JOURNAL OF ANIMAL BEHAVIOUR AND BIOMETEOROLOGY

REVIEW ARTICLE
Published Online: September 22, 2022
https://doi.org/10.31893/jabb.22033

Anatomical, physiological, and behavioral mechanisms of thermoregulation in elephants

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Abstract Elephants use different thermoregulatory mechanisms that depend on the anatomical and morphological characteristics of the species. The crevices and wrinkles of the skin enhance the water-retention capacity of the epidermis. The highly vascularized ear is another region of particular interest, as its movement and vasomotor changes promote heat dissipation. Generally, these mechanisms are modulated by the hypothalamic thermoregulatory center and by the peripheral response of animals. Nonetheless, elephants are currently exposed to alterations in their habitats, such as global warming and climatic changes, which challenge their homeothermy. This article aims to discuss the thermoregulation mechanisms of African (*Loxodonta africana*) and Asian (*Elephas maximus*) elephants from an anatomical, physiological, and behavioral basis. The practical implications of these elements will be analyzed to implement tools, such as infrared thermography, or environmental enrichment, as strategies to promote the thermal balance of elephants.

Keywords: *Loxodonta africana*, *Elephas maximus*, elephant anatomy, thermal state

1. Introduction

Elephants are species adapted to life in extreme climatic conditions (Mole et al 2016). Asian and African elephants are considered water-dependent animals because they rely on behaviors such as bathing, mud, or dust-bathing to thermoregulate and maintain skin moisture (Rees 2002a; Dunkin et al 2013). Their ears, a thermoregulatory organ, promote convective heat loss through movement and vascularization (Mikota 2006). Despite the characteristics that facilitate elephant homeothermy (Bansiddhi et al 2020), extreme climatic conditions, global warming, and ecological alterations can affect the physiology, thermoregulation, health, and conservation of the species (Mumby et al 2015).

Due to their lack of sweat glands (Mota-Rojas et al 2021a), elephants rely on evaporative cooling because their metabolic heat production exceeds the rate of heat loss (Rowe et al 2013; Dunkin et al 2013). However, evaporative cooling hinders thermoregulatory processes when exposed to adverse climatic conditions (Bansiddhi et al 2020). This response begins with the cold- or heat-sensitive fibers in the skin and is mediated by the spinal dorsal horn and integrated by the preoptic area of the hypothalamus (POA), known as the thermoregulatory center (Uchida et al 2017). POA neurons project to other supraspinal structures and descending pathways to avoid hyperthermia and its adverse effects by generating central and peripheral responses (e.g., neurotransmitter release and vasomotor changes, respectively) (Mota-Rojas et al 2021b,c) and behavioral modifications (Thaker et al 2019).

This review aims to discuss anatomical, physiological, and behavioral thermoregulatory mechanisms in African (*Loxodonta africana*) and Asian (*Elephas maximus*) elephants to prevent hyperthermia when environmental conditions challenge their homeothermia, as well as the differences between species. Considering these aspects, strategies such as infrared thermography (IRT) and environmental enrichment protocols will be analyzed to assess and promote thermal comfort in elephants.

2. Importance of thermoregulation

Thermoregulation is a vital process to survive and maintain proper organ and cellular function (Shelton and Alberts 2018). In most mammals, core temperature oscillates around 37 °C and is mediated by a complex central neural network that responds to environmental temperature (Shelton and Alberts 2018). These mechanisms are activated with deviations from the thermoneutrality zone, defined as the environmental temperature range where metabolic heat production or evaporative heat loss do not require changes (Kingma 2012). When the temperature is below this range, it promotes thermogenesis by activating brown adipose tissue (BAT) and shivering. In contrast, environments above thermoneutrality trigger heat loss through vasomotor and evaporative cooling changes (Morrison and Nakamura 2019).

 Received: July 27, 2022 | Accepted: September 7, 2022

Environmental conditions such as habitat or climate change represent a physiological challenge for elephants and depend on the anatomy, physiology, and natural behavior of pachyderms, influencing their conservation status (Wenwen et al 2019).

3. Impact of climate change

In recent years, climate change and global warming have become serious issues as increases in environmental temperature of up to 1.6 °C have been recorded from 2019 to 2020, affecting human and animal health (Wang et al 2021). By 2050, Mpakairi et al (2020) predict that the habitat of pachyderms will reduce by 40% in Zimbabwe, an area inhabited by elephants, due to a temperature increase of up to 2 °C. These insights provide a perspective on how elephants are exposed to threats like global warming and its adverse effects on the health of elephants and their thermoregulatory mechanisms, including behavior (Morrison and Nakamura 2019).

One of the main challenges is heat stress (Thaker et al 2019) since elephants have a large size and low surface-to-volume ratio that make heat dissipation inefficient when ambient temperatures exceed body temperature (Williams' 1990). This also affects pachyderms' immune, reproductive, and behavioral responses (Hansen 2009). A study in southern Africa evaluated the relationship between environmental temperature and the natural behaviors (e.g., walking, resting, feeding, drinking, and wetting) of seven free-ranging African elephants (*Loxodonta africana*). At temperatures above 35 °C, elephants spent more time in the shade (29.5 ± 18.1%), resting (1.7 ± 2.7%), and engaged in water-related behaviors like swimming, mud bathing, and squirting (3.0 ± 3.5%). In contrast, walking time was reduced (6.5 ± 2.8%) in temperatures above 33 °C. They also recorded an increase in skin surface temperature as a function of black globe temperature ($p<0.0001$) (Mole et al 2016), determining that African elephants can maintain homeothermy through compensatory thermoregulatory behaviors to dissipate heat even in high-temperature conditions because there were no observable fluctuations in body temperature above 1.5 °C (Mole et al 2016; Mota-Rojas et al 2021b). In recent studies with African elephants (*Loxodonta africana*), it was found that resting during the hottest hours is a behavioral modification that counteracts the metabolic costs associated with thermoregulation (Du Plessis et al 2021).

These results show the importance of providing resources such as water, food, and shade to maintain the thermal health of elephants. However, one of the adverse effects of climate change is extreme droughts in the areas they inhabit. In Asian elephants (*Elephas maximus*) situated in forests and grasslands in Xishuangbanna, China, the habitat shrinkage causes food shortages of herbaceous and shrub plants that constitute the food base species. This has led to territorial conflicts with humans because animals migrate to fields or towns, an important aspect of climate change (Wang et al 2021).

This migration effect and the resulting human-animal conflicts were reported by Wang et al (2021), who studied the possible causes of the migration of over 500 km of wild Asian elephants across northern China from MengYang to Kunming from March 2020 to June 2021. The reasons mentioned were increased population density, habitat loss, and food shortages. A similar case was seen in India, where the habitat has been shrinking since 1950, forcing elephants to migrate and raid crops (Choudhury 2004).

Through conservation programs, elephant population density in China increased from 150 animals in 1960 to almost 300 in 2020. However, the extreme drought in 2020 contributed to food shortages, and the range of Asian elephants (*Elephas maximus*) was also reduced due to agriculture and human settlements (Wang et al 2021). For Asian elephants, suitable habitat is an area of approximately 5228.18 km^2, but it is projected that 45.71% will be lost by 2050 due to climate change (2836.76 km^2 remaining) (Wenwen et al 2019). This reflects the impact of global temperature change on elephants and many other species, including humans, and their anthropocentric activities that drive animals to respond.

The habitat damage due to high temperatures, human disturbance, and restricted space use makes elephants susceptible to chronic stress, generating a facultative refuge behavioral response characterized by a reserve use reduction by up to 20% and increased fecal glucocorticoid metabolites (FGM) concentrations for more than six years after translocation (Jachowski et al 2012). Likewise, glucocorticoid secretion alters animals' immune function and health when they are chronically exposed to adverse factors (Mason 2010).

Thus, they can compensate for heat stress when elephants have covered their habitat, food, water use, shade, and space requirements. However, climate change-induced phenomena such as drought or migration and physiological limitations of wild elephants or under human care can hinder their ability to dissipate heat and start the central or peripheral thermoregulatory mechanisms.

4. Physiology of thermoregulation in elephants

Coping with thermal challenges involves two main pathways to maintain homeothermia: central and peripheral responses.

4.1. Central thermoregulatory mechanisms

Elephants, considered endotherms, reside in various habitats, from savannas to deserts, exposing them to extreme temperatures ranging from 8 °C at night and 50 °C during the day (Kinahan et al 2007a). Given the elephants' size and small volume-to-surface area ratio (Hidden 2009), thermal homeostasis is achieved through physiological pathways that enhance metabolic, immune, and neural systems (Mota-Rojas et al 2021d). Ishiwata et al (2005) mention that the anterior hypothalamus and the POA are brain structures that integrate thermal signals obtained from various body parts and develop heat production or loss mechanisms, depending on the species and the environment (Napolitano et al 2020; Mota-Rojas et al 2021dg).

The POA is a brain structure containing afferent and efferent thermosensitive neurons that increase or decrease their activity (Mota-Rojas et al 2021d; Mota-Rojas et al 2022). Heat-sensitive neurons in the spinal cord and hypothalamus induce responses such as vasodilation and sweating. However, the latter is not observed in elephants due to the absence of sweat glands (Martins et al 2018). In contrast, cold-sensitive neurons promote non-shivering (BAT) and shivering thermogenesis, and peripheral vasoconstriction (Uchida et al 2017). These neurons receive information from viscera or skin through thermoreceptors, which transduce and transmit peripheral signals to the POA (Mota-Rojas et al 2021d). The spinal dorsal horn and supraspinal regions, such as the lateral parabrachial nucleus (LPBN) and the median preoptic nucleus (MnPO) process cold and warm sensory stimuli. The descending GABAergic projection neurons in the medial preoptic area (MPO) also participate in this process and inhibit the activity of sympathetic BAT neurons in the dorsomedial hypothalamus (DMH) (Mota-Rojas et al 2021d).

Normal temperature in adult elephants ranges from 36-37 °C, while in neonates, the values may be slightly higher (Fowler 2006). When the temperature of individuals is above this range, hyperthermia occurs, implying an increase in heat production and a decreased heat loss (Mota-Rojas et al 2021d). After thermoreceptors detect hyperthermia, the information is projected to the dorsal part of the LPB (LPBd), activating heat-sensible axons that stimulate the POA. Within the POA, GABAergic interneurons are stimulated in the MnPO and the MPO. From these centers and their communication with the DMH and the rostral raphe pallidus (rRPa) in the spinal cord, the main peripheral response (vasodilation) is stimulated to lose heat in conjunction with evaporative mechanisms like sweating or panting when an animal is exposed to heat stress (Kruk and Davydov 1977).

In other mammalian species, sweating from eccrine sweat glands (located in different anatomical body regions) responds to preganglionic and postganglionic cholinergic sympathetic stimulation. However, elephants lack sweat glands and are incapable of panting, so they require other means to dissipate heat and prevent hyperthermia (Mota-Rojas et al 2021d). Selective brain cooling and heterothermia are mechanisms that lower brain temperature below arterial temperature by contacting cold venous blood with warmer arterial blood before it enters the brain cavity to mitigate the effects of global warming and aridification. Black wildebeests (*Connochaetes gnu*) perform this adaptive heat exchange mechanism through carotid and intracranial vascular networks. Although a similar carotid network is suspected in elephants, it is still unclear whether they can generate selective brain cooling, and further research is required (Mitchell et al 2002; Hidden 2009; Strauss et al 2017). The importance of preventing hyperthermia and the activation of central mechanisms lies in the systemic alterations that can develop, such as coagulative necrosis, hypotension, cerebral hypoxia, and electrolyte alterations that change neuronal functionality and communication (Fowler 2006).

On the other hand, when an organism responds to a decrease in core temperature, the Sympathetic Nervous System (SNS) promotes thermogenesis through vasodilation, shivering, heat-seeking behaviors (Mota-Rojas et al 2021d; Mota-Rojas et al 2022), and BAT activation (Morrison and Nakamura 2019; Mota-Rojas et al 2021b). Although there are two types of adipose tissue: white adipose tissue (WAT) (which stores energy in the form of triglycerides) and BAT, only in the latter is thermogenesis driven by hypothalamic-medullary glutamatergic signals. This action produces heat through mitochondrial uncoupling and is regulated by the interaction of norepinephrine with β3 adrenoreceptors in the BAT (Mota-Rojas et al 2021d). Mota-Rojas et al (2021d) mention that BAT heat production and WAT browning depend on SNS stimulation to control energy balance and regulate fat tissues. Similarly, acetylcholine neurotransmitters stimulate musculature to transform stored chemical energy into thermal energy, increasing metabolic body rates.

Secreted catecholamines also act on α-adrenoreceptors in blood vessels to divert blood flow from the periphery to central organs, causing a reduction in heat release by radiation (or cutaneous vasoconstriction) (Ikoma et al 2018; Morrison and Nakamura 2019; Mota-Rojas et al 2021e). These mechanisms constitute the afferent response of central temperature modulation, which is reflected in the changes observed or assessed at the peripheral level.

4.2. Peripheral thermoregulatory mechanism

Body temperature results from a balance between mechanisms of heat production and dissipation in large homeotherms like elephants (Kinahan et al 2007a). These mechanisms are regulated by thermoreceptors in the POA that induce vascular changes in response to cold or heat stimuli (Morf and Schibler 2013; Mota-Rojas et al 2021d) (Figure 1).

In POA-derived central responses, the vasodilation of capillaries when elephants are exposed to warm temperatures is perceived by Ruffini corpuscles, which transmit the signal to spinal sensory neurons in the dorsal root ganglia (DRG) (Mole et al 2016). The involvement of the LPBd, its axons to the POA, and communication with the MnPO and MPO, which project to the DMH and rRPa and the ventral horn, stimulates sympathetic fibers that promote vasodilation, especially in regions with high vascularization like the ears (Tupone et al 2014; Morrison 2016; Mota-Rojas et al 2021ab).

When elephants are in cold environments, POA initiates vasoconstriction of superficial capillaries to redistribute blood flow to critical organs, thereby increasing temperature (Mole et al 2016). In contrast to heat response, this process begins in Krause's corpuscles and uses the external lateral part of the LPB (LPBel), the MnPO, and MPO. In these sites, the stimulation of sympathetic fibers promotes vasoconstriction of limb blood capillaries and stimulates somatic motor fibers to activate shivering thermogenesis (Yang and Ruan 2015; Morrison 2016; Mota-Rojas et al 2021a).

Mole et al (2016) mention that dermal evaporative cooling is one of the main mechanisms elephants use to modulate their temperature, and water plays an essential role. If they do not access it, elephants deplete their body reserves, affecting osmoregulation. For example, it has been reported that elephants lose more moisture through skin evaporation (2500 ml/h in an 11 m2 elephant) (Kinahan et al 2007a; Hidden 2009) and from metabolic heat through the lungs and skin (approximately 20%) (Wright and Luck 1984), than through sweating mechanisms, due to the absence of sweat glands (Lamps et al 2001). Likewise, the non-evaporative strategies mentioned by Dunkin et al (2013), such as the movement of the ears or shade seeking, are other tools that favor heat loss.

Heterothermy is another adaptive process that has been proposed in elephants exposed to hot climates. An animal can store body heat by reducing the need to dissipate it through evaporation and, therefore, preserving body water (Mitchell et al 2002). This mechanism has been observed in desert animals like camels (*Camelus dromedarius*) and antelopes, aiming at diurnal heat storage and nocturnal heat dissipation, which allows the animal to conserve energy and water in dry and hot conditions. This effect has been studied by Weissenböck et al (2012) with 13 Asian elephants (*Elephas maximus*) in two different environmental conditions, one at Hellabrunn Zoo in Munich, Germany at a moderate temperature of 21 °C and the other at Samphran Elephant Ground and Zoo in Thailand at an average temperature of 30 °C. They found that elephants activated heterothermy even at moderate temperatures when the ambient temperature was below body temperature, compared to the antelope that only performs this mechanism when exposed to temperatures above 40 °C. This difference could be explained by the size of both species, where large mammals such as elephants have a small surface: volume ratio because they have limited areas available to dissipate body heat efficiently at temperatures above 35 °C (Kinahan et al 2007a; Weissenböck et al 2012). In addition, Rowe et al (2013) mention that elephants and leatherback sea turtles (*Dermochelys coriacea*) perform endothermic gigantothermy, an event consisting of a series of vascular changes (vasoconstriction and vasodilation) to store metabolic heat produced by exercise (approximately 56-100%) in central tissues, dissipating it through behaviors such as bathing, mud- and dust-bathing. The importance of these behaviors is associated not only with the size of the elephants but also with the anatomy of pachyderms, a trait that can influence how they respond to thermal challenges.

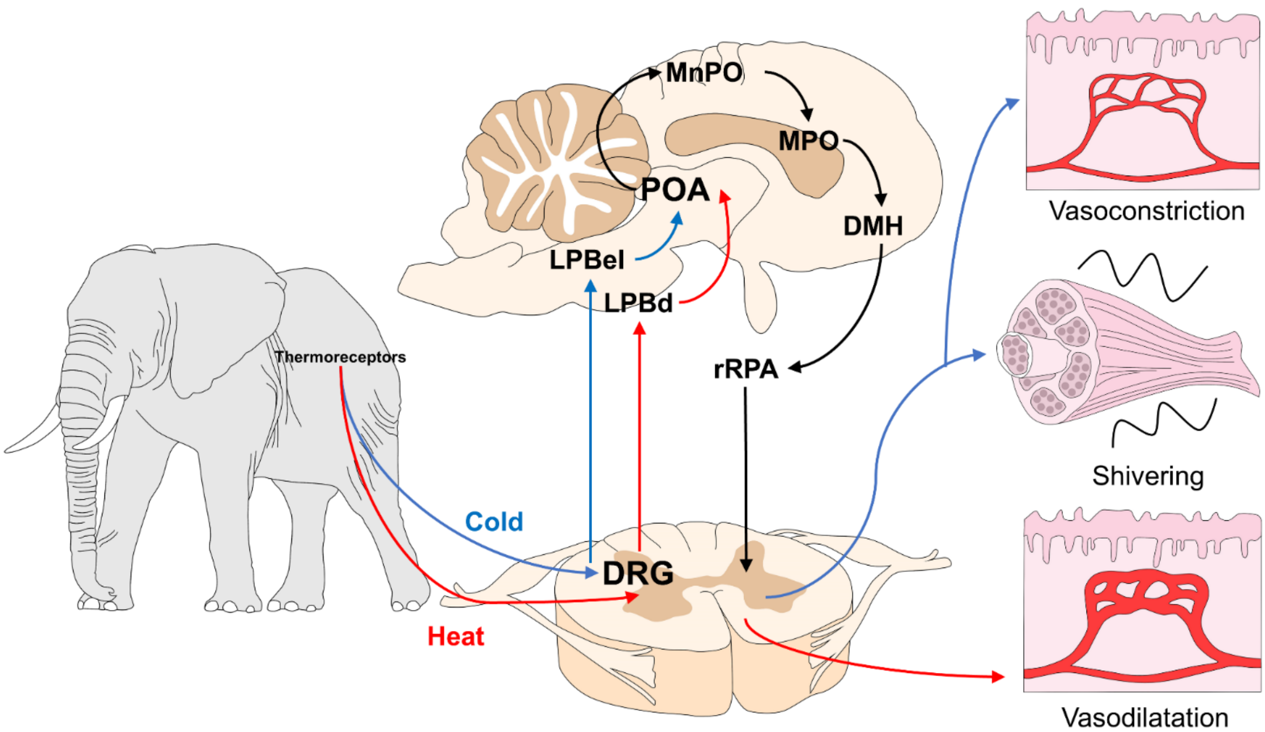

Figure 1 Mechanisms of central and peripheral thermoregulation. The image illustrates the integration of the thermal stimuli detected by the corpuscles of Ruffini or Krause in the face of heat or cold, respectively. Although the central pathways in both cases are very similar and use the DRG, POA, MnPO, or rRPA (black lines), the main difference is observed in the LPBN regions that are activated by stimuli of a different nature. The red lines show the thermoregulatory mechanisms in warm environments, where LPBd neurons produce vasodilation. In contrast, with cold stimuli (blue lines), the LPBel neurons are stimulated to generate sympathetic vasoconstriction and stimulate motor fibers that promote shivering and non-shivering thermogenesis. DRG: dorsal root ganglia; LPBd: dorsal part of the lateral parabrachial nucleus; LPBeL: Lateral parabrachial nucleus in its external region; POA: preoptic area of the hypothalamus; MnPO: median preoptic nucleus; MPO: medial preoptic area; DMH: dorsomedial hypothalamus; rRPA: rostral raphe pallidus.

5. Anatomical aspects and their influence on thermoregulation

The adverse effects of global warming on the thermoregulatory mechanisms of elephants depend on the habitat characteristics and adaptability of the animal. However, it is necessary to analyze the structures involved in thermoregulation and their differences depending on the species since these responses are based on the anatomical and morphological particularities of elephants.

5.1. Skin

The term "pachyderm" means "thick skin". The skin is a structure whose main function is as a protective barrier against physical, chemical, and biological elements (Low et al 2020). It is composed of two layers: the nonvascular epidermis, and the dermis, in which collagen, blood vessels (Mikota 2006), and free nerve endings are found (Lezama-García et al 2022). These endings are composed of ion channels that respond to noxious heat (above 43 °C) (Low et al 2020) or cold (between 18 and 23 °C) (Zakharian et al 2010). It also protects against parasites and intense solar radiation and is a key sensory organ for thermoregulation.

Elephant skin is characterized by its gray color with brownish hues, with wrinkles and crevices distributed geometrically on the surface of the epidermis. The epidermis and dermis are connected by complex polygonal columns or studs (Mikota 2006). These 1-2 mm wide tubercles, mixed with cracks or wrinkles, create the honeycomb effect in the skin (Lillywhite and Stein 1987). A histological study on two 2-year-old Asian elephants (*Elephas maximus*) calves showed the absence of a stratum lucidum and the presence of many melanocytes in the *stratum basale* and *stratum spinosum* (Thitaram et al 2018).

Computed tomography work has shown that cracks in the stratum corneum result from hyperkeratinization, deficient skin desquamation, and growth of dermal elevations (Martins et al 2018). Deficient desquamation contributes to the thickening of the *stratum corneum* (thickness that can exceed 300-400 μm). It permits the adsorption and movement of water over the body's surface through interconnected crevices (Martins et al 2018).

Although the characteristics that have been described are observed in Asian and African elephants (Peeks and Badarnah 2021), it is important to mention some differences since the environment inhabited by the *Elephantidae* family influences their degree of adaptation. For example, African elephants reside in the African continent and areas with extreme climates, having two recognized subspecies: the savanna elephant (*Loxodonta africana*) and the forest elephant (*Loxodonta cyclotis*) (Grubb et al 2000). They have larger ears and tusks, reach heights of approximately 2.2 to 4 m, and weigh up to 7000 kg (Lee and Moss 1995; Morgan and Lee 2003; Feldhamer et al 2020). In contrast, Asian elephants (*Elephas maximus*) are smaller, with average heights of 2.24 m, weighing from 2720 kg to 4500 kg, and inhabit the southern Himalayas, mountains of India and Indonesia (Shoshani and Eisenberg 1982; Feldhamer et al 2020).

The differences between the two species can be observed in their physical appearance and histological skin structure (Figure 2). In African elephants, the thickness can range from 30-40 mm (Spearman 1970; Rubio-Martínez et al 2014), while in Asian species, it is 18-30 mm (Shoshani and Eisenberg 1982). The thickness of the epidermis depends on the body region observed. For example, the skin thickness of the ear is 1.8 mm on the medial surface, on the medial side of the legs, it is 1 cm, and on the dorsum, it reaches up to 3.2 cm (Mikota 2006). The thickness and presence of wrinkles improve the water retention capacity of elephant skin. This parameter is 4 to 10 times higher than on smooth surfaces, preventing epidermis dehydration and contributing to evaporative heat loss (Lillywhite and Stein 1987).

Water retention capacity depends on the crevices' morphology, and both species are placed between 0.03 and 0.2 mm in width, with 0.1-2 mm in depth. An experimental study with two *Loxodonta africana* and two *Elephas maximus* has shown that African elephants have a greater capacity to retain water ($P < 0.01$) because the cracks and fissures of their skin are deeply sculptured, reaching up to 1 cm in depth. Therefore, the amount of water that can be adsorbed by an African elephant weighing 2500 kg is a minimum of approximately 225 g of water, while an Asian elephant of the same weight would only absorb 144 g (Lillywhite and Stein 1987). Another unique trait of *Loxodonta* is the channel pattern of dermo-epidermal protuberances, which is an environmental adaptation effect to withstand the extreme temperatures of the African continent (Martins et al 2018).

This dermal adaptation is associated with the frequency of water-dependent thermoregulatory behaviors (e.g., bathing with water, dust-bathing, or wallowing) (Stoinski et al 2000) or spraying (Barandongo et al 2018). Cracks and wrinkles hydrate the stratum corneum (Shoshani and Foley 2000), allowing mud to adhere and prolonging the hydrating effect of water. For example, mud maintains dermal moisture for more than 18 h and with a maximum of 26 h in elephant skin models (Lillywhite and Stein 1987), promoting evaporative heat loss (Dunkin et al 2013). Cutaneous evaporative water loss was evaluated in seven African and six Asian elephants exposed to various ambient temperatures for five years. Losses showed no differences between species but were higher in moist skins, ranging from 0.31 to 8.9 g/min/m in Asian elephants and 0.26 to 6.5 g/min/m in African elephants (Dunkin et al 2013). Therefore, when individuals are exposed to arid climates without a water source, the risk of dehydration and decreased rate of evaporative water loss may cause heat shock (Mole et al 2018).

Another dermal deficiency linked to constant moisture requirements in elephants is the lack of sweat glands and sebum glands that keep the stratum corneum moist (Mole et al 2018; Martins et al 2018). The lack of these glands means that elephants cannot sweat and that transepidermal water losses are low (Lillywhite and Stein

1987). However, in *Elephas maximus,* interdigital glands (one gland every 10-15 blocks) have been reported in the reticular dermis and have a similar function to the eccrine glands of humans (Lamps et al 2001). Although they lack sympathetic control of sweating, elephants can compensate through increased cutaneous permeability of water to lose heat through evaporation (Dunkin et al 2013). Also, hair follicles' absence (or near absence) exacerbates thermoregulation and dermal water balance issues (Anastassakis 2022). Although Asian elephants have sparsely distributed hair around the eyes, ears, genitalia, chin, and tail, studies in three Indian elephants (*Elephas indicus*) fetuses revealed the absence of hair follicles, sebaceous and sweat glands, as well as a lack of development or differentiation of the arrector pilorum muscles (Ayer and Mariappa 1950).

Dermal blood vessels and peripheral vasomotor control are other important elements that contribute to evaporative heat loss by vasoconstriction or vasodilation (Fowler 2006). In this structure, arteriovenous anastomoses and venous plexuses in the skin regulate blood pressure and heat dissipation (Barlett 2006), particularly in the ears, one of the essential thermoregulatory zones in elephants.

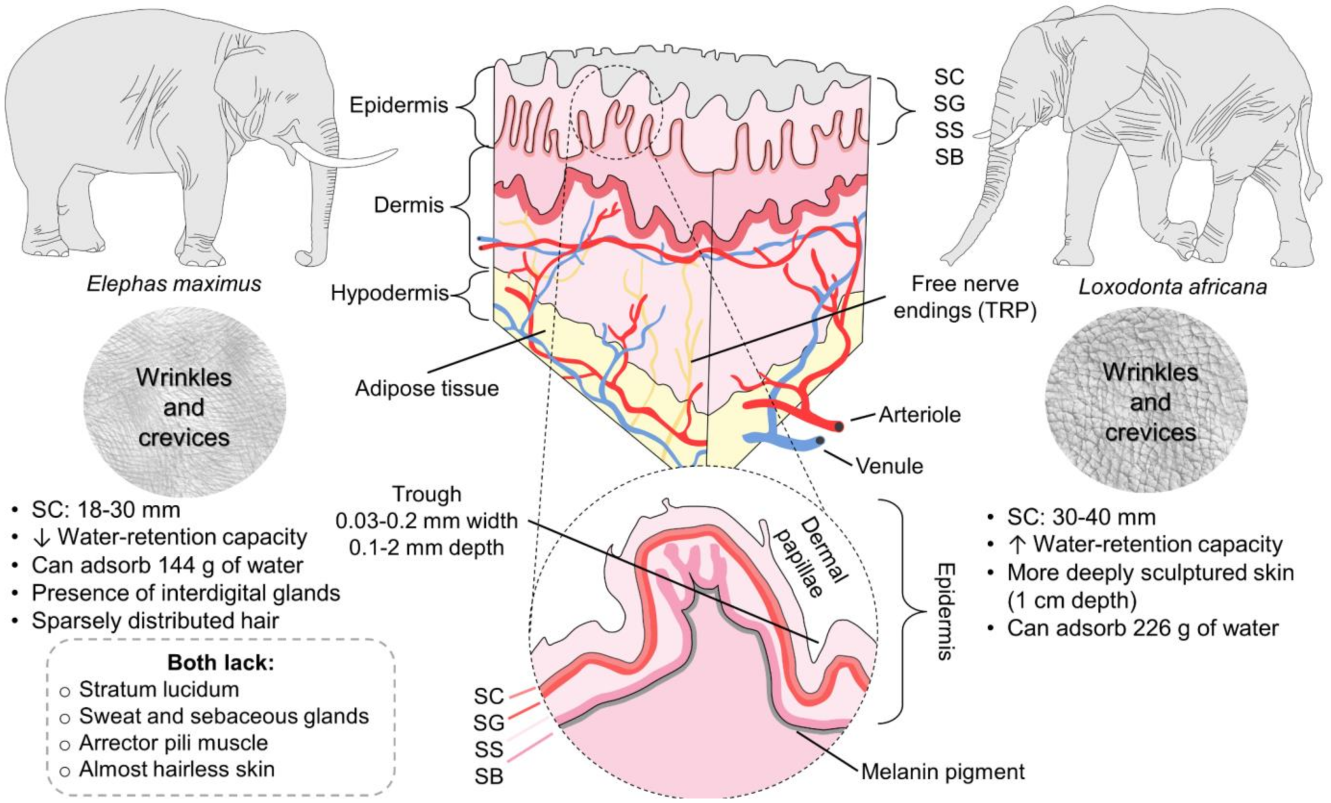

Figure 2 Morphology of the skin, its layers, and differences between Asian (*Elephas maximus*) and African (*Loxodonta africana*) elephants. In general, the skin of the *Elephantidae* family is characterized by epidermis with an SC with wrinkles and crevices, which promote water retention in the skin. In both species, stratum lucidum, sweat and sebaceous glands, and hair follicles are absent, and the arrector pili muscle is not developed. However, significant differences have been reported: the African elephants have a more deeply sculptured skin that enhances their water-retention capacity, while Asian elephants' skin is less thick, they have a lower water-retention capacity, but also have sparsely distributed hair follicles, and interdigital glands similar to sweat glands present in humans have been reported. SB: stratum basale; SC: stratum corneum; SG: stratum granulosum; SS: stratum spinosum: TRP: transient receptor potential.

5.2. Ears

Ears are highly vascularized structures with movements that promote heat loss through convection (Mikota 2006). The previously mentioned differences in body size are also reflected in the ears and respond to the different environmental temperatures (Terrien 2011). According to Phillips and Heath (1992), in the case of African species, elephants with larger ears, the measure of four females were 106.7-137 cm and 63.5-88.9 cm in length and width, respectively, and the pinna extended from above the neck (Mikota 2006). In contrast, in Asian elephants, the pinna, with a trapezoid shape, is positioned below the neck (Mikota 2006) and is about one-third the size of the African elephant (Carrington 1959).

Ear shape also affects thermoregulation as African species have up to twice the ear surface area (Dunkin et al 2013). This variation is attributed to the higher requirements of *Loxodonta* to dissipate heat due to the exposure to high ambient temperatures (40-50 °C) (Narasimhan 2008; Terrien 2011). In these species, the high surface-to-volume ratio, vascularization, and constant flapping of the ears represent an area of between 13-20% to dissipate heat at temperatures above 25 °C (Fowler 2006). In contrast, in Asian species, the smaller size of their ears gives them only 7-10% (Fowler 2006).

The constant movement of the pinna is a key element for heat loss by radiation and convection (Phillips and Heath 1992). This movement is controlled by the *rotator, auriculo occipitalis, postauricularis, zygomatico auricularis, platysma myoides* y *sphinctor profundus* muscles (Figure 3) (Boas and Paulli 1908). These fibers are innervated by the facial nerve and the anterior branches of the temporal portion or the ramus auricularis posterior (Marchant and Shoshani 2007). The movement exposes the medial side of the ears, where the complex network of blood vessels promotes heat loss when exposed to air currents (Athurupana et al 2015).

The irrigation in this area is provided by the auricular veins (Barlett 2006), which are branches of the lateral auricular vein and the middle auricular branch (Isaza and Hunter 2004). The thickness of the skin in this area (1 to 2 mm) favors the effects of cutaneous vasodilation when elephants need to dissipate heat, thereby exchanging heat (Phillips and Heath 1995; Narasimhan 2008).

The characteristics of skin and ears are two thermoregulatory organs that serve as a thermal window to dissipate heat (Feldhamer et al 2020). They are also associated with animals' various behaviors to achieve an adequate thermal state.

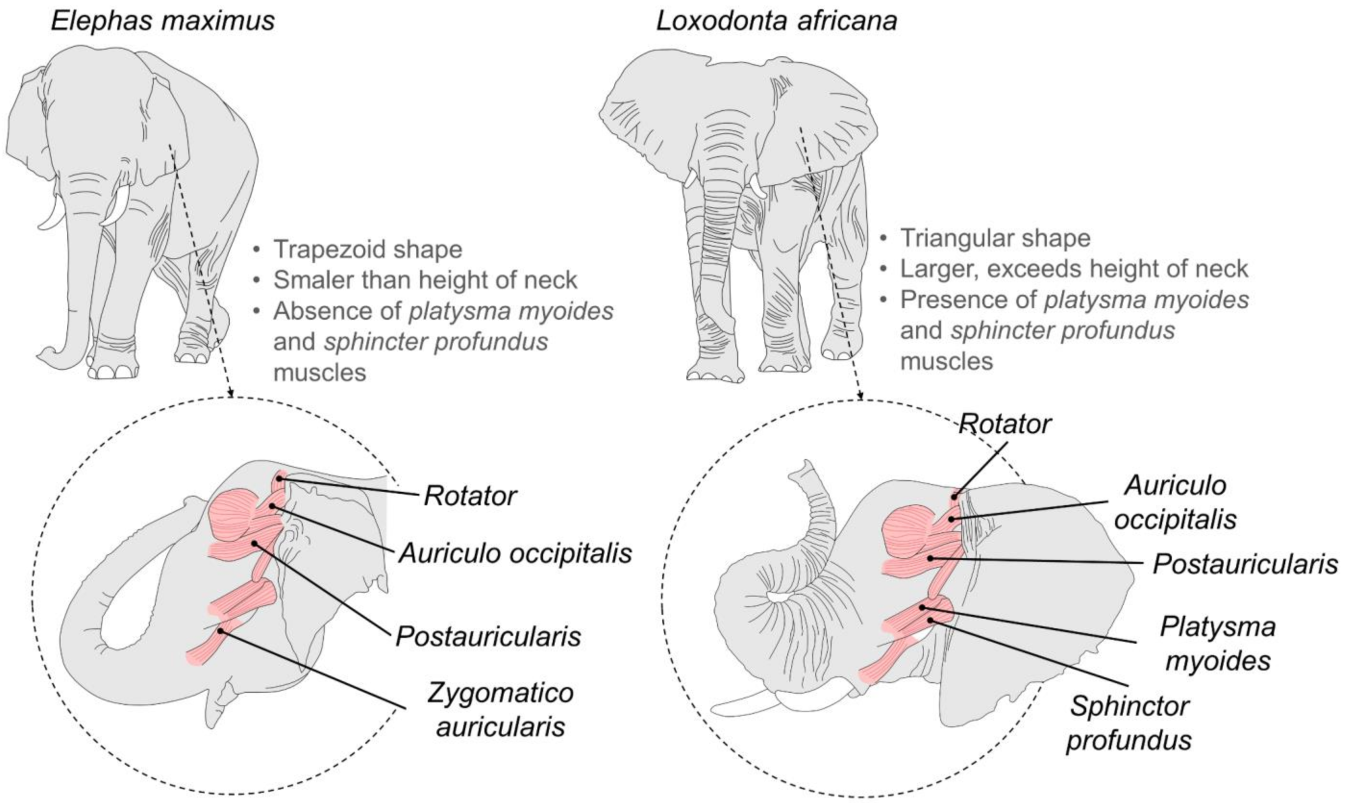

Figure 3 Morphoanatomical ear differences between Asian (*Elephas maximus*) and African (*Loxodonta africana*) elephants. For elephants, the ears represent the largest thermoregulatory organ. Due to its high vascularization and the movement provided by the auricular muscles, heat loss is made through convection. In Asian elephants, whose ears shape is a trapezoid, the platysma myoides and sphincter profundus is absent. In contrast, the triangular shape of the ears, their larger size, and the presence of the muscles are characteristics of the Loxodonta.

6. Thermoregulatory behaviors

In addition to the physiological response, elephants also adopt behaviors to reduce heat load in areas where diurnal ambient temperatures (up to 50 °C) exceed core body temperatures (Cole 1986; Kinahan et al 2007b). These include resting in the shade, mud bathing, dust bathing, and ear flapping (Hiley 1975; Baskaran 1998; Rees 2002b).

6.1. Bathing, mud bathing and dust bathing

As previously mentioned, elephants are considered water-dependent due to the large amounts of water intake (up to 100 liters/day) (Feldhamer et al 2020), the lack of sweat glands (Wright and Luck 1984), and the high index of water turnover due to water loss through the skin and respiratory evaporation (Dunkin et al 2013; Purdon and van Aarde 2017). To promote this effect, elephants use mud bathing, swimming, and splashing to thermoregulate (Dunkin et al 2013; Mole et al 2016; Purdon and van Aarde 2017). According to Rees (2002b), these behaviors (bathing, mud bathing, and dust bathing), serve for social cohesion among conspecifics, modulating body temperature and protecting the skin from insects, parasites, and radiation.

The study by Purdon y van Aarde (2017) assessed how water management patterns, source type (natural or artificial waterholes), and availability affect the spatial use of 26 female elephants (*Loxodonta africana*) in Kruger National Park, South Africa. Global position system telemetry collars were used to identify trips to water sources from June 2012 to March 2014 (Chamaille-Jammes et al 2013; Purdon and van Aarde 2017). Results showed that the probability of pachyderms visiting water bodies depended on the hottest hours of the day, increase in ambient temperature above 20 °C, the season, and visiting rivers (estimated 1⁄4 0.25 ± 0.04; z 1⁄4 5.77; $P < 0.0001$) and artificial waterholes (estimated 1⁄4 0.90 ± 0.16; z 1⁄4 5.55; $P < 0.0001$) during the dry season.

In the case of dust bathing, this behavior was studied in a herd of eight Asian elephants (*Elephas maximus*) that were being held captive at the National Elephant Centre of the Zoological Society of Northern England (Chester Zoo) in Cheshire, England, from February 10 to September 21, 1999. Data collected through instant scan sampling (Martin and Bateson 1993; Rees 2002b) revealed that the elephants' technique for applying sand to the body was to roll the trunk all over the ground, take a portion of the soil, and then throw or blowing the sand over the head, back, sides, or onto their forelegs. In younger individuals, another method of bathing was lying and rolling on the ground. Also, in this study, it was determined that the greatest amount of dust bathing (27.3%) was recorded on days when the average ambient temperature was 19.91 °C and the maximum was 25.11 °C (Rees 2002b), serving as a protective barrier from solar radiation since they lack hair follicles.

6.2. Movement and shade-seeking

Exposure to hot, arid environments leads elephants to decide where and how fast they should move to reduce thermal stress (Thaker et al 2019). Movement patterns and their spatial distribution are influenced by factors such as vegetation greenness, distribution of water sources, and ambient temperature (Diaz et al 2021). Kinahan et al (2007b) also mention that, in high temperatures, elephants prefer relocation to landscapes that cool faster to facilitate heat loss. The same happens during low ambient temperatures, where they move to more rapid warming territories to reduce heat loss or increase heat gain. The proximity of water also influences elephant movement speed. This parameter increases during wet seasons and decreases in dry seasons, particularly in densely wooded habitats, to reduce water loss due when moving at high temperatures (Codron et al 2006; Kinahan et al 2007a; Birkett et al 2012; Chamaille-Jammes et al 2013; Thaker et al 2019).

6.3. Ears

Phillips and Heath (1992) mention that ear movement and vasodilation of dermal capillaries can satisfy 100% of an elephant's heat loss requirements. The frequency of ear flapping increases with rising environmental temperature (Rees 2002b), while airflow through the pinna facilitates heat loss by radiation and convection, in which anatomical differences have an influence (Wright and Luck 1984; Phillips and Heath 1992).

In the study by Athurupana et al (2015), the flapping ear rate in large elephants was higher (10.7 ± 0.5), while in medium and small elephants, the rate was 5.4 ± 0.3 and 1.6 ± 0.1, respectively, demonstrating that their dimensions may affect heat exchange (Williams' 1990). Also, size, climatic and habitat conditions are associated with the frequency of auricular movements and specific patterns. Temperatures between 30-31 °C and relative humidity of 59-61% affect the frequency of movements, an event that decreases when the animal is located in the shade (Athurupana et al 2015).

The influence of environmental temperature and its link with season and roofing material has been studied by Vanitha y Baskaran (2010) with the thermoregulation of six Asian elephants (*Elephas maximus*) under human care. In this study, ear movement rates were compared between the frequency of ear movements and those elephants housed in enclosures made of different materials (asbestos sheets, coconut frond thatching, and reinforced cement concrete (RCC)). They reported that ear movements increased gradually from 6:00 to 18:00 hrs, reaching a maximum peak between 13:00 and 14:00 hrs, then gradually decreasing. The highest frequency of ear movement (9.2 times/minute) was recorded during the months of May-June with an average maximum temperature of 36 ± 3.42 °C, and decreased by almost half (5.7 times/minute) during December-January, with an average minimum temperature of 28 ± 3.38 °C. Regarding the enclosure material, the highest frequency of ear movement was observed in houses made of asbestos sheets with 6 times per minute between 11:00 and 12:00 and 8 times per minute between 12:00 and 13:00 hrs. This was followed by houses made of RCC with a gradual increase after 12:00 h, reaching its peak at 13:00 h, contrarily to the coconut frond thatching houses that had a noticeable decrease in the frequency of ear movement. These factors are fundamental elements that must be considered, especially in elephants under human care to avoid the consequences of heat stress related to the enclosure characteristics.

7. Recent findings and future directions on thermoregulation

7.1. Use and importance of IRT

The study and understanding of elephant thermoregulatory mechanisms serve to understand the thermal physiology of elephants and to apply methods to promote thermal equilibrium in wild and captive elephants. In this sense, IRT is a non-invasive tool that detects surface temperature distribution patterns (McCafferty 2007). In veterinary medicine, this method is a complementary tool for diagnosing diseases, controlling reproductive processes, analyzing animal behavior, and estimating species' thermal state. One of its advantages, especially in wildlife, is that it can be used remotely, so the animal does not need physical or chemical restraint, thereby reducing stress levels (Cilulko et al 2013).

In the case of elephants, Williams (1990) measured dermal heat loss by convection, radiation, and conduction using IRT on different anatomical sites (body, legs, head, trunk, neck, and ears) of an African (*Loxodonta africana*; adult; 3500 kg) and Indian elephant (*Elephas maximus*; immature; 2000 kg). The results showed that convection and radiation account for almost 90% of total heat loss for both species. This heat transfer occurs in thermal windows, which, according to Šumbera et al (2007) and Mota-Rojas et al (2021f), are body regions with a high density of blood vessels and arteriovenous anastomoses close to the body surface and lack fur. These characteristics facilitate heat exchange through vasoconstriction or vasodilation.

Following these elements, the anatomy of elephant ears is a thermal window (Figura 4) (Phillips and Heath 1992). In addition to the pinna, Weissenböck et al (2010) determined with six African elephants (*Loxodonta africana*, four adult females, and two juveniles) that the body surface of the torso and limbs are also regions that can be used to assess the thermal status of pachyderms.

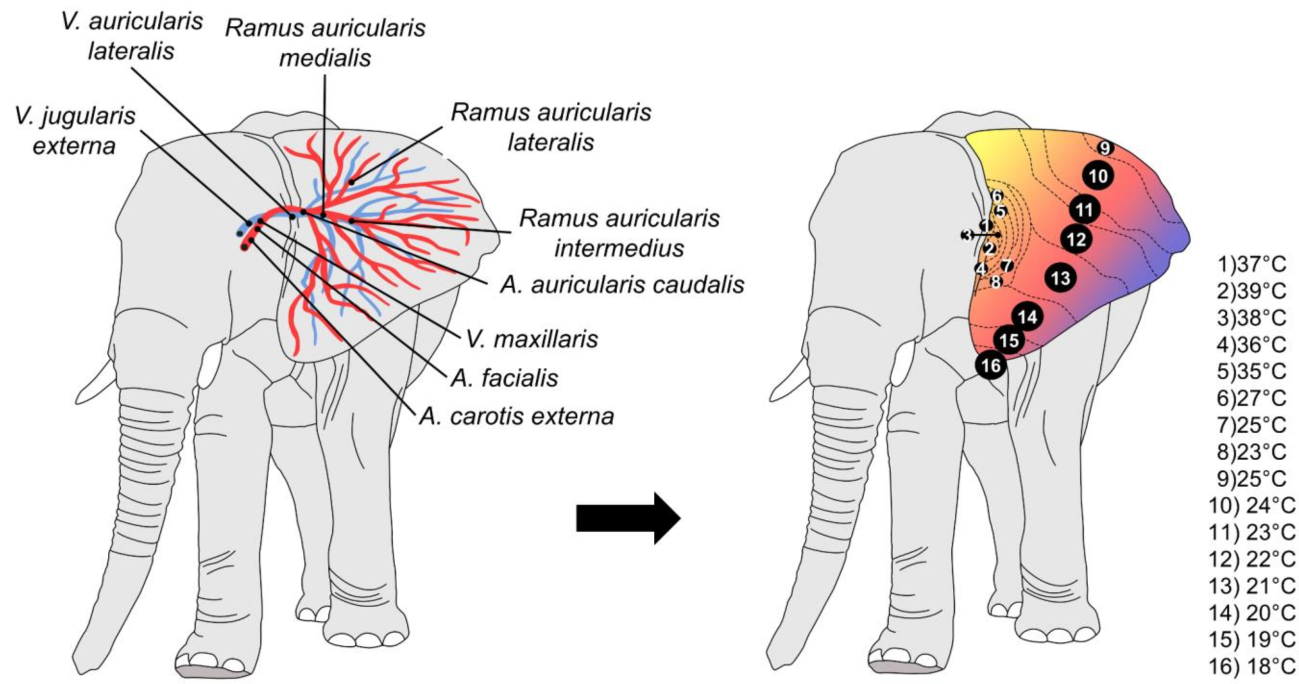

Figure 4 Auricular vascularization and its influence on the thermal response. The ramus auricularis medialis, lateralis, and intermedius, ramifications from the a. external carotid and v. external jugularis, are the blood vessels that supply the pinna of elephants. Due to the vasomotor changes in these blood vessels, the temperature of the pavilion has differences. The highest temperatures are in the medial part of the ear, while the lowest values are registered at the periphery.

Another example of the use of IRT was shown in the study by Avni-Magen et al (2017) in four Asian elephants (*Elephas maximus*), where they employed IRT as a complementary method for the early detection of pathological inflammatory lesions in the ears. The results indicated local temperature increases before the clinical identification of the lesion and a positive correlation ($P < 0.001$) between the clinical diagnosis of inflammatory lesions and the area of hyperthermia recorded by IRT.

Although IRT is suggested as a supportive tool in animals, it has environmental, individual, or technical limitations. As mentioned by (Cilulko et al 2013), weather conditions include direct solar radiation, precipitation, wind, and air humidity, while technical conditions refer to the distance between the object and camera and the field of view (recommended field of 90° to 50°, maximum). As for the individual characteristics of the animals, the coat, its thickness, color, quality, and length affect the precision of IRT to quantify thermal variations (Mota-Rojas et al 2021c). Furthermore, stressors, physical activity, and pharmacological agents can modify blood circulation and changes in surface body temperature and must be considered when using IRT.

7.2. Environmental enrichment and enclosure design to promote thermoregulation

The knowledge of elephant thermoregulation and the techniques currently used to assess this process is a way to ensure the welfare of pachyderms, especially when they are placed in enclosures under human care.

Housing characteristics, resource-based and outcome-based measures help interpret animal responses to varying environmental parameters (Meehan et al 2016). Enclosure design should be based on species-specific biological needs and animal responses (Mason 2010). In the case of elephants, based on their thermoregulatory physiology, the environment should promote natural behaviors, which serve as an indicator of physical and mental welfare (Glaeser et al 2021) (Figure 5).

Given that elephants move to reduce thermal stress (Thaker et al 2019), an ideal enclosure should provide an artificial microclimate for heat exchange (Langman et al 2003) while also considering the differences between species and the characteristics of their natural habitat. For example, because Asian elephants (*Elephas maximus*) and African forest elephants (*Loxodonta cyclotis*) inhabit forested areas, they are likely to have a higher ecological affinity than African elephants (*Loxodonta africana*), whose habitat is usually in open savanna grasslands (Pastorini et al 2010).

The application of these premises and the implementation of different enrichments employed within zoos and reserves place these parameters as a priority. In the study by Glaeser et al (2021), the concentration of adrenal hormones -cortisol and corticosterone-, reproductive hormones, and behavioral data were analyzed to evaluate the effectiveness of the design features of habitat for Asian elephants (*Elephas maximus*) at the Oregon Zoo. In this enclosure pools, shade structures, drinking fountains, temperature-controlled rooms, a splash pad, a water cannon, and a sprinkler were installed to simulate rain. These structures provide various options for elephants to thermoregulate (Thaker et al 2019). The use of shaded areas within elephant enclosures was evaluated by Langman et al (2003) at Zoo Atlanta. It was recorded that shaded areas covered approximately 11% of the enclosure and helped to reduce the radiant heat load to 278 Wm^{-2}, or 36% of the calculated maximum heat reduction of 766 Wm^{-2} (Thaker et al 2019) mention that shade provided by dense vegetation supports thermoregulation and constitutes a naturalized environment for elephants.

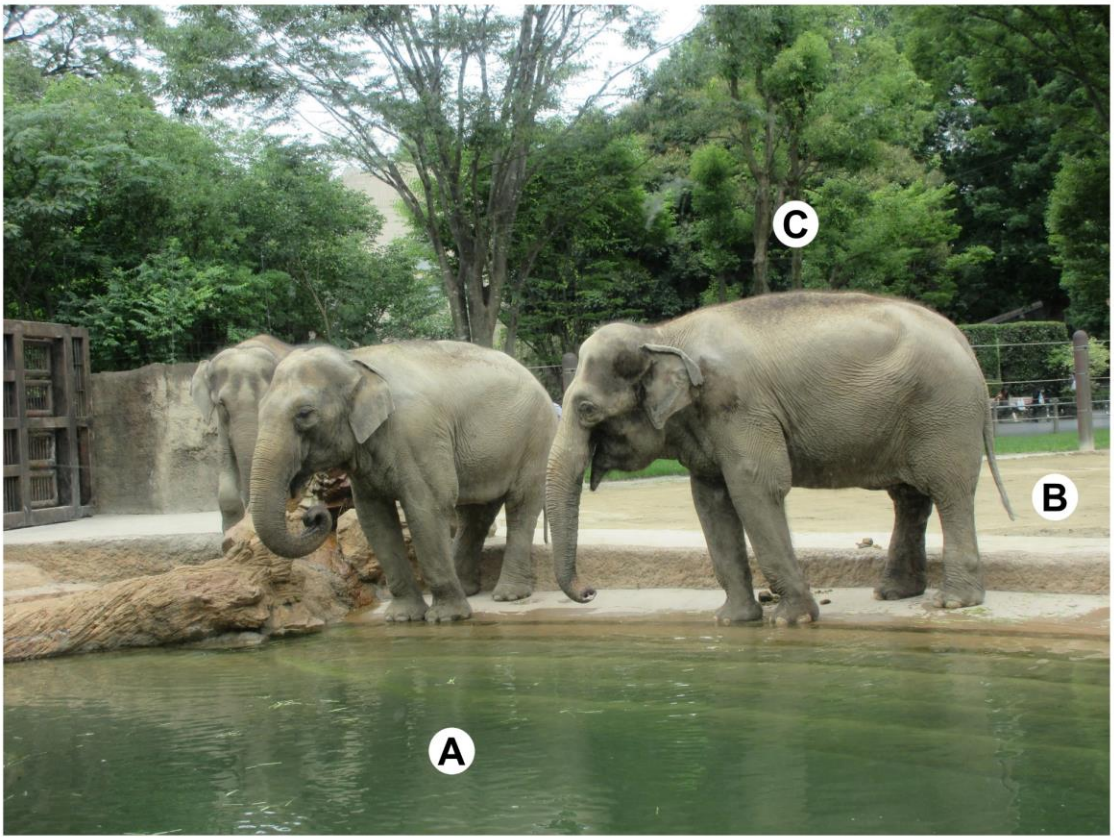

Figure 5 Asian elephant (*Elephas maximus*) enclosure at Ueno zoological gardens, Japan. In this photograph taken by the authors, the enclosure has a large pond enough to provide a source of water for the individuals (A). The space available to move (B) allows them to walk to warmer or cooler areas. (C) represents the use of dense vegetation as a natural shade to prevent hyperthermia.

Water bodies are essential for elephants to meet their daily physiological demands and to perform thermoregulatory behaviors to moisten and cool the skin (Pontzer et al 2020). In recent years, elephant tourist camps have implemented activities promoting the coexistence of people and wildlife. They also represent environmental enrichment for the elephants by engaging them in natural behaviors. For example, Kosaruk et al (2020) reported that tourist camps with 44 elephants in Thailand include recreational activities such as bathing in the river, splashing water on the elephants, and applying mud to the elephants' skin. These activities encourage behaviors typical of the species' repertoire, promote positive human-animal interaction (Escobar-Ibarra et al 2021), and increase fecal and salivary IgA concentrations, a biomarker often associated with positive welfare. The water body size has also been associated with elephant preferences in the study by Pastorini et al (2010), where it is mentioned that elephants prefer larger tanks and this is related to perennial water content.

Therefore, understanding the thermoregulatory physiology of elephants is the basis for implementing appropriate measures for their conservation and management (Mole et al 2016), thus promoting the good welfare of elephants under human care by satisfying their biological needs (Mason 2010). Considering this, it is essential to adopt environmental enrichment techniques within the enclosure to contribute to the thermal comfort of these pachyderms. Amongst these techniques are increased water availability (Pastorini et al 2010), construction of shaded areas, controlled microclimates (Langman et al 2003), and areas that allow the movement of the animal for its thermoregulation (Thaker et al 2019).

8. Final considerations

Elephants are mammals predisposed to heat stress when their ability to cope with climatic variations is hampered if their habitat resources are limited or when their physiological and morphological mechanisms of thermoregulation are altered.

In this regard, the lack of sweat glands hinders efficient heat dissipation. However, cracks in the skin promote water retention and evaporative heat loss. In addition, behaviors such as bathing with sand and water and ear movements also serve as a cooling mechanism and contribute to maintaining homeothermia by exposing the auricular blood vessels to the environment.

Innovative technologies such as IRT represent a useful alternative to assess the thermal status of elephants in determining thermal windows that use the anatomical characteristics of the animals as a physiological basis. The importance of evaluating these parameters helps to ensure the thermal well-being of Asian and African elephants and to improve the habitat and enclosures of wild elephants or animals under human care.

Conflict of Interest

The authors declare that there is no conflict of interest with this work.

Funding

This research did not receive any financial support.

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