

Recent advances in insect thermoregulation

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ABSTRACT

Ambient temperature (T_a) is a critical abiotic factor for insects that cannot maintain a constant body temperature (T_b). Interestingly, T_a varies during the day, between seasons and habitats; insects must constantly cope with these variations to avoid reaching the deleterious effects of thermal stress. To minimize these risks, insects have evolved a set of physiological and behavioral thermoregulatory processes as well as molecular responses that allow them to survive and perform under various thermal conditions. These strategies range from actively seeking an adequate environment, to cooling down through the evaporation of body fluids and synthesizing heat shock proteins to prevent damage at the cellular level after heat exposure. In contrast, endothermy may allow an insect to fight parasitic infections, fly within a large range of T_a and facilitate nest defense. Since May (1979), Casey (1988) and Heinrich (1993) reviewed the literature on insect thermoregulation, hundreds of scientific articles have been published on the subject and new insights in several insect groups have emerged. In particular, technical advancements have provided a better understanding of the mechanisms underlying thermoregulatory processes. This present Review aims to provide an overview of these findings with a focus on various insect groups, including blood-feeding arthropods, as well as to explore the impact of thermoregulation and heat exposure on insect immunity and pathogen development. Finally, it provides insights into current knowledge gaps in the field and discusses insect thermoregulation in the context of climate change.

KEY WORDS: Thermoregulatory processes, Thermal stress, Thermotolerance, Thermal adaptation, Endothermy, Evaporative cooling

Introduction

Insects live in a wide range of habitats and some species can survive under extreme thermal conditions. Yet, unlike warm-blooded animals (i.e. homeotherms), insects cannot maintain a constant body temperature (T_b) independently of the temperature of their environment (T_a) for extensive periods of time and must adapt or adjust depending on their physiological needs. In response to the thermal heterogeneity of their environment in both time and space, insects have developed multiple strategies to minimize the risks of deleterious effects associated with sub-optimal T_a , including thermal stress and ultimately death. These mechanisms, which include thermoregulation, contribute to maintaining metabolic functions, maximize their fitness and ensure their survival.

In homeotherms, contrary to poikilotherms (including insects), T_b is held relatively constant despite complex interactions among radiation, convection, evaporation and the organism's metabolic activity. In insects, the rate of thermal exchange varies depending on several factors, both biotic and abiotic, including T_a , humidity and wind speed, as well as the color and size of the insect, and the thickness and texture of its cuticle (Digby, 1955; May, 1979; Willmer and Unwin, 1981; Shi et al., 2015). Abiotic and biotic factors can influence T_b in homeotherms as well, although the range of shift in T_b is minimal compared with that in poikilotherms.

Interestingly, the idea that insects can thermoregulate was considered rather peculiar until the 1970s (Heinrich, 2007). Nevertheless, research published in the early 1920s mentioned some insects' ability to use evaporative cooling to regulate their T_b (e.g. Pirsch, 1923; Buxton, 1924; Necheles, 1924). The number of studies on insect thermoregulation has since greatly increased, particularly after the seminal work of researchers such as Heinrich (1993), May (1979) and Casey (1988), to cite just a few. An increase in the number of studies on insect thermoregulation in the early 2000s (listed on PubMed) may be linked to the development of new technological advances that allowed us to more fully understand the mechanisms underlying these thermoregulatory processes (see Box 1).

This Review highlights recent studies focusing on both model and new non-model organisms that have emerged in the field. After providing an overview of the thermoregulatory processes, I discuss findings related to thermoregulation during blood-feeding and insect immunity. I close by highlighting future challenges, particularly in the context of global climate change. Although my focus has been on studies published over the past 30 years, I chose to mention several landmark studies to illustrate general concepts, but readers with the desire to dive in publications prior to the 1990s may refer to several reviews published before then (e.g. May, 1979; Casey, 1988; Heinrich, 1993; Prange, 1996).

Thermoregulatory processes and mechanisms

Thermoregulatory processes in insects can be divided into two main categories aimed either at warming (e.g. endogenous heat production) or cooling (e.g. evaporative cooling). Additionally, insects may behaviorally alter their T_b by modifying their posture, their daily activity pattern or their microhabitat selection (Fig. 1). These strategies are often used in combination and as a function of the environmental conditions (see Box 2).

Endothermy

Heat production through the simultaneous contraction of antagonist flight muscles, either before or during flight, is a strategy used to warm up, perform under sub-optimal environmental conditions (e.g. freezing temperatures) and minimize the risk of cold stress (Fig. 1). The challenge is then to produce the necessary heat endogenously to perform optimally while controlling and managing it to avoid the potential risk of overheating. Shivering (i.e. pre-flight rapid contractions of the thoracic muscles) allows for a rapid

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Glossary

Ant bivouac

Structure formed by moving/migratory ants.

Coxal fluid

The coxal gland collects and excretes urine and is present in some arthropod species such as ticks.

Cibarial and pharyngeal pumps

Muscular structures localized in the head of insects that mediate food intake.

Collective endothermy

Heat production found in social insects such as bees.

Heat transfer

This can occur via radiation, convection, conduction and evaporation between insects and their environment.

Imago

The last stage of insect development (i.e. adult).

Multivoltine

Species that has two or more offspring per year.

Univoltine

Species that has one offspring per year.

Semivoltine

Species that takes more than a year to complete its life cycle.

increase in the thoracic temperature (T_{th}) which can be stabilized, at least for a given time. This is in part due to adaptations of the circulatory system which is at the core of the thoracic muscles in many flying insects. To warm up and increase T_{th} , overall hemolymph circulation is reduced, and the thorax is thus isolated with minimal transfer of hemolymph to the abdomen (Heinrich, 1993). In this case, $T_{th} > \text{head temperature } (T_h) > \text{abdominal temperature } (T_{abd})$ (i.e. heterothermy) with T_{abd} being closer to T_a . In moths and bumblebees, other features – including a coat of insulating ‘fur’ – participates in the process as well by limiting heat dissipation by convection at the thoracic cuticle. This allows some species to fly at very low T_a (Heinrich, 1972, 1987; Heinrich and Mommsen, 1985; Stone, 1993). Interestingly, other species such as *Operophtera bruceata* can take off with a T_{th} close to 0°C and do not produce heat endogenously (Heinrich and Mommsen, 1985). Flight muscle properties (e.g. contraction velocity, force-generating capacity) directly impact the way insects can maintain T_{th} (Marden, 1995). For example, intermittent shivering can be used by honeybees between plant visits to optimize their flight performance (Esch et al., 1991). Tsetse flies activate their alary (i.e. flight) muscles post-feeding (i.e. ‘buzzing’) to improve take-off immediately after ingesting a blood meal (Howe and Lehane, 1986; Lahondère and Lazzari, 2015), which provides a fitness advantage by reducing the risk of being killed by the host.

Although the thorax warms up during endogenous heat production, the abdomen tends to be cooler and can be used as a radiator. To cool down and avoid overheating, cool hemolymph present in the abdomen enters the heart through the ostia and is then pushed by peristaltic contractions in the aorta before it reaches the head. It warms when in contact with the flight muscles and is then projected back through the general cavity, as the aorta is open on its anterior part (Heinrich, 1993; Lahondère et al., 2017). By adjusting hemolymph circulation to the abdomen, insects can thus reduce T_{th} . In this case, the abdomen acts as a heat transfer system (see Glossary) or ‘thermal window’ to dissipate heat through the cuticle, by convection and radiation. This system is more likely to be used in larger insects such as moths, beetles and dragonflies (Heinrich, 1996). Specific conformations of the aorta allow for enhanced and optimized heat exchanges (e.g. countercurrent heat exchanges),

Box 1. New and improved methods and the emergence of non-model organisms

Although early experiments on insect thermoregulation were mostly conducted in the laboratory, field experiments have become more common over the years. This is due, in part, to improvements in instrument portability, which has rendered field studies easier to conduct. Moreover, whereas the first temperature measurements to determine T_{th} for example, were conducted using thermocouples (which must be inserted into the thoracic cavity of a captured insect, resulting in their death), the development of non-invasive techniques for temperature measurements – such as thermographic cameras – have led to a sharp increase in studies on insect thermoregulatory abilities. These high-resolution cameras, equipped with macro lenses, allow for precise and continuous measurements of insect T_b . It is worth noting that the resolution of these cameras is critical to obtain reliable results in insect studies. Other techniques, although not originally associated with studying insect thermoregulation, have allowed for a better understanding of the mechanisms underlying these processes. Microtomography and the advances in CT scanning are two examples (e.g. Verdú et al., 2012; Lahondère et al., 2017), while radiotelemetry has contributed to studying behavioral thermoregulation (Ørskov et al., 2019). Combining various techniques such as flow-through respirometry and thermography (e.g. Stabentheiner et al., 2012; Hadley et al., 1991) allows for a finer and more in-depth analysis of insect thermoregulation ability. Overall, these new technologies have also allowed for work on new non-model organisms, which may not be easily reared in laboratories, as well as with endangered and rare species. Indeed, bees, moths, ants, dragonflies, grasshoppers, beetles and flies have long been the primary study models, either because of their size or because they were easy to catch or rear. However, new insect models have emerged in studies on thermoregulation over the past decade. Among them are blood-sucking arthropods, which were ignored in these studies until the early 2010s but have been shown to use thermoregulation strategies to overcome the stress associated with blood-feeding on warm-blooded hosts (see section on ‘Thermoregulation associated with blood feeding’). Interestingly, studying aquatic insects and stages still seems to be challenging because of technical limitations and most studies are conducted on flying or terrestrial insects.

which have been found in bumblebees (Heinrich, 1976), moths (Heinrich, 1987), carpenter bees (Heinrich and Buchmann, 1986) and kissing bugs (Lahondère et al., 2017). It is worth mentioning that the conformation of the heart (e.g. location of the ostia), the aorta and the location of the countercurrent heat exchanger (e.g. head, thorax, petiole) vary greatly across species. Other specific features of structures such as wings (e.g. cuticle thickness, diversity of scale structure, hemolymph flow) can participate in reducing the risk of overheating in butterflies (Tsai et al., 2020). Interestingly, heat can also be transferred to the abdomen via hemolymph circulation to increase its temperature for brood incubation as demonstrated in bumblebees (Heinrich, 1993).

Endothermy presents many advantages for insects, allowing them to optimize the exploitation of their environment in both time and space. Indeed, endothermic insects may be active for longer periods of time (e.g. earlier/later in the day or the season) compared with ectothermic insects and are consequently less impacted by T_a , at least within a given range. May (1976) has shown that dragonfly species that perform long flights and produce heat endogenously are active before sunrise and after sunset, which is not the case in species that are mainly perchers (i.e. warming up primarily by basking). Additionally, in *Anax junius* dragonflies, circulation of hemolymph is critical to regulate T_{th} , including during flight (May, 1995). In sympatric beetle species (*Scarabaeus sacer* and *Scarabaeus cicatricosus*), strategies can differ greatly allowing species to use specific thermal niches which may reduce competition

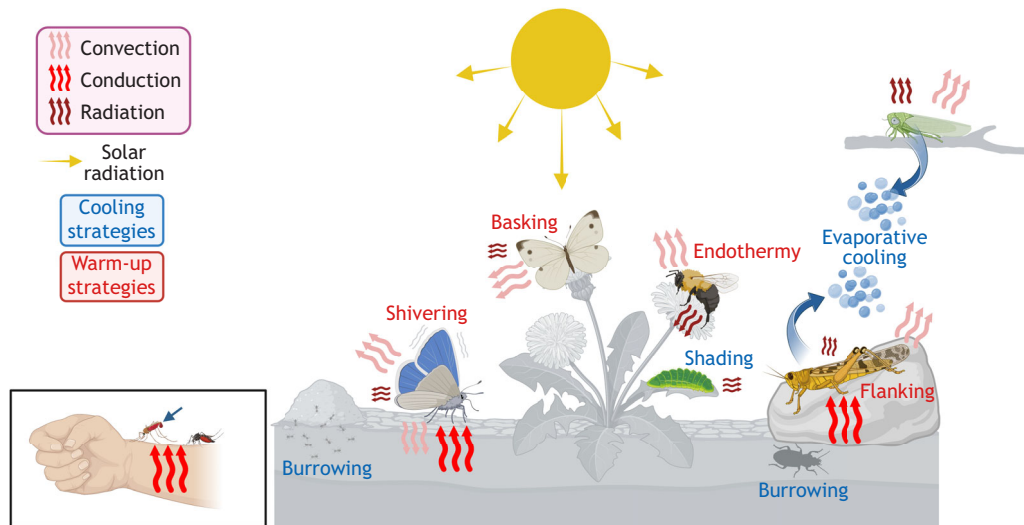


Fig. 1. Schematic representing examples of the major processes of heat exchange that occur between insects and their environment. These include convection (light pink arrows), conduction (red arrows), radiation (maroon arrows and yellow arrows) and evaporation (blue bubbles). Strategies to warm up (in red) or cool down (in blue) are also highlighted. Inset: strategies used by mosquitoes during blood feeding. *Anopheles* mosquitoes (inset, left) use evaporative cooling of urine and blood droplets (blue arrow) to reduce T_{abd} , while *Aedes* mosquitoes (inset, right) tend to have a T_{abd} closer to the temperature of the host and do not exhibit cooling mechanism while blood-feeding.

and affect distribution (Verdú et al., 2012). Besides optimizing flight, endothermy is beneficial for insects that produce sounds by activating their flight muscles and may lead to fitness advantages. In Tettigoniidae, thoracic heat production leads to more powerful (i.e. louder) sounds that are attractive to females (Heath and Josephson, 1970; Josephson, 1973). Cicadas, which produce heat endogenously during flight, also do so at rest by activating their flight muscles (Sanborn, 2000; Sanborn et al., 1995, 2003, 2004). Finally, collective endothermy (see Glossary) certainly provides an advantage to social insects, as shown in the ant *Eciton burchellii parvispinum* (Baudier et al., 2019). In this case, metabolic heating varies with T_a and depends on colony development stages. Consequently, ant bivouacs (see Glossary) can conserve energy by limiting metabolic heating in areas with cooler T_a at high elevation.

Evaporative cooling

Evaporating water to cool down has long been thought to only be possible in vertebrates (i.e. perspiration, panting). However, many insects use evaporative cooling (EC) to reduce T_b (Prange, 1996). In some instances where behavioral thermoregulation is not possible (e.g. seeking a cooler resting site), EC can be the only strategy to decrease T_b and avoid overheating (Fig. 1). Because ectotherms cannot maintain a constant T_b and because of their high surface to volume ratio, the risk of desiccation is relatively high, in particular in environments with low humidity levels such as arid regions (Zachariassen, 1996; Chown, 2002). Thus, it is critical to make careful use of stored water to maintain a stable water balance. Consequently, this cooling mechanism is used mostly in species that have a diet rich in water (e.g. sap, nectar and blood feeders). Access to water in food sources, as well as the environmental conditions in which the insects live (e.g. desert versus tropical forest), impact EC (Hadley et al., 1991; Draney, 1993). Several factors impact water loss rates, including the surface to volume ratio, T_a , atmospheric humidity and air circulation (either caused by wind or movements of insects' appendages) around the evaporation site (Chown, 2002). EC can be split into three categories (discussed below), which are either passive or active mechanisms, but insects may use a

combination of these strategies (Prange, 1996; Roxburgh et al., 1996). Interestingly, water loss rates might change after acclimation to various T_a and humidity levels (reviewed in Chown, 2002 and Chown et al., 2011), as shown in tsetse flies, for example (Kleynhans and Terblanche, 2009, 2011) indicating that both passive and active mechanisms are at play during EC.

Transcuticular evaporative cooling

Water emission through pores present in the cuticle has been reported in several insect groups, including cicadas (Toolson, 1987; Hadley et al., 1991; Sanborn et al., 1992), beetles (Zachariassen, 1991) and ants (Schilman et al., 2005). This is a passive cooling mechanism, and it is worth noting that the rate of transcuticular water loss varies between species (reviewed in Chown, 2002). This variation is mainly linked to differences in cuticular composition (in particular in lipid types and amounts), which affects permeability and can vary depending on the insect body areas (e.g. Hadley et al., 1989; Hadley, 1979) and T_a (Toolson, 1982; Gibbs et al., 1998), as well as other abiotic factors such as level of humidity (Chown, 2002). Toolson and Toolson (1991) showed that *Magicicada tredecim* cicadas use transcuticular water loss to reduce T_b . Toolson (1987) made similar observations in *Diceroprocta apache* cicadas that inhabit the Sonoran Desert, highlighting that transcuticular water is facilitated by a high cuticular permeability in this species. Managing water loss efficiently is particularly important for insects living in desert regions where water balance is critical for survival (e.g. Schilman et al., 2005; Zachariassen, 1991). While it appears advantageous for insects to use transcuticular water loss as a mean of cooling down, studies that directly correlate it with a reduction of T_b remain limited and more research is needed to fully understand its contribution to overall insect body heat loss.

Respiratory evaporative cooling

The tracheal (i.e. breathing) system of insects can be involved in cooling (Prange, 1996; Chown, 2002). Air in the tracheae may be saturated with water vapor and cyclic respiration – combined with control of the opening of the spiracles – limits its loss. The opening

Box 2. To thermoconform or to thermoregulate?

Insects can maintain activities (e.g. foraging, mating, developing) within a species-specific range of environmental temperatures depending on both biotic and abiotic factors. Their overall performance and success will depend on T_a . Their performance peaks at a given T_b and the activity becomes impossible beyond a critical thermal minimum and maximum temperatures (i.e. CT_{min} , CT_{max}). This determines the overall level of thermosensitivity in a species, which will vary with T_a . Some species are considered thermal specialists, having a narrow range of operating T_a , whereas thermal generalists can operate within a larger range of T_a (Huey and Stevenson, 1979; Angilletta, 2009). Because of the dependence on T_a to meet their physiological needs, most insects tend to oscillate between being thermoconformers (i.e. $T_b = T_a$) and thermoregulators (i.e. $T_b > \text{or} < T_a$). Trade-offs between thermoregulating and thermoconforming occur as the costs of thermoregulation can be high. Indeed, endogenous heat production and resting site selection can be energetically costly (May, 1979). The same is true for cooling strategies: maintaining water balance and avoiding the risk of desiccation as well as moving to avoid overheating is energetically costly. For some insects, it might be more advantageous to face thermal stress than to avoid the associated costs. However, this will depend on many factors associated with thermotolerance in a species, including its size, water content and ability to recover from the effects associated with thermal stress through the deployment of other strategies such as the synthesis of heat shock proteins. In holometabolous insects, there might be a higher chance of needing to thermoconform because early life stages (e.g. egg, larva, pupa) cannot escape or move to another microhabitat, contrary to the imago (see Glossary). Daily or seasonal changes in the environmental conditions may also drive the need to thermoconform. For example, summer larvae of the high arctic caterpillar, *Gynaephora groenlandica* thermoconform, whereas winter larvae are considered thermoconformers (Kukal et al., 1988). *Tibicen chloromerus* and *Tibicen winnemanna* cicadas thermoregulate during the day and are thermoconformers during the evening and at night (Sanborn, 2000). Acridid species *Locustana pardalina* and *Hieroglyphus daganensis* exhibit rather distinct thermoregulatory behaviors which are linked to their habitat characteristics (Blanford and Thomas, 2000). *Locustana pardalina* is considered a thermoregulator, which uses postural adjustments and microhabitat selection to maintain a high T_b (38–41°C), whereas *H. daganensis*, which lives in a more humid habitat, does not exhibit any of these characteristics and is considered a thermoconformer ($T_b = 32^\circ\text{C}$). Factors inherent to the insect species, such as the size, also determine the strategies used by insects in their environment (e.g. Kaspari et al., 2015). For example, larger species of beetles tend to thermoregulate (i.e. endothermy), whereas small species of beetles tend to thermoconform (Verdú et al., 2006).

of the spiracles is often linked with T_a to optimize gas exchange and water balance (e.g. Schilman et al., 2005). This active cooling mechanism allows some grasshopper species to maintain T_b 8°C below T_a for example (Prange, 1990; Prange and Modi, 1990; Prange and Pinshow, 1994). Edney and Barrass (1962) noted that tsetse flies decreased T_b by 2°C by opening their spiracles, and that the average temperature decrease was proportional to T_a . The respiratory physiology and its possible role in EC have also been studied in tenebrionid beetle species in the Namib desert, which differ in their cooling strategy based on their size (Duncan, 2021). The larger species (*Onymacris plana*) – a fog harvester – tends to use water to cool down using its respiratory surface, whereas two others (*Metriopus depressus* and *Zophosis amabilis*) do not exhibit respiratory water loss, but rather conserve water. Indeed, no water intake has been noticed in *Metriopus depressus* and *Zophosis amabilis* and these two species live in a different type of habitat (i.e. gravel plains) compared with *O. plana*, which inhabits dunes. Miller (1962) described movements of the thoracic spiracles in dragonflies

and discussed their importance for cooling in parallel to their respiratory role. In grasshoppers (*Romalea guttata*), Hadley and Quinlan (1993) showed that the ventilatory patterns are correlated with respiratory EC. It is worth mentioning that the contribution of respiratory transpiration to water loss has long been debated in the field, in particular for insects with discontinuous gas exchange cycles (DGCs) (reviewed in Chown, 2002).

Head and abdominal evaporative cooling

Droplet regurgitation and excretion is another active mechanism used by some insects to cool the head and the abdomen, respectively. Adam and Heath (1964) observed that the butterfly (*Pholus achemon*) cools down its head by flying with a droplet on its proboscis. Bees regurgitate droplets of nectar, and by moving the droplet on their proboscis in and out ('tongue wagging'), they reduce T_h and T_{th} (Heinrich, 1979; Cooper et al., 1985). Thus, maintaining constant access to water in the colony is critical to avoid overheating (Ostwald et al., 2016). This can also be paired with a form of cuticular evaporative cooling: bees spread regurgitated droplets on their body with their front legs to increase evaporation and decrease T_b . This allows the bees to reduce T_{th} as well, because of the close contact between the two body segments. In yellowjacket wasp workers, the frequency of regurgitation increases with T_a (Coelho and Ross, 1996). More recently, studies have found that several species of flies (Hendrichs et al., 1992, 1993; Stoffolano et al., 2008; Larson and Stoffolano, 2011) also use the same strategy (i.e. 'bubbling'). As in bees, flies usually emit a droplet and re-ingest it. Apple maggot flies (*Rhagoletis pomonella*) may deposit the droplets on the substrate and then re-ingest them (Hendrichs et al., 1992). It has been argued that this mechanism also allows for the crop content to be concentrated by eliminating water from the food source (Stoffolano et al., 2008). However, Larson and Stoffolano (2011) showed that the proportion of bubbling was higher in flies that ate a more concentrated sugar solution, which does not support this hypothesis. Hendrichs et al. (1993) reported that 'bubbling' in *R. pomonella*, increased based on food volume and concentration, and as a function of T_a . Overall, these studies indicate that 'bubbling' probably functions to both concentrate food and reduce T_h .

Strategies for cooling the abdomen are similar to those for cooling the head with liquids. Some species cool their abdomen by excreting honeydew (aphids) or urine (*Anopheles stephensi* and *Culex quinquefasciatus* mosquitoes) (Mittler, 1958; Lahondère and Lazzari, 2012; Reinhold et al., 2021). The droplets are maintained at the tip of the abdomen, which cools down in contact with the surrounding air. Seymour (1974) noted that sawflies spread excreted liquid on their body surface, which causes T_b to decrease by 6°C. Ticks also use coxal fluids (see Glossary) to reduce T_b (Lazzari et al., 2021) (see section on Thermoregulation associated with blood feeding).

Behavioral thermoregulation

Posture adjustments

To warm up, many species modify their posture towards the sun to maximize radiative heat gain (i.e. basking). This behavior has been observed in percher dragonflies (May, 1976), ants (Kadochová et al., 2017), grasshoppers (Whitman, 1987; Blanford and Thomas, 2000), cicadas (Sanborn et al., 1995; Sanborn, 2000) and butterflies (Tsai et al., 2020). In butterflies, heat is accumulated by spreading the wings (i.e. dorsal basking) or by closing them and rotating to maximize solar input laterally (i.e. lateral basking). Solar input is reduced by closing the wings and changing the orientation towards

the sun (Clench, 1966; reviewed in Casey, 1988). Perching on vegetation can also help maximize solar input (May, 2017) (Fig. 1). In dragonflies, the posture of the obelisk – which consists of lifting the abdomen vertically above the head – allows them to minimize solar input. In this case, the abdomen acts as a parasol to protect the thorax from heat radiation (May, 1976). *Zenithoptera lanei* dragonflies possess distinct features on their wings, including wax nanocrystals that reflect ultraviolet (UV) and infrared (IR) light, as well as a network of wing tracheae which are thought to participate in heat accumulation and dissipation depending on the positioning of the wing itself (Guillermo-Ferreira and Gorb, 2021). By perching in a crouched position, the robber flies *Machimus occidentalis* and *Machimus formosus* maximize solar input, allowing them to forage at low T_a (O'Neill and Kemp, 1992).

Another way for insects to collect heat to adjust T_b is by using heat accumulated in the substrate. Heat is thus transferred to the insects through both conduction and radiation (Fig. 1). Among these postures, 'flanking' has been observed in grasshoppers, which lay on their side to warm up (Whitman, 1987). Tiger beetles have been shown to apply their abdomen to the substrate when T_a is under 20°C but when T_a increases and the substrate warms, they extend their legs and keep their body away from the surface when walking (Dreisig, 1980). This behavior has also been shown in insects living in desert areas where shelter options are limited (Remmert, 1985), as well as in grasshoppers (Whitman, 1987), in particular when ground temperature exceeds 50°C (Piou et al., 2022). Desert tenebrionids, which have long legs, either collect heat from the substrate or use 'stilting' to avoid overheating. Moreover, very little hemolymph circulates in the tarsi to further minimize heat intake by direct contact (Henwood, 1975). Finally, dung beetles use their dung ball as a thermal refuge when the ground exceed 60°C. The insects climb on the dung ball and the humidity within the dung ball aids in reducing T_b (Smolka et al., 2012).

Daily activity pattern

In addition to posture adjustments, insects may modify their daily activity patterns to operate under favorable environmental conditions or simply withdraw from unfavorable ones. This may imply daily (i.e. diurnal/nocturnal) or seasonal changes in activity. Insects tend to avoid foraging during the peak heat of mid-day. For example, desert Tenebrionidae modify their overall activity pattern depending on the season and time of day (reviewed in Draney, 1993) and Johnson et al. (2022) reported that the Sonoran Desert bee, *Centris caesalpiniae*, ceased flying midday when T_a is the highest. Some insects, such as the carabid beetle *Thermophilum sexmaculatum*, may be active during the day in winter but shift to being nocturnal during the summer (Erbeling and Paarmann, 1985). Moreover, changes in T_a during the day and overall solar input can affect activity. For example, *Angoleus nitidus* ground beetles have bimodal activity patterns when T_a is relatively high but show unimodal activity patterns on cloudy days (Atienza et al., 1996).

Microhabitat selection

As thermoregulatory abilities increase, thermal constraints associated with the environment decrease. However, for species with minimal thermoregulatory capacities, it is even more critical to select appropriate microhabitats to meet their physiological needs, avoid thermal stress and maintain their performance, which will ultimately impact their fitness (Huey, 1991). Minimal shelter options or harsh conditions can lead insects to pursue microhabitat selection to avoid death. A species' main mode of locomotion (flying versus walking), as well as its speed, drastically influences

habitat selection and is a means to obtain heat without the insect overheating.

In many species, minimizing heat dispersion by convection is necessary for survival. Shade availability and consequently sun exposure may also affect a species' distribution and abundance, as seen in dragonflies (Remsburg et al., 2008). Building a temporary or permanent shelter (e.g. protective case) or taking advantage of the topology of the terrain (e.g. cracks in rocks, holes in trees, animal burrows) can also be critical for survival. For example, Blanford and Thomas (2000) showed that *Locustana pardalina* shelters during the day to avoid thermal stress. Desert ants avoid high sand temperatures by retreating to their nest while other desert insects, including tenebrionid beetles, may burrow under the sand to avoid heat stress (Henwood, 1975). In dung beetles, body mass affects T_b and thermoregulatory strategies, and may play a role in thermal niche selection and overall population distribution (Verdú et al., 2006; Giménez Gómez et al., 2020). Cicadas, which produce heat endogenously, may be able to use habitats otherwise unavailable (Sanborn et al., 1995) and this may also reduce predation (Sanborn et al., 1995; Sanborn, 2000). Pygmy grasshoppers, which vary in color also differ in their habitat selection, depending on both T_a and the risk of predation (Ahnesjö and Forsman, 2006). Finally, some insects such as Dynasty scarab beetles (*Cyclocephala colasi*) rely on endothermy only facultatively and rarely when T_a is above 28°C (Seymour et al., 2009). These beetles are associated with the thermogenic plant *Philodendron solimoesense*, which can maintain an inflorescence temperature higher than T_a owing to floral thermogenesis, which directly benefits these insects.

As well as selecting microhabitats, some insects build or produce them. These structures, which can be considered extended phenotypes, are microclimatic niches that reduce the pressure of environmental fluctuations on the insects that build them. Traits associated with each extended phenotype (e.g. thickness of material, depth of burrow) have various thermal functions (e.g. heat or cold buffers) (Woods et al., 2021). For example, spittlebug nymphs (*Mahanarva fimbriolata*) produce foam to create a stable thermal microhabitat near the roots of plants (Tonelli et al., 2018). Embids (communal web-spinners), which build silk shelters, do so depending on their environment and habitat conditions, including T_a and sun exposure (e.g. Edgerly et al., 2005). Poitou et al. (2021) have shown that the nest of pine processionary caterpillars (*Thaumetopoea pityocampa*), constituted an ideal habitat for larvae to develop during the winter, highlighting the ability of this species to build its own thermal niche. It has also been shown that termite mound construction and geometry vary with internal T_a , among other factors (Ocko et al., 2019). Finally, in *Onthophagus* spp. dung beetles, females bury their brood ball deeper at higher T_a , which affects the development time of the offspring (Mamantov and Sheldon, 2021).

Thermoregulation associated with blood feeding

Although most insects that are exposed to excessive amounts of heat in their environment can find ways to escape and reduce the risk of thermal stress and potential death, insects feeding on warm-blooded vertebrates cannot. Indeed, during each meal they rapidly imbibe a liquid (i.e. blood) that greatly exceeds T_b and evidence of heat stress [i.e. synthesis of heat shock proteins (HSPs)] has been found in several species (e.g. Benoit et al., 2011). This difference ($T_{\text{blood}} - T_b$) can be as high as 20–25°C, depending on the host [e.g. birds have higher body temperature compared with mammals (Prinzinger et al., 1991)]. Moreover, as the host plays the double role of prey (i.e. blood meal source) and predator (i.e. anti-parasitic behavior, grooming), insects need to take as much blood as possible in a minimum of time to avoid being killed during the blood intake

(Lehane, 2005; Lazzari, 2021). Yet, some species can feed quickly (e.g. tsetse flies) whereas others might take up to 20 min (e.g. kissing bugs) or even several days (e.g. hard ticks) to obtain a full blood-meal. Strategies to evade anti-parasitic behaviors include feeding at night when the hosts are resting, as well as producing a set of molecules in the saliva that reduce inflammation and itching and, consequently, the risk of being detected by the host. This leads to a trade-off between being able to minimize the time spent on the host to avoid anti-parasitic behaviors and the exposure to heat stress due to the blood meal ingestion. Some blood-sucking species have evolved thermoregulatory strategies to minimize heat stress by actively cooling down during feeding (see Box 3). These strategies are discussed in more detail below.

Thermoregulatory mechanisms

Evaporative cooling

In mosquitoes, as in many blood-sucking insects, urine excretion begins during blood-feeding (i.e. pre-diuresis). This allows females to concentrate the nutrients present in the host blood and maintain water balance (Briegleb and Rezzonico, 1985). Excreting urine also acts to reduce mosquito weight which increases mobility and may decrease the predation risk (Vaughan et al., 1991). Interestingly, several *Anopheles* species also excrete red blood cells, which might appear as a waste of freshly ingested blood. Lahondère and Lazzari (2012) hypothesized that the production and retention of urine droplets at the tip of the abdomen during feeding could reduce T_{abd} through evaporative cooling. Consequently, the fresh blood excreted would not be wasted but rather could be considered as invested in a cooling mechanism to avoid overheating. More recently, Reinhold et al. (2021) showed that *Culex quinquefasciatus* mosquitoes also cool down during feeding through the same process. Interestingly, this species does not excrete red blood cells and the cooling is

achieved solely using urine. This mechanism leads to a decrease in T_{abd} by an average of 2–4°C.

Although hard ticks may take up to several days to feed to repletion, soft ticks complete their feeding in only 5 to 25 min (Davis, 1941). This leads, once again, to a fast rise in T_b , which may trigger a heat stress response. Lazzari et al. (2021) found that the soft tick *Ornithodoros rostratus* cools down during blood-feeding by excreting coxal gland fluid that spreads on the dorsal cuticular surface. Maldonado-Ruiz et al. (2022) showed that evaporation of the dermal secretion leads to a quick decrease in T_b in the hard tick species *Amblyomma americanum* when exposed to high T_a . However, it remains unclear how hard ticks manage heat stress during blood ingestion.

Countercurrent heat exchanger

Kissing bugs imbibe a large amount of blood when feeding on a host (i.e. up to 12 times their unfed weight) (Lehane, 2005). These insects are feeding mainly at night, and they can take a full blood-meal in minutes, depending on the stage of the insects and T_{blood} (Lahondère et al., 2019 preprint). Using thermography, Lahondère et al. (2017) analyzed T_b in *Rhodnius prolixus* while feeding and found that kissing bugs maintain a strong heterothermy along their body. Whereas T_h is close to T_{blood} , the temperature of the abdomen (T_{abd}) remains lower and closer to T_a . This difference can reach up to 10°C. This is due to an elaborate system located in the kissing bug head that was revealed by functional anatomy and X-ray synchrotron analyses (Lahondère et al., 2017). The ingested blood circulates in the alimentary canal that is separated from the aorta, in which hemolymph circulates, by only a thin layer of cells. This provides an ideal medium for heat exchange. Moreover, these two fluids circulate in opposite directions: blood circulates from anterior to posterior, whereas the hemolymph enters the heart at the tip of the abdomen and is then pulsed in the aorta from posterior to anterior. When the heart is severed, Lahondère et al. (2017) showed that heterothermy during feeding disappeared because of the lack of cool hemolymph supplied to the head, which cools down the ingested blood before it reaches the mosquito thorax and abdomen. Moreover, increasing T_{blood} increases the insect heart rate (Lahondère et al., 2019 preprint), possibly to provide hemolymph to the cooling system more efficiently. By analyzing the activity of the ingestion pumps, Lahondère et al. (2017) demonstrated that the cibarial pump (see Glossary) acts as a piston, working anti-phase to the pharyngeal pump (see Glossary) to create a constant flow of ingested blood. This supports the hypothesis of a countercurrent heat-exchanger in the head of *R. prolixus*, which is responsible for maintaining heterothermy during blood-feeding. This also functions to prevent overheating the abdomen which contains temperature-sensitive organs such as testes and ovaries.

Trade-offs during blood-feeding: cooling or not cooling?

Several blood-feeding insects feed so quickly that no thermoregulatory processes can be put in place while feeding. This is exemplified by tsetse flies, which feed to repletion in less than a minute but still ingest two to three times their unfed weight (Lehane, 2005). This has the advantage of reducing the time spent on the host and thus avoiding anti-parasitic behaviors. Lahondère and Lazzari (2015) studied tsetse fly T_b during blood feeding and found little to no heterothermy; this indicates that these flies are able to sustain heat stress associated with the ingestion of a warm blood meal (Fig. 2). This heat tolerance might be associated with the synthesis of HSPs, allowing the insect to recover from heat stress post-exposure, as found in bed bugs and some mosquito species (Benoit et al., 2011). In mosquitoes, a peak of HSP70 synthesis was noted one hour after a warm blood meal. This has since

Box 3. Open questions on other blood-feeding insects/arthropods

Exploring the thermal biology of blood-sucking insects is a relatively recent field of research, and many questions remain unanswered. Among them, is the potential role of the circulatory system, in particular the heart, in thermoregulation and thermal stress avoidance. Although the role of the heart in thermoregulation in kissing bugs is relatively well understood (Lahondère et al., 2017, 2019), the question remains unanswered for all other blood-sucking insects. Moreover, the underlying mechanisms (e.g. role of neurohormones) need to be explored further. Determining the fitness consequences of thermoregulation during feeding will also allow for understanding the advantages insects may gain through this process other than avoiding overheating. For example, what is the impact on reproductive output (e.g. number of eggs laid, hatching rate)? Whether hyperventilation (and thus respiratory EC) also allows these insects to bring cool air in their tracheal system and around their organs remains unknown. Tsetse flies can reduce their T_b (up to -2°C) when T_a increases (Edney and Barrass, 1962); but what about during blood feeding? Another question is how other blood-sucking insects such as lice, fleas and horseflies, cope with the ingestion of a warm blood meal? Finally, exploring strategies and tolerance of insects feeding on cold-blooded hosts seems relevant, particularly to learn more about the evolutionary processes that have led insects to feed on endotherms (Reinhold et al., 2022). For example, mosquitoes feeding on frogs may take up to 2 h to feed to repletion (personal observation): why take the risk to stay on the host for such a long time and possibly be killed in the attempt? Could it be a strategy to avoid heat stress? Are these species less thermotolerant compared with those feeding on warm-blooded hosts?

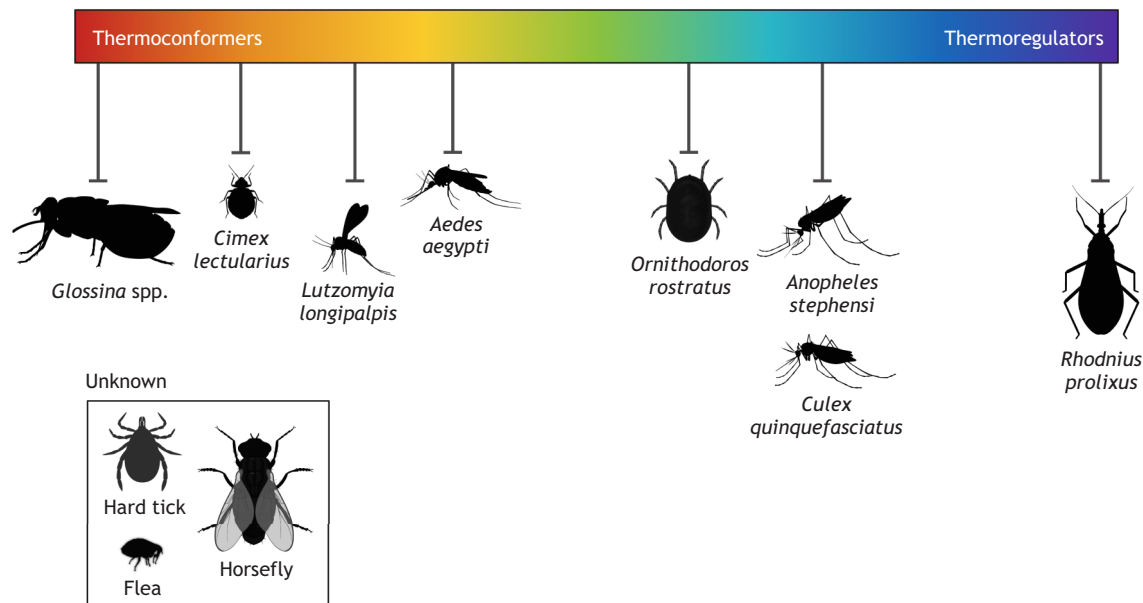


Fig. 2. A summary of the range of thermoregulatory strategies observed in blood-sucking arthropods during blood-feeding. This scale comprises efficient thermoregulators (e.g. *Rhodnius prolixus*) which can cool down during feeding and maintain T_b up to 10°C under T_{blood} and insects which do not display thermoregulation strategies (e.g. *Glossina* spp.) and for which $T_b = T_{\text{blood}}$ (i.e. thermoconformers) during blood-feeding. The responses of many blood-sucking genera, including fleas, horseflies and hard ticks, remain unknown. It is hypothesized that horseflies and fleas are thermoconformers because of their short duration of feeding and/or size, whereas hard ticks might be either thermoconformers or thermoregulators based on their extensive duration of feeding. Synthesis of heat shock proteins is expected to occur in all three genera.

been shown in ticks (Oleaga et al., 2017) and kissing bugs (Paim et al., 2016), which also use thermoregulatory strategies to protect themselves from overheating during feeding, as well as in the sandfly *Lutzomyia longipalpis* (Martins et al., 2022), which do not thermoregulate while feeding. Thus, it appears that HSP synthesis may come as a complementary strategy of protection rather than as a replacement for thermoregulation for several species. Interestingly, keeping a high T_b during feeding can have certain fitness advantages. For example, in tsetse flies, which feed milk to their larva *in utero*, a warm blood meal leads to an increase in milk production in these insects, which directly benefits their progeny (Benoit et al., 2022). More recently, it has been found that *L. longipalpis* do not thermoregulate while feeding either (Martins et al., 2022), but synthesize HSPs to prevent damage at the cellular level.

A potential advantage of cooling during feeding is to reduce the risk of cannibalism from conspecifics. This risk is likely high in kissing bugs and ticks, which can live in close association either on the hosts or in shelters (i.e. gregarious behavior). Indeed, as heat is an important cue for kissing bugs to initiate feeding (Fresquet and Lazzari, 2011; Barrozo et al., 2017), when a warm kissing bug returns to the shelter after a blood meal, it might become an easy target for conspecifics (Schaub et al., 1989). Lazzari et al. (2018) showed that insects that were artificially warmed up after ingesting a blood meal, thus mimicking the absence of a cooling mechanism, were targeted by younger larvae which were ultimately able to obtain a blood meal by piercing the cuticle of the warmed-up individual. This validates the idea that cooling down during feeding allows kissing bugs to avoid cannibalism.

Post-feeding thermophily

Although managing heat exposure during feeding is essential to avoid heat stress in blood-sucking arthropods, it is worth noting that seeking a higher temperature after feeding presents several

advantages (i.e. postprandial thermophily). This has been shown in many cold-blooded vertebrates such as snakes (Toledo et al., 2003) and toads (Clemente et al., 2020), and other invertebrates such as leeches (Petersen et al., 2011) and scorpions (Raviv and Gefen, 2021). Tsetse flies (*Glossina brevipalpis*) and kissing bugs prefer warmer temperatures directly after imbibing a blood meal (McCue et al., 2016; Lazzari, 1991; Schilman and Lazzari, 2004). This may be because higher temperatures boost metabolism and allow insects to digest faster and more efficiently. T_b gradually decreases with time after blood ingestion, which is linked to the digestion of the meal. Whether this is a common response in other blood-sucking insects is unclear and remains to be tested in a broad range of species. Yet, we have evidence that this is not the case in two species of mosquitoes, *Aedes aegypti* and *Aedes japonicus* (Verhulst et al., 2020), as well as in *L. longipalpis* (Martins et al., 2022). A possible explanation for this is that digestion is faster in mosquitoes and sandflies compared with tsetse flies and kissing bugs, which take much larger blood meals. Moreover, mosquitoes tend to perform a lot of pre-diuresis to concentrate the blood during feeding which may contribute to speeding the digestion process. Urine production during feeding is reduced in tsetse and kissing bugs. Urine produced by kissing bugs and tsetse flies is partly produced on the host skin but remains minimal in comparison to the volume that mosquitoes can excrete during feeding. Future studies comparing thermopreference (T_p) in hard ticks, which also need more time to feed and can digest over the course of several days, may help better understand this mechanism.

Behavioral fever, immunity, parasite transmission and defense

Endotherms often exhibit an increase in T_b in response to an infection (i.e. fever). Interestingly, endothermy has restricted most fungi from being potential harmful pathogens in vertebrates (Robert and Casadevall, 2009). In insects, which cannot maintain a constant

T_b , warming up to fight a fungal infection can be achieved by producing heat endogenously or by selecting a microhabitat with a higher T_a to increase T_b (i.e. behavioral fever), without reaching thermal stress. Moreover, some parasites and pathogens can also affect and manipulate the host's physiology and behavior, sometimes for the benefit of their development (e.g. Maitland, 1994; Thomas et al., 2003; Suito et al., 2022). Previous reviews have summarized the impact of the host temperature and T_a on pathogen development as well as on insect immunity (e.g. Thomas and Blanford, 2003; Wojda, 2017; Reinhold et al., 2018). Below, I highlight recent work on the effects of temperature on insect immunity.

Fighting infection and behavioral fever

Increasing T_b above the parasite's lethal temperature can prevent their development and lead to a clearance of the parasites within the insect's body. One of the first studies to demonstrate the existence of behavioral fever in insects was conducted by Louis et al. (1986), who showed that *Gryllus bimaculatus* crickets infected with *Rickettsiella grylli* tended to have a higher T_b , which led to a higher survival rate. Since then, many studies in various species have shown similar behavioral fever effects in response to an infection. For example, Karban (1998) showed that *Platyrepia virginialis* caterpillars infected with the *Thelaira americana* parasitoid tend to bask more than unparasitized ones and immune-challenged mealworms (*Tenebrio molitor*) displayed a higher T_p compared with uninfected ones (Catalán et al., 2012). *Musca domestica* flies infected with the *Entomophthora* fungus prefer warmer sites in the field compared with uninfected ones (Kalsbeek et al., 2001), while in *Oedaleus senegalensis* grasshoppers, infection with the *Metarhizium flavoviride* fungus in the field led to an increase in T_p (Blanford et al., 1998). Similar observations were obtained under laboratory conditions with *Locusta migratoria migratorioides*, following infection with *Metarhizium anisopliae* var. *Acridum* (Ouedraogo et al., 2004) and in *Locusta migratoria manilensis* infected with *Beauveria bassiana* (Sangbaramou et al., 2018). In both cases, the infected insects tended to exhibit a higher T_p compared with uninfected individuals.

Besides extending survival in infected insects, Elliot et al. (2002) found that behavioral fever in infected *Schistocerca gregaria* led to the production of viable offspring while those unable to use 'heat therapy' did not produce viable offspring. This illustrates the importance of behavioral fever to boost fitness in infected individuals. Honeybees increase the temperature of their nest in response to an infection by the heat-sensitive brood pathogen, *Ascosphaera apis* (Starks et al., 2000). This 'social fever' allows the colony to minimize the spread of the pathogen (Goblirsch et al., 2020). Interestingly, other species have been shown to seek cooler temperatures when infected, which may reduce the probability of successful parasite development, whereas some others, such as *R. prolixus*, exhibit a different T_p depending on the species of pathogen infecting them (Hinestroza et al., 2016). Finally, it is worth noting that some species (e.g. *Anopheles stephensi* mosquitoes) infected with a pathogen do not seem to exhibit behavioral fever (e.g. Blanford et al., 2000, 2009). Whether and how this behavior is affected by T_a remains unclear and more studies are needed to better understand of abiotic factors may influence T_p in insects which exhibit this behavior.

Warming as a defense and protective mechanism

Using endogenous heat production to fight a predator has been demonstrated in honeybees. Ono et al. (1995) showed that *Apis*

cerana japonica can defend their hive from attacking intruder hornets (*Vespa mandarinia japonica*) by exhibiting a collective defensive behavior, gathering and forming a ball around the intruders and increasing their T_{th} by shivering. This leads to an increase in temperature (up to 47°C) at the center of the ball where the hornet is located, causing its death without harming the honeybees, which have a slightly higher critical thermal maximum (CT_{max}) temperature. This defense mechanism has only been shown in these insects. Another way some insects take advantage of T_a as a defense mechanism is by occupying ecological niches or being active at times of day when predators are not active as discussed above. This is the case for some ants whose foraging occurs at times of day when the desert can reach 60°C and vertebrates predators need to hide (Wehner et al., 1992).

Effects of pesticides on thermoregulation

Recently, pesticides have been shown to negatively affect insect thermoregulation. For example, Tosi et al. (2016) showed that neonicotinoid pesticide affects African honeybees (*Apis mellifera scutellata*) thermoregulation. In this case, sublethal levels of thiamethoxam altered T_{th} which may, in turn, affect the insects' foraging ability. Tong et al. (2019) showed that the pesticide flupyradifurone negatively affects bee fitness and their thermoregulatory abilities, while the pesticide methoxyfenozide disrupts honeybee thermoregulation when ingested (Meikle et al., 2019). In bumblebee workers, Crall et al. (2018) found that field-realistic levels of imidacloprid negatively impacted colony thermoregulation by affecting the construction of insulating structures in the nest, and Potts et al. (2018) noticed similar negative effects in *Bombus terrestris* when the insects were fed with either imidacloprid or thiamethoxam. In these two studies, the insects had more difficulties warming up after a cold shock. More recently, Weidenmüller et al. (2022) found that the herbicide glyphosate negatively impacts bumblebees' collective thermoregulation behavior, reducing the ability of the hive to maintain high brood temperatures by 25%. The effects of these pesticides on thermoregulatory abilities of other insects including butterflies, moths and other nectar feeders have yet to be tested.

Knowledge gaps and future research

Thermosensation in insects

Although temperature sensing is critical for insects to prevent overheating by being able to locate suitable microenvironments for instance, it remains understudied in most insect species, other than *Drosophila melanogaster* (reviewed in Li et al., 2020; Barbagallo and Garrity, 2015; Xiao and Xu, 2021) and more recently, in some blood-sucking insects, including kissing bugs (reviewed in Lazzari, 2019) and mosquitoes (reviewed in Greppi et al., 2020; Greppi and Garrity, 2022). However, temperature sensing remains poorly understood in other insects. Yet, a better understanding of insect thermosensation along with deciphering the underlying processing mechanisms at the level of both peripheral and central nervous systems would allow for deeper knowledge regarding the evolutionary mechanisms that have led insects to blood feed on endotherms, for example.

The need for an integrative and multidisciplinary approach

Integrating behavioral and physiological data along with biophysical studies remains critical to provide an accurate understanding of the various mechanisms that insects use to cope with thermal stress or to attain a desirable T_b to perform more efficiently (Casey, 1988). Moreover, predicting the response of a given species to climate change may be achieved through both laboratory and field studies that

incorporate realistic environmental data along with species-specific key physiological and behavioral traits (Buckley, 2022; Johnson et al., 2022; Lahondère and Bonizzoni, 2022). Finally, when measuring thermotolerance, it is important to consider other factors, including tolerance to drought. Indeed, water balance management is critical in insects, but its study remains separated from the impact of T_a while in the field, although it is probably correlated.

A note on thermoregulation, thermotolerance and climate change

As the global climate changes along with an increase in extreme weather events, the question of how insects will cope with these changes arises (Chown et al., 2011; Sinclair et al., 2016; Buckley and Kingsolver, 2021). Indeed, insects with low thermotolerance and low phenotypic plasticity may be rapidly threatened by sudden increases in temperature or drought (Sgrò et al., 2016; González-Tokman et al., 2020). However, although species which have a higher degree of behavioral plasticity may benefit in the short term, they may not be able to adapt to long-term climatic changes (Buckley et al., 2015). Factors inherent to the type of ecosystems the insects live in as well as their access to microhabitats and shelters will also affect their response (Pincebourde and Woods, 2020). For example, some species might have the opportunity to gradually shift their geographic distribution and start colonizing areas at higher altitudes to cope with an increase in T_a (Baudier et al., 2019). Intra- and inter-population differences might be observed, particularly in populations inhabiting temperate and tropical environments (Andrew et al., 2013). For tropical species, which usually experience less variation in T_a , the risks of overheating and the costs associated with coping are higher, compared to temperate species (Halsch et al., 2021; de Farias-Silva and Freitas, 2021). However, there is clear evidence that most ectotherms do not possess a “thermal safety margin” and require behavioral thermoregulation to avoid thermal stress (Sunday et al., 2014). Rapid thermal adaptation will be necessary for most species to survive, which may be easier to achieve for species with shorter development times or for multivoltine species (see Glossary) compared to semivoltine and univoltine species (see Glossary). Finally, besides impacts on performance and fitness, it has been suggested that climate change will also have an impact on disease resistance in some species (Adamo and Lovett, 2011).

The evolution of thermoregulatory strategies has allowed insects to colonize ecosystems that are otherwise impossible to survive, including deserts and mountains, as well as to perform under sub-optimal thermal conditions and optimize their overall performance. The mechanisms underlying such processes have become better understood thanks to the development of new tools and non-invasive techniques (e.g. thermographic camera and synchrotron imaging) which allow for monitoring T_b in live insects and to determine the role of various structures and organs in these processes (e.g. tracheal and circulatory systems). Yet, knowledge gaps remain, along with the need for a multidisciplinary approach in studying insect thermoregulation. Future research will help finely decipher how species respond to thermal stress, especially in the context of climate change, and how they respond to other anthropogenic disturbances including habitat fragmentation, urbanization and pollution.

Acknowledgements

I would first like to thank Dr John Terblanche for the invitation to write this review and for helpful discussions regarding this manuscript. I would also like to thank Dr Claudio Lazzari and Dr Clément Vinauger for helpful comments and suggestions on the manuscript. Figures 1 and 2 were created using BioRender.com.

Competing interests

The author declares no competing or financial interests.

Funding

This work was supported by grants from the National Science Foundation (IOS 2114127), USDA National Institute of Food and Agriculture (VA160160) as well as by the Department of Biochemistry and the Fralin Life Science Institute at Virginia Tech.

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