asian circus elephants, after only 10 minutes of walking (Toscano, 2001), a result which was inconsistent with my findings. In the elephants that I studied, there did not appear to be a hyperthermia associated with periods of increased activity during the afternoon, despite the additional factor of a large environmental heat load in the hot period. And in the morning, body temperature decreased despite the elephants' increased activity; the 24 h minimum often occurred during the ride. So it seems that walking has no effect on internal body temperature. However, as mentioned above, no comparison to a "normal" pattern of body temperature could be made, and the activity might have influenced the pattern of body temperature. It is also probable that the rides did not represent an increase in metabolic rate sufficient to raise internal body temperature. Investigation of the influence of higher-intensity activity on elephant body temperature is needed.

Chapter 6

Summary and conclusions

Elephants are a keystone species (Sukumar, 2003) and play an important role in the ecosystems of which they are a part (Pringle, 2008). Although the data regarding elephant numbers across Africa is not reliable due to inconsistent or poor sampling techniques in many regions (Blanc *et al.*, 2005), several trends are evident. The populations in southern and eastern Africa have recovered remarkably from the heavy poaching and hunting which took place in the eighteen and nineteen hundreds (Carruthers *et al.*, in press), even to the point where concern regarding the effects of certain elephant populations on biodiversity has been expressed (Cumming *et al.*, 1997; Kerley *et al.*, in press). In other regions, such as the western parts of Africa, the continued existence of elephant populations is uncertain (Barnes, 1999; Blanc *et al.*, 2007). The African elephant is still classified as Vulnerable by the IUCN (AfESG, 2004), and the destruction of habitat, as well as increasing conflict between humans and elephants (Blanc *et al.*, 2007), does indeed mean that this species may remain, on a continent-wide scale, in a vulnerable position.

Efficient management of elephant populations across Africa will be crucial for the long-term survival of the species. An understanding of the factors which influence elephants' survival, as well as their distribution and use of their habitat, is important for their efficient management. One such factor is elephant physiology. The importance of an understanding of animal physiology to studies of ecology is widely recognised, as an animal's physiology plays an important role in determining how it interacts with its environment (Hiley, 1975; Schmidt-Nielsen, 1977; Parker & Robbins, 1985; Wikelski & Cooke, 2006). An animal's physiological requirements may even be used to "predict the limits of the climatic habitat it must occupy to survive" (Porter & Gates, 1969). Environmental temperature may be a limiting factor in the distribution of species as an animal may select a particular habitat based on its thermoregulatory requirements (Huey, 1991).

The influence of environmental temperature on elephants' use of habitats has been demonstrated (Kinahan *et al.*, 2007b) but no attempt to assess the elephants' thermal state was made during the study. Several other investigations of elephant thermoregulation have been conducted, and each has made a valuable contribution to our understanding of elephant thermoregulatory physiology. However, continuous measurements of body temperature were not made, and the subjects of previous investigations either were living in zoos or circuses, or were deceased when measurements of body temperature were recorded. The studies which considered the role of behaviour in thermoregulation did not include measurements of body temperature at all. It was in the absence of such data that I undertook my investigation.

I was unable to investigate thermoregulation in truly free-living elephants, and as a compromise, worked with animals which were semi free-living. The elephants I studied were working elephants and as a consequence could not be implanted surgically with temperature-sensitive data loggers. Using several designs of ingestible device, I was able to record the gastrointestinal temperature of four elephant bulls. The use of ingestible data loggers for the measurement of body temperature is not a novel technique. However, studies which have previously employed the technique in large animals did not attempt to use ingestible data loggers in animals given the freedom to move through large areas of their natural habitat. Also, the issue of damage to devices during transit had not received adequate attention. Covering devices in insulation tape and wax appears to provide adequate protection against moisture, as well as any other chemical and mechanical forces to which devices are most likely subjected during transit though an elephant's gastrointestinal tract. By a process of trial and error, I found that the most successful technique involved the attachment of a length of ribbon to a data logger, which was covered in wax. I acknowledge that the use of such a technique may not be feasible in studies of the thermoregulatory physiology of wild elephants, and cannot be used in studies that require real-time data. However, I believe that the technique provides a reliable means of recording multiple measurements of internal body temperature in tame elephants and may have application in other large animals, given that investigators are aware of the possible limitations.

Differences in temperature along the gastrointestinal tract were a potential concern, but no significant differences in temperature along the gastrointestinal tract were observed, and the position of a data logger did not affect the 24 h pattern of body temperature which was recorded. However, I acknowledge that the use of gastrointestinal temperature as a measure of "core" body temperature in animals of very large body size remains to be validated. Gastrointestinal temperature may differ from blood temperature in the speed with which short-term changes occur, and in the magnitude of these changes. Nevertheless, I was able to assess the daily pattern of elephant body temperature and how body temperature responded to environmental temperature. Despite their large size, the elephants' internal temperature exhibited a greater number of short-term changes, and 24 h amplitude was similar to that of animals of considerably smaller body mass. As observed for several other

African mammals, the 24 h pattern of body temperature appeared to be endogenous, and was independent of environmental temperature. I did not see a shift in the pattern of body temperature across the climatic periods, but I acknowledge that the data recorded during the cold and warm periods were limited. I found no evidence of adaptive heterothermy in the elephants I studied, but it is possible that adaptive heterothermy is employed by individuals exposed to high water and heat stress, especially if their ability to thermoregulate behaviourally (for example seeking shade) is limited by the habitat they occupy.

Although not many large deviations of body temperature were observed in the elephants I studied, substantial short-term changes in body temperature were evident occasionally. These changes might have been a consequence of the technique of body temperature measurement, but I was compelled to determine whether they were the result of certain behaviour. I investigated the influence of selected behaviour on elephant body temperature and found that drinking, swimming and splashing did not consistently produce a decrease in elephant body temperature. Furthermore, high body temperatures did not appear to prompt the elephants to engage in swimming or splashing behaviour. I did not consider all thermoregulatory behaviours in my study, and activities such as shade seeking and dust bathing should perhaps be included in future investigations. I did consider ear flapping and found that it too did not cause a decrease in body temperature, and I found that an increase in ear flapping was not prompted by an increase in internal body temperature. The frequency of ear flapping was influenced mostly by air temperature and to some extent by wind speed, but not by solar radiation. I was unable to assess the influence of environmental temperature on the frequency of the other behaviours I considered, but believe that elephants may employ behaviour such as swimming or splashing simply for the pleasure of it. Alternatively, the elephants might have employed these behaviours, and possibly ear flapping, in response to an increase in environmental heat load, through its effect on skin temperature. By responding proactively to an increase in environmental temperature, sensed by thermoreceptors in the skin, elephants may avoid increases in internal body temperature. Further study, including the measurement of skin temperature, is required to determine how African elephants respond behaviourally to changes in environmental heat load and how behavioural adjustments influence skin temperature.

It seems from my results that behaviours previously considered to exert an influence on the body temperature of large mammals (Allbrook *et al.*, 1958; Luck & Wright, 1959) do not result in the dissipation of large amounts of body heat, in spite of any effect on skin temperature. However, I believe that changes in the conductance of the skin, as effected by changes in peripheral vasomotor tone, are likely to be important in the regulation of elephant body temperature. I attempted to assess the interaction between internal and skin temperature, but I recorded insufficient data to be able to draw any conclusions. An understanding of the relationship between the 24 h patterns of internal and skin temperatures would assist our understanding of how elephants regulate their internal body temperature, and I recommend the undertaking of such research.

It is possible that, even under the harsh climatic conditions of the African savanna, elephants are not as heat-stressed as previously supposed. Because of their small surface area to volume ratio, elephants do not gain heat from their environment as quickly as do animals of smaller body size (Taylor, 1970a). Also, it seems that elephant locomotion is particularly efficient (Langman *et al.*, 1995) and, therefore, elephants probably do not produce as much metabolic heat (per gram of body tissue) during increased activity as animals of smaller body size. Nevertheless, it is likely that an elephant must dissipate some amount of heat in order to maintain a stable core body temperature. The dissipation of excess body heat by increasing the flow of blood through the skin is only effective when the temperature gradient favours loss in the direction of the environment; when environmental heat load exceeds body temperature, evaporative cooling is the only means by which an organism can lose body heat. The African elephant's capacity to dissipate body heat through the evaporation of water lost passively through the skin has been demonstrated (Wright & Luck, 1984), and I attempted to measure cutaneous moisture loss in my study animals, but was unable to record quantifiable results. There remains an inadequate understanding of the relationship between changes in cutaneous moisture loss and environmental heat load, and between changes in cutaneous moisture loss and internal body temperature, and further research is required. If elephants are especially dependent upon this means of dissipating excess body heat, it may explain their dependence on drinking water.

With the advance of global climate change, Africa is going to become both hotter and drier. The results of a recent study show that ambient temperatures across southern and western Africa have increased steadily over the last four decades, mainly evidenced in higher minimum temperatures, fewer "cold" days, and a greater number of "hot" days (New *et al.*, 2006). Although the net amount of rainfall per year did not decrease significantly over the same period, the dry season significantly increased in length (New *et al.*, 2006). A conservative prediction of future changes in rainfall, and of the resulting changes in surface water availability, showed that even small decreases in annual rainfall will have disastrous consequences across large portions of Africa (de Wit & Stankiewicz, 2006). Surface water availability determines the distribution and abundance of large herbivores in dry regions, although the extent of limitation depends on a species' water requirements, its capacity (and freedom) to move, and its physiology (Chamaillé-Jammes *et al.*, 2007a). The predicted changes in water availability and ambient temperature across Africa are likely to have serious impacts on body water balance and temperature regulation in terrestrial species (Martin & Nagy, 2002) and I believe that elephants will be no exception.

Elephants are strongly dependent on water (Skinner and Chimimba, 2005). The distribution of individuals varies with the availability of surface water (Chamaillé-Jammes *et al.*, 2007b) and potentially, as water becomes scarce, higher concentrations of elephants may be forced upon areas which may not able to cope with the increased pressure on vegetation (Van Aarde *et al.*, 2006). Elephants do survive in extremely arid regions such as the Namib (Viljoen, 1989) and Sahel (Blake *et al.*, 2003) deserts, but these populations are small and their continued existence in these regions is precarious. Also, increasing competition for resources with humans may mean that we will see extensive declines in elephant populations across Africa in the future. Investigations of thermoregulation in wild elephants, exposed to heat and water stress, will provide a better understanding of the African elephants' capacity to cope with the challenge of a hotter and drier climate.

In conclusion, it appears from the results of my study that the African savanna elephant, given access to sufficient water, is able to defend its body temperature in environmental (black globe) temperatures ranging from about -1 to 52°C. Our understanding of elephant thermoregulation is not yet complete, but I am of the firm conviction that an understanding of how an elephant's thermoregulatory requirements affect its use of its habitat and, therefore, its survival, will assist the management and conservation of one of Africa's iconic megafauna.

Chapter 7

References

Acocks J. (1988). *Veld types of South Africa. Memoirs of the Botanical Survey of South Africa, 3rd edition.* Botanical Research Institute, Department of Agriculture and Water Supply, South Africa.

African Elephant Specialist Group. (2004). *Loxodonta africana*. In: IUCN 2007 Red List of Threatened Species. <http://www.iucnredlist.org> Downloaded on 22 April 2008.

Allbrook D, Harthoorn A, Luck C & Wright P. (1958). Temperature regulation in the white rhinoceros. *Journal of Physiology* **143,** 51P - 52P.

Aschoff J. (1982). The circadian rhythm of body temperature as a function of body size. In: *A Companion to Animal Physiology*, ed. Taylor C, Johansen K & Bolis L, pp. 173 - 187. Cambridge University Press, Cambridge.

Baker M. (1979). A brain-cooling system in mammals. *Scientific American* **240,** 114 - 122.

Barnes R. (1999). Is there a future for elephants in West Africa? *Mammalian Review* **29,** 175 - 199.

Bartholomew G. (1964). The roles of physiology and behaviour in the maintenance of homeostasis in the desert environment. In: *Symposia of the Society of Experimental Biology*, ed. Hughes G, pp. 7 - 29. Cambridge University Press, Cambridge.

Bartholomew G. (1987). Interspecific comparison as a tool for ecological physiologists. In: *New Directions in Ecological Physiology*, ed. Feder M, Bennett A, Burggren W & Huey R, pp. 11 - 37. Cambridge University Press, Cambridge.

Benedict F, Fox E & Baker M. (1921). The skin temperature of pachyderms. *Proceedings of the National Academy of Science* **7,** 154 - 156.

Benedict F. (1936). The Physiology of the Elephant. Nutrition Laboratory, Carnegie Institution of Washington, Washington.

Benedict F & Lee R. (1936). Studies on the body temperatures of elephants. *Proceedings of the National Academy of Science* **22,** 405 - 408.

Benedict F & Lee R. (1938). Further observations on the physiology of the elephant. *Journal of Mammalogy* **19,** 175 - 194.

Blake S, Bouché P, Rasmussen H, Orlando A & Douglas-Hamilton I. (2003). *The last Sahelian elephants: ranging behaviour, population status, and recent history of the desert elephants of Mali*. Save the Elephants, Nairobi.

Blanc J, Barnes R, Craig C, Douglas-Hamilton I, Dublin H, Hart J & Thouless C. (2005). Changes in elephant numbers in major savanna populations in eastern and southern Africa. *Pachyderm* **38,** 19 - 28.

Blanc J, Barnes R, Craig C, Dublin H, Thouless C, Douglas-Hamilton I & Hart J. (2007). *African Elephant Status Report 2007: an update from the African Elephant Database*. Occasional Paper Series of the IUCN Species Survival Commission, No 33. IUCN/SCC African Elephant Specialist Group, Switzerland.

Bland J & Altman D. (1986). Statistical methods for assessing agreement between two methods of clinical measurement. *Lancet* **1,** 307 - 310.

Bligh J & Harthoorn A. (1965). Continuous radiotelemetric records of the deep body temperature of some unrestrained African mammals under near-natural conditions. *Journal of Physiology* **176,** 145 - 162.

Bligh J, Ingram D, Keynes R & Robinson S. (1965). The deep body temperature of an unrestrained Welsh mountain sheep recorded by a radiotelemetric technique during a 12-month period. *Journal of Physiology* **176,** 136 - 144.

Boulant J. (1991). Thermoregulation. In: *Fever Basic Mechanisms and Management*, ed. Mackowiak P, pp. 1 - 22. Raven Press, New York.

Brengelmann G. (1987). Dilemma of body temperature measurement. In: *Man in Stressful Environments - Thermal and Work Physiology*, ed. Shiraki K & Yousef M, pp. 5 - 22. Thomas Springfield.

Brown-Brandl T, Yanagi T, Xin H, Gates R, Bucklin R & Ross G. (2003). A new telemetry system for measuring core body temperature in livestock and poultry. *Applied Engineering in Agriculture* **19,** 583 - 589.

Buss I & Wallner A. (1965). Body temperature of the African elephant. *Journal of Mammalogy* **46,** 104 - 107.

Buss I & Estes J. (1971). The functional significance of movements and positions of the pinnae of the African elephant, *Loxodonta africana*. *Journal of Mammalogy* **52,** 21 - 27.

Byrne C, Lee J, Chew S, Lim C & Tan E. (2006). Continuous thermoregulatory responses to mass-participation distance running in heat. *Medicine and Science in Sports and Exercise* **38,** 803 - 810.

Byrne C & Lim C. (2007). The ingestible telemetric core temperature sensor: a review of validity and exercise applications. *British Journal of Sports Medicine* **41,** 126 - 133.

Carruthers J, Boshoff A, Slotow R, Biggs H, Avery G & Matthews W. (in press). The elephant in South Africa: History and distribution. In: *Assessment of South African*

Elephant Management, ed. Scholes R & Mennell K, pp. 1 - 50. Witwatersrand University Press, Johannesburg.

Casa D, Becker S, Ganio M, Brown C, Yeargin S, Roti M, Siegler J, Blowers J, Glaviano N, Huggins R, Armstrong L & Maresh C. (2007). Validity of devices that assess body temperature during outdoor exercise in the heat. *Journal of Athletic Training* **42,** 333 - 342.

Cave A & Allbrook D. (1958). The skin and nuchal eminence of the white rhinoceros. *Proceedings of the Zoological Society of London* **132,** 99 - 107.

Cena K & Clark J. (1973). Thermographic measurements of the surface temperatures of animals. *Journal of Mammalogy* **54,** 1003 - 1007.

Chamaillé-Jammes S, Fritz H & Murindagomo F. (2007a). Climate-driven fluctuations in surface-water availability and the buffering role of artificial pumping in an African savanna: potential implication for herbivore dynamics. *Australian Ecology* **32,** 740 - 748.

Chamaillé-Jammes S, Valeix M & Fritz H. (2007b). Managing heterogeneity in elephant distribution: interactions between elephant population density and surface water availability. *Journal of Applied Ecology* **44,** 625 - 633.

Cole P. (1953). Further observations on the conditioning of respiratory air. *Journal of Laryngology and Otology* **67,** 669 - 681.

Cooke S, Hinch S, Wikelski M, Andrews R, Kuchel L, Wolcott T & Butler P. (2004). Biotelemetry: a mechanistic approach to ecology. *Trends in Ecology and Evolution* **19,** 334 - 343.

Craighead J, Varney J, Craighead F & Sumner J. (1976). Telemetry experiments with a hibernating Black bear. In: *Bears: their Biology and Management.* A selection of papers from the 3rd International Conference on Bear Research and Management, IUCN Publications New Series no. 40, pp. 357 - 371.

Cumming D, Fenton M, Rautenbach I, Taylor R, Cumming G, Cumming M, Dunlop J, Ford A, Hovorka M, Johnston D, Kalcounis M, Mahlangu Z & Portfors C. (1997). Elephants, woodlands and biodiversity in southern Africa. *South African Journal of Science* **93,** 231 - 236.

de Wit M & Stankiewicz J. (2006). Changes in surface water supply across Africa with predicted climate change. *Science* **311,** 1917 - 1921.

Durotoye A & Grayson J. (1971). Heat production in the gastro-intestinal tract of the dog. *Journal of Physiology* **214,** 417 - 426.

Eigenberg R, Brown-Brandl T & Nienaber J. (2008). Sensors for dynamic physiological measurements. *Computers and Electronics in Agriculture* **62,** 41 - 47.

Elder W & Rodgers D. (1975). Body temperature in the African elephant as related to ambient temperature. *Mammalia* **39,** 395 - 399.

Erasmus B, van Jaarsveld A, Chown S, Kshatriya M & Wessels K. (2002). Vulnerability of South African animal taxa to climate change. *Global Change Biology* **8,** 679 - 693.

Finch V. (1972). Thermoregulation and heat balance in the East African eland and hartebeest. *American Journal of Physiology* **222,** 1374 - 1379.

Fuller A, Moss D, Skinner J, Jessen P, Mitchell G & Mitchell D. (1999a). Brain, abdominal and arterial blood temperatures of free-ranging eland in their natural habitat. *Pflügers Archives - European Journal of Applied Physiology* **438,** 671 - 680.

Fuller A, Oosthuyse T, Maloney S & Mitchell D. (1999b). Evaluation of miniature data loggers for body temperature measurement during sporting activities. *Pflügers Archives - European Journal of Applied Physiology* **79,** 341 - 346.

Fuller A, Maloney S, Kamerman P, Mitchell G & Mitchell D. (2000). Absence of selective brain cooling in free-ranging zebras in their natural habitat. *Experimental Physiology* **85,** 209 - 217.

Fuller A, Maloney S, Mitchell G & Mitchell D. (2004). The eland and the oryx revisited: body and brain temperatures of free-living animals. *International Congress Series* **1275,** 275 - 282.

Fuller A, Kamerman P, Maloney S, Matthee A, Mitchell G & Mitchell D. (2005). A year in the thermal life of a free-ranging herd of springbok (*Antidorcas marsupialis*). *Journal of Experimental Biology* **208,** 2855 - 2864.

Gant N, Atkinson G & Williams C. (2006). The validity and reliability of intestinal temperature during intermittent running. *Medicine and Science in Sports and Exercise* **38,** 1926 - 1931.

Gebremedhin K & Wu B. (2001). A model of evaporative cooling of wet skin surface and fur layer. *Journal of Thermal Biology* **26,** 537 - 545.

Goddard J. (1967). Home range, behaviour, and recruitment rates of two black rhinoceros populations. *East African Wildlife Journal* **5,** 133 - 150.

Gordon M, Bartholomew G, Grinnell A, Barker Jørgensen C & White F. (1982). *Animal Physiology: principles and adaptations, 4th edition*. Macmillan Publishing Co., New York.

Green A, Gates R & Lawrence L. (2005). Measurement of horse core body temperature. *Journal of Thermal Biology* **30,** 370 - 377.

Green A, Gates R, Lawrence L & Wheeler E. (2008). Continuous recording reliability analysis of three monitoring systems for horse core body temperature. *Computers and Electronics in Agriculture* **61,** 88 - 95.

Harris G, Russell G, Van Aarde R & Pimm S. (2008). Rules of habitat use by elephants Loxodonta africana in southern Africa: insights for regional management. *Oryx* **42,** 66 - 75.

Hetem R, Maloney S, Fuller A, Meyer L & Mitchell D. (2007). Validation of a biotelemetric technique, using ambulatory miniature black globe thermometers, to quantify thermoregulatory behaviour in ungulates. *Journal of Experimental Biology* **307,** 342 - 356.

Hetem R, Mitchell D, Maloney S, Meyer L, Fick L, Kerley G & Fuller A. (2008). Fever and sickness behavior during an opportunistic infection in a free-living antelope, the greater kudu (*Tragelaphus strepsiceros*). *American Journal of Physiology* **294,** R246 - R254.

Hiley P. (1972). *A comparison of the thermoregulation in a number of East African mammals*. MSc Thesis, University of Nairobi, Nairobi.

Hiley P. (1975). How the elephant keeps its cool. *Natural History* **84,** 34 - 40.

Hiley P. (1977). The thermoregulatory response of the rhinoceros (*Diceros bicornis* and *Ceratotherium simum*) and the zebra (*Equus burchelli*) to diurnal temperature change. *East African Wildlife Journal* **15,** 337.

Huey R. (1991). Physiological consequences of habitat selection. *The American Naturalist* **137,** S91 - S115.

Hulme P. (2005). Adapting to climate change: is there scope for ecological management in the face of a global threat? *Journal of Applied Ecology* **42,** 784 - 794.

Hutchinson J, Famini D, Lair R & Kram R. (2003). Are fast-moving elephants really running? *Nature* **422,** 493 - 494.

Ingram D. (1965). Evaporative cooling in the pig. *Nature* **207,** 415 - 416.

Jessen C, Laburn H, Knight M, Kuhnen G, Goelst K & Mitchell D. (1994). Blood and brain temperatures of free-ranging black wildebeest in their natural environment. *American Journal of Physiology* **36,** R1528 - R1536.

Jessen C. (2001). *Temperature Regulation in Humans and Other Animals*. Springer, Berlin, Germany.

Kerley G, Landman M, Kruger L, Owen-Smith N, Balfour D, de Boer W, Gaylard A, Lindsay K & Slotow R. (in press). Effects of elephant on ecosystems and biodiversity. In: *Assessment of South African Elephant Management*, ed. Scholes R & Mennell K, pp. 101 - 147. Witwatersrand University Press, Johannesburg.

Kinahan A, Inge-moller R, Bateman P, Kotze A & Scantlebury M. (2007a). Body temperature daily rhythm adaptations in African savanna elephants (*Loxodonta africana*). *Physiology and Behavior* **92,** 560 - 565.

Kinahan A, Pimm S & van Aarde R. (2007b). Ambient temperature as a determinant of landscape use in the savanna elephant, *Loxodonta africana*. *Journal of Thermal Biology* **32,** 47 - 58.

Kuhnen G. (1997). Selective brain cooling reduces respiratory water loss during heat stress. *Comparative Biochemistry and Physiology A* **118,** 891 - 895.

Langman V, Maloiy G, Schmidt-Nielsen K & Schroter R. (1979). Nasal heat exchange in the giraffe and other large mammals. *Respiration Physiology* **37,** 325 - 333.

Langman V, Bamford O & Maloiy G. (1982). Respiration and metabolism in the giraffe. *Respiration Physiology* **50,** 141 - 152.

Langman V & Maloiy G. (1989). Passive obligatory heterothermy of the giraffe. *Journal of Physiology* **415,** 89P.

Langman VA, Roberts TJ, Black J, Maloiy GMO, Heglund NC, Weber JM, Kram R & Taylor CR. (1995). Moving cheaply: energetics of walking in the African elephant. *Journal of Experimental Biology* **198,** 629 - 632.

Leggett K. (2004). Coprophagy and unusual thermoregulatory behaviour in desert-dwelling elephants of north-western Namibia. *Pachyderm* **36,** 113 - 115.

Lehmer E, Bossenbroek J & Van Horne B. (2003). The influence of environment, sex, and innate timing mechanisms on body temperature patterns of free-ranging black-tailed prairie dogs (Cynomys ludovicianus). *Physiological and Biochemical Zoology* **76,** 72 - 83.

Li H & Reynolds J. (1995). On definition and quantification of heterogeneity. *Oikos* **73,** 280 - 284.

Lillywhite H & Stein B. (1987). Surface sculpturing and water retention of elephant skin. *Journal of Zoology* **211,** 727 - 734.

Luck C & Wright P. (1959). The body temperature of the hippopotamus. *Journal of Physiology* **147,** 53P - 54P.

Luck C & Wright P. (1964). Aspects of the anatomy and physiology of the skin of the hippopotamus (*H. amphibius*). *Experimental Physiology* **49,** 1-14.

Mackay R. (1964). Deep body temperature of untethered dolphin recorded by ingested radio transmitter. *Science* **144,** 864 - 866.

Maloney S, Fuller A, Mitchell G & Mitchell D. (2002). Brain and arterial blood temperatures of free-ranging oryx (*Oryx gazella*). *Pflügers Archives - European Journal of Applied Physiology* **443,** 437 - 445.

Maluf N. (1995). Kidney of elephants. *The Anatomical Record* **242,** 491 - 514.

Martin K & Nagy K. (2002). Animal physiology and global environmental change. In: *The Earth system: biological and ecological dimensions of global environmental change*, ed. Mooney H & Canadell J, pp. 136 - 139. John Wiley & Sons, Ltd, Chichester.

McCarty J. (2001). Ecological consequences of recent climate change. *Conservation Biology* **15,** 320 - 331.

McGinnis S & Southworth T. (1967). Body temperature fluctuations in the Northern elephant seal. *Journal of Mammalogy* **48,** 484 - 485.

McKenzie J & Osgood D. (2004). Validation of a new telemetric core temperature monitor. *Journal of Thermal Biology* **29,** 605 - 611.

McNab B. (1970). Body weight and the energetics of temperature regulation. *Journal of Experimental Biology* **53,** 329 - 348.

Mitchell D. (1977). Physical basis of thermoregulation. In: *International Review of Physiology, Environmental Physiology II*, ed. Robertshaw D, pp. 1 - 27. University Park Press, Baltimore.

Mitchell D, Maloney S, Laburn H, Knight M, Kuhnen G & Jessen C. (1997). Activity, blood temperature and brain temperature of free-ranging springbok. *Comparative Biochemistry and Physiology B* **167,** 335 - 343.

Mitchell D, Maloney S, Jessen C, Laburn H, Kamerman P, Mitchell G & Fuller A. (2002). Adaptive heterothermy and selective brain cooling in arid-zone mammals. *Comparative Biochemistry and Physiology B* **131,** 571 - 585.

Mitchell G & Skinner J. (2004). Giraffe thermoregulation: a review. *Transactions of the Royal Society of South Africa* **59,** 109 - 118.

Moran D, Pandolf K, Shapiro Y, Heled Y, Shani Y, Mathew W & Gonzalez R. (2001). An environmental stress index (ESI) as a substitute for the wet bulb globe temperature (WBGT). *Journal of Thermal Biology* **26,** 427 - 431.

Moran J. (1973). Heat tolerance of Brahman cross, buffalo, banting and shorthorn steers during exposure to sun as a result of exercise. *Australian Journal of Agricultural Research* **24,** 775 - 782.

Mortola J & Lanthier C. (2004). Scaling the amplitudes of the circadian pattern of resting oxygen consumption, body temperature and heart rate in mammals. *Comparative Biochemistry and Physiology A* **139,** 83 - 95.

Nagl L, Schmitz R, Warren S, Hildreth T, Erickson H & Andresen D. (2003). Wearable sensor system for wireless state-of-health determination in cattle. Engineering in

Medicine and Biology Society, *Proceedings of the 25th Annual International Conference of the IEEE*, pp. 3012 - 3015.

Nevill C & Friend T. (2003). The behavior of circus tigers during transport. *Applied Animal Behaviour Science* **82,** 329 - 337.

New M, Hewitson B, Stephenson D, Tsiga A, Kruger A, Manhique A, Gomez B, Coelho C, Masisi D, Kululanga E, Mbambalala E, Adesina F, Saleh H, Kanyanga J, Adosi J, Bulane L, Fortunata L, Mdoka M & Lajoie R. (2006). Evidence of trends in daily climate extremes over southern and west Africa. *Journal of Geophysical Research* **111,** D14102.

Nogués-Bravo D, Rodríguez J, Hortal J, Batra P & Araujo M. (2008). Climate change, humans and the extinction of the woolly mammoth. *PLoS Biology* **6,** e79.

Noirard C, Le Berre M, Ramousse R & Lena J. (2008). Seasonal variation of thermoregulatory behaviour in the hippopotamus (*Hippopotamus amphibius*). *Journal of Ethology* **26,** 191 - 193.

Ogutu J & Owen-Smith N. (2003). ENSO, rainfall and temperature influences on extreme population declines among African savanna ungulates. *Ecology Letters* **6,** 412 - 419.

Ostrowski S, Williams J & Ismael K. (2003). Heterothermy and the water economy of free-living Arabian oryx (*Oryx leucoryx*). *Journal of Experimental Biology* **206,** 1471 - 1478.

Ostrowski S & Williams J. (2006). Heterothermy of free-living Arabian sand gazelles (*Gazella subgutturosa marica*) in a desert environment. *Journal of Experimental Biology* **209,** 1421 - 1429.

Owen-Smith N. (1988). *Megaherbivores. The influence of very large body size on ecology*. Cambridge University Press, Johannesburg, South Africa.

Parker K & Robbins C. (1985). Thermoregulation in ungulates. In: *Bioenergetics of Wild Herbivores*, ed. Hudson R & White R, pp. 161 - 182. CRC Press, Inc., Florida.

Phillips P & Heath J. (1992). Heat exchange by the pinna of the African elephant (*Loxodonta africana*). *Comparative Biochemistry and Physiology A* **101,** 693 - 699.

Phillips P & Heath J. (1995). Dependency of surface temperature regulation on body size in terrestrial mammals. *Journal of Thermal Biology* **20,** 281 - 289.

Piccione G, Caola G & Mortola J. (2005). Scaling the daily oscillation of breathing frequency and skin temperature in mammals. *Comparative Biochemistry and Physiology A* **140,** 477 - 486.

Porter W & Gates D. (1969). Thermodynamic equilibria of animals with environment. *Ecological Monographs* **39,** 227 - 244.

Prendiville D, Lowe J, Earley B, Spahr C & Kettlewell P. (2002). *Radiotelemetry systems for measuring body temperature*. Beef Production Series No 57. Grange Research Centre, Dunsany, Co. Meath.

Pringle R. (2008). Elephants as agents of habitat creation for small vertebrates at the patch scale. *Ecology* **89,** 26 - 33.

Raath J. (1993). Chemical capture of the African elephant *Loxodonta africana*. In: *The Capture and Care Manual Capture, Care, Accommodation and Transportation of Wild African Animals*, ed. McKenzie A, pp. 484 - 492. Wildlife Decision Support Services and the South African Veterinary Foundation, South Africa.

Refinetti R & Menaker M. (1992). The circadian rhythm of body temperature. *Physiology and Behavior* **51,** 613 - 637.

Robertshaw D & Taylor C. (1969). A comparison of sweat gland activity in eight species of East African bovid. *Journal of Physiology* **203,** 135 - 143.

Robertshaw D. (2006). Mechanisms for the control of respiratory evaporative heat loss in panting animals. *Journal of Applied Physiology* **101,** 664 - 668.

Sargeant G, Eberhardt L & Peek J. (1994). Thermoregulation by Mule deer in arid rangelands of Southcentral Washington. *Journal of Mammalogy* **75,** 536 - 544.

Schmidt-Nielsen K, Schmidt-Nielsen B, Jarnum S & Houpt T. (1957). Body temperature of the camel and its relation to water economy. *American Journal of Physiology* **188,** 103 - 112.

Schmidt-Nielsen K. (1977). The physiology of wild animals. *Proceedings of the Royal Society of London Series B, Biological Sciences* **199,** 345 - 360.

Schmidt-Nielsen K, Schroter R & Shkolnik A. (1981). Desaturation of exhaled air in camels. *Proceedings of the Royal Society of London Series B, Biological Sciences* **211,** 305 - 319.

Schmidt-Nielsen K. (1984). *Scaling: Why is animal size so important?* Cambridge University Press, Cambridge.

Schmidt-Nielsen K. (1997). *Animal Physiology: Adaptation and Environment, 5th edition*. Cambridge University Press, Cambridge.

Schoenig S, Hildreth T, Nagl L, Erickson H, Spire M, Andresen D & Warren S. (2004). Ambulatory instrumentation suitable for long-term monitoring of cattle health.

Engineering in Medicine and Biology Society, *Proceedings of the 26th Annual International Conference of the IEEE*, pp. 2379 - 2382.

Scholander P. (1955). Evolution of climatic adaptation in homeotherms. *Evolution* **9,** 15 - 26.

Shoshani J, Kupsky W & Marchant G. (2006). Elephant brain. Part I: Gross morphology, functions, comparative anatomy, and evolution. *Brain Research Bulletin* **70,** 124 - 157.

Sikes S. (1971). *The Natural History of the African Elephant*. Weidenfeld and Nicolson, London.

Sinclair A. (1977). *The African Buffalo. A study of resource limitation of populations*. The University of Chicago Press, Chicago.

Skinner J & Chimimba C. (2005). *The Mammals of the Southern African Subregion, 3rd edition*. Cambridge University Press, Cape Town, South Africa.

Spearman R. (1970). The epidermis and its keratinisation in the African elephant (*Loxodonta africana*). *Zoologica Africana* **5,** 327 - 338.

Sukumar R. (2003). *The Living Elephants - Evolution, Ecology, Behaviour and Conservation*. Oxford University Press, Oxford.

Taylor C & Lyman C. (1967). A comparative study of the environmental physiology of an East African antelope, the eland, and the Hereford steer. *Physiogical Zoology* **40,** 280 - 295.

Taylor C. (1969). The eland and the oryx. *Scientific American* **220,** 88 - 97.

Taylor C. (1970a). Strategies of temperature regulation: effect on evaporation in East African ungulates. *American Journal of Physiology* **219,** 1131 - 1135.

Taylor C. (1970b). Dehydration and heat: effects on temperature regulation of East African ungulates. *American Journal of Physiology* **219,** 1136 - 1139.

Taylor C. (1977). Exercise and environmental heat loads: different mechanisms for solving different problems. In: *International Review of Physiology, Environmental Physiology II*, ed. Robertshaw D, pp. 119 - 146. University Park Press, Baltimore.

Thuiller W, Broennimann O, Hughes G, Alkemade R, Midgley G & Corsi F. (2006). Vulnerability of African mammals to anthropogenic climate change under conservative land transformation assumptions. *Global Change Biology* **12,** 424 - 440.

Thuiller W. (2007). Climate change and the ecologist. *Nature* **448,** 550 - 552.

Toscano M. (2001). *Environmental conditions and responses of circus elephants transported by truck and railcar during relatively high and low temperature conditions*. MSc Thesis, A&M University, Texas.

Van Aarde R, Jackson T & Ferreira S. (2006). Conservation science and elephant management in southern Africa. *South African Journal of Science* **102,** 385 - 388.

van Hoven W, Prins R & Lankhorst A. (1981). Fermentative digestion in the African elephant. *South African Journal of Wildlife Research* **11,** 78 - 86.

Vernon H. (1930). The measurement of radiant heat in relation to human comfort. *Journal of Physiology* **70,** 15 - 17.

Viljoen P. (1989). Spatial distribution and movements of elephants (*Loxodonta africana*) in the northern Namib Desert region of the Kaokoveld, South West Africa/Namibia. *Journal of Zoology* **219,** 1 - 19.

Viljoen P & Bothma J. (1990). Daily movements of desert-dwelling elephants in the northern Namib desert. *South African Journal of Wildlife Research* **20,** 69 - 72.

Wikelski M & Cooke S. (2006). Conservation physiology. *Trends in Ecology and Evolution* **21,** 38 - 46.

Williams T. (1990). Heat transfer in elephants: thermal partitioning based on skin temperature profiles. *Journal of Zoology* **222,** 235 - 245.

Wright P. (1984). Why do elephants flap their ears? *South African Journal of Zoology* **19,** 266 - 269.

Wright P & Luck C. (1984). Do elephants need to sweat? *South African Journal of Zoology* **19,** 270 - 274.

Wright P. (1987). Thermoregulation in the hippopotamus on land. *South African Journal of Zoology* **22,** 237 - 242.

Chapter 8

Appendix

Appendix A

Outlined below is the process used to calculate the amount of water which would need to have been ingested by Elephant 4 to produce the decrease in body temperature observed on the morning of 16 Dec 2007 after the elephant was observed to be have been drinking.

$M_1T_1 = M_2T_2$ (calorimetric principle)

If $M_1T_1 = MxTx + MyTy$

And $M_2T_2 = MfTf$

Then $MxTx + My\ Ty = MfTf$

Where Mx = mass of water ingested

Tx = temperature of ingested water

My = mass of elephant

Ty = Temperature of elephant before drinking

Mf = mass of water and elephant (final)

Tf = temperature of water and elephant (final)

If $Mf = Mx + My$

Then $MxTx + MyTy = (Mx + My)Tf$

$$MxTx + MyTy = MxTf + MyTf$$

$$MxTx - MxTf = MyTf - MyTy$$

$$Mx(Tx - Tf) = My(Tf - Ty)$$

Thus $Mx = \frac{My(Tf - Ty)}{(Tx - Tf)}$

SO

Where Mx = mass of water ingested = unknown

Tx = 25.1°C

My = 4000 kg

Ty = 36.5°C

Tf = 35.8°C

Then $$Mx = \frac{4000\ \text{kg}\ (35.8\text{C} - 36.5°\text{C})}{(25.1\text{C} - 35.8°\text{C})}$$

$$= \frac{4000\ \text{kg}\ (-0.7°\text{C})}{-10.7°\text{C}}$$

= 261.7 kg of water (about 260 l)