Behavioral thermoregulation in mammals: a review

Jeremy Terrien[1,2], Martine Perret[1], Fabienne Aujard[1]

[1] Adaptive Mechanisms and Evolution, UMR 7179, National Centre for Scientific Research, National Museum of Natural History, Brunoy, France, [2] Department of Neuroscience, University of Texas Southwestern Medical Center, Dallas, TX 7539, USA

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1. ABSTRACT

In mammals, thermoregulation is a key feature in the maintenance of homeostasis. Thermoregulatory capacities are strongly related to energy balance and animals are constantly seeking to limit the energy costs of normothermia. In case of thermal changes, physiological mechanisms are enhanced, increasing rates of energy expenditure. However, behavioral adjustments are available for species to lower the autonomic work, and thus reduce the energy costs of thermoregulatory responses. Hence, thermogenesis-induced metabolic costs can be reduced during cold exposure, and hyperthermia associated to dehydration can be avoided during heat exposure. Hypothermia avoidance consists in a concomitant decrease in heat dissipation and increase in heat production. Inversely, heat exchange is enhanced and body heat production is reduced when avoiding hyperthermia. The different behavioral strategies available for mammal species to cope with both decreased and increased levels of ambient temperature are reviewed. Moreover, thermoregulation function is under the control of central, metabolic, energetic and endocrine systems, which induces that parameters such as hour of the day, season, gender or aging may affect thermoregulatory adjustments. Some examples will be given.

2. INTRODUCTION

Thermoregulation plays a major role in organism homeostasis, involving central, endocrine and metabolic functions. Homeothermia is defined as the ability of an organism to maintain its core temperature (Tc) within a narrow range over a relatively wide range of environmental temperatures (1). This physiological process leads to the internal thermal stability of the organism regardless the environmental variations. Such internal protection accounts for cell integrity and is supposed to improve survival throughout the life. Failure to maintain Tc within the physiological narrow range, that is when reaching abnormal low or high Tc, leads to pathophysiological states (hypo- or hyperthermia). Normothermia maintenance, defined as Tc varying within the physiological range, involves a balance between thermogenic and thermolytic mechanisms.

Mammals, and more particularly humans, have been able to adapt to a great diversity of climates. Nevertheless, exposure to low or high ambient temperatures (Tas) is very stressful for the organism, placing it in great danger of hypo- or hyperthermia until possible death. However, numerous physiological and

behavioral adaptations are available for mammals in order to prevent such homeostasis disruption.

Autonomic thermo-effectors are critical physiological mechanisms to maintain normothermia in the absence of behavioral thermoregulatory options. Autonomic mechanisms, via the activation of thermoregulatory pathways in the anterior hypothalamus, ensure a balance between heat production and heat loss (2, 3). The hypothalamus is thus able to trigger body heat production or dissipation in response to environmental stimuli. In fact, adaptive thermoregulation results in a balance between thermogenesis and thermolysis processes, which are enhanced during cold or heat responses, respectively. Thermogenesis is the process by which body heat is produced while thermolysis is defined as the overall process to dissipate excess body heat. Thermogenesis involves changes in metabolism, muscle activity and hormones levels. The major part of heat produced by the organism comes from muscular activity and involves mechanisms that are very demanding in energy. In comparison, thermolysis mechanisms consist in the enhancement of excess body heat dissipation by vasodilatation, sweating and panting that are the most common ways to decrease Tc in mammals.

As compared to cold-induced responses, physiological adjustments in response to elevated Tc are few and this probably contributes to increase the frailty of individuals towards elevated Ta. Indeed, efficient responses to increased Tc levels above the higher critical point mainly rely on passive mechanisms, that is the concomitant decreased production and increased dissipation of body heat. Processes of radiation, conduction, convection and evaporation are then involved to promote heat transfer from the organism to the environment (4). A failure to control either production or dissipation of body heat may contribute to impair the maintenance of the thermal comfort. Physiological responses to thermal changes are very complex, involving anabolic and catabolic reactions, which won't be exposed here.

As alternative options for mammals, numerous behavioral adjustments are available to support autonomic thermoregulation and possibly counteract autonomic dysfunction (5, 6). The detection of abnormal Tc values below or above physiological thresholds is integrated by the central nervous system that triggers appropriate behaviors (4). These adjustments contribute to facilitate the management of cold- and heat-induced responses, and mainly rely on body heat exchanges between the organism and the changing environment. Hence, behavioral adjustments will be displayed in order to improve either body heat keeping or body heat loss, via the modulation of the skin-air interface. In humans, the use of clothes, air conditioning… are artificial adjustments that soften the selective pressure on the energy needs and metabolic costs and that highly contribute to reduce the influence of environmental changes on the human organism. However, parameters such as aging may impair the accuracy of behavioral adjustment, thus threatening homeostasis maintenance. Indeed, thermal perception is impaired in

aged individuals (4, 7), and inappropriate thermal adjustments in response to Ta variations have also been described in the elderly (8-10). Such results suggest that there is a disruption between the changing environment and the operant mechanisms to efficiently respond to these variations in aged individuals.

In addition to age, thermoregulatory behaviors can also be modulated by season and gender. Indeed, as some mammals exhibit very robust seasonal acclimation, thus inducing strong endocrine and metabolic modifications with seasons, thermal choice is also supposed to be related to season alternation (11). Gender is also well known to strongly interfere with thermoregulatory capacities (12, 13) and is thus supposed to induce differences in the behavioral adjustments operated by males and females.

There are many reviews describing each thermoregulatory behavior and their benefits on organism homeostasis. However, no manuscript, to the best of our knowledge, summarizes all the behavioral processes available for animals in response to Ta variations. The aim of this review is thus to focus on behavioral adjustments available for mammals, including humans, during cold and heat exposures and to explain their potential roles in the maintenance of organism homeostasis. Then, modulations induced by parameters such as season and gender will be described. Finally, the effects of age on the accuracy of behavioral thermoregulation will be discussed.

3. THERMO-PREFERENDUM

Animals are constantly seeking for the best environment in accordance with a specific thermo-preferendum, over a range of Tas corresponding to the thermal comfort of the animal (14). The notion of thermal preference is strongly associated to metabolic activity which efficiency is optimal within a specific range of Tcs. Cell integrity is endangered in the case of severe increase or decrease in Tc beyond the acceptable physiological limits. Thermo-preferendum seeking behavior tends to decrease the temperature difference between the environment and the organism, by reducing the temperature gradient between internal and external compartments. This strategy induces limited metabolic energetic costs in adult individuals to maintain normothermia (Figure 1), as there is an overlap between the range of preferred Ta and the thermoneutral zone (TNZ). Actually, TNZ definitions are numerous but all converge to the fact that thermal stress and energetic costs are minimal within the TNZ (15).

The determination of TNZ and thermo-preferendum can easily be assessed when experimenting animals in a thermal gradient. The principle of the thermal gradient is to give access to several distinct Tas and to allow spontaneous selection of the preferred Ta. Numerous species have been already experimented in such device and data have been collected in golden hamsters (16-18), desert hamsters (19), ground squirrels (18), rats (20-27), mice (5, 28), tree shrews (29), flying squirrels (29), Chilean degus (30), marsupials (31), bats (32), chipmunks (33), kangaroo rats (34), rabbits (35), naked-mole rats (36), mouse lemurs
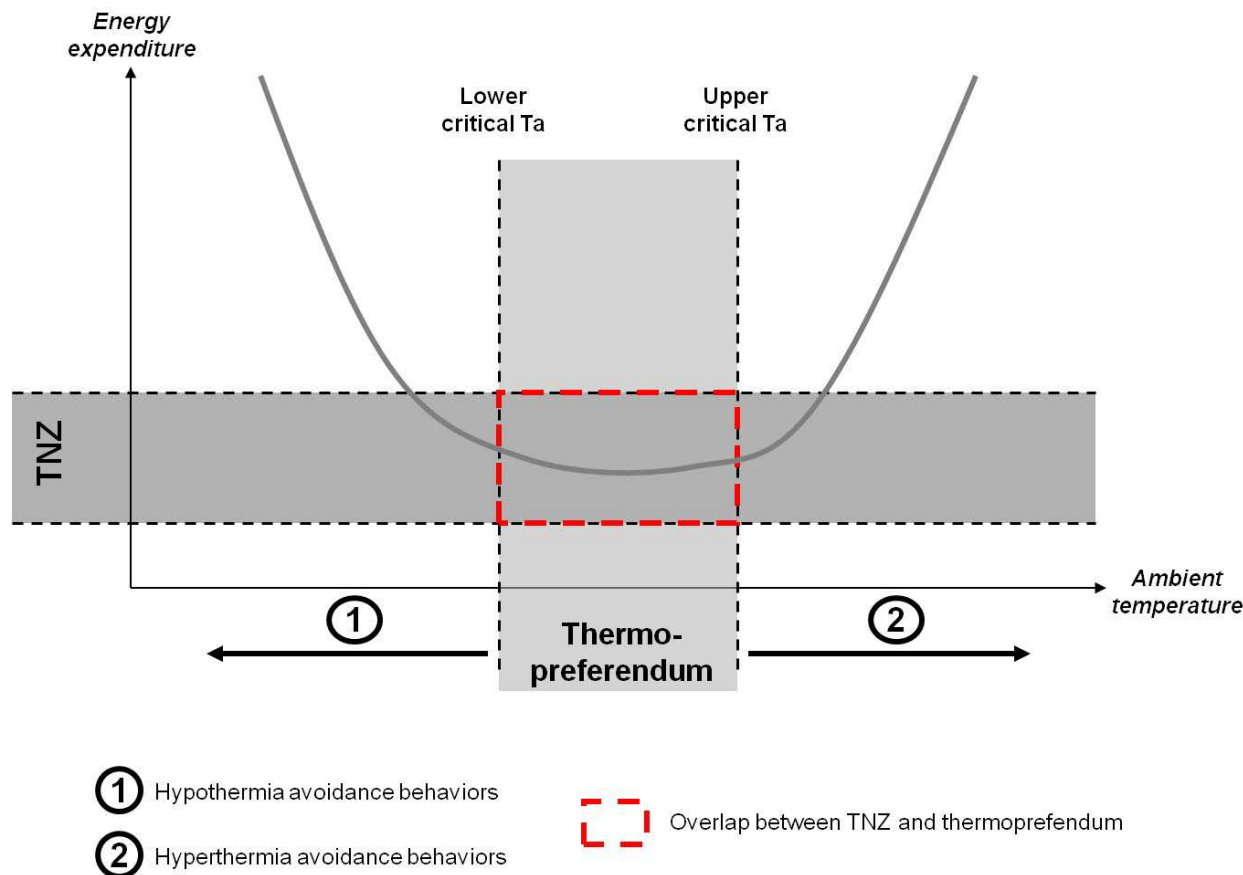
Figure 1. Schematic representation of the variations of energy expenditure in response to ambient temperature (Ta) changes. The graph shows that energy costs are the lowest when the animal selects a Ta within the thermopreferendum zone, leading to an overlap between minimal energy requirements, i.e. the thermoneutral zone (TNZ), and the thermal comfort zone. When Ta varies beyond lower or upper critical values, energy needs increases and triggers cold- or heat-induced thermoregulatory responses. Behavioral adjustments thus occur to avoid hypo- or hyperthermia.

(37) These data demonstrated that thermal preference was species-dependent, as energy needs differ among species. Gordon *et al.* showed that preferred Ta averaged 30.9°C in mice (5), 30.6°C in guinea pigs (6), 28.2°C in golden hamsters and 23.4°C in Fischer rats (27).

Moreover, the thermo-preferendum could depend on the daytime in some species, but not in all (18). Actually, day/night changes in thermo-preferendum are due to daily variations in the needs for body heat production (38). Such observations were already made in a non-human primate (37) and in humans (39). Such result is in accordance with the hypothesis that behavioral adjustments oppose to the daily variations in Tc. This was also observed in rats which preferred 24°C during their active nocturnal periods, and 27°C during the resting diurnal phases (40). In regards to the robustness of daily rhythms in Tc in heterotherm mammal species, it is noteworthy that day/night variations in preferred Ta would be greater in such species. There are studies discussing the importance of temperature selection during the torpor phase of the animal or during normothermia. Actually, torpor is a physiological mechanism that is displayed to save energy.

This process is characterized by a drastic depression of metabolic activity, thus inducing a drop in Tc. Energy savings are possible if Ta is lower than Tc, thus inducing Tc decrease. Song and collaborators suggested that thermal adjustments were particularly used during normothermia maintenance, after reaching the daily plateau of Tc, rather than during torpor (31). By this way, heterotherm species would realize greater energy savings, by performing both torpor and high Ta selection during normothermia phase.

4. HYPOTHERMIA AVOIDANCE

The defense of organism integrity is partly due to the necessity for keeping Tc above the lower critical threshold. Decreased levels of Tc following metabolic depression have to be actively controlled by the hypothalamus, to prevent severe body cooling. When exposed to low Tas, a two-step response is enhanced. First, the dissipation of body heat is reduced to promote the maintenance of body heat produced by the organism. Vasoconstriction is the primary process involved to limit body heat dissipation. Then, thermogenesis mechanisms are triggered.
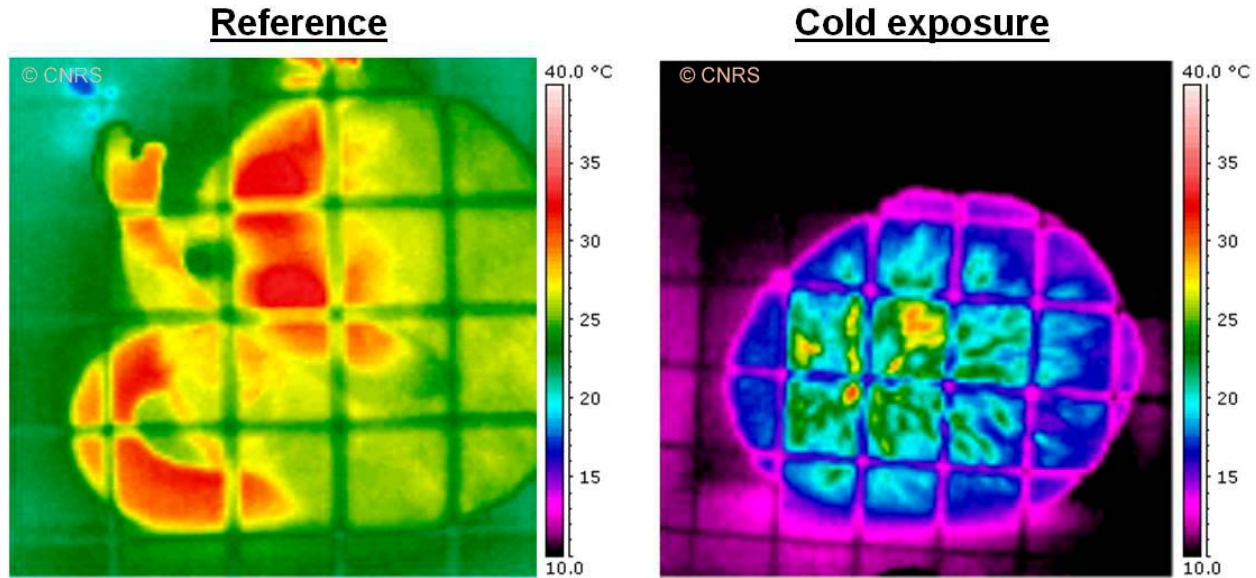
Reference

Cold exposure

Figure 2. Thermography representation of a non-human primate individual performing ball-like posture in response to cold exposure. The two pictures represent a non-human primate species (*Microcebus murinus*) that uses ball-like posture during cold exposure (right) as compared to a common resting posture in reference conditions (left). It is clear that the aim of this behavior is to reduce the surface-to-volume ratio to limit the skin contact with air and thus reduce the heat loss. The scales of temperature, ranging from 10 to 40°C, are the same on the two pictures and clearly show the differences in surface temperature between the two thermal situations.

Behavioral adjustments can support each part of autonomic mechanisms in both strategies for keeping body heat and sustaining high-level thermogenesis activity. The main impact of such adjustment is to reduce the energetic costs of cold-induced physiological responses. Actually, behavioral adjustments during cold exposure consist in a trade-off between acquiring and conserving energy. The increase of ingested food is the best way to increase energy availability, while nest-sharing and basking behaviors are the most useful to save energy (41).

4.1. Strategies to keep body heat

The ability to preserve heat mainly involves behavioral strategies, such as observed in humans (42) and rodents (43). Behavioral adjustments in body posture provide efficient mechanisms to minimize heat loss. Among such strategies, resting in nest, huddling or grouping strategies, using solar radiant heat or Ta increase are efficient ways to decrease the energetic costs of thermoregulation.

4.1.1. Specific postures
4.1.1.1. Ball-like posture

Mammal species use specific energy-conserving postures to limit heat dissipation (Figure 2). Such postures reduce the surface-to-volume ratio to minimize the contact surface with air and thus to reduce the area of heat dissipation. The ball-like posture is particularly useful to reduce this ratio, and is widely used in small mammals. Ball-like postures or hunched sitting position have also been observed in monkeys (44), lemurs (45), rodents (46), seals (47), and are particularly observed during seasonal periods of low Tas or during cold exposure. Another

advantage of ball-like postures is the conservation of lost body heat in the inner part of the ball which contributes to create a microclimate. Such postures can be modulated in response to environmental conditions. For example, Stelzner and Hausfater demonstrated that free-ranging yellow baboons were able to change trunk orientation and posture according to wind direction and air temperature, respectively (48).

4.1.1.2. Basking

Basking has been identified as a way to decrease energetic demand in many species from many orders such as ice rats (49), marsupials (50-54), elephant shrews (55), bats (56), rock hyraxes (57), noki or dassie-rats (58), lemurs (59, 60) and other primates (61). Most examples come from species living in arid or semi-arid habitats. The principle of basking is to transfer solar radiation into heat and then passively warm up the body. Such passive heating can be operated via the exposure of skin surface (especially dark skinned surface) to sunlight, or via increased Ta while being inside a shelter. Basking duration increases with decreased Ta or food availability, pointing out the relationship between such behaviour and energy requirements (45, 61, 62). Torpor arousals in heterotherm species are very costly and passive heating is a very efficient way to reduce the energy costs of organism rewarming (Figure 3). As most experimental protocols were conducted at constant Ta, conclusions on energy benefits were probably underestimated in captive conditions as compared to field ones (55). Nevertheless, radiant heat has a positive impact on animals' thermal energetics as exemplified in captive dunnarts for which the energetic costs of torpor arousal could be decreased by 6 fold when compared to active rewarming (53) or in the
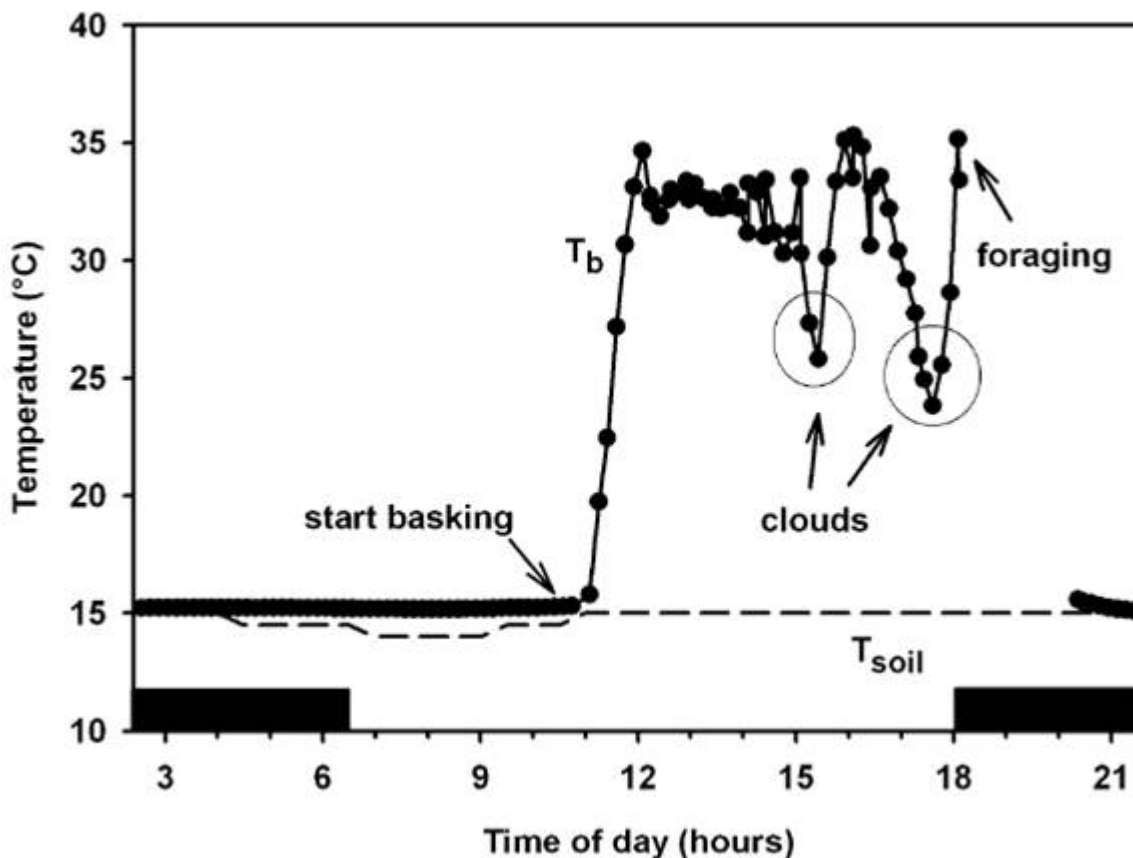
Figure 3. Representation of the impact of basking behavior on the levels of body temperature (Tb) in a marsupial species (from 50). This graph shows that the arousal from the Tb of 15°C started when the dunnart moved out of its shelter and began basking. Consequently, Tb rose to values averaging almost 33°C. Interestingly, clouds decreased the beneficial effects of basking on Tb. Reproduced with permission from Springer.

Gile's planigale exhibiting a reduction of metabolic rate due to basking by more than 50% (63). Although basking initiates torpor arousals, a complete rewarming of the organism requires the enhancement of physiological mechanisms such as shivering and non-shivering thermogenesis (54, 64, 65).

4.1.2. Nest-housing and nest-building
4.1.2.1. Nest-housing

Nesting in a buffered shelter is the most common way to prevent severe cooling and to rest into a protective and stable environment. The role of nest-housing as an anti-predator strategy is also not negligible and could contribute significantly to improve survival in small mammal species (66). Nest-housing has been proposed to be a good alternative to huddling strategy for solitary species (66). Only little is known on the spontaneous choice of Ta in heterotherm species and results remain controversial (11, 32, 67-70). Housing in nests is a strategy that is also used among small-sized primates (71-73). The principle of nest-housing is based on the constitution of a micro-environment which prevents from environmental changes. Thus, the nest characteristics become strongly influenced

by the organism living in. Indeed, the heat lost by the organism is conserved into the nest and contributes to increase the Ta inside the shelter. In addition, evaporative heat loss induces increased humidity into the nest which may soften water loss during resting phases. This characteristic is particularly important during cold and dry episodes, when environmental water is scarce, which becomes a major metabolic constraint.

The choice for a shelter that has good insulation properties is essential for survival in small mammal species (41, 74-77) and the incidence of tree holes properties on the Tc daily rhythms has been already described (77, 78). Indeed, higher energetic costs were recorded in animals sleeping in tree holes with poor insulation properties, i.e. in which high amplitude of Ta variations were recorded. In comparison, resting in trees with thicker walls prevents animals from severe daily variations in Ta, thus limiting energy expenditure. As reported, the main benefit of sleeping in nests is to reduce the energetic costs of thermoregulation (75, 79). For example, the Siberian hamster does not perform hypometabolism when given the possibility to adjust Ta in a thermal gradient (80). The
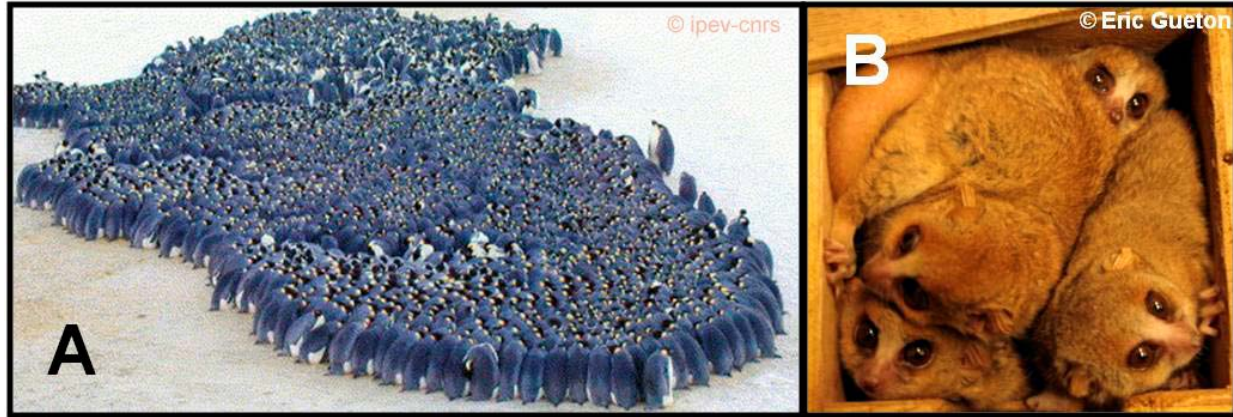
Figure 4. Pictures representative of grouping strategies used to counteract low ambient temperature levels. One of the most famous behaviors to avoid hypothermia during cold exposure is huddling as observed in penguins (A). This strategy is observed in open spaces but can also be performed in shelters and be assimilated to a nest-sharing strategy (B). Both strategies are very common among mammal species to lower the energetic costs of normothermia maintenance but this implies high degrees of tolerance with regard to the closeness between individuals.

importance of shelter choice to optimize the energy savings has been also demonstrated in bats, even during hibernation (81, 82), and in lemur species (78, 83).

4.1.2.2. Nest-building

Animals resting in a shelter can either use an existing nest, that is a nest that which has been deserted by its previous occupant, or build a new nest. Nest-building commonly starts with the finding of a natural shelter (a tree hole for example) that will be specifically improved with the possible use of tools (84). Glaser and Lustick described in 1975 the nest-building strategy in white-footed mice (*Peromyscus leucopus noveboracensis*) observed during cold exposure (75). Nest-building strategy is strongly associated to parental care, the females anticipating birth by providing shelter with insulation capacities to protect their future offspring. Such behavior is observable in mammal species and has been described in sows (85, 86), mice (87), primates (66, 88), rabbits (89)…

4.1.3. Grouping strategies

In this section, we will distinguish two specific strategies: outside grouping behavior that will be called huddling, and inside-nest grouping strategy that will be called nest-sharing. Actually, both can be considered as huddling and are observed in gregarious species. The distinction between the two strategies relies on the occurrence of such behaviors in closed or open spaces in the presence or not of a shelter, respectively.

4.1.3.1. Huddling

Huddling strategy consists in the aggregation of numerous individuals to limit energy dissipation and thus decrease the energetic needs for body heat production. Huddling has been recently reviewed (90) and can be observed in numerous species such as pigs, seals, bats, rabbits, rats, voles, hamsters, mice, marmots, lemurs, monkeys…. The most famous example of huddling individuals is the penguin (Figure 4A). The use of huddling mainly results in a reduced surface-area-to-volume ratio

associated to a drop in thermal conductance. Hence, a microclimate is created between animals that maintain psycho-physiological interactions. Such adjustments have been shown to induce decreased levels of energy expenditure from 6 to 53% (46).

4.1.3.2. Nest-sharing

Nest-sharing (Figure 4B), is particularly useful to reduce the energetic costs of thermogenic mechanisms. In heterotherm species, nest-sharing buffers the effects of cold or food scarcity on torpor expression of each shelter inhabitant. The arousing of the group becomes less demanding in energy, the part of each individual involved in the group arousal being decreased (91). This strategy has been observed in many species such as marsupials (92), mice (28, 92), white-footed mice (93), mouse lemurs (73)…As small mammals, most bats use sheltered day roosts and thus profit energetically from social thermoregulation by mutual warming and warm microclimate in roosting cavities. More, roost temperature has great influence on torpor expression and reproduction (81, 94, 95). Energy saved by social thermoregulation may vary from 7 to up to 50% depending on the group size and on the species (75). Such strategy could be used in solitary species when environmental conditions become harsher, and more particularly during food scarcity periods (96-98). In addition to energetic benefits, nest-sharing behavior has also been recently demonstrated to improve immunological status in a non-human primate species (99).

Grouping behavior implies that individuals must be tolerant to each other to support social aggregation in an enclosed space. Several genetic studies revealed that individuals that congregate were genetically related (96, 100). Nest-sharing and huddling behaviors appear thus as a compromise between different factors including ecological constraints, physiological demands, protection against predators, and relatedness components.
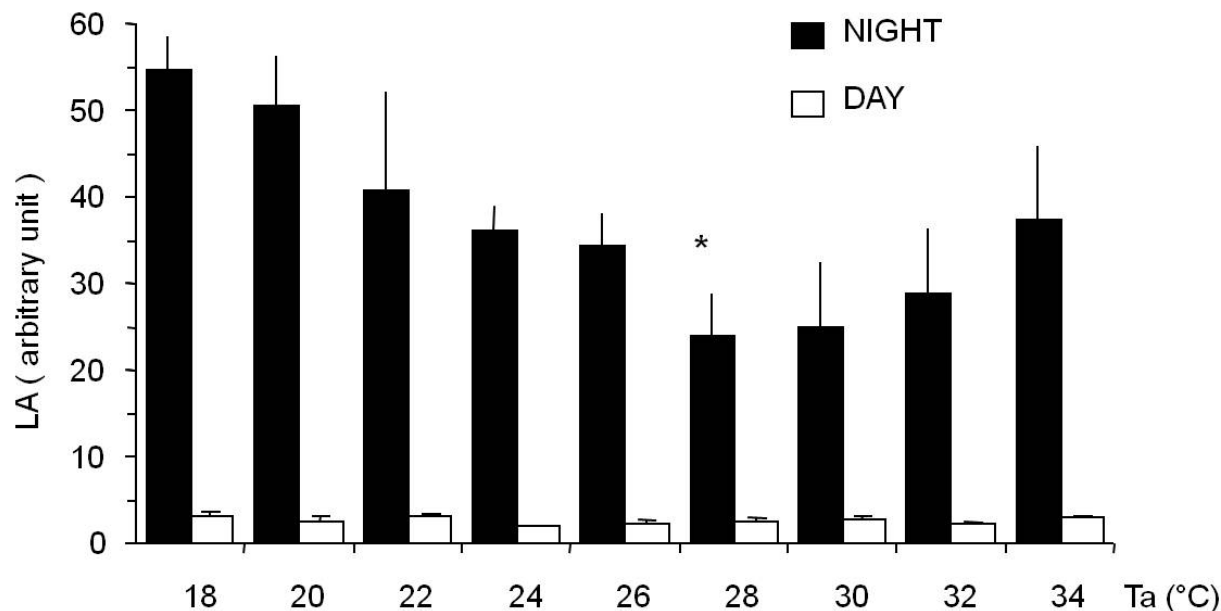
Figure 5. Representation of the ambient temperature dependent changes in locomotor activity in a non-human primate species (from 104). Variations of nocturnal and diurnal locomotor activity (LA, mean/5 min ± SEM, arbitrary unit) in response to ambient temperature varying from 18 °C to 34 °C. * p < 0.05. Reproduced with permission from Springer.

4.2. Strategies to enhance body heat production

The high needs for increased thermogenesis during cold exposure can be behaviorally supported by the enhancement of motor activities and the increase in energy intake.

4.2.1. Increased locomotor activity

Among the available sources of body heat production, muscular work is one of the most efficient. The contribution of muscular activity in thermogenesis responses to mild cold exposure has been already discussed (97, 101). As an example, locomotor activity recorded in a non-human primate exposed to Ta below the TNZ increased significantly and especially during the resting period (Figure 5 – (102-104)). Such changes in activity/rest rhythms were also evidenced in hamsters, in which high levels of locomotor activity during cold exposure were dependent of the motivational context (105). However, even though muscular work constitutes a huge source of body heat, it is very costly and needs to be constantly fuelled with high levels of energy intake.

4.2.2 Increased energy intake

To fuel the increased needs in energy and maintain a positive energy balance during cold exposure, animals need to adapt their food intake behaviour in consequence. Many years ago, food has been proposed to take part in temperature regulation (106). Actually, increase in caloric intake has been widely described in many species, adults or juveniles, to counteract cold-induced costs of thermoregulation (103, 107-110). In response to cold exposure, catabolic mechanisms are enhanced, promoting energy intake and energy expenditure. A specific endocrine signalling involving orexigenic hormones is triggered, increasing caloric intake (111). As

an indirect consequence of increased food intake, body heat derivated from food digestion is produced and represents 5-15% of total energy expenditure (112). The magnitude of the post-prandial thermogenic effect is assumed to average 10% of the ingested calories over a given time period, though the effect substantially varies according to food composition and the cost devoted to food seeking behaviour.

5. HYPERTHERMIA AVOIDANCE

Hyperthermia may occur from two different processes, one depending on the organism (i.e. fever), and the other depending on environmental factors. Increase in Tc during fever is due to a change in Tc set point, a physiological mechanism known to improve immune system defense. Fever occurrence after pyrogen administration reflects both increase in oxygen consumption and reduction of heat loss (113). More, to optimize immune response, selected Ta by organisms would be biased towards warm Ta, as demonstrated in rats (22). However, when fever is associated with inflammation, cold-seeking behaviors were evidenced in rats (114).

Hyperthermia following a heat stress causes deleterious effects on metabolism and water loss and may lead to potential cellular damages in the central nervous system. When exposed to extreme heat, animals have to move to cooler places (housing in buffered shelters, thermal refuge in a burrow, immersion in water) and/or to promote heat dissipation through adaptive behaviors (115-117). Such behaviors are driven by the pre-optic and anterior hypothalamus (4) and are underlined by the dopamine system (114). Indeed, when the dopamine system is inactivated, mice do not exhibit escape behaviour in

response to elevated Ta (118). From experimental studies on heatstroke, behavioural thermoregulation to prevent hyperthermia was achieved by selection of cool Ta (119). Fluid intake to ensure sufficient hydration and to avoid water stress is well documented in animals exposed to heat environment (115-119).

5.1. Strategies to dissipate body heat
5.1.1. Habitat selection and specific postures.
Most mammals avoid the heat of their environment during the hours of the day by retreating in shaded cooler places. Nocturnal small species, especially those inhabiting arid or semi-arid ecosystems, decrease their energy and water expenditure by spending day time in a thermal refuge, burrow or tree hole (66, 120). The retreat in a burrow can consistently reduce body temperature by 1 to 2 degrees as exemplified in the ground squirrel (121). Moreover, in diurnal species changes in daily activity have been observed to face extreme or hot conditions, (122).

Only a few postures are available for mammal species to promote body heat loss. Behavioral posture strategies mainly consist in increasing the surface-area ratio or the gradient between the organism and the air to promote the conductive heat exchanges between the warm skin and the air. Within these strategies, exposition to wind, prone position, posting on rocks are regularly observed during the warm season in many species. The heat dissipation has been clearly demonstrated to be dependent on mammal fur characteristics: with less than 1000 hairs/cm², a 14-km/h wind may penetrate deep into the fur, while at a greater fur density, even a 32-km/h wind penetrates little into the fur (120). Haired species exhibit thus difficulties to dissipate excess body heat. More, the main part of body heat dissipation comes from sweat through evaporative water loss which remains extremely limited to peripheral regions such as nose, ears, hands and feet in furred species (123). In rodents, the role of tail has been stressed as an effective heat loss process, involving the sympathic fibers regulating tail blood flow (121, 124).

One famous behavior for promoting heat loss and Tc regulation is ear movements in elephants (102, 103). The ears are highly vascularized and muscular movements improve the convection on ears surface. African species have larger ears than Indian ones and this size difference would be related to higher Ta between the two continents (123), requiring higher heat dissipation in African species. However, owing to the difference in body mass between the two species, the heat dissipation might be less challenging for Indian species.

5.1.2. Panting
The increase in respiratory rhythm frequency via panting contributes to dissipate huge amounts of body heat induced by water loss (125). This mechanism is a good alternative to sweating in small mammal species and is particularly observed in dogs (126), but also in sheeps (127). Panting mechanism is related to thermosensitivity and integration by the hypothalamus (109). In addition, this pathway to dissipate excess body heat has been identified to be particularly efficient to cool the brain. This process

has been observed in many mammalian species, but not in humans.

5.2. Strategies to decrease body heat production
During hyperthermia risk, a decrease in body heat production can be behaviorally achieved via the reduction of energy intake and motor activities, inversely to what observed to enhance heat production.

5.2.1. Decreased energy intake
Exposure to high Tas has been already described to be a potential modulator of energy intake (106, 110, 128-130). Because heat exposure induces reduced energetic costs, needs for caloric intake are reduced. Besides, energy intake is source of heat generating, meaning that an accurate adaptation to high Ta would be to decrease energy intake. Such behavior has been observed in piglets (128, 131). Anorexigenic pathways are actually activated, inducing catabolic reactions to decrease energy intake (111).

5.2.2. Decreased locomotor activity
Decreased levels of physical activity in response to elevated Ta, such as observed in rats (132), should be the most appropriate response to limit hyperthermia risk. However, the reduction of motor activities is not systematically observed (115), owing to the complex control of locomotor activity patterns. Lastly, the stress induced by heat exposure probably induces severe physiological disturbances that could impede animals to trigger accurate behavioral adjustments.

6. FACTORS AFFECTING BEHAVIORAL THERMOREGULATION

Thermoregulation is a key function in homeostasis maintenance and is controlled by central, metabolic, energetic and endocrine systems. Some characteristics such as body mass and body geometry through their relation to basal metabolic rate (133, 134) but also more subtle morphological parameters such as fur color (44), can affect the use of behavioral adjustments. Thermoregulatory capacities play a determinant adaptive role to survive in an environment when resources and Ta vary. This implies that local conditions, season, gender and aging may have major effects on the display of thermoregulatory behaviors and their frequency.

6.1. Season
Thermoregulatory capacities are highly dependent on seasonal changes (116, 135-138) and refer to seasonal changes in body composition, thermal conductance and hormonal status. According to season-dependent effects on autonomic thermoregulation, behavioral adjustments and their efficiency were described in many species to vary along seasons (49, 60, 73, 139). For example, the Golden Hamster exhibits preference for Ta averaging 8°C in pre-hibernating state, but a preference for Ta over 24°C in the post-hibernating period (12). In bats, thermal preferences and group size also vary with the season (81, 94, 140). Likely, thermoregulatory behaviors such as selection of Ta and nest-sharing seasonally differ in
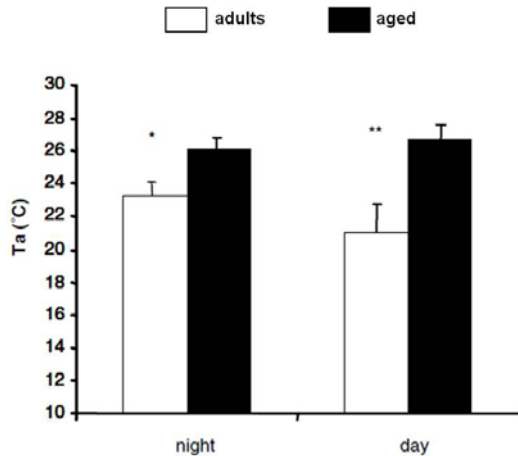
Figure 6. Effect of aging on the spontaneous selection of ambient temperature (Ta) in a non-human primate species (from 37). Aging induced selection of higher levels of Ta during both night and day periods in a nocturnal primate species (*Microcebus murinus*) experimented in a thermal gradient. Reproduced with permission from Elsevier.

the mouse lemur, evidencing that cold-induced behavioral adjustments during winter are switched to heat-induced strategies during summer (37).

6.2. Gender

Gender is today well known to affect thermoregulatory capacities (12, 13). Effects of gender on behavioral adjustments have been described in various species such as rodents and primates (44, 96, 141). In female rodents that exhibit greater capacities for cold-induced heat production (142, 143), gender has been proposed to interfere with vasomotor capacities rather than with heat production feature (144). Females would particularly promote Tc stability as compared to males in regards to the trade-off between energy required for thermoregulation and energy allocated to their reproductive fitness. Indeed, energetic constraints during the breeding period rely on energy allocation for offspring growth and parental care. Females would thus promote behavioral thermoregulation and thereby maintain low levels of energy expenditure. In field conditions, female mouse lemurs use torpor to a greater extent than males do (96, 141, 145) and congregate in larger groups with greater insulation properties comparatively to males (77). Likely, female bats change their thermoregulatory behavior to optimize the juvenile development by selecting warm places in order to limit torpor occurrence (95, 146).

6.3. Aging

Numerous epidemiological studies describe increased prevalence of death in the elderly from hypo- or hyperthermia (147-151), suggesting that thermoregulation, as well as other biological functions, is impaired with age. Indeed, among deleterious effects of age on autonomic thermoregulation can be listed impaired vasomotor capacities (4, 152-160), which strongly disturb the interaction between the organism and the changing environment. During cold exposure, data show that physiological capacities for producing body heat are decreased with age (161-168). In addition, evaporative heat loss capacity has been shown to decline during aging (8, 169) and could participate to increase the risk of dehydration during heat exposure (4).

Regarding the effects of aging on autonomic thermoregulatory capacities, the needs for behavioral adjustments become greater with age to counter physiological deficiencies, especially during harsh environmental conditions. Recent studies in a non-human primate species (Figure 6) demonstrated that aging induced greater use of behavioral adjustments in aged animals as compared to adults (37). These results confirmed that behavioral thermoregulation is very useful to limit the energetic costs of normothermia maintenance and might be beneficial to counteract the negative energy balance evidenced during cold exposure (170, 171). This association between behavioral adjustments and metabolic requirements has also been demonstrated in rodents (5, 172). Such data may reflect that aging is associated with decreased levels of sex steroids (173, 174), these hormones participating to thermogenesis mechanisms.

However, impaired behavioral adjustments in response to Ta challenges have been evidenced in humans (7), partly due to decreased sensitivity for thermal changes leading to inappropriate adjustments of Ta. Indeed, the decline in thermo-sensitivity described in the elderly (4, 7, 156, 175, 176) could contribute to delay the detection of Ta variations, and consequently delay the appropriate operating adjustments (4, 9, 153). Moreover, aging has been associated with impaired capacities for regulating the indoor Ta when given the possibility to adjust Ta in response to thermal changes (9), which could be related to decreased cognitive performances as already demonstrated in non-human primate species (177, 178). Although the subjective thermal comfort zone does not seem to be changed with age (4), the accuracy of the control of Tc variations, which is operated by the hypothalamus (2, 3, 179, 180), could be defective in aged individuals and lead to abnormal Tc values during cold or high events. Central impairments (4) are potential sources to explaining the age-related deteriorations observed in behavioral thermoregulation capacities. For example, aging impairs cold-induced increase in locomotor activity levels (163). During heat exposure, dehydration is a consequence of reduced thirst sensation and lack of fluid intake to restore a positive water balance in old rats (181), as well as in elderly people (182). Finally, aging could be characterized by a disruption in the overlap between TNZ and thermo-preferendum described in adult individuals. For example, aged mouse lemurs showed greater preference for warm Tas as compared to adults (37), but this behaviour could not reach the energy/water requirements for homeostasis maintenance, thus threatening survival.

7. CONCLUSIONS

The first aim of this review was to give an overall catalogue of all the behavioral processes used by

mammals to counteract thermal challenges. To date, there were only specific reviews on each adjustment available, but none summarizing all the strategies known.

The diversity of thermoregulatory behaviors becomes larger when extending the considerations to whole animal reign, as metabolic reactions only depends on Ta management in ectothermic species.

Thermoregulatory behaviors are primarily used to reduce the energetic costs of autonomic thermoregulation and to adjust Ta to the thermal comfort zone of the animals. However, we can notice that behavioral strategies, such as nest-housing or huddling, have also been proposed to have beneficial effects on longevity (183, 184). These strategies would be beneficial only in extreme environmental conditions, i.e. during severe cold or food scarcity periods, and their role on longevity could be reduced as compared to the anti-predation or social transmission of information benefits (185).

Behavioral adjustments towards increased Tas are only few as compared to cold-induced behavioral responses, increasing the risk of deleterious effects during heat episodes, *a fortiori* with age. Such failure to behaviorally avoid hyperthermia and dehydration would be at the origin of high prevalence of deaths during heat wave episodes as recorded in US or in Europe in 2003.

The use for thermoregulatory behaviors depends on organism needs and is complementary to autonomic responses. Hence, gender, season and aging are parameters that strongly interfere with behavior occurrence and can modify their efficiency. Thus, because of the importance of behavioral adjustments on energy balance maintenance, greater attention should be paid to thermoregulatory behaviors in the understanding of overall thermoregulation function. Finally, if climate changes (global warming and current upward trend in heat wave incidence) and anthropic constraints continue, behavioral studies have to be a necessary component for conservation ecologists to preserve the key elements of habitats required for efficient expression of thermoregulatory behaviors within small mammalian species, especially those with low thermoregulation flexibility.

8. REFERENCES

1. A. W. Crompton, C. R. Taylor and J. A. Jagger: Evolution of homeothermy in mammals. *Nature*, 272(5651), 333-6 (1978)

2. G. L. Florant and H. C. Heller: CNS regulation of body temperature in euthermic and hibernating marmots (*Marmota flaviventris*). *American Journal of Physiology-Regulatory Integrative and Comparative Physiology*, 232(5), R203-8 (1977)

3. H. C. Heller and H. T. Hammel: CNS control of body temperature during hibernation. *Comparative Biochemistry and Physiology. A, Comparative Physiology*, 41(2), 349-59 (1972)

4. E. J. Van Someren, R. J. Raymann, E. J. Scherder, H. A. Daanen and D. F. Swaab: Circadian and age-related modulation of thermoreception and temperature regulation: mechanisms and functional implications. *Ageing Research Reviews*, 1(4), 721-78 (2002)

5. C. J. Gordon: Relationship between autonomic and behavioral thermoregulation in the mouse. *Physiology & behavior*, 34(5), 687-90 (1985)

6. C. J. Gordon: Relationship between behavioral and autonomic thermoregulation in the guinea pig. *Physiology & behavior*, 38(6), 827-31 (1986)

7. N. A. Taylor, N. K. Allsopp and D. G. Parkes: Preferred room temperature of young vs aged males: the influence of thermal sensation, thermal comfort, and affect. *Journal of Gerontology. Series A, Biological Sciences and Medical Sciences*, 50(4), M216-21 (1995)

8. K. J. Collins and A. N. Exton-Smith: 1983 Henderson Award Lecture. Thermal homeostasis in old age. *Journal of the American Geriatrics Society*, 31(9), 519-24 (1983)

9. K. J. Collins: Thermal comfort and hypothermia. *Royal Society of Health journal*, 101(1), 16-8 (1981)

10. K. J. Collins, A. N. Exton-Smith and C. Dore: Urban hypothermia: preferred temperature and thermal perception in old age. *British Medical Journal (Clinical Research Edition)*, 282(6259), 175-7 (1981)

11. M. R. Gumma and F. E. South: Hypothermia and behavioral thermoregulatory temperature preference. *Cryobiology*, 3(5), 363-& (1967)

12. H. Kaciuba-Uscilko and R. Grucza: Gender differences in thermoregulation. *Current opinion in clinical nutrition and metabolic care*, 4(6), 533-6 (2001)

13. M. Lopez, D. I. Sessler, K. Walter, T. Emerick and M. Ozaki: Rate and gender dependance of the sweating, vasoconstriction, and shivering thresholds in humans. *Anesthesiology*, 80(4), 780-788 (1994)

14. R. Refinetti and S. M. Horvath: Thermopreferendum of the rat - Inter-subject and intra-subject variabilities. *Behavioral and Neural Biology*, 52(1), 87-94 (1989)

15. A. A. Romanovsky, A. I. Ivanov and Y. P. Shimansky: Selected contribution: ambient temperature for experiments in rats: a new method for determining the zone of thermal neutrality. *Journal of Applied Physiology*, 92(6), 2667-79 (2002)

16. M. Jefimow, M. S. Wojciechowski and E. Tegowska: Effects of prolonged acclimation to intermediate photoperiod and photo-schedule reversal in photosensitive golden hamsters. *Journal of Experimental Zoology. Part A, Comparative Experimental Biology*, 303(11), 987-97 (2005)

17. M. Jefimow, M. Wojciechowski and E. Tegowska: Seasonal changes in the thermoregulation of laboratory golden hamsters during acclimation to seminatural outdoor conditions. *Comparative Biochemistry and Physiology. Part A, Molecular and Integrative Physiology*, 139(3), 379-88 (2004)

18. R. Refinetti: Body temperature and behavior of golden-hamsters (*Mesocricetus-auratus*) and ground-squirrels (*Spermophilus-tridecemlineatus*) in a thermal gradient. *Journal of Comparative Physiology a-Sensory Neural and Behavioral Physiology*, 177(6), 701-705 (1995)

19. M. Jefimow: Effects of summer- and winter-like acclimation on the thermoregulatory behavior of fed and fasted desert hamsters, *Phodopus roborovskii. Journal of Thermal Biology*, 32(4), 212-219 (2007) doi:10.1016/j.jtherbio.2007.01.002

20. S. Sakurada, O. Shido, N. Sugimoto, Y. Hiratsuka, T. Yoda and K. Kanosue: Autonomic and behavioural thermoregulation in starved rats. *Journal of Physiology*, 526 Pt 2, 417-24 (2000)

21. M. Florez-Duquet, E. Peloso and E. Satinoff: Fever and behavioral thermoregulation in young and old rats. *American Journal of Physiology-Regulatory Integrative and Comparative Physiology*, 280(5), R1457-61 (2001)

22. E. Briese: Selected temperature correlates with intensity of fever in rats. *Physiology & Behavior*, 61(5), 659-660 (1997)

23. M. Bodurka, M. Caputa and J. Bodurka: A comparison of febrile responses induced by LPS from *E-coli* and *S-abortus* in unrestrained rats placed in a thermal gradient. *Journal of Physiology & Pharmacology*, 48(1), 81-88 (1997)

24. W. J. Farrell and J. R. Alberts: Rat behavioral thermoregulation integrates with nonshivering thermogenesis during postnatal development. *Behavioral Neuroscience*, 121(6), 1333-1341 (2007) doi:10.1037/0735-7044.121.6.1333

25. H. Tanaka, M. Yasumatsu and H. Hasegawa: Changes in selected ambient temperatures following physical training in rats. *Japanese Journal of Physiology*, 53(4), 309-312 (2003)

26. O. Shido, S. Sakurada, N. Sugimoto, F. Furuyama and T. Nagasaka: Thermoeffector thresholds and preferred ambient temperatures of the FOK rat. *American Journal of Physiology-Regulatory Integrative and Comparative Physiology*, 274(3), R604-R609 (1998)

27. C. J. Gordon: Relationship between preferred ambient-temperature and autonomic thermoregulatory function in rat. *American Journal of Physiology*, 252(6), R1130-R1137 (1987)

28. C. J. Gordon, P. Becker and J. S. Ali: Behavioral thermoregulatory responses of single- and group-housed mice. *Physiology & Behavior*, 65(2), 255-62 (1998)

29. R. Refinetti: Body temperature and behavior of tree shrews and flying squirrels in a thermal gradient. *Physiology & Behavior*, 63(4), 517-520 (1998)

30. R. Refinetti: Rhythms of body temperature and temperature selection are out of phase in a diurnal rodent, *Octodon degus. Physiology & Behavior*, 60(3), 959-61 (1996)

31. X. Song, G. Kortner and F. Geiser: Temperature selection and use of torpor by the marsupial *Sminthopsis macroura. Physiology & Behavior*, 64(5), 675-82 (1998)

32. C. R. Brown and R. T. F. Bernard: Thermal preference of Schreiber long-fingered (*Miniopterus-schreiberisi*) and cape-horseschoe (*Rhinolophus-capensis*) bats. *Comparative Biochemistry and Physiology. A, Comparative Physiology*, 107(3), 439-449 (1994)

33. D. L. Levesque and G. J. Tattersall: Seasonal changes in thermoregulatory responses to hypoxia in the Eastern chipmunk (*Tamias striatus*). *Journal of Experimental Biology*, 212(12), 1801-1810 (2009) doi:10.1242/jeb.027094

34. M. R. Banta: Merriam's kangaroo rats (*Dipodomys merriami*) voluntarily select temperatures that conserve energy rather than water. *Physiological & Biochemical Zoology*, 76(4), 522-532 (2003)

35. N. Sugimoto, S. Sakurada and O. Shido: Selected ambient temperatures of rats acclimated to heat given on various schedules. *Pflugers Archiv-European Journal of Physiology*, 438(6), 766-770 (1999)

36. R. Buffenstein, N. T. Urison, R. Woodley, L. A. VanderWesthuizen and J. Jarvis: Temperature changes during pregnancy in the subterranean naked mole-rat (*Heterocephalus glaber*); The role of altered body composition and basking behaviour. *Mammalia*, 60(4), 619-628 (1996)

37. F. Aujard, M. Seguy, J. Terrien, R. Botalla, S. Blanc and M. Perret: Behavioral thermoregulation in a non human primate: effects of age and photoperiod on temperature selection. *Experimental Gerontology*, 41(8), 784-92 (2006)

38. M. Jefimow, M. Wojciechowski and E. Tegowska: Daily variations in the influence of noradrenaline on preferred ambient temperature of the Siberian hamster. *Comparative Biochemistry and Physiology. Part A, Molecular and Integrative Physiology*, 134(4), 717-26 (2003)

39. J. A. Shoemaker and R. Refinetti: Day-night difference in the preferred ambient temperature of human subjects. *Physiology & behavior*, 59(4-5), 1001-3 (1996)

40. B. Ray, H. N. Mallick and V. M. Kumar: Changes in thermal preference, sleep-wakefulness, body temperature and locomotor activity of rats during continuous recording for 24 hours. *Behavioural brain research*, 154(2), 519-26 (2004)

41. L. A. Schultz, G. Collier and D. F. Johnson: Behavioral strategies in the cold: Effects of feeding and nesting costs. *Physiology & Behavior*, 67(1), 107-115 (1999)

42. M. A. MacKenzie, A. R. Hermus, H. C. Wollersheim, G. F. Pieters, A. G. Smals, R. A. Binkhorst, T. Thien and P. W. Kloppenborg: Poikilothermia in man: pathophysiology and clinical implications. *Medicine*, 70(4), 257-68 (1991)

43. M. I. Talan, H. M. Tatelman and B. T. Engel: Cold tolerance and metabolic heat production in male C57BL/6J mice at different times of day. *Physiology & Behavior*, 50(3), 613-6 (1991)

44. J. C. Bicca-Marques and C. Calegaro-Marques: Behavioral thermoregulation in a sexually and developmentally dichromatic neotropical primate, the black-and-gold howling monkey (*Alouatta caraya*). *American Journal of Physical Anthropology*, 106(4), 533-546 (1998)

45. H. S. Morland: Seasonal behavioral variation and its relationship to thermoregulation in ruffed lemurs (*Varecia variegata variegata*). Plenum Press Div Plenum Publishing Corp, New York (1993)

46. C. Moinard, C. P. Doncaster and H. Barre: Indirect calorimetry measurments on behavioral thermoregulation in a semiaquatic social rodent, *Myocastor coypus*. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 70(5), 907-911 (1992)

47. R. L. Gentry: Thermoregulatory behavior of eared seals. *Behaviour*, 46, 73-& (1973)

48. J. K. Stelzner and G. Hausfater: Posture, microclimate, and thermoregulation in yellow baboons. *Primates*, 27(4), 449-463 (1986)

49. U. Schwaibold and N. Pillay: Behavioral strategies of the African ice rat *Otomys sloggetti robertsi* in the cold. *Physiology & Behavior*, 88(4-5), 567-74 (2006)

50. L. Warnecke, J. M. Turner and F. Geiser: Torpor and basking in a small arid zone marsupial. *Naturwissenschaften*, 95(1), 73-8 (2008)

51. G. Kortner and F. Geiser: The key to winter survival: daily torpor in a small arid-zone marsupial. *Naturwissenschaften*, 96(4), 525-30 (2009)

52. F. Geiser, N. Goodship and C. R. Pavey: Was basking important in the evolution of mammalian endothermy? *Naturwissenschaften*, 89(9), 412-4 (2002)

53. F. Geiser and R. L. Drury: Radiant heat affects thermoregulation and energy expenditure during rewarming from torpor. *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology*, 173(1), 55-60 (2003) doi:10.1007/s00360-002-0311-y

54. G. Lovegrove, G. Kortner and F. Geiser: The energetic cost of arousal from torpor in the marsupial *Sminthopsis macroura*: benefits of summer ambient temperature cycles. *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology*, 169(1), 11-8 (1999)

55. N. Mzilikazi, B. G. Lovegrove and D. O. Ribble: Exogenous passive heating during torpor arousal in free-ranging rock elephant shrews, *Elephantulus myurus*. *Oecologia*, 133(3), 307-314 (2002) doi:10.1007/s00422-002-1052-z

56. T. A. Vaughan: Behavioral thermoregulation in the African yellow-winged bat. *Journal of Mammalogy*, 68(2), 376-378 (1987)

57. K. J. Brown and C. T. Downs: Basking behaviour in the rock hyrax (*Procavia capensis*) during winter. *African Zoology*, 42(1), 70-79 (2007)

58. G. B. Rathbun and C. D. Rathbun: Sheltering, basking, and petrophily in the noki or dassie-rat (*Petromus typicus*) in Namibia. *Mammalia*, 70(3-4), 269-275 (2006) doi:10.1515/mamm.2006.038

59. K. H. Dausmann, J. U. Ganzhorn and G. Heldmaier: Body temperature and metabolic rate of a hibernating primate in Madagascar: Preliminary results from a field study. In: *Life in the Cold*. Ed G. Heldmaier&M. Klingenspor. Springer-Verlag Berlin, Berlin (2000)

60. H. S. Morland: Seasonal variation in the social structure of wild ruffed lemurs (*Varecia variegata*). *American Journal of Physical Anthropology*, 81(2), 272-272 (1990)

61. G. Hanya, M. Kiyono and S. Hayaishi: Behavioral thermoregulation of wild Japanese macaques: comparisons between two subpopulations. *American Journal of Primatology*, 69(7), 802-15 (2007) doi:10.1002/ajp.20397

62. L. Warnecke, E. Schleucher and F. Geiser: Basking behaviour in relation to energy use and food availability in one of the smallest marsupials. *Physiology & Behavior* (2010) doi:S0031-9384(10)00258-1 [pii]

10.1016/j.physbeh.2010.07.003

63. L. Warnecke and F. Geiser: The energetics of basking behaviour and torpor in a small marsupial exposed to simulated natural conditions. *J Comp Physiol B*, 180(3), 437-45 (2010) doi:10.1007/s00360-009-0417-6

64. S. Ortmann, J. Schmid, J. U. Ganzhorn and G. Heldmaier: Body temperature and torpor in a Malagasy small primate, the mouse lemur. In: *Adapatations to the cold: Tenth International Hibernation Symposium*. Ed F. Geiser. University of England Press, Armidale (1996)

65. J. Schmid: Oxygen consumption and torpor in mouse lemurs (*Mircocebus murinus* and *M. myoxinus*): preliminary results of a study in western Madagascar. In: *Adapatations to the cold: Tenth International Hibernation Symposium*. Ed F. Geiser. University of New England Press, Armidale (1996)

66. P. M. Kappeler: Nests, tree holes, and the evolution of primate life histories. *American Journal of Primatology*, 46(1), 7-33 (1998)

67. A. R. French: Selection of high-temperatures for hibernation by pocket mouse, *Perognathus-longimembris* - Ecological advantages and energetic consequences. *Ecology*, 57(1), 185-191 (1976)

68. M. R. Gumma, F. E. South and J. N. Allen: Temperature preference in Golden hamsters. *Animal Behaviour*, 15(4), 534-& (1967)

69. A. Nagel and R. Nagel: How do bats choose optimal temperatures for hibernation. *Comparative Biochemistry and Physiology. A, Comparative Physiology*, 99(3), 323-326 (1991)

70. P. I. Webb, J. R. Speakman and P. A. Racey: How hot is a hibernaculum? A review of the temperatures at which bats hibernate. *Canadian Journal of Zoology*, 74(4), 761-765 (1996)

71. E. F. Muller: Basal metabolic rates in Primates - The possible role of phylogenetic and ecological factors. *Comparative Biochemistry and Physiology. A, Comparative Physiology*, 81(4), 707-711 (1985)

72. C. M. Knox and P. G. Wright: Thermoregulation and energy-metabolism in the lesser bushbaby, *Galago-galago-senegalensis-moholi*. *South African Journal of Zoology*, 24(2), 89-94 (1989)

73. M. Perret: Energetic advantage of nest-sharing in a solitary primate, the lesser mouse lemur (*Microcebus murinus*). *Journal of Mammalogy*, 79(4), 1093-1102 (1998)

74. W. Arnold, G. Heldmaier, S. Ortmann, H. Pohl, T. Ruf and S. Steinlechner: Ambient -temperatures in hibernacula and their energetic consequences for alpine marmots (*Marmota marmota*). *Journal of Thermal Biology*, 16(4), 223-226 (1991)

75. H. Glaser and S. Lustick: Energetics and nesting-behavior of northern white-footed mouse, *Peromyscus leucopus-noveboracensis*. *Physiological Zoology*, 48(2), 105-113 (1975)

76. S. K. Maloney, G. N. Bronner and R. Buffenstein: Thermoregulation in the Angolan free-tailed bat *Mops condylurus*: A small mammal that uses hot roosts. *Physiological & Biochemical Zoology*, 72(4), 385-396 (1999)

77. J. Schmid: Tree holes used for resting by gray mouse lemurs (*Microcebus murinus*) in Madagascar: Insulation capacities and energetic consequences. *International Journal of Primatology*, 19(5), 797-809 (1998)

78. K. H. Dausmann, J. Glos and G. Heldmaier: Energetics of tropical hibernation. *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology*, 179(3), 345-57 (2009)

79. F. D. Vogt and G. R. Lynch: Influence of ambient-temperature, nest availability, huddling, and daily torpor on energy-expenditure in the white-footed mouse *Peromyscus leucopus*. *Physiological Zoology*, 55(1), 56-63 (1982)

80. M. S. Wojciechowski and M. Jefimow: Is torpor only an advantage? Effect of thermal environment on torpor use in the Siberian hamsters (*Phodopus sungorus*). *Journal of Physiology & Pharmacology*, 57 Suppl 8, 83-92 (2006)

81. G. Kerth, K. Weissmann and B. Konig: Day roost selection in female Bechstein's bats (*Myotis bechsteinii*): a field experiment to determine the influence of roost temperature. *Oecologia*, 126(1), 1-9 (2001)

82. J. G. Boyles, J. J. Storm and V. Brack: Thermal benefits of clustering during hibernation: a field test of competing hypotheses on *Myotis sodalis*. *Functional Ecology*, 22(4), 632-636 (2008) doi:10.1111/j.1365-2435.2008.01423.x

83. K. H. Dausmann, J. Glos, J. U. Ganzhorn and G. Heldmaier: Physiology: hibernation in a tropical primate. *Nature*, 429(6994), 825-6 (2004)

84. M. Hansell and G. D. Ruxton: Setting tool use within the context of animal construction behaviour. *Trends in Ecology & Evolution*, 23(2), 73-78 (2008) doi:10.1016/j.tree.2007.10.006

85. D. Wischner, N. Kemper and J. Krieter: Nest-building behaviour in sows and consequences for pig husbandry. *Livestock Science*, 124(1-3), 1-8 (2009) doi:10.1016/j.livsci.2009.01.015

86. B. Algers and K. Uvnas-Moberg: Matemal behavior in pigs. *Hormones & Behavior*, 52(1), 78-85 (2007) doi:10.1016/j.yhbeh.2007.03.022

87. E. M. Weber and I. A. S. Olsson: Maternal behaviour in *Mus musculus sp.*: An ethological review. *Applied Animal Behaviour Science*, 114(1-2), 1-22 (2008) doi:10.1016/j.applanim.2008.06.006

88. J. R. Anderson: Sleep-related behavioural adaptations in free-ranging anthropoid primates. *Sleep Medicine Reviews*, 4(4), 355-373 (2000)

89. K. L. Hoffman and R. I. R. Morales: Toward an understanding of the neurobiology of "just right" perceptions: Nest building in the female rabbit as a possible model for compulsive behavior and the perception of task completion. *Behavioural Brain Research*, 204(1), 182-191 (2009) doi:10.1016/j.bbr.2009.06.010

90. C. Gilbert, D. McCafferty, Y. Le Maho, J. M. Martrette, S. Giroud, S. Blanc and A. Ancel: One for all and all for

one: the energetic benefits of huddling in endotherms. *Biological Reviews of the Cambridge Philosophical Society* (2010)

91. L. A. Ebensperger: A review of the evolutionary causes of rodent group-living. *Acta Theriologica*, 46(2), 115-144 (2001)

92. S. R. Morton: Torpor and nest-sharing in free-living *Sminthopsis crassicaudata* (Marsupialia) and *Mus musculus* (Rodentia). *Journal of Mammalogy*, 59(3), 569-575 (1978)

93. F. D. Vogt and P. Kakooza: The influence of nest-sharing on the expression of daily torpor in the White-footed mouse. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 71(7), 1297-1302 (1993)

94. I. Pretzlaff, G. Kerth and K. H. Dausmann: Communally breeding bats use physiological and behavioural adjustments to optimise daily energy expenditure. *Naturwissenschaften*, 97(4), 353-363 (2010) doi:10.1007/s00114-010-0647-1

95. M. Dietz and E. K. Kalko: Seasonal changes in daily torpor patterns of free-ranging female and male Daubenton's bats (*Myotis daubentonii*). *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology*, 176(3), 223-31 (2006)

96. U. Radespiel, Z. Sarikaya, E. Zimmermann and M. W. Bruford: Sociogenetic structure in a free-living nocturnal primate population: sex-specific differences in the grey mouse lemur (*Microcebus murinus*). *Behavioral Ecology & Sociobiology*, 50(6), 493-502 (2001)

97. M. J. Dauncey: Activity and energy expenditure. *Canadian Journal of Physiology & Pharmacology*, 68(1), 17-27 (1990)

98. A. Haim: Behavior patterns of cold-resistant golden spiny mouse *Acomys russatus*. *Physiology & Behavior*, 50(3), 641-643 (1991)

99. F. Aujard and M. Perret: Health status and nesting pattern in male gray mouse lemurs (*Microcebus murinus*). *Revue D Ecologie-La Terre Et La Vie*, 64(3), 197-205 (2009)

100. E. Pages-Feuillade: Modalités de l'occupation de l'espace et relations interindividuelles chez un prosimien nocturne malgache (*Microcebus murinus*). *Folia Primatologica*, 50, 204-220 (1988)

101. D. Brown, G. Livesey and M. J. Dauncey: Influence of mild cold on the components of 24 hour thermogenesis in rats. *Journal of Physiology*, 441, 137-54 (1991)

102. P. G. Wright: Why do elephants flap their ears? *South African Journal of Zoology*, 19(4), 266-269 (1984)

103. P. K. Phillips and J. E. Heath: Heat loss in Dumbo: a theoretical approach. *Journal of Thermal Biology*, 26(2), 117-120 (2001)

104. F. Aujard and F. Vasseur: Effect of ambient temperature on the body temperature rhythm of male gray mouse lemurs (*Microcebus murinus*). *International Journal of Primatology*, 22(1), 43-56 (2001)

105. N. Mrosovsky and S. M. Biello: Nonphotic phase-shifting in the old and the cold. *Chronobiology International*, 11(4), 232-252 (1994)

106. J. R. Brobeck: Food intake as a mechanism of temperature regulation. *Yale Journal of Biology & Medicine*, 20(6), 545-552 (1948)

107. A. S. Kauffman, A. Cabrera and I. Zucker: Energy intake and fur in summer- and winter-acclimated Siberian hamsters (*Phodopus sungorus*). *American Journal of Physiology-Regulatory Integrative and Comparative Physiology*, 281(2), R519-R527 (2001)

108. M. J. Paul, C. Tuthill, A. S. Kauffman and I. Zucker: Pelage insulation, litter size, and ambient temperature impact maternal energy intake and offspring development during lactation. *Physiology & Behavior*, 100(2), 128-134 (2010) doi:10.1016/j.physbeh.2010.02.012

109. J. T. Stitt: Regulation of respiratory evaporative heat loss in Rabbit. *Journal of Physiology-London*, 258(1), 157-171 (1976)

110. M. S. Westerterp-Plantenga: Effects of extreme environments on food intake in human subjects. *Proceedings of the Nutrition Society*, 58(4), 791-798 (1999)

111. M. Szekely, E. Petervari and Z. Szelenyi: Orexigenic vs. anorexigenic peptides and feeding status in the modulation of fever and hypothermia. *Frontiers in Bioscience*, 9, 2746-2763 (2004)

112. K. R. Westerterp: Diet induced thermogenesis. *Nutrition and metabolism*, 1(1), 5 (2004)

113. J. B. Buchanan, E. Peloso and E. Satinoff: Thermoregulatory and metabolic changes during fever in young and old rats. *American Journal of Physiology-Regulatory Integrative and Comparative Physiology*, 285(5), R1165-R1169 (2003)

114. M. C. Almeida, A. A. Steiner, L. G. S. Branco and A. A. Romanovsky: Cold-seeking behavior as a thermoregulatory strategy in systemic inflammation. *European Journal of Neuroscience*, 23(12), 3359-3367 (2006) doi:10.1111/j.1460-9568.2006.04854.x

115. K. Ishii, M. Kuwahara, H. Tsubone and S. Sugano: The telemetric monitoring of heart rate, locomotor activity, and body temperature in mice and voles (*Microtus arvalis*) during ambient temperature changes. *Laboratory Animals*, 30(1), 7-12 (1996)

116. G. Heldmaier, S. Steinlechner, T. Ruf, H. Wiesinger and M. Klingenspor: Photoperiod and thermoregulation in vertebrates: body temperature rhythms and thermogenic acclimation. *Journal of Biological Rhythms*, 4(2), 251-65 (1989)

117. C. R. Jackson, T. H. Setsaas, M. P. Robertson, M. Scantlebury and N. C. Bennett: Insights into torpor and behavioural thermoregulation of the endangered Juliana's golden mole. *Journal of Zoology*, 278(4), 299-307 (2009) doi:10.1111/j.1469-7998.2009.00575.x

118. N. Harikai, T. Sugawara, K. Tomogane, K. Mizuno and S. I. Tashiro: Dopamine 2 antagonists suppress the jumping escape behavior of mice exposed to heat. *Journal of Thermal Biology*, 33(6), 369-373 (2008) doi:10.1016/j.jtherbio.2008.06.001

119. L. R. Leon, C. J. Gordon, B. G. Helwig, D. M. Rufolo and M. D. Blaha: Thermoregulatory, behavioral, and metabolic responses to heatstroke in a conscious mouse model. *American Journal of Physiology-Regulatory Integrative and Comparative Physiology*, 299(1), R241-R248 (2010) doi:10.1152/ajpregu.00309.2009

120. J. Kotze, N. C. Bennett and M. Scantlebury: The energetics of huddling in two species of mole-rat (Rodentia: Bathyergidae). *Physiology & Behavior*, 93(1-2), 215-21 (2008) doi:S0031-9384(07)00353-8 [pii]

10.1016/j.physbeh.2007.08.016

121. L. G. Fick, T. A. Kucio, A. Fuller, A. Matthee and D. Mitchell: The relative roles of the parasol-like tail and burrow shuttling in thermoregulation of free-ranging Cape ground squirrels, *Xerus inauris*. *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology*, 152(3), 334-340 (2009) doi:10.1016/j.cbpa.2008.11.004

122. A. Haim, A. Alma and A. Neuman: Body mass is a thermoregulatory adaptation of diurnal rodents to the desert environment. *Journal of Thermal Biology*, 31(1-2), 168-171 (2006) doi:10.1016/j.jtherbio.2005.11.016

123. R. Sumbera, J. Zelova, P. Kunc, I. Knizkova and H. Burda: Patterns of surface temperatures in two mole-rats (Bathyergidae) with different social systems as revealed by IR-thermography. *Physiology & Behavior*, 92(3), 526-532 (2007)

124. K. Nagashima: Central mechanisms for thermoregulation in a hot environment. *Industrial Health*, 44(3), 359-367 (2006)

125. D. Robertshaw: Mechanisms for the control of respiratory evaporative heat loss in panting animals. *Journal of Applied Physiology*, 101(2), 664-8 (2006)

126. M. B. Goldberg, V. A. Langman and C. R. Taylor: Panting in dogs: paths of air flow in response to heat and exercise. *Respiration physiology*, 43(3), 327-38 (1981)

127. J. R. S. Hales and G. D. Brown: Net energetic and thermoregulatory efficiency during panting in sheep. *Comparative Biochemistry and Physiology. A, Comparative Physiology*, 49(3A), 413-422 (1974)

128. A. Collin, J. van Milgen and J. Le Dividich: Modelling the effect of high, constant temperature on food intake in young growing pigs. *Journal of Animal Science*, 72, 519-527 (2001)

129. A. Collin, Y. Lebreton, M. Fillaut, A. Vincent, F. Thomas and P. Herpin: Effects of exposure to high temperature and feeding level on regional blood flow and oxidative capacity of tissues in piglets. *Experimental Physiology*, 86(1), 83-91 (2001)

130. C. L. Hamilton: Interactions of food intake and temperature regulation in rat. *Journal of Comparative & Physiological Psychology*, 56(3), 476-& (1963)

131. A. Collin, J. van Milgen, S. Dubois and J. Noblet: Effect of high temperature on feeding behaviour and heat production in group-housed young pigs. *British journal of nutrition*, 86(1), 63-70 (2001)

132. O. Shido, S. Sakurada and T. Nagasaka: Effect of heat acclimation on diurnal changes in body temperature and locomotor activity in rats. *Journal of Physiology-London*, 433, 59-71 (1991)

133. M. Canals, M. Rosenmann and F. Bozinovic: Energetics and geometry of huddling in small mammals. *Journal of Theoretical Biology*, 141(2), 181-189 (1989)

134. C. E. Cooper and F. Geiser: The "minimal boundary curve for endothermy" as a predictor of heterothermy in mammals and birds: a review. *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology*, 178(1), 1-8 (2008)

135. G. Heldmaier, H. Böckler, A. Buchberger, G. R. Lynch, W. Puchalski, S. Steinlechner and H. Wiesinger: Seasonal acclimation and thermogenesis. In: *Circulation, Respiration, and Metabolism*. Ed R. Gilles. Springer-Verlag, Berlin (1985)

136. G. Heldmaier, S. Klaus and H. Wiesinger: Seasonal adaptation of thermoregulatory heat production in small mammals. In: *Thermoreception and temperature regulation*. Ed J. Blight&K. Voigt. Springer-Verlag, Berlin (1990)

137. G. T. Ellison, J. D. Skinner and A. Haim: The relative importance of photoperiod and temperature as cues for seasonal acclimation of thermoregulation in pouched mice (*Saccostomus campestris*: Cricetidae) from southern Africa. *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology*, 162(8), 740-6 (1992)

138. B. G. Lovegrove: Seasonal thermoregulatory responses in mammals. *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology*, 175(4), 231-47 (2005)

139. M. Dagosto: Seasonal-variation in positional behavior of Malagasy lemurs. *International Journal of Primatology*, 16(5), 807-833 (1995)

140. D. I. Solick and R. M. R. Barclay: Thermoregulation and roosting behaviour of reproductive and nonreproductive female western long-eared bats (*Myotis evotis*) in the Rocky Mountains of Alberta. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 84(4), 589-599 (2006) doi:10.1139/z06-028

141. P. Lahann: Habitat utilization of three sympatric cheirogaleid lemur species in a littoral rain forest of southeastern Madagascar. *International Journal of Primatology*, 29(1), 117-134 (2008) doi:10.1007/s10764-007-9138-4

142. S. Rodriguez-Cuenca, E. Pujol, R. Justo, M. Frontera, J. Oliver, M. Gianotti and P. Roca: Sex-dependent thermogenesis, differences in mitochondrial morphology and function, and adrenergic response in brown adipose tissue. *Journal of Biological Chemistry*, 277(45), 42958-63 (2002)

143. A. Valle, F. J. Garcia-Palmer, J. Oliver and P. Roca: Sex differences in brown adipose tissue thermogenic features during caloric restriction. *Cellular Physiology and Biochemestry*, 19(1-4), 195-204 (2007)

144. R. B. McDonald, C. Day, K. Carlson, J. S. Stern and B. A. Horwitz: Effect of age and gender on thermoregulation. *American Journal of Physiology-Regulatory Integrative and Comparative Physiology*, 257(4), R700-R704 (1989)

145. J. Schmid and J. U. Ganzhorn: Optional strategies for reduced metabolism in gray mouse lemurs. *Naturwissenschaften*, 96(6), 737-41 (2009)

146. C. K. R. Willis and R. M. Brigham: Social thermoregulation exerts more influence than microclimate on forest roost preferences by a cavity-dwelling bat. *Behavioral Ecology & Sociobiology*, 62, 97-108 (2007) doi:10.1007/s00265-007-0442-y

147. A. Fouillet, G. Rey, F. Laurent, G. Pavillon, S. Bellec, C. Guihenneuc-Jouyaux, J. Clavel, E. Jougla and D. Hemon: Excess mortality related to the August 2003 heat wave in France. *International Archives of Occupational & Environmental Health*, 80(1), 16-24 (2006) doi:10.1007/s00420-006-0089-4

148. G. Rey, E. Jougla, A. Fouillet, G. Pavillon, P. Bessemoulin, P. Frayssinet, J. Clavel and D. Hemon: The impact of major heat waves on all-cause and cause-specific mortality in France from 1971 to 2003. *International Archives of Occupational & Environmental Health*, 80(7), 615-26 (2007)

149. D. N. Slater: Death from hypothermia: are current views on causative factors well founded? *British Medical Journal (Clinical Research Edition)*, 296(6637), 1643-4 (1988)

150. M. Tanaka and S. Tokudome: Accidental hypothermia and death from cold in urban areas. *International Journal of Biometeorology*, 34(4), 242-6 (1991)

151. M. E. Ward and A. R. Cowley: Hypothermia: a natural cause of death. *American Journal of Forensic Medicine & Pathology*, 20(4), 383-6 (1999)

152. W. L. Kenney and T. A. Munce: Invited review: aging and human temperature regulation. *Journal of Applied Physiology*, 95(6), 2598-603 (2003)

153. S. M. Frank, S. N. Raja, C. Bulcao and D. S. Goldstein: Age-related thermoregulatory differences during core cooling in humans. *American Journal of Physiology-Regulatory Integrative and Comparative Physiology*, 279(1), R349-54 (2000)

154. D. Richardson, J. Tyra and A. McCray: Attenuation of the cutaneous vasoconstrictor response to cold in elderly men. *Journal of Gerontology*, 47(6), M211-4 (1992)

155. Y. Inoue, T. Kuwahara and T. Araki: Maturation- and aging-related changes in heat loss effector function. *Journal of Physiological Anthropology & Applied Human Science*, 23(6), 289-94 (2004)

156. W. L. Kenney, A. L. Morgan, W. B. Farquhar, E. M. Brooks, J. M. Pierzga and J. A. Derr: Decreased active vasodilator sensitivity in aged skin. *American Journal of Physiology-Heart and circulatory physiology*, 272(4 Pt 2), H1609-14 (1997)

157. L. A. Holowatz, C. S. Thompson-Torgerson and W. L. Kenney: Altered mechanisms of vasodilation in aged human skin. *Exercise & Sport Sciences Reviews*, 35(3), 119-25 (2007)

158. C. G. Armstrong and W. L. Kenney: Effects of age and acclimation on responses to passive heat exposure. *Journal of Applied Physiology*, 75(5), 2162-7 (1993)

159. S. Sagawa, K. Shiraki, M. K. Yousef and K. Miki: Sweating and cardiovascular responses of aged men to heat exposure. *Journal of gerontology*, 43(1), M1-8 (1988)

160. W. L. Kenney: Control of heat-induced cutaneous vasodilatation in relation to age. *European journal of applied physiology and occupational physiology*, 57(1), 120-5 (1988)

161. E. T. Poehlman: Regulation of energy expenditure in aging humans. *Journal of the American Geriatrics Society*, 41(5), 552-9 (1993)

162. M. Elia, P. Ritz and R. J. Stubbs: Total energy expenditure in the elderly. *European Journal of Clinical Nutrition*, 54 Suppl 3, S92-103 (2000)

163. M. Florez-Duquet and R. B. McDonald: Cold-induced thermoregulation and biological aging. *Physiological Reviews*, 78(2), 339-58 (1998)

164. M. Talan: Age-related changes in thermoregulation of mice. *Annals of the New York Academy of Sciences*, 813, 95-100 (1997)

165. R. B. McDonald and B. A. Horwitz: Brown adipose tissue thermogenesis during aging and senescence. *Journal of Bioenergetics & Biomembranes*, 31(5), 507-16 (1999)

166. M. A. Horan, R. A. Little, N. J. Rothwell and M. J. Stock: Changes in body composition, brown adipose tissue activity and thermogenic capacity in BN/BiRij rats undergoing senescence. *Experimental Gerontology*, 23(6), 455-61 (1988)

167. A. Vermeulen: Dehydroepiandrosterone sulfate and aging. *Annals of the New York Academy of Sciences*, 774, 121-7 (1995)

168. E. Ferrari, L. Cravello, F. Falvo, L. Barili, S. B. Solerte, M. Fioravanti and F. Magri: Neuroendocrine features in extreme longevity. *Experimental Gerontology*, 43(2), 88-94 (2008)

169. H. Hensel: Thermoreception and temperature regulation. *Monographs of the Physiological Society*, 38, 1-321 (1981)

170. J. Terrien, A. Zahariev, S. Blanc and F. Aujard: Impaired Control of Body Cooling during Heterothermia Represents the Major Energetic Constraint in an Aging Non-Human Primate Exposed to Cold. *PLoS One*, 4(10), e7587 (2009)

171. J. Terrien, P. Zizzari, M. T. Bluet-Pajot, P. Y. Henry, M. Perret, J. Epelbaum and F. Aujard: Effects of age on thermoregulatory responses during cold exposure in a nonhuman primate, *Microcebus murinus*. *American Journal of Physiology - Regulatory Integrative & Comparative Physiology*, 295(2), R696-703 (2008)

172. C. J. Gordon, K. S. Fehlner and M. D. Long: Relationship between autonomic and behavioral thermoregulation in the golden hamster. *American Journal of Physiology-Regulatory Integrative and Comparative Physiology*, 251(2 Pt 2), R320-4 (1986)

173. M. Perret and F. Aujard: Aging and season affect plasma dehydroepiandrosterone sulfate (DHEA-S) levels in a primate. *Experimental Gerontology*, 40(7), 582-7 (2005)

174. F. Aujard and M. Perret: Age-related effects on reproductive function and sexual competition in the male prosimian primate, *Microcebus murinus*. *Physiology & Behavior*, 64(4), 513-9 (1998)

175. C. S. Thompson, L. A. Holowatz and W. L. Kenney: Attenuated noradrenergic sensitivity during local cooling in aged human skin. *Journal of Physiology*, 564(Pt 1), 313-9 (2005)

176. E. L. Glickman, N. Caine-Bish, C. C. Cheatham, M. Blegen and E. S. Potkanowicz: The influence of age on thermosensitivity during cold water immersion. *Wilderness & Environmental Medicine*, 13(3), 194-202 (2002)

177. J. L. Picq: Effects of aging upon recent memory in *Microcebus murinus*. *Aging*, 7(1), 17-22 (1995)

178. J. L. Picq: Aging affects executive functions and memory in mouse lemur primates. *Experimental Gerontology*, 42(3), 223-32 (2006)

179. H. C. Heller, G. W. Colliver and J. Bread: Thermoregulation during entrance into hibernation. *Pflugers Archiv (European Journal of Physiology)*, 369(1), 55-9 (1977)

180. H. C. Heller and S. F. Glotzbach: Thermoregulation during sleep and hibernation. *International Review of Physiology*, 15, 147-88 (1977)

181. D. G. Whyte, R. L. Thunhorst and A. K. Johnson: Reduced thirst in old, thermally dehydrated rats. *Physiology & Behavior*, 81(4), 569-576 (2004) doi:10.1016/j.physbeh.2004.02.030

182. W. L. Kenney and P. Chiu: Influence of age on thirst and fluid intake. *Medicine and Science in Sports and Exercise*, 33(9), 1524-1532 (2001)

183. J. A. Sealander: The relationship of nest protection and huddling to survival of *Peromyscus* at low temperature. *Ecology*, 33(1), 63-71 (1952)

184. G. J. Kenagy and O. P. Pearson: Life with fur and without: experimental field energetics and survival of naked meadow voles. *Oecologia*, 122(2), 220-224 (2000)

185. D. Berteaux, J. M. Bergeron, D. W. Thomas and H. Lapierre: Solitude versus gregariousness: Do physical benefits drive the choice in overwintering meadow voles? *Oikos*, 76(2), 330-336 (1996)