

BEHAVIOURAL AND AUTONOMIC THERMOREGULATION
IN MALAYAN SUN BEARS (*HELARCTOS MALAYANUS*)
AND POLAR BEARS (*URSUS MARITIMUS*)

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LIST OF ABBREVIATIONS

AVA	Arteriovenous anastomoses
BM	Body mass
BMR	Basal metabolic rate
CITES	Convention on International Trade in Endangered Species
IPCC	Intergovernmental Panel on Climate Change
IUCN	International Union for the Conservation of Nature
MR	Metabolic rate
T _A	Ambient temperature
T _B	Body core temperature
T _S	Surface temperature
T _{LC}	Lower critical temperature
TNZ	Thermoneutral zone
T _{UC}	Upper critical temperature
W	Watt

ABSTRACT

The aim of the study was to examine the effect of different meteorological variables on behavioural and autonomic thermoregulatory mechanisms in polar bears (*Ursus maritimus*) and Malayan sun bears (*Helarctos malayanus*) and to determine to which degree behavioural thermoregulation complements autonomic mechanisms to keep energy expenditure for the maintenance of body temperature low.

The study took place in nine European zoos including a total of 17 polar bears and 10 sun bears. Infrared thermography was used to non-invasively determine surface temperature distribution in relation to ambient temperature and to detect body surfaces specialized for heat dissipation. Thermographic measurements were made on 10 adult Malayan sun bears at air temperatures between 5 °C and 30 °C and on 11 adult polar bears and two cubs between 0 °C and 20 °C.

To assess behaviours that contribute to thermoregulation, observations were conducted by instantaneous scan sampling at ambient temperatures ranging from 5 °C to 34 °C in nine adult sun bears and between -2 °C and 35 °C in 10 adult polar bears. Activity, body posture while resting, selection of substrate to rest on, choice of shady resting places, and the occurrence of shivering and panting were recorded in 60 second intervals for a total of 721 hours of direct observations. Simultaneously, ambient temperature, humidity, wind speed and solar radiation were recorded four times per hour.

Thermographic measurements revealed that the thermoneutral zone of sun bears that lies between 24 °C and 28 °C. The assumption that polar bears possess body surfaces specialised for the dissipation of excess heat in the shoulder region and limbs, so called thermal windows, could be confirmed.

Behavioural data showed that behaviours related to thermoregulation, such as changes in activity, body posture while resting, and the choice of shade and substrates for resting occurred in advance of heat dissipation and panting, which would increase the physiological

costs, and were highly correlated to ambient temperature and solar radiation. Temperature thresholds for the initiation of various thermoregulatory behaviours could be defined. The results are discussed with respect to *ex-situ* und *in-situ* conservation.

ZUSAMMENFASSUNG

Ziel der Studie war es, den Einfluss meteorologischer Variablen auf verhaltensgesteuerte und autonome Thermoregulation bei Eisbären (*Ursus maritimus*) und Malaienbären (*Helarctos malayanus*) zu untersuchen und zu bestimmen, bis zu welchem Grad Verhalten autonome Mechanismen ergänzt, um die energetischen Kosten für die Aufrechterhaltung der Körpertemperatur möglichst gering zu halten. Die Untersuchungen wurden in neun Europäischen Zoos an insgesamt 17 Eisbären und zehn Malaienbären durchgeführt. Mithilfe der Infrarotthermographie, einer nicht invasiven Methode zur Ermittlung von Oberflächentemperaturen in Abhängigkeit von der Außentemperatur sowie von Oberflächen, die auf die Abgabe überschüssiger Wärme spezialisiert sind, wurden zehn adulte Malaienbären zwischen 5 °C und 30 °C und elf adulte Eisbären und zwei Jungtiere zwischen 0 °C und 20 °C untersucht. Zur Ermittlung von Verhaltensweisen, die zur Thermoregulation beitragen, wurden Verhaltensbeobachtungen mithilfe von instantaneous scan sampling bei Temperaturen zwischen 5 °C und 34 °C bei neun adulten Malaienbären und zwischen -2 °C und 35 °C bei zehn adulten Eisbären durchgeführt.

Aktivität sowie Körperhaltung, Wahl des Substrates und das Aufsuchen von Schatten beim Ruhen und das Auftreten von Hecheln wurden mittels direkter Verhaltensbeobachtungen alle 60 Sekunden über insgesamt 721 Stunden protokolliert. Lufttemperatur, relative Luftfeuchte, Windgeschwindigkeit und Sonnenstrahlung wurden viermal stündlich gemessen.

Die thermographischen Untersuchungen ergaben, dass die thermoneutrale Zone von Malaienbären zwischen 24 °C und 28 °C liegt. Die Annahme, dass Eisbären Oberflächen, die

auf die Abgabe überschüssiger Wärme spezialisiert sind, so genannte Thermofenster, in der Schulterregion und den Beinen besitzen, konnte bestätigt werden.

Die Beobachtungen konnten zeigen, das Verhaltensweisen, welche zur Thermoregulation beitragen, wie Änderungen der Aktivität, Körperhaltung beim Ruhen und das Aufsuchen schattiger Ruheplätze, auftreten bevor Wärmeabgabe und Hecheln, was energetisch kostspielig wäre, eingesetzt werden und stark mit Lufttemperatur und Sonnenstrahlung korrelieren. Es konnten Temperaturschwellen für den Einsatz verschiedener thermoregulatorischer Mechanismen bestimmt werden. Die Ergebnisse wurden mit Hinblick auf *ex-situ* und *in-situ* Artenschutz diskutiert.

1. INTRODUCTION

Ursids have adapted to a wide variety of climates, ranging from the Arctic to the tropical rainforest (Derocher 2000). Polar bears and Malayan sun bears live in regions with considerable differing demands regarding thermoregulation. While air temperatures in the arctic and sub arctic, the natural environment of polar bears, vary between $-60\text{ }^{\circ}\text{C}$ in winter and $12\text{ }^{\circ}\text{C}$ in summer (Barry and Hare 1974, McBean *et al.* 2005, Serreze *et al.* 2007), in their most southern range even up to $20\text{ }^{\circ}\text{C}$ (Stirling 1998), annual temperature in the tropical rain forest, the habitat of sun bears, averages $26.5\text{ }^{\circ}\text{C}$ and does not vary with season (Oates 1987, Wong 2002, Fredriksson *et al.* 2006, Fredriksson 2012). In the course of their evolution, bears have developed several morphological, physiological and behavioural adaptations, which correspond to the climatic conditions of their respective habitats.

In zoos they often live under climatic conditions deviating considerably from their original range. Thus *ex situ* research offers the opportunity to investigate the species' thermoregulatory potential and provide information necessary to improve husbandry conditions and might furthermore help to estimate whether and to which extent the species will be able to cope with climate change and habitat destruction which is occurring in the natural range of both species.

The aim of this study was to identify the currently unknown thermoneutral zone of Malayan sun bears and to investigate behavioural and autonomic thermoregulatory mechanisms of polar bears and sun bears with respect to temperature thresholds for their occurrence, which are mainly unknown.

1.1 General aspects of mammalian thermoregulation

Being endotherms, mammals and birds are able to maintain a high and relatively constant body temperature (T_B), at which biochemical processes and physiological functions are optimized, independent of changes in ambient temperature (T_A) or internal heat production

(Schmidt-Nielsen 1990, McNab 2002). A stable T_B is maintained by balancing heat gain and heat loss. Accordingly, heat produced during metabolic processes or physical activity must be efficiently conserved or dissipated. Endogenous produced heat has to be transported from the body core to the surface before it can be transferred to the environment (Aschoff and Wever 1958). Heat flow always occurs from regions of higher to those of lower temperature (Schmidt-Nielsen 1990). Consequently, the temperature of an organism is not uniformly distributed. While T_B remains nearly constant throughout the body core, surface temperatures (T_S) can vary greatly dependent on T_A and the need for heat dissipation or heat conservation (Aschoff 1971). In combination with T_A , humidity, air flow and solar radiation also affect the amount of heat transfer (Schmidt-Nielsen 1990).

Heat exchange between an animal and its environment can occur via radiation, conduction, convection and evaporation. Radiation is the dissipation of heat in form of electromagnetic waves and takes place without direct contact between objects. Conduction describes heat transfer between objects that are in direct contact with each other and between an object and a non-moving fluid or gas, whereas heat transfer by convection takes place between an object and a moving fluid or gas. Evaporation is the dissipation of heat through vaporization of fluids (Schmidt-Nielsen 1990, IUPS 2003, Incropera *et al.* 2007). The rate of heat transfer is proportional to the involved surface area (Scholander *et al.* 1950c) and, except for evaporative water loss, proportional to the temperature gradient between the animal and its environment (Frappell and Cummings 2008).

Temperature regulation in endotherms is achieved by both behavioural and autonomic means (Schmidt-Nielsen 1990, IUPS 2003). Behavioural thermoregulation includes changes in activity to alter the rate of internal produced heat (Limberger *et al.* 1986, Rees 2004, Hill 2006, Cain *et al.* 2008), selection of an appropriate microclimate (Limberger *et al.* 1986, Hill 2006, Kinahan *et al.* 2007, Cain *et al.* 2008, Noirard *et al.* 2008), and alterations of body

posture and orientation to vary the exposed surface area and thus the amount of heat exchange with the environment (Bianca 1977, De Lamo *et al.* 1998, Ward *et al.* 2008). Wetting of body surfaces through mud bathing (Hiley 1975, Rees 2002), saliva spreading (Buffenstein 1984) or excretion of dilute urine on the legs (Kahl 1966) enable evaporative cooling. Social thermoregulation through contact lying, referred to as huddling (Arnold 1988, McKechnie and Lovegrove 2001, Kauffman *et al.* 2003, Gilbert *et al.* 2010), as well as nest building (Thieme and Kolter 1995, Kurt 2000, Kauffman *et al.* 2003) reduce heat loss to the environment.

Furthermore, T_B is regulated by autonomic mechanisms. Heat production can be elevated by muscular activity, involuntary tremor of skeletal muscles, so called shivering, or by metabolic heat production (Schmidt-Nielsen 1990, Cannon and Nedergaard 2004). Non shivering thermogenesis in the brown adipose tissue, that consists of fat cells with high mitochondrial content and which is specialised in the production of heat (Willmer *et al.* 2009), is restricted to small hibernators and in large mammals to neonates (Geiser and Baudinette 1990, Carey *et al.* 2003, Cannon and Nedergaard 2004).

The rate of heat transfer can be varied through piloerection by raising or flattening hairs or feathers and thereby modifying the insulative air layer surrounding the body (Cena and Monteith 1975, Vogel 2005, Chaplin *et al.* 2013).

Countercurrent heat exchangers, vascular arrangements that are found in the appendages of marine or cold adapted endotherms, act preventing heat loss, as adjacent vessels with opposite blood flow direction exchange heat between arterial and venous blood (Scholander and Schevill 1955, Schmidt-Nielsen 1990, Kvadsheim and Folkow 1997). Insulation can further be altered by peripheral blood flow control, which is usually seen in large endothermic animals (Schmidt-Nielsen 1990). By increasing or decreasing blood flow to the skin, heat can be dissipated through vasodilation or conserved by vasoconstriction of capillaries (Clark *et al.*

1977, Johnson *et al.* 1986, Sessler *et al.* 1990, Savage and Brengelmann 1996).

Beside general heat dissipation over the whole body surface, vasomotion may also occur in specific tissues causing a localized reduction or increase in blood flow to the skin. Specialized connections between arterial and venous vessels, arteriovenous anastomoses (AVA), bypass capillaries and allow an increased blood flow to the body surface, such that heat dissipation is increased in those regions (Daanen 1991). Several species are documented to effectively control heat loss by regulating surface temperature of special body regions called thermal windows which are referred to as areas with temporary higher temperatures than the surrounding body surface and ambient temperature (Phillips and Heath 1992, Mauck *et al.* 2003, Willis *et al.* 2005, Schneider and Kolter 2009, Khamas *et al.* 2012).

Transpiration through sweat glands (Hattingh 1972, de Lamo *et al.* 2001) as well as thermal panting, that leads to evaporative water loss from the respiratory tract (Best 1982, Schmidt-Nielsen 1990), provide cooling through evaporation. However, constant sweating and panting exceed water sources and is energetically much more unfavourable than sensible heat loss (Schmidt-Nielsen 1990, Sawka *et al.* 2001).

Heat balance must be achieved without exhausting limited resources. Behavioural adaptations function in combination with morphological and physiological mechanisms and are of critical importance for the maintenance of temperature and water balance (Cain *et al.* 2008). The energetic costs for endothermy are considerable and must be compensated by a higher energetic intake or by reducing energy expenditure through behaviour (Bennett and Ruben 1979, Bennett 1986, Grahn and Heller 2004). It has been reported that in the guanaco (*Lama guanicoe*) body position could contribute to a reduction of energetic costs of 67% (De Lamo *et al.* 1998). In the white-tailed deer (*Odocoileus virginianus*) reduced activity levels at low T_A led to energy conservation up to 1000 kcal/day (Moen 1976).

Behavioural mechanisms such as changes in activity, postural changes and the selection of suitable microclimates, as well as piloerection or variations in heat transfer through variations in blood circulation, require little energy expenditure and are thus implemented before energetically costly and physically constraining mechanisms such as evaporation of water or metabolic heat production occur (Scholander *et al.* 1950b, Bianca 1977, Grahn and Heller 2004). The activation of the various thermoregulatory mechanisms is hierarchical and aims at minimising energy expenditure (Bianca 1977, Grahn and Heller 2004).

The range of T_A within which temperature regulation in an endotherm is achieved without increases in metabolic rate above basal level is referred to as the thermoneutral zone (TNZ) (Figure 1).

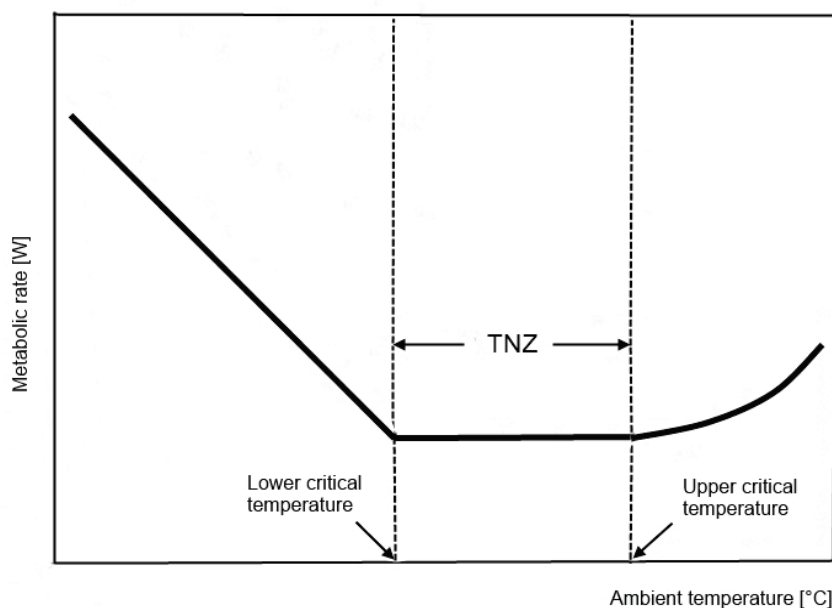


Figure 1. Thermoneutral zone, lower and upper critical temperature (modified after Pflumm 1989).

Below the lower critical temperature (T_{LC}) metabolic rate, and hence energy expenditure, increases linearly with decreasing T_A , since metabolic heat is produced to compensate for increased heat loss to the environment. Above the upper critical temperature an animal must also increase its metabolism in order to activate and maintain heat dissipating mechanisms

(Schmidt-Nielsen 1990, IUPS 2003). Within the TNZ, T_B is maintained by modifying insulation and thereby altering the temperature difference between body surface and environment, and through behavioural responses (Müller 1995, Vogel 2005). Behavioural mechanisms in general tend to keep an animal within its TNZ to keep energy expenditure low (Müller 1995, Willmer *et al.* 2009). When the TNZ is exceeded, regulation of T_B adds to the physiological costs.

The range of the TNZ is mainly determined by morphological and physiological features relevant for body insulation. In species living in habitats with distinct seasonality, those adaptations include summer and winter fur (Hart 1956), seasonal changing subcutaneous fat layers (Scholander *et al.* 1950c, Irving and Hart 1957, Thiemann *et al.* 2006), as well as peripheral AVA in the blood vessels (Schmidt-Nielsen 1990). Species inhabiting tropical zones have a short, less insulating fur throughout the year and do not develop insulating fat layers (Scholander *et al.* 1950a).

Animals adapted to cold environments tend to have a relatively broad TNZ, whereas in most tropical mammals the range of thermoneutrality is quite narrow (Scholander *et al.* 1950c). The breadth of the TNZ varies greatly among species, ranging from 1.1 °C in the feathertail glider (*Acrobates pygmaeus*) to 40 °C in the American bison (*Bison bison*) (Christopherson *et al.* 1979) and corresponds to those T_A , which predominate in the climate a species has evolved in, such that the main functions can be performed without additional energy expenditure.

1.2 Malayan sun bears

Sun bears are the smallest of the eight bear species (Dathe 1979), with body weights of 65 kg reported for males and 45 kg for females (Garshelis *et al.* 2009). They occur in 11 Southeast Asian countries (Fredriksson *et al.* 2008), in two of which, Bangladesh and Southern China, they are likely extinct (Fredriksson 2014, pers. comm.). While sun bear populations

historically have been wide dispersed throughout the tropical Southeast Asian rainforests (Figure 2), quantitative data of their current population size and trends are lacking (Fredriksson *et al.* 2008). Commercial exploitation and deforestation throughout their range have dramatically reduced population size and suitable habitat for sun bears, which rely on tropical forest. It is estimated that the global population of Malayan sun bears has declined by > 30% over the past 30 years (Fredriksson *et al.* 2008). Accordingly the species has been upgraded from Data Deficient to Vulnerable in the IUCN (International Union for Conservation of Nature) Red List of Threatened Species. The currently running re-assessment confirms that decision (Fredriksson 2014, pers. comm.). Since 1979 Malayan sun bears are listed in Appendix I of CITES (Convention on International Trade in Endangered Species) (Fredriksson *et al.* 2008).

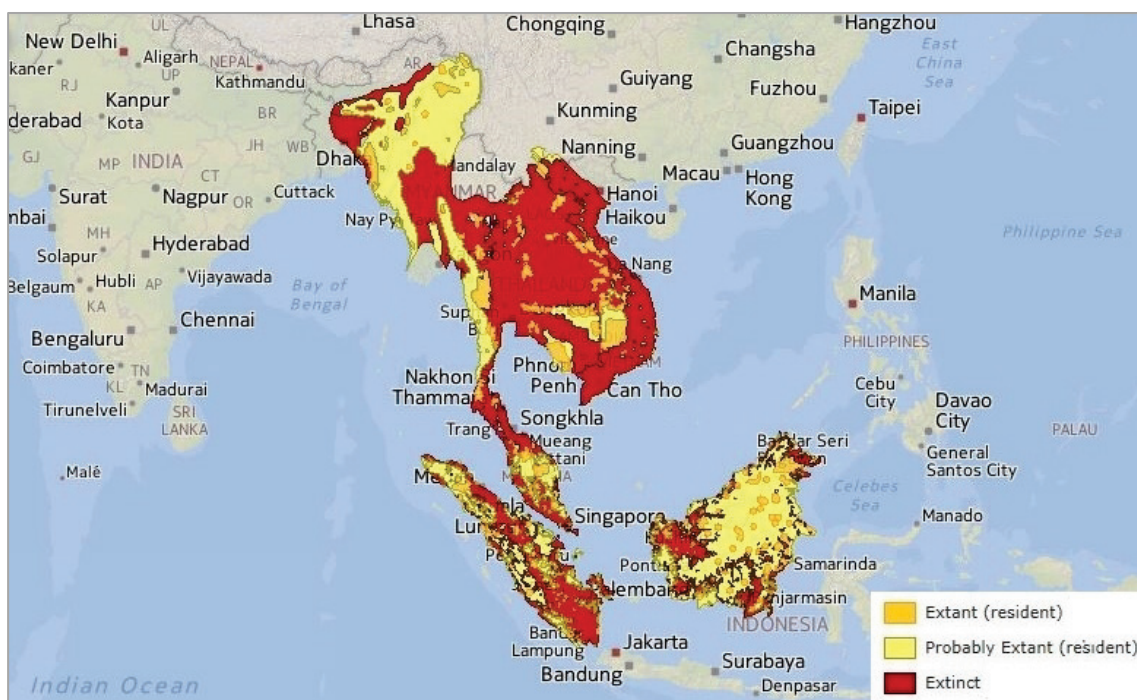


Figure 2. Current and historical range of sun bears (IUCN Red List of Threatened Species. Version 2014.2).

Currently, there is no scientific information on thermoregulation in Malayan sun bears. They inhabit a warm, humid climate, which is characterised by low seasonal and diurnal temperature fluctuations (Oates 1987, Wong 2002, Fredriksson *et al.* 2006, Fredriksson 2012)

ranging from 23 °C to 30 °C (Fredriksson *et al.* 2006). Accordingly, they have a short and thin fur throughout the year (Servheen 1999) and furless food pads (Dathe 1979).

In intact environments, which are undisturbed by humans, sun bears are active during most of the day while they rest during the warmest midday hours and at night (Wong *et al.* 2004, Fredriksson 2005). Hence, a shift of activity towards the slightly cooler hours during the night does not seem to occur. However, there is evidence that sun bears avoid direct solar radiation by selectively using open palm oil plantations only during crepuscule, independent of the presence of humans (Normua *et al.* 2004).

Like other semi–arboreal ursids, sun bears use tree nests built of branches high up the ground (Domico *et al.* 1995, McConkey and Galetti 1999) or in hollow trunks with dry, soft substratum (Wong *et al.* 2004). Nest building is also described for Andean bears (*Tremarctos ornatus*) (Peyton 1980, Goldstein 2002) and Asiatic black bears (*Ursus thibetanus*) (Thieme and Kolter 1995, Kurt 2000) and presumably contributes to a reduction in heat loss from the body surface to the environment.

Unlike the northern bear species, Malayan sun bears do not hibernate during times of low food availability (Domico *et al.* 1995), but switch to insects and larvae when fruits are not available (Wong 2002, Fredriksson *et al.* 2006). Food accessibility in the tropical rainforest is neither predictable nor are there external zeitgeber (Fittkau 1973, Knott 1998). Probably sun bears attempt to maximize food intake during high fruit availability in order to store energy for the upcoming dry season, but they do not develop significant subcutaneous fat layers (Wong 2002). During multi–annually periodic mast fruiting events, fruits makes up most of the diet, providing the opportunity to build up, or recover, fat and energy reserves for the prolonged inter–mast intervals (Fredriksson 2005, Fredriksson *et al.* 2006). However, it is unlikely that these fat reserves contribute to body insulation. Sections of sun bears from zoos, where food availability is high year round and the animals generally achieve higher body

weights than in the wild, revealed only poorly developed subcutaneous fat layers (pers. observ.). Thermographic measurements in several zoo housed ursid species indicate that sun bears are the least insulated bears (Hilsberg 2000). Precise information about their critical temperatures and their environmental requirements for proper thermoregulation is lacking.

1.3 Polar bears

Polar bears are the largest of the extant bears (DeMaster and Stirling 1981) with body weights of 350–650 kg reported for males and 150–250 kg for females (Stirling 1998). They are distributed throughout the annual reformative pack ice of the circumpolar Arctic with their range being limited by the southern extent of sea ice (Stirling 1998). As they primarily feed on seals caught from the sea ice surface, they are considered ecologically to be marine mammals (Vongraven *et al.* 2012). Polar bears have recently been reclassified as Vulnerable on the IUCN Red List, primary due to climate change induced loss of sea ice habitat (Schliebe 2008a).



Figure 3. The 19 polar bear subpopulations currently defined by the IUCN Polar Bear Specialist Group.

During the arctic winter T_A reaches $-60\text{ }^\circ\text{C}$ with periodically upcoming high wind chills (Best 1982), which add to heat loss by both forced convection and by decreasing the insulating air layer inside the fur (Gebremedhin 1987). These extreme climatic conditions impose high energetic demands on polar bears. They must maintain a high T_B and simultaneously store sufficient energy in order to overcome periods of food scarcity. Several morphological, physiological and behavioural adaptations enable them to cope with these conditions.

Polar bears have adapted to the arctic environment by effective thermal insulation. Due to their large body size, the ratio of heat producing volume to heat dissipating body surface reduces the risk of hypothermia (McNab 1983). Their thick and dense white fur consists of long guard hairs of different length up to 11 cm (Øritsland 1970) and underlying dense underwool (Frisch *et al.* 1974). Polar bears are completely furred except for the tip of the nose. Pelage density in the ventrally and in axillary areas is more even than in other ursids, which are more sparsely furred in those regions. Winter fur is much more dense and provides a better insulation than summer fur (Frisch *et al.* 1974), whereby the moult progressively proceeds from May to August (Kolenosky 1987). The skin is black (Wiig 2000), facilitating heat conservation. Under the skin lies an up to 11 cm thick fat layer, which acts as an energy reserve (Pond *et al.* 1992) but also provides insulation (Derocher 2000). The densely furred food pads contribute to the reduction of heat loss to ice and snow (Derocher 2000).

Air and fur have relatively low heat capacities and accordingly high insulation values (Hammel 1955). Inside water, the insulation of the fur decreases significantly, and heat loss is 24 times higher than in air of the same temperature (Scholander *et al.* 1950a, Frisch *et al.* 1974) due to the high thermal conductance and heat capacity of water (Schmidt-Nielsen 1990). During swimming, heat loss can be up to 50 times higher due to forced convection and because water penetrates the fur and displaces the insulative air layer. Inside water, insulation is mainly provided by the subcutaneous fat layer, which has a low conductance and thus

provides an effective insulation (Øritsland 1970). Accordingly, polar bears avoid swimming. To feed on seals, they rely on the sea ice (Stirling and Parkinson 2006).

When energy expenditure for foraging exceeds energy gain through the food, it is favourable to reduce metabolic rate and T_B and thereby minimizing heat loss and energy expenditure. To cope with extreme climatic conditions and limited food resources, many endotherms periodically undergo alternative physiological states such as hibernation, aestivation or torpor, during which MR, heart rate and respiratory frequency are reduced, leading to significant energy saving (Heldmaier and Ruf 1992, Ortmann *et al.* 1997, Geiser and Brigham 2000, Heldmaier *et al.* 2004), which decreases with increasing body size (Heldmaier *et al.* 2004).

Most of the northern bear species undergo hibernation during times of low food availability. While hibernating, bears reduce their T_B (Hellgren 1998), lower their heart-rate (Nelson *et al.* 1983, Tøien *et al.* 2011), and slow their metabolism (Tøien *et al.* 2011). Unlike true hibernators, in which T_B may approach freezing point, and basal metabolic rate (BMR) is reduced to 1% (Barnes 1989, Carey *et al.* 2003), T_B in brown bears (*Ursus arctos*) and American black bears (*Ursus americanus*) decreases to 31 °C – 35 °C (Hellgren 1998). In polar bears T_B decreases only to 35 °C – 37 °C (Nelson 1980, Watts and Hansen 1987) and BMR is reduced to 73% of the normal value (Hellgren 1998). Bears maintain a much higher T_B than true hibernators. Large mammals are prevented from being true hibernators by the high energetic costs associated with arousal (Feldhamer *et al.* 1999). Furthermore, females have to be able to meet physiological requirements like lactation and warming of cubs (Stirling 1998). During hibernation, bears do not urinate or defecate (Nelson *et al.* 1973) and rely on their fat reserves (Nelson 1980, Messier *et al.* 1992).

Unlike most populations of brown bears, American black bears, and the northern populations of Asiatic black bears, where both sexes hibernate, among polar bears only pregnant females hibernate in winter dens (Watts and Hansen 1987, Amstrup 2003) and remain on land until

February or March, when they return to the sea ice with cubs (Derocher *et al.* 1993). The remaining population is active year round (Derocher *et al.* 1990, Atkinson and Ramsay 1995). For polar bears with continuous access to sea ice, seals are available throughout the year. In those areas where the sea ice melts completely from July through early November, polar bears are not able to hunt their primary food, ringed seals (*Phoca hispida*), and are forced to spend several months on land, fasting and utilising stored fat reserves until freeze up (Jonkel *et al.* 1972, Knudsen 1978, Derocher and Stirling 1990, Schliebe *et al.* 2008b).

Contrasting other ursids (Watts and Hansen 1987) and true hibernators (Heldmaier *et al.* 1989) in which hibernation is induced by day length or air temperature, hibernation in polar bears is dependent on food availability (Derocher *et al.* 1990). Unlike other bear species, which are able to reduce their MR only in fall, polar bears can undergo a hibernation like state at any time of the year when food is not sufficiently available, provided that they possess sufficient fat reserves (Nelson *et al.* 1983, Derocher *et al.* 1990, Ramsay *et al.* 1991). Since during this time they are rarely active (Stirling 1974, Knudsen 1978, Derocher and Stirling 1990), this physiological state is often referred to as walking hibernation (Derocher *et al.* 1990) and is characterized by a low serum urea to serum creatinine ratio, comparable to that found in fasting black bears and female polar bears immediately after leaving the maternity den (Nelson *et al.* 1973, Adams *et al.* 1988, Derocher *et al.* 1990). However, bears feeding on garbage in Hudson Bay during food scarcity showed biochemical values typical for a normal metabolism (Stirling 1998). Apparently polar bears are able to shift between a fasting and a feeding metabolism throughout the year, dependent on access to food (Derocher *et al.* 1990). Normal T_B in resting polar bears is 36.9 ± 0.5 °C, similar to other mammals. As long as they remain inactive and there is low wind chill, their MR and T_B remain constant and independent of T_A between -30 °C and 5 °C, representing their TNZ (Best 1982).

The TNZ in arctic mammals is considerably larger and the metabolic response less pronounced than in tropical ones, and they have a lower T_{UC} than those from tropical regions (Scholander *et al.* 1950a). The consequence of an effective insulation is the potential risk of overheating at high T_A or when internal heat production increases due to food intake and subsequent digestive processes or increased physical activity. The latter became obvious in experiments with polar bears walking on a treadmill in a climatic chamber. At T_A between $-40\text{ }^{\circ}\text{C}$ and $0\text{ }^{\circ}\text{C}$ and a walking speed up to 4 km/h, T_B remained constant. At walking speeds of 7 km/h, T_B increased up to $39.0\text{ }^{\circ}\text{C}$ (Hurst and Øritsland 1982, Hurst *et al.* 1982). This increase in T_B however is not only due to the effective insulation. Polar bears consume more than twice the amount of energy that would be expected referring from their body mass and therefore produce more heat (Øritsland and Lavigne 1976, Best 1982).

Overheating causes additional energy expenditure to increase heart rate and to provide water for evaporative cooling. Consequently, polar bears move slowly, even if they can walk up to 40 km/h (Derocher 2000). Especially at high T_A they remain inactive to avoid the high cost of locomotion and the risk of overheating.

When resting, polar bears adopt different body postures, depending on the need to dissipate or conserve heat. At low T_A they curl up and cover the sparsely furred snout with their paws to reduce heat loss (Øritsland 1970). During summer, adult bears use shallow excavations for temporary resting and cooling during the relatively warm ice-free season (Jonkel *et al.* 1972). In late summer and autumn polar bears dig pits to rest on (Stirling 1998, Kolter 2007b). When pregnant females of the Hudson Bay population come ashore in summer, they only move inlands to occupy their cool dens when T_A has decreased or during rainfall (Stirling 1998). Accordingly, polar bears have adapted their behaviour to avoid overheating and to efficiently use energy.

Endotherms can cope less with high than with low T_A , the possibilities to dissipate heat are limited compared to those for heat conservation (Pflumm 1989). While adaptations to cold have been thoroughly documented in polar bears, their responses to high temperatures are not well understood.

Besides sweating, which does not occur in bears, respiratory evaporation through thermal panting is an effective thermoregulatory mechanism to avoid overheating. Polar bears begin to pant when moving fast or at high T_A (Øritsland *et al.* 1974), while respiratory frequency is positively correlated with an increase in T_B at a threshold of 39 °C (Best 1982). Several zoo housed bear species are documented to perform thermal panting at high T_A or after strenuous activity (Phillips 1992). However, constant panting exceed water sources and might further result in respiratory alkalosis due to higher losses of CO_2 and thus an increased blood pH (Schmidt-Nielsen 1990, Sawka *et al.* 2001) and is therefore unfavourable in the long term.

An efficient mechanism to dissipate excess heat is the control of blood flow to the skin by circumventing the subcutaneous insulative fat layer and thereby varying insulation (Hokkanen 1990, Mauck *et al.* 2003, Van Sant and Bakken 2006). Fur however is an effective insulator (Scholander *et al.* 1950c). Since the major part of the body must be insulated for maximal heat conservation, less furred body surfaces are necessary to dissipate excess heat due to high T_A or increased activity. Several mammals show differences in the density of fur in different body parts (Scholander *et al.* 1950a, Scholander *et al.* 1950b) and thinner areas of fur have been shown to permit heat dissipation (Klir and Heath 1992). Also in polar bears the fur is not uniformly distributed over the body in terms of both density and length (Øritsland 1970). Generally, thermoregulatory vasomotor responses in ursids are reported to be limited to non insulated body surface regions (Tøien *et al.*, 1999). According to current knowledge, heat loss in polar bears is restricted to the less insulated parts of the body such as eyes, ears, snout and the inside of the thighs (Øritsland 1970, DeMaster and Stirling 1981, Best 1982, Stirling

1998, Hilsberg 2000, Stirling 2011). Dissections of polar bears however revealed thin layers of muscles, which are richly supplied with blood vessels lying under the skin in the shoulder region and the legs. The author hypothesized that these anatomical structures function as areas for heat dissipation (Øritsland 1970). However, around freezing point, which lies clearly within the TNZ of polar bears, those body regions could not be identified by infrared measurements (Øritsland *et al.* 1974, Adams *et al.* 1988, Stirling 1998, 2011) and no further investigations have been made to date.

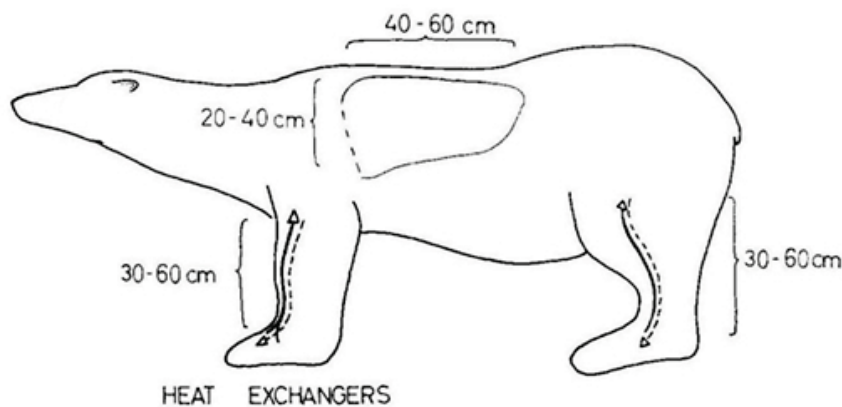


Figure 4. Anatomical features observed in 12 polar bears 1–25 years old. Main arteries and veins circulating the legs are running in close contact over a length of 30 to 60 cm (Øritsland 1970).

Whereas the insulation properties of polar bears and their advantages in a cold climate are well studied, it is unclear whether there are special physiological mechanisms to avoid overheating. For the most southern populations that spend the ice free period during summer on land (Derocher *et al.* 1993, Stirling 1998), temperatures exceed 12 °C and might increase to 20 °C, which is well above the reported T_{UC} of 5 °C of polar bears, leading to the assumption that beside behavioural adaptations, they might have developed morphological and physiological mechanisms that act before energy exhausting mechanisms such as panting are initiated.

1.4 Impact of climate change

Global warming is affecting ecosystems worldwide, with major temperature changes occurring in the Arctic (Parmesan 2006), where air temperatures have increased about 5 °C over the past 100 years (Serreze *et al.* 2000, Gagnon and Gough 2005, Comiso 2006, Serreze and Francis 2006, Serreze and Barry 2011) and the extent of sea ice has declined by six percent over the past 20 years (Stroeve *et al.* 2007, Serreze and Barry 2011, Stroeve *et al.* 2012) with increasing trend (Hamilton *et al.* 2014).

First effects on polar bears have become evident in the northern region through a decrease in summer sea ice. Polar bears use the marine ice for hunting seals, their primary prey. Across a part of their range the ice melts completely in summer and reforms in fall, forcing them ashore for months. During this time, they do not have access to seals and must rely on stored energy reserves for survival.

Due to a warmer climate, the ice free period in summer is progressively extending, shortening the time when polar bears can hunt seals and accumulate fat reserves which are essential for survival and reproduction (Atkinson and Ramsay 1995, Stirling 1997, Stirling and Parkinson 2006, Stirling *et al.* 2008). Due to their high body fat content, seals are the most important prey for polar bears (Stirling *et al.* 1999). Each additional ice free week is associated to a loss of 10 kg of stored body fat (Stirling and Derocher 1993, Stirling *et al.* 1999). Accordingly, longer ice-free periods affect polar bears in these regions through nutritional stress resulting from both a reduction in time available to accumulate energy reserves, and longer periods of time relying on fat stores while living on land (Regehr *et al.* 2007).

This has a severe impact on the reproductive output. Pregnant females, that enter maternity dens in autumn, may fast for up to eight months (Ramsay and Stirling 1988) in addition to meeting the nutritional demands of gestation and lactation. Implantation of the blastocyste is delayed and only takes place if females have accumulated sufficient fat reserves. It has been

suggested that 190 kg approximates a minimum weight below which females are no longer able to successfully reproduce (Derocher *et al.* 1992).

In addition, with increasing air temperatures caused by global warming, the T_{UC} of polar bears is exceeded for prolonged periods in summer, compromising their energy budget even more.

Declines of population sizes, body size and birth rates have already been documented in some polar bear populations (Stirling *et al.* 1999, Regehr *et al.* 2007, Schliebe *et al.* 2008b, Regehr *et al.* 2010, Rode *et al.* 2010, Stirling and Derocher 2012). If this trend proceeds, it can be expected that in large parts of their distribution polar bears will be extinct within the next 100 years (Derocher *et al.* 2004, Schliebe *et al.* 2006).

In the long term, effects of climate change on the other ursid species can be expected (Edwards *et al.* 2005, Carroll 2007, Pigeon 2007). This applies in particular to Malayan sun bears. As a consequence of global warming, the occurrence of El Niño events has become more frequent over the past decades (Timmermann *et al.* 1999, Solomon *et al.* 2007, Stocker 2013). The thereby caused forest fires have drastically reduced tree populations in sun bear habitat (Fredriksson *et al.* 2007), aggravating the effects of the continuing decline of tropical rain forest and the fragmentation of natural habitat due to large scale forest clearings to grow cash crops and establish palm oil plantations in Southeast Asia. Sun bears rely on forests, they do not occur in other habitats. Trees are not only essential for food production, but might also provide protection against direct solar radiation (Normua *et al.* 2004). Lack of shelter from direct solar radiation presents another factor contributing to the reduction in suitable habitat for Malayan sun bears.

1.5 *Ex situ* conservation

Beside *in situ* conservation efforts in their natural habitat (Servheen 1999, Brower *et al.* 2002), there are coordinated captive breeding programmes established in Europe and North America for both species (Kolter 2007a). Captive ursids play an important role for conservation education as well as for applied research to improve husbandry conditions, and increasingly for research relevant for conservation to approach problems which are hard to solve in the field (Kolter pers. comm.). In particular for the least studied sun bear, precise knowledge on thermal requirements is crucial for both captive propagation and for the identification of suitable habitat and the recognition of protected areas (Wong 2002, Linkie *et al.* 2007). Most tropical mammals have a thermoneutral range between 20 °C and 30 °C (Scholander *et al.* 1950c). Inferring from the climatic conditions in their natural habitat, it can be assumed that the TNZ in sun bears is relatively narrow and lies within the range of tropical temperatures. In North America as well as in Europe, sun bears face thermal conditions far below this temperature range for most of the year. Thus they have to thermoregulate and invest considerable energy for prolonged periods, which might impact their reproduction, which is energetically costly too. Reproductive output of sun bears in captivity is low (Kolter 1995).

1.6 Study aim

The aim of the study was to determine the autonomic and behavioural mechanisms for thermoregulation used by the examined species, to identify temperature thresholds for the activation of these mechanisms and to estimate the range of the thermoneutral zone for Malayan sun bears. The purpose was to provide scientifically based information on the thermal requirements of the two species in order to optimise facilities in terms of structures, substrates and indoor temperatures. Additionally, the findings might help to estimate the species specific limits of the adaption potential with respect to the effects of climate change.

The following hypotheses and expectations have been tested:

(1) The TNZ of Malayan sun bears is narrow and close to T_A occurring in their natural range.

(2) In sun bears heat dissipation is equally distributed over the body surface.

(3) Polar bears possess body surfaces specialized for the dissipation of excess heat in the back region, so called thermal windows, which are activated above of 5 °C, their T_{UC} .

(4) Above the T_{UC} with increasing T_A both species are expected to

- reduce activity
- increase the use of substrates with higher thermal conductivity
- increase the proportion of time resting in a most extended body position
- increase the proportion of time resting in the shade
- increase the proportion of time of staying in water

(5) Below their T_{LC} , with decreasing T_A sun bears are expected to¹

- increase activity
- increase the use of substrates with lower thermal conductivity
- increase the proportion of time resting in a curled up position
- increase the proportion of resting in the sun
- increase the use of the indoor enclosure

(6) As autonomic mechanisms such as panting and shivering are energetically costly, they should rarely occur and if appropriate cooler respectively warmer microclimates are not available.

¹ The T_{LC} of polar bears is not expected to occur in the latitudes where the study takes place.

2. MATERIAL AND METHODS

2.1 Animals and keeping conditions

The study took place in nine European zoos (Table 1) at latitudes between 46° and 57°. In order to evaluate the bears' responses to different ambient conditions, relatively large and naturalistic enclosures were chosen, which provide appropriate conditions and options for behavioural thermoregulation in terms of structures, substrate and water sources that allow for the selection of different microclimates while maintaining inter individual distances. The chosen facilities correspond to the EAZA husbandry guidelines for ursids (Kolter 2007a).

Table 1. Information on study animals, enclosures and used methods (body mass was either measured or, when weighing was not possible, estimated using bears of known weight as references).

Zoo	Species	Identity	Studbook no.	Gender	Date of birth	BM (kg)	Method
Köln	Sun bear	Chika	206	male	07.1989	70	Observations / Thermography
Köln	Sun bear	Bao	192	female	28.06.1993	65	Observations / Thermography
Köln	Sun bear	Bali	193	female	28.06.1993	65	Observations / Thermography
Köln	Sun bear	Charlotte	226	female	04.12.2006	60	Thermography
Köln	Sun bear	Gula	233	female	25.08.2008	60	Observations / Thermography
Köln/Arnhem	Sun bear	Bunga	211	female	29.01.2000	70/65	Observations / Thermography
Köln/Arnhem	Sun bear	Bola	213	female	04.08.2000	60	Observations / Thermography
Arnhem	Sun bear	Frodo	218	male	30.05.2004	65	Observations / Thermography
Münster	Sun bear	Josefine	212	female	17.10.1986	70	Observations / Thermography
Münster	Sun bear	Klaus	164	male	19.03.2000	65	Observations / Thermography
Rhenen	Polar bear	Victor	1622	male	18.12.1998	440	Observations / Thermography
Rhenen	Polar bear	Hygis	1428	female	1994	220	Observations / Thermography
Rhenen	Polar bear	Freedom	1708	female	06.12.2001	300	Observations / Thermography
Rhenen	Polar bear	Walker	2900	male	07.12.2008	225	Observations
Rhenen	Polar bear	Taiko	3081	male	24.11.2010	13	Thermography
Rhenen	Polar bear	Sesi	3082	female	24.11.2010	13	Thermography
Hannover	Polar bear	Nanuq	2886	male	30.11.2007	300	Observations / Thermography
Hannover	Polar bear	Arctos	2887	male	30.11.2007	300	Observations / Thermography
Hannover	Polar bear	Sprinter	2888	male	13.12.2007	300	Observations / Thermography
Karlsruhe	Polar bear	Vitus	1674	male	02.12.2000	450	Observations
Karlsruhe	Polar bear	Larissa	1252	female	05.12.1990	270	Observations
Karlsruhe	Polar bear	Nika	1678	female	26.11.2000	300	Observations
Wuppertal	Polar bear	Boris	130	male	1978	500	Thermography
Wuppertal	Polar bear	Jerka	1361	female	23.11.1989	300	Thermography
Wuppertal	Polar bear	Lars	785	male	12.12.1993	400	Thermography
Rotterdam	Polar bear	Eric	1497	male	08.12.1993	350	Thermography
Rotterdam/Amsterdam	Polar bear	Tania	1319	female	23.12.1990	325	Thermography

2.2 Data collection

2.2.1 Meteorological variables

During both behavioural observations and thermographic measurements, meteorological data were recorded in 15 minutes intervals. The installation of measurement stations in order to measure the accessible microclimates (Kinahan *et al.* 2007) was not feasible due to the explorative and destructive nature of the studied species. Since it was not possible to obtain T_A of the microclimates within the enclosure, meteorological data were obtained in its immediate vicinity at a representative location. T_A (°C), and relative humidity (%) were measured using a digital thermohygrometer (Dewpoint Pro, scale -40 °C to 70 °C, resolution 0.1 °C, precision ± 0.5 °C). Measurements were made complying with international standard at the height of 2 m above ground in the shadow, in order to preclude errors due to direct solar radiation or radiation from the ground. Wind velocity (m/s) was obtained using an anemometer (Windmaster 2, resolution 0.1, precision $\pm 4\%$). Solar radiation (W/m^2) was measured using a solar measuring device (MacSolar, scale: 0 – 1500 W/m^2 , resolution 1, precision $\pm 2\%$). Furthermore, occurrence and intensity of precipitation were recorded (low, moderate and high). Since thermal conductance can be much higher in wet substrates than in the same material in dry condition, it was noted if the soil was wet due to prior precipitation. In one case, in Zoo Hannover, water temperature (°C) was measured via a fix installed data logger. Otherwise, water temperatures were obtained with a standard bath thermometer. Water temperature and indoor T_A measurements, when animals had access to the indoor enclosure, were conducted opportunistically.

2.2.2 Thermographic measurements

In order to examine surface temperature distribution in relation to ambient temperature, thermographic measurements were conducted at T_A between 5 °C and 30 °C in 10 adult sun

bears, and between 0 °C and 20 °C in 11 adult and polar bears and two cubs, using the camera Model ThermoCAM™ S65 HS (temperature range –40 °C – 1500 °C, resolution 0.05 °C, precision $\pm 2\%$), providing accurate high resolution thermal images in real time. Prior to the measurements, the following object parameters were programmed: T_A and humidity were obtained as described above. The distance to the measured object was measured by a distance meter (Leica LRF 1200 Rangemaster, range 0.05 m – 1097 m). An emission coefficient of $\epsilon = 0.98$, usually used for animal fur, was used (Speakman and Ward 1998, McCafferty *et al.* 2007). To minimize solar interference, measurements were made under overcast conditions when solar radiation was low and when the animals were positioned at a minimal distance of 2 m to heat radiating objects (McCafferty 2007). To avoid false interpretations of the infrared images, wetting of the fur, inflammations or scars were recorded and the animals were additionally photographed with a digital camera.

Measurements were carried out by a qualified thermographic technician (Thermotec Fischer OHG) allowing for simultaneously conducted behavioural measurements in order to link the infrared images to physical activity.

Due to the restrictive nature of the above described conditions for infrared image acquisition, measurements were conducted whenever the conditions were appropriate rather than at defined intervals.

2.2.3 Behavioural observations

In order to determine the contribution of behaviours to thermoregulation, behavioural observations were conducted at T_A ranging from –2 °C to 35 °C in 10 adult polar bears and between 5 °C and 34 °C in nine adult sun bears. Data were collected between 9:00 and 18:00, covering the time the animals were in the outdoor enclosure. Intermissions took place at differing times of the day, such that all hours of the day were equally represented in the final sample (Martin and Bateson 2007).

To test the effect of different ambient conditions on behaviours related to thermoregulation, activity, choice of substrate, shade and body position while resting were recorded by instantaneous sampling (Martin and Bateson 2007), recording each individual's activity simultaneously at 1 min intervals.

The category resting was further subdivided into three categories of lying in different body positions depending on the proportion of body surface area exposed to the air and ground respectively (see Table 2). Individuals were considered to rest in the sun when more than 50% of their body was exposed to direct sunlight (Kendall *et al.* 2006). When exactly half of the body was in the shade, the animal was considered to rest in the sun when their head was exposed to solar radiation. Rarely occurring patterns such as panting or shivering were recorded separately. Behavioural data were collected for a total of 721 hours and 43260 scans, resulting in a total of 54060 data points for polar bears and 44025 for sun bears.

Table 2. Definitions of recorded behaviours.

Behaviour	Description
Standing	Standing quadrupedally, showing no activity
Resting	The category resting was subdivided into three categories of resting in different body postures: (1) Lying in a curled up posture, contact with environment is minimal, snout may be covered with paws (2) Sitting with the trunk fold forward while maintaining an upright position, sometimes the head touches the paws, sitting erect or semi-erect with the forelimbs elevated, lateral lying with the front and rear legs all to one side, lying or sitting front legs supported by a tree or other similarly elevated objects (3) Lying in an extended posture on the belly or back with all extremities stretched forward and backward, dorsal lying with all legs extended upwards, ventral lying with four legs extended forward on both sides, large body surface exposed to the environment
Sitting / standing active	Activities which do not require a high degree of physical activity, such as exploration or object manipulation while sitting or standing, excluding nest building activities, or other light activities such as maintenance behaviour (e.g., scratch, lick, stretch any part of body) while sitting or standing, defecation and urination
Nest building	Manipulation of such as straw, branches, jute or other insulating material to rest on
Exploration	All explorative behaviours when no food was available, such as walking while sniffing the ground, digging soil, scratching wood or manipulating objects intensively, or tearing apart trunks with forelegs,
Foraging	Feeding and all explorative behaviours described above when food was available; water intake has not been documented because access to drinking water was not always visible to the observer
Walking	Terrestrial locomotion at a moderate speed
Pacing	Repetitive movement pattern performed on land, here typically walking over the same path back and forth
Running	Locomotion on land at a more accelerated speed than when walking
Climbing	Vertical quadrupedal movements over trees or tree trunks, typically performed by sun bears
Social play	Play fighting on land or in water while sitting, running or climbing, at a high level of activity
Swimming	Any activity in water, such as swimming or diving, often includes exploration, object play or social play; typically performed by polar bears
Out of sight	The animal or its behaviour is not clearly visible to the observer
Shivering	Shivering becomes evident by fast muscular contractions
Panting	Mouth opened high frequent respiration

2.3 Data analysis

2.3.1 Thermographic measurements

Body surface temperature distribution, and hence heat loss to the environment, can be determined by measuring the quantity of radiation emitted from the body (McCafferty 2007). Thermal images were analysed using the ThermaCAM Researcher™ software. For analysis of T_S in relation to T_A , only images taken in conditions where the animals were dry were used, as water alters the emissivity (McCafferty 2007) and, most notably, the insulating properties of the fur. Contrasting to Malayan sun bears, polar bears were often found wet after swimming or after wallowing in mud or soil, resulting in a reduced number of images available for analyses. In total, 1160 thermal images of eight polar bears (T_A 1 °C – 19°C) and 4237 of 10 sun bears (T_A 5 °C – 30 °C) were analysed.

Quantitative analyses of thermal images were performed on different body surfaces (eyes, snout, face, trunk, shoulder region, outer leg, and inner leg). T_S were obtained by measuring the resulting temperature at randomly chosen points situated within each chosen area.

The intensity of emitted radiation is affected by the angle at which the thermal image of an object is taken, since electromagnetic radiation travels in straight lines. Thus if an object is viewed at a very shallow angle, the intensity of thermal radiation received is reduced, resulting in a lower T_S (Speakman and Ward 1998). Therefore, the outer borders of the body surfaces were excluded from analyses.

T_S (mean \pm SD) of the respective surface area and differences between mean T_S and T_A were calculated and plotted against T_A in order to evaluate heat dissipation in relation to T_A .

The amount of heat exchange is proportional to the temperature difference between body surface and ambient temperature. However, for a substantial heat exchange to occur, a temperature gradient between the surface of an individual and its environment is required

(Tracy 1972). It has been suggested that a temperature gradient of less than 1.5 °C is likely too small for meaningful heat exchange (Phillips and Heath 1995).

An estimation of the critical temperatures of Malayan sun bears was made based on differences between T_S and T_A measured by infrared thermography at different T_A , by determining the range of temperatures where T_S is nearly identical to T_A (± 1.5 °C) (Romanovsky *et al.* 2002, Autio *et al.* 2007). Since the TNZ is measured in animals in a resting and post-absorptive state, data derived from animals during or immediately following activity were excluded from analyses for the estimation of the TNZ.

For the detection of body surfaces specialized for heat loss however, also images that were taken during locomotion can be analysed. A thermal window was defined as an area on the body with a difference of T_S of at least 1.0 °C to the surrounding body surface (Erdsack *et al.* 2012). In order to identify body surfaces specialized for the dissipation of excess heat, thermograms were analysed as follows: (1) Body surfaces which show T_S close to T_A , were not considered to contribute to heat loss, (2) Body surfaces that exhibit consistently T_S above T_A were considered to dissipate heat to the environment, but not specialized for the regulation of heat exchange, (3) Body surfaces that vary greatly in T_S in relation to T_A , were considered to be specialized for the exchange of heat (Phillips and Sanborn 1994).

2.3.2 Behavioural observations

In order to assess the contribution of behaviours related to thermoregulation, the percentage of time spent in each recorded behaviour pattern was calculated and plotted against T_A .

2.3.3 Statistical analysis

Spearman rank correlation was calculated to determine the relationship between solar radiation, humidity and T_A .

Prior to pooling the behavioural data, between-group and within-group comparisons were carried out using a Friedman test, in order to identify differences between individuals as well as between different zoo groups, which might have been due to confounding variables such as age, sex or local keeping conditions. Since there were no statistically differences between individuals or different zoo housed groups ($P > 0.05$, Friedman test), the data were pooled for subsequent analyses.

The proportion of time spent in each recorded behaviour pattern in relation to T_A was calculated and the relationship between behaviours and T_A was calculated using Spearman rank correlation. The correlation coefficient, r_s , ranges from -1 to $+1$. A correlation of ± 1.0 indicates a perfect association, a correlation of 0 means there is no linear association between the two measures (Martin and Bateson 2007). Informal phrases to interpret statistically significant correlation coefficients of various sizes were used after Martin and Bateson (2007). Comparisons of the proportion of time spent in each behaviour pattern at different subgroups of T_A ranges that were determined after plotting the data were analysed using Mann-Whitney U one-tailed test.

Changes of T_S of different body surfaces in relation to T_A were calculated using Spearman rank correlation. Differences between mean T_S measured in different body parts were calculated using Wilcoxon signed-rank one-tailed test. A Mann Whitney- U -test, one-tailed, was employed to test for significant differences of mean T_S between individuals.

Differences were considered statistically significant at $P < 0.05$ (Lamprecht 1992).

3. RESULTS

3.1 Meteorological variables

Wind speed was constantly below 1 m/s. Air velocities below 1.6 m/s have no significant effect on T_A and are therefore negligible (Ames and Insley 1975). The relationship between solar radiation, humidity and T_A is shown in Figure 5. The positive correlation between solar radiation and T_A ($r_s = 0.97$, $P = 0.000000$) as well as the negative correlation between humidity and T_A ($r_s = -0.95$, $P = 0.000000$) were highly significant. Due to these very high correlations, and thus dependency, all behavioural data were analysed in relation to T_A , assuming a combined effect of air temperature, solar radiation, and humidity.

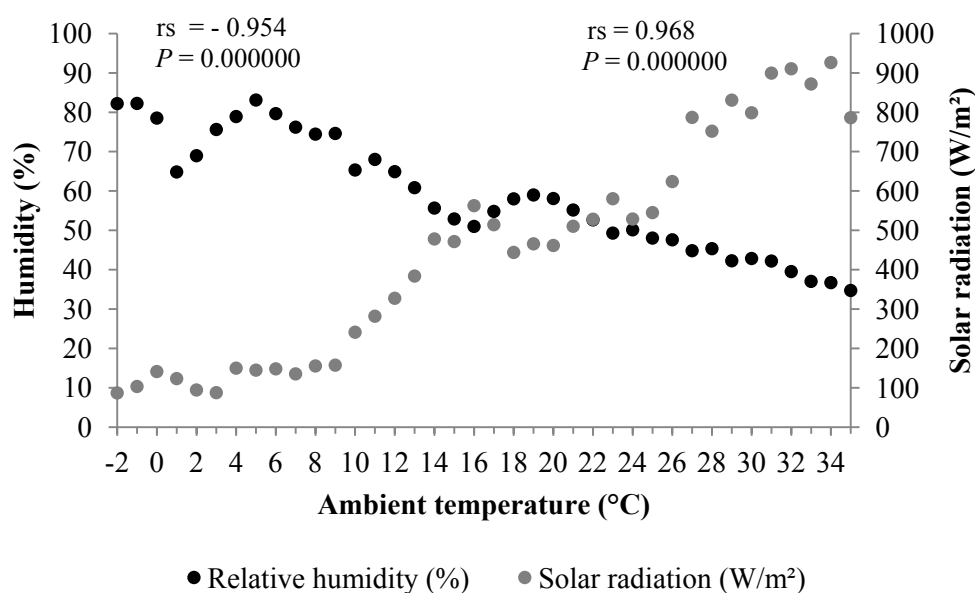


Figure 5. Mean relative humidity (%) and solar radiation (W/m^2) in relation to T_A ($^{\circ}C$).

3.2 Thermographic measurements of Malayan sun bears

The TNZ of sun bears was estimated by identifying the range of T_A , where T_S is close to T_A . Figure 6 shows typical thermal images taken from adult sun bears at different T_A while they were post-absorptive and inactive or immediately after resting. At T_A of $28^{\circ}C$, T_S of most body parts correspond to T_A , indicating that there is no substantial heat exchange between

body and environment and that this T_A lies within the TNZ. Below 24 °C and above 28 °C heat is dissipated equally over the body surface, resulting in T_S higher than T_A . However, there were not sufficient thermographic images available from resting animals to test the data statistically.

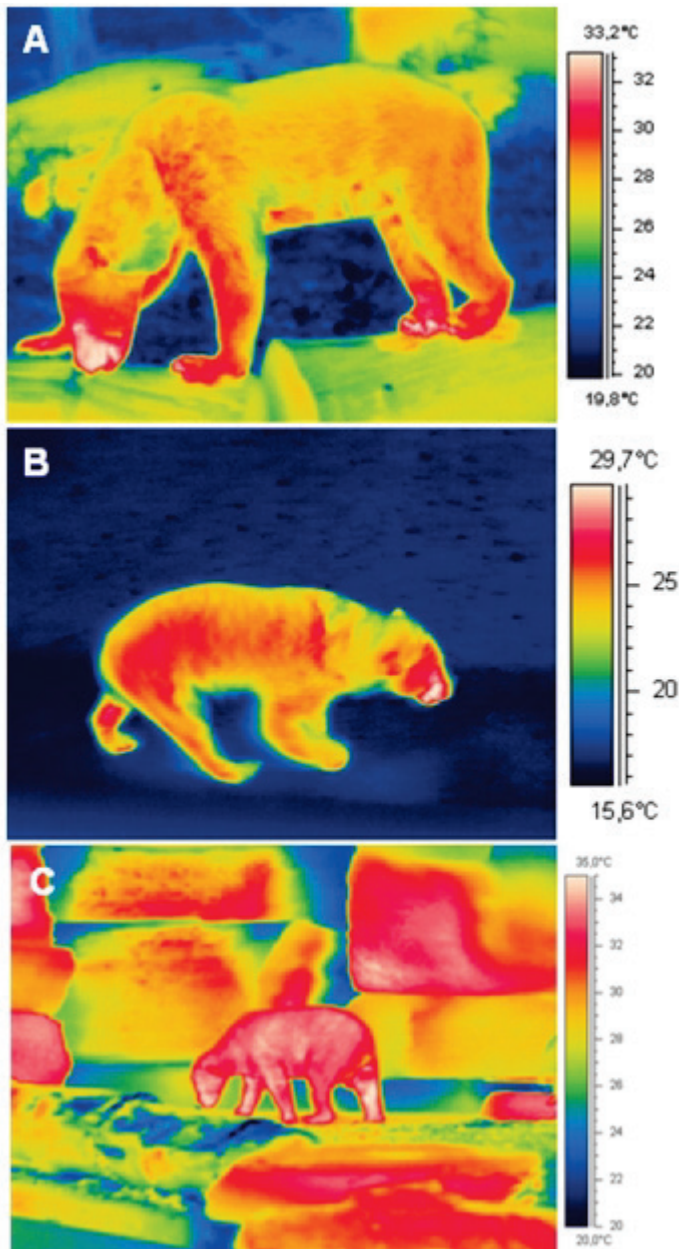


Figure 6. Typical thermographic images of adult Malayan sun bears taken at $T_A = 28$ °C (A), $T_A = 23$ °C (B), and $T_A = 29$ °C (C). Data obtained during or immediately following activity were excluded from analyses.

The TNZ is measured in a resting and post-absorptive state, when only basic metabolic processes take place, whereas food intake as well as activity causes additional internal heat production. Thus, thermographic images taken from active sun bears were analysed in order to quantify the variation of heat dissipation in relation to T_A during normal activity.

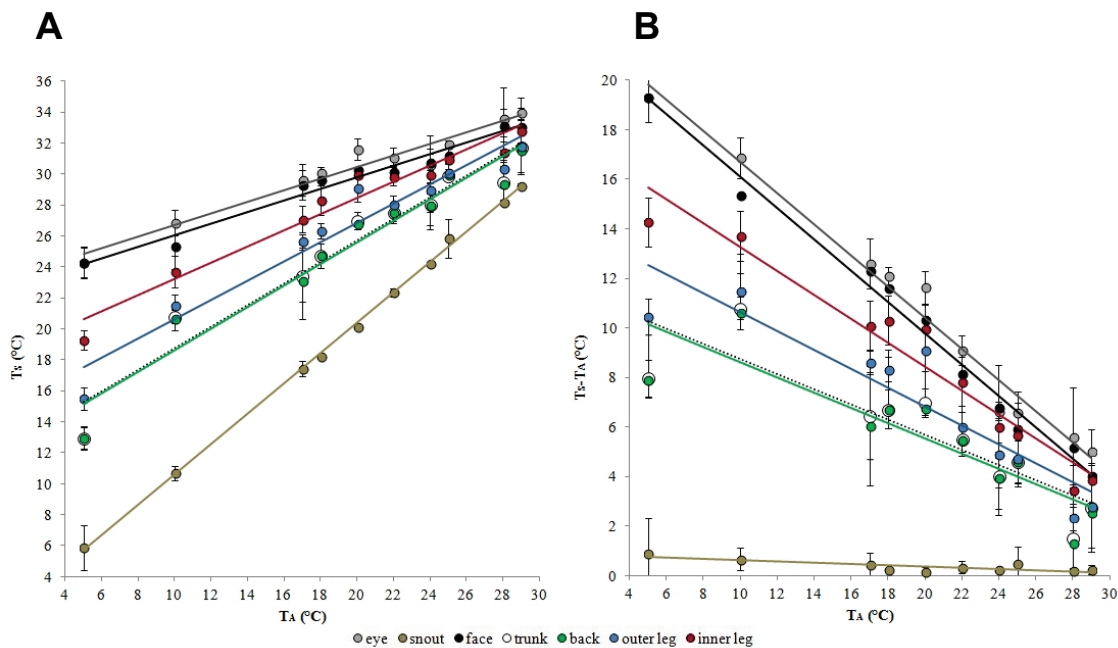


Figure 7. Mean T_S of different body parts in relation to T_A (A) and the temperature gradient between mean T_S and T_A in relation to T_A (B). Shown are means \pm SD. Values for r_s and P (Spearman rank correlation) are provided in the text.

Figure 7 shows T_S (mean \pm SD) of different body parts in relation to T_A , measured in the sun bears while the animals were active, and $\Delta T_S - T_A$ in relation to T_A . At all T_A , T_S of the eyes was highest, followed by facial surface temperatures, whereas those of the snout were lowest and always close to T_A . The surface temperatures T_S of all body parts increased linearly with T_A . All correlations were very high and strongly significant (eye: $r_s = 0.95$, $P = 0.000023$, snout: $r_s = 1.0$, $P = 0.000000$, face: $r_s = 0.98$, $P = 0.000001$, trunk: $r_s = 0.99$, $P = 0.000000$, back: $r_s = 0.99$, $P = 0.000000$, outer leg: $r_s = 0.96$, $P = 0.000007$, inner leg: $r_s = 0.98$, $P = 0.000001$). Heat was dissipated equally over the trunk, back and outer legs, hence the major body parts (see Figure 6). Merely the inner legs showed T_S that were significantly higher than T_S of the outer legs ($P = 0.00098$). T_S of the snout were constantly close to T_A .

3.3 Thermographic measurements of polar bears

Figure 8 shows a typical thermographic image taken from a polar bear immediately after rest at T_A of 5 °C, the reported T_{UC} of polar bears. At T_A of 5 °C, T_S in major body parts of an inactive animal are close to T_A , indicating that there is no heat exchange between body surface and environment and that this T_A lies within the TNZ of polar bears.

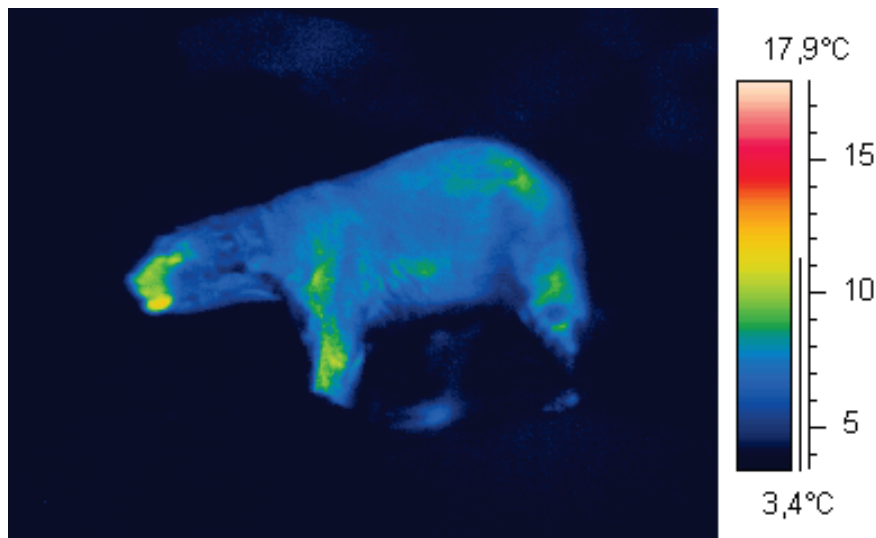


Figure 8. Typical thermal image of an adult male polar bear taken at $T_A = 5$ °C immediately after resting.

Figure 9, however, shows that at T_A of 12 °C, 17 °C and 19 °C and during physical activity, the shoulder and the back regions show T_S above those of the surrounding areas with increasing differences between mean T_S and T_A with increasing T_A and thus increasing heat loss via convection.

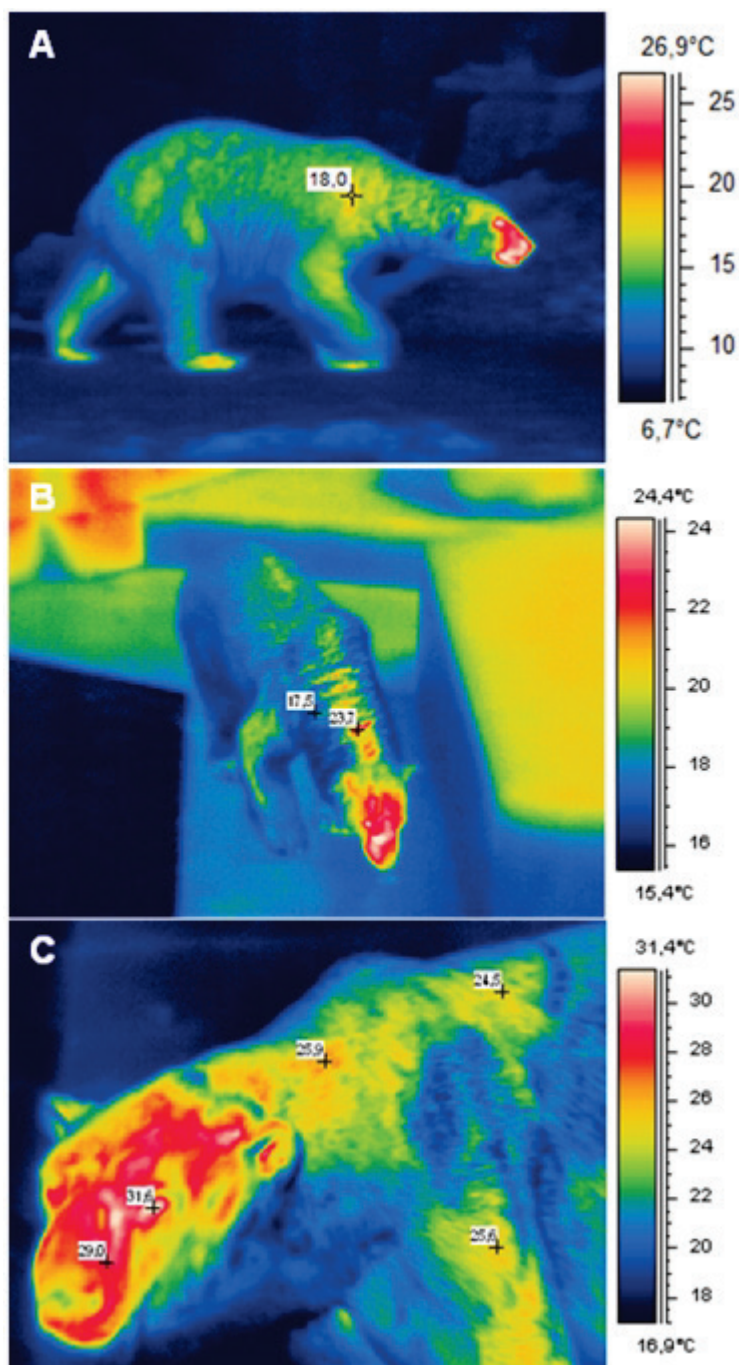


Figure 9. Thermographic images of active adult polar bears taken at $T_A = 12\text{ °C}$ (A), $T_A = 17\text{ °C}$ (B), and $T_A = 19\text{ °C}$ (C).

Figure 10 shows thermal images of two four months old polar bear cubs during social play at $T_A = 7\text{ }^\circ\text{C}$. T_S of major parts of the body surface are slightly above T_A , indicating slight heat loss to the environment. After a few minutes of extensive social play, thermal windows in the shoulder and back region, as well as in the legs, became obvious.

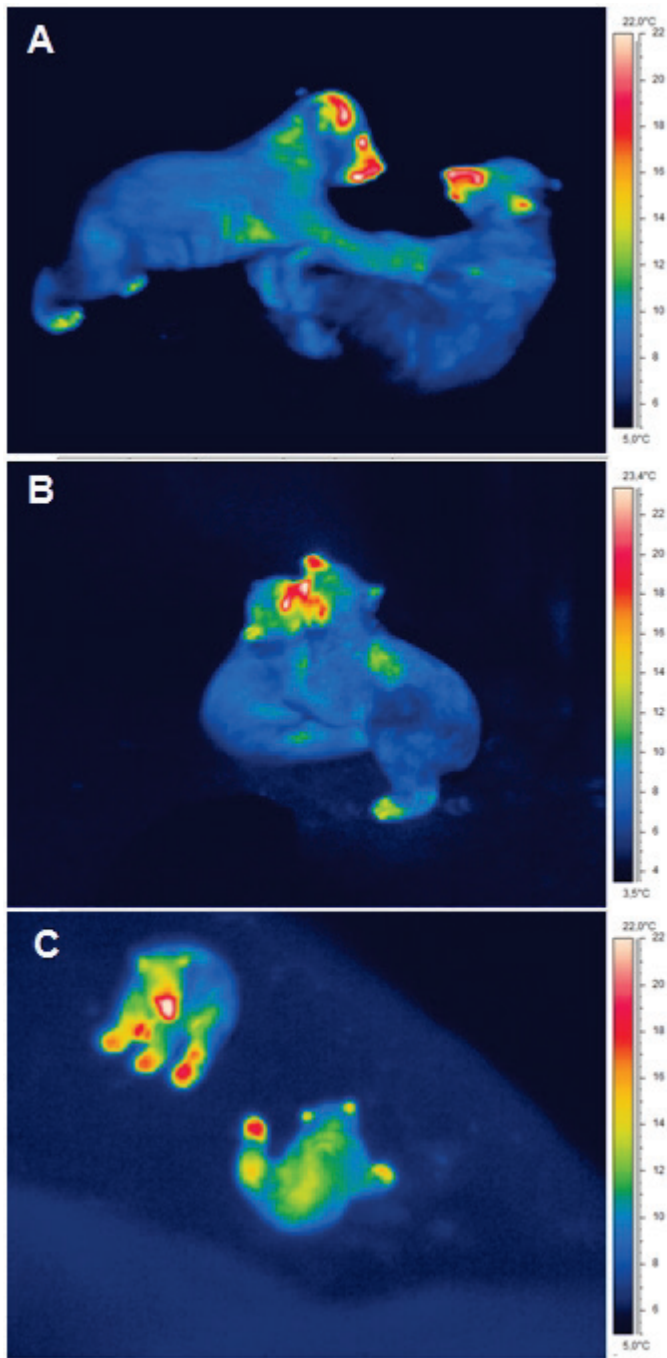


Figure 10. Thermographic images of four months old playing polar bear cubs taken at $T_A = 7\text{ }^\circ\text{C}$ immediately after the beginning (A), after 2 minutes (B), and after seven minutes (C) of intensive social play.

T_S (mean \pm SD) of different body surfaces in relation to T_A , measured in active polar bears, and $\Delta T_S - T_A$ in relation to T_A are shown in Figure 11. At all T_A , the eyes showed the highest T_S . In all measured body surfaces, T_S increased linearly with T_A . Whereas correlations were highly significant for the eyes ($r_s = 1.0$, $P = 0.000000$), the trunk ($r_s = 1.0$, $P = 0.000000$), the inner leg ($r_s = 1.0$, $P = 0.000000$) and the outer leg ($r_s = 1.0$, $P = 0.000000$), the relationship between T_A and T_S was not significant for the face ($r_s = 0.8$, $P = 0.2$) respectively the back region ($r_s = 0.8$, $P = 0.2$).

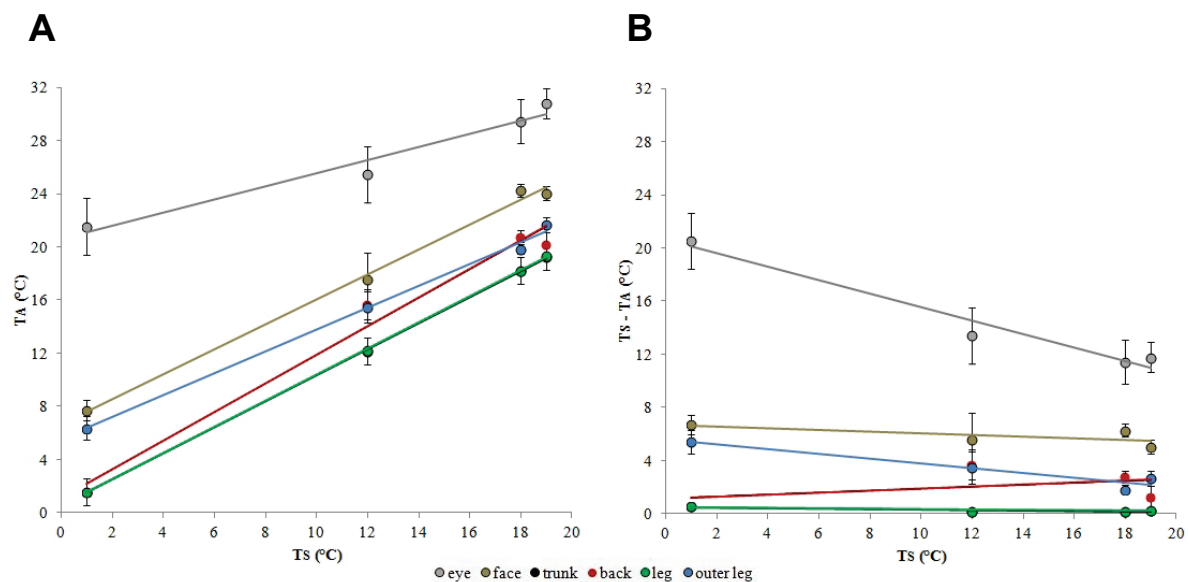


Figure 11. Mean T_S of different body surfaces in relation to T_A (A) and the temperature gradient between mean T_S and T_A in relation to T_A (B). Shown are means \pm SD. Values for r_s and P (Spearman rank correlation) are provided in the text.

Mean T_S of the back region and the trunk measured in several polar bears at different T_A and ΔT_S back– T_S trunk are shown in Figure 12. All measured bears showed thermal windows in the back region with strongly significant higher T_S than the rest of the trunk, independent of sex, age and body mass.

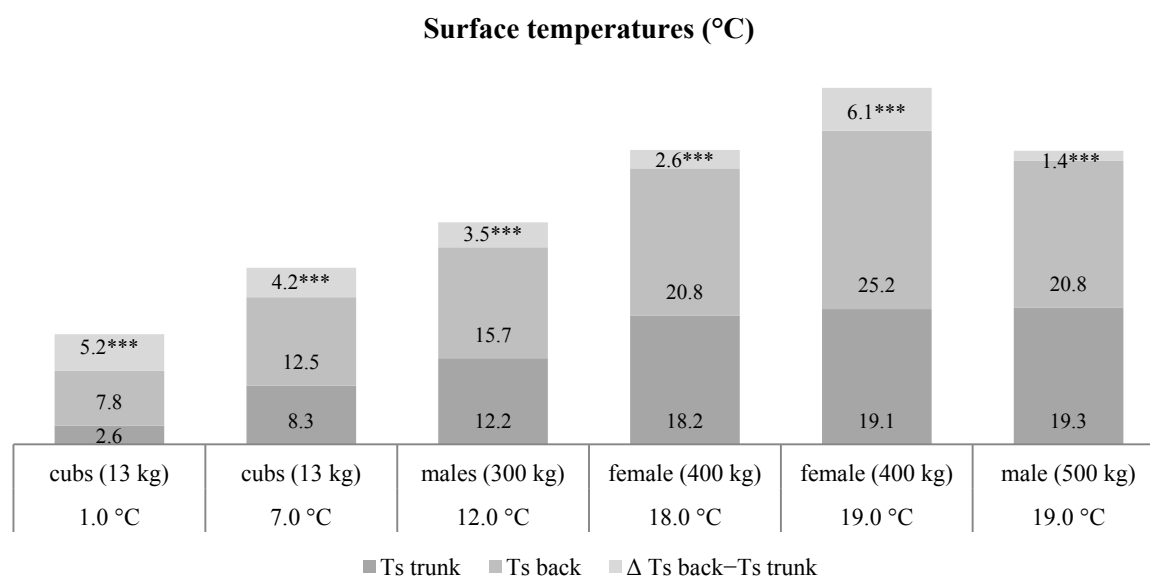


Figure 12. Mean T_S of back, trunk and ΔT_S back– T_S trunk measured in different polar bears at the T_A indicated (***) $P < 0.001$, Wilcoxon signed-rank test, one-tailed).

Mean T_S of the outer legs and the surrounding surface of the legs as well as ΔT_S outer leg– T_S leg measured in several bears at different T_A are shown in Figure 13. Differences between T_S of the legs and the outer legs were highly significant at $T_A = 1$ °C in an adult female ($P = 0.000000$) ($N = 96$), at $T_A = 12$ °C in three adult males ($P = 0.000000$) ($N = 54$), at $T_A = 18$ °C in an adult female ($P = 0.000000$) ($N = 257$), at $T_A = 19$ °C in an inactive adult female ($P = 0.000004$) ($N = 18$) and at $T_A = 19$ °C in an adult male ($P = 0.000000$) ($N = 525$).

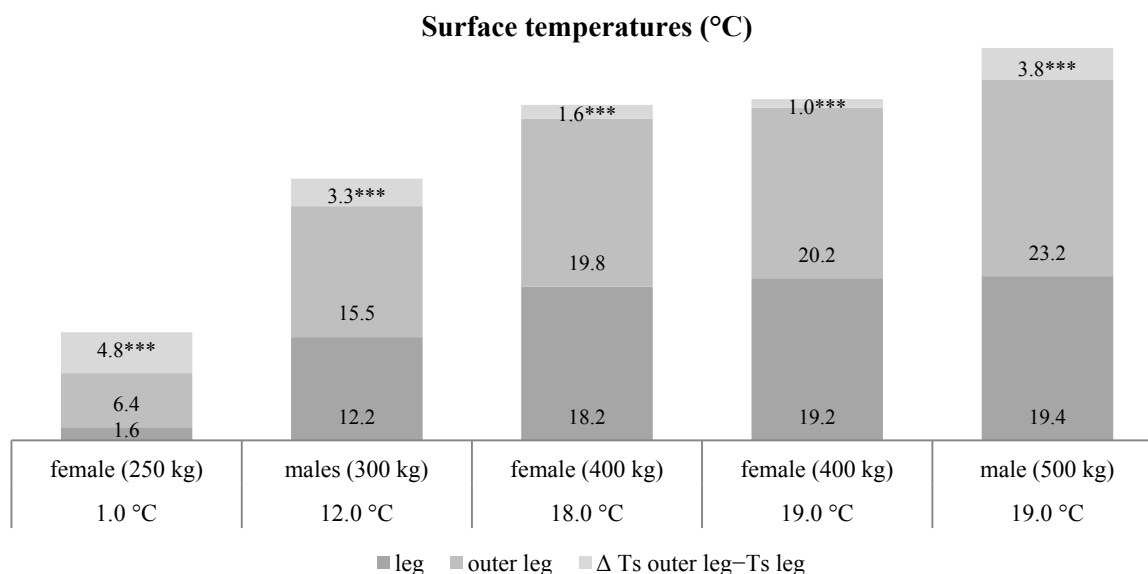


Figure 13. Mean T_S of the outer legs and the surrounding surface of the legs and ΔT_S outer leg - T_S leg measured in polar bears at the T_A indicated (***) $P < 0.001$, Wilcoxon signed-rank test, one-tailed).

3.4 Behavioural observations in Malayan sun bears

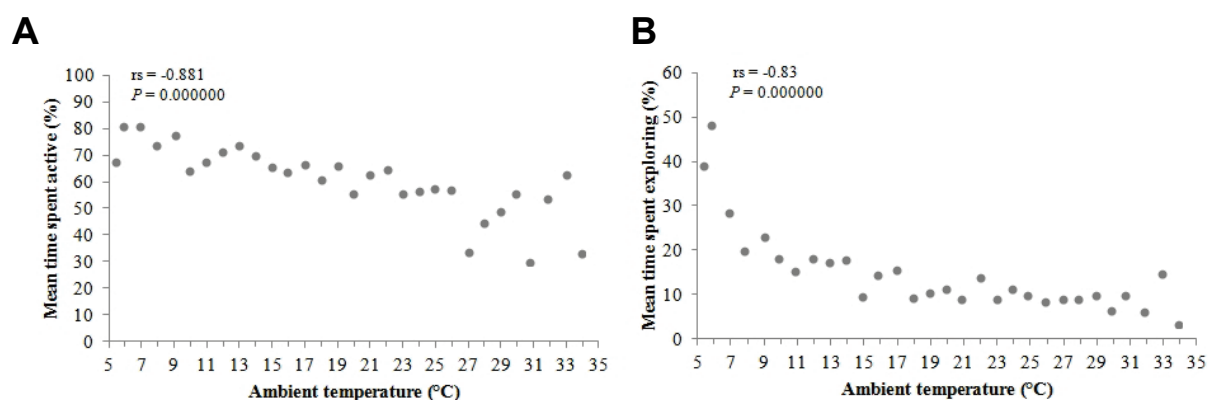
3.4.1 Time budget

The proportions of time spent in each recorded behaviour pattern are summarised in Table 3. The percentage of resting was highly correlated to T_A ($r_s = 0.79$, $P = 0.000000$). Furthermore, there was a moderate correlation between the amount of standing and T_A ($r_s = 0.40$, $P = 0.03$). Ambient conditions had no effect on light activities while sitting or standing ($r_s = -0.08$, $P > 0.05$), whereas exploration, that required a moderate degree of physical activity, decreased significantly with increasing T_A ($r_s = -0.83$, $P = 0.000000$) and showed a marked relationship across the entire temperature range (see Figure 14). The time spent walking was moderately negatively correlated to T_A ($r_s = -0.45$, $P = 0.01$), whereas foraging was not influenced by T_A ($r_s = 0.31$, $P > 0.05$). Among activities that required a higher degree of physical activity, running ($r_s = -0.18$, $P > 0.05$) and pacing ($r_s = 0.28$, $P > 0.05$) have not been affected by T_A . In contrast, the proportion of climbing ($r_s = -0.89$, $P = 0.000000$) and social play ($r_s = -0.41$, $P = 0.02$) significantly decreased with increasing T_A .

Table 3. Mean percentages spent in each recorded behaviour (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, Spearman rank correlation).

T_A (°C)	Standing *	Resting ***	Sitting/ standing active	Nest building ***	Exploration ***	Foraging	Walking *	Running	Pacing	Climbing ***	Social play *
5	0.0	32.6	17.1	0.7	39.1	0.0	4.5	0.0	0.0	5.9	0.0
6	3.2	16.1	11.1	2.7	48.4	6.1	7.5	0.0	0.2	3.5	1.3
7	2.0	17.0	12.1	0.2	28.6	15.1	19.0	1.5	0.0	4.4	0.0
8	8.1	18.2	7.9	0.0	20.0	9.3	26.7	0.2	3.1	3.6	3.0
9	5.8	16.9	10.4	3.8	23.2	12.9	15.5	1.1	2.0	5.1	3.1
10	8.5	27.4	10.9	0.4	18.2	6.6	20.3	0.8	0.7	1.9	4.2
11	8.3	24.2	8.6	0.8	15.4	12.5	20.8	0.3	2.8	3.1	3.3
12	10.0	18.8	17.2	0.7	18.2	4.3	21.8	0.4	3.9	2.5	2.2
13	8.7	17.5	10.5	0.1	17.4	18.5	18.2	0.0	5.1	1.7	2.2
14	4.7	25.7	13.1	1.2	17.8	7.7	17.7	0.0	4.2	1.6	6.2
15	8.2	21.9	11.3	2.8	9.7	17.3	18.5	0.0	3.9	0.5	1.5
16	4.4	31.9	7.5	1.1	14.5	16.7	16.9	0.6	1.7	1.6	3.1
17	6.6	26.9	20.4	0.2	15.5	7.9	17.3	0.0	2.1	1.2	1.6
18	6.2	32.9	13.3	0.0	9.5	21.1	12.5	0.0	2.2	1.7	0.6
19	7.1	26.9	16.1	0.1	10.5	19.4	15.9	0.1	0.3	1.1	2.4
20	9.2	35.3	12.7	0.0	11.4	12.3	11.9	0.1	1.4	1.2	4.4
21	8.4	29.0	16.1	0.1	9.1	17.0	13.9	0.3	1.4	1.3	3.5
22	7.6	27.6	9.0	0.1	13.8	21.3	16.1	0.1	1.2	1.5	1.7
23	8.0	36.3	11.4	0.0	9.0	14.8	15.3	0.4	1.0	1.5	2.1
24	7.1	36.5	10.7	0.2	11.5	11.9	16.3	0.3	2.0	1.3	2.2
25	6.3	36.5	12.7	0.0	10.0	15.4	17.3	0.1	0.2	0.8	0.8
26	9.2	34.1	5.0	0.1	8.4	23.3	16.8	0.1	0.3	0.9	1.6
27	10.9	55.5	2.5	0.0	9.1	4.1	12.2	0.1	1.7	1.3	2.6
28	8.4	47.1	3.2	0.0	9.1	9.2	19.0	0.2	1.5	0.9	1.4
29	14.0	37.2	5.9	0.0	10.1	12.7	17.3	0.4	0.9	1.1	0.6
30	4.9	39.6	9.7	0.0	6.4	31.7	6.6	0.6	0.0	0.3	0.0
31	4.3	65.8	10.7	0.0	9.9	7.0	1.5	0.0	0.0	0.8	0.0
32	6.8	39.7	23.3	0.0	6.1	15.5	8.7	0.0	0.0	0.0	0.0
33	11.9	25.5	19.6	0.0	14.9	16.5	7.9	0.0	3.7	0.0	0.0
34	12.8	54.1	11.2	0.0	3.4	15.0	3.4	0.0	0.0	0.0	0.0

The mean time spent active (all recorded behaviours excluding resting and standing) and the proportion of time spent exploring are displayed in Figure 14. The total time spent active was highly significantly correlated to T_A ($r_s = -0.88$, $P = 0.000000$) and there was a marked negative relationship between the two variables across the entire temperature range.

**Figure 14.** Mean time (A) spent active and (B) the proportion of time spent with exploration in relation to ambient temperature.

The proportion of nest building activities in relation to T_A is illustrated separately in Figure 15. Nest building was significantly negatively correlated to T_A ($r_s = -0.73$, $P = 0.000005$) and could be distinguished between distinct temperature ranges. Below 16 °C the proportion of nest building was significantly higher than between 16 °C and 26 °C ($P = 0.003$) and significantly lower above 26 °C, where this behaviour did not occur at all ($P = 0.01$).

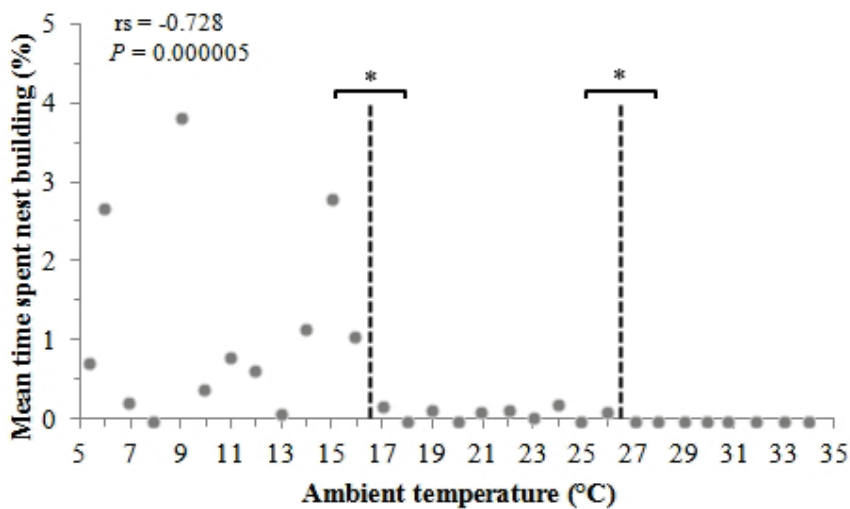


Figure 15. Proportions of time spent nest building (* $P < 0.05$, Mann-Whitney U one-tailed test).

3.4.2 Substrate chosen to rest on

The proportion of time spent resting on different substrates in relation to T_A are summarised in Figure 16. Temperatures were post hoc subdivided into two or three sub-groups based on obvious behavioural changes in relation to T_A and compared for statistical differences.

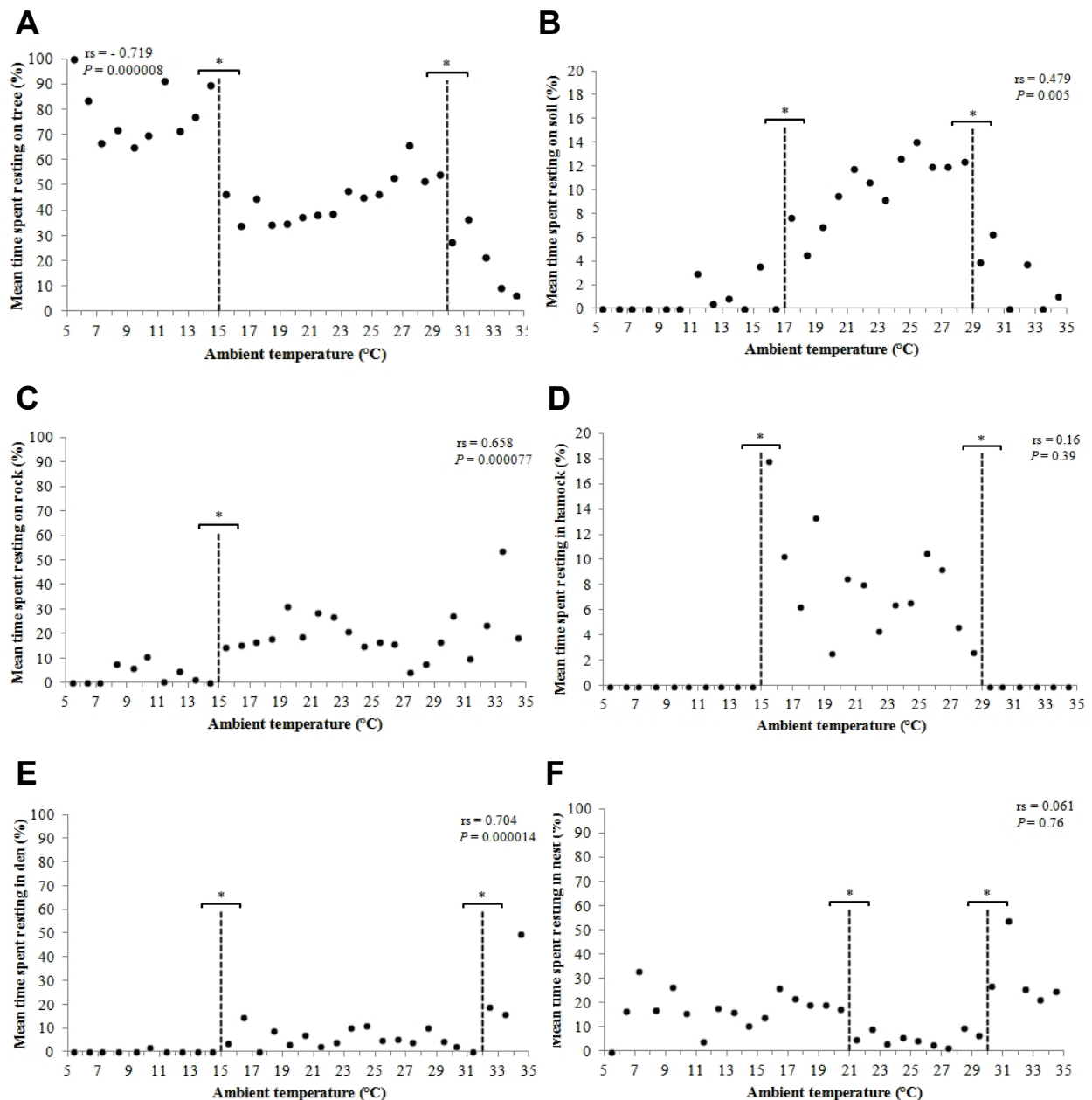


Figure 16. Proportions of time spent resting on (A) tree, (B) soil, (C) rock, (D) hammock, (E) den and (F) nest in relation to T_A (* $P < 0.05$, Mann-Whitney U one-tailed test).

The substrate which was selected to rest on varied greatly with T_A . Resting on tree trunks was strongly negatively correlated to T_A ($r_s = 0.72$, $P = 0.000008$) with significant higher proportions between 5 $^{\circ}\text{C}$ and 14 $^{\circ}\text{C}$ than from 15 $^{\circ}\text{C}$ to 29 $^{\circ}\text{C}$ ($P = 0.00001$). Above 29 $^{\circ}\text{C}$ the use of tree trunks to rest on dropped again significantly ($P = 0.0005$). There was a moderate significant positive correlation between the proportion of resting on soil and T_A (r_s

= 0.48, $P = 0.005$), showing an inversely U-shaped relationship between the two variables. The use of soil for resting was significantly higher between 17 °C and 28 °C than below ($P = 0.000000$) and above ($P = 0.0001$) this temperature range. The use of rocks to rest on increased significantly with increasing T_A ($r_s = 0.66$, $P = 0.00008$) and occurred significantly less below 15 °C ($P = 0.000001$). Although there was no overall correlation between resting in a hammock and T_A ($r_s = 0.16$, $P > 0.005$), the sample was composed of distinct sub-groups. The use of hammocks for resting was significantly higher between 15 °C and 28 °C, when compared to T_A below and above this temperature range ($P = 0.000001$ respectively 0.00003). Resting in a den was significantly correlated to T_A ($r_s = 0.70$, $P = 0.00001$) across the entire range of T_A . However, below 16 °C dens were used significantly less to rest ($P = 0.000000$) whereas above 31 °C the proportion of resting in dens was highest ($P = 0.001$). The proportion of resting in a nest could not linearly be correlated to T_A ($r_s = 0.06$, $P > 0.005$) but was significantly higher below 21 °C and above 29 °C ($P = 0.0003$ respectively 0.0005).

3.4.3 Body posture while resting

The relation between body position while resting and T_A is illustrated in Figure 17. The proportion of sitting was constantly high when compared to resting in a curled up or an extended body position. Resting in a curled up position was significantly inversely correlated to T_A ($r_s = 0.84$, $P = 0.000000$) and occurred significantly more often below 15 °C ($P = 0.000000$). Resting in an extended position could be correlated to increasing T_A ($r_s = 0.85$, $P = 0.000000$) and increased significantly above 25 °C ($P = 0.000000$).

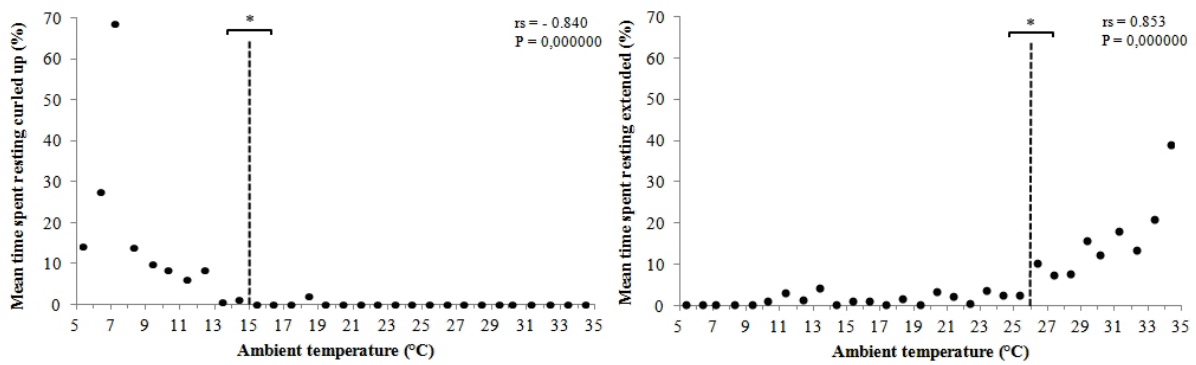


Figure 17. Proportions of time spent resting (A) in a curled up and (B) in an extended body position ($* P < 0.05$, Mann-Whitney U one-tailed test).

3.4.4 Resting in the shade vs. sun

The proportions of resting in the shade in relation to T_A are shown in Figure 18. With increasing T_A , time spent in shady places significantly increased ($r_s = 0.94$, $P = 0.000000$). Whereas below 16 °C the amount of resting in the shade was significantly lower ($P = 0.00004$), above 26 °C, resting in the shade increased significantly ($P = 0.00001$).

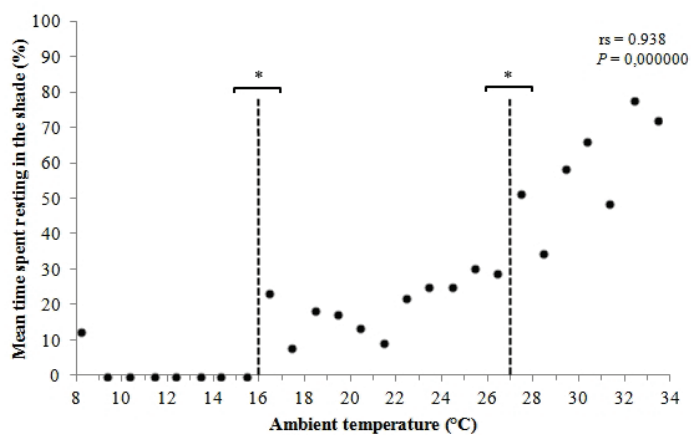


Figure 18. Proportions of time spent resting in the shade in relation to T_A ($* P < 0.05$, Mann-Whitney U one-tailed test). Data derived from observations during the absence of sunshine were excluded from analyses.

3.4.5 Time spent in water

The proportions of time spent in water, whether active or not, in relation to T_A are given in Figure 19. The use of water varied greatly with T_A . The time the bears spent inside water was significantly correlated to T_A ($r_s = 0.93$, $P = 0.000000$). Below 16 °C the time spent in water

was significantly lower when compared to T_A between 16 °C and 26 °C ($P = 0.0001$). Above 26 °C the proportion of time spent in water significantly increased ($P = 0.00001$).

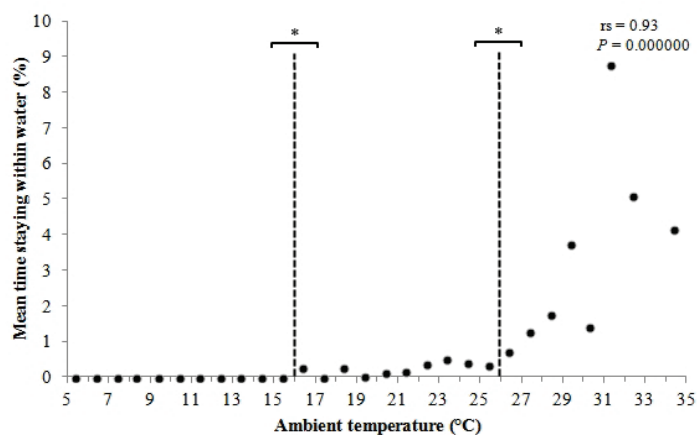


Figure 19. Proportion of time spent in water in relation to T_A .

3.4.6 Use of the indoor enclosure

The proportion of staying indoors in relation to T_A is illustrated in Figure 20. There was a moderate negative correlation between staying indoors and T_A ($r_s = -0.40$, $P = 0.03$), when analysed across the entire temperature range. However both, below 18 °C and above 28 °C the indoor enclosure was used significantly more often than within this temperature range ($P = 0.000001$ and 0.00006 respectively).

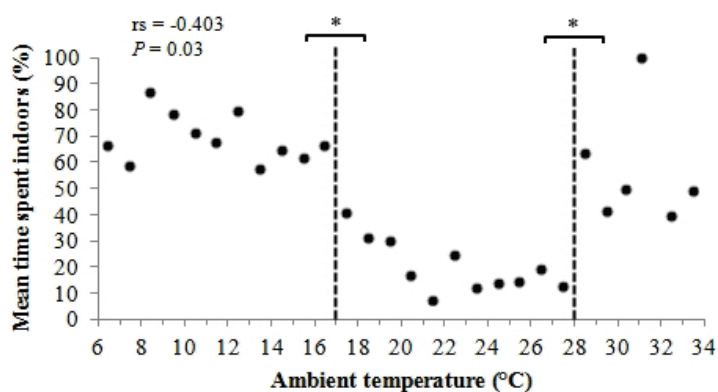


Figure 20. Proportion of time spent indoors in relation to T_A . Data derived from observations when the bears had no access to the indoor enclosure were excluded from analysis.

3.4.7 Panting and shivering

Panting did only occur on a few occasions after strenuous social play between a male and a female sun bear in one location, which was forced by the male. During none of the observations shivering could be observed.

3.5 Behavioural observations in polar bears

3.5.1 Time budget

The proportion of time spent in each recorded behaviour pattern are summarised in Table 4.

Table 4. Mean percentages spent in each recorded behaviour (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, Spearman rank correlation).

T _A (°C)	Standing ***	Resting	Sitting/ standing active	Exploration ***	Foraging	Walking ***	Running **	Pacing*	Social play***	Swimming ***
-2	18.1	12.6	0.8	14.3	11.1	14.9	0.6	0.0	21.5	6.1
-1	4.7	25.5	1.3	16.3	7.8	12.1	0.3	0.8	11.1	20.1
0	10.4	32.7	5.4	1.3	0.0	27.5	0.0	0.9	4.6	17.1
1	15.6	32.5	1.8	11.4	5.0	15.0	0.1	12.9	4.1	1.7
2	17.5	20.3	2.2	12.8	2.4	19.3	0.1	15.6	3.7	6.3
3	10.9	36.0	4.8	6.0	0.2	12.2	0.0	14.0	2.6	13.2
4	12.8	24.3	5.6	4.0	4.7	24.9	0.0	15.7	3.8	4.3
5	15.1	26.1	3.1	2.0	0.4	20.3	0.2	16.7	1.2	14.9
6	11.0	37.9	4.5	0.7	4.2	21.5	0.0	6.6	0.4	13.2
7	11.2	23.3	1.4	1.4	9.3	22.7	0.0	24.4	0.0	6.3
8	14.0	22.8	1.4	1.3	6.1	21.1	0.1	28.6	0.0	4.6
9	10.9	36.4	4.1	1.7	9.6	12.9	0.0	11.0	0.0	13.4
10	13.6	18.2	3.4	2.0	13.9	12.5	0.0	10.3	1.4	24.8
11	9.6	24.9	3.4	1.6	1.8	8.5	0.0	19.1	0.5	30.4
12	11.8	30.4	2.5	2.3	8.2	17.4	0.0	14.0	1.9	11.6
13	6.3	31.4	3.2	1.5	2.8	11.0	0.0	17.6	1.4	25.8
14	13.7	23.3	2.2	1.3	4.7	15.5	0.0	22.2	0.6	18.9
15	7.4	34.1	6.8	0.7	1.0	7.2	0.0	17.9	0.8	28.8
16	3.8	12.4	12.2	3.5	8.4	8.9	0.3	9.3	1.2	46.0
17	10.1	20.8	1.8	1.4	11.2	9.7	0.0	14.1	1.9	35.9
18	11.1	17.2	1.6	0.8	6.5	11.3	0.0	14.8	0.3	45.0
19	7.4	22.8	5.3	1.3	7.8	10.6	0.1	12.6	0.1	41.9
20	12.2	35.3	2.4	0.6	4.0	7.8	0.0	12.9	0.0	29.7
21	11.6	33.4	3.4	1.8	9.9	10.3	0.1	11.0	0.0	23.7
22	16.1	30.5	4.2	0.9	1.5	11.2	0.2	14.7	0.0	28.4
23	13.8	32.2	5.3	2.5	2.7	8.9	0.0	12.0	0.0	27.4
24	9.3	19.4	4.8	0.7	8.9	12.0	0.0	15.2	0.0	34.3
25	9.8	40.9	3.6	0.8	4.7	3.9	0.0	10.6	0.0	28.0
26	3.0	31.9	3.0	1.0	6.3	4.2	0.0	15.4	0.0	35.2
27	1.4	25.3	1.1	0.7	0.0	4.1	0.0	21.6	0.0	45.8
28	1.5	22.2	3.9	1.1	14.8	2.8	0.0	14.7	0.0	39.1
29	3.7	40.8	3.8	0.6	0.0	3.9	0.0	18.8	0.0	28.5
30	1.2	22.5	0.4	0.0	0.0	6.1	0.0	27.5	0.0	42.4
31	3.4	23.7	1.3	0.0	0.0	4.4	0.0	27.7	0.0	39.5
32	0.2	35.7	1.9	0.0	18.2	1.0	0.0	20.0	0.0	23.1
33	3.0	47.9	0.6	0.0	0.0	2.3	0.0	21.1	0.0	25.1
34	3.6	24.4	2.6	0.0	20.0	4.0	0.0	6.2	0.0	39.2
35	3.7	33.3	0.7	0.0	2.2	5.9	0.0	23.7	0.0	30.4

The time spent inactive while standing markedly decreased with increasing T_A ($r_s = -0.67$, $P = 0.000004$). There was no significant relationship between the time spent resting and T_A ($r_s = 0.16$, $P > 0.1$). Whereas mean overall activity was not correlated to T_A ($r_s = 0.2$, $P > 0.1$), activities performed on land significantly decreased with increasing T_A ($r_s = -0.75$, $P = 0.000000$) (see Figure 21).

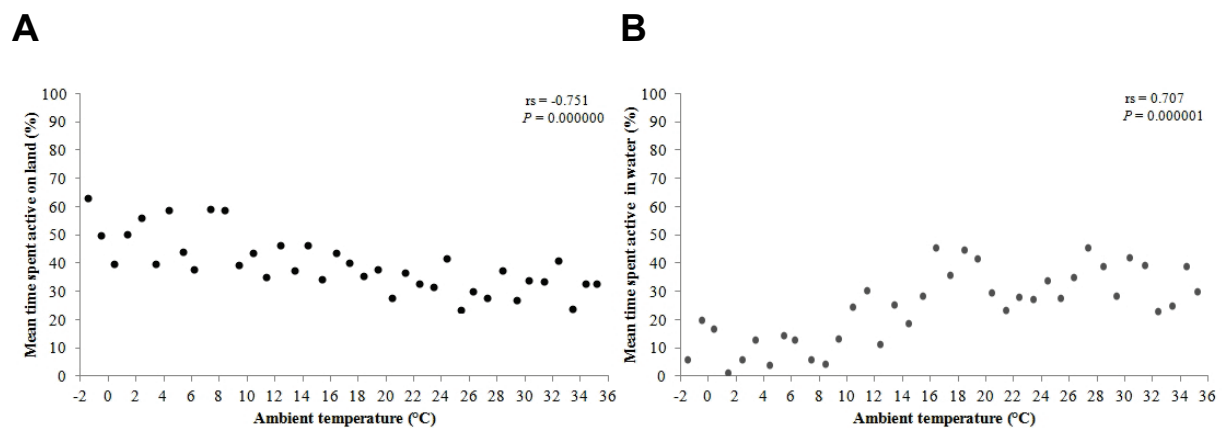


Figure 21. Mean time spent active (A) on land and (B) in water in relation to T_A .

These activities were associated to varying T_A as follows: Foraging was the only activity performed on land that was not associated with varying T_A ($r_s = -0.07$, $P > 0.5$) (see Figure 22). Exploration ($r_s = -0.80$, $P = 0.000000$) as well as walking ($r_s = -0.86$, $P = 0.000000$) decreased with increasing T_A . The decrease in the proportion of running was less pronounced, but significant ($r_s = -0.42$, $P = 0.009$). Social play decreased with increasing T_A ($r_s = -0.80$, $P = 0.000000$) (see Figure 22). Above 5 °C, there was a sharp decrease in time spent exploring on land ($P = 0.000000$). The same is true for social play ($P = 0.000000$) (see Figure 22). Pacing was the only active behaviour performed ashore that could be correlated to T_A , although the relationship was very low ($r_s = 0.36$, $P = 0.03$). The proportion of time spent actively in water, increased with T_A ($r_s = 0.71$, $P = 0.000001$) (see Figure 21).

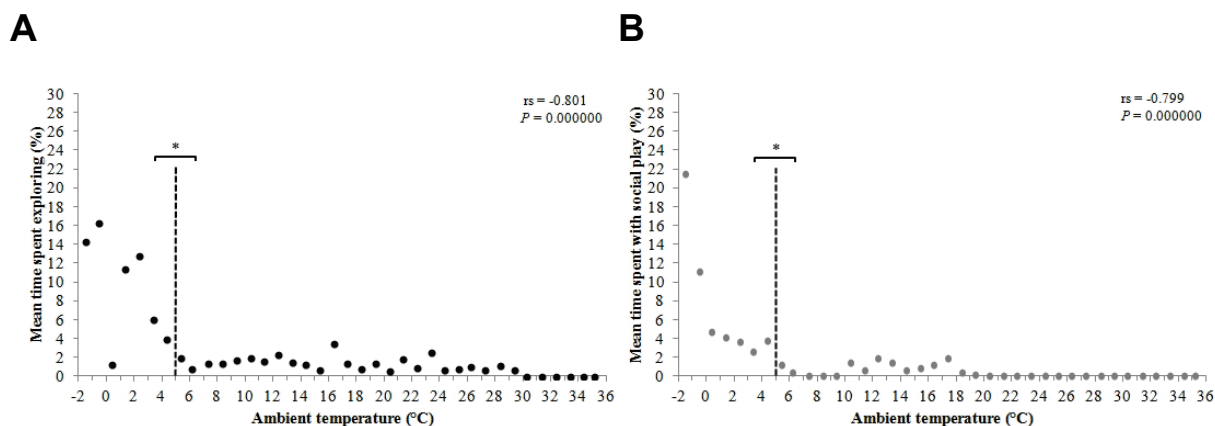


Figure 22. Mean time spent with (A) exploration and (B) with social play in relation to T_A (* $P < 0.05$, Mann-Whitney U one-tailed test).

3.5.2 Substrate chosen to rest on

The proportion of time spent resting on different substrates in relation to T_A are summarised in Figure 23. There was a significant negative correlation between the amount of resting on sand and T_A ($r_s = -0.54$, $P = 0.0005$) and a definite but small positive relationship between resting on soil and T_A ($r_s = 0.33$, $P < 0.05$). In contrast, no correlation between resting on rocks and T_A was found ($r_s = 0.03$, $P > 0.05$). However, although the overall correlation was close to zero, there may be a more complex association of rocks as resting substrate and T_A .

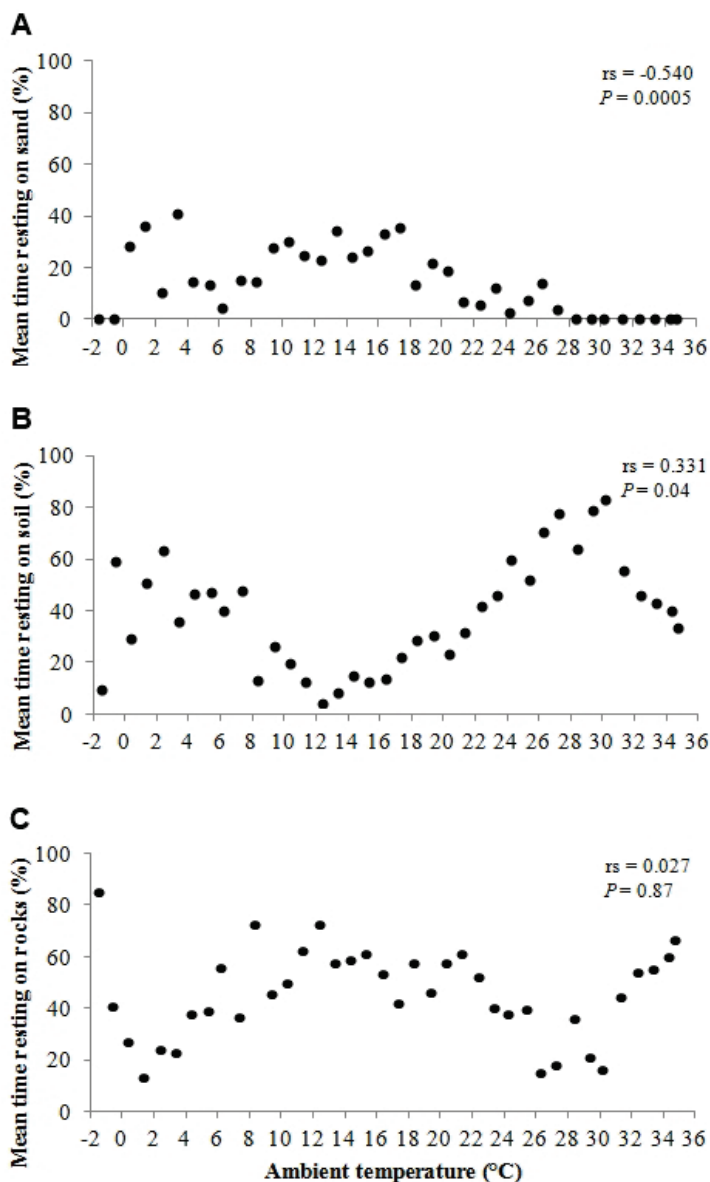


Figure 23. Proportions of time spent resting on (A) sand, (B) soil and (C) rock to T_A .

3.5.3 Body posture while resting

There was a marked relationship between resting in an extended body position and T_A ($r_s = 0.73$, $P = 0.000$) (Figure 24). Resting in a curled up position did never occur during the observation periods.

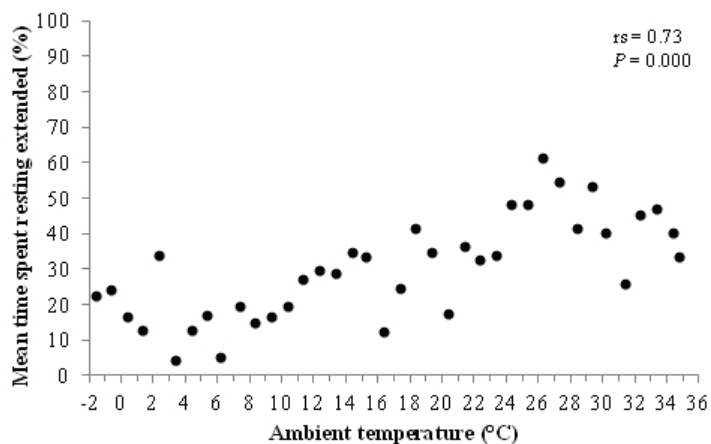


Figure 24. Proportions of time spent resting in an extended body position.

3.5.4 Resting in the shade vs. sun

No relationship could be found between the use of shady resting places and T_A ($r_s = -0.2$, $P > 0.05$) as can be seen in Figure 25.

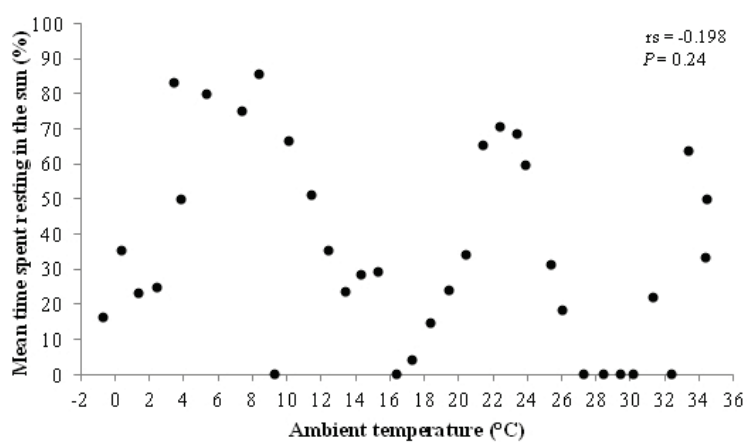


Figure 25. Proportions of time spent resting in the shade in relation to T_A . Data derived from observations during the absence of sunshine were excluded from analyses.

3.5.5 Panting and shivering

Neither shivering nor panting could be observed. However, polar bears were often seen walking with the mouth slightly opened, which was not further investigated within the scope of this study.

4. DISCUSSION

The purpose of the present study was to test the effect of different meteorological parameters on both autonomic and behavioural thermoregulation in Malayan sun bears and polar bears by a combination of behavioural observations and infrared thermography and to determine thresholds of T_A for associated regulatory mechanisms and behaviours.

4.1 Heat dissipation

Thermographic measurements of Malayan sun bears at rest revealed that the range of ambient temperature where T_S is close to T_A lies between 24 °C and 28 °C, supporting the assumption that their TNZ is relatively narrow and corresponds to T_A occurring in their natural habitat, which lie between 23 °C and 30 °C (Fredriksson *et al.* 2006). This is consistent with findings for several tropical mammals, which are reported to have TNZ between 20 °C and 30 °C, most of which with T_{LC} between 25 °C and 27 °C (Scholander *et al.* 1950c). However, there were only a limited number of recordings of sun bears that were inactive and in a post-absorptive state, which is required to measure the TNZ. Therefore the findings can only represent an approximation. For further conclusions about the range of the TNZ, a greater number of systematic measurements is required.

Outside of the TNZ and during activity, merely the inner legs showed a higher degree of heat loss to the environment, which might be due to the low density of the fur in this region (Servheen 1999). Apart from that, heat was dissipated equally over the trunk, back and outer legs, with a positive linear relationship to T_A , supporting the assumption that in sun bears heat is dissipated equally over the body surface. The increase of heat loss indicated by the increase of $T_S - T_A$ with decreasing ambient temperature can be due to either low insulating properties of fur, lack of fat or low ability to control vasomotion. Sun bears have a very short and thin fur (Servheen 1999), and do not develop significant fat layers (Wong 2002), so any control of T_S would have to occur via vasomotion, which is obviously not well pronounced.

Contrasting to sun bears, in polar bears the outer legs and the shoulder region were the only regions where considerable temperature fluctuations could be observed in resting animals above 5 ° C, the T_{UC} of polar bears (Best 1982), or during activity. The shoulder region and the outer legs can be considered to be an important avenue for heat loss in polar bears.

The results provide evidence that polar bears are able to open so called thermal windows in the shoulder region and the legs. These are referred to as areas with temporary higher temperatures than the surrounding body surfaces as well as ambient temperature, due to the control of blood flow to the to the body surface in order to dissipate excess heat (Phillips and Sanborn 1994, Mauck *et al.* 2003, Willis *et al.* 2005, Khamas *et al.* 2012). The findings confirm the hypothesis that polar bears possess specialised body parts for the dissipation of excess heat, which is consistent with earlier anatomical findings of vascular structures in polar bears (Øritsland 1970).

Thermal windows are not evident in other ursid species, where no differences in T_S between abdomen and back were found in American black bears, brown bears, sloth bears and Andean bears (Phillips 1992). Obviously, among ursids this mechanism is unique for polar bears. Thermal windows are well described for other marine mammals, the pinnipeds (Mauck *et al.* 2003, Willis *et al.* 2005, Khamas *et al.* 2012), which are even better insulated than polar bears. In both, seals and polar bears these mechanisms in order to bypass insulating fat layers by vascular structures and to transport heat to the surfaces might help to reduce the risk of overheating, which in polar bears is mainly due to insulative properties of their fur that provide an effective insulation (Øritsland 1970, Frisch *et al.* 1974). Whereas in pinnipeds, which are mainly insulated by fat layers (blubber), locations of thermal windows are highly variable and can occur over their whole body, in polar bears heat loss over the body surface is restricted to areas with less dense fur (Øritsland 1970). Differences in T_S between outer and inner leg were only detected in American black bears at T_A of 31 °C and 32 °C, but not below

these T_A , and could not be detected in brown bears, sloth bears or Andean bears (Phillips 1992). Single measurements of brown bears, polar bears and Andean bears at T_A of 1 °C as well as of Asiatic black bears, sloth bears and sun bears at 5 °C showed no differences between T_S of body and legs and heat dissipation was equally distributed over the whole body (Hilsberg 2000).

In both species, surface temperatures in the eye region was constantly high at all T_A , indicating continuous blood flow to the naked skin around the eye regardless of T_A , most probably to maintain physiological function of sensory organs (Mauck *et al.* 2000, Tattersall *et al.* 2009), such that these regions are not assumed to function as body regions for heat dissipation.

The fluctuation of surface temperature in direct proportion to T_A observed in both species is a thermoregulatory mechanism regulated by vasoconstriction and vasodilation of cutaneous blood vessels. However, this does not imply that within the TNZ vasomotion is not used. Blood flow through the subcutaneous shunt vessels and the capillary beds are still instrumental regulating body temperature and heat loss within the zone of thermally neutral ambient temperatures (Johnson *et al.* 1986).

The TNZ of a species provides a first insight in its insulative properties and indicates at which temperature levels energy expenditure for the maintenance of body temperature becomes necessary in resting animals. Conversely, food intake and locomotor activity increase MR, thus shifting the ideal temperature range (Müller 1995). Heat loss was proportional to the temperature gradient between body surface and air temperature in both species, indicating that with increasing T_A , the amount of heat dissipation, and thus energy expenditure, increases. Thus, behavioural observations were conducted in order to estimate at which temperature thresholds various behavioural mechanisms are implemented to reduce the energetic cost of autonomic thermoregulation (Terrien *et al.* 2011).

4.2 Behavioural thermoregulation

In sun bears, locomotor activity, which leads to internal heat production (Schmidt-Nielsen 1990, Cannon and Nedergaard 2004), significantly decreased with increasing T_A , indicating that this mechanism is used to limit energy expenditure at high T_A , what is consistent with previous studies in various mammalian species, where activity declined in relation to increasing T_A (Moen 1976, Limberger *et al.* 1986, Hill 2006). The time spent with explorative behaviours out of feeding times, also decreased with increasing T_A , supporting the above mentioned assumption. In contrast, the amount of time spent foraging when food was present was not affected by T_A , indicating that food, and thus energy intake, is an important variable, which is independent of abiotic factors, at least of those within the temperate zone.

The decrease in the proportion of time spent active was also evident in polar bears, when analysing active behaviours performed on land. Both exploration and social play showed a sharp decrease above 5 °C, the reported T_{UC} for polar bears, highlighting the dispensability of such behaviour patterns in order to preserve energy. These findings are in accordance with activity levels reported for free ranging polar bears (Stirling 1998, Derocher 2000) and support the assumption, that alterations in activity are used to keep energy expenditure low in order to avoid overheating. Similar to sun bears, in polar bears the time spent feeding showed no relation to T_A , supporting the aforementioned assumption that, at least in the temperate zone, such essential behaviours cannot be spared despite the associated energetic cost.

Behavioural data revealed a strong relationship between the substrate which was chosen to rest on and T_A . Tree trunks are the substrate which is used most often by sun bears below their T_{UC} of 28 °C. The lesser use of trees for resting by sun bears above their T_{UC} was unexpected, since trees usually provide a cool microclimate (Briscoe *et al.* 2014). This, however, might be explained by the fact that most trees provided in zoos are cut trunks which do not evaporate water and hence, lack cooling properties.

However, above 15 °C tree trunks are used less in favour of rocks as well as soil and hammocks. At lower T_A (~ 5 °C–15 °C) sun bears preferred trees as a resting substrate, at medium T_A (~ 16 °C–29 °C) soil and hammocks were increasingly used and at high T_A (~ 30 °C–35 °C) rocks and dens were selected for resting. The latter also provided shade offering a cooler microclimate.

Resting in nests was observed both, at low and high T_A . This is presumably explained by insulating properties of nest material in the cold, favouring the increase of nest building activities at low T_A , and the option of shade at high T_A , since the nests were roofed. The use of nests in mammals can have various purposes such as breeding (Jensen 1989, Wechsler and Heggin 1997), resting (Stewart *et al.* 2007) or temperature regulation (Lynch and Hegmann 1972). In the current study, a considerable amount of nest building activity merely occurred below 16 °C. Since the outcome of nest building activities provides insulation, they can be regarded as thermoregulatory behaviour that contributes to the prevention of heat loss to the environment. Thus, the underlying motivation for the use of nests at low T_A can be linked to thermoregulation. However, nest building in free ranging sun bears (McConkey and Galetti 1999) has not been studied in relation to T_A .

In polar bears, distribution patterns of the use of substrates to rest on were more complex. While the use of sand for resting decreased with increasing T_A , the use of soil and rocks was inversely related, being high for soil at low (below 9 °C) and very high T_A (above 23 °C) and high for rocks at a medium range of T_A . While T_S of substrates, obtained from infrared measurements at low solar radiation, increased with T_A , the thermal properties of substrates better explain the exhibited preferences (see Appendix). Rocks have the highest thermal conductance, followed by soil while sand exhibits the lowest, whereby conductance increases when a substrate is wet (Monteith and Unsworth 1990). During high solar radiation higher thermal conductances involve that a substrate remains warm for a longer period than a

substrate with a low thermal conductance. The use of sand to rest was negatively correlated to T_A which can be explained by the low thermal conductance that results in higher T_S for a longer period during solar radiation. Wild polar bears are reported to use a variety of resting places for cooling (Jonkel *et al.* 1972, Stirling 1998). The complex patterns of substrate use found in the current study emphasise the importance to provide sufficient options of appropriate substrates with varying thermal properties.

In addition to T_A , thermal properties of substrates have influenced the body posture while resting, which enables to dissipate or prevent heat loss to the environment via conduction, convection and radiation, and thus can lead to considerable energy savings (De Lamo *et al.* 1998, Ward *et al.* 2008) could be related to T_A in both species.

In sun bears, a curled up posture, thus decreasing the exposed body surface was displayed at T_A below 15 °C, when the animals mainly rested on wood, the substrate with the lowest heat extracting capacity that was available, while an extended body position was mainly observed above their T_{UC} , when also rocks, with the highest thermal conductance, were selected.

In polar bears resting in an extended body position was highly correlated to T_A , similarly reported for wild polar bears (Øritsland 1970), whereas resting in a curled up position was never observed. This however was not expected since T_A during the study never dropped to values as low as in their natural range.

The selection of an appropriate microclimate provided further means of regulating body temperature by behaviour. In sun bears, the proportion of resting in the shade was highly positively correlated to T_A , showing the same threshold pattern as seen for substrate selection and body posture, with 15 °C representing the temperature threshold for the avoidance of shade and 28 °C, their T_{UC} , for a significantly higher use of shady resting places. This supports the observation that free ranging sun bears avoid direct solar radiation (Normua *et al.*

2004) and emphasises the need for the provision of shade for behavioural thermoregulation (Hill 2006, Cain *et al.* 2008).

Contrary to expectations, in polar bears, the amount of resting in the sun was unaffected by T_A and solar radiation. This could be due to their fur, which is denser than in sun bears, providing an effective insulation against solar radiation. The fur of mammals offers insulation that restricts heat loss at low T_A , but also impedes the transfer of heat into the body at high T_A (Schmidt-Nielsen 1965). In hot regions, external insulation deflects solar radiation away from the skin surface and reduces the flow of heat from the surface of the insulation layer to the skin (Grahn and Heller 2004). However, this applies only for resting as long as internal heat production is low, thus food intake (Swaminathan *et al.* 1985) or physical activity quickly exceed benefits of preventing heat impact by radiation.

Water represents another medium, which is often sought by both species, in order to prevent overheating and to lose heat by convection, since conductivity of water is substantially higher than that of air. Once again, in sun bears thresholds for the selection of water adhered to the threshold pattern mentioned above, being absent at low, rarely shown at medium and highly prevalent at high T_A ranges, again with a sharp increase above their T_{UC} . Due to the high thermal conductance and heat capacity of water, which is 24 times higher than that of air of the same temperature (Schmidt-Nielsen 1990), insulation of the fur decreases significantly in water (Scholander *et al.* 1950a, Frisch *et al.* 1974). Thus, water represents a highly important source for behavioural thermoregulation. During swimming, heat loss is even higher due to forced convection (Øritsland 1970) which might explain the high activity levels in water found in polar bears with increasing T_A .

The use of the indoor enclosure by sun bears was high at low as well as at high temperature ranges, while being moderate at the medium range of T_A . This indicates that the animals seek

an approximation of the medium temperature range, since at low T_A indoor enclosures are heated, whereas at high T_A they provide a cooler environment and shade.

Shivering did occur in neither species. The T_{LC} of polar bears was not reached during the study and conclusions about that mechanism cannot be drawn from the present data. In sun bears however, it can be assumed that behavioural thermoregulation is implemented before autonomic mechanisms become necessary, provided that they have enough options to do so.

Except for few occasions, where panting occurred in sun bears after extensive social play, this mechanism could not be observed in either species, which is consistent with the previously described disadvantages of panting such as high energetic costs, water loss and the risk of respiratory alkalosis (Schmidt-Nielsen 1990, Sawka *et al.* 2001). Such shortcomings are presumably avoided by implementing behavioural thermoregulation first.

Furthermore, respiratory frequency in polar bears is reported to be closely correlated with T_B . 39.0 °C is the threshold T_B for the initiation of panting (Best 1982). Thus it could be argued that due to the absence of panting no rises in T_B occurred. However, several zoo housed bear species performed panting (Phillips 1992), underlining the importance of options for behavioural thermoregulation that can be implemented prior to the need of panting, which is disadvantageous as mentioned above.

Referring from these findings it can be concluded that both studied species use a high proportion of behavioural mechanisms in order to keep energetic costs for thermoregulation low.

4.3 Temperature thresholds

In response to varying T_A and solar radiation, both species altered the time spent active, body posture while resting, the use of shady and sunny resting places and the selection of microclimates, supporting the hypothesis that these behaviours occur prior to the

implementation of energetic costly autonomic thermoregulation (Scholander *et al.* 1950b, Bianca 1977, Grahn and Heller 2004).

For sun bears, 15 °C seems to be an important temperature threshold as most behavioural mechanisms to prevent cooling were initiated at that T_A . While this ambient temperature lies considerably below 24 °C, the estimated T_{LC} found in the current study, the onset for behaviours to prevent overheating occurred immediately at 28 °C, the estimated T_{UC} , which is true for all tested variables.

As mentioned above, the thermoneutral zone is measured at rest and in a post absorptive state. Both food intake and locomotor activity lead to internal heat production, thus shifting the temperature range where metabolic rate is minimal. This could explain why all measured behaviours that prevent heat loss to the environment are implemented well below the T_{LC} .

However, the temperature threshold for the onset of behaviours that prevent overheating was around 28 °C, the estimated T_{UC} for sun bears found in this study. This can be explained by the fact that endotherms can cope less with high than with low T_A , since the possibilities for heat dissipation are limited compared to those for heat conservation (Pflumm 1989).

While in polar bears resting in a most extended position, which aims at maximising body surface for heat dissipation, increased linearly with increasing T_A , it could be shown that a T_A of 5 °C, the reported T_{UC} for polar bears, represents a distinct temperature threshold for the onset of thermoregulatory behaviours that help to prevent overheating. Whereas the proportion of time spent in water, which enables heat dissipation via convection, significantly increased above 5 °C, explorative behaviour and social play, significantly decreased above this T_A . The results highlight the important role of behavioural thermoregulation as a strategy to keep energy expenditure low.

4.4 Implications for husbandry

Referring from the estimated TNZ of sun bears found in this study, as well as from the T_{UC} reported for polar bears, which could be confirmed by behavioural data from the present study, it can be assumed that in zoos in the temperate zone the T_{UC} of polar bears and the TNZ of sun bears might be exceeded during the major part of the year. This should be regarded in management practises by providing sufficient options for behavioural thermoregulation in terms of substrates, structures that provide shade, water and indoor temperatures.

The high degree of behavioural thermoregulation performed by both species as well as the fact that the respective T_{UC} is a distinct temperature threshold for the initiation of behaviours that prevent overheating, support the assumption that autonomic responses to avoid overheating are limited compared to mechanisms that prevent cooling (Pflumm 1989) and underlines the importance of the provision of options for behavioural thermoregulation in captive environments to avoid thermal stress.

The findings support the assumption that various species choose a range of T_A which is close to their respective TNZ (Müller 1995). It is evident that the species specific TNZ plays an important role in selecting an optimal value for T_A for indoor enclosures for captive animals. However, as mentioned above, the TNZ is defined as the range of T_A within which thermoregulatory needs of fasting and resting endotherms can be met by minimal energetic efforts. This zone of minimal metabolic rate cannot simply be equated with optimal thermal conditions for indoor enclosures. Animals are rarely post-absorptive and hence have a higher heat production than during measurements of the TNZ. Locomotor activity also increases metabolic rate, thus further lowering the ideal temperature range. This could be shown in the present study by the determined temperature threshold for the initiation of thermoregulatory behaviours that were performed considerably below the estimated T_{LC} of sun bears.

4.5 Consequences for wild living bears

Global warming has been reported to increase T_A and reduce arctic sea ice (Serreze and Barry 2011) and thereby increase the length of fasting in summer when polar bears have no access to seals, resulting in less fat reserves due to longer ice-free periods (Stirling *et al.* 2008). The problems polar bears have to face from hunting, toxic pollution and oil developments in the Arctic come on top of the impacts of global warming. In addition, with increasing T_A due to climate change, the T_{UC} of polar bears is exceeded considerably for prolonged periods in summer. The fact that polar bears are able to dissipate heat via thermal windows might prevent them from overheating, but adds considerably to the physiological costs. The greater the temperature gradient between body surface and the surrounding air, the greater the heat transfer and thus energy expenditure. In harbour seals, the calculation of heat loss through thermal windows resulted in considerable values (Erdsack *et al.* 2012). Staying in water, which might help to dissipate heat, is as well energetically costly due to its high thermal conductivity and heat capacity.

With fewer fat reserves due to longer ice free periods summer reported for polar bears (Regehr *et al.* 2007, Regehr *et al.* 2010, Rode *et al.* 2010), additional physiological costs for thermoregulation could compromise their energy budget even more. Higher energetic costs for thermoregulation have an impact on the energetics of the species and might have negative consequences for the long term conservation of polar bears.

A higher number of El Niño phenomena caused by global warming, has led to a higher frequency of forest fires (Timmermann *et al.* 1999, Solomon *et al.* 2007, Stocker 2013), and thereby loss of suitable habitat for Malayan sun bears (Fredriksson *et al.* 2007). The results of the present study show that trees are essential for behavioural thermoregulation since they offer an appropriate substrate and shelter from direct solar radiation.

Both species are facing multiple extinction threats although their energy budget is already compromised. Additional costs for thermoregulation might exceed their adaptability in the long term.

CONCLUSIONS

- (1) The findings suggest that the TNZ of Malayan sun bears lies between 24 °C and 28 °C.
- (2) The assumption that polar bears possess body surfaces specialised for the dissipation of excess heat in the shoulder region and limbs, so called thermal windows, could be confirmed.
- (3) Behaviours related to thermoregulation, such as changes in activity, alterations in body posture and the choice of shade and substrates while resting as well as the selection of appropriate microclimates occurred in advance of energetically costly autonomic mechanisms, and were highly correlated to T_A and solar radiation.
- (4) The temperature threshold for the onset of thermoregulative behaviour in sun bears below the TNZ lies around 15 °C which is well below the T_{LC} .
- (5) The temperature threshold for the initiation of behavioural mechanisms above the TNZ is linked to the respective T_{UC} in both species.

OUTLOOK

Future studies should attempt to determine the total heat flow from the body surface to the environment and then to relate it to the energetic economy of the respective species in its natural habitat. Quantifying energetic costs under the problems both species have to face in the wild is important for population management and conservation. Calculation of energy expenditure via heat loss measured by infrared thermography to assess the energetic costs associated to higher thermoregulatory demands is therefore a long term goal of this study.

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APPENDIX

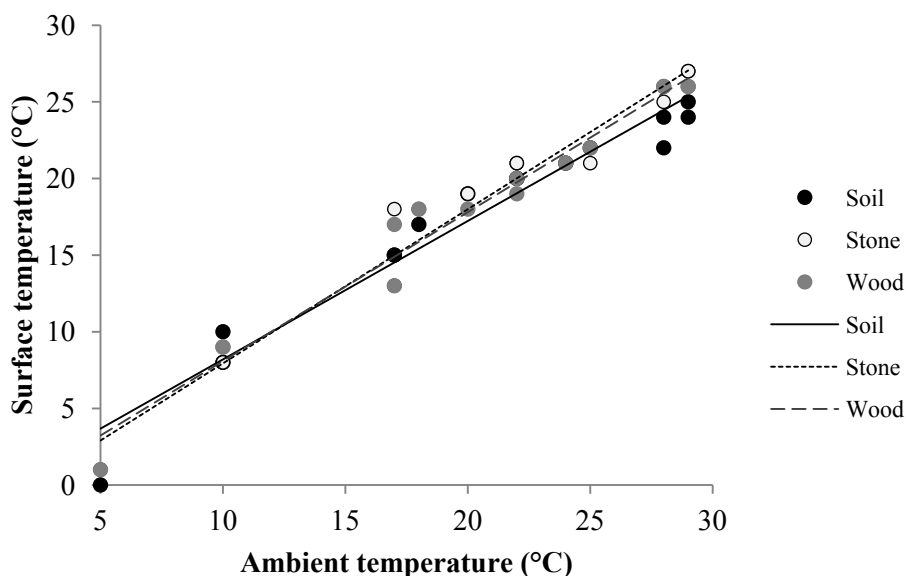


Figure 26. Mean surface temperatures of substrates in all involved sun bear enclosures at different air temperatures obtained from thermographic measurements. Note that those measurements were exclusively made under overcast conditions.

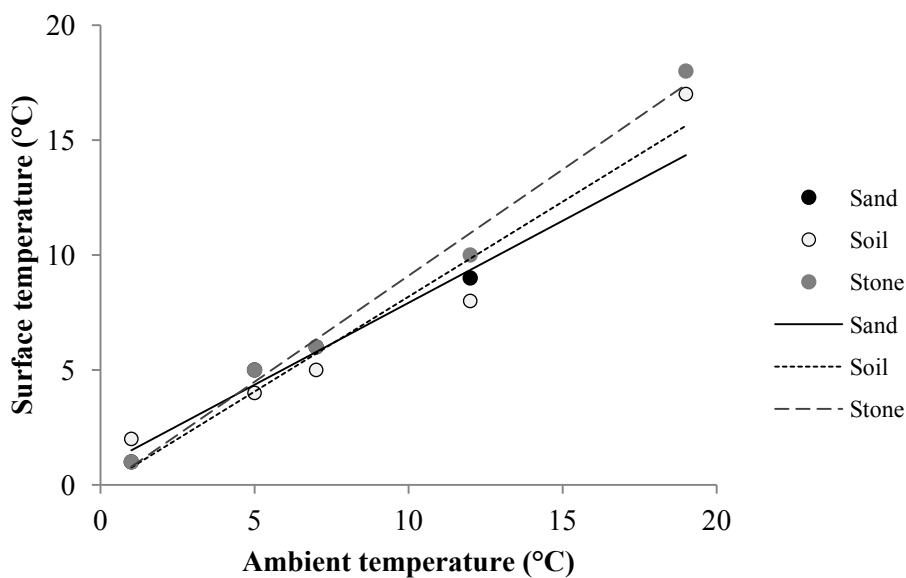


Figure 27. Mean surface temperatures of substrates in all involved polar bear enclosures at different air temperatures obtained from thermographic measurements. Note that those measurements were exclusively made under overcast conditions.

Table 5. Thermal conductances of different substrates after Monteith and Unsworth (1990)

Substrate	Thermal conductances (W/(m*K))
Soil (dry)	0.15-0.60
Soil (10% humidity)	0.50-2.00
Soil (20% humidity)	0.75-2.70
Sand (dry)	0.70
Sand (10% humidity)	0.90
Sand (20% humidity)	1.25
Artificial Stone	1.30
Natural stone / rock	2.30-3.50
Wood (tree)	0.13-0.20
Plywood	0.15
Water	0.58
Air	0.025

ERKLÄRUNG

Ich versichere, dass ich die von mir vorgelegte Dissertation selbständig angefertigt, die benutzten Quellen und Hilfsmittel vollständig angegeben und die Stellen der Arbeit – einschließlich Tabellen, Karten und Abbildungen –, die anderen Werken im Wortlaut oder dem Sinn nach entnommen sind, in jedem Einzelfall als Entlehnung kenntlich gemacht habe. Diese Dissertation hat noch keiner anderen Fakultät oder Universität zur Prüfung vorgelegen. Darüber hinaus versichere ich, dass die vorliegende Dissertation, abgesehen von unten angegebenen Konferenzbeiträgen, noch nicht veröffentlicht worden ist sowie, dass ich eine solche Veröffentlichung vor Abschluss des Promotionsverfahrens nicht vornehmen werde. Die Bestimmungen der Promotionsordnung sind mir bekannt. Die von mir vorgelegte Dissertation ist von Priv.-Doz. Dr. Thomas Ziegler betreut worden

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KONFERENZBEITRÄGE

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