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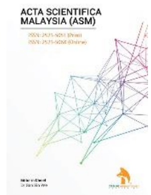

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RESEARCH ARTICLE

INSIGHTS OF CASTE DETERMINATIONS IN SOCIAL INSECTS

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ABSTRACT

Eusocial insects display caste structures in which reproductive ability is possessed by a single or a few queens while all other colony members act as workers. In social insects like ants, bees, and termites, vital physiological processes are regulated at the colony scale. Females in social insects have at least one reproductive caste and one nonreproductive caste; many termites have at least two male castes. The castes have considerable anatomical, physiological, and behavioural differences in higher social insects. Organismal systems, such as pheromone sensing, hormone signaling, and brain signaling pathways, are deployed in novel circumstances to impact nestmate and colony behaviours due to physiological decentralization over evolutionary time. Significant morphogenesis with region-specific cellular proliferation and degradation occurs during soldier development through two moulting via a presoldier stage in termite. JH action has been developed, in which a high JH titer causes soldier differentiation and a low JH titer causes alate differentiation. A monogamous pair of primary reproductives (one king and one queen) generated from alates normally establishes termite colonies (winged adults). The nymph-alate pathway (sexual pathway) or the worker pathway differentiates larvae in *Reticulitermes* termites (neuter pathway). Haplo-diploid sex determination controls the first developmental transition, in which unfertilized (haploid) embryos become males and fertilized (diploid) embryos become females in the case of *Cataglyphis* ant genus. The queen's mandibular gland secretion, a mix of fatty acids and aromatic chemicals, is critical for maintaining the reproductive division of labour in honeybees (*Apis mellifera*), suppressing ovary growth in workers. Besides this, the brood produced by the queen also inhibits ovary development in workers by emitting two pheromones: the brood pheromone (BP), mainly composed of esters, and the highly volatile E-b-ocimene.

KEYWORDS

Social Insect, Caste, Physiology, Hormone.

1. INTRODUCTION

Social insects exhibit cooperative brood care with organized overlapping generations within a colony of adults, and a division of labor into reproductive and non-reproductive groups. The division of labor creates specialized behavioral groups within an insect society which are referred to as 'castes'. Termites, ants, bees, and wasps are social insects with structured communities. One or very few females are in charge of all laying eggs, while other colony members (typically sterile females) collect food and do other activities. Individuals in social insect colonies can be significantly varied in shape and function. As if it were a single individual, a colony of social insects is referred to as a "superorganism" (Hölldobler and Wilson, 2009). Castes of social insects are a group of phenotypically, behaviorally, and morphologically diverse individuals who work together to complete colony activities (Miura, 2004). One of the distinct characteristics of social insects is that they have morphologies that specialize in duties that are assigned in a colony (Wilson, 1971). Several factors can impact the caste differentiation process in social insects. Environmental factors like temperature and social factors like nestmate caste composition can significantly impact whether caste distinction happens or not. In order to have an effective division of labour, caste difference is essential. Colonies must figure out how to maintain caste differences within this system because inappropriate regulation might lead to an overabundance or lack of certain castes, rendering colony duties like food acquisition, reproduction, grooming, and defence difficult or impossible (Tarver et al., 2009). Individual progress within social insect colonies is regulated mainly by the effect of social circumstances and the social environment, whether through physical interaction or chemical signals (Robinson et al., 2008).

Depending on the species and level of sociality, caste differences can range from being completely behavioural and physiological through showing dramatically different alternate morphological phenotypes or polyphenisms (Ross et al., 1991). Social insects are essential to examining physiology concerning caste determination because of various distinguishing characteristics. Physiological processes that optimize caste ratios, particularly behavioural castes, focus on social physiology because they increase colony production (Johnson and Linksvayer, 2010). Termites are ideal for exploring caste regulation systems because of several distinguishing traits(Howard and Thorn, 2010). For example, termites construct diverse, huge, and complex nests, including enormous individuals (Noirot and Darlington 2010). Ants are some of the most complex polyphenisms, with females developing into a broad range of morphological castes, such as workers, soldiers, queens, and ergatoid queens (Molet et al., 2012).

In ants, parental factors such as JH, vitellogenin, and ecdysone deposited in eggs can impact the size and push larvae towards the worker or queen formation (Trible and kronauer, 2017). In honeybees, qualitative variations in larval feeding at critical times throughout development (e.g., royal jelly fed) cause epigenetic and endocrine alterations in individuals, leading to queen's and worker's development (Hartfelder ,

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2000). Taxonomically distinct populations can show resemblance in caste systems in proportion to the environmental condition they have developed, which is an intriguing aspect. The mechanisms of sex determination in termite, ant, honeybee with reference to hormonal and behavioural interaction will be discussed in this review. Besides that, the physiological and functional range of social insects in relation to their castes will be reviewed in understanding different castes.

2. Reviews of Findings

2.1 Physiology Affecting Insect Caste Development

The insects are distinguished from other animals by their abundance, diversity, and significant economic importance and physiology**.** All social insects have caste systems and the division of work they allow. An insect colony is more than just a collection of individuals; it's also a functional entity. In addition to coordinating the physiological state in each individual, the entire colony is coordinated via interactions among colony members to accomplish adaptive social behaviour in variable environmental conditions (Watanabe et al., 2014). Social anatomy is analogous to specialized anatomy (e.g., organs, tissues) in a metazoan body, while social physiology plays a similar role to organismal physiology in a metazoan body (Figure 1). Ants, termites, bees, and wasps are virtually totally female-dominated communities. Inequalities in female members build communities; these might be modest, affecting merely physiology, or they can be significant, including enormous size differences and hundreds of physical features. Organisms regulate their body physiology via neural and molecular mechanisms. In eusocial insect colonies, physiological mechanisms include these neural and molecular types and the physical interactions among colony members. The regulation of nestmate and colony traits arises from interactions within and across castes, task groups, and developmental stages.

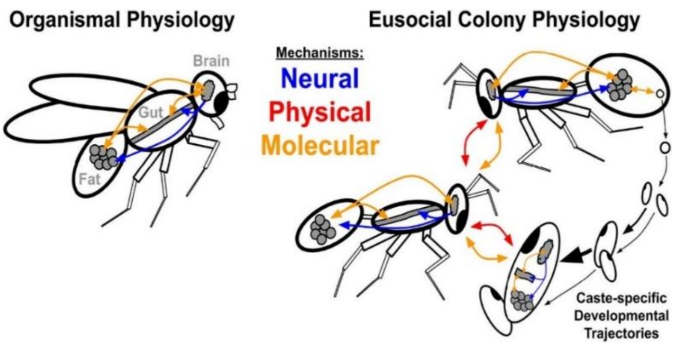

Figure 1: Organismal and eusocial colony physiology (Friedman et al., 2020)

2.2 Termites

2.2.1 Developmental Process: Metamorphogenesis

Except for a few ancestors with secondary loss, all termite species with th e soldier caste have defensive morphologies that are not present in any of the other castes, such as larger mandibles, brushlike labrum, and frontal projections or nasus (Koshikawa et al., 2002). Significant morphogenesis with region-specific cellular proliferation and degradation occurs during soldier development through two moulting via a presoldier stage (Toga and Maekawa, 2013). As a result, before the moult to presoldier, folding structures of epithelial tissues and cuticle layers that form weapon structures such as mandibles and/or nasus are observed under the cuticle of the previous developmental stage. Soldier differentiation is a hemimetabolous moulting process with distinct morphogenesis; endocrine systems, namely hormonal effects, developmental variables, and associated signalling pathways, have been studied to date.

2.2.2 Endocrine Factor: Ecdysone

Although it has been observed that ecdysone titers changed among castes and/or developmental stages, there have been far fewer investigations on the effect of ecdysone in caste differentiation insects like termites (Korb et al., 2009). The use of 20hydroxyecdysone (20E, the active form of ecdysone) was also demonstrated to cause *Reticulitermes speratus* to moult from worker to worker stages (Masuoka et al., 2013). The genes encoding enzymes involved in the 20E synthetic pathway, commonly known as the 6 Halloween genes, are thought to have a role in termite caste distinction, as some of them displayed queen or worker biased in the three termite species having genomic information (Harrison et al., 2018). As it is generally known that the JH and 20E signalling pathways are interconnected with each other (Jindra et al., 2013). The interaction between the two pathways might possibly play a role in termite caste differentiation. The transforming growth factor (TGF) pathway, for example, is thought to be involved in this crosstalk, as well as morphogenesis during soldier development in *Zootermopsis nevadensis* (Masuka et al., 2018). The acquisition of JH dependent 20E regulatory system mediated by the TGFβ signaling might then allow presoldier morphogenesis and complete soldier differentiation via the double molting process (Figure 2).

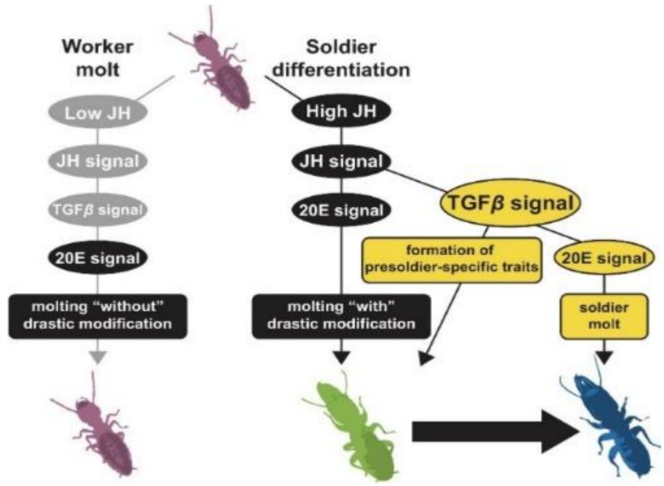

Figure 2: A schematic model on the role of TGFβ signaling for soldier differentiation (Masuka et al., 2018)

2.2.3 Endocrine Factor: Juvenile Hormone (JH)

JH, an endocrine regulator that governs caste distinction in social insects such as termites, has received much attention (Miura, 2019). It has been identified as the essential endocrine element in caste differentiation. JH action has been developed, in which a high JH titer causes soldier differentiation and a low JH titer causes alate differentiation (Nijhout and Wheeler, 1982). Indeed, expression analyses of some JH pathway genes between queens and workers in three termite species with genome information (*Zootermopsis nevadensis, Cryptotermes secundus, and Macrotermes natalensis*) suggested that JH signalling would be diversified among termite lineages, particularly between lower (first two) and higher (third) termites (Jongepier et al., 2018). Recently, genes related to the JH action, that is, up-and downstream factors in the JH signalling pathway, have been analyzed in detail.

2.2.4 Social Interactions

Only a small percentage of genetically related colony members differentiate into soldiers; extrinsic signals should be used to determine soldier differentiation. Social interactions should play a crucial role in coordinating the sophisticated social networks in termites as environmental signals that impact caste determination and differentiation (Watanabe et al., 2014). In contrast to the inhibitory effects of primary reproductives, the alate production was shown to be accelerated by the presence of soldiers in *Z. nevadensis*. Similarly, the differentiation of secondary reproductives of *Kalotermes flavicollis* was accelerated by soldiers (Springhetti, 1969). Both cases indicate that the differentiation to reproductives seemed to be induced by the presence of soldiers. When the soldier was removed from an incipient colony, another worker started to differentiate into a new soldier.

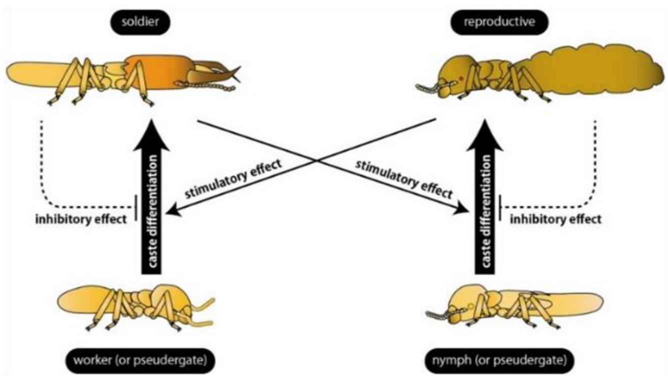

Figure 3: Summary of the regulation of caste differentiation by social

interactions (Watanabe et al., 2014)

By using individuals collected from mature colonies, the inhibitory effects of soldiers on the additional soldier differentiation were demonstrated in *K. flavicollis* (Figure 3). Differentiation into reproductives and soldiers (bold arrows) are stimulated by different castes (thin arrows) and inhibited by the same castes (broken arrows).

2.2.5 Sex and Caste

The regulation of caste distinction in termites is also influenced by sexuality. The percentage of soldiers in a colony of termites is frequently biased. In *Reticulitermes*, for example, the female-biased soldier ratio is thought to have evolved due to females' size dimorphism (Matsuura, 2006). However, this is not always the case in higher termites, the family Termitidae (Bourguignon et al., 2012). The sex-biased manifestation in termites could be linked to sex-determination and/or sex-differentiation pathways. Some investigations found a link between JH titer and gonadal development in *R. speratus and Z. nevadensi* reproductive that might trigger the sex-biased caste differentiation pathways (Saiki et al., 2015). Although the developmental physiology of reproductive soldiers is not clarified, changes in the reproductive composition may stimulate the differentiation of this caste (Johnson et al., 2011).

2.2.6 Caste Syndromes and Their Functioning

A monogamous pair of primary reproductives (one king and one queen) generated from alates normally establishes termite colonies (winged adults). The nymph-alate pathway (sexual pathway) or the worker pathway differentiates larvae in *Reticulitermes* termites (neuter pathway; figure 4). Most nymphs mature into alates and fly out to start new colonies. On the death of the primary king and queen, neotenic (also known as secondary reproductives or supplementary reproductives) are created from within the colony and take over reproduction (Vargo and Husseneder, 2009).

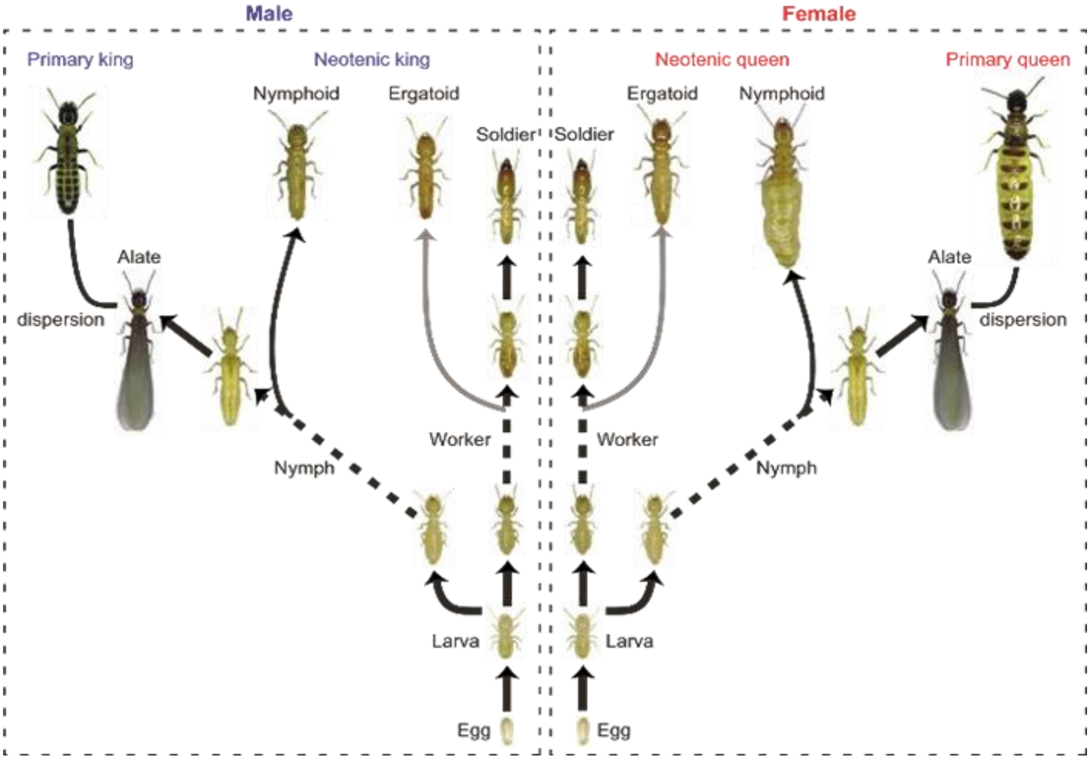

Figure 4: Caste differentiation pathway of *Reticulitermes* termites (Vargo and Husseneder, 2009).

2.2.7 Evolutionary Implications

Caste differentiation in social insects is an example of polyphenism, which occurs when a single species has numerous distinct phenotypes (Nijhout, 2003). Individuals in termite castes are primarily separated into two types: fertile (reproductives) and sterile (neuters) (Throne, 1996; Abe et al., 2000). Workers, presoldiers, and soldiers are among the sterile castes, whereas alates are primary reproductives and secondary reproductives are among the fertile castes. Alates perform nuptial flights with imaginal traits (wings, testes, ovaries) that grow during the nymphal stages. They lose their wings, mate, establish new colonies, and become primary reproductives (i.e., kings and queens). Some individuals develop into secondary reproductives when primary reproductives die, become senescent, or when colonies grow. In the relatively primary termite lineages, late-stage larvae that act as workers are called "pseudergates" (Thorne , 1996). However, it should also be noted that the caste fates are also affected by coexisting castes (Hayashi et al., 2007).

2.3 In Ants

2.3.1 Inhibition of the Soldier Program: Pheromones

Adult soldiers negatively regulate soldier production when they affect soldier production in the next generation; increasing the proportion of soldiers reduces soldier production while decreasing the proportion of soldiers increases soldier production. Although the role of the queens in the reduction or inhibition of queen rearing in ant colonies has been demonstrated, there is also evidence for the existence and function of queen pheromones (Gregg, 1942). Distribution of ant queen pheromones during grooming or feeding (1), carrying queen-laid eggs(2), contacting egg piles(3) indicated as blue dots in Figure 5.

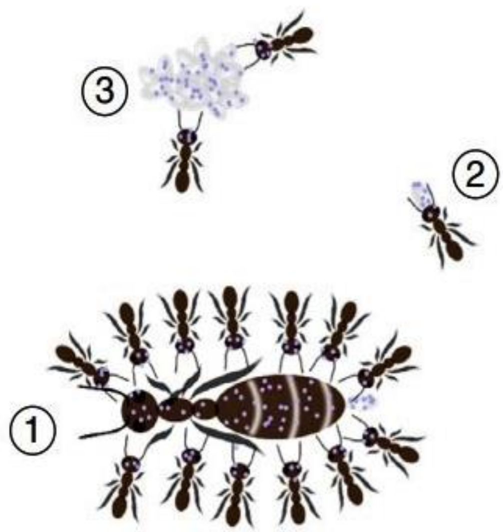

Figure 5: Distribution of queen pheromones (indicated as blue dots) (Gregg, 1942)

2.3.2 Endocrine Factor: Juvenile Hormone (JH)

Ant colonies usually feature a wingless worker caste and a winged queen.

However, novel forms of queens (such as wingless queens) and workers (such as soldiers) have evolved frequently in ants. The second developmental transition, which is mediated by Juvenile Hormone (JH) and occurs shortly after the first, happens when individuals differentiate into reproductive queens or sterile workers. The third developmental switch differentiates worker larvae into either soldiers or minor workers. This change is also influenced by JH and is thought to be largely influenced by nutrition; a high-protein diet stimulates JH production, prolonging development and triggering the soldier program (Figure 6) (Passera and Suzzonoi, 1979).

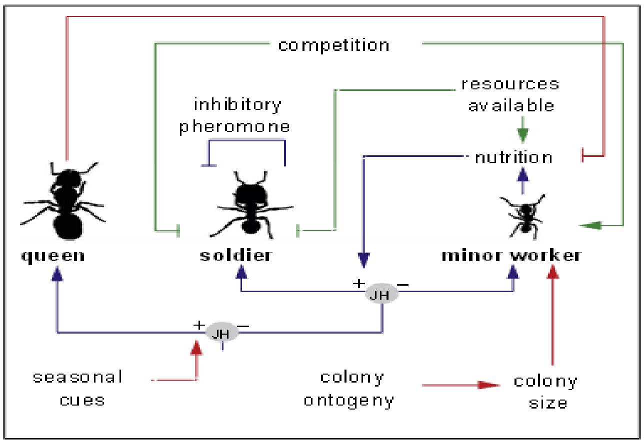

Figure 6: Network model of the major factors regulating subcaste ratios in *Pheidole* (Passera and Suzzonoi, 1979)

Solid lines indicate regulatory mechanisms supported by sufficient evidence, while dashed lines indicate regulatory mechanisms. Lines with arrowheads indicate activation, while lines with perpendicular bars indicate repression. Internal influences (blue lines). Two developmental switches mediated by JH: an early switch in embryogenesis determines queen or worker fate, while a late switch in larvae determines soldier or minor worker fate. Nutrition promotes soldier production by activating JH. Soldiers suppress soldier production through the soldier inhibitory pheromone. External influences (green lines). Resources available in the habitat promote soldier production by providing more nutrition to the colony or effectively decreasing the numbers of soldiers in the colony by recruiting them to significant finds. Competition increases soldier production by promoting the feeding of larvae by minor workers or increasing the death of adult soldiers, thereby alleviating the effect of the soldier inhibitory pheromone on larvae. Colony development and life cycle influences (red lines). Seasonal cues increase the production of virgin queens by promoting JH. Virgin queens reduce the amount of nutrition available to activate the soldier program, thereby reducing soldier production.

2.3.3 Caste Evolution

Multiple extinct lineages of early ants with winged queens and wingless workers have been discovered in the ant fossil record, suggesting that the most recent common ancestor of current ants included these two castes as well. The last common ancestor of extant ants likely possessed morphologically distinct worker and queen castes, but many species have subsequently gained or lost castes (Barden and Grimaldi, 2016). In addition to nutrients, saliva contains juvenile hormones and other molecules, including proteins, microRNAs, and cuticular hydrocarbons (Figure 7), which influence individual ants' roles in ant colonies (Knaden, 2016).

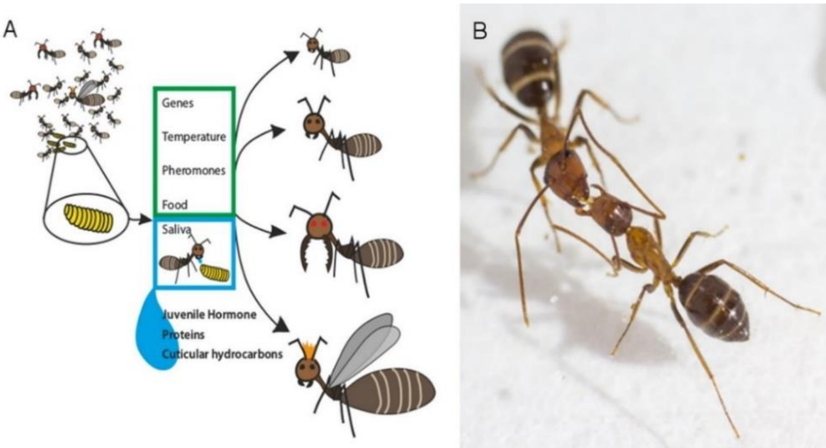

Figure 7: Several factors influence the roles of individual ants in ant colonies (Knaden, 2016).

(A) As a larva (yellow) prepares to transform into an adult ant, the number of factors determine whether it will develop into, for example, a nurse, a forager, a soldier, or a queen (right: top-to-bottom). Previous studies have shown that genetic factors and environmental cues can influence this outcome (green box). Adult ants feed larvae mouth-to-mouth (blue box), a variety of signal molecules are transferred alongside the nutrients in the adult's saliva. These molecules include juvenile hormone, which alters caste fate, and numerous proteins that control how social insects grow and develop. Molecules known as cuticular hydrocarbons (which allow ants to distinguish between nestmates and non-nestmates) are also transferred. (**B**) Adult ants also exchange fluid mouth-to-mouth, as demonstrated in this photograph of two carpenter ants.

2.3.4 Rescue Behaviour

A unique candidate for task specialization, which suggests we should think differently about ants' division of labour, is rescue behaviour. Documented in only a tiny fraction of ant species rescue requires a worker to respond to a call for help from an entrapped nestmate and attempt to free that victim with precisely targeted behaviour that avoids injuring the victim (Nowbahari et al., 2009). Rescue behaviour in *Cataglyphis cursor* is thus an act of individual altruism. Once whatever is restraining the victim has been revealed, rescuers precisely target that object. Workers who contacted the victim and performed one or more behavioural rescue patterns (Table 2) for at least 60 s were transferred to a second ring, where another nestmate victim from the same colony was located.

Table 1: Rescue Behaviour Performed by *Cataglyphis Cursor* Ants

Rescue Behaviour	Operational definition
Sand Digging	Ant positions itself within 2 cm of the trapped victim and flicks sand backward, away from the victim, using its anterior legs.
Limb Pulling	Ant grabs a victim's limb with mandibles and drags backwards with frequent antennation.
Sand Transport	Ant picks up sand particles in contact with a victim, filters paper or snare using mandibles, and moves it at least 5 mm from the snare.
Snare Biting	Ant bites and tugs at the nylon snare using mandibles.

Source: (Knaden, 2016)

2.3.5 Sex and Caste

Workers make up the vast bulk of ants in a colony, and the workers develop from the colony's queen's eggs (Wheeler, 1991). A few eggs develop into winged alates – either queens (fertile females) or haploid males which hatch from unfertilized eggs (White, 1984). Haplo-diploid sex determination controls the first developmental transition, in which unfertilized (haploid) embryos become males and fertilized (diploid) embryos become females (Crozier, 1971). Apparent caste determination may result from temporal variation in sperm use rather than from fertilization bias among male ejaculates. Males die soon after mating, and queens maintain the sperm in a specialized organ (Wheeler and Krutzsch, 1994). In some species, queens produce workers sexually but produce new queens by fertilizing their own eggs. This is called conditional use of sex (Figure 8). Their colonies are made robust by variation among workers, while reproductive offspring receive only the queen's DNA (Pearcy et al., 2004).

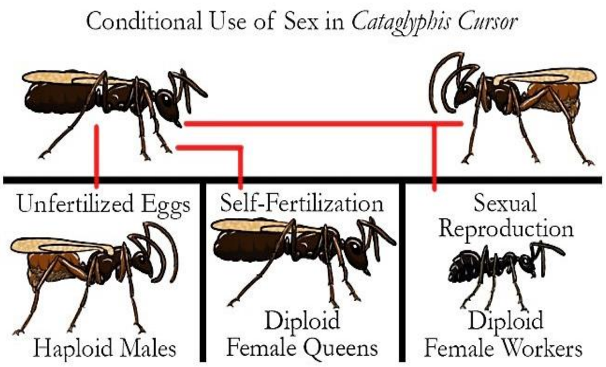

Figure 8: Conditional reproductive system in *Cataglyphis* genus (Meurville and LeBoeuf, 2021).

2.4 Honey bee

2.4.1 Pheromone

In social insects, queen pheromones prevent worker reproduction. The queen's mandibular gland secretion, a mix of fatty acids and aromatic chemicals, is critical for maintaining the reproductive division of labour in honeybees (*Apis mellifera*), suppressing ovary growth in workers (Strauss et al., 2008). Pheromones can affect adults, causing them to treat larvae differently, resulting in the development of either workers or queens. Adult workers are inhibited from developing new queens by queen pheromones regulating what larvae are fed or if workers destroy larvae that have moved to the queen developmental route. Besides this, the brood produced by the queen also inhibits ovary development in workers by emitting two pheromones: the brood pheromone (BP), mainly composed of esters and the highly volatile E-b-ocimene (Arnold et al., 1994; Maisonnasse et al., 2009).

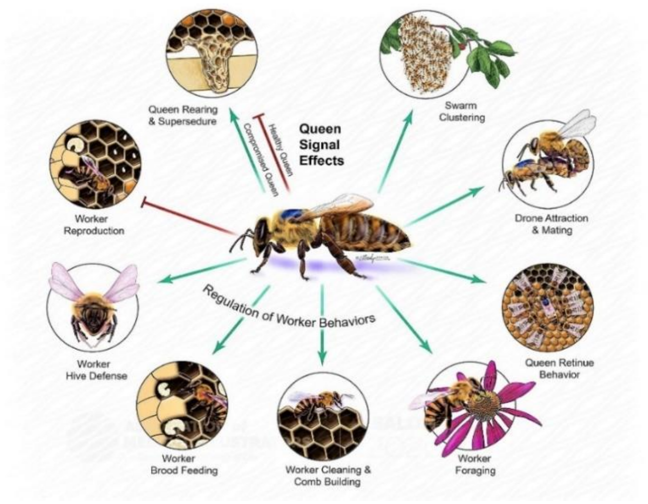

Figure 9: Queen Honey Bee Pheromone Communication (AMI meeting 2021)

Honeybees are a great example of pheromone effects on worker activity that result in variable larval nutrition; queen rearing appears to be fully controlled by worker activities (Figure 9). Workers make queen cells when the queen fails or die or when the colony prepares to reproduce to undergo fission, and this is how caste is determined in honeybees (Alaux et al., 2006).

2.4.2 Reproduction and Development

In the honeybee, *A. mellifera*, secretions of female's Dufours gland differ in composition between the queen and her cohort worker bees (Katzav-Gozansky et al., 1997). A fertile queen's Dufours gland produces a blend of esters (queen pheromone) that control worker bee behaviour (Katzav-Gozansky et al., 2003). Worker bees do not make these esters in a colony with a reproductive queen; instead, they produce comparable alcohols. However, their Dufours glands can be encouraged to produce esters in vitro behaviour (Katzav-Gozansky et al., 2000). When a queen is removed from a colony, the workers' Dufours glands begin to generate esters in vivo, encouraging ovary maturation. Thus, it appears that a fertilized queen's gonadal gland generates esters that regulate the caste and ester production of her colony's workers. Workers can use the queen's social rank and gonadal glands' ability to create these esters in her absence, whether physical or functional.

2.4.3 Food Collection Behaviour

The majority of bee species are solitary, with females searching for nectar and pollen, which they store in large quantities in cells where they lay their eggs. The queen and drones never visit flowers in honey bee colonies; foraging is done exclusively by a specialized caste of sterile female workers. Honeybee workers progress through behavioural tasks within the colony as they grow older, but genes and environmental factors impact their behaviour. (Figure 10) (Robinson, 2002).

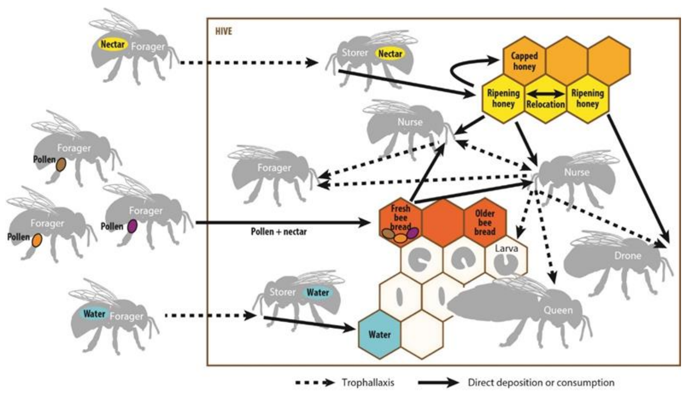

Figure 10: The flow of food and water in a honey bee colony by foragers (Robinson, 2002)

Foragers gather nectar (and honeydew), pollen, water, and tree resin (for propolis); the colony keeps track of foraging effort for each of these items based on the demands of the colony. The pollen-hoarding behaviour of the colony and the possibility of a forager obtaining pollen or nectar are influenced by the queen's and worker patrilines' genetics (Robinson and Page, 1989).

2.4.4 Royal Jelly

Honey bees are the only bee species to convert the food they eat into royal jelly, a nutritional material that is supplied to their larvae. In the heads of bees, the mandibular and hypopharyngeal glands create royal jelly. Nurses distribute it in worker cells and queen larvae cells; queen larvae are given an abundance of jelly, whereas workers are given much less food and fed on-demand in the later stages of growth (Haydak, 1970). Honey bee eggs could be grafted into queen cells and develop into queens. The chemical composition of royal jelly has effects on honey bee development. Only when honeybee larvae are given a substantial amount of royal jelly and they grow into queen bees (Weaver, 1957).

3. Conclusion

Caste determination is an aspect of physiology. Hormones and pheromones play a significant impact. Of the first category, juvenile hormone stands out. It is clear that royal jelly's quantity and factors are essential elements in the caste differentiation of social Hymenopteran insects. In termites, and most probably in other social Hymenoptera as well, the effect of an increased JH-titre is only visible after several moults and metamorphosis have elapsed. This includes the division of labour and the seasonal state of the worker. The endocrine basis of caste differentiation has important consequences for the application of juvenoid insect growth regulators. Developmental programming and the Functioning of castes, modified by hormones, and the underlying trigger mechanisms of endocrine activity, offer a fascinating field of sufficient complexity to provide themes of research for generations of insect physiologists.

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