Adaptations to thermal stress in social insects: recent advances and future directions

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ABSTRACT

Thermal stress is a major driver of population declines and extinctions. Shifts in thermal regimes create new environmental conditions, leading to trait adaptation, population migration, and/or species extinction. Extensive research has examined thermal adaptations in terrestrial arthropods. However, little is known about social insects, despite their major role in ecosystems. It is only within the last few years that the adaptations of social insects to thermal stress have received attention. Herein, we discuss what is currently known about thermal tolerance and thermal adaptation in social insects – namely ants, termites, social bees, and social wasps. We describe the behavioural, morphological, physiological, and molecular adaptations that social insects have evolved to cope with thermal stress. We examine individual and collective responses to both temporary and persistent changes in thermal conditions and explore the extent to which individuals can exploit genetic variability to acclimatise. Finally, we consider the costs and benefits of sociality in the face of thermal stress, and we propose some future research directions that should advance our knowledge of individual and collective thermal adaptations in social insects.

Key words: social insects, thermal tolerance, thermoregulation, adaptation, heat shock proteins, morphology, physiology, behaviour

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I. INTRODUCTION

Over the last decade, an increasing number of studies have explored how natural populations are responding to the unnatural temperature shifts associated with global climate change. It has become clear that both vertebrate and invertebrate taxa are experiencing range shifts, population declines, and even extinction (Araújo, Thuiller, & Pearson, 2006; Loboda *et al.*, 2018). To predict species' responses to global warming better, we must first understand how species adapt to natural temperature variation.

Temperature is one of the most stressful abiotic pressures. Thermal stress disrupts the thermodynamic equilibrium of macromolecules such as DNA, proteins, and membrane lipids, leading to a loss of structure and function (Quinn, 1988; Feder & Hofmann, 1999; Daniel et al., 2008; Evgen'ev, Garbuz, & Zatsepina, 2014; Abram et al., 2016). Severe thermal stress can lead to cell death, tissue necrosis, and, ultimately, the death of the afflicted individual. While endotherms harness metabolic heat to keep body temperature constant, ectotherms lack this ability, and their biological functions are thus more directly affected by the thermal conditions in their environment (Neven, 2000; Paaijmans et al., 2013). Thermal tolerance range is defined as the temperature range between the coldest temperature (critical thermal minimum, CT_{min}) and hottest temperature (critical thermal maximum, CT_{max}) at which an organism can maintain muscle control. Consequently, both thermal tolerance and its degree of plasticity play key roles in determining the geographical distribution of ectotherms: species with greater tolerance ranges tend to be more broadly distributed (Kellermann et al., 2009; Sunday, Bates, & Dulvy, 2011).

The ability of animal species to tolerate temporary or persistent thermal stress depends on two complementary adaptive mechanisms. First, there are adaptations that help organisms resist thermal stress by 'immunising' them against cell damage (Fineblum & Rausher, 1995). Resistance mechanisms exploit the thermodynamic properties of cells, such as those related to membrane composition or the intrinsic characteristics of proteins. Second, there are adaptations that help organisms tolerate thermal stress. In these mechanisms, the denaturation of molecules induces an active physiological response, limiting the further deterioration of cell components and contributing to their repair if degraded (Huey & Kingsolver, 1989; Richter, Haslbeck, & Buchner, 2010).

Social insects (ants, termites, social bees, and social wasps) are found in most terrestrial ecosystems, from the subarctic tundra to the hottest deserts (Hölldobler & Wilson, 1990). They are among the most abundant, diverse, and broadly distributed taxonomic groups (Wilson, 1971; Hölldobler & Wilson, 1990). For example, more than 15,600 ant species

have been described to date (AntWiki, 2020). The unparalleled ecological dominance of social insects is rooted in the division of labour between (i) queens and males (kings in termites) that are specialised for reproduction and (i) sterile workers that promote colony development and growth (Wilson, 1971; Oster & Wilson, 1978). Within the worker caste, further specialisation often occurs because a worker's tasks can be influenced by age, genotypic effects, and morphological adaptations (Oster & Wilson, 1978; Hölldobler & Wilson, 1990; Hughes et al., 2003; Smith et al., 2008). For example, in some ant species, two morphologically distinct worker castes have evolved: large individuals with large heads that specialise in colony defence, and small individuals with normal-sized heads that specialise in brood care and foraging. Social insect colonies are typically sedentary, and colony members must therefore deal with variability in environmental temperatures. As a result, in recent years, increasing attention has been paid to both the individual and collective mechanisms used by social insects to cope with thermal stress.

In this review, we summarise what is currently known about adaptations to thermal stress in social insects. We focus on thermal tolerance range and explore the main behavioural, morphological, and physiological adaptations that social insects have evolved to cope with temperature variation. It can be challenging to compare thermal tolerance in social insects because tolerance (CT_{max} and CT_{min}) and responses to thermal stress have been characterised using different methods; consequently, results cannot be reliably compared across studies (Terblanche et al., 2007; Ribeiro, Camacho, & Navas, 2012). We will not address resistance mechanisms due to the absence of research. Here, our goal is not exhaustively to describe any single adaptation, but rather to provide an overview of the major ways in which social insects cope with thermal stress. We discuss major similarities and differences in adaptations to thermal stress between social and solitary insect species, and we highlight important directions that future research should take to advance our understanding of thermal adaptation in insect societies.

II. THERMAL TOLERANCE AND ENVIRONMENTAL CONDITIONS

(1) Variation in thermal tolerance with latitude

In ectotherms, thermal tolerance is generally correlated with latitude (Addo-Bediako, Chown, & Gaston, 2000; Sunday, Bates, & Dulvy, 2011), and social insects are no exception. Indeed, social insect species living in more mesic habitats further north were found to have a lower CT_{max} than those living in more xeric habitats further south [ants (Marsh, 1985; Morton & Christian, 1994; Oberg, del Toro, & Pelini, 2012); bees (Ruttner, 1988; Abou-Shaara, 2015); termites (Janowiecki *et al.*, 2019)]. Northern European species of *Polistes* wasps were found to have a lower CT_{min} than species from the Mediterranean (Kovac *et al.*, 2017). Ants display within-species variation in thermal tolerance: populations from higher latitudes were shown to have a lower CT_{min} than populations from lower latitudes (*Leptothorax acervorum*; Heinze *et al.*, 1998).

Likewise, species living in sympatry often display similar thermal limits (Sponsler & Appel, 1991; Cerdá & Retana, 2000). For example, sympatric honeybee populations were seen to have similar CT_{max} values [Apis mellifera carnica 49.2°C \pm 2°C and A. m. ligustica 50°C \pm 1°C (mean \pm SD); Kovac *et al.*, 2014]; the same was true for sympatric termite species (Coptotermes formosanus $46.3^{\circ}C \pm 0.23^{\circ}C$ and Reticulitermes flavipes $45.3^{\circ}C \pm 0.17^{\circ}C$; Sponsler & Appel, 1991). However, such is not always the case, and sympatric species can also display marked differences in thermal tolerance. The ants Temnothorax curvispinosus and Aphaenogaster rudis both live in eastern North American forests. Workers of T. curvispinosus were observed to forage at higher temperatures and display greater heat tolerance than workers of A. rudis (CT_{max} 46.3 \pm 1.26 and 41.3 \pm 0.95, respectively; Penick et al., 2016).

(2) Species living under extreme thermal conditions

Some social insect species are endemic to hot and arid areas (Atmowidjojo et al., 1997; Cerdá, Retana, & Cros, 2011; Boulay et al., 2017). In contrast to many other desert animals that escape the heat by being nocturnal or crepuscular, these species are active even during the warmest hours of the day, thanks to their high degree of tolerance to heat and desiccation. This strategy provides a tremendous competitive advantage because they can forage under climatic conditions that none of their potential competitors or predators can withstand (Wehner, Marsh, & Wehner, 1992; Wehner & Wehner, 2011). Seed-harvester ants (Pogomyrmex spp.) in North American deserts were found to have CT_{max} values above 50°C (Lighton & Turner, 2004). Even more impressive are the three ant genera Cataglyphis, Ocymyrmex and Melophorus, which occur in Palaearctic, Afrotropic, and Australasian deserts, respectively (Fig. 1). They are among the most heat-tolerant animals described to date (Marsh, 1985; Christian & Morton, 1992; Andersen, 2007; Wehner & Wehner, 2011; Boulay et al., 2017). Foragers of C. bombycina, O. robustior, and M. bagoti are active at midday and can thus withstand air temperatures exceeding 45°C and soil temperatures of 70°C. These species have evolved convergently an array of behavioural, morphological, and physiological adaptations to face these extreme conditions (see Sections III.2, IV.2, IV.3 & V.3).

Few social insects occur at higher latitudes, as cold conditions pose challenges for ectotherms (Heinze & Hölldobler, 1994; Addo-Bediako, Chown, & Gaston, 2000; Sunday, Bates, & Dulvy, 2011). That said, the ant *Leptothorax acervorum* inhabits the plains of the Siberian tundra, where nest temperatures can drop below -20° C in the winter (Heinze, Stahl, & Hölldobler, 1996). In termites, workers of *Reticulitermes flavipes* were found to remain active at temperatures as low as 5.7°C (Clarke, Thompson, & Sinclair, 2013). Workers of *Porotermes adamseni* and *Stolotermes victoriensis* display even greater cold tolerance: activity levels are maintained at temperatures as low as -5° C and -6° C, respectively (Lacey, Lenz, & Evans, 2010). These two species have low CT_{min} values and supercooling points (i.e. the temperature at which body fluids start to freeze; Ring, 1982).

(3) Altitudinal and urban-rural variation in thermal tolerance

Thermal conditions vary across altitudinal gradients. In several ant species, a negative correlation between CT_{min} and altitude has been reported (Bishop *et al.*, 2017; Baudier *et al.*, 2018). In bumblebees (*Bombus* spp.), species from higher altitudes are more cold tolerant than species from lower altitudes: they have lower CT_{min} values and are able to recover from cold exposure at air temperatures that are 3–4°C lower (Oyen, Giri, & Dillon, 2016).

Thermal conditions also vary between urban and rural areas. Urban areas often function as heat islands, with temperatures that are up to 12°C higher than in surrounding rural areas (Zele⊠áková *et al.*, 2015). As a result, thermophilic bee species have been able to expand their distribution ranges northward (Banaszak-Cibicka, 2014). Leaf-cutter ants (*Atta sexdens*) from urban areas tolerate higher temperatures than those from rural areas (Angilletta *et al.*, 2007). In the acorn ant (*Temnothorax curvispinosus*), populations from urban habitats have a slightly greater thermal range: CT_{min} and CT_{max} were 1°C higher in urban populations (Diamond *et al.*, 2017). A similar trend was documented in the honeybee (*Apis mellifera*; Sánchez-Echeverría *et al.*, 2019).

(4) Microhabitat and thermal tolerance

Species can have the same geographical range but display differences in thermal tolerance because they occupy different microhabitats. Such disparities are most commonly seen in species that live above versus below ground because soils can buffer temperature variation. A comparative study of thermal tolerance among Neotropical army ants (Ecitoninae) found that, compared to above-ground species, below-ground species were more thermosensitive and had lower CT_{max} values (Baudier et al., 2015). Comparable results were seen in leaf-cutter ants (Atta laevigata and A. capiguara; Bouchebti et al., 2015). In tropical forests, air temperature can be 8°C higher in the canopy than at ground level, and it was found that the CT_{max} of canopy ants was 3.5-5°C higher, on average, than the CT_{max} of species nesting in the shaded understorey (Kaspari et al., 2015).



Fig 1. Workers of the ant species (A) Cataglyphis holgerseni, (B) Ocymyrmex velox, (C) Melophorus bagoti, and (D) Pogonomyrmex californicus. These species are among the most heat-tolerant animals in the world and have evolved behavioural, morphological, and physiological adaptations to withstand the extremely hot temperatures of the deserts in which they live. Photograph credits: A and B, A. Kuhn; C, A. Wystrach; D, A. Wild.

Taken together, these observations indicate that thermal tolerance in social insects is greatly shaped by local environmental conditions.

III. BEHAVIOURAL ADAPTATIONS

Most ectotherms regulate their body temperature using behavioural adaptations (May, 1979; Kronenberg & Heller, 1982). In social insects, thermoregulation can occur at both societal and individual levels.

(1) Social thermoregulation

The ecological success of social insects is largely based on their ability to maintain climatic conditions in the nest that promote brood development. There is strong selective pressure on nest site location. Colonies can also benefit from situating their nests in or on top of the ground and covering them with leaves, stones, or pieces of wood for protection. When temperatures shift, social insects may then employ passive or active nest temperature regulation (Korb, 2003; Jones & Oldroyd, 2006).

(a) Passive nest thermoregulation

Nest temperature can be regulated passively using three mechanisms: nest orientation, architecture, and/or construction material (Gallé, 1973; Jones & Oldroyd, 2006;

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Kadochová & Frouz, 2014). Nests may be oriented so that the level of solar radiation intercepted corresponds to colony needs (i.e. to heat up the nest or keep the nest cool). In the winter and summer, when temperatures become more extreme, ant and termite workers can dig deeper into the ground for their colonies to be better buffered (Strack & Myles, 1997; Hu & Song, 2007; Bentley *et al.*, 2015).

The relationship between nest architecture and thermoregulation remains poorly understood in social insects even though it has been the focus of several studies. In termite nests, open ridges, turrets, and chimneys (Fig. 2A) play a central role in gas exchange; however, it is unclear whether or not thev contribute to nest thermoregulation (Turner, 1994; Turner & Soar, 2008). For example, obstructing ventilation has not been found to impair nest temperature regulation significantly. That said, in Africa, Macrotermes species construct mounds that are among the largest and most complex structures built by invertebrates (Fig. 2B), and ambient temperature clearly influences mound architecture because nests in cooler habitats do not contain ventilation structures and display reduced surface complexity. In M. bellicosus, the structure of large colonies allows to maintain a constant temperature in the nest independent of external temperature fluctuations and that is optimal for colony development (Korb & Linsenmair, 1998b, 2000). Recently, Vesala et al. (2019) demonstrated that mound size and ventilation type may have a major effect on nest temperature in M. subhyalinus. Large mounds with open ventilation systems always had relatively cooler nest temperatures, while small mounds with closed ventilation systems always had





Fig 2. Termite nests. (A) Open-chimney mounds built by an *Odontotermes* termite species in the Nkayamba Natural Forest Reserve, Burundi. Chimneys promote nest ventilation and, to a lesser extent, can be used in nest thermoregulation when thermal conditions are favourable. (B) Cathedral termite mound of *Macrotermes bellicosus* in the Parc National de la Comoé, Côte d'Ivoire. The yellow and white bar placed next to the mound indicates 1 m height. Photograph credits: A, Y. Roisin; B, J. Korb.

relatively warmer nest temperatures. These studies suggest that ventilation structures mainly ensure gas exchange but can also help contribute to nest thermoregulation when thermal conditions are favourable. By contrast, when thermal conditions are unfavourable, the use of these structures is limited to promote heat retention.

Nest wall thickness also appears to influence gas exchange and thermoregulation in *M. bellicosus* in Côte d'Ivoire) (Korb & Linsenmair, 1998*a*, 1999). Under favourable thermal conditions, nests have thin walls that enhance gas



Fig 3. Infrared thermogram of honey bees (*Apis mellifera*) on the central combs of a winter cluster at an ambient air temperature of 5.5° C. Some of the bees have warm thoraces (yellow and white spots). The heat they produce with their flight muscles helps keep the temperature at the outer surface of the cluster above $10-12^{\circ}$ C. At temperatures below 10° C, bee muscle function and respiration fail, and any afflicted individuals ultimately fall off the cluster. Modified from Stabentheiner *et al.* (2003). Photograph credit: A. Stabentheiner.

exchange. Under unfavourable thermal conditions, nests have thicker walls that limit heat loss, albeit at the expense of gas exchange. Wall thickness also appears to be key to nest temperature regulation in *Melipona* bees (Jones & Oldroyd, 2006). In warmer environments, workers build nests with thin walls, promoting heat dissipation; in cooler environments, they build nests with thick walls, enhancing heat retention.

Nest construction materials also greatly affect nest temperature. In colder areas, heat absorption and retention are important. In wood ants (*Formica rufa* group), nest mounds are made of pine and spruce needles, which absorb solar radiation and keep nest temperatures high (Rosengren *et al.*, 1987). Bumblebees (*Bombus* spp.) pile plant matter, such as grass, on top of their nests to improve insulation; they also build a canopy of wax over their nests to trap metabolic heat (Jones & Oldroyd, 2006). In warmer areas, it is important to be able to shunt heat away. Grass-cutter ants (*Acromyrmex* spp.) build thatched mounds and thus maintain thermal homeostasis in their nests by enhancing heat diffusion (Bollazzi & Roces, 2010).

Passive thermoregulation can also take place outside the nest via behavioural mechanisms. For example, workers of most termite species and many ant species forage underground in or around the nest (Hölldobler & Wilson, 1990; Traniello & Leuthold, 2000). In the hot central Australian desert, Ochetellus flavipes workers construct covered runways using sand and plant matter, which help shield them from solar radiation (Christian & Morton, 1992; Morton & Christian, 1994). In other species, foraging activity is modified based on daily temperature patterns: workers may forage in the morning and evening, when temperatures are more bearable [e.g. Monomorium vatranum (Marsh, 1988); Pogonomyrmex pronotalis (Pol & de Casenave, 2004)], or they may strictly



Fig 4. Infrared thermograms of a *Vespula* wasp showing the temperature of the thorax (Th) and the abdomen (Ab) during (A) normal conditions and (B) after the rapid contraction and release of the thoracic muscles to generate heat. H, head; W, wings. The ambient temperature was 42.5°C. Photograph credit: A. Stabentheiner, H. Kovac, and H. Käfer.

forage at night [e.g. Myrmecia pyriformis (Briese & Macauley, 1980); Monomorium salomonis (Narendra, Kamhi, & Ogawa, 2017)].

(b) Active nest thermoregulation

Nest temperature can also be actively regulated via behavioural mechanisms (Höcherl, Kennedy, & Tautz, 2016). In colder areas, social insects need to keep their nest warm. They can accomplish this via clustering: ants and bees have been observed to huddle close together (Rosengren et al., 1987). This behaviour, coupled with the metabolic heat produced via the rapid contraction and release of the workers' thoracic muscles, can increase nest temperature and maintain thermal homeostasis (Figs 3 and 4) (Coenen-StaB, Schaarschmidt, & Lamprecht, 1980; Jones & Oldrovd, 2006; Stabentheiner, Kovac, & Brodschneider, 2010; Käfer, Kovac, & Stabentheiner, 2012; Modlmeier et al., 2012; Kadochová & Frouz, 2014). Additionally, in the honeybee (Apis mellifera), nest temperature is kept stable through changes in insect density, with individuals entering or exiting the nest (Stabentheiner, Kovac, & Brodschneider, 2010). In wood ants (Formica spp.), workers leave the nest to bask in the sun; when they re-enter the nest, the heat stored in their bodies is released (Kadochová, Frouz, & Roces, 2017; Kadochová, Frouz, & Tószögyová, 2019).

Under heat stress, social insects need to cool their nests. Workers are known actively to fan hot air out of their nests in the honeybee (*Apis mellifera*; Jones *et al.*, 2004), bumblebees [*Bombus huntii* (O'Donnell & Foster, 2001); *B. bifarius* (Gardner, Foster, & O'Donnell, 2007); *B. terrestris* (Weidenmüller, 2004; Westhus *et al.*, 2013)], and wasps (*Polistes biglumis*, A. Stabentheiner, H. Kovac & H. Käfer, personal communication). Furthermore, in the honeybee, workers may act as 'heat shields', positioning themselves on the hottest parts of the hive's walls to protect the brood from overheating (Starks & Gilley, 1999). Additionally, the proportion of workers serving as water foragers can increase (Bordier *et al.*, 2017), and they may spread water around the comb, allowing evaporative cooling (Li *et al.*, 2018). Evaporative cooling is also used by a paper wasp (*Polistes biglumis*): workers have been seen to regurgitate droplets of fresh water into nest cells so as to prevent overheating (Fig. 5) (A. Stabentheiner, personal communication).

(2) Individual thermoregulation

Ants, bees, and wasps also display individual thermoregulation mechanisms. To warm up, workers can absorb solar radiation (Heinrich, 1974, 1995; Jones & Oldrovd, 2006; Kovac, Stabentheiner, & Schmaranzer, 2010; Stabentheiner et al., 2012; Kovac, Käfer, & Stabentheiner, 2019). In the honeybee (Apis mellifera), workers can remain in a hive cell and increase their metabolic activity via rapid and continuous respiration (Kleinhenz et al., 2003). By contrast, when workers need to cool down because their body temperature is over the thermal optimum $(\pm 35^{\circ}C)$, they can shunt excess heat into their abdomens, which is then dissipated through intersegmental membranes, allowing convective cooling (Coelho, 1991; Guo et al., 2018). They can also regurgitate gut fluids, expelling the heat they contain and enhancing evaporative cooling (Cooper, Schaffer, & Buchmann, 1985; Coelho, 1991). This regurgitation behaviour is also seen in Vespula social wasps and can decrease head temperature by 4°C (Coelho & Ross, 1996).

Among all of the workers in a colony, foragers face the greatest thermal risks. In arid or semi-arid regions, environmental temperatures may be at or above the lethal limits for most species. Workers in the thermophilic ant genera Cataglyphis, Melophorus and Ocymyrmex actively use thermal refuges to avoid overheating (Marsh, 1985; Christian & Morton, 1992). These refuges are usually shadows, but may also be slightly elevated points, where the air temperature is cooler. Just 4 mm above the ground, air temperature may be 5-10°C lower (Marsh, 1985; Wehner, Marsh, & Wehner, 1992; Sommer & Wehner, 2012). In the Namib desert, where soil temperatures may exceed 67°C, Ocymyrmex *robustior* foragers can drop their body temperature by 6°C within 7 s by using thermal refuges (Marsh, 1985); when they are out foraging, workers spend as much as 50% of their time in thermal refuges, thus avoiding the risk of muscle paralysis and death (Fig. 6).

A remarkable trait seen in some desert ants is the ability to raise their gasters to a vertical position (Fig. 7). This ability is associated with the presence of a nodiform or cubiform (rather than a squamiform) petiolus. It is characteristic of *Cataglyphis* species in the *bicolor* and *albicans* groups and is also seen in *Melophorus bagoti* (R. Perez, personal observations). It has long been considered that lifting the gaster in this way, and thus maximising its distance from the hot ground, is a strategy for reducing the risk of overheating (Cerdá & Retana, 2000). Another non-mutually exclusive explanation is that raising the abdomen reduces an individual's moment of inertia, facilitating dynamic changes in direction and allowing desert ants to run faster along tortuous paths (McMeeking, Artz, & Wehner, 2012).



Fig 5. Infrared thermogram of a nest of the paper wasp *Polistes* biglumis. This wasp is commonly found in montane habitats. Its nests are built to face east-southeast for maximum exposure to the morning sun, which helps speed up brood development. To prevent the brood from overheating during the warmer parts of the day, individuals use fanning (note the wasp on top of the nest) and spread water droplets (black spots) to cool the nest convectively and evaporatively, respectively (A. Stabentheiner, unpublished data). Photograph credit: A. Stabentheiner, H. Kovac, and H. Käfer.

IV. MORPHOLOGICAL ADAPTATIONS

(1) Body size

Bergmann's rule (Bergmann, 1847) states that thermal tolerance should be positively correlated with body size. Evidence supporting this prediction has been observed in a broad range of endotherms: within species or among closely related species, larger individuals with greater body mass are predominantly found in colder environments, while smaller individuals with lower body mass are predominantly found in warmer environments. Although Bergmann's rule has been upheld in a number of different species, there are certain groups of organisms in which body size is not correlated with latitude because specific thermoregulatory mechanisms and/or other factors are present (Ashton, Tracy, & de Queiroz, 2000; Gohli & Voje, 2016; Salewski & Watt, 2017; Nwaogu et al., 2018). For ectotherms in general, and social insects in particular, this hypothetical relationship between thermal tolerance and body size remains a source of debate, and no general pattern has been observed among taxa (Atkinson, 1994; Mousseau, 1997; Zamora-Camacho, Reguera, & Moreno-Rueda, 2014; Makaure, Caston, & Sithole, 2015; Ramírez-Delgado et al., 2016; Santo & Lobel, 2017). A recent study analysed more than 140,000 distribution records for 615 bee species across a broad altitudinal gradient (Gérard et al., 2018). Taking into account seasonal variation, social organisation, and life-history traits, it showed that variation in body size was generally consistent with Bergmann's rule. In ants, Aphaenogaster iberica workers have been found to be larger at higher latitudes (Shik et al., 2019). Furthermore, in a number of social insect



Fig 6. Relationship between sand surface temperature and the frequency of thermal refuge used by foragers of the Namib ant *Ocymprmex barbiger*. During thermal-respite behaviour, the ants stay in the shade or climb on a object above the ground. The great majority of pauses ranges between 0 and 20 s (modified from Marsh, 1985).

species, researchers have observed a positive relationship between body size and heat tolerance, where larger workers were more heat resistant than smaller workers [ants (Cerdá & Retana, 1997, Cerdá & Retana, 2000, Clémencet *et al.*, 2010, Oberg, del Toro, & Pelini, 2012, Baudier *et al.*, 2015, Baudier & O'Donnell, 2016, 2017, Wendt & Verble-Pearson, 2016); termites (Janowiecki *et al.*, 2019)].

However, these relationships are not consistent. In an extensive study on ants in eastern North America, there was no relationship between body size and latitude (Geraghty, Dunn, & Sanders, 2007). In another study on wasps (Polistes versicolor, Polybia ignobilis and Polybia paulista), there was no association between body size and thermal tolerance (Michelutti et al., 2018). On the Iberian Peninsula, thermal tolerance in ants was similar for small workers (4.5 mm long) of Cataglyphis rosenhaueri and large workers (12 mm long) of C. velox (Cerdá & Retana, 2000). A study that looked at 14 North American ant species from 12 genera even found the surprising result that CT_{max} was negatively correlated with body size (Verble-Pearson, Gifford, & Yanoviak, 2015). The same negative relationship was found in a comparative study examining 37 bee species (some solitary, some social) from five families (Peters, Peisker, &



Fig 7. *Cataglyphis cubica* worker with (A) a vertically raised gaster and (B) an unraised gaster. It is thought that workers hold their gasters in this vertical position to increase gaster distance from the hot ground and to facilitate dynamic changes in direction. Photograph credit: R. Perez.

Steffan-Dewenter, 2016). The reasons for such discrepancies remain unclear.

Research on the relationship between cold tolerance and body size in social insects is less extensive but has yielded similarly inconsistent results. In the fire ant (*Solenopsis invicta*), larger workers appear to be less cold tolerant: their supercooling point is 3°C higher than that of smaller workers (Hahn, Martin, & Porter, 2008). The opposite pattern was documented in Alaskan bees, where larger workers display greater cold tolerance (Bishop & Armbruster, 1999).

Overall, these observations show that body size is not consistently associated with thermal tolerance in social insects. They underscore that thermal tolerance involves adaptations above and beyond simple radiative heat transfer.

(2) Leg length

Desert ants in the genera *Cataglyphis*, *Ocymymex*, *Melophorus* and *Pogonomymex* convergently evolved legs that are relatively long for their body size (Fig. 1). As a result, foragers can hold their bodies up off the hot ground; an increase of just a few millimetres in leg length can reduce the air temperature surrounding the body by as much as 4°C (Sommer & Wehner, 2012; Centorame *et al.*, 2019). In addition, longer legs allow foragers to run faster, thereby maximising convective cooling and reducing the time spent outside the nest (Hurlbert, Ballantyne, & Powell, 2008; Sommer & Wehner, 2012; Pfeffer *et al.*, 2019). Valley carpenter bees (*Xylocopa varipuncta*) also use active convective cooling to fly at very high temperatures without overheating (Heinrich & Esch, 2018).

(3) Hair

One of the most remarkable morphological adaptations for dealing with extreme thermal conditions can be seen in the Saharan silver ant *Cataglyphis bombycina* (Fig. 8; Shi *et al.*, 2015; Willot *et al.*, 2016). In workers of this species, the dorsal sides of the head, thorax, and abdomen are covered with densely packed hairs with a highly specialised

structure. This coat of hairs is responsible for the ant's silvery appearance and, more importantly, allows the ant to contend with extremely high temperatures. First, the hairs have a prism-like shape, which maximises the amount of light that is reflected off their surfaces via a combination of scattering and total internal reflection (i.e. light bounces off the hair's bottom plane and back out through one of the sides, away from the body). This fact, combined with the high hair density, means that little light reaches the body surface. Second, the hairs reflect light mostly in the visible and near-infrared range, two regions of the electromagnetic spectrum where solar radiation is the most powerful. Third, the hairs' shape also allows the ant to offload heat by emitting radiation in the mid-infrared range. Taken together, these effects result in extraordinary thermoregulatory abilities, enabling C. bombycina foragers to maintain non-lethal body temperatures despite the extreme heat of their natural environment.

In cold environments, flying insects need to have warm thoracic muscles to produce enough power to fly (Roberts & Harrison, 1998; Weiner *et al.*, 2011). Bumblebees have flight muscles capable of intense metabolic activity: they produce enough heat to allow flight during mild winters (Heinrich, 1974, 1993). The heat generated by these flight muscles is retained due to the hairs covering the thorax, which limit heat loss (Church, 1960; Heinrich & Esch, 2018). Hair length is positively correlated with cold tolerance (Peters, Peisker, & Steffan-Dewenter, 2016).

V. PHYSIOLOGICAL AND MOLECULAR ADAPTATIONS

When behavioural and morphological adaptations fail to provide sufficient protection against thermal conditions, physiological adaptations can be used to mitigate thermal stress. Diapause-related cold adaptations have been extensively reviewed in both social (Cannon & Fell, 1992; Berman *et al.*, 2010) and solitary (Denlinger, 1991; Pullin, 1996; Koštál, 2006) insect species, and we will not address them here. Apart from diapause, physiological



Fig 8. Saharan silver ant Cataglyphis bombycina workers are covered in hairs with highly specialised thermoregulatory qualities. (A) Workers have a metallic sheen when exposed to sunlight. (B) The ant's silvery appearance results from the dense array of hairs that cover the dorsal side of the head, thorax, and abdomen. (C) With their triangular shape, the hairs act as prisms and maximise the amount of light that is reflected off their surfaces via a combination of scattering and total internal reflection (i.e. light bounces off the hair's bottom plane and back out through one of the sides, away from the body). They notably reflect light in the visible and nearinfrared range and also offload heat by emitting radiation in the mid-infrared range. These effects help explain the remarkable thermoregulatory abilities of workers (Shi et al., 2015; Willot et al., 2016). Photograph credit: A, H. Darras; B and C, P. Simonis.

and molecular adaptations to thermal stress remain poorly studied in social insects. Below, we discuss the adaptive mechanisms that have received the most attention, namely those involving cuticular hydrocarbons, cryoprotectants, membrane components, heat shock proteins, and antioxidants.

(1) Cuticular hydrocarbons (CHCs)

One of the most harmful effects of heat stress is desiccation (Neven, 2000; Woon et al., 2019). Insects have cuticles that are covered by a viscous wax of hydrophobic hydrocarbons (mostly long-chain hydrocarbons containing 20-35 carbon atoms) that likely evolved to prevent water loss and to protect against infection (Blomquist & Bagnères, 2010; Ferveur et al., 2018). Typical compounds include n-alkanes, alkenes, and methyl-branched alkanes. The degree to which the cuticle is waterproof depends on alkane and alkene type and relative abundance. Greater alkane abundance and length result in lower water loss. In accordance with these physiological findings, researchers observed that four thermophilic ants (Cataglyphis livida, C. velox, C. mauritanica and C. niger) had relatively greater amounts of long linear alkanes in their CHC profiles than did the common red ant (Myrmica rubra), which lives in temperate regions (Lenoir et al., 2009). In the North American seed-harvester Pogonomyrmex barbatus, foragers and patrollers have a higher proportion of *n*-alkanes in their CHC profiles than do workers who remain in the nest (Wagner, Tissot, & Gordon, 2001). More recent work has shown that experimentally induced thermal stress can increase the production of long linear cuticular alkanes in ants [Temnothorax longispinosus and T. ambiguous (Menzel, Zumbusch, & Feldmeyer, 2017); Myrmica rubra and M. ruginodis (Sprenger et al., 2018)], termites (Cryptotermes brevis; Woodrow et al., 2000), and wasps (Polistes versicolor, Polybia ignobilis and Polybia paulista; Michelutti et al., 2018).

(2) Cryoprotectants and membrane composition

It is well documented that insects can cope with cold stress by producing various metabolites and by changing the composition of their cell membranes (Block, 1990; Lee *et al.*, 2006). However, few studies have explored the use of such mechanisms in social species. Two cold-adapted termites (*Porotermes adamsoni* and *Stolotermes victoriensis*) display seasonal fluctuations in trehalose production, with levels being higher in the winter (Lacey, Lenz, & Evans, 2010). Like glycerol, trehalose decreases the supercooling point and protects cells from freezing (Storey & Storey, 1997; Lee, Chang, & Kim, 2002). Similarly, in paper wasps (*Polistes exclamans* and *P. annularis*), workers synthesise high levels of trehalose in the haemolymph after prolonged exposure to cold stress (Strassmann *et al.*, 1984).

Temperature can also affect the fluidity of cell membranes: heat stress makes membranes more fluid, while cold stress stiffens them. It is crucial that membrane fluidity remains optimal to ensure cellular homeostasis and the membrane molecular roles. There are two mechanisms for maintaining membrane function (Quinn, 1988; Overgaard *et al.*, 2005; Dufourc, 2008). First, during heat stress, cells can increase levels of saturated fatty acids and sterols



Fig 9. Schematic representation of how heat shock proteins (Hsps) operate. Small heat shock proteins (sHsps) help prevent the aggregation of denatured proteins by binding to hydrophobic residues. Hsp70, with Hsp40 as a co-factor, binds to denatured proteins, initiating a process that facilitates their return to a partially unfolded form or to their native state. If the protein remains partially unfolded, the process can be repeated until folding is completed. The Hsp40–Hsp70–Hsp100 complex solubilises protein aggregates so that the proteins unfold. The unfolded proteins are then subjected to various forms of proteolysis, like the ubiquitin–proteasome system in which proteins are degraded by a complex of proteases following conjugation with multiple ubiquitin molecules. The 'catalytic core' of the complex is a complex of proteases known as the proteasome.



Fig 10. Relative expression of thermoprotective genes in mesophilic (solid line) and thermophilic (hatched line) species subject to different temperature treatments. Thermophilic species had a higher induction threshold for heat shock protein genes *hsp*, and gene expression continued at higher temperatures.

(cholesterols), rendering the cytoplasmic membrane and organelle membranes more rigid. To the best of our knowledge, changes in cell membrane composition in response to heat stress remain completely unstudied in social insects. Second, during cold stress, cells can increase levels of unsaturated fatty acids, rendering membranes more fluid. In this case, high levels of unsaturated fatty acids have been observed in cold-adapted termites (*Stolotermes victoriensis*; Lacey, Lenz, & Evans, 2010) and bumblebees (*Bombus vosnesenskii*; Keaveny *et al.*, 2019). In ectotherms, one adaptation to cold conditions is significantly to increase mitochondrial density, which enhances heat production (Johnston & Dunn, 1987; Lane, 2018). In honeybee (*Apis mellifera*) populations adapted to colder climates, major energy-producing mitochondrial pathways were found to be upregulated (Parker *et al.*, 2010). In both ants (*Aphaenogaster iberica*; Shik *et al.*, 2019) and wasps (*Polistes dominula*, Kovac *et al.*, 2017), workers from populations found at higher altitudes had higher metabolic rates than did workers from populations found at lower altitudes.

(3) Heat shock proteins

Just like other environmental and physiological stressors such as pathogens, ultraviolet rays, pesticides, ageing, dehydration, and food deprivation, thermal stress can disturb the thermodynamic equilibrium of macromolecules (e.g. DNA, RNA, proteins) and can eventually cause proteins to become denatured, lose biological function, and form aggregates Garbuz, & Zatsepina, (Evgen'ev, 2014;Nguyen et al., 2017). Protein denaturation triggers the synthesis of molecular chaperones that are responsible for preventing and/or repairing cell damage (Evgen'ev, Garbuz, & Zatsepina, 2014). Heat shock proteins (Hsps) are a crucial type of molecular chaperone. They belong to several subfamilies, the most common being Hsp100, Hsp90, Hsp70, Hsp60, Hsp40, and Hsp20 (i.e. small Hsps) (Lindquist & Craig, 1988; Feder & Hofmann, 1999; Wirth *et al.*, 2002; Evgen'ev, Garbuz, & Zatsepina, 2014). Their primary roles are to (i) transport newly formed proteins, (ii) stabilise the optimal conformations of newly formed proteins, (iii) promote three-dimensional refolding of denatured proteins due to cellular stresses, and (iv) facilitate the degradation of aggregated proteins (Fig. 9) (Feder & Hofmann, 1999; Sørensen, Kristensen, & Loeschcke, 2003; Evgen'ev, Garbuz, & Zatsepina, 2014).

In ectotherms, *hsp* gene expression dynamics differ among species and populations based on local thermal conditions and life-history strategies (Krebs & Bettencourt, 1999; Evgen'ev, Garbuz, & Zatsepina, 2014; Stucki, Freitak, & Sundström, 2017). For instance, thermophilic species usually display higher gene induction thresholds, and they continue to express thermoprotective genes at much higher temperatures (Fig. 10). Consistent with this finding, workers of a thermophilic seed-harvester ant species (Pogonomyrmex barbatus) displayed greater constitutive expression and induction of hsp genes (hsp83, hsc70-4 h1, hsc70-4 h2, and hsp 40) in response to heat stress, compared to workers of a species found in more mesic habitats (Aphaenogaster picea) (Nguyen, Gotelli, & Cahan, 2016; Stanton-Geddes et al., 2016). In a study comparing *Cataglyphis* ants, constitutive expression of hsp70 was found to be correlated with local thermal conditions (Willot, Gueydan, & Aron, 2017; Willot et al., 2018). Workers of the Saharan silver ant (C. bombycina) had high constitutive levels of Hsp70, even when they were in the nest, where the temperature was around 25°C (Gehring & Wehner, 1995; Willot, Gueydan, & Aron, 2017). This feature is thought to be a physiological adaptation that, in addition to behavioural and morphological traits (see Sections III.2, IV.2 & IV.3), allows workers to cope immediately with the extreme temperatures that they face when they leave the nest to forage. By contrast, C. mauritanica workers from the Atlas Mountains, where the climate is semi-arid and cold, were found to have lower constitutive levels of Hsp70. Similarly, in the thermophilic ant species Formica cinereal, expression patterns of hsp90, hsp75 and hsp60 did not differ between foraging workers and their nestmates in the nest, suggesting that constitutive levels of Hsps are always high to

allow foragers safely to face the abrupt change in temperature when they leave the nest (X lipiński, Pomorski, & Kowalewska, 2015). Thus, it appears that higher constitutive levels of thermoprotective Hsps have been selected for in species inhabiting high-temperature environments (Gehring & Wehner, 1995; Moseley, 1997; Cahan *et al.*, 2017; Willot, Gueydan, & Aron, 2017).

The physiological role of *hsp* upregulation as part of the response to occasional thermal stress remains poorly studied in social insects (Table 1). In the Saharan silver ant (C. bomby*cina*), heat stress induces strong upregulation of *hsp* genes (Willot et al., 2018), including hsc70-5 and hsp60, which encode Hsps involved in safeguarding mitochondrial integrity and function; unc-89, which encodes proteins involved in sarcomere assembly and organisation; and l(2)efl (from the Hsp20 family), which encodes proteins that affect the structural integrity of the cytoskeleton, organelle morphology, and the myofilaments. In this ant, it is crucial that muscle function is both structurally and metabolically maintained given that individuals need to run at high speeds to enhance convective cooling, reach thermal refuges as quickly as possible, and limit the time spent foraging on hot ground (Sommer & Wehner, 2012; Boulay et al., 2017; Willot et al., 2018). In the eastern honeybee (Apis cerana), upregulation of DnaJC3 (a member of the Hsp40 family) has been observed in the muscles and epidermis during both cold and heat stress (Zhang et al., 2014; Zhang et al., 2019). Apis mellifera honeybees have extremely thermotolerant thoracic muscles (Elekonich, 2009). The expression of hsp70 is 10 times greater in the flight muscles of foragers capable of flight than in the flight muscles of one-day-old bees incapable of flight. Thoracic muscles can become extremely hot during foraging trips in the summer and have evolved to display exceptional thermostability relative to other tissues. In the ants Myrmica ruginodis and M. rubra, hsp70 expression seems to be a key component of cold adaptation in the species' northernmost populations (Maisov, Podlipaeva, & Kipvatkov, 2007).

The production of thermoprotective molecules (e.g. Hsps, antioxidants) following exposure to non-lethal albeit stressful temperatures often equips individuals to tolerate subsequent incidents of extreme thermal stress better. Heat- or cold-hardening (as a result of acclimatisation to high or low temperatures, respectively) greatly enhances the plasticity of thermal tolerance (Bowler, 2005; Jensen *et al.*, 2019). The ability to regulate *hsp* genes following heat stress remains poorly studied in social insects. To date, only a few ant species [*Aphaenogaster picea* and *A. rudis* (Cahan *et al.*, 2017); *Cataglyphis mauritanica* (Willot, Gueydan, & Aron, 2017)] are known to display heat-hardening in association with the upregulation of genes in the *hsp70* family.

(4) Antioxidants

Reactive oxygen species (ROS) are the byproducts of mitchondrial oxygen metabolism and can lead to the toxic oxidation of cell compounds. ROS are usually produced in small Table 1. Major behavioural, morphological and physiological/molecular mechanisms underlying thermal tolerance in social insects. For heat-shock proteins (Hsps), changes in expression of *hsp* genes after a heat or a cold stress are shown. The number of transcripts (isoforms + identified genes) is indicated in parentheses. Data based on different methodological approaches [RNA-sequencing or real-time quantitative PCR (RT-qPCR)] according to studies. n/a, no data available

Adaptive responses					
Cold stress	Ants	Bees	Wasps	Termites	
Behavioural	workers cluster close to each other to maintain thermal homeostasis; workers bask in the sun, then re-enter the nest where heat is released; dig deeper into the ground to buffer extreme temperatures; use of nest construction materials that absorb solar radiation	workers cluster close to each other to maintain thermal homeostasis; workers bask in the sun to absorb solar radiation; use of nest-construction materials to trap metabolic heat	workers bask in the sun to absorb solar radiation	subterranean lifestyle; orientation of the nest to increase solar radiation; building nests with thick walls to limit heat dissipation	
Morphological Physiological	n/a enhanced metabolic heat <i>via</i> contraction of thoracic muscles; production of Hsps [<i>hsp70</i> (2)]	fur coat limiting heat loss enhanced metabolic heat <i>via</i> contraction of flight muscles; production of antioxidants (proline, ascorbate dismutase); increased synthesis of unsaturated fatty acids in cellular membranes; production of Hsps [<i>hsp90</i> (1); <i>hsp70</i> (2); <i>hsp60</i> (1): <i>hsp40</i> (1): <i>shs</i> (4)]	n/a production of trehalose	n/a production of trehalose; increased synthesis of unsaturated fatty acids in cellular membranes	
Heat stress Behavioural	Ants use of thermal refuges to enhance heat dissipation; workers run at high speed allowing convective cooling; dig deeper into the ground to buffer extreme temperatures; use of nest-construction materials that protect from solar radiation; changes in timing of forgaging activity	(1), <i>hspto</i> (1), <i>stap</i> (4)] Bees workers fly at high speed to force convective cooling; wing fanning to increase convective cooling; regurgitation of gut fluids to enhance evaporative cooling; protection of the brood by the body of the workers	Wasps wing fanning to increase convective cooling; regurgitation of gut fluids to enhance evaporative cooling; spread of water droplets to increase evaporative cooling	Termites orientation of the nest to limit sun exposure; dig deeper into the ground to buffer extreme temperatures; construction of nests whose structure favours heat dissipation	
Morphological	prismatic hairs that maximise reflection of solar radiation; long legs increase distance of the body from the hot ground and allow foragers to run faster thereby maximising convective cooling; capability to hold the gaster in the vertical position to increase its distance from the hot ground	n/a	n/a	n/a	
Physiological	production of large amounts of long linear alkanes in the cuticular	production of antioxydants (gluthatione reductase, gluthatione peroxidase,	production of large amounts of long linear alkanes in the CHC	production of large amounts of long linear alkanes in the CHC	

(Continues)

Table 1. (Cont.)

Adaptive responses						
Cold stress	Ants	Bees	Wasps	Termites		
	hydrocarbons (CHCs) reducing water loss; production of Hsps [<i>hsp90</i> (4); <i>hsp70</i> (18); <i>hsp60</i> (2); <i>hsp40</i> (3); <i>shsp</i> (2)]	superoxide dismutase, catalase carboxylesterase, clofenotane dehydrochlorinase, cytochrome P450 (CYP450), gluthatione transferase, acetyl cholinesterase, phosphoprotein 1, vitellogenin); production of Hsps [hsp90 (2); hsp70 (6); hsp60 (1); hsp40 (1); shsps [1]]	profile reducing water loss	profile reducing water loss		

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quantities and eliminated by antioxidant defences (e.g. superoxide dismutase, gluthathione, ascorbic acid, proline). Environmental and physiological stressors can disrupt macromolecules and cause reactions in the electron transport chain to fail, resulting in the increased production of ROS, which antioxidant defences are incapable of handling (Birben et al., 2012; Gagné, 2014; Slimen et al., 2014). Among the various antioxidant defences, proline captures ROS produced during cell stress, preventing them from carrying out toxic oxidation (Hayat et al., 2012). High levels of proline have been observed in high-latitude populations of bumblebees (Bombus vosnesenskii; Keaveny et al., 2019). In the honeybee (A. mellifera), heat stress induces the upregulation of genes encoding the antioxidant enzyme ascorbate dismutase (POD) and the detoxification enzyme cytochrome P450 (CYP450) (Ma et al., 2019). It was also found that, following heat stress, the honeybee (A. mellifera) and the eastern honeybee (A. cerana) had enhanced activity levels for several antioxidant enzymes [gluthatione reductase (GSR), POD, gluthatione peroxidase (GPX), superoxide dismutase (SOD), and catalase CAT)] and detoxification enzymes [carboxylesterase (CES), clofenotane dehydrochlorinase DDTase, CYP450, gluthatione transferase (GST), and acetyl cholinesterase (AchE)] (Li et al., 2019). In addition, heatstressed honeybee workers overproduced stress-induced phosphoprotein 1 (STIP1) and vitellogenin, two proteins involved in defence against oxidative stress (e.g. STIP1 interacts with Hsp70 and Hsp90) (Bordier et al., 2017; Zhai et al., 2018).

VI. DISCUSSION AND FUTURE DIRECTIONS

Sociality allowed insects to evolve thermoregulatory mechanisms rarely found in non-social species. Social insects can precisely regulate nest temperatures thanks to collective mechanisms (nest location, architecture, and construction material) and individual mechanisms (e.g. behaviour). Workers vary in their response thresholds and intensities, which generates pronounced plasticity that colonies can exploit to control nest temperature and to cope with fluctuating thermal conditions in their environment. Such differences among individuals may stem from genetic and/or epigenetic variability (Weitekamp, Libbrecht, & Keller, 2017) or could be rooted in variable past exposure to heat stress (e.g. Westhus et al., 2013). These thermoregulatory abilities could have been selected for, at least in part, because social insect colonies are typically sedentary and rarely relocate to areas with more favourable thermal conditions. Compared to solitary species, social species can also benefit from the polymorphism of their workers. Variation in worker body size is common in both ants and termites. It is likely that both body size and variation in body size are under strong selection because they influence the effectiveness of activities like foraging behaviour, prey selection, defence, and/or competitive interactions and thus shape colony fitness (Davidson, 1978; Oster & Wilson, 1978; Powell, 2009; Wills et al., 2018). In ants, worker size polymorphism has been shown to expand the thermal window during which colonies can be active since workers with different body sizes have different thermal limits and different heating or cooling rates. As a result, colonies can spend more time foraging during the day or across seasons, increasing colony output (Kaspari & Vargo, 1995; Cerdá & Retana, 1997; Baudier & O'Donnell, 2017). While worker size polymorphism may be a trait unique to social species, there are morphological characteristics that evolved convergently in both solitary and social insects to aid with thermoregulation. For example, elongated limbs that allow individuals both to lift their bodies up off the hot ground and to run at incredibly high speeds are common in social insects (e.g. Cataglyphis, Ocymyrmex, Melophorus and Pogonomyrmex ants) and solitary insects (e.g. Stenocara gracilipes and Onymacris plana beetles) that inhabit hot deserts (Medvedev, 1965; Nicolson, Bartholomew, & Seely, 1984; Sommer & Wehner, 2012).

Although sociality may have pronounced thermoregulatory benefits, it may also result in significant trade-offs, as illustrated by CHCs. In insects and other arthropods, CHCs can help limit water loss and the risk of desiccation (Blomquist & Bagnères, 2010; Moussian, 2013). CHC quantity and composition vary greatly based on abiotic and biotic environmental conditions (Gefen et al., 2015; Nation, 2015; Otte, Hilker, & Geiselhardt, 2018). In social insects, CHCs also serve as signals, largely in the context of nestmate recognition (Greene & Gordon, 2003; d'Ettorre & Lenoir, 2010; Leonhardt et al., 2016). In insects, CHCs are synthesised in fat bodies. They are then transported to the cuticle, although they can pass through the postpharyngeal gland, which serves as a *gestalt* organ that facilitates odour exchange among nestmates. Since termites do not possess such a gland, their CHCs are probably shipped directly to the cuticle (Billen & Morgan, 1998; d'Ettorre & Lenoir, 2010). CHCs can be linear alkanes as well as branched alkanes. While the former are best for waterproofing, the latter convey more information. Hence, workers may be affected by a trade-off between their ability to limit heat stress and their ability to communicate, which is a key component of social life.

Molecular and physiological adaptations for coping with extreme thermal conditions have been well conserved over the course of evolution and are seen in organisms ranging from bacteria to humans (Neven, 2000; Evgen'ev, Garbuz, & Zatsepina, 2014). Solitary and social insects employ the same molecular mechanisms to enhance cold tolerance: increased metabolic rates, synthesis of cryoprotectants, and changes in membrane composition (Strassmann et al., 1984; Zachariassen, 1985; Block, 1990; Roberts & Harrison, 1998; Sinclair et al., 2003; Lacey, Lenz, & Evans, 2010; Kadochová & Frouz, 2014). Furthermore, species occupying similar habitats have evolved the same gene expression dynamics in response to thermal stress. For example, a large study comparing several species of Diptera from four families showed that more heat-tolerant species had higher levels of basal hsp expression than did less heattolerant species (Garbuz et al., 2008; Zatsepina et al., 2016), a pattern that has also been observed in social insects (Gehring & Wehner, 1995; Willot, Gueydan, & Aron, 2017).

The emergence of new DNA sequencing techniques should allow us to make considerable progress in identifying how ecological factors affect gene structure, expression, and evolution. In tandem with the results of proteomics studies exploring protein composition, structure, and function, we should be able to achieve new breakthroughs in our understanding of how organisms adapt to static and shifting thermal conditions. For example, recent research has highlighted the role of intrinsically disordered proteins (IDPs), which lack a folded structure and do not decline in solubility at elevated temperatures, in the remarkable thermal tolerance of tardigrades (Tantos, Friedrich, & Tompa, 2009; Boothby et al., 2017). Variation in the spatial distribution and number of copies of hsps, which likely resulted from adaptation to contrasting thermal environments, has also been documented in insects (Garbuz et al., 2011) and nematodes (Jones et al., 2018). In social insects, research examining genomic and proteomic variation in response to ecological conditions is still in the early stages compared to in other organisms. Next-generation sequencing could be used to analyse large numbers of proteins from warm- and cold-adapted species with a view to identifying structural changes associated with thermal adaptations, such as differences in the proportion of non-covalent bonds and the presence of certain types of amino acids. Comparative analyses of genomic variation in populations of the same species found in contrasting habitats (and thus subject to different thermal pressures) should help identify candidate genes and the potential genetic modifications (e.g. mutations, duplications, genetic rearrangements) that are involved in shaping adaptations that enhance thermal tolerance. Ultimately, such studies could help elucidate how populations adapt to different thermal environments.

In addition to genomics and proteomics studies, differential gene expression (DGE) analyses can be used to identify both qualitative (e.g. genetic diversity, isoforms, molecular functions, and cellular functions) and quantitative (e.g. the number of genes that are differentially expressed) differences in responses to environmental pressures in a variety of organisms, including plants, insects, molluscs, crustaceans, and fish (Ye et al., 2014; Zhao et al., 2014; Cañas et al., 2015; Faddeeva et al., 2015; Cheng, Hui, & Sha, 2019; Jesus et al., 2019). In recent years, DGE studies in social insects have highlighted a number of genes that are involved in colony organisation and adaptation to environmental constraints (Ferreira et al., 2013; Helmkampf et al., 2016; Lucas, Romiguier, & Keller, 2017; Willot et al., 2018; Holman et al., 2019). However, such studies remain fairly rare, and many taxa are currently ignored. For example, in social insects, only a single study has examined DGE in response to cold stress (Xu et al., 2017). Furthermore, little is known about how termites and wasps have adapted to deal with thermal stress (Table 1). Indeed, although most termite species occur in the tropics and are adapted to stable warm temperatures, the few studies on termite thermotolerance have been carried out on cold-tolerant species. Furthermore, comparative studies that explore whether exposure to similar environmental conditions has led to the evolution of convergent or divergent traits in different lineages remain scarce for social insects. We therefore encourage researchers to compare heat shock responses among phylogenetically close species native to different climatic zones and among phylogenetically distant species occupying the same types of habitats. Furthemore, while tissue-specific gene expression (TGE) has been used investigate thermal tolerance in insects (e.g. Krebs & Feder, 1997; Singh & Lakhotia, 2000; Duman, Verleye, & Li, 2002; Keshan et al., 2014), few studies have looked at correlations between gene expression patterns and ecophysiological factors. For example, TGE data for muscle or nervous tissue could provide major insights into how highly thermophilic species, such as desert ants and bees, can maintain high running or flying speeds despite the crippling effects of extreme heat in their environments.

We also wish to highlight the need for functional approaches based on RNA interference (RNAi) or pharmacological inhibitors that can be used to identify gene variants and proteins involved in the thermal stress response in social insects. However, RNAi-based approaches present certain challenges since, for example, Hsps are not produced exclusively in response to thermal stress. Consequently, artificially inhibiting their levels may greatly affect other functions, including some of potentially vital importance to cells. Future research should also aim to clarify the roles of certain metabolic products. For example, trehalose is the key carbohydrate used by flying insects for storing energy. It has also been found to play a role in resistance to desiccation and thermal stress in yeasts, fungi, plants, and animals (Eleutherio, Araujo, & Panek, 1993; Doehlemann, Berndt, & Hahn, 2006; Iordachescu & Imai, 2008; Jin et al., 2018). However, the physiological significance of this compound for the heat stress response remains completely unstudied in social insects. Clearly, if we wish to predict better how social insects will respond to climatic shifts, which will affect their future distributions, we need a better understanding of the behavioural, morphological, and physiological mechanisms underlying adaptations to thermal stress, thermal tolerance, and the degree of plasticity in thermal tolerance.

VII. CONCLUSIONS

(1) Social insects are found in most terrestrial ecosystems, from the subarctic tundra to the hottest deserts. This fact underscores their high degree of thermal adaptability.

(2) In addition to utilising individual thermoregulatory mechanisms, workers can act collectively to cope with thermal stress and ensure thermal homeostasis in the nest.

(3) Social insects have evolved remarkable morphological adaptations, including long legs and coats of hair to protect themselves from thermal stress. In addition, worker size polymorphism is a unique trait that generates pronounced plasticity in thermal tolerance that colonies can exploit.

(4) While sociality provides thermoregulatory benefits at the colony level, it may also result in a trade-off between thermal tolerance and communication.

(5) New DNA- and RNA-sequencing techniques should help identify how ecological factors affect gene structure and expression and elucidate how populations adapt to different thermal environments.

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