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REVIEW

# Adaptation of *Apis mellifera jemenitica* (Hymenoptera: Apidae) to high temperatures: Morphological, behavioural, and physiological aspects

**YEHYA ALATTAL**

Department of Plant Protection, College of Food and Agriculture Sciences, King Saud University, Riyadh, Saudi Arabia;
e-mail: Yalattal@ksu.edu.sa

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**Abstract.** Temperature affects the distribution and success of *Apis mellifera* subspecies. To survive high temperatures in their natural habitats, unique adaptive traits have been evolved by various *A. mellifera* subspecies. *A. mellifera jemenitica* is a subtropical subspecies that is native to the Arabian Peninsula. It is one of the most thermotolerant *A. mellifera* subspecies and the only subspecies that can successfully survive long summers with daily temperatures exceeding 45°C in the Arabian Peninsula. In hot, dry conditions and short seasons, *A. m. jemenitica* can successfully establish its colonies. In this article, the different morphological, behavioural and physiological aspects of the thermal adaptation of *A. m. jemenitica,* which are its size, pigmentation, brood cell size, seasonal cycle, foraging behaviour, heat shock proteins and life genes are discussed. These aspects account for how *A. m. jemenitica* can withstand and survive the high summer temperatures on the Arabian Peninsula.

## INTRODUCTION

*Apis mellifera* is a cosmopolitan insect of high importance for human beings with more than 30 subspecies that are well-adapted to different climatic zones (Ruttner, 1988; Engel, 1999; Ilyasov et al., 2020). However, the successful occurrence *A. mellifera* subspecies in non-native habitats is very dependent on the temperature conditions (Adam, 1983; Ruttner, 1988). Some subspecies are exceptional in terms of their distributions, such as *A. m. mellifera* (toward the poles) and *A. m. jemenitica* (in deserts) (Ruttner, 1988). Nevertheless, the natural occurrence of *A. mellifera* might change as it adapts to temperature changes in most places in the world (UNEP, 2022). Thus, investigating mechanisms of thermal adaptation in different subspecies of *A. mellifera* is very valuable. *A. m. jemenitica* is the Arabian or Nubian Honeybee (Ruttner, 1988; Engel, 1999), it has the most unique ecological, morphological and physiological features of all subspecies of *A. mellifera* (Ruttner, 1988; Alqarni et al., 2019; Alattal & Alghamdi, 2023). It occurs naturally in the Arabian Peninsula and sub-Saharan zones of eastern Africa, such as Yemen (Ruttner, 1975) Saudi Arabia (Ruttner, 1975; Alqarni et al., 2011; Alattal & Alghamdi, 2022), Oman (Dutton et al., 1981), Sudan (Ruttner, 1975; Rashad & Al-Sarrag, 1978), Chad (Gadbin et al., 1979), Uganda, Somalia, Ethiopia and Cameron (Ruttner, 1975; Radloff & Hepburn, 1997). At these localities, *A. m. jemenitica* is well adapted to drought and high summer temperatures (Ruttner, 1975; Alqarni et al., 2011; Alattal & Alghamdi, 2015), with the most xerothermic populations in Saudi Arabia and Sudan (Rutner, 1988; Alqarni, 1995; Alattal & Alghamdi, 2022). This accounts for its survival under extreme thermal conditions. Only *A. m. jemenitica* can survive the high summer temperatures (>40°C) that occur in Saudi Arabia, whereas *A. m. carnica*, *A. m. ligustica* and Egyptian landraces of *A. m. lamarckii* (Alqarni, 1995; Alattal & Alghamdi, 2015) suffer very high colony losses within the first summer season. Abou-Shaara et al. (2012) report a 4-degree difference in the upper critical temperatures between *A. m. jemenitica* (61.0°C) and *A. m. carnica* (57.5°C). Exotic subspecies of *A. mellifera* have been imported to Saudi Arabia over the last few decades (MEWA, 2023), which may threaten the genetic composition and biodiversity of the local subspecies, *A. m. jemenitica*. Nevertheless, the over-summering and drought adaptation of *A. m. jemenitica* in Saudi Arabia can be considered unique (Ruttner, 1988).

Ectothermic insects have evolved different morphological, behavioural, and physiological traits, for example, the unique morphological leg traits and foraging behaviour of the desert ant *Cataglyphis bombycina* (Hymenoptera: Formicidae), enable it to forage at temperatures exceeding 60°C (Wehner et al., 1992). At the molecular level, this exceptional adaptation of *Cataglyphis bombycina* (Hymenoptera: Formicidae) is associated with increased expression and synthesis of HSPs (Gehring & Wehner, 1995). At the other extreme, the Arctic woolly bear moth *Gynaephora groenlandica*, a non-social insect, may require 14 years to complete its life cycle because of the need to avoid freezing (Kukal, 1995), whereas in northern Europe, social behaviour and physiological aspects of *A. m. carnica* and *A. m. mellifera* enable them to develop well and withstand long periods of freezing temperatures (Ruttner, 1988). Other desert insects avoid high temperatures by occupying suitable microhabitats, in which the ambient temperature is 30°C less than in the open desert (Sanborn, 2008). In *Drosophila*, plastic responses, microhabitat selection and micro-evolution increase its thermotolerance (Austin & Moehring, 2019; Xue et al., 2019).

Thermal adaptation of *A. m. jemenitica* involves: (a) the general eusocial structure and behaviour of its colonies in terms of the cooperative association of colony members in foraging activity, foraging duration, evaporative cooling and fanning, swarming, selection of colonization sites, reproduction, and seasonal growth cycle (Heinrich, 1974; Seeley & Heinrich 1981; Kronenberg & Heller, 1982; Southwick, 1983; Ruttner, 1988; Kühnholz & Seeley, 1997) and (b) the inherited adaptive morphological and physiological traits of the worker bees associated with thermal adaptation, such as body size, colour, brood cell size, synthesis of HSPs and expression of other essential genes. Without such individual and colony-based adaptive traits, *A. m. jemenitica* could not survive the high summer temperatures in Saudi Arabia. In this review, the different morphological, behavioural, and molecular characteristics of *A. m. jemenitica* associated with thermal adaptation are discussed.

## MORPHOLOGICAL AND STRUCTURAL ASPECTS

### Body size

Body size is associated with thermal adaptation in *A. mellifera*, with the small subspecies occurring in hotter and dryer climatic zones than the large temperate zone subspecies (Ruttner, 1988). *A. m. jemenitica* is the smallest of all subspecies and is described by Ruttner (1988) as the most thermotolerant subspecies of *A. mellifera*. It is a similar size to *A. cerana* from regions with high temperatures (Ruttner, 1988; Alattal et al., 2014; Yancan et al., 2019). Comparing the morphometric data (Table 1) of *A. m. jemenitica* with that of the temperate zone subspecies, such as *A. m. carnica* and *A. m. mellifera*, reveals differences in body size (T3+T4) and forewing length and width of both subspecies (Fig. 1). The body size (T3+T4) of *A m. jemenitica* is ~20% smaller than that of *A. m. carnica* (Fig. 1) (Ruttner, 1988; Alqarni, 1995; Alghamdi et al., 2012; Alattal & Alghamdi, 2022) and the forewing length and width are ~15% and ~30% less, respectively, in *A. m. jemenitica* than in *A. m. carnica* (Ruttner, 1988; Alghamdi et al., 2012; Alqarni, 1995). In addition, the body of *A. m. jemenitica* is not as slender (86.04±4.23) as that of *A. m. carnica* (83.7±1.02) (Ruttner, 1988; Alghamdi et al., 2012; Alattal & Alghamdi, 2022).

The mechanisms of thermal adaptation associated with body size in *A. mellifera* are based on: (I) Small subspecies of *A. mellifera* have a relatively higher body surface area and can consequently dissipate heat faster and consequently regulate their body temperature faster (Sanborn, 2008). (II) Body size influences metabolic rates of individuals under stress (Verma et al., 1970; Gillooly et al., 2001), with the metabolic rate increasing exponentially in response to heat stress much faster in large-bodied organisms than small ones, which determines their probability of survival (Gillooly et al., 2001). This indicates that the effect of heat stress on *A. m. jemenitica* is less than on large subspecies of *A. mellifera* (Gillooly et al., 2001). (III) Body size determines the porosity (spaces) between bees in brood frames and honey frames and affects heat insulation (Ruttner, 1988; Mitchell, 2022). When small nurse bees are working on brood frames, they have higher porosity and provide less heat insulation, which might minimize brood overheating. The high porosity of worker frames might be an adaptive trait of sub-saharan subspecies of *A. mellifera,* including *A. m. jemenitica* (Ruttner, 1988; Mitchell, 2022). In contrast, broad and large subspecies are efficient brood warmers and insulators (Mitchell, 2022), an essential adaptive trait for temperate zone *A. mellifera*, which is not suitable for a tropical climate (Ruttner, 1988; Mitchell, 2022). The small body size of *A. m. jemenitica* may be one of the main mechanisms by which this subspecies can survive in hot climates.

**Fig. 1.** Photographic comparison at the same magnification of the body size of *A. m. carnica* on the left and *A. m. jemenitca* on the right.

### Pigmentation and tergal hairs

Body pigmentation is also associated with the distribution of *A. mellifera* subspecies, with dark subspecies (black) occurring naturally in temperate regions, such as *A. m. carnica*, *A. m. caucasica*, and *A. m. mellifera*, whereas light (yellow) subspecies occur in hotter and drier areas, such as *A. m. ligustica*, *A. m. meda*, *A. m. syriaca* and *A. m. jemenitica* (Ruttner, 1988). The colour classification of *A. mellifera* ranges from 0 (completely black) to 9 (completely yellow) (Ruttner, 1988). *A. m. jemenitica* is very yellow, with pale yellow terga (T2 = 8.81±0.43; T3 = 8.73±0.51; T4 = 5.02±0.56) compared with, for example, the very dark pigmentation in *A. m.carnica* (T2 = 0.85±1.21; T3 = 2.35±0.74; T4 = 1.1±0.43) (Fig. 2 and Table 1) (Hepburn & Radloff, 1998; Ruttner, 1988; Yancan et al., 2019; Alattal & Alghamdi, 2022). Similarly, the scutellum of *A. m. jemenitica* is a yellowish colour (6.26) compared to black (0.13) in *A. m. carnica*.

**Table 1.** Comparison of morphological, behavioural, and physiological traits associated with thermal adaptation in Arabian *A. m. jemenitica*, African *A. m. jemenitica*, *A. m. carnica* and *A. cerana*.

| Criteria | Arabian, *A. m. jemenitica* | African, *A. m. jemenitica* | *A. m. carnica* | *A. cerana* | References |
|---|---|---|---|---|---|
| Natural Occurrence | Arabian Peninsula | Tropical Africa | Europe (Temperate zone) | East of Iran and south of the great mountain ranges | Ruttner, 1988 |
| Adult body size (T3+T4) | The smallest<br>3.75±0.15 (mm) | Small<br>3.94±0.14 (mm) | Large<br>4.51±0.18 (mm) | Small<br>3.86±0.15 | Ruttner, 1988; Yancan et al., 2019 |
| Wing length | 7.87±0.224 (mm) | 8.136±0.141 (mm) | 9.40±0.150 (mm) | 7.54±0.14 (mm) | Seeley & Heinrich, 1981; Ruttner, 1988; Alattal & Alghamdi, 2022 |
| T2 pigmentation | Brilliant yellow<br>8.81±0.43 | Yellow<br>770±1.09 | Brown<br>1.39±1.07 | Dark yellow<br>4.64±1.78 | Ruttner, 1988; Hepburn & Radloff, 1998; Yancan et al., 2019; Alattal & Alghamdi, 2022; Reference data* |
| T3 pigmentation | Brilliant yellow<br>8.7±0.51 | Yellow<br>7.50±1.13 | Brown<br>2.35±0.74 | Brown<br>2.76±1.43 | Ruttner, 1988; Yancan et al., 2019 |
| T4 pigmentation | Pale<br>5.01±0.57 | Pale<br>4.8±1.6 | Brown<br>0.97±0.74 | Brownish<br>3.33±1.70 | Yancan et al., 2019; Reference data* |
| Scutellum | Pale yellow<br>6.26±1.02 | Yellowish<br>5.87±1.96 | Brown<br>0.13 | Pale yellow<br>6.49±1.49 | Ruttner, 1988; Hepburn & Radloff, 1998; Yancan et al., 2019; Reference data* |
| Hair length | Short<br>0.172±0.021 (mm) | Medium<br>0.211±0.019 (mm) | Long<br>0.288±0.065 (mm) | Long<br>0.287 (mm) | Dyer & Seeley, 1987; Ruttner, 1988 |
| Brood cell size | Smallest<br>4.07 (mm) | Small<br>4.7 (mm) | Large<br>5.51 (mm) | Small<br>4.83±0.003 (mm) | Gadbin et al., 1979; Ruttner, 1988; Adgaba et al., 2016; Yang et al., 2021 |
| Egg water-content | 90.1% | — | 88.7% | — | Alghamdi et al., 2014 |
| Post-capping period | Short | Short | Long | Shortest | Ruttner, 1988; Single, 2015 |
| Foraging | Earlier and longer | Earlier and longer | Later and shorter | Earlier and longer | Yang, 2005; Alattal & Alghamdi, 2015 |
| Colony size | Small | Relatively small | Large | Large | Ruttner, 1988 |
| Colony growth | Rapid | Rapid | Slow | Rapid | Ruttner, 1988 |
| Incidence of swarming | Low | High | Low | Average | Ruttner, 1988; Adgaba et al., 2002 |
| Absconding | Absent | Present | Absent | Present | Ruttner, 1988 |
| Expression of HSP | High | — | Low | — | Alghamdi & Alattal, 2023 |

*Reference morphometric data obtained from the State Institute of Apiculture, Oberursel, Germany.

Dark colours absorb high amounts of radiation of all wavelengths compared to light colours (Ruttner, 1988; Gaffin et al., 2010). Thus, dark coloured insects warm up faster than yellow or light-colored ones that reflect part of the radiation (Ruttner, 1988; Freoa et al., 2023). Differences in the temperature of light and dark-coloured surfaces can be very high, for example, it can be 17°C or more for black and white surfaces under the same conditions (Hermans, 2007; Gaffin et al., 2010). Therefore, natural selection favours lighter-coloured individuals in hot geographical zones (Ruttner, 1988; Suni & Dela Cruz, 2021).

Similarly, subspecies of *A. mellifera* with a covering of short hairs are less well insulated than those with a covering of long or dense hairs (Ruttner, 1988). The hair covering of *A. m. jemenitica* is the shortest of all the subspecies of *A. mellifera* (Ruttner, 1988) and that of *A. m. carnica* (0.288±0.06) is about 1.7× that of *A. m. jemenitica* (0.177±0.12). Short hairs are characteristic of subspecies of *A. mellifera* in hot climatic zones (Ruttner, 1985) and are one of the few characteristics of proven adaptive value (Ruttner, 1988). The bright yellowish colour of *A. mellifera* is also negatively correlated with its body size and hair length (Ruttner, 1988; Alghamdi et al., 2012; Alattal & Alghamdi, 2022).

## Brood and brood-cell size

*A. mellifera* brood are stenothermous with a narrow temperature range (32–36°C) (Petz et al., 2004; Becher et al., 2009). Brood cooling and warming depend on the adaptive characteristics of the honeybee colony and might increase tolerance limits with no significant effect on brood development (Petz et al., 2004). In this context, two characteristics of *A. m. jemenitica* brood and brood cells increase its tolerance to hot conditions. First: in colonies of *A. m. jemenitica*, the brood (larvae or pupa) surface-area-to-volume ratio is higher than that of other subspecies of *A. mellifera*, which means their brood is more efficient at radiating body heat (Ruttner, 1988; Bogin et al., 2022). Second, the brood cell diameter of Arabian *A. m. jemenitica* (4.07±0.17) is the smallest of all the subspecies of *A. mellifera* after *A. m. litorea* and *A. m. scutellata* (Chandler, 1975; Ruttner, 1988; Adgaba et al., 2016). Consequently, the number of brood cells per unit area of brood frame is ~20% more for *A. m. jemenitica* than for *A. m. carnica* (Ruttner, 1988), thus small brood sizes with more condensed brood areas indicate a greater porosity (spaces) during brood development. This trait is characteristic of most tropical honeybees, because control of brood temperature is of less importance in

**Fig. 2.** Photographs of the inside of colonies showing the clear yellow colour of the T2 and T3 of adult *A. m. jemenitica* workers (upper) and the brown colour of T2 and T3 of adult *A. m. carnica* workers (lower), obtained, with permission, from J. Krauter (2024).

hot climates (Ruttner, 1988), and that the brood cell size of *A. m. jemenitica* is adaptive in hot climates (Oldroyd & Pratt, 2015).

## COLONY FUNCTIONING AND PHYSIOLOGICAL ASPECTS

### Oviposition rate and egg traits

Different subspecies of *A. mellifera* produce eggs of different sizes and adjust their egg-laying rate to habitat conditions (Ruttner, 1988; Amiri et al., 2020). It is reported that queens of *A. mellifera* in small colonies lay large eggs and those in large colonies lay small eggs (Han et al., 2022), this difference might be non-adaptive, however, as queens might increase egg size and decrease fecundity in response to environmental conditions (Amiri et al., 2020), this plasticity in egg size in response to environmental conditions, such as drought and high temperatures, is adaptive (Fox & Czesak, 2000). Similarly, the differences in the egg size among *A. mellifera* subspecies are also associated with differences in egg water content under different temperature regimes (Alghamdi et al., 2014). Adaptive variation in egg composition/morphology and changes in egg laying rates ensure a higher percentage of egg hatch and healthy development of brood under certain conditions (Amiri et al., 2020; Han et al., 2022). In the case of *A. m. jemenitica*, (I) its egg is longer (1.58 mm) and has a higher average water content (90.1%) than that of *A. m. carnica* (1.54 mm and 88.7% respectively) (Alghamdi et al., 2014), (II) percentage of egg hatch for *A. m. jemenitica* is significantly higher than that for *A. m. carnica* in Saudi Arabia (Alghamdi et al., 2014), (III) based on population density studies, the egg laying rate of *A. m. jemenitica* is higher than that of exotic *A. mellifera* subspecies (i.e. *A. m. carnica* and *A. m. ligustica*) under the same conditions, which ensures rapid colony growth (Alghamdi et al., 2014, 2017; Alqarni et al., 2014; Hatjina et al., 2014; Single, 2015). These aspects of egg structure and egg-laying rates are associated with thermal adaptation in *A. m. jemenitica*.

### Brood developmental time (post-capping period)

Tropical subspecies of *A. mellifera* characteristically have a short brood post-capping period, which is a biological trait of *A. mellifera* inhabiting hot climates (Ruttner, 1988). For example, the mean post-capping period of *A. m. unicolor* is 280.1±0.12 h, which is 10 h less than that of *A. m. carnica* (Jobart et al., 2023). For *A. m. jemenitica*, the worker brood post-capping period is 11 h shorter than that of *A. m. carnica* (Khanbash, 2002). Moreover, Alattal & Alghamdi (2015) report a shorter post-capping period for *A. m. jemenitica* than for *A. m. carnica* in the deserts of Saudi Arabia. In addition, the percentage distribution of the post-capping periods in both subspecies could be important. Only 3.0% of the worker brood cells of *A. m. carnica* require less than 260 h for emergence, this percentage is 6.2% in *A. m. jemenitica*. Consistently, the percentage of cells that require more than 290 h to complete the post-capping period is 32.1% and 25.8% in *A. m. carnica* and *A. m. jemenitica*, respectively (Alattal & Alghamdi, 2015). The short developmental time of *A. m. jemenitica* accounts for rapid colony growth and high fitness in short seasons characterized by high temperatures in Saudi Arabia. In addition to that, the short post-capping period in *A. m. jemenitica* might adversely affect the reproductive success of some brood parasites, such as *Varroa destructor*, as Buechler & Dreschner (1990) estimate that a one-hour reduction in the post-capping period results in a 9% reduction in population density of the *Varroa* mite in *A. mellifera* colonies.

### Colony size and population dynamics

The size and growth pattern *A. m. jemenitica* colonies indicate a strong effect of seasonal temperature changes (Ruttner, 1998). Colonies of *A. m. jemenitica* are small to moderate sizes, but nevertheless larger colonies than exotic honeybee colonies living under the same conditions in Saudi conditions (Alqarni, 1995; Ali, 2011; Alqarni et al., 2014; Single, 2015; Alghamdi et al., 2017). Three phases in population growth are documented for *A. m. jemenitica* colonies in Saudi Arabia, with the main population peak before summer and a minor peak before winter (Alqarni, 1995; Alqarni et al., 2014; Single, 2015; Alghamdi et al., 2017). The peaks occur when pollen is abundant from March to June (main peak) and from October to November (minor peak) (Alqarni, 1995). Then, colonies rapidly decrease during the hottest summer months from July to September and slightly in winter after the second minor population peak (Alqarni, 1995; Alqarni et al., 2014; Single, 2015). The winter population is generally higher than that at the end of summer (Single, 2015; Alghamdi et al., 2017). No cluster bees are documented for *A. m. jemenitica* and brood rearing is relatively continuous throughout the year with a very significant decrease during summer and winter (Alqarni, 1995). Drones develop during both population peaks, but the number is low compared to that reported for other subspecies of *A. mellifera*, such as *A. m. carnica* or even *A. m. syriaca* (Liebig, 1993; Alqarni, 1995; Renz, 2003; Alattal, 2006; Single, 2015). Comparing the colony size and growth pattern of *A. m. jemenitica* with temperate zone subspecies, such as *A. m. carnica*, it is clear that *A. m. carnica* colonies generally have one high population peak at the beginning of summer, which grows relatively slowly, produce swarms and there is no rearing of brood during winter and a gradual decrease in population density from summer until the beginning of next spring (Renz, 2003; Hatjina et al., 2014).

In Single (2015) study, the highest average adult population in colonies of *A. m. jemenitica* is 20488±4679 (May–July), and the lowest 5207±2987 (October–November), the maxima for capped and open brood cells are (13804±3451) and (9792±1017), respectively. Comparison of these densities with the adult worker population and numbers of capped brood cells for *A. m. carnica* under temperate conditions, reveals that the *A. m. jemenitica* values are less than 50% of those reported for *A. m. carnica* (Liebig, 1993; Renz, 2003). In southern Germany, for example, the population maxima of *A. m. carnica* is more than 40,000 adult bees and 35,000 adult worker bees and capped brood cells, respectively (Liebig, 1993; Renz, 2003).

Comparison of the population dynamics of *A. m. carnica* and *A. m. jemenitica* colonies under the same conditions in Saudi Arabia, reveals that those of *A. m. jemenitica* have higher adult and brood population densities (Alqarni, 1995; Alattal, 2006; Ali, 2011; Single, 2015; Adgaba et al., 2017). For example, the adult worker population is lower in *A. m. carnica* (9945±442) than in *A. m. jemenitica* (11597±6549), with a higher brood/adult worker ratio in spring in *A. m. jemenitica* (1.5) than in *A. m. carnica* (1.2) (Single, 2015). After summer, the Carniolan Honeybee adult worker population is 3516±3412 compared to 5207±2987 in *A. m. jemenitica* (Single, 2015). During summer a small percentage of diseased or starving colonies of *A. m. jemenitica* are lost, yet more than 90% of the exotic subspecies, such as *A. m. carnica* or its hybrids are usually lost (Alattal, 2015). Similarly, population density and colony size are higher in *A. m. jemenitica* than in the Egyptian Honeybee *A. m. lamarckii* in Saudi Arabia (Alqarni, 1995; Ali, 2011).

It is suggested that colony development in *A m. jemenitica* is an adaptation to living in hot and dry environments in terms of (1) establishing small colonies to avoid a dramatic reduction in the adult worker population when ambient temperature increases in summer, (2) rapid rearing of brood and population growth with a relatively high brood/adult ratio during the reproductive phase of the colony, (3) compensating summer second minor population peak from September to November associated with a slight increase in plant resources in Autumn, (4) drone production occurs before and after winter to avoid the stress of the summer months and drone sterility.

## Heat shock protein

Increased expression of heat shock proteins (HSPs) is a well-documented mechanism associated with the thermal tolerance of subspecies of *A. mellifera* (Severson et al., 1990; Elekonich, 2009; Zhao & Johns, 2012; Alghamdi & Alattal, 2023). Two studies on colonies of *A. m. jemenitica* indicate high basal and phenotypic thermal tolerance compared to that of the temperate zone subspecies *A. m. carnica* and *A. m. ligustica* (Alqarni et al., 2019; Alghamdi & Alattal, 2023). In the first study, day-long higher expression levels of *hsp70ab*, *hsc70cb*, *hsp83*, *hsp90*, *hsp10*, and *hsp28* are reported in foragers of *A. m. jemenitica* than in *A. m. carnica* in response to desert summer conditions in Saudi Arabia (Alghamdi & Alattal, 2023). Changes in day-long expression levels of *hsp70 mRNAs* are more than 10× higher in *A. m. jemenitica* than in *A. m. carnica* under the same conditions. Furthermore, expression levels of different *hsps* (*hsp70ab*, *hsc70cb*, *hsp83*, *hsp90*, *hsp10*, and *hsp28*) are also higher in *A. m. jemenitica* under normal temperatures (22–30°C) than in *A. m. carnica* (Alghamdi & Alattal, 2023). It is suggested that higher basal expression of *hsp*s induced by heat stress is an important component of thermal adaptation in *A. m. jemenitica*. In the second study, based on SDS-page analyses, *hsp70*, and *hsp82* are expressed in nurse bees of *A. m. jemenitica, A. m. carnica,* and *A. m. ligustica* after exposure to 40 and 45°C. However, in foragers, only *hsp70* is expressed in *A. m. jemenitica* at 40°C (Alqarni et al., 2019), this might indicate a higher response threshold to heat stress in *A. m. jemenitica*. A third study on *A. m. jemenitica*, linked expression levels of *hsps mRNAs* with histone post-translation modifications (HPTM), indicating an epigenetic layer of HSP regulation in *A. m. jemenitica* in response to heat stress (Alattal & Alghamdi, 2023).

## Life-essential genes

The *lethal(2)essential-for-life-like* gene family *(l(2)efl)* has a key role in protein homeostasis and proteostasis (Bakthisaran et al., 2015; Qin et al., 2019). High expression levels of *l(2)efl* gene family are associated with heat tolerance in *A. mellifera* (McMenamin et al., 2020; Runtuwene et al., 2020; Shih et al., 2021). For example, a higher increase in *l(2)efl* transcripts is reported in midguts of *A. mellifera* after exposure to 45°C for 4 h than in the control (Shih et al., 2021). In *A. m. carnica*, higher expression levels of *l(2)efl* mRNAs are reported in heat-stressed foragers than in the control (McMenamin et al., 2020; Runtuwene et al., 2020). Another study reports higher day-long real-time expression levels of *l(2)efl* genes in *A. m. jemenitica* than in *A. m. carnica*. This study states that under desert and semi-arid conditions in Saudi Arabia, day-long expression levels of *l(2)efl* genes in *A. m. jemenitica* are much higher than in *A. m. carnica* (Algamdi & Alattal, 2023), which may imply a higher basal and phenotypic tolerance in this subspecies of *A. mellifera*. In response to the summer desert conditions in Saudi Arabia, changes in the levels of expression of *l(2)efl* are ~100× higher in *A. m. jemenitica* than in *A. m. carnica* under semi-arid conditions (the calibrator) (Alattal & Alghamdi, 2024; Alghamdi & Alattal, 2024). It is concluded that increases in the level of expression of *l(2) efl* mRNAs are associated with the thermal adaptation and higher fitness of *A. m. jemenitica* at high temperatures in Saudi Arabia and can be considered to be an adaptive trait of this subspecies.

## COLONY BEHAVIOUR

### Foraging behaviour

Before *A. mellifera* foragers fly, they increase their thoracic temperature by shivering, the minimum thoracic temperature for flight must be maintained above 30°C (Heinrich, 1993). Many researchers report a relationship between foraging activity and body temperature (Nachtigall et al., 1989; Heinrich, 1993). This might be less challenging in hot climates, where the ambient temperature suitable for flight occurs on most days. However, *A. mellifera* can regulate the thoracic temperature while they are on the ground, but when inflight the muscles operate myogenically (Heinrich, 1993). Therefore, under high summer temperatures, bees may stop foraging to avoid overheating and death. In this context, *A. m. jemenitica* workers are better foragers than exotic subspecies of *A. mellifera*, such as *A. m. carnica* and *A. m. ligustica* at high summer temperatures in central Saudi Arabia (Ali, 2011; Alattal & Alghamdi, 2015; Adgaba et al., 2017; Alqarni et al., 2021, 2023). *A. m. jemenitica* foragers are 2× more with >3× foraging pollen than the exotic *A. m. carnica* (Adgaba et al., 2017; Alqarni et al., 2021). Alattal & Alghamdi (2015) report a higher day-long foraging for *A. m. jemenitica*, which unlike in *A. m. carnica* starts at sunrise and may be linked to a faster warming-up of the smaller *A. m. jemenitica* and better utilization of the content of the honey-crop during flight. Then, after sunrise, the number of *A. m. carnica* foragers decreases significantly as temperature increases compared to *A. m. jemenitica,* with minimal foraging activity of *A. m. carnica* at mid-day in summer, this mid-day foraging activity might prevent overheating of flight muscle at a lower threshold compared to *A. m. jemenitica*. Likewise, at sunset, foragers of *A. m. jemenitica* return later to their colonies than those of *A. m. carnica* (Ali, 2011; Alattal & Alghamdi, 2015). During drought and out-of-season, *A. m. jemenitica* also forages more actively flowers that provide little nectar and pollen (Alqarni, 1995; Ali, 2011; Alqarni et al., 2021), which is associated with the higher responsiveness of *A. m. jemenitica* to glucose and sucrose than *A. m. carnica* and *A. m ligustica* under Saudi Arabia conditions (Alqarni et al., 2023). In summary, *A. m. jemenitica* has a higher number of foragers, longer foraging span and foraging range in its natural habitats than exotic subspecies, which increases their fitness and survival under such conditions.

### Swarming behaviour

Swarming behaviour is an evolutionary process, which is retained by subspecies of *A. mellifera* even if moved to new localities (Ruttner, 1988). High swarming rates are reported for subspecies of tropical *A. mellifera* and the situation with *A. m. jemenitica* is very specific, with African populations of *A. m. jemenitica*, such as, those in Ethiopia and Chad swarming frequently, similar to *A. m scutellata* (Taylor, 1985; Ruttner, 1988; Adgaba et al., 2002). In Oman 10–12 swarms per *A. m. jemenitica* colony are reported in good seasons (Dutton et al., 1981). However, *A. m. jemenitica* in Saudi Arabia has a low swarming tendency (Alqarni, 1995) and is very similar in this respect to subspecies in the temperate zone. The low swarming tendency of *A. m. jemenitica* in Saudi Arabia and that of temperate zone subspecies, such as *A m. carnica* and *A. m. ligustica* might have evolved as a consequence of their habitat conditions. Swarming is hazardous in regions with very hot summers or long cold winters, where suitable nesting sites with sufficient floral resources are rare (Ruttner, 1988).

### Absconding

Absconding is reported for all tropical subspecies of *A. mellifera*, therefore, the African populations of *A. m. jemenitica* are highly mobile (Rashad & El-Sarrag, 1978; Gadbin et al., 1979; Woyke, 1993; Hepburn & Radloff, 1998). "Hunger Swarms" are also reported for temperate zone subspecies of *A. mellifera*, but, some colonies starve rather than abscond (Zander & Weiss, 1964; Ruttner, 1988). *A. m. jemenitica* in Saudi Arabia, Yemen, and Oman is exceptional in not absconding (Alqarni, 1995), which can also be associated with their specific habitat conditions. Low swarming and the absconding tendency of *A. m. jemenitica* in Saudi Arabia are adaptive to the high temperatures prevailing there.

## CONCLUSION

Recently several significant studies have been published on thermal adaptation in *A. m. jemenitica*. In this short review, morphological, behavioural and molecular aspects of thermal adaptation in *A. m. jemenitica* in Saudi Arabia are discussed. It is concluded that thermal tolerance in *A. m. jemenitica* is multi-faceted, with adult body size and expression of *hsp*s (basal/phenotypic) being the most important. Comparative morphological data on the temperate zone subspecies, *A. m. carnica* is also presented. Further studies are needed on the following topics. (I) The effectiveness of behavioural thermoregulation, such as evaporative cooling and fanning in *A. m. jemenitica*. (II) The upper thermal limit for *A. m. jemenitica* measured in more realistic conditions. (III) Differences in the thermal adaption of sub-populations or along geographical clines of *A. m. jemenitica*. (IV) The consequences of hybridization and crosses between *A. m. jemenitica* and other subspecies of *A. mellifera* on the thermal adaption of their offspring. With climate change and an increase in the earth's temperature, *A. m. jemenitica* could become more important. The potential ability of *A. m. jemenitica* to survive future climate changes might not be straightforward, but, the evolutionary potential and preadaptation of *A. m. jemenitica,* in terms of its high upper thermal limits, make it very valuable for future beekeeping. On the other hand, monitoring the performance of *A. m. jemenitica* colonies in temperate climates (outside their natural range) may increase our understanding of *A. m. jemenitica* survival and potential productivity. Efforts should also be directed at conserving the Arabian Honeybee *A. m. jemenitica* and preventing the introduction of exotic subspecies of honeybees.

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