# THE ROLE OF BROOD IN EUSOCIAL HYMENOPTERA

Eva Schultner

*Centre of Excellence in Biological Interactions, Department of Biosciences, University of Helsinki*

*00014 Helsinki, Finland*

*Tvärminne Zoological Station*

*10900 Hanko, Finland*

*Institut für Zoologie, Universität Regensburg*

*93053 Regensburg, Germany*

e-mail: eva.schultner@gmail.com


Jan Oettler

*Institut für Zoologie, Universität Regensburg*

*93053 Regensburg, Germany*

e-mail: joettler@gmail.com


Heikki Helanterä

*Centre of Excellence in Biological Interactions, Department of Biosciences, University of Helsinki*

*00014 Helsinki, Finland*

*Tvärminne Zoological Station*

*10900 Hanko, Finland*

e-mail: heikki.helantera@helsinki.fi

keywords
eusocial Hymenoptera, brood, development, cooperation, conflict

abstract
*Study of social traits in offspring traditionally reflects on interactions in simple family groups, with famous examples including parent-offspring conflict and sibling rivalry in birds and mammals. In contrast, studies of complex social groups such as the societies of ants, bees, and wasps focus mainly on adults and, in particular, on traits and interests of queens and workers. The social role of developing individuals in complex societies remains poorly understood. We attempt to fill this gap by illustrating*

*that development in social Hymenoptera constitutes a crucial life stage with important consequences for the individual as well as the colony. We begin by describing the complex social regulatory network that modulates development in Hymenoptera societies. By highlighting the inclusive fitness interests of developing individuals, we show that they may differ from those of other colony members. We then demonstrate that offspring have evolved specialized traits that allow them to play a functional, cooperative role within colonies and give them the potential power to act toward increasing their inclusive fitness. We conclude by providing testable predictions for investigating the role of brood in colony interactions and giving a general outlook on what can be learned from studying offspring traits in hymenopteran societies.*

## Introduction

LIFE is social and it is the interactions among molecules, cells, or individuals that have created functional genomes from simple replicators, multicellular organisms from a unicellular ancestor, and animal societies from solitary organisms. Across these evolutionary transitions (Maynard Smith and Szathmáry 1995), similar ultimate factors underlie how single entities form and maintain cohesive social groups. On one hand, genetic relatedness between individual entities facilitates cooperation because partners gain indirect fitness from helping relatives (Hamilton 1964). On the other hand, because partners are rarely genetically identical and do not overlap perfectly in their fitness interests, potential for conflict remains and complex control mechanisms are predicted to evolve in order to keep selfishness in check (Bourke 2011). Both cooperation and conflict are thus crucial determinants of social cohesion.

Insects have evolved an especially large range of social complexity (Figure 1), which reaches its apex in the colonies of eusocial insects that are characterized by reproductive division of labor between individuals, cooperative brood care, and the presence of individuals from overlapping generations (Wilson 1971). The Hymenoptera—ants, bees, and wasps—stand out across the range of insect sociality for several reasons. First, this group exhibits the entire range of sociality, from the solitary lifestyles of parasitic wasps over the semisocial groups of sweat bees to the irreversibly eusocial superorganismal societies of ants and honey bees, with their morphologically separated queen and worker castes and high levels of social cohesion (Helanterä 2016). The same species can even display different levels of sociality depending on environmental conditions (e.g., in bees; Michener 1974). Second, eusociality within the Hymenoptera has evolved several times independently (Johnson et al. 2013). Finally, there is large variation in social ecological complexity even within eusocial Hymenoptera, from the annual, simple family groups of bumble bees to the complex nest networks of supercolonial wood ants (Schultner et al. 2016), making this taxon ideal for understanding the evolutionary dynamics that govern the formation, maintenance, and cohesion of complex social groups (Bourke 2011).

The evolution of eusociality in the Hymenoptera is anchored in simple family groups, with adult offspring staying in their parental nest to help their mother reproduce instead of dispersing and reproducing themselves (Hughes et al. 2008). A typical eusocial Hymenoptera colony is characterized by reproductive division of labor between adult females of overlapping generations—the reproductive queen(s) and her (facultatively) sterile daughter workers. In primitively eusocial species, differences between queens and workers are subtle, involving mainly changes in adult physiology and/or behavior (O'Donnell 1998), and individuals are capable of switching between roles. Although the reproductive capacity of workers is constrained, for instance, via dominance hierarchies or queen pheromonal control (Van Oystaeyen et al. 2014), they usually retain the ability to reproduce sexually, for example, in wasps (Suzuki 1985; Chandrashekara and Gadagkar 1991) and bees (Michener 1990). When a queen dies, one of her daughters will take over the nest—in many cases her success depends

on her physical dominance over nestmates (Michener 1990; Kukuk and May 1991; Kukuk 1994). In advanced eusocial species, reproductive division of labor is generally permanent and queens and workers exhibit strong morphological differences. Queens are specialized for dispersal, colony founding, and egg laying, and workers are structurally adapted for cooperative tasks such as colony defense, nursing, and foraging (Wilson 1953, 1971; Oster and Wilson 1978; Wheeler 1986). Workers are morphologically constrained in their reproductive options because they lack functional organs for sexual reproduction (e.g., loss of functional sperm-storing organs in honey bee workers, Gotoh et al. 2013, 2016; and most ants, Hölldobler and Wilson 1990; Gobin et al. 2008; Gotoh et al. 2016). Although workers of many advanced eusocial species have retained the ability to produce unfertilized eggs that develop into males (Bourke 1988; Helanterä and Sundström 2007), some species have lost worker reproductive organs altogether (Hölldobler and Wilson 1990; Boleli et al. 1999; Gotoh et al. 2016).

The presence of individuals from several generations within the same nest adds a layer of social complexity to eusocial colonies compared to subsocial or semisocial taxa (Figure 1), and social interactions in eusocial species involve parent-offspring and offspring-offspring interactions on several levels: between queens and workers, between queens and their developing offspring, between workers and developing individuals, and among developing individuals. Nevertheless, study of eusocial Hymenoptera has largely concentrated on the social interactions between adult queens and workers, and colony offspring production has been seen as a simple consequence of adult actions. This is perhaps not surprising, since queens and workers share expensive stakes in colony reproduction and, consequently, in lifetime fitness. However, as mentioned above, adult queens and workers can be behaviorally, physiologically, and morphologically restricted to their reproductive roles.

In contrast to adults, the eggs of eusocial Hymenoptera species are generally toti-potent, leaving developing individuals with more reproductive options (Khila and Abouheif 2008, 2010). Hymenoptera develop with complete metamorphosis (so-called holometabolous development) and individuals undergo several developmental steps from egg to adult (Figure 2). An important consequence of development with complete metamorphosis is that growth occurs only during development so that morphological traits such as overall body size and size and allometry of specific body parts are irreversibly determined by the time individuals reach the adult stage. For advanced eusocial Hymenoptera species with morphological reproductive castes, holometabolous development has particularly important consequences: whether a female egg develops into a reproductive queen or a sterile worker is irreversibly determined during larval development (Wheeler 1986). As a result, adult queens and workers are fixed in their reproductive roles when they reach the adult stage. Development is similarly decisive for males, who typically produce sperm only during this life stage, after which the testes degenerate (Hölldobler and Bartz 1985; Boomsma et al. 2005; Stürup et al. 2013).

Within Hymenoptera colonies, developing individuals embody future generations of sexuals and workers with individual fitness interests. At the same time, they represent the combined current reproductive investment of all colony members and much of a colony's social life revolves around brood care and the attempts of adult individuals to follow their inclusive fitness interests by influencing offspring production and development. Brood becomes a source of conflict within colonies when adults follow contrasting fitness interests (Sundström and Boomsma 2001; Beekman and Ratnieks 2003; Beekman et al. 2003; Helanterä and Ratnieks 2009), making them central to the evolution of both cooperation and conflict within societies.

Fully understanding the social complexity of Hymenoptera societies therefore hardly seems possible without a closer look at the biology of brood. Surprisingly, however, developing individuals as a distinct social entity have been largely neglected in studies

Cannibalistic fruit fly larva

Earwig offspring and their mother

Ambrosia beetle larvae cooperatively digging a tunnel

Juvenile termite workers and soldiers

HIGH

Relative importance of indirect fitness

LOW

Adults (and juveniles) of several generations live together

Cooperative brood care

Little or no parental care

Extended parental care

Adults of same generation live together

Reproductive division of labor

Morphological castes

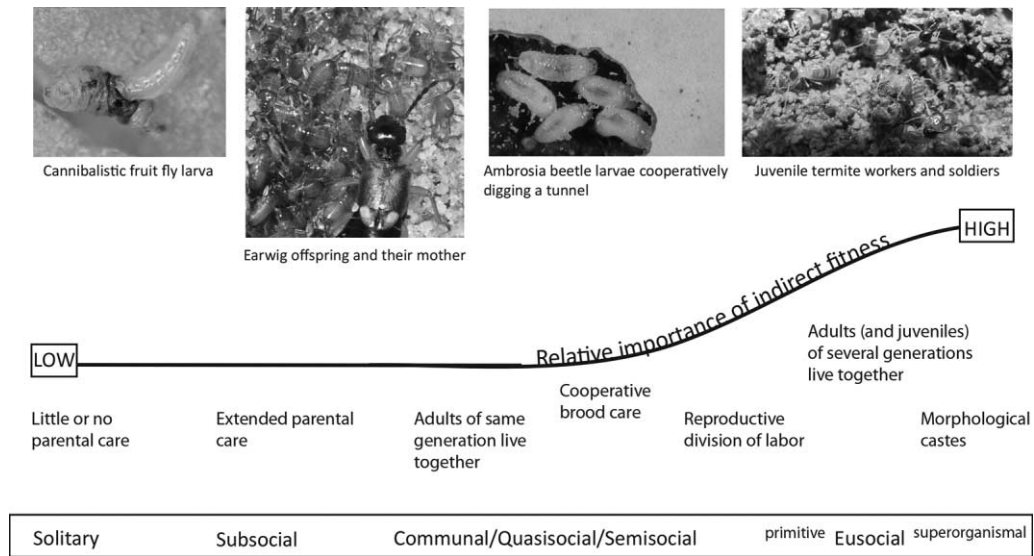| Solitary | Subsocial | Communal/Quasisocial/Semisocial | primitive Eusocial superorganismal |
|----------|-----------|----------------------------------|------------------------------------|

Figure 1. Insect Sociality and the Role of Offspring in the Other Insect Societies

Insects have evolved a wide range of social lifestyles (Wilson 1971; Costa 2006). Main characteristics of this sociality continuum are variation in the social interactions between offspring and adults and among offspring (Wong et al. 2013), and variation in the contributions of indirect and direct fitness to overall inclusive fitness of individuals within groups.

In **solitary** insects offspring typically develop in isolation from parents, so that parent-offspring interactions are nonexistent or limited to short-term parental care such as egg guarding and mass provisioning. However, solitary juveniles can display intense social interactions. Well-known examples include cannibalism among developing stages (e.g., in ladybugs and fruit flies; Michaud and Grant 2004; Vijendravarma et al. 2013) and cooperative foraging in caterpillars (Fitzgerald and Peterson 1988).

In **subsocial** species, parents exhibit extended periods of offspring care, for instance, by engaging in progressive provisioning. With longer periods of parental care, developing individuals also spend more time together, providing further opportunities for interaction. Earwigs are one intriguing example; here mothers defend and provision their mobile offspring for several weeks after hatching (Costa 2006). During this time, offspring can engage in competitive interactions such as cannibalism (Dobler and Kölliker 2010, 2011), but also behave cooperatively by sharing food via direct feedings and consumption of broodmate feces (Falk et al. 2014). Cooperative food sharing has been linked to the transition from simple to highly social groups in the order Blattodea, which contains social cockroaches and termites (Lihoreau et al. 2012). In the termite lineage, food sharing may have played a role in the evolution of eusociality by facilitating transfer of the microbial fauna needed for wood digestion (Bell et al. 2007).

Social insect species comprise **communal**, **quasisocial**, **semisocial**, and primitive and superorganismal eusocial species. In communal species members of the same generation live together but do not engage in cooperative brood care. Quasisocial and semisocial species form groups of members of the same generation and engage in cooperative brood care, and sometimes even division of reproductive labor. Nesting behavior of adults creates a novel social environment, which now includes adult-juvenile interactions that do not involve parents and their offspring. Quasisocial and semisocial insect groups are often only temporary—occurring throughout the colony cycle of several species of bees and wasps (Crespi and Yanega 1995).

Social complexity is most pronounced in obligately **eusocial** insects, which form permanent social groups characterized by reproductive division of labor, cooperative brood care, and the presence of individuals from overlapping generations. With individuals from several generations living in the same nest, social interactions in eusocial species involve parent-offspring and offspring-offspring interactions on several different levels. This complexity can be further increased by the huge variation in colony structures exhibited by eusocial species, which ranges from family groups with a single pair of reproductives and their offspring to huge colonies containing hundreds of reproductives and their respective helper and developing offspring. The diversity of social lifestyles is striking even within the eusocial insects, ranging from the small colonies of primitively

of social Hymenoptera. In fact, developing Hymenoptera are often thought to possess little power, i.e., the ability to act (Beekman and Ratnieks 2003), because of their low mobility and overall dependence on workers. This is in contrast to the other major group of eusocial insects—the termites. Termites are hemimetabolous insects that develop with incomplete metamorphosis. Termite colonies are largely comprised of juvenile workers in different larval (without visible wing buds) and nymphal (with visible wing buds) stages, in addition to reproductive adults (the queen and king). This allows for a more flexible determination of reproductive caste since workers can develop into reproductives late in life. These fundamental differences in developmental strategies have important consequences for individual and colony life history. Furthermore, the ultimate factors driving cooperative behavior appear to differ between eusocial Hymenoptera (benefits from brood care) and termites (benefits from cooperative nest defense). We therefore restrict this review to the role of brood in eusocial Hymenoptera and refer to Korb et al. (2012) for a discussion of brood from a termite perspective.

In the following review, we demonstrate that development in eusocial Hymenoptera constitutes a crucial life stage with important consequences for the individual as well as the colony. We focus mainly on the developing stages of eusocial species because these have been studied most closely. The wealth of literature on queen-worker interactions underlines that eusocial Hymenoptera are especially intriguing for study of social traits because of the large variation in the magnitude of division of labor (e.g.,

ranging from clonal ant species with monomorphic queens and workers to leafcutter ants with several morphological worker castes), ecological strategies (exemplified by differential nesting and brood-rearing strategies in bees and wasps compared to ants), and social structures (from tight-knit family groups to large, genetically diverse colonies; Figure 2).

We begin our review by presenting an overview of the social regulatory network that modulates development in eusocial species and describing the complex fitness interactions between developing individuals and their adult nestmates. We go on to illustrate that, contrary to the common view that brood is powerless, developing individuals are a diverse, functional group that plays an active role in colony life. We conclude by presenting promising avenues of future research on brood biology that will help provide new perspectives on social evolution.

### Development in a Social Environment

There are several features of social hymenopteran biology that are important for understanding the developmental, ecological, and evolutionary processes shaping brood traits within societies. For simplicity, we have summarized these characteristics in Figure 2. We begin our review by focusing on one of these fundamental properties—polyphenic development of female eggs into queens or workers—to illustrate the complex regulation of development in the social environments of hymenopteran colonies. We then zoom in on the fitness interests of developing individuals, who are predicted to evolve traits that allow them

---

eusocial species lacking morphological reproductive castes (e.g., hover wasps, sweat bees) to the huge societies of superorganismal eusocial species with distinct morphological castes (e.g., termites, army ants, honey bees). The social role of developing individuals is surely most pronounced in termites, where juveniles resemble adults in morphology and can carry out all kinds of colony tasks. One of the most fascinating social offspring behaviors is displayed by Ambrosia beetle larvae that cooperate with their adult siblings in brood care, gallery maintenance, and fungus gardening (Biedermann and Taborsky 2011). Discovery of such elaborate behaviors affirms that it is worthwhile to take a closer look at the social role of brood in insect societies.

Photo credits: R. Vijendravarma (fly), J. Meunier (earwig), P. Biedermann (beetle), E. Schultner (termite). See the online edition for a color version of this figure.
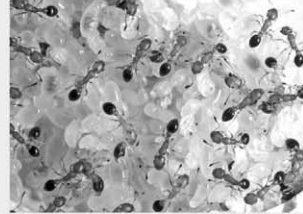
## ECOLOGY

### Colony founding

One thing all eusocial Hymenoptera species have in common is nesting behavior. As a consequence of different colony founding strategies, mature colonies contain either a single queen (monogyny) or multiple queens (polygyny). There are three main ways new colonies are initiated. In independent, solitary founding species a single newly mated queen finds a nest site and produces her first eggs. She then either forages for food (semiclaustral founding) or uses only her reserves (claustral founding) to feed hatching larvae (Johnson 2006). Once the first workers hatch, they take over foraging and brood care. Independent pleometrotic colony foundation involves several mated queens that cooperate during colony foundation—depending on the species, queens then reproduce cooperatively (primary polygyny) or one of the foundresses becomes the dominant queen (secondary monogyny). In dependently founding species, a newly mated queen joins her maternal or a nearby nest. Newly adopted queens either remain in the nest, resulting in secondary polygyny, or leave the nest with a group of workers (so-called budding or fission).

### Nesting

The majority of eusocial bees and wasps rear offspring in separate cells so that developing individuals have no or little contact with their developing nestmates (with some rare exceptions—brood of allodapine bees, for instance, is not reared in cells; Kukuk 1994). In contrast, ants rear their brood in loose piles so that developing individuals can be in contact with other eggs, larvae, and pupae. Some ant species sort brood by age and/or development stage, others keep all development stages together.
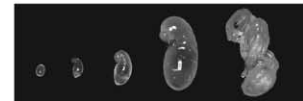
### Brood provisioning

Eusocial Hymenoptera can be divided into groups according to the way they provision their brood. In mass provisioning species (sweat bees, carpenter bees, stingless bees) workers deposit a fixed amount of food in each cell, after which a queen (or worker) lays an egg and the cell is sealed. Progressively provisioning species feed larvae continuously throughout development—cells are only sealed shortly before pupation. Some eusocial bees (Allodapinae, bumble bees, honey bees) and all eusocial wasps (hover wasps, paper wasps, yellow jackets) and ants are progressive provisioners.
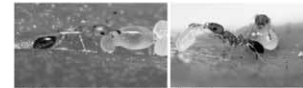


Honey bee worker emerging from brood cell



Ant workers tending a brood pile

## DEVELOPMENT

### Holometaboly

Hymenoptera undergo complete metamorphosis, which means that their development consists of four distinct stages: egg, larva, pupa, and adult (or imago). A key consequence of holometabolous development is that fitness-related traits such as overall body size and size and allometry of body parts are irreversibly determined by the time individuals reach the adult stage. In species with morphological castes, this strongly affects the fitness options of adults (direct fitness through own offspring versus indirect fitness through benefiting offspring of relatives, see Eusociality and inclusive fitness below) since they are morphologically restricted to their reproductive roles. Holometaboly distinguishes eusocial Hymenoptera from the hemimetabolous termites, which develop with incomplete metamorphosis so that juveniles resemble adults in morphology. The stark differences between life stages in holometabolous insects can allow them to occupy distinct niches. Even in Hymenoptera colonies, where juveniles and adults share a strictly controlled nest environment their distinct morphologies can influence their ecological niche. For instance, the thread waist of adult ants, wasps, and bees restricts them to ingesting liquid food. Their larvae have not yet developed a narrow waist, allowing them to take over digestion of large solid food items (Hunt and Nalepa 1994).
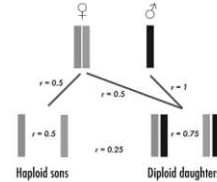
### Haplodiploidy

A prominent feature of Hymenopteran development is haplodiploid sex determination. Through this process, male ants, bees, and wasps develop from unfertilized, haploid eggs while females, i.e., workers and queens, develop from fertilized, diploid eggs. Haplodiploidy affects the relatedness (r) structure between groups of individuals within colonies. When a single-mated queen reproduces, her daughters (workers and gynes) will share identical paternal genes ($r = 1$) in addition to, on average, half of the same maternal genes ($r = 0.5$). Sons, on the other hand, carry only a single copy of maternal genes. On average, sisters are therefore more closely related to each other ($r = 0.75$) than to their mother ($r = 0.5$) or brothers ($r = 0.25$). The mother queen in contrast is equally related to daughters and sons ($r = 0.5$).



Developmental stages in the ant
*Cardiocondyla obscurior*



Adult *C. obscurior* queen and wingless, sterile worker



## EVOLUTION

### Eusociality and inclusive fitness

Reproductive altruism was long considered an evolutionary puzzle. Put simply, how can worker individuals evolve that never pass their genes onto the next generation? Inclusive fitness theory (Hamilton 1964) provides an answer to this paradox by showing that altruism can evolve if the fitness benefit b to the recipient outweighs the fitness loss c to the donor, weighted by the relatedness r between recipient and donor (Hamilton's rule: $b * r > c$). An individual can thus forego own reproduction (direct fitness) in order to gain indirect fitness (in terms of the genes passed onto the next generation) by helping a related individual reproduce because both share copies of the same genes more often than random individuals in the population. The more closely related two individuals are, the higher the indirect fitness gains for the helper. Inclusive fitness theory has received vast empirical support and it is commonly agreed that it explains the evolution of eusociality (Maynard Smith 1964; Abbot et al. 2011; Bourke 2011).
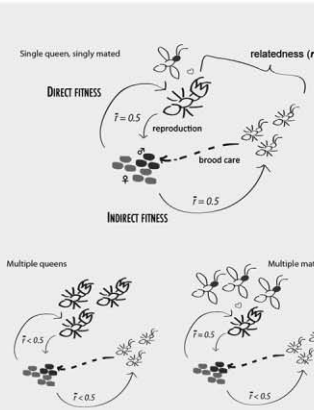
### Kin structure variation

Social Hymenoptera are powerful models for testing inclusive fitness predictions because of the extreme variation in the relatedness structure of their colonies (Crozier and Pamilo 1996). Relatedness between nestmates is largely determined by the number of reproducing queens, which can vary within and between species (e.g., in ants: Bourke and Franks 1995). Relatedness also varies with queen mating frequency. Finally, haplodiploid sex determination results in relatedness asymmetries between groups of individuals within colonies. Variation in kin structure explains variation in many features of colony allocation strategies, for instance, regarding sex ratios and male parentage.



FIGURE 2. FUNDAMENTAL FEATURES OF SOCIAL HYMENOPTERA BIOLOGY

to maximize their inclusive fitness, and explore how these tie-in with the inclusive fitness interests of other colony members.

## COMPLEX SOCIAL REGULATION OF DEVELOPMENT

Like in other organisms, developmental outcome in social Hymenoptera depends on individual genotype, environment, and direct maternal effects (West-Eberhard 2003). Social environment adds another layer of complexity to this regulatory developmental network (Wheeler 1986, 1991; Linksvayer and Wade 2005) as expression of larval phenotypes can be regulated by the genotypes of adult colony members through modification of the internal environment independently of outside factors (Linksvayer and Wade 2005; Linksvayer 2006, 2007; Linksvayer et al. 2009, 2011). Developing in a Hymenoptera colony thus entails exposure to an intricate social network, providing developing individuals with ample opportunity to participate in social processes, while at the same time allowing adult nestmates to influence larval environment.

The complexity of social regulation of development is best exemplified by differential queen-worker development. This fundamental property of eusocial Hymenoptera colonies has received much attention and presenting a comprehensive account of the proximate mechanisms involved is outside the scope of this review—we instead refer readers to more thorough reviews of this topic (e.g., Wheeler 1986; Anderson et al. 2008; Smith et al. 2008b; Corona et al. 2016; Kapheim 2016). In the following we use differential queen-worker development to illustrate the complexity of developmental regulation in eusocial colonies.

Contrasting queen and worker phenotypes result from differential expression of core developmental pathways (West-Eberhard 2003) that are *cis*-regulated by methylation (Bonasio et al. 2012; Simola et al. 2013) and transcription factors (Schrader et al. 2015; Klein et al. 2016). Alternative developmental trajectories can be initiated by factors such as genetic predisposition (Julian et al. 2002; Volny and Gordon 2002; Helms Cahan and Keller 2003; Anderson et al. 2006, 2008; Schwander and Keller 2008), maternal effects (Bier 1952, 1954a; Schwander et al. 2008; Libbrecht et al. 2013), and by social developmental environment, particularly nutrition (Michener 1974; Ishay et al. 1976; Wheeler 1986, 1994; Hölldobler and Wilson 1990; Gadagkar et al. 1991; Kukuk 1994; O'Donnell 1998; Karsai and Hunt 2002; Smith et al. 2008a; Jeanne and Suryanarayanan 2011; Kamakura 2011; Linksvayer et al. 2011; Judd et al. 2015). Food quality and quantity, in particular, seem to play a role in triggering worker development by acting on diverse molecular and physiological processes (Corona et al. 2016). In primitively eusocial species, environmental variation in resource levels can underlie female caste differences (Knerer and Atwood 1966). In most species, however, nutrition levels of larvae are assumed to be (at least to some extent) under worker control. In mass provisioning species such as stingless bees, for example, larvae are reared in closed cells and workers deposit more than twice the amount of food in the larger queen cells compared to worker cells (Sakagami 1982). Workers can also manipulate the quality of larval provisions. In primitively eusocial sweat bees, larvae reared on provisions with relatively higher sugar content are more likely to attain queen status (Richards and Packer 1994). Similarly, in the progressively provisioning honey bee where cells remain open until pupation and larvae are fed successively, workers exert

control over caste determination by feeding queen-destined larvae with high-quality royal jelly instead of pollen ( Jung-Hoffmann 1966). Apart from provisioning behavior, workers can also influence female development via mechanical signals ( Jeanne 2009) or directed aggression (Brian 1973; Penick and Liebig 2012).

In many cases, worker brood care behavior is modulated by the queen(s). Indeed, queens play a role in social control of caste fate, for example, via pheromonal control of worker feeding behavior (Vargo and Passera 1991; Vargo 1998), through mechanical signals directed at developing females ( Jeanne 2009; Jeanne and Suryanarayanan 2011; Suryanarayanan et al. 2011), via pheromones that cause workers to kill sexual larvae (Edwards Adas 1991; Vargo and Passera 1991; Keller et al. 1996; Klobuchar and Deslippe 2002), or through direct pheromonal inhibition (Röseler and Röseler 1974; Passera 1980). Although queen signaling appears to act like an enforcement strategy, the widespread occurrence and evolutionary stability of inhibitory signals (Van Oystaeyen et al. 2014) suggests that the colony as a whole, and possibly individual larvae, may benefit from queen control of female caste (Keller and Nonacs 1993). Conditions experienced by queens may also translate into different female phenotypes via maternal effects (Schwander et al. 2008; Meunier and Chapuisat 2009; Cahan et al. 2011; Libbrecht et al. 2013). In wood ants, for example, queens develop from eggs laid in spring, while summer eggs develop into workers (Bier 1954a). Predisposition toward queen caste in the egg stage arises because spring eggs are associated with larger nurse cells in the ovaries (Bier 1952, 1954b). However, predetermination of caste in these species is not absolute and worker-modulated nutritional conditions experienced by female larvae play a substantial role in influencing adult caste (Bier 1954a; Gösswald and Bier 1954).

These examples show that the influence of individual genotype, environment, maternal effects, and sibsocial effects on development are often difficult to tease apart (Linksvayer and Wade 2005). With the help of cross-fostering approaches, experimental studies are now beginning to reveal how these factors interact to create different phenotypes. In ants, for example, caste fate of female larvae can be determined by an interaction between larval genotypes and genotypes of adult nestmates (Linksvayer 2006, 2007; Teseo et al. 2014; Villalta et al. 2016b). These interactions are likely modulated by individual differences between larvae regarding sensitivity to social environmental input and individual worker differences in key behaviors like provisioning. Similar effects of worker genotypes on female caste development have been demonstrated in the honey bee (Linksvayer et al. 2011), where interplay between larval and nurse worker gene expression regulates differential development of female larvae (Vojvodic et al. 2015). Interplay of individual genotypic, maternal, and sibsocial effects can also influence expression of more general traits, such as body size and survival. In acorn ants, interaction between larval and worker genotypes determines adult worker body size (Linksvayer 2007). In contrast, worker and larvae genotypes interact to modulate survival but not worker size in the alpine ant (Purcell and Chapuisat 2012).

Further excellent evidence for the complexity and flexibility of the social developmental regulatory network comes from the study of ants, where so-called intercastes commonly occur (cf. Heinze 1998). Intercaste individuals are thought to result from abnormal development because they display an uncoordinated expression of queen and worker traits. However, aberrantly produced intercastes can become accommodated into stable intermorph phenotypes when their presence increases colony fitness (Molet et al. 2012), underlining the importance of development for evolutionary processes. Intermorphs with a functional spermatheca and active ovaries have been found in a ponerine ant (Ohkawara et al. 1993), where they may represent a novel caste specialized in brood production. In *Crematogaster* ants intermorph-laid eggs are redistributed to the queen and the larvae (Heinze et al. 1999; Peeters et al. 2013) and

**MARCH 2017**

thus serve as food sinks without affecting male parentage or sexual production (Oettler et al. 2013), indicating that developing into an intermorph is altruistic at the colony level.

To conclude, the wealth of studies on female caste determination in eusocial Hymenoptera provide an excellent backbone for investigating regulation of development in social environments. In the future, the combination of experimental and molecular methods should help further unravel the mechanisms associated with such genotype by (social) environment interactions.

<div align="center">

FITNESS INTERESTS OF
DEVELOPING INDIVIDUALS
</div>

Evolution of social developmental regulation is tightly linked with selective processes acting on individual as well as colony-level traits (Figure 3). On one hand, male and female sexuals mate and produce offspring, which allows them to gain direct fitness from reproduction. Workers in species with distinct morphological castes, on the other hand, are typically restricted to gaining indirect fitness by helping to rear related offspring. Both sexuals and workers ultimately depend on colony reproductive output for inclusive fitness, and total offspring production depends on the quality of the queen(s) and her mate(s) as well as on the ability of workers to cooperate efficiently (Korb and Heinze 2016). Colonies as groups of cooperating individuals can thus become direct targets of selection and be seen as adaptive "superorganismal" units if within group competition is obviated (Gardner and Grafen 2009), e.g., when efficient control of brood rearing by workers resolves the conflict over caste fate of developing females (Ratnieks et al. 2006; Ratnieks and Helanterä 2009). When the fitness interests of developing individuals differ from those of their nestmates based, for instance, on relatedness asymmetries within complex societies, potential for social conflict exists (Ratnieks and Reeve 1992; Ratnieks et al. 2006). In the next section, we zoom in on key traits linked to the fitness interests of developing individuals, and explore whether these concur or are in conflict with the inclusive fitness interests of other colony members. Furthermore, we highlight the features that determine whether individuals are able to capitalize on potentially conflicting inclusive fitness interests and the factors that may constrain them from doing so.

<div align="center">

Female Caste Fate
</div>

Perhaps the most important trait for a developing female is whether she develops into a reproductive queen or a (functionally) sterile worker. Because a female is more closely related to her own offspring than to offspring of other developing individuals, female larvae are predicted to be under selection to increase their chances of developing into a queen rather than a worker (Bourke and Ratnieks 1999; Ratnieks 2001; Reuter and Keller 2001; Wenseleers et al. 2003; Dobata 2012). Adult queens and workers generally differ in their relatedness to developing females because of haplodiploidy, with workers more closely related to their queen-destined sisters than to their mother queen. This can cause them to exhibit differing fitness interests regarding allocation of resources toward new queens versus workers (Strassmann et al. 2002; Ratnieks et al. 2006). Additionally, variation in colony queen number or queen mating frequency may lead them to differ in their interests regarding the identity of queen-destined larvae (i.e., nepotism; Ratnieks et al. 2006). Similarly, decreasing relatedness may increase levels of selfishness in developing females, resulting in conflict over female caste both among female larvae and between female larvae and their adult nestmates (Dobata 2012). However, conflict between queens and workers over which individual female larva develops into a queen may be constrained from breaking out because within-colony kin discrimination and the cues that underlie it are predicted to be selected against (Ratnieks 1991; Keller 1997). Similarly, multiple mating by queens should reduce actual levels of within-colony conflict over female caste fate by increasing caste fate policing (Dobata 2012).
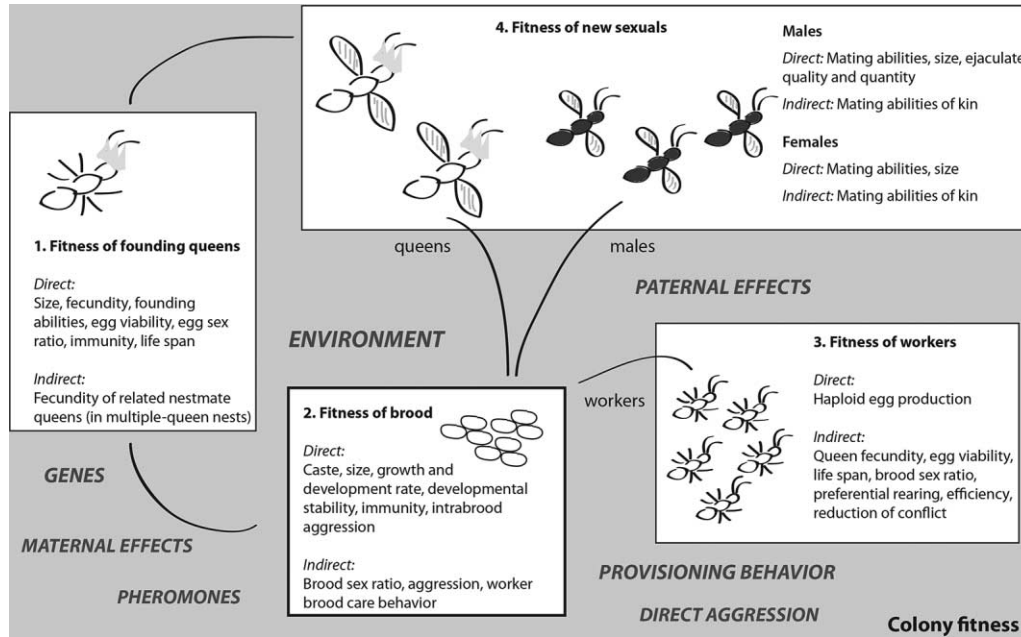
Figure 3. Determinants of Fitness in Hymenoptera Colonies

The life cycle of a stereotypical social hymenopteran colony begins with a single queen. Prior to colony foundation, the queen mates with one or several males whose sperm she stores in her spermatheca for the entire duration of her life. Although the males die soon after mating, the queen goes on to found a new colony. During the early phases of colony foundation, she produces female eggs that develop into the first generations of workers. After a phase of colony growth during which only workers are reared, the queen starts to lay male eggs and workers begin rearing female larvae into new queens. Upon maturation, males and new queens leave their natal nest to mate, and the cycle starts anew. Individual fitness depends on an array of factors in each life stage, including caste (e.g., queen or worker), morphology, physiology, fecundity, and behavior. These fitness-determining factors are in turn strongly influenced by genes, epigenetic mechanisms, and abiotic and social environment. Colony fitness is also determined by these factors and their interactions, as well as by their consequences on collective behavior, colony efficiency, and social cohesion. See the online edition for a color version of this figure.

There are many potential ways in which a female larva can influence her caste fate; these are strongly linked to species-specific mechanisms of caste determination. The best example for selfish queen caste determination comes from taxa where queen-worker size dimorphism is absent (Ratnieks 2001). In *Melipona* stingless bees, queens and workers are reared in identically sized cells provisioned with the same amount of food. Around one-fifth of female larvae develop into queens (Kerr 1950; Wenseleers and Ratnieks 2004), even though very few of them end up as swarming queens (Bourke and Ratnieks 1999; Wenseleers et al. 2003). However, queens that do manage to join a swarm and found a new colony reap immense fitness benefits. At the same time, selfish female larvae are costly to the colony overall, probably because queen development demands high resource investment. Workers kill a large proportion of excess queens immediately after emergence (Engels and Imperatriz-Fonseca 1990; Wenseleers et al. 2004a), which suggests that individual- and colony-level selection are opposing forces in this conflict. Alternatively, production and culling of excess queens may be a way for workers to select the highest quality queen. Although these bees have long served as models in social insect research, how selfish larvae actually influence their caste fate is not well understood. With today's genomic resources (Kapheim et al.

2015), this fascinating system seems predestined for studying the proximate link between genetic and/or environmental factors and selfish queen determination, and promises to shed light on general processes coordinating developmental switches in eusocial insects.

Another way female larvae may selfishly attain queen caste is by developing into miniature queens (Bourke and Ratnieks 1999; Wolf and Seppä 2016). Females that develop into queens in spite of only being fed worker rations have been observed in ants (McInnes and Tschinkel 1995; Rüppell et al. 1998; Lenoir et al. 2010) and stingless bees, where developing into a miniature queen has clear fitness benefits as "dwarf" queens are frequently observed to head colonies (Wenseleers et al. 2005; Ribeiro et al. 2006). Instead of founding their own colonies, small queens of the fire ant *Solenopsis invicta* take over unrelated, queenless nests (McInnes and Tschinkel 1995) in order to exploit the resident worker force (Tschinkel 1996). Over one-third of colonies produce small queens in the field, indicating that conspecific colony takeover pays off (McInnes and Tschinkel 1995). Here, developing into a small queen allows female larvae to engage in an alternative reproductive tactic (Wolf and Seppä 2016), potentially resulting in large fitness benefits. This mode of colony foundation is common in socially parasitic (inquiline) ants, where queens are of similar size as their heterospecific host workers; miniaturization of queens appears to be an evolutionary mechanism allowing parasites to produce queens even when larvae are fed worker rations (Nonacs and Tobin 1992; Aron et al. 1999). When female larvae in nonparasitic species employ similar tactics to attain queen status, they may in fact be acting as intraspecific parasites (Savolainen and Vepsäläinen 2003; Lenoir et al. 2010). Prevalence of clear queen-size dimorphism and altogether smaller queen sizes in polygynous species (Heinze and Tsuji 1995; Rüppell and Heinze 1999; Heinze and Keller 2000; Rüppell et al. 2002) suggests that small queens may represent a successful strategy in species where queens stay in their natal nest or join already established nests instead of founding their own colonies (Lenoir et al. 2010). Theory predicts potential conflict among workers, resident queens, and the future queens regarding queen development, recruitment, and dispersal in polygynous species (Crozier and Pamilo 1996), but empirical tests are still lacking.

## Female Quality

In holometabolous insects, morphological traits such as overall body size are irreversibly determined during development (Shingleton et al. 2007). Substantial evidence shows that these traits play a role in determining adult fitness (Roff 1992; Stearns 1992). For instance, overall body size is positively correlated with female potential fecundity in butterflies (Bauerfeind and Fischer 2005; Boggs and Freeman 2005).

Likewise, large ant queens have higher chances of surviving independent colony foundation (Bourke and Franks 1995; Wiernasz and Cole 2003; Enzmann et al. 2014). In addition, queen body weight is positively correlated with oviposition rate (Wagner and Gordon 1999) and overall brood production (Fjerdingstad and Keller 2004). Although increased weight can be a result of both pre- and posteclosion feeding, these studies indicate that well-endowed queens outcompete smaller conspecifics. Similarly, a queen that concludes development with a slight size advantage may increase her chances of winning struggles over reproductive dominance that involve direct aggression or fighting (Bernasconi and Strassmann 1999; Beekman and Ratnieks 2003; Beekman et al. 2003; Ratnieks et al. 2006). This is the case in the fire ant *Solenopsis invicta* (Bernasconi and Keller 1998) and the garden ant *Lasius niger* (Aron et al. 2009), where the largest queens typically win contests among cooperatively founding queens. Queen-destined larvae may be confronted with a tradeoff between adult body size and timing of emergence if fast development confers a fitness advantage but results in smaller adult size with potentially lower fecundity and/or longevity. In the honey bee, the virgin queen that hatches first rou-

tinely attempts to kill any remaining queen pupae in order to assure her takeover of the maternal colony (Seeley 1985). Here, competition over future reproductive dominance between queen-destined larvae may become apparent in differential developmental rates.

The outcome of competition between females in species without morphological castes may also be influenced by size advantages accumulated during development (Kukuk 1994). In the eusocial halictine bee *Lasioglossum zephyrum*, for instance, the probability that a female will emerge as queen increases with body size (Michener 1990) and large queens are better at inhibiting worker reproduction (Kukuk and May 1991). Finally, it is often overlooked that developmentally determined adult traits can play a role for worker inclusive fitness. For example, in a carpenter ant where workers have retained the ability to produce haploid, male-destined eggs, worker size is positively correlated with ovariole number (Wheeler 1994). In honey bees, workers that are pollen-deprived during development grow up to be poor foragers (Scofield and Mattila 2015).

Generally, workers should have an interest in controlling female size if a certain size is linked to higher fitness per unit of investment (Fjerdingstad 2005), whereas a developing female might simply prefer larger size. Variation in resource availability should lead workers to adjust the number of queens they rear, while maintaining optimal queen size (Rosenheim et al. 1996; Fjerdingstad 2005). However, many species show considerable variability when it comes to queen size (Sundström 1995; Fjerdingstad and Boomsma 1997; Rüppell et al. 2002; Wiernasz and Cole 2003; Fjerdingstad 2004, 2005; Meunier and Chapuisat 2009), which indicates that although workers may retain partial control of size through allocation of provisions to larvae, plastic developmental responses may limit their ability to control female size (Fjerdingstad 2005). Indeed, size variation within species or even colonies likely reflects variation in developmental trajectories brought about by environmental factors, worker provisioning behavior, and larval developmental and behavioral

responses (Linksvayer 2006). Cross-fostering approaches that take differential larval responses into account can help resolve whether variability in queen size reflects the outcome of conflict between developing queens and workers, or simply represents noise in the system.

## Male Quality

Eusocial Hymenoptera males spend the majority of their lives as developing individuals, usually surviving as adults only long enough to mate (Hölldobler and Bartz 1985). Male reproductive success has been linked to sperm quantity and quality (Wiernasz et al. 2001; Baer and Boomsma 2004; Lawson et al. 2012), seminal fluid composition (den Boer et al. 2009, 2010; King et al. 2011), and the presence of mating plugs (Roberston 1995; Duvoisin et al. 1999; Baer et al. 2001). Because of their short adult life span males typically only produce sperm during development, after which the testes degenerate (Hölldobler and Bartz 1985; Passera and Keller 1992; Simmons 2001; Boomsma et al. 2005); the only known exception to this rule are the wingless males in the ant genus *Cardiocondyla* (Heinze and Hölldobler 1993). With spermatogenesis restricted to development, ejaculate quantity and viability are invariably fixed by the time the adult male emerges. Given the fitness benefits from lifelong pair-bonding, male larvae should thus have a strong interest in maximizing ejaculate production (Boomsma et al. 2005). However, few studies have investigated how conditions experienced during development impact characteristics of the male ejaculate. Correlative evidence for the importance of development and growth in determining male reproductive success has been found in the harvester ant, where large males transfer up to five times more sperm than small males (Wiernasz et al. 2001). Similarly, large honey bee drones carry significantly more sperm than small drones (Schlüns et al. 2003). Recently, it has also been shown that protein intake during adulthood does not affect sperm viability in drones, indicating that larval nutrition plays a central role in determining male fitness (Stürup et al. 2013).

Prior to mating a male must search for, find, and court a prospective queen while facing strong competition from rival males (Shik et al. 2013). Similar to queens, adult body size and timing of emergence is thus predicted to be crucial for male quality and reproductive success. An association between overall male body size and fitness has been demonstrated in harvester ants (Davidson 1982; Wiernasz et al. 1995; Abell et al. 1999), where the size and the shape of legs and wings correlate with male mating success (Wiernasz et al. 1995). In the honey bee, mating flights seem to have selected for wing symmetry in males, a trait linked to developmental stability (Jaffé and Moritz 2010). Male quality may be particularly linked to fitness when competition for matings is fierce (Wiernasz et al. 1995; Abell et al. 1999; Boomsma et al. 2005). As is the case for queens, workers should prefer male sizes with the highest fitness payoff per unit investment (Fjerdingstad 2005), and worker and larval genotypes together with environmental factors likely determine adult male size. Although social Hymenoptera males are generally short-lived and do not contribute to social life, there are exceptions such as the long-lived males in the ant genus *Cardiocondyla*, which allow for more detailed study of the dynamics of male quality (Heinze 2016).

## Brood Sex

The fitness optima of queens and workers in regard to brood sex allocation are determined by relatedness asymmetries between individuals resulting from haplodiploidy, variation in queen mating frequency, queen number and relatedness, and the production of males by workers (Bourke and Franks 1995; Ratnieks et al. 2006). In the simplest scenario with one singly mated queen as sole reproductive, workers should prefer threefold investment in female sexuals while the queen prefers equal investment in both sexes (Trivers and Hare 1976). Conflict between these parties of interest becomes apparent when workers execute male brood (Keller et al. 1996; Passera and Aron 1996; Sundström et al. 1996; Chapuisat et al. 1997)

or selectively bias the caste fate of female larvae, thus decreasing production of workers but increasing allocation to female sexuals (Hammond et al. 2002). Because of the extreme consequences of such behavior, each male larva should prefer to escape execution (Nonacs 1993) while each female larva should prefer to be a recipient of preferential treatment (as long as they can effectively turn the extra resources into fitness). As is the case among adults, colony kin structure may play a role in determining the potential for this conflict. In particular, selection on workers to detect and remove queen-laid male larvae should be stronger in singly mated, single-queen colonies. Male larvae in single-queen colonies should therefore, both as individuals and as a collective (since they prefer an equal sex ratio, as do the queens), have an increased interest in escaping detection by workers compared to their counterparts in multiple-queen colonies. Female larvae in single-queen colonies may benefit from advertising their sex in order to facilitate selective removal of males. Although queens determine primary sex ratios via control of egg fertilization, brood phenotype is decisive in influencing the ability of workers to manipulate secondary sex ratios via selective brood rearing (Mehdiabadi et al. 2003).

## Brood Parentage

In species where workers have retained the ability to produce haploid male eggs, a further conflict arises over male parentage. Although male larvae and their worker mothers share an interest in individual male survival, nestmate workers and queens should prefer to lay their own eggs and/or rear only queen-laid male eggs. The potential for conflict is predicted to vary with kin structure, with higher levels of worker reproduction in colonies with a single, singly mated queen where workers are on average more related to sons of other workers than to sons of the queen. Here, workers are predicted to be under selection to produce their own sons instead of rearing the queen's sons. Accordingly, worker-laid males in such colonies should have an interest in signaling

their maternity to promote preferential rearing. In contrast, in colonies with multiply mated queens, workers are selected to police other egg-laying workers as they are more closely related to queen sons than worker sons, even if each individual worker is still most closely related to her own sons (Ratnieks 1988; Wenseleers et al. 2013). Here, worker-laid males should have an interest in masking maternity. Although relatedness variation seems to explain a considerable proportion of variation in worker policing (Bourke 1988; Wenseleers and Ratnieks 2006b), worker policing can also evolve if there are substantial costs to unchecked worker reproduction, i.e., through decreases in colony efficiency (Ratnieks 1988; Hammond and Keller 2004). Ultimately, policing behavior should select against worker egg laying (Wenseleers et al. 2004b), which has been shown to be the case in honey bees and social wasps (Wenseleers and Ratnieks 2006a).

Conflict over parentage of both male and female brood can arise between queens in multiple queen colonies (Reeve and Ratnieks 1993; Keller and Reeve 1994; Keller 1995, 1997). Here, kin-preferential behavior or nepotism is predicted to evolve because individual workers and groups of workers vary in their relatedness to brood produced by different queens. Brood may be selected to either signal maternity in order to facilitate kin-preferential rearing or mask maternity to avoid nepotistic brood removal. Although theory predicts selection against sufficient chemical information for kin-preferential rearing (Ratnieks 1991), it does not preclude selection on larvae to advertise parentage and empirical data show that genetic relatedness can be reflected by chemical similarity (Dani et al. 2004; Nehring et al. 2011; Helanterä et al. 2013; Helanterä and d'Ettorre 2015).

## The Social Role of Developing Individuals

In the previous section, we described why development is an important life stage both for the individual and the colony and illus-trated how social environment influences individual development. We now change perspective and examine how developing individuals themselves can influence social processes within a colony.

The mere presence or absence of brood affects ecological, behavioral, and physiological processes within colonies. For example, ant larvae influence periodic activity, foraging strategies, and ovarian activity of workers (Cole and Hoeg 1996; Dussutour and Simpson 2009; Ulrich et al. 2016). In wasps, absence of brood causes workers to abandon colonies (Kumano and Kasuya 2001) and can induce physiological changes in individual workers that lead to the development of queen-like features (Solis and Strassmann 1990). Brood can also be involved in influencing ecological processes outside the colony—larval demand for protein in aphid-tending ants, for instance, directly impacts growth rates of aphid colonies (Oliver et al. 2012).

Brood thus clearly modulates processes on both the individual and the colony level. Such modulation can be passive (e.g., when workers respond to larger numbers of larvae by increasing foraging efforts) and thus strongly resemble the limited parent-offspring interactions in subsocial insects (Wong et al. 2013). Brood can also actively influence the behavior and physiology of their nestmates, as well as their own development. This seems intuitive when thinking of social interactions in simple groups such as the classic case of family conflict in birds, where chicks adjust their begging intensities to maximize their own food intake (Smith and Montgomerie 1991; Ottosson et al. 1997), often to the detriment of their siblings or parents (Mock and Parker 1998; Johnstone 2004). So far, little attention has been paid to active manipulation by eusocial Hymenoptera offspring and few studies have aimed at distinguishing between passive and active mechanisms. Similarly, the importance of brood traits for determining individual and colony developmental processes and their effects on fitness trajectories remains underappreciated. So although there is ample evidence that de-

veloping individuals are as social as adults, in many cases it remains unclear to which extent brood social traits serve cooperative and selfish purposes, whether they can be used in different contexts, and how they influence social processes.

In the second part of our review, we provide a synthesis on the morphological, behavioral, and physiological traits that allow developing offspring to modulate individual- and colony-level processes. We roughly classify offspring traits according to features of social life, but ask readers to remember that traits may be used in different contexts. We highlight cases where developing individuals may be actively manipulating their social environment and discuss the relevance of specific traits for the acting developing individual, its nestmates, and the colony as a collective whole.

## BROOD EXHIBITS MORPHOLOGIES ADAPTED TO SOCIAL LIFE

Compared to the striking diversity of adult ants, bees, and wasps, at first glance brood looks surprisingly similar across taxa. Legless and grub-like, social Hymenoptera larvae seem to display few distinct features. However, a closer look reveals a large diversity in morphology (Wheeler and Wheeler 1976) even within single groups—e.g., in ants (Wheeler 1918; Wheeler and Wheeler 1953; Petralia and Vinson 1979; Hölldobler and Wilson 1990; Masuko 1990a, 2008; Peeters and Hölldobler 1992; Baratte et al. 2005; Bueno et al. 2011; Solis et al. 2010a,b, 2011, 2012). Indeed, morphological specializations linked to the specific ecology of larvae are visible in developing stages. Larvae of many ant species use their sharp, sclerotized mandibles to feed directly on insect prey brought back to the nest (Wheeler 1918; Wilson 1958). *Myrmecina* ant larvae have specialized, elongated head morphologies that allow them to consume the contents of their mite prey (Masuko 1994, 2008). In contrast, in ants with largely immobile larvae that are fed directly by workers, mandibles are often rudimentary (Wheeler and Wheeler 1953). Some ant larvae have unique

structures that are used to hold solid food items (Petralia and Vinson 1978, 1979; Buschinger and Schaefer 2006). Others carry specialized tubercles through which they secrete substances that workers ingest during brood care (Wheeler 1918; Villet et al. 1990).

Brood has also evolved features that are important to colony survival, defense, and organization. Ant colonies take advantage of the superior buoyancy of brood and its resistance to submersion by forming living rafts with which they escape floods in their unpredictable habitats (Adams et al. 2011; Purcell et al. 2014). In the weaver ant *Polyrhachis muelleri*, larvae and pupae possess mimetic green coloration that is thought to reduce the conspicuousness of nest contents in this tree-living species (Dorow et al. 1990). Weaver ant larvae are also unique in that their silk glands, instead of being used to spin cocoons, have been co-opted to produce nest construction material (Hölldobler and Wilson 1977). Strikingly, in some taxa, mainly female larvae are used for silk spinning, which represents a kind of division of labor among larvae (Wilson and Hölldobler 1980). In other cases, morphological adaptations are restricted to certain development stages, for example, in the desert ant *Pheidole rhea*, whose fourth instar larvae have anchor-tipped hairs that serve to attach them to the ceiling of underground nests (Penick et al. 2012). In wood ants, larval hairs help attach larvae to one another, thus facilitating their transport by workers (Otto 2005), while ponerine ant larvae exhibit sticky tubercles which serve to attach them to nest walls (Peeters and Hölldobler 1992).

Recent studies suggest that morphological characters also play a role in communication between adults and brood. Wasp larvae are thought to use specialized hairs to sense vibrations caused by workers and queens (Suryanarayanan et al. 2011), while *Myrmica* ant pupae possess stridulatory organs with which they signal their status to attending workers (Casacci et al. 2013). These studies highlight how studying the functional morphology of brood can help in understanding its social role in hymenopteran societies.

## BROOD AS A FOOD SOURCE

One passive way for brood to take part in colony life is as a direct food source for nestmates (Wilson 1971); in the context of this review, such cannibalism of viable brood is not to be confused with consumption of nonviable, trophic eggs produced by adult females in many species (Crespi 1992; Hunt and Nalepa 1994; Khila and Abouheif 2008). Across species, adults resort to brood cannibalism and/or feed eggs and pupae to larvae in times of resource shortages (Woyke 1977; Sorensen et al. 1983a; Hölldobler and Wilson 1990; Heinze et al. 1999; Schmickl and Crailsheim 2001; Kudô and Shirai 2012) and high brood-to-worker ratios can significantly increase colony resistance to starvation (Rueppell and Kirkman 2005). Selective destruction of viable brood by workers and queens is typically seen as a consequence of conflict over reproductive dominance, male production, and/or sex allocation (e.g., in ants; Bourke and Franks 1995; Hora et al. 2007), but can have a simple trophic function as well (Oettler et al. 2013). In some ants, workers and/or queens regularly drink larval hemolymph by puncturing the larval cuticle (Masuko 1986) through hemolymph ducts located on the abdomen of larvae (Masuko 1989, 1990b) or by squeezing a larva's neck until it produces a droplet of saliva (Traniello 1982). This provides adults with essential nutrients but does not kill the larvae. In this way, brood plays a cooperative role in within-colony interactions.

## BROOD MODULATES COLONY NUTRITION

Adult ants, bees, and wasps cannot process large food items due to their thread waist, which restricts the size of food particles that can pass through their esophagus to the midgut (Hölldobler and Wilson 1990; Hunt 1991, 1994). Processing of solid prey—in many species a colony's main protein source—is therefore often performed by larvae earning them the name "communal stomach" (Wheeler 1918; Markin 1970; Went et al. 1972; Sorensen et al. 1983b; Cassill and Tschinkel 1999; Dussutour and Simpson 2009). Nestmate solicitation of lar-

val secretions is thus a key feature of brood-adult interactions in social Hymenoptera colonies (Hölldobler and Wilson 1990; Hunt and Nalepa 1994). A prime example of larval food processing is found in poneromorph ants, whose larvae digest solid insect prey extra-intestinally with the help of proteolytic salivary secretions (Wheeler 1918). Larval predigestion of prey is then followed by ingestion and redistribution of the liquefied food by workers (Cassill et al. 2005). Larvae also act as a digestive caste due to the high levels of proteases and amylases in their labial secretions and midgut (Wheeler 1918; Went et al. 1972; Petralia et al. 1980; Sorensen et al. 1983b). Enzymes and degraded proteins that are passed from larvae to adults during trophallaxis lead to a significant increase of proteinase activity in worker midguts (Sorensen et al. 1983b)—which do not usually contain proteases (Petralia et al. 1980; Hölldobler and Wilson 1990). In wasps, larval saliva resembles floral nectar and contains essential amino acids (Hunt et al. 1982). Many of these are not produced by adults themselves, and thus queens and workers must solicit saliva donations to aid in protein degradation (Ishay and Ikan 1968; Hunt 1984).

For colony as well as individual fitness, the importance of this social interaction is immense. In ants, brood can process excess protein that otherwise would have detrimental effects on individual worker and colony survival (Dussutour and Simpson 2012). Lack of protein-processing late instar larvae prohibits production of new sexuals in pharaoh ants, giving larvae a role in caste regulation (Warner et al. 2016). When paper wasp adults are denied access to larval saliva, nests exhibit decreased survival, smaller size, and produce fewer offspring (Hunt and Dove 2002). Wasp larvae respond actively to solicitation with specialized appendages that they use to signal their reluctance to share (Hunt 1988) and retain saliva in response to lateral vibrations caused by queens, showing that larvae actively respond to physical cues (Cummings et al. 1999). In fire ants, queen egg-laying rate is significantly correlated with the number of protein-processing larvae (Tschinkel 1995;

Cassill and Vinson 2007). Addition of larvae to colonies maximizes egg laying, while removal of larvae causes egg-laying rates to drop to almost zero (Tschinkel 1988). When larval secretions constitute the main food source of queens (Wilson 1974; Børgesen 1989; Børgesen and Jensen 1995), the effects of abstinence can be far-reaching. Pharaoh ant queens that are denied access to larvae have lower levels of both vitellogenin and vitellin in their abdomens (Jensen and Børgesen 1995) and significantly decrease their egg production (Børgesen 1989; Børgesen and Jensen 1995). Intriguingly, larvae seem to only respond to solicitation by mature, mated queens but deny young, mated queens and virgin queens access to saliva (Børgesen 1989). This indicates that larvae can differentiate between queens of varying fecundity, perhaps with the help of honest chemical signals, and suggests that secretion donation is an active behavioral response.

### BROOD ACTIVELY REGULATES FOOD INTAKE

The quantity and quality of nutrition is one of the most important factors implicated in insect development (Scriber and Slansky 1981), and has been linked to a diversity of fitness-related traits such as survival (Hódar et al. 2002), developmental rate (Shafiei et al. 2001), body size (Chapman 1998; Davidowitz et al. 2003), and reproductive success (Delisle and Hardy 1997; Engels and Sauer 2007). In social Hymenoptera, developmental nutrition is furthermore tightly linked to female reproductive caste and the fitness payoffs associated with developing into a queen. Selection should therefore favor traits that allow developing individuals to regulate their food intake.

One common way offspring influence their food intake is through begging (Kilner and Johnstone 1997; Johnstone 2004; Mas and Kölliker 2008). Although the first observations of begging in social Hymenoptera date back some 60 years (Le Masne 1953; Brian 1966), the consequences of this behavior have only been studied more recently. In a *Myrmica* ant, larvae that beg for food by extending the head upward are fed more frequently by workers (Creemers et al. 2003), while others signal their hunger by swaying, with hungry larvae displaying this begging behavior more often than well-fed nestmates (Kaptein et al. 2005). *Vespa* wasp larvae signal hunger acoustically by scraping their mandibles against the cell walls, which attracts feeding workers (Ishay and Landau 1972; Barenholz-Paniry et al. 1986). Worker, male, and queen larvae produce distinct hunger signals (Ishay and Schwartz 1973), which suggests that workers may respond differently to varying signals. Likewise, stridulation of mandible surfaces (Wheeler and Bailey 1920) and nonvolatile chemical cues (Cassill and Tschinkel 1995) may function as hunger signals in ant larvae. In bumble bees, differential feeding behavior of workers has been associated with hunger status of larvae (Smeets and Duchateau 2001; Pereboom et al. 2003), and recently this has been linked to differences in the chemical compounds on the cuticles of hungry and satiated larvae (den Boer and Duchateau 2006).

Larvae may also increase their food consumption directly. How a larva goes about doing this is strongly linked to species biology. In social bees and wasps, brood is reared in cells that are either mass-provisioned prior to ovipositioning and then sealed, or progressively provisioned throughout development. Brood rearing in mass provisioned, sealed cells limits resources available to brood, but also removes some of the control workers may exert over larval nutrition, thus giving larvae potential power over food intake (Bourke and Ratnieks 1999; Ratnieks 2001). A prime example is egg cannibalism in the stingless bee *Trigona postica,* which occurs when several eggs are laid in the same cell (Beig 1972). Similarly, larvae in some mass-provisioning wasps increase their provisions by entering neighboring brood cells and consuming their contents (Engels and Imperatriz-Fonseca 1990; Velthuis and Sommeijer 1991; Faustino et al. 2002).

In contrast to bees and wasps, ant brood is reared in piles without any physical boundaries between individuals (Hölldobler and Wilson 1990). This has important conse-

quences for both the developing individuals and the colony as a whole because ant larvae typically have the opportunity to selfishly increase provisions by cannibalizing nearby brood items (Hölldobler and Wilson 1990). Indeed, ant larvae increase their provisions by feeding on larvae (Rüger et al. 2008) and cannibalizing eggs (Baroni Urbani 1991; Heinze et al. 1996; Schultner et al. 2013, 2014), a behavior that can increase their survival (Schultner et al. 2013). Cannibalism levels in *Formica* ant larvae are mediated by inclusive fitness constraints, with larvae cannibalizing less often when presented with highly related eggs (Schultner et al. 2014). However, although female larvae significantly decreased cannibalism intensities in high-relatedness broods, cannibalism levels in male larvae remained constant (Schultner et al. 2014). Together with data showing that larvae preferentially cannibalize eggs from a foreign population compared to sibling eggs (Schultner et al. 2013), this confirms that factors such as individual genotype and colony kin structure play a decisive role in mediating larval behavior. Finally, cannibalism provides a good example for how interactions among developing individuals can have far-reaching consequences for colony organization: the spatial separation of brood by age and/or size in many ant taxa has been suggested to be a means for colonies to prevent costly cannibalism among brood (Wheeler 1910; Le Masne 1953; Carlin 1988; Baroni Urbani 1991)—and thus qualifies as an example of coercion.

### BROOD MODULATES DIVISION OF LABOR WITHIN COLONIES

Excellent evidence for how brood can modulate division of labor comes from the study of honey bee brood pheromone. Developing honey bee larvae secrete brood pheromone, a blend of substances produced by their salivary glands (Le Conte et al. 2006) that induces workers to cap brood cells (Le Conte et al. 1990; Trouiller et al. 1991). Adult workers exposed to the pheromone also begin foraging later (Le Conte et al. 2001) and decrease their foraging turnaround time (Pankiw 2007). Brood pheromone furthermore increases foraging time (Traynor et al. 2015) and worker pollen consumption (Pankiw et al. 2008), and primes preforagers to begin pollen foraging (Pankiw and Page 2001), resulting in an increase in the number of foragers (Pankiw et al. 1998) and their pollen loads (Pankiw 2004). Specific compounds in brood pheromone modulate worker feeding behavior, and experimental application of these compounds on larval cuticle results in increased deposition of royal jelly and higher larvae weights (Le Conte et al. 1995). In queenless colonies, brood pheromone induces emergency queen rearing, and workers are more likely to choose female larvae that exhibit high pheromone concentrations as future queens (Le Conte et al. 1994). Many of these behavioral changes seem modulated by brood pheromone effects on worker physiology. In particular, decreasing titres of juvenile hormone (Le Conte et al. 2001), inhibition of ovary development and/or activation (Arnold et al. 1994; Mohammedi et al. 1998; Maisonnasse et al. 2010; Traynor et al. 2014), increasing activity of hypopharyngeal glands (Mohammedi et al. 1996), and decreasing vitellogenin stores (Smedal et al. 2009) have all been linked to brood pheromone.

Numerous past studies have attempted to characterize brood pheromones in ants (Watkins and Cole 1966; Walsh and Tschinkel 1974; Bigley and Vinson 1975; Brian 1975), but unequivocal evidence for brood pheromone-mediated effects on worker behavior has proven difficult to obtain (see the review by Morel and Vander Meer 1988). Since then, however, several studies have demonstrated that brood regulates worker egg-laying in ants (Heinze et al. 1996; Endler et al. 2004; Teseo et al. 2013; Ebie et al. 2015; Ulrich et al. 2016), and it appears that both queen-derived odors on egg surfaces (Morel and Vander Meer 1988; Endler et al. 2006; Holman et al. 2010) and larval odors (Villalta et al. 2015) are responsible for inducing changes in worker behavior and physiology. With the availability of modern quantitative technologies, now is the time to readdress the question of ant brood pheromones in more detail.

An important consequence of physiological changes induced by brood odors is worker sterility; thus brood can signal workers to refrain from egg laying and instead concentrate their efforts on brood rearing (Keller and Nonacs 1993). Brood odors also provide a way for offspring to advertise their status or quality and influence provisioning behavior of workers (He et al. 2016). Seen from this perspective, brood odors are no different than the chemical begging signals employed by offspring of other insect taxa to manipulate parental provisioning behavior (Mas and Kölliker 2008). Because brood odors signal workers to refrain from egg laying and their production influences colony ecology and survival (Smedal et al. 2009), they are a crucial determinant of the inclusive fitness of developing individuals. Although clearly a brood phenotype, brood odors are often seen as a chemical means for queens to suppress worker reproduction. Indeed, it is likely that queens benefit from inhibition of worker reproduction mediated by the odors of their offspring. Thus mother and offspring interests may align concerning brood odor production, adding an additional level of complexity to this central social interaction. As brood pheromone effects are so strongly associated with the regulation of social processes such as worker foraging and brood rearing behavior, brood signaling is also likely to play a key role in the evolution of cooperative brood care in bees and other social Hymenoptera (Traynor et al. 2014).

### BROOD ODORS MEDIATE CONFLICT AMONG ADULTS

Brood odors are furthermore associated with selective brood treatment (Klahn and Gamboa 1983; Page et al. 1989; Panek and Gamboa 2000; Hannonen and Sundström 2003), for instance, in the context of sex allocation conflict where workers need to discriminate between male and female brood. Here, brood phenotype directly influences worker behavior. Social Hymenoptera typically use long-chained hydrocarbons embedded in the cuticle as discrimination cues

(van Zweden and d'Ettorre 2010), and like adults brood can display nest-specific odor profiles (Klahn and Gamboa 1983; Cotoneschi et al. 2007). Additionally, information about sex is conveyed in wasp brood odor profiles, although workers do not seem to use this information (Cotoneschi et al. 2009). Ant workers can discriminate between brood according to sex, parentage, and/or caste (Jemielity and Keller 2003; Endler et al. 2004, 2006; Shimoji et al. 2012; Ebie et al. 2015; Villalta et al. 2016a). Intriguingly, discrimination abilities of adult workers appear to be linked to their experience as larvae (Signorotti et al. 2013), providing yet another argument to include brood when studying insect societies.

Brood odors can play a key role in regulating adult traits, for instance, in the honey bee where queens mate multiply and workers have retained the ability to lay male eggs. Honey bee workers are selected to remove eggs laid by other workers, since the inclusive fitness interests of workers align with both the queen and her sons (Beekman and Ratnieks 2003). Indeed, queen-laid eggs differ from worker-laid eggs in their odor profiles (Katzav-Gozansky et al. 2003; Martin et al. 2005) and removal rates (Ratnieks and Visscher 1989), indicating that queens are under selection to produce male eggs that display maternal origin in order to facilitate discrimination and avoid destruction through policing workers (Seeley 1985, 1995; Ratnieks 1988, 1995; Keller and Nonacs 1993; Oldroyd et al. 2002). However, low removal rates of worker-laid eggs in so-called anarchistic honey bee societies suggest that worker-laid males can sometimes escape detection (Oldroyd et al. 1994; Oldroyd and Ratnieks 2000; Barron et al. 2001), possibly by carrying queen-like odors (Oldroyd and Ratnieks 2000; Oldroyd et al. 2002). In ants, differences in odor profiles of worker and queen-laid eggs can allow workers to selectively kill worker-laid eggs (d'Ettorre et al. 2004; van Zweden et al. 2009). Brood odors may also play a role in regulating the production of new sexuals, for instance, in the ant *Aphaenogaster senilis*, where workers preferentially kill queen-destined larvae even though the chemical

profiles of worker and queen-destined larvae are highly similar (Villalta et al. 2016a). Clearly, brood odor regulation of adult behavior is complex and the mere presence or absence of odor variation does not justify inferences about differential behavior.

Overall, the diversity of brood odors appears to play a crucial role in determining adult treatment of offspring. For now, however, data on individual variation in odor profiles is too scarce to provide conclusive evidence that offspring are under selection to mask or advertise their parentage, sex, or caste. Moreover, we are only beginning to understand the proximate mechanisms associated with odor perception (Gronenberg 2008; Zube et al. 2008; Brandstaetter et al. 2011; Roat and Cruz-Landim 2011; Brill et al. 2013; Sharma et al. 2015; McKenzie et al. 2016; Wang et al. 2016). Understanding evolution of offspring odors in social Hymenoptera will therefore require detailed exploration of offspring odor production and adult perception and discrimination abilities, as well as study of the factors that facilitate and constrain odor diversity evolution. Together, such studies will be paramount in providing a better understanding of the role of brood odors in influencing colony social processes.

## Studying Developing Individuals Reveals a New Perspective on Social Evolution

The above sections show how developing ants, bees, and wasps play a crucial role in colony life, and that they have both fitness interests and the power to attempt to reach their fitness optima. Table 1 summarizes central aspects of colony life that brood can influence, elaborates on how the fitness interests of brood, the power of conflicting parties of interest, and taxon-specific constraints may influence social processes, and provides testable predictions of brood power. In the final section, we present a short overview of how the study of developing individuals can provide a new perspective on the biology of social Hymenoptera.

Larval food processing (see the section, The Social Role of Developing Individuals;

Hunt and Nalepa 1994) has been suggested to play a key role in the repeated evolution of eusociality in the Hymenoptera (Hunt 1991; Johnson et al. 2013). The food-sharing behavior that is also found in subsocial taxa such as earwigs provides support to the idea that offspring feeding interactions lie at the basis of complex sociality in insects (Falk et al. 2014). In several eusocial taxa, this has turned into an obligately expressed offspring behavior without which colonies cannot function optimally (e.g., decreased egg-laying rates in fire ant queens denied access to larval saliva, Tschinkel 1995; failure to produce new queens in pharaoh ant colonies deprived of larvae, Warner et al. 2016; lower survival of larvae-deprived, green-headed ant colonies due to the inability to process excess proteins, Dussutour and Simpson 2009; and lower survivorship and fecundity of paper wasp colonies deprived of larval secretions, Hunt and Dove 2002). Nevertheless, this crucial social interaction has received very little attention from social insect researchers, with the exception of seminal work published over 20 years ago (Hunt 1991; Hunt and Nalepa 1994). Hunt (1991) also called attention to a conflict-related aspect of this behavior by suggesting that evolution of saliva donorism in wasps may be intertwined with developmental conflict. If, for example, donorism carries a developmental cost for larvae and/or reduces future reproductive potential, reluctance to share saliva may in fact be the result of selection on larvae to control the timing and amount of saliva surrendered (Hunt 1991). Possibly, larvae that selectively refuse soliciting adults benefit from increased growth rates compared to more cooperative brood mates. Should increasing growth lead to queen development, the incentive for females to withhold saliva may be particularly strong. Such speculation is, in our opinion, worth pursuing in empirical tests in order to understand the proximate mechanisms (e.g., physiological regulation of sharing/refusing) and ultimate factors (e.g., costs and benefits of sharing/refusing) underlying the evolution of this primary social interaction, and its role in the evolution of complex sociality.

TABLE 1

*The influence of brood on individual and colony-level traits in eusocial Hymenoptera*

| INDIVIDUAL- and COLONY-LEVEL traits | BROOD influence via | Are there CONFLICTS OF INTEREST? | Does KIN STRUCTURE affect conflict potential/outcome? | POTENTIAL CONSTRAINTS on brood power | Testable PREDICTIONS |
|---|---|---|---|---|---|
| *Whole Colony* | | | | | |
| Colony organization, defense, foraging, productivity | Presence, morphology, behavior | Yes—cooperative traits may be used in selfish contexts[a]. Selfish brood traits can underlie evolution of colony-level traits[b] | Possibly—payoffs from cooperation may be higher when relatedness is high | Physical dominance of adult queens and workers | If brood behavior (e.g., food processing) is shaped by similar evolutionary processes as adult behavior, degree of cooperative behaviors should increase with social complexity |
| *Workers* | | | | | |
| Provisioning behavior | Begging. Chemical signaling (e.g., brood pheromone) | Yes—brood as a whole and individual offspring may have different optima in worker provisioning. Workers and individual brood can disagree over optimal resource allocation if there is a tradeoff between optimal offspring size and number[c] | Yes—selfishness of individual offspring should be higher in low-relatedness societies. Worker and brood interests over optimal allocation into offspring size versus number are predicted to diverge more strongly when relatedness is low | Workers control resource intake and brood provisioning | Selfish behavior (e.g., begging, cannibalism, dishonest signaling of need) should be negatively correlated with relatedness, both inter- and intraspecifically. If kin structure affects the degree of divergence between brood and worker interests, variation in, for example, offspring size and number should be higher in low-relatedness settings |
| Physiology and reproduction | Chemical signaling (e.g., brood pheromone) | Yes—brood has an interest in acting on worker physiology so that egg-laying workers refrain from costly reproduction | Yes—whether brood agrees with egg-laying workers on male parentage depends on mating frequency of the queen and queen number | Brood pheromones are shaped by selection on queens as well | Primer effect on worker physiology should increase with decreasing relatedness |

TABLE 1
*Continued*

| INDIVIDUAL- and COLONY-LEVEL traits | BROOD influence via | Are there CONFLICTS OF INTEREST? | Does KIN STRUCTURE affect conflict potential/outcome? | POTENTIAL CONSTRAINTS on brood power | Testable PREDICTIONS |
|---|---|---|---|---|---|
| | | | Brood signals should be released from primer function in high-relatedness societies | | Honesty of brood signals should increase with relatedness levels |
| *Queens* | | | | | |
| Fecundity | Saliva/hemolymph donorism and retention | Yes—individual offspring have an interest in maximizing survival and may refuse donorism if this negatively affects growth and development | Yes—individual offspring may retain saliva more often or preferentially donate saliva to related queens in multiple queen colonies, if they are not equally related to all queens | Adults have a physical advantage over larvae | Levels of saliva donorism should increase with relatedness levels |
| | Self-sacrifice | Queens are predicted to exploit brood as a resource in multiple queen colonies if its increases fitness | Workers may be more likely to sacrifice less related brood | | If male and female larvae differ in the benefits gained from saliva retention, they may adjust donorism levels accordingly |
| *Whole Brood* | | | | | |
| Sex Allocation | Regulating food intake | Yes—brood, workers, and queens differ in their sex-ratio optima because of relatedness asymmetries | Yes—conflict potential among all parties of interest is highest in single-queen colonies where relatedness asymmetries are maximized | Queen controls fertilization | Individual male and female offspring should differ in levels of selfishness across kin structures[e] |
| | Removing competitors | Generally, interests of female brood align with worker interests while interests of male brood align with queen interests[d] | | Workers control brood care | Female larvae should be under strong selection to signal sex in single queen colonies while male larvae should be selected to mask sex |
| | Masking/advertizing sex | | | | |

TABLE 1
*Continued*

| | | | *Individual offspring* | | |
|---|---|---|---|---|---|
| Female caste | Regulating food intake | Yes—queens and workers prefer producing fewer new queens than is optimal for an individual female larva | Yes—levels of selfishness in individual female larvae are predicted to increase when relatedness is low[e] | Workers control resource flow | If female offspring retain power over their caste fate, the proportion of female larvae that develop into queens should reflect the larval rather than adult optimum[k] |
| | Attaining critical size before nestmates[f] | | | Queen pheromones with primer function | |
| | Alternative developmental pathways | | Low relatedness causes queens and workers to prefer rearing closely related female larvae into queens | Large QW size dimorphism[g] | |
| | Removing competitors | | | Maternal effects | |
| | Masking identity | | | Brood rearing in cells[h] | |
| | | | | Access to information about colony size[i] | |
| | | | | Constraints on larval ability to recognize competitors[j] | |
| Male and queen quality | Regulating food intake | Yes—workers prefer an optimal tradeoff between size and number of new queens and males[c] | Yes—adult and brood interests concerning optimal allocation into offspring size versus number are predicted to diverge more strongly when relatedness is low | Workers control resource flow | Degree of selfish behavior should be higher in species where competition for matings, nesting sites, or reproductive dominance is fierce[l] |
| | Removing competitors | | | Allometric growth/physiological tradeoffs | |
| | Novel developmental pathways | Individual offspring prefer maximizing investment in themselves | | Constraints on larval ability to recognize competitors[j] | |
| | Masking/advertizing identity | | | | |

TABLE 1
*Continued*

| INDIVIDUAL- and COLONY-LEVEL traits | BROOD influence via | Are there CONFLICTS OF INTEREST? | Does KIN STRUCTURE affect conflict potential/outcome? | POTENTIAL CONSTRAINTS on brood power | Testable PREDICTIONS |
|---|---|---|---|---|---|
| | | | | Less worker control of quality in species with alternative sexual morphs? | If both workers and larvae retain partial control over development, variation in adult phenotype should be larger in low relatedness settings |
| Male parentage | Masking/advertizing parentage | Yes—individual male offspring, workers, and queens are predicted to disagree about which males are reared to adulthood | Yes—in single-queen colonies, interests of the queen and her sons align; workers collectively prefer workers' sons based on kinship alone and interests of workers' sons align with their mothers<br><br>In multiple-queen colonies, interests of queen sons, queens, and workers collectively align but individual workers prefer own sons over queen sons | Lack of functional ovaries/reproductive constraints restricts/limits worker reproduction<br><br>Policing (which may be constrained by lack of matriline-specific brood odors) | If male offspring are under selection to signal parentage, worker sons should advertise their parentage in singly mated, single-queen colonies while queen sons should mask parentage; this should be reversed in multiply mated or multiple-queen colonies |

TABLE 1
Continued

| Female parentage | Masking/advertising parentage | | | |
|---|---|---|---|---|
| | Yes—in multiple-queen/mating societies, individual female offspring, workers, and queens are predicted to disagree over which queen-destined larvae are reared to adulthood | Yes—in multiple-queen colonies, workers may attempt to preferentially rear full sisters into queens | Lack of matriline-specific brood odors may constrain preferential brood rearing | In multiple-queen nests, queens should produce female brood-carrying matriline specific odors in order to facilitate preferential rearing (unless costs of being discriminated against are high), irrespective of queen fitness—this can be tested by comparing matriline specificity of brood odors in single- and multiple-queen colonies of socially polymorphic species |

[a] Evolution of cooperative larval traits such as saliva donorism may be intertwined with developmental conflict, e.g., if such behaviors carry a cost and/or reduce future reproductive potential (Hunt 1991).

[b] One example is spatial separation of brood by age and/or size in ants, which has been suggested to be a means for colonies to prevent costly cannibalism among brood (Wheeler 1910; Le Masne 1953; Carlin 1988; Baroni Urbani 1991).

[c] Workers should have an interest in controlling the size of sexuals if a certain size is linked to higher sexual fitness per unit of investment (Fjerdingstad 2005). A developing larva may prefer a larger size than the worker optimum.

[d] In populations where colonies are headed by both singly and multiply mated queens or contain both single and multiple queens, sex ratios can be split so that singly mated/single-queen colonies produce female-biased sex ratios while multiply mated/multiple-queen colonies produce male-biased sex ratios (Meunier et al. 2008). In such populations, fitness interests of workers will depend on their colony of origin.

[e] When larval selfishness in the form of egg cannibalism is modeled in a kin selection framework, levels of cannibalism are predicted to vary with mean nestmate relatedness, the size of sex-specific benefits, and brood sex ratio. As variation in queen number and relatedness differentially affects relatedness between males and nestmates and females and nestmates (due to haplodiploidy), cannibalism levels in male larvae are predicted to stay constant across relatedness levels, while female levels drop sharply with decreasing queen number (Schultner et al. 2014).

[f] Female larvae that reach a critical minimum size before their female brood mates may increase their chances of being reared into queens if workers preferentially rear relatively larger female larvae into queens, as is the case in the ant Myrmica rubra (Brian and Hibble 1963).

[g] In taxa with strong morphological differences between castes, developmental switches typically occur early in development to allow for sufficient divergent growth periods (Wheeler 1986). The need for relatively more resources to trigger queen development in particular in species with large size differences between queens and workers may thus constrain larvae in their power to influence caste, especially if they must act within a restricted time window.

[h] Rearing of brood in separate cells in social bees and wasps may limit the power of brood to regulate their food intake. In some cases larvae can overcome this constraint by biting through cell walls to enter and consume provisions of neighboring cells (Engels and Imperatriz-Fonseca 1990; Faustino et al. 2002). Ant larvae potentially retain much more power to engage in selfish provisioning because brood is reared in batches and larvae often have easy access to eggs (Hölldobler and Wilson 1990).

[i] In annual species where queens and workers are reared in separate cohorts, colony size is the main trigger of queen rearing (Bourke and Ratnieks 1999). Access to information about colony size may therefore be another crucial determinant of larvae power.

[j] For larvae to selectively remove same-sex competitors, they need to be able to discriminate among brood of different sexes. At the same time, individuals should be selected to avoid detection.

[k] Ratnieks 1991; Dobata 2012.

[l] Competition over access to resources between queen-destined larvae may be especially strong in species where queens found colonies together and then fight for reproductive dominance until only one queen remains (Bernasconi and Keller 1998; Aron et al. 2009). Competition between males in some ants can be fierce when they compete for matings (Wiernasz et al. 1995; Abell et al. 1999; Boomsma et al. 2005).

Another example of a social interaction worth pursuing in more detail is parent-offspring conflict—an interaction typically studied from the perspective of both adults and juveniles. Although Hymenoptera conflict studies are built on the same theoretical scaffold, the focus has mainly been on conflict between parents (i.e., queens/males) and their adult helper offspring (i.e., workers). This may explain why classic conflict traits such as begging have been largely overlooked in social insects (with the few notable exceptions mentioned in the section, The Social Role of Developing Individuals). Begging can function as an honest signal of need or reflect the competitive ability of individuals, i.e., their ability to carry the costs of begging (Kilner and Johnstone 1997; Royle et al. 2002). The only study of begging honesty in eusocial Hymenoptera revealed that hungry ant larvae beg more frequently than well-fed ones, indicating that this signal honestly reflects needs (Kaptein et al. 2005). Insect offspring often signal their hunger chemically (Mas and Kölliker 2008)— social earwig offspring signal their quality by secreting higher relative amounts of particular compounds on their cuticle, which induces differential feeding behavior in mothers (Mas et al. 2009). Again, to our knowledge, only one study has looked at chemical signals as a way for individual larvae to signal hunger and directly influence worker provisioning behavior in eusocial Hymenoptera (den Boer and Duchateau 2006). Seeing how important chemical communication is in social insect colonies (Blomquist and Bagnères 2010), offspring chemical signaling traits such as honey bee brood pheromones and ant larvae odors merit further attention. Understanding the evolution of offspring signaling in social Hymenoptera will demand studies focusing on signal production and perception, as well as exploration of the costs and benefits of signaling, the effects of signaling on individuals and the colony, and the potential effects of colony kin structure on signal intensity and honesty. At the moment, this field is wide open.

Finally, the expanding field of ecological evolutionary developmental biology (eco-evo-devo) spurs renewed interest in the role of development in evolution (West-Eberhard 2003; Abouheif et al. 2014). Social Hymenoptera are excellent models due to their extreme developmental polyphenism, which is regulated by genetic, epigenetic, environmental, and social factors. Much like the study of evolutionary conflict, traditionally the study of social insect polyphenism has focused on adult individuals. Only recently has this shifted to center on molecular traits of developing individuals. This has revealed a central role of transcriptional regulation (Kucharski et al. 2008, 2015; Kamakura 2011; Forêt et al. 2012; Guo et al. 2013; Shi et al. 2013; Bonasio 2014; Klein et al. 2016) underlying differential gene expression during development (Corona et al. 1999; Evans and Wheeler 1999, 2001; Abouheif and Wray 2002; Santana et al. 2006; Wheeler et al. 2006, 2014; Barchuk et al. 2007; Hoffman and Goodisman 2007; Patel et al. 2007; Mackert et al. 2008; Hunt et al. 2010b; Li et al. 2010; Azevedo et al. 2011; Colgan et al. 2011; Mutti et al. 2011; Wolschin et al. 2011; Chen et al. 2012; Cameron et al. 2013; Berens et al. 2015; Brito et al. 2015; Schrader et al. 2015; Vojvodic et al. 2015), with important consequences for gene evolution (Hunt et al. 2010a, 2011, 2013; Hall et al. 2013; Harpur et al. 2014; Helanterä and Uller 2014; Mikheyev and Linksvayer 2015; Schrader et al. 2016). These efforts have substantially heightened our understanding of the proximate mechanisms associated with polyphenic development. Within the eco-evo-devo framework, experimental studies on emerging social insect model species promise to provide answers to fundamental questions in evolutionary biology.

## Conclusions

Social Hymenoptera have proven ideal models for studying the evolution of sociality, contributing to our understanding of the interplay between cooperation and conflict in social systems, and the factors associated with maintaining social cohesion (Bourke 2011). However, the majority of studies have focused on interactions between adults.

This is surprising, since important physiological processes that determine lifetime fitness coincide with development. In addition, developing individuals often dominate colonies numerically and their needs dictate worker behavior, physiology, and colony-level task division. Far from powerless, developing individuals have evolved specialized traits that serve complex interactions with nestmates and play a central role in social cohesion. In light of the ideas presented here, the study of cooperation and conflict in social insect brood promises to be a fruitful avenue for future research.

## REFERENCES

Abbot P., Abe J., Alcock J., et al. 2011. Inclusive fitness theory and eusociality. *Nature* 471:E1–E4.

Abell A. J., Cole B. J., Reyes R., Wiernasz D. C. 1999. Sexual selection on body size and shape in the western harvester ant, *Pogonomyrmex occidentalis* Cresson. *Evolution* 53:535–545.

Abouheif E., Wray G. A. 2002. Evolution of the gene network underlying wing polymorphism in ants. *Science* 297:249–252.

Abouheif E., Favé M.-J., Ibarrarán-Viniegra A. S., Lesoway M. P., Rafiqi A. M., Rajakumar R. 2014. Eco-evo-devo: the time has come. *Advances in Experimental Medicine and Biology* 781:107–125.

Adams B. J., Hooper-Bùi L. M., Strecker R. M., O'Brien D. M. 2011. Raft formation by the red imported fire ant, *Solenopsis invicta*. *Journal of Insect Science* 11:171.

Anderson K. E., Gadau J., Mott B. M., Johnson R. A., Altamirano A., Strehl C., Fewell J. H. 2006. Distribution and evolution of genetic caste determination in *Pogonomyrmex* seed-harvester ants. *Ecology* 87:2171–2184.

Anderson K. E., Linksvayer T. A., Smith C. R. 2008. The causes and consequences of genetic caste determination in ants (Hymenoptera: Formicidae). *Myrmecological News* 11:119–132.

Arnold G., Le Conte Y., Trouiller J., Hervet H., Chappe B., Masson C. 1994. Inhibition of worker honeybee ovaries development by a mixture of fatty acid esters from larvae. *Comptes rendus de l'Académie des sciences, Série III, Sciences de la vie* 317:511–515.

Aron S., Passera L., Keller L. 1999. Evolution of social parasitism in ants: size of sexuals, sex ratio and mechanisms of caste determination. *Proceedings of the Royal Society B: Biological Sciences* 266:173–177.

Aron S., Steinhauer N., Fournier D. 2009. Influence of queen phenotype, investment and maternity apportionment on the outcome of fights in cooperative foundations of the ant *Lasius niger*. *Animal Behaviour* 77:1067–1074.

Azevedo S. V., Caranton O. A. M., de Oliveira T. L., Hartfelder K. 2011. Differential expression of hypoxia pathway genes in honey bee (*Apis mellifera* L.) caste development. *Journal of Insect Physiology* 57:38–45.

Baer B., Boomsma J. J. 2004. Male reproductive investment and queen mating-frequency in fungus-growing ants. *Behavioral Ecology* 15:426–432.

Baer B., Morgan E. D., Schmid-Hempel P. 2001. A nonspecific fatty acid within the bumblebee mating plug prevents females from remating. *Proceedings of the National Academy of Sciences of the United States of America* 98:3926–3928.

Baratte S., Cobb M., Deutsch J., Peeters C. 2005. Morphological variations in the pre-imaginal development of the ponerine ant *Diacamma ceylonense*. *Acta Zoologica* 86:25–31.

Barchuk A. R., Cristino A. S., Kucharski R., Costa L. F., Simões Z. L. P., Maleszka R. 2007. Molecular determinants of caste differentiation in the highly eusocial honeybee *Apis mellifera*. *BMC Developmental Biology* 7:70.

Barenholz-Paniry V., Ishay J. S., Karin J., Akselrod S. 1986. Rhythm of sounds produced by larvae of the oriental hornet *Vespa orientalis*: spectral analysis. *BioSystems* 19:299–305.

Baroni Urbani C. 1991. Indiscriminate oophagy by ant larvae: an explanation for brood serial organization? *Insectes Sociaux* 38:229–239.

Barron A. B., Oldroyd B. P., Ratnieks F. L. W. 2001. Worker reproduction in honey-bees (*Apis*) and the anarchic syndrome: a review. *Behavioral Ecology and Sociobiology* 50:199–208.

Bauerfeind S. S., Fischer K. 2005. Effects of food stress and density in different life stages on reproduction in a butterfly. *Oikos* 111:514–524.

Beekman M., Ratnieks F. L. W. 2003. Power over reproduction in social Hymenoptera. *Philosophical Transactions of the Royal Society B: Biological Sciences* 358:1741–1753.

Beekman M., Komdeur J., Ratnieks F. L. W. 2003. Reproductive conflicts in social animals: who has power? *Trends in Ecology and Evolution* 18:277–282.

Beig D. 1972. The production of males in queenright colonies of *Trigona (Scaptotrigona) postica. Journal of Apicultural Research* 11:33–39.

Bell W. J., Roth L. M., Nalepa C. A. 2007. *Cockroaches: Ecology, Behavior, and Natural History.* Balitmore (Maryland): Johns Hopkins University Press.

Berens A. J., Hunt J. H., Toth A. L. 2015. Nourishment level affects caste-related gene expression in *Polistes* wasps. *BMC Genomics* 16:235.

Bernasconi G., Keller L. 1998. Phenotype and individual investment in cooperative foundress associations of the fire ant, *Solenopsis invicta. Behavioral Ecology* 9:478–485.

Bernasconi G., Strassmann J. E. 1999. Cooperation among unrelated individuals: the ant foundress case. *Trends in Ecology and Evolution* 14:477–482.

Biedermann P. H. W., Taborsky M. 2011. Larval helpers and age polyethism in ambrosia beetles. *Proceedings of the National Academy of Sciences of the United States of America* 108:17064–17069.

Bier K. 1952. Beziehungen zwischen Nährzellkerngröße und Ausbildung ribonukleinsäurehaltiger Strukturen in den Oocyten von Formica rufa rufo-pratensis minor Gößwald. *Verhandlungen der Deutschen Zoologischen Gesellschaft Freiburg* 40:369–374.

Bier K. 1954a. Über den Saisondimorphismus der Oogenese von Formica rufa rufo-pratensis minor Gössw. und dessen Bedeutung für die Kastendetermination. *Biologisches Zentralblatt* 73:2.

Bier K. 1954b. Über Phasen gesteigerter Protein- und Kohlehydrateinlagerung und die Fettverteilung im Hymenopterenovar. *Zoologischer Anzeiger* 18:422–429.

Bigley W. S., Vinson S. B. 1975. Characterization of a brood pheromone isolated from sexual brood of the imported fire ant, *Solenopsis invicta. Annals of the Entomological Society of America* 68:301–304.

Blomquist G. J., Bagnères A.-G. 2010. *Insect Hydrocarbons: Biology, Biochemistry, and Chemical Ecology.* Cambridge (United Kingdom): Cambridge University Press.

Boggs C. L., Freeman K. D. 2005. Larval food limitation in butterflies: effects on adult resource allocation and fitness. *Oecologia* 144:353–361.

Boleli I. C., Paulino-Simões Z. L., Bitondi M. M. G. 1999. Cell death in ovarioles causes permanent sterility in *Frieseomelitta varia* worker bees. *Journal of Morphology* 242:271–282.

Bonasio R. 2014. The role of chromatin and epigenetics in the polyphenisms of ant castes. *Briefings in Functional Genomics* 13:235–245.

Bonasio R., Li Q., Lian J., Mutti N. S., Jin L., Zhao H., Zhang P., Wen P., Xiang H., Ding Y., Jin Z., Shen S. S., Wang Z., Wang W., Wang J., Berger S. L., Liebig J., Zhang G., Reinberg D. 2012. Genome-wide and caste-specific DNA methylomes of the ants *Camponotus floridanus* and *Harpegnathos saltator. Current Biology* 22:1755–1764.

Boomsma J. J., Baer B., Heinze J. 2005. The evolution of male traits in social insects. *Annual Review of Entomology* 50:395–420.

Børgesen L. W. 1989. A new aspect of the role of larvae in the pharaoh's ant society (*Monomorium pharaonis* (L.)-Formicidae, Myrmicinae): producer of fecundity-increasing substances to the queen. *Insectes Sociaux* 36:313–327.

Børgesen L. W., Jensen P. V. 1995. Influence of larvae and workers on egg production of queens of the pharaoh's ant, *Monomorium pharaonis* (L.). *Insectes Sociaux* 42:103–112.

Bourke A. F. G. 1988. Worker reproduction in the higher eusocial Hymenoptera. *Quarterly Review of Biology* 63:291–311.

Bourke A. F. G. 2011. *Principles of Social Evolution.* Oxford (United Kingdom): Oxford University Press.

Bourke A. F. G., Franks N. R. 1995. *Social Evolution in Ants.* Princeton (New Jersey): Princeton University Press.

Bourke A. F. G., Ratnieks F. L. W. 1999. Kin conflict over caste determination in social Hymenoptera. *Behavioral Ecology and Sociobiology* 46:287–297.

Brandstaetter A. S., Rössler W., Kleineidam C. J. 2011. Friends and foes from an ant brain's point of view—neuronal correlates of colony odors in a social insect. *PLOS ONE* 6:e21383.

Brian M. V. 1966. *Social Insect Populations.* London (United Kingdom): Academic Press.

Brian M. V. 1973. Caste control through worker attack in the ant *Myrmica. Insectes Sociaux* 20:87–102.

Brian M. V. 1975. Larval recognition by workers of the ant *Myrmica. Animal Behaviour* 23:745–756.

Brian M. V., Hibble J. 1963. Larval size and the influence of the queen on growth in *Myrmica. Insectes Sociaux* 10:71–81.

Brill M. F., Rosenbaum T., Reus I., Kleinedam C. J., Nawrot M. P., Rössler W. 2013. Parallel processing via a dual olfactory pathway in the honeybee. *Journal of Neuroscience* 33:2443–2456.

Brito D. V., Silva C. G. N., Hasselmann M., Viana L. S., Astolfi-Filho S., Carvalho-Zilse G. A. 2015. Molecular characterization of the gene *feminizer* in the stingless bee *Melipona interrupta* (Hymenoptera: Apidae) reveals association to sex and caste development. *Insect Biochemistry and Molecular Biology* 66:24–30.

Bueno O. C., Mathias M. I. C., Ortiz G. 2011. Morphological organization of the dorsal protuberance of *Linepithema humile* (Mayr, 1868) ant's larvae (Hymenoptera, Formicidae). *Microscopy Research and Technique* 74:551–558.

Buschinger A., Schaefer M. 2006. Larval nourishment in *Leptothorax acervorum* (Fabricius, 1793) (Hymenoptera: Formicidae), with description of a larval mensarium as a trophophoretic structure for the handling of food particles. *Myrmecologische Nachrichten* 9:35–41.

Cahan S. H., Graves C. J., Brent C. S. 2011. Intergenerational effect of juvenile hormone on offspring in *Pogonomyrmex* harvester ants. *Journal of Comparative Physiology B: Biochemical, Systems, and Environmental Physiology* 181:991–999.

Cameron R. C., Duncan E. J., Dearden P. K. 2013. Biased gene expression in early honeybee larval development. *BMC Genomics* 14:903.

Carlin N. F. 1988. Species, kin and other forms of recognition in the brood discrimination of ants. Pages 267–295 in *Advances in Myrmecology*, edited by J. C. Trager. Leiden (The Netherlands): E. J. Brill.

Casacci L. P., Thomas J. A., Sala M., Treanor D., Bonelli S., Balletto E., Schönrogge K. 2013. Ant pupae employ acoustics to communicate social status in their colony's hierarchy. *Current Biology* 23:323–327.

Cassill D. L., Tschinkel W. R. 1995. Allocation of liquid food to larvae via trophallaxis in colonies of the fire ant, *Solenopsis invicta*. *Animal Behaviour* 50:801–813.

Cassill D. L., Tschinkel W. R. 1999. Regulation of diet in the fire ant, *Solenopsis invicta*. *Journal of Insect Behavior* 12:307–328.

Cassill D. L., Vinson S. B. 2007. Effects of larval secretions on queen fecundity in the fire ant. *Annals of the Entomological Society of America* 100:327–332.

Cassill D. L., Butler J., Vinson S. B., Wheeler D. E. 2005. Cooperation during prey digestion between workers and larvae in the ant, *Pheidole spadonia*. *Insectes Sociaux* 52:339–343.

Chandrashekara K., Gadagkar R. 1991. Behavioural castes, dominance and division of labour in a primitively eusocial wasp. *Ethology* 87:269–283.

Chapman R. F. 1998. *The Insects: Structure and Function*. Fourth Edition. Cambridge (United Kingdom): Cambridge University Press.

Chapuisat M., Sundström L., Keller L. 1997. Sex-ratio regulation: the economics of fratricide in ants. *Proceedings of the Royal Society B: Biological Sciences* 264:1255–1260.

Chen X., Hu Y., Zheng H., Cao L., Niu D., Yu D., Sun Y., Hu S., Hu F. 2012. Transcriptome comparison between honey bee queen- and worker-destined larvae. *Insect Biochemistry and Molecular Biology* 42: 665–673.

Cole B. J., Hoeg L. 1996. The influence of brood type on activity cycles in *Leptothorax allardycei* (Hymenoptera: Faruicidae). *Journal of Insect Behavior* 9:539–547.

Colgan T. J., Carolan J. C., Bridgett S. J., Sumner S., Blaxter M. L., Brown M. J. F. 2011. Polyphenism in social insects: insights from a transcriptome-wide analysis of gene expression in the life stages of the key pollinator, *Bombus terrestris*. *BMC Genomics* 12:623.

Corona M., Estrada E., Zurita M. 1999. Differential expression of mitochondrial genes between queens and workers during caste determination in the honeybee *Apis mellifera*. *Journal of Experimental Biology* 202:929–938.

Corona M., Libbrecht R., Wheeler D. E. 2016. Molecular mechanisms of phenotypic plasticity in social insects. *Current Opinion in Insect Science* 13:55–60.

Costa J. T. 2006. *The Other Insect Societies*. Cambridge (Massachusetts): Belknap Press of Harvard University Press.

Cotoneschi C., Dani F. R., Cervo R., Sledge M. F., Turillazzi S. 2007. *Polistes dominulus* (Hymenoptera: Vespidae) larvae possess their own chemical signatures. *Journal of Insect Physiology* 53:954–963.

Cotoneschi C., Dani F. R., Cervo R., Scala C., Strassmann J. E., Queller D. C., Turillazzi S. 2009. *Polistes dominulus* (Hymenoptera, Vespidae) larvae show different cuticular patterns according to their sex: workers seem not use this chemical information. *Chemical Senses* 34:195–202.

Creemers B., Billen J., Gobin B. 2003. Larval begging behaviour in the ant *Myrmica rubra*. *Ethology, Ecology and Evolution* 15:261–272.

Crespi B. J. 1992. Cannibalism and trophic eggs in subsocial and eusocial insects. Pages 176–213 in *Cannibalism: Ecology and Evolution Among Diverse Taxa*, edited by M. A. Elgar and B. J. Crespi. Oxford (United Kingdom): Oxford University Press.

Crespi B. J., Yanega D. 1995. The definition of eusociality. *Behavioral Ecology* 6:109–115.

Crozier R. H., Pamilo P. 1996. *Evolution of Social Insect Colonies: Sex Allocation and Kin Selection*. Oxford (United Kingdom): Oxford University Press.

Cummings D. L. D., Gamboa G. J., Harding B. J. 1999. Lateral vibrations by social wasps signal larvae to withhold salivary secretions (*Polistes fuscatus*, Hymenoptera: Vespidae). *Journal of Insect Behavior* 12: 465–473.

d'Ettorre P., Heinze J., Ratnieks F. L. W. 2004. Worker policing by egg eating in the ponerine ant *Pachycondyla inversa*. *Proceedings of the Royal Society B: Biological Sciences* 271:1427–1434.

Dani F. R., Foster K. R., Zacchi F., Seppä P., Massolo A., Carelli A., Arévalo E., Queller D. C., Strassmann J. E., Turillazzi S. 2004. Can cuticular lipids provide sufficient information for within-colony nepotism in wasps? *Proceedings of the Royal Society B: Biological Sciences* 271:745–753.

Davidowitz G., D'Amico L. J., Nijhout H. F. 2003. Critical weight in the development of insect body size. *Evolution and Development* 5:188–197.

Davidson D. W. 1982. Sexual selection in harvester ants (Hymenoptera: Formicidae: *Pogonomyrmex*). *Behavioral Ecology and Sociobiology* 10:245–250.

Delisle J., Hardy M. 1997. Male larval nutrition influences the reproductive success of both sexes of the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). *Functional Ecology* 11: 451–463.

den Boer S. P. A., Duchateau M. J. H. M. 2006. A larval hunger signal in the bumblebee *Bombus terrestris*. *Insectes Sociaux* 53:369–373.

den Boer S. P. A., Boomsma J. J., Baer B. 2009. Honey bee males and queens use glandular secretions to enhance sperm viability before and after storage. *Journal of Insect Physiology* 55:538–543.

den Boer S. P. A., Baer B., Boomsma J. J. 2010. Seminal fluid mediates ejaculate competition in social insects. *Science* 327:1506–1509.

Dobata S. 2012. Arms race between selfishness and policing: two-trait quantitative genetic model for caste fate conflict in eusocial Hymenoptera. *Evolution* 66:3754–3764.

Dobler R., Kölliker M. 2010. Kin-selected siblicide and cannibalism in the European earwig. *Behavioral Ecology* 21:257–263.

Dobler R., Kölliker M. 2011. Influence of weight asymmetry and kinship on siblicidal and cannibalistic behaviour in earwigs. *Animal Behaviour* 82:667–672.

Dorow W. H. O., Maschwitz U., Rapp S. 1990. The natural history of *Polyrhachis (Myrmhopla) muelleri* Forel 1893 (Formicidae Formicinae), a weaver ant with mimetic larvae and an unusual nesting behaviour. *Tropical Zoology* 3:181–190.

Dussutour A., Simpson S. J. 2009. Communal nutrition in ants. *Current Biology* 19:740–744.

Dussutour A., Simpson S. J. 2012. Ant workers die young and colonies collapse when fed a high-protein diet. *Proceedings of the Royal Society B: Biological Sciences* 279:2402–2408.

Duvoisin N., Baer B., Schmid-Hempel P. 1999. Sperm transfer and male competition in a bumblebee. *Animal Behaviour* 58:743–749.

Ebie J. D., Hölldobler B., Liebig J. 2015. Larval regulation of worker reproduction in the polydomous ant *Novomessor cockerelli*. *Science of Nature* 102:72.

Edwards Adas J. P. 1991. Caste regulation in the pharaoh's ant *Monomorium pharaonis*: recognition and cannibalism of sexual brood by workers. *Physiological Entomology* 16:263–271.

Endler A., Liebig J., Schmitt T., Parker J. E., Jones G. R., Schreier P., Hölldobler B. 2004. Surface hydrocarbons of queen eggs regulate worker reproduction in a social insect. *Proceedings of the National Academy of Sciences of the United States of America* 101:2945–2950.

Endler A., Liebig J., Hölldobler B. 2006. Queen fertility, egg marking and colony size in the ant *Cam-*

*ponotus floridanus*. *Behavioral Ecology and Sociobiology* 59:490–499.

Engels S., Sauer K. P. 2007. Energy beyond the pupal stage: larval nutrition and its long-time consequences for male mating performance in a scorpionfly. *Journal of Insect Physiology* 53:633–638.

Engels W., Imperatriz-Fonseca V.-L. 1990. Caste development, reproductive strategies, and control of fertility in honey bees and stingless bees. Pages 167–230 in *Social Insects: An Evolutionary Approach to Castes and Reproduction*, edited by W. Engles. Berlin (Germany): Springer.

Enzmann B. L., Gibbs A. G., Nonacs P. 2014. The cost of being queen: investment across *Pogonomyrmex* harvester ant gynes that differ in degree of claustrality. *Journal of Insect Physiology* 70:134–142.

Evans J. D., Wheeler D. E. 1999. Differential gene expression between developing queens and workers in the honey bee, *Apis mellifera*. *Proceedings of the National Academy of Sciences of the United States of America* 96:5575–5580.

Evans J. D., Wheeler D. E. 2001. Gene expression and the evolution of insect polyphenisms. *BioEssays* 23:62–68.

Falk J., Wong J. W. Y., Kölliker M., Meunier J. 2014. Sibling cooperation in earwig families provides insights into the early evolution of social life. *American Naturalist* 183:547–557.

Faustino C. D., Silva-Matos E. V., Mateus S., Zucchi R. 2002. First record of emergency queen rearing in stingless bees (Hymenoptera, Apinae, Meliponini). *Insectes Sociaux* 49:111–113.

Fitzgerald T. D., Peterson S. C. 1988. Cooperative foraging and communication in caterpillars: silk and chemical markers may catalyze social evolution. *BioScience* 38:20–25.

Fjerdingstad E. J. 2004. Multiple paternity and colony homeostasis in *Lasius niger* ants. *Behavioral Ecology and Sociobiology* 56:50–58.

Fjerdingstad E. J. 2005. Control of body size of *Lasius niger* ant sexuals—worker interests, genes and environment. *Molecular Ecology* 14:3123–3132.

Fjerdingstad E. J., Boomsma J. J. 1997. Variation in size and sperm content of sexuals in the leafcutter ant *Atta colombica*. *Insectes Sociaux* 44:209–218.

Fjerdingstad E. J., Keller L. 2004. Relationships between phenotype, mating behavior, and fitness of queens in the ant *Lasius niger*. *Evolution* 58:1056–1063.

Forêt S., Kucharski R., Pellegrini M., Feng S., Jacobsen S. E., Robinson G. E., Maleszka R. 2012. DNA methylation dynamics, metabolic fluxes, gene splicing, and alternative phenotypes in honey bees. *Proceedings of the National Academy of Sciences of the United States of America* 109:4968–4973.

Gadagkar R., Bhagavan S., Chandrashekara K., Vinutha C. 1991. The role of larval nutrition in pre-imaginal biasing of caste in the primitively

eusocial wasp *Ropalidia marginata* (Hymenoptera: Vespidae). *Ecological Entomology* 16:435–440.

Gardner A., Grafen A. 2009. Capturing the superorganism: a formal theory of group adaptation. *Journal of Evolutionary Biology* 22:659–671.

Gobin B., Ito F., Billen J., Peeters C. 2008. Degeneration of sperm reservoir and the loss of mating ability in worker ants. *Naturwissenschaften* 95:1041–1048.

Gösswald K., Bier K. 1954. Untersuchungen zur Kastendetermination in der Gattung *Formica*. *Insectes Sociaux* 1:229–246.

Gotoh A., Ito F., Billen J. 2013. Vestigial spermatheca morphology in honeybee workers, *Apis cerana* and *Apis mellifera*, from Japan. *Apidologie* 44:133–143.

Gotoh A., Billen J., Hashim R., Ito F. 2016. Degeneration patterns of the worker spermatheca during morphogenesis in ants (Hymenoptera: Formicidae). *Evolution and Development* 18:96–104.

Gronenberg W. 2008. Structure and function of ant (Hymenoptera: Formicidae) brains: strength in numbers. *Myrmecological News* 11:25–36.

Guo X., Su S., Skogerboe G., Dai S., Li W., Li Z., Liu F., Ni R., Guo Y., Chen S., Zhang S., Chen R. 2013. Recipe for a busy bee: microRNAs in honey bee caste determination. *PLOS ONE* 8:e81661.

Hall D. W., Yi S. V., Goodisman M. A. D. 2013. Kin selection, genomics and caste-antagonistic pleiotropy. *Biology Letters* 9:20130309.

Hamilton W. D. 1964. The genetical evolution of social behaviour. *Journal of Theoretical Biology* 7:1–52.

Hammond R. L., Keller L. 2004. Conflict over male parentage in social insects. *PLOS Biology* 2:e248.

Hammond R. L., Bruford M. W., Bourke A. F. G. 2002. Ant workers selfishly bias sex ratios by manipulating female development. *Proceedings of the Royal Society B: Biological Sciences* 269:173–178.

Hannonen M., Sundström L. 2003. Worker nepotism among polygynous ants. *Nature* 421:910.

Harpur B. A., Kent C. F., Molodtsova D., Lebon J. M. D., Alqarni A. S., Owayss A. A., Zayed A. 2014. Population genomics of the honey bee reveals strong signatures of positive selection on worker traits. *Proceedings of the National Academy of Sciences of the United States of America* 111:2614–2619.

He X. J., Zhang X. C., Jiang W. J., Barron A. B., Zhang J. H., Zeng Z. J. 2016. Starving honey bee (*Apis mellifera*) larvae signal pheromonally to worker bees. *Scientific Reports* 6:22359.

Heinze J. 1998. Intercastes, intermorphs, and ergatoid queens: who is who in ant reproduction? *Insectes Sociaux* 45:113–124.

Heinze J. 2016. The male has done his work—the male may go. *Current Opinion in Insect Science* 16:22–27.

Heinze J., Hölldobler B. 1993. Fighting for a harem of queens: physiology of reproduction in Cardiocondyla male ants. *Proceedings of the National Academy of Sciences of the United States of America* 90:8412–8414.

Heinze J., Keller L. 2000. Alternative reproductive strategies: a queen perspective in ants. *Trends in Ecology and Evolution* 15:508–512.

Heinze J., Tsuji K. 1995. Ant reproductive strategies. *Researches on Population Ecology* 37:135–149.

Heinze J., Trunzer B., Oliveira P. S., Hölldobler B. 1996. Regulation of reproduction in the neotropical ponerine ant, *Pachycondyla villosa*. *Journal of Insect Behavior* 9:441–450.

Heinze J., Foitzik S., Oberstadt B., Rüppell O., Hölldobler B. 1999. A female caste specialized for the production of unfertilized eggs in the ant *Crematogaster smithi*. *Naturwissenschaften* 86:93–95.

Helanterä H. 2016. An organismal perpective on the evolution of insect societies. *Frontiers in Ecology and Evolution* 4:6.

Helanterä H., d'Ettorre P. 2015. A comparative study of egg recognition signature mixtures in *Formica* ants. *Evolution* 69:520–529.

Helanterä H., Ratnieks F. L. W. 2009. Sex allocation conflict in insect societies: who wins? *Biology Letters* 5:700–704.

Helanterä H., Sundström L. 2007. Worker reproduction in *Formica* ants. *American Naturalist* 170:E14–E25.

Helanterä H., Uller T. 2014. Neutral and adaptive explanations for an association between caste-biased gene expression and rate of sequence evolution. *Frontiers in Genetics* 5:297.

Helanterä H., Aehle O., Roux M., Heinze J., d'Ettorre P. 2013. Family-based guilds in the ant *Pachycondyla inversa*. *Biology Letters* 9:20130125.

Helms Cahan S., Keller L. 2003. Complex hybrid origin of genetic caste determination in harvester ants. *Nature* 424:306–309.

Hódar J. A., Zamora R., Castro J. 2002. Host utilisation by moth and larval survival of pine processionary caterpillar *Thaumetopoea pityocampa* in relation to food quality in three *Pinus* species. *Ecological Entomology* 27:292–301.

Hoffman E. A., Goodisman M. A. D. 2007. Gene expression and the evolution of phenotypic diversity in social wasps. *BMC Biology* 5:23.

Hölldobler B., Bartz S. 1985. Sociobiology of reproduction in ants. Pages 237–257 in *Experimental Behavioral Ecology and Sociobiology*, edited by B. Hölldobler, M. Lindauer, and K. von Frisch. Sunderland (Massachusetts): Sinauer Associates.

Hölldobler B., Wilson E. O. 1977. Weaver ants. *Scientific American* 237:146–154.

Hölldobler B., Wilson E. O. 1990. *The Ants*. Cambridge (Massachusetts): Belknap Press of Harvard University Press.

Holman L., Jørgensen C. G., Nielsen J., d'Ettorre P. 2010. Identification of an ant queen pheromone

regulating worker sterility. *Proceedings of the Royal Society B: Biological Sciences* 277:3793–3800.

Hora R. R., Poteaux C., Doums C., Fresneau D., Fénéron R. 2007. Egg cannibalism in a facultative polygynous ant: conflict for reproduction or strategy to survive? *Ethology* 113:909–916.

Hughes W. O. H., Oldroyd B. P., Beekman M., Ratnieks F. L. W. 2008. Ancestral monogamy shows kin selection is key to the evolution of eusociality. *Science* 320:1213–1216.

Hunt B. G., Wyder S., Elango N., Werren J. H., Zdobnov E. M., Yi S. V., Goodisman M. A. D. 2010a. Sociality is linked to rates of protein evolution in a highly social insect. *Molecular Biology and Evolution* 27:497–500.

Hunt B. G., Ometto L., Wurm Y., Shoemaker D., Yi S. V., Keller L., Goodisman M. A. D. 2011. Relaxed selection is a precursor to the evolution of phenotypic plasticity. *Proceedings of the National Academy of Sciences of the United States of America* 108:15936–15941.

Hunt B. G., Ometto L., Keller L., Goodisman M. A. D. 2013. Evolution at two levels in fire ants: the relationship between patterns of gene expression and protein sequence evolution. *Molecular Biology and Evolution* 30:263–271.

Hunt J. H. 1984. Adult nourishment during larval provisioning in a primitively eusocial wasp, *Polistes metricus* Say. *Insectes Sociaux* 31:452–460.

Hunt J. H. 1988. Lobe erection behavior and its possible social role in larvae of *Mischocyttarus* paper wasps. *Journal of Insect Behavior* 1:379–386.

Hunt J. H. 1991. Nourishment and the evolution of the social Vespidae. Pages 426–450 in *The Social Biology of Wasps*, edited by K. G. Ross and R. W. Matthews. Ithaca (New York): Cornell University Press.

Hunt J. H. 1994. Nourishment and evolution in wasps *sensu lato*. Pages 211–244 in *Nourishment and Evolution in Insect Societies*, edited by J. H. Hunt and C. A. Nalepa. Boulder (Colorado): Westview Press.

Hunt J. H., Dove M. A. 2002. Nourishment affects colony demographics in the paper wasp *Polistes metricus*. *Ecological Entomology* 27:467–474.

Hunt J. H., Nalepa C. A. 1994. *Nourishment and Evolution in Insect Societies*. Boulder (Colorado): Westview Press.

Hunt J. H., Baker I., Baker H. G. 1982. Similarity of amino acids in nectar and larval saliva: the nutritional basis of trophallaxis in social wasps. *Evolution* 36:1318–1322.

Hunt J. H., Wolschin F., Henshaw M. T., Newman T. C., Toth A. L., Amdam G. V. 2010b. Differential gene expression and protein abundance evince ontogenetic bias toward castes in a primitively eusocial wasp. *PLOS ONE* 5:e10674.

Ishay J., Ikan R. 1968. Food exchange between adults and larvae in *Vespa orientalis* F. *Animal Behaviour* 16:298–303.

Ishay J., Landau E. M. 1972. *Vespa* larvae send out rhythmic hunger signals. *Nature* 237:286–287.

Ishay J., Schwartz A. 1973. Acoustical communication between members of the oriental hornet (*Vespa orientalis*) colony. *Journal of the Acoustical Society of America* 53:640–649.

Ishay J., Fischl J., Alpern G. 1976. Study of honeybee caste differentiation by glucose level differences during development. *Insectes Sociaux* 23:23–28.

Jaffé R., Moritz R. F. A. 2010. Mating flights select for symmetry in honeybee drones (*Apis mellifera*). *Naturwissenschaften* 97:337–343.

Jeanne R. L. 2009. Vibrational signals in social wasps: a role in caste determination? Pages 243–265 in *Organization of Insect Societies: From Genome to Sociocomplexity*, edited by J. Gadau and J. Fewell. Cambridge (Massachusetts): Harvard University Press.

Jeanne R. L., Suryanarayanan S. 2011. A new model for caste development in social wasps. *Communicative and Integrative Biology* 4:373–377.

Jemielity S., Keller L. 2003. Queen control over reproductive decisions—no sexual deception in the ant *Lasius niger*. *Molecular Ecology* 12:1589–1597.

Jensen P. V., Børgesen L. W. 1995. Yolk protein in the pharaoh's ant: influence of larvae and workers on vitellogenin and vitellin content in queens. *Insectes Sociaux* 42:397–409.

Johnson B. R., Borowiec M. L., Chiu J. C., Lee E. K., Atallah J., Ward P. S. 2013. Phylogenomics resolves evolutionary relationships among ants, bees, and wasps. *Current Biology* 23:2565.

Johnson R. A. 2006. Capital and income breeding and the evolution of colony founding strategies in ants. *Insectes Sociaux* 53:316–322.

Johnstone R. A. 2004. Begging and sibling competition: how should offspring respond to their rivals? *American Naturalist* 163:388–406.

Judd T. M., Teal P. E. A., Hernandez E. J., Choudhury T., Hunt J. H. 2015. Quantitative differences in nourishment affect caste-related physiology and development in the paper wasp *Polistes metricus*. *PLOS ONE* 10:e0116199.

Julian G. E., Fewell J. H., Gadau J., Johnson R. A., Larrabee D. 2002. Genetic determination of the queen caste in an ant hybrid zone. *Proceedings of the National Academy of Sciences of the United States of America* 99:8157–8160.

Jung-Hoffmann I. 1966. Die Determination von Königin und Arbeiterin der Honigbiene. *Zeitschrift für Bienenforschung* 8:296–322.

Kamakura M. 2011. Royalactin induces queen differentiation in honeybees. *Nature* 473:478–483.

Kapheim K. M. 2016. Genomic sources of phenotypic novelty in the evolution of eusociality in insects. *Current Opinion in Insect Science* 13:24–32.

Kapheim K. M., Pan H., Li C., et al. 2015. Genomic signatures of evolutionary transitions from solitary to group living. *Science* 348:1139–1143.

Kaptein N., Billen J., Gobin B. 2005. Larval begging for food enhances reproductive options in the ponerine ant *Gnamptogenys striatula*. *Animal Behaviour* 69:293–299.

Karsai I., Hunt J. H. 2002. Food quantity affects traits of offspring in the paper wasp *Polistes metricus* (Hymenoptera: Vespidae). *Environmental Entomology* 31:99–106.

Katzav-Gozansky T., Soroker V., Kamer J., Schulz C. M., Francke W., Hefetz A. 2003. Ultrastructural and chemical characterization of egg surface of honeybee worker and queen-laid eggs. *Chemoecology* 13: 129–134.

Keller L. 1995. Social life: the paradox of multiple-queen colonies. *Trends in Ecology and Evolution* 10:355–360.

Keller L. 1997. Indiscriminate altruism: unduly nice parents and siblings. *Trends in Ecology and Evolution* 12:99–103.

Keller L., Nonacs P. 1993. The role of queen pheromones in social insects: queen control or queen signal? *Animal Behaviour* 45:787–794.

Keller L., Reeve H. K. 1994. Partitioning of reproduction in animal societies. *Trends in Ecology and Evolution* 9:98–102.

Keller L., Aron S., Passera L. 1996. Internest sex-ratio variation and male brood survival in the ant *Pheidole pallidula*. *Behavioral Ecology* 7:292–298.

Kerr W. E. 1950. Genetic determination of castes in the genus *Melipona*. *Genetics* 35:143–152.

Khila A., Abouheif E. 2008. Reproductive constraint is a developmental mechanism that maintains social harmony in advanced ant societies. *Proceedings of the National Academy of Sciences of the United States of America* 105:17884–17889.

Khila A., Abouheif E. 2010. Evaluating the role of reproductive constraints in ant social evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:617–630.

Kilner R., Johnstone R. A. 1997. Begging the question: are offspring solicitation behaviours signals of need? *Trends in Ecology and Evolution* 12:11–15.

King M., Eubel H., Millar A. H., Baer B. 2011. Proteins within the seminal fluid are crucial to keep sperm viable in the honeybee *Apis mellifera*. *Journal of Insect Physiology* 57:409–414.

Klahn J. E., Gamboa G. J. 1983. Social wasps: discrimination between kin and nonkin brood. *Science* 221:482–484.

Klein A., Schultner E., Lowak H., Schrader L., Heinze J., Holman L., Oettler J. 2016. Evolution of social insect polyphenism facilitated by the sex differentiation cascade. *PLOS Genetics* 12:e1005952.

Klobuchar E., Deslippe R. J. 2002. A queen pheromone induces workers to kill sexual larvae in colonies of the red imported fire ant (*Solenopsis invicta*). *Naturwissenschaften* 89:302–304.

Knerer G., Atwood C. E. 1966. Polymorphism in some neartic halictine bees. *Science* 152:1262–1263.

Korb J., Heinze J. 2016. Major hurdles for the evolution of sociality. *Annual Review of Entomology* 61:297–316.

Korb J., Buschmann M., Schafberg S., Liebig J., Bagnères A.-G. 2012. Brood care and social evolution in termites. *Proceedings of the Royal Society B: Biological Sciences* 279:2662–2671.

Kucharski R., Maleszka J., Foret S., Maleszka R. 2008. Nutritional control of reproductive status in honeybees via DNA methylation. *Science* 319:1827–1830.

Kucharski R., Foret S., Maleszka R. 2015. EGFR gene methylation is not involved in Royalactin controlled phenotypic polymorphism in honey bees. *Scientific Reports* 5:14070.

Kudô K., Shirai A. 2012. Effect of food availability on larval cannibalism by foundresses of the paper wasp *Polistes chinensis antennalis*. *Insectes Sociaux* 59:279–284.

Kukuk P. F. 1994. Nutrient transfer and reproduction in primitively social bees. Pages 329–343 in *Nourishment and Evolution in Insect Societies*, edited by J. H. Hunt and C. A. Nalepa. Boulder (Colorado): Westview Press.

Kukuk P. F., May B. 1991. Colony dynamics in a primitively eusocial halictine bee *Lasioglossum (Dialictus) zephyrum* (Hymenoptera: Halictidae). *Insectes Sociaux* 38:171–188.

Kumano N., Kasuya E. 2001. Why do workers of the primitively eusocial wasp *Polistes chinensis antennalis* remain at their natal nest? *Animal Behaviour* 61:655–660.

Lawson L. P., Vander Meer R. K., Shoemaker D. 2012. Male reproductive fitness and queen polyandry are linked to variation in the supergene *Gp-9* in the fire ant *Solenopsis invicta*. *Proceedings of the Royal Society B: Biological Sciences* 279:3217–3222.

Le Conte Y., Arnold G., Trouiller J., Masson C., Chappe B. 1990. Identification of a brood pheromone in honeybees. *Naturwissenschaften* 77:334–336.

Le Conte Y., Sreng L., Trouiller J. 1994. The recognition of larvae by worker honeybees. *Naturwissenschaften* 81:462–465.

Le Conte Y., Sreng L., Poitout S. H. 1995. Brood pheromone can modulate the feeding behavior of *Apis*

*mellifera* workers (Hymenoptera: Apidae). *Journal of Economic Entomology* 88:798–804.

Le Conte Y., Mohammedi A., Robinson G. E. 2001. Primer effects of a brood pheromone on honey-bee behavioural development. *Proceedings of the Royal Society B: Biological Sciences* 268:163–168.

Le Conte Y., Bécard J.-M., Costagliola G., de Vaublanc G., El Maâtaoui M., Crauser D., Plettner E., Slessor K. N. 2006. Larval salivary glands are a source of primer and releaser pheromone in honey bee (*Apis mellifera* L.). *Naturwissenschaften* 93:237–241.

Le Masne G. 1953. Observations sur les relations entre le couvain et les adultes chez les fourmis. *Annales des Sciences Naturelles Zoologiques* 15:1–56.

Lenoir A., Devers S., Marchand P., Bressac C., Savolainen R. 2010. Microgynous queens in the Palearctic ant, *Manica rubida*: dispersal morphs or social parasites? *Journal of Insect Science* 10:17.

Li J., Wu J., Rundassa D. B., Song F., Zheng A., Fang Y. 2010. Differential protein expression in honeybee (*Apis mellifera* L.) larvae: underlying caste differentiation. *PLOS ONE* 5:e13455.

Libbrecht R., Corona M., Wende F., Azevedo D. O., Serrão J. E., Keller L. 2013. Interplay between insulin signaling, juvenile hormone, and vitellogenin regulates maternal effects on polyphenism in ants. *Proceedings of the National Academy of Sciences of the United States of America* 110:11050–11055.

Lihoreau M., Costa J. T., Rivault C. 2012. The social biology of domiciliary cockroaches: colony structure, kin recognition and collective decisions. *Insectes Sociaux* 59:445–452.

Linksvayer T. A. 2006. Direct, maternal, and sibsocial genetic effects on individual and colony traits in an ant. *Evolution* 60:2552–2561.

Linksvayer T. A. 2007. Ant species differences determined by epistasis between brood and worker genomes. *PLOS ONE* 2:e994.

Linksvayer T. A., Wade M. J. 2005. The evolutionary origin and elaboration of sociality in the aculeate Hymenoptera: maternal effects, sib-social effects, and heterochrony. *Quarterly Review of Biology* 80:317–336.

Linksvayer T. A., Fondrk M. K., Page R. E. Jr. 2009. Honeybee social regulatory networks are shaped by colony-level selection. *American Naturalist* 173:E99–E107.

Linksvayer T. A., Kaftanoglu O., Akyol E., Blatch S., Amdam G. V., Page R. E. Jr. 2011. Larval and nurse worker control of developmental plasticity and the evolution of honey bee queen-worker dimorphism. *Journal of Evolutionary Biology* 24:1939–1948.

Mackert A., do Nascimento A. M., Bitondi M. M. G., Hartfelder K., Simões Z. L. P. 2008. Identification of a juvenile hormone esterase-like gene in the honey bee, *Apis mellifera* L.—expression analysis and functional assays. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology* 150:33–44.

Maisonnasse A., Lenoir J.-C., Beslay D., Crauser D., Le Conte Y. 2010. E-β-ocimene, a volatile brood pheromone involved in social regulation in the honey bee colony (*Apis mellifera*). *PLOS ONE* 5:e13531.

Markin G. 1970. Food distribution within laboratory colonies of the Argentine ant, *Tridomyrmex humilis* (Mayr). *Insectes Sociaux* 17:127–157.

Martin S. J., Châline N. G., Ratnieks F. L. W., Jones G. R. 2005. Searching for the egg-marking signal in honeybees. *Journal of Negative Results* 2:1–9.

Mas F., Kölliker M. 2008. Maternal care and offspring begging in social insects: chemical signalling, hormonal regulation and evolution. *Animal Behaviour* 76:1121–1131.

Mas F., Haynes K. F., Kölliker M. 2009. A chemical signal of offspring quality affects maternal care in a social insect. *Proceedings of the Royal Society B: Biological Sciences* 276:2847–2853.

Masuko K. 1986. Larval hemolymph feeding: a nondestructive parental cannibalism in the primitive ant *Amblyopone silvestrii* Wheeler (Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology* 19:249–255.

Masuko K. 1989. Larval hemolymph feeding in the ant *Leptanilla japonica* by use of a specialized duct organ, the "larval hemolymph tap" (Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology* 24:127–132.

Masuko K. 1990a. The instars of the ant *Amblyopone silvestrii* (Hymenoptera: Formicidae). *Sociobiology* 17:221–244.

Masuko K. 1990b. Behavior and ecology of the enigmatic ant *Leptanilla japonica* Baroni Urbani (Hymenoptera: Formicidae: Leptanillinae). *Insectes Sociaux* 37:31–57.

Masuko K. 1994. Specialized predation on oribatid mites by two species of the ant genus *Myrmecina* (Hymenoptera: Formicidae). *Psyche* 101:159–173.

Masuko K. 2008. Larval stenocephaly related to specialized feeding in the ant genera *Amblyopone*, *Leptanilla* and *Myrmecina* (Hymenoptera: Formicidae). *Arthropod Structure and Development* 37:109–117.

Maynard Smith J. 1964. Group selection and kin selection. *Nature* 201:1145–1147.

Maynard Smith J., Szathmáry E. 1995. *The Major Transitions in Evolution.* Oxford (United Kingdom): Oxford University Press.

McInnes D. A., Tschinkel W. R. 1995. Queen dimorphism and reproductive strategies in the fire ant *Solenopsis geminata* (Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology* 36:367–375.

McKenzie S. K., Fetter-Pruneda I., Ruta V., Kronauer D. J. C. 2016. Transcriptomics and neuroanatomy of the clonal raider ant implicate an expanded clade of odorant receptors in chemical communication.

*Proceedings of the National Academy of Sciences of the United States of America* 113:14091–14096.

Mehdiabadi N. J., Reeve H. K., Mueller U. G. 2003. Queens versus workers: sex-ratio conflict in eusocial Hymenoptera. *Trends in Ecology and Evolution* 18:88–93.

Meunier J., Chapuisat M. 2009. The determinants of queen size in a socially polymorphic ant. *Journal of Evolutionary Biology* 22:1906–1913.

Meunier J., West S. A., Chapuisat M. 2008. Split sex ratios in the social Hymenoptera: a meta-analysis. *Behavioral Ecology* 19:382–390.

Michaud J. P., Grant A. K. 2004. Adaptive significance of sibling egg cannibalism in Coccinellidae: comparative evidence from three species. *Annals of the Entomological Society of America* 97:710–719.

Michener C. D. 1974. *The Social Behavior of the Bees: A Comparative Study.* Cambridge (Massachusetts): Belknap Press of Harvard University Press.

Michener C. D. 1990. Reproduction and castes in social Halictine bees. Pages 77–121 in *Social Insects: An Evolutionary Approach to Castes and Reproduction,* edited by W. Engles. Berlin (Germany): Springer.

Mikheyev A. S., Linksvayer T. A. 2015. Genes associated with ant social behavior show distinct transcriptional and evolutionary patterns. *eLife* 4:e04775.

Mock D. W., Parker G. A. 1998. Siblicide, family conflict and the evolutionary limits of selfishness. *Animal Behaviour* 56:1–10.

Mohammedi A., Crauser D., Paris A., Le Conte Y. 1996. Effect of a brood pheromone on honeybee hypopharyngeal glands. *Comptes rendus de l'Académie des sciences, Série III, Sciences de la vie* 319:769–772.

Mohammedi A., Paris A., Crauser D., Le Conte Y. 1998. Effect of aliphatic esters on ovary development of queenless bees (*Apis mellifera* L.). *Naturwissenschaften* 85:455–458.

Molet M., Wheeler D. E., Peeters C. 2012. Evolution of novel mosaic castes in ants: modularity, phenotypic plasticity, and colonial buffering. *American Naturalist* 180:328–341.

Morel L., Vander Meer R. K. 1988. Do ant brood pheromones exist? *Annals of the Entomological Society of America* 81:705–710.

Mutti N. S., Dolezal A. G., Wolschin F., Mutti J. S., Gill K. S., Amdam G. V. 2011. IRS and TOR nutrient-signaling pathways act *via* juvenile hormone to influence honey bee caste fate. *Journal of Experimental Biology* 214:3977–3984.

Nehring V., Evison S. E. F., Santorelli L. A., d'Ettorre P., Hughes W. O. H. 2011. Kin-informative recognition cues in ants. *Proceedings of the Royal Society B: Biological Sciences* 278:1942–1948.

Nonacs P. 1993. Male parentage and sexual deception in the social Hymenoptera. Pages 384–401 in *Evolution and Diversity of Sex Ratio in Insects and Mites,*

edited by D. L. Wrensch and M. A. Ebbert. New York: Chapman and Hall.

Nonacs P., Tobin J. E. 1992. Selfish larvae: development and the evolution of parasitic behavior in the Hymenoptera. *Evolution* 46:1605–1620.

O'Donnell S. 1998. Reproductive caste determination in eusocial wasps (Hymenoptera: Vespidae). *Annual Review of Entomology* 43:323–346.

Oettler J., Dijkstra M. B., Heinze J. 2013. Egg-laying "intermorphs" in the ant *Crematogaster smithi* neither affect sexual production nor male parentage. *PLOS ONE* 8:e75278.

Ohkawara K., Ito F., Higashi S. 1993. Production and reproductive function of intercastes in *Myrmecina graminicola nipponica* colonies (Hymenoptera: Formicidae). *Insectes Sociaux* 40:1–10.

Oldroyd B. P., Ratnieks F. L. W. 2000. Evolution of worker sterility in honey-bees (*Apis mellifera*): how anarchistic workers evade policing by laying eggs that have low removal rates. *Behavioral Ecology and Sociobiology* 47:268–273.

Oldroyd B. P., Smolenski A. J., Cornuet J.-M., Crozler R. H. 1994. Anarchy in the beehive. *Nature* 371:749.

Oldroyd B. P., Ratnieks F. L. W., Wossler T. C. 2002. Egg-marking pheromones in honey-bees *Apis mellifera. Behavioral Ecology and Sociobiology* 51:590–591.

Oliver T. H., Leather S. R., Cook J. M. 2012. Ant larval demand reduces aphid colony growth rates in an ant-aphid interaction. *Insects* 3:120–130.

Oster G. F., Wilson E. O. 1978. *Caste and Ecology in Social Insects.* Princeton (New Jersey): Princeton University Press.

Otto D. 2005. *Die roten Waldameisen: Die Baumeister der grossen Hügelbauten im Walde:* Formica ruta *L. und* Formica polyctena *Först.* Hohenwarsleben (Germany): Westarp Wissenschaften.

Ottosson U., Bäckman J., Smith H. G. 1997. Begging affects parental effort in the pied flycatcher, *Ficedula hypoleuca. Behavioral Ecology and Sociobiology* 41:381–384.

Page R. E. Jr., Robinson G. E., Fondrk M. K. 1989. Genetic specialists, kin recognition and nepotism in honey-bee colonies. *Nature* 338:576–579.

Panek L. M., Gamboa G. J. 2000. Queens of the paper wasp *Polistes fuscatus* (Hymenoptera: Vespidae) discriminate among larvae on the basis of relatedness. *Ethology* 106:159–170.

Pankiw T. 2004. Brood pheromone regulates foraging activity of honey bees (Hymenoptera: Apidae). *Journal of Economic Entomology* 97:748–751.

Pankiw T. 2007. Brood pheromone modulation of pollen forager turnaround time in the honey bee (*Apis mellifera* L.). *Journal of Insect Behavior* 20:173–180.

Pankiw T., Page R. E. Jr. 2001. Brood pheromone modulates honeybee (*Apis mellifera* L.) sucrose response thresholds. *Behavioral Ecology and Sociobiology* 49:206–213.

Pankiw T., Page R. E. Jr., Fondrk M. K. 1998. Brood pheromone stimulates pollen foraging in honey bees (*Apis mellifera*). *Behavioral Ecology and Sociobiology* 44:193–198.

Pankiw T., Sagili R. R., Metz B. N. 2008. Brood pheromone effects on colony protein supplement consumption and growth in the honey bee (Hymenoptera: Apidae) in a subtropical winter climate. *Journal of Economic Entomology* 101:1749–1755.

Passera L. 1980. La fonction inhibitrice des reines de la fourmi *Plagiolepis pygmae* Latr.: role des pheromones. *Insectes Sociaux* 27:212–225.

Passera L., Aron S. 1996. Early sex discrimination and male brood elimination by workers of the Argentine ant. *Proceedings of the Royal Society B: Biological Sciences* 263:1041–1046.

Passera L., Keller L. 1992. The period of sexual maturation and the age at mating in *Iridomyrmex humilis*, an ant with intranidal mating. *Journal of Zoology* 228:141–153.

Patel A., Fondrk M. K., Kaftanoglu O., Emore C., Hunt G., Frederick K., Amdam G. V. 2007. The making of a queen: TOR pathway is a key player in diphenic caste development. *PLOS ONE* 2:e509.

Peeters C., Hölldobler B. 1992. Notes on the morphology of the sticky "doorknobs" of larvae in an Australian Hypoponera sp. (Formicidae; Ponerinae). *Psyche* 99:23–30.

Peeters C., Lin C.-C., Quinet Y., Martins Segundo G., Billen J. 2013. Evolution of a soldier caste specialized to lay unfertilized eggs in the ant genus *Crematogaster* (subgenus *Orthocrema*). *Arthropod Structure and Development* 42:257–264.

Penick C. A., Liebig J. 2012. Regulation of queen development through worker aggression in a predatory ant. *Behavioral Ecology* 23:992–998.

Penick C. A., Copple R. N., Mendez R. A., Smith A. A. 2012. The role of anchor-tipped larval hairs in the organization of ant colonies. *PLOS ONE* 7: e41595.

Pereboom J. J. M., Velthuis H. H. W., Duchateau M. J. 2003. The organisation of larval feeding in bumblebees (Hymenoptera, Apidae) and its significance to caste differentiation. *Insectes Sociaux* 50:127–133.

Petralia R. S., Vinson S. B. 1978. Feeding in the larvae of the imported fire ant, *Solenopsis invicta*: behavior and morphological adaptations. *Annals of the Entomological Society of America* 71:643–648.

Petralia R. S., Vinson S. B. 1979. Comparative anatomy of the ventral region of ant larvae, and its relation to feeding behavior. *Psyche* 86:375–394.

Petralia R. S., Sorensen A. A., Vinson S. B. 1980. The labial gland system of larvae of the imported fire ant, *Solenopsis invicta* Buren. *Cell and Tissue Research* 206:145–156.

Purcell J., Chapuisat M. 2012. The influence of social structure on brood survival and development in a socially polymorphic ant: insights from a cross-fostering experiment. *Journal of Evolutionary Biology* 25:2288–2297.

Purcell J., Avril A., Jaffuel G., Bates S., Chapuisat M. 2014. Ant brood function as life preservers during floods. *PLOS ONE* 9:e89211.

Ratnieks F. L. W. 1988. Reproductive harmony via mutual policing by workers in eusocial Hymenoptera. *American Naturalist* 132:217–236.

Ratnieks F. L. W. 1991. The evolution of genetic odorcue diversity in social Hymenoptera. *American Naturalist* 137:202–226.

Ratnieks F. L. W. 1995. Evidence for a queen-produced egg-marking pheromone and its use in worker policing in the honey bee. *Journal of Apicultural Research* 34:31–37.

Ratnieks F. L. W. 2001. Heirs and spares: caste conflict and excess queen production in *Melipona* bees. *Behavioral Ecology and Sociobiology* 50:467–473.

Ratnieks F. L. W., Helanterä H. 2009. The evolution of extreme altruism and inequality in insect societies. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364:3169–3179.

Ratnieks F. L. W., Reeve H. K. 1992. Conflict in single-queen Hymenopteran societies: the structure of conflict and processes that reduce conflict in advanced eusocial species. *Journal of Theoretical Biology* 158:33–65.

Ratnieks F. L. W., Visscher P. K. 1989. Worker policing in the honeybee. *Nature* 342:796–797.

Ratnieks F. L. W., Foster K. R., Wenseleers T. 2006. Conflict resolution in insect societies. *Annual Review of Entomology* 51:581–608.

Reeve H. K., Ratnieks F. L. W. 1993. Queen-queen conflicts in polygynous societies: mutual tolerance and reproductive skew. Pages 45–85 in *Queen Number and Sociality in Insects*, edited by L. Keller. Oxford (United Kingdom): Oxford University Press.

Reuter M., Keller L. 2001. Sex ratio conflict and worker production in eusocial Hymenoptera. *American Naturalist* 158:166–177.

Ribeiro M. de F., Wenseleers T., Filho P. de S. S., Alves D. de A. 2006. Miniature queens in stingless bees: basic facts and evolutionary hypotheses. *Apidologie* 37:191–206.

Richards M. H., Packer L. 1994. Trophic aspects of caste determination in *Halictus ligatus*, a primitively eusocial sweat bee. *Behavioral Ecology and Sociobiology* 34:385–391.

Roat T. C., da Cruz-Landim C. 2011. Differentiation of the honey bee (*Apis mellifera* L.) antennal lobes during metamorphosis: a comparative study among castes and sexes. *Animal Biology* 61:153–161.

Roberston H. G. 1995. Sperm transfer in the ant *Carebara vidua* F. Smith (Hymenoptera: Formicidae). *Insectes Sociaux* 42:411–418.

Roff D. A. 1992. *The Evolution of Life Histories: Theory and Analysis*. New York: Chapman and Hall.

Röseler P. F., Röseler I. 1974. Morphologische und physiologische Differenzierung der Kasten bei den Hummelarten *Bombus hypnorum* (L.) und *Bombus terrestris* (L.). *Zoologische Jahrbucher Abteilung fuer Allegmeine Zoologie und Physiologie der Tierre* 78:175–198.

Rosenheim J. A., Nonacs P., Mangel M. 1996. Sex ratios and multifaceted parental investment. *American Naturalist* 148:501–535.

Royle N. J., Hartley I. R., Parker G. A. 2002. Begging for control: when are offspring solicitation behaviours honest? *Trends in Ecology and Evolution* 17:434–440.

Rueppell O., Kirkman R. W. 2005. Extraordinary starvation resistance in *Temnothorax rugatulus* (Hymenoptera, Formicidae) colonies: demography and adaptive behavior. *Insectes Sociaux* 52:282–290.

Rüger M. H., Fröba J., Foitzik S. 2008. Larval cannibalism and worker-induced separation of larvae in *Hypoponera* ants: a case of conflict over caste determination? *Insectes Sociaux* 55:12–21.

Rüppell O., Heinze J. 1999. Alternative reproductive tactics in females: the case of size polymorphism in winged ant queens. *Insectes Sociaux* 46:6–17.

Rüppell O., Heinze J., Hölldobler B. 1998. Size-dimorphism in the queens of the North American ant *Leptothorax rugatulus* (Emery). *Insectes Sociaux* 45:67–77.

Rüppell O., Heinze J., Hölldobler B. 2002. Intracolonial patterns of reproduction in the queen-size dimorphic ant *Leptothorax rugatulus*. *Behavioral Ecology* 13:239–247.

Sakagami S. 1982. Stingless bees. Pages 361–423 in *Social Insects*, edited by H. R. Herman. New York: Academic Press.

Santana F. A., Nunes F. M. F., Vieira C. U., Machado M. A. M. S, Kerr W. E., Silva W. A. Jr., Bonetti A. M. 2006. Differentially displayed expressed sequence tags in *Melipona scutellaris* (Hymenoptera, Apidae, Meliponini) development. *Anais da Academia Brasileira de Ciencias* 78:69–75.

Savolainen R., Vepsäläinen K. 2003. Sympatric speciation through intraspecific social parasitism. *Proceedings of the National Academy of Sciences of the United States of America* 100:7169–7174.

Schlüns H., Schlüns E. A., van Praagh J., Moritz R. F. A. 2003. Sperm numbers in drone honeybees (*Apis mellifera*) depend on body size. *Apidologie* 34:577–584.

Schmickl T., Crailsheim K. 2001. Cannibalism and early capping: strategy of honeybee colonies in times of experimental pollen shortages. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology* 187:541–547.

Schrader L., Simola D. F., Heinze J., Oettler J. 2015. Sphingolipids, transcription factors, and conserved toolkit genes: developmental plasticity in the ant *Cardiocondyla obscurior*. *Molecular Biology and Evolution* 32:1474–1486.

Schrader L., Helanterä H., Oettler J. 2016. Accelerated evolution of developmentally biased genes in the tetraphenic ant *Cardiocondyla obscurior*. *Molecular Biology and Evolution* doi: 10.1093/molbev/msw240.

Schultner E., d'Ettorre P., Helanterä H. 2013. Social conflict in ant larvae: egg cannibalism occurs mainly in males and larvae prefer alien eggs. *Behavioral Ecology* 24:1306–1311.

Schultner E., Gardner A., Karhunen M., Helanterä H. 2014. Ant larvae as players in social conflict: relatedness and individual identity mediate cannibalism intensity. *American Naturalist* 184:E161–E174.

Schultner E., Saramäki J., Helanterä H. 2016. Genetic structure of native ant supercolonies varies in space and time. *Molecular Ecology* 25:6196–6213.

Schwander T., Keller L. 2008. Genetic compatibility affects queen and worker caste determination. *Science* 322:552.

Schwander T., Humbert J.-Y., Brent C. S., Cahan S. H., Chapuis L., Renai E., Keller L. 2008. Maternal effect on female caste determination in a social insect. *Current Biology* 18:265–269.

Scofield H. N., Mattila H. R. 2015. Honey bee workers that are pollen stressed as larvae become poor foragers and waggle dancers as adults. *PLOS ONE* 10:e0121731.

Scriber J. M., Slansky F. Jr. 1981. The nutritional ecology of immature insects. *Annual Review of Entomology* 26:183–211.

Seeley T. D. 1985. *Honeybee Ecology: A Study of Adaptation in Social Life*. Princeton (New Jersey): Princeton University Press.

Seeley T. D. 1995. *The Wisdom of the Hive: The Social Physiology of Honey Bee Colonies*. Cambridge (Massachusetts): Harvard University Press.

Shafiei M., Moczek A. P., Nijhout H. F. 2001. Food availability controls the onset of metamorphosis in the dung beetle *Onthophagus taurus* (Coleoptera: Scarabaeidae). *Physiological Entomology* 26:173–180.

Sharma K. R., Enzmann B. L., Schmidt Y., Moore D., Jones G. R., Parker J., Berger S. L., Reinberg D., Zwiebel L. J., Breit B., Liebig J., Ray A. 2015. Cuticular hydrocarbon pheromones for social behavior and their coding in the ant antenna. *Cell Reports* 12:1261–1271.

Shi Y. Y., Yan W. Y., Huang Z. Y., Wang Z. L., Wu X. B., Zheng Z. J. 2013. Genomewide analysis indicates that queen larvae have lower methylation levels in the honey bee (*Apis mellifera*). *Naturwissenschaften* 100:193–197.

Shik J. Z., Donoso D. A., Kaspari M. 2013. The life history continuum hypothesis links traits of male ants with life outside the nest. *Entomologia Experimentalis et Applicata* 149:99–109.

Shimoji H., Fujiki Y., Yamaoka R., Tsuji K. 2012. Egg discrimination by workers in *Diacamma* sp. from Japan. *Insectes Sociaux* 59:201–206.

Shingleton A. W., Frankino W. A., Flatt T., Nijhout H. F., Emlen D. J. 2007. Size and shape: the developmental regulation of static allometry in insects. *BioEssays* 29:536–548.

Signorotti L., Jaisson P., d'Ettorre P. 2013. Larval memory affects adult nest-mate recognition in the ant *Aphaenogaster senilis. Proceedings of the Royal Society B: Biological Sciences* 281:20132579.

Simmons L. W. 2001. Social insects. Pages 319–341 in *Sperm Competition and Its Evolutionary Consequences in the Insects*, by L. W. Simmons. Princeton (New Jersey): Princeton University Press.

Simola D. F., Ye C., Mutti N. S., Dolezal K., Bonasio R., Liebig J., Reinberg D., Berger S. L. 2013. A chromatin link to caste identity in the carpenter ant *Camponotus floridanus. Genome Research* 23:486–496.

Smedal B., Brynem M., Kreibich C. D., Amdam G. V. 2009. Brood pheromone suppresses physiology of extreme longevity in honeybees (*Apis mellifera*). *Journal of Experimental Biology* 212:3795–3801.

Smeets P., Duchateau M. J. 2001. Feeding behaviour in the bumble bee *Bombus terrestris. Belgian Journal of Zoology* 131:119–126.

Smith C. R., Anderson K. E., Tillberg C. V., Gadau J., Suarez A. V. 2008a. Caste determination in a polymorphic social insect: nutritional, social, and genetic factors. *American Naturalist* 172:497–507.

Smith C. R., Toth A. L., Suarez A. V., Robinson G. E. 2008b. Genetic and genomic analyses of the division of labour in insect societies. *Nature Reviews Genetics* 9:735–748.

Smith H. G., Montgomerie R. 1991. Nestling American robins compete with siblings by begging. *Behavioral Ecology and Sociobiology* 29:307–312.

Solis C. R., Strassmann J. E. 1990. Presence of brood affects caste differentiation in the social wasp, *Polistes exclamans* Viereck (Hymenoptera: Vespidae). *Functional Ecology* 4:531–541.

Solis D. R., Fox E. G. P., Kato L. M., de Jesus C. M., Yabuki A. T., de Carvalho Campos A. E., Bueno O. C. 2010a. Morphological description of the immatures of the ant, *Monomorium floricola. Journal of Insect Science* 10:15.

Solis D. R., Fox E. G. P., Rossi M. L., Bueno O. C. 2010b. Description of the immatures of *Linepithema humile* Mayr (Hymenoptera: Formicidae). *Biological Research* 43:19–30.

Solis D. R., Nakano M. A., Fox E. G. P., Rossi M. L., Feitosa R. M., Bueno O. C., de Castro Morini M. S. 2011. Description of the immatures of the ant, *Myrmelachista catharinae. Journal of Insect Science* 11:24.

Solis D. R., Fox E. G. P., Ceccato M., Reiss I. C., Décio P., Lorenzon N., DaSilva N. C., Bueno O. C. 2012.

On the morphology of the worker immatures of the leafcutter ant *Atta sexdens* Linnaeus (Hymenoptera: Formicidae). *Microscopy Research and Technique* 75:1059–1065.

Sorensen A. A., Busch T. M., Vinson S. B. 1983a. Factors affecting brood cannibalism in laboratory colonies of the imported fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae). *Journal of the Kansas Entomological Society* 56:140–150.

Sorensen A. A., Kamas R. S., Vinson S. B. 1983b. The influence of oral secretions from larvae on levels of proteinases in colony members of *Solenopsis invicta* Buren (Hymenoptera: Formicidae). *Journal of Insect Physiology* 29:163–168.

Stearns S. C. 1992. *The Evolution of Life Histories.* Oxford (United Kingdom): Oxford University Press.

Strassmann J. E., Sullender B. W., Queller D. C. 2002. Caste totipotency and conflict in a large-colony social insect. *Proceedings of the Royal Society B: Biological Sciences* 269:263–270.

Stürup M., Baer-Imhoof B., Nash D. R., Boomsma J. J., Baer B. 2013. When every sperm counts: factors affecting male fertility in the honeybee *Apis mellifera. Behavioral Ecology* 24:1192–1198.

Sundström L. 1995. Dispersal polymorphism and physiological condition of males and females in the ant, *Formica truncorum. Behavioral Ecology* 6:132–139.

Sundström L., Boomsma J. J. 2001. Conflicts and alliances in insect families. *Heredity* 86:515–521.

Sundström L., Chapuisat M., Keller L. 1996. Conditional manipulation of sex ratios by ant workers: a test of kin selection theory. *Science* 274:993–995.

Suryanarayanan S., Hermanson J. C., Jeanne R. L. 2011. A mechanical signal biases caste development in a social wasp. *Current Biology* 21:231–235.

Suzuki T. 1985. Mating and laying of female-producing eggs by orphaned workers of a paper wasp, *Polistes snelleni* (Hymenoptera: Vespidae). *Annals of the Entomological Society of America* 78:736–739.

Teseo S., Kronauer D. J. C., Jaisson P., Châline N. 2013. Enforcement of reproductive synchrony via policing in a clonal ant. *Current Biology* 23:328–332.

Teseo S., Châline N., Jaisson P., Kronauer D. J. C. 2014. Epistasis between adults and larvae underlies caste fate and fitness in a clonal ant. *Nature Communications* 5:3363.

Traniello J. F. A. 1982. Population structure and social organization in the primitive ant *Amblyopone pallipes* (Hymenoptera: Formicidae). *Psyche* 89:65–80.

Traynor K. S., Le Conte Y., Page R. E. Jr. 2014. Queen and young larval pheromones impact nursing and reproductive physiology of honey bee (*Apis mellifera*) workers. *Behavioral Ecology and Sociobiology* 68:2059–2073.

Traynor K. S., Le Conte Y., Page R. E. Jr. 2015. Age matters: pheromone profiles of larvae differentially

influence foraging behaviour in the honeybee, *Apis mellifera. Animal Behaviour* 99:1–8.

Trivers R. L., Hare H. 1976. Haplodiploidy and the evolution of the social insect. *Science* 191:249–263.

Trouiller J., Arnold G., Le Conte Y., Masson C., Chappe B. 1991. Temporal pheromonal and kairomonal secretion in the brood of honeybees. *Naturwissenschaften* 78:368–370.

Tschinkel W. R. 1988. Social control of egg-laying rate in queens of the fire ant, *Solenopsis invicta. Physiological Entomology* 13:327–350.

Tschinkel W. R. 1995. Stimulation of fire ant queen fecundity by a highly specific brood stage. *Annals of the Entomological Society of America* 88:876–882.

Tschinkel W. R. 1996. A newly-discovered mode of colony founding among fire ants. *Insectes Sociaux* 43:267–276.

Ulrich Y., Burns D., Libbrecht R., Kronauer D. J. C. 2016. Ant larvae regulate worker foraging behavior and ovarian activity in a dose-dependent manner. *Behavioral Ecology and Sociobiology* 70:1011–1018.

Van Oystaeyen A., Oliveira R. C., Holman L., van Zweden J. S., Romero C., Oi C. A., d'Ettorre P., Khalesi M., Billen J., Wäckers F., Millar J. G., Wenseleers T. 2014. Conserved class of queen pheromones stops social insect workers from reproducing. *Science* 343:287–290.

van Zweden J. S., d'Ettorre P. 2010. Nestmate recognition in social insects and the role of hydrocarbons. Pages 222–243 in *Insect Hydrocarbons: Biology, Biochemistry and Chemical Ecology*, edited by G. J. Blomquist and A.-G. Bagnères. Cambridge (United Kingdom): Cambridge University Press.

van Zweden J. S., Heinze J., Boomsma J. J., d'Ettorre P. 2009. Ant queen egg-marking signals: Matching deceptive laboratory simplicity with natural complexity. *PLOS ONE* 4:e4718.

Vargo E. L. 1998. Primer pheromones in ants. Pages 293–313 in *Pheromone Communication in Social Insects: Ants, Wasps, Bees, and Termites*, edited by R. K. Vander Meer, M. D. Breed, M. Winston, and K. E. Espelie. Boulder (Colorado): Westview Press.

Vargo E. L., Passera L. 1991. Pheromonal and behavioral queen control over the production of gynes in the Argentine ant *Iridomyrmex humilis* (Mayr). *Behavioral Ecology and Sociobiology* 28:161–169.

Velthuis H., Sommeijer M. J. 1991. Roles of morphogenetic hormones in caste polymorphism in stingless bees. Pages 346–383 in *Morphogenetic Hormones of Arthropods*, edited by A. P. Gupta. New Brunswick (New Jersey): Rutgers University Press.

Vijendravarma R. K., Narasimha S., Kawecki T. J. 2013. Predatory cannibalism in *Drosophila melanogaster* larvae. *Nature Communications* 4:1789.

Villalta I., Angulo E., Devers S., Cerdá X., Boulay R. 2015. Regulation of worker egg laying by lar-

vae in a fission-performing ant. *Animal Behaviour* 106:149–156.

Villalta I., Amor F., Cerdá X., Boulay R. 2016a. Social coercion of larval development in an ant species. *Science of Nature* 103:18.

Villalta I., Blight O., Angulo E., Cerdá X., Boulay R. 2016b. Early developmental processes limit socially mediated phenotypic plasticity in an ant. *Behavioral Ecology and Sociobiology* 70:285–291.

Villet M. H., Hanrahan S. A., Walther C. 1990. Larval structures associated with larval-to-adult trophallaxis in *Platythyrea* (Hymenoptera: Formicidae). *International Journal of Insect Morphology and Embryology* 19:243–256.

Vojvodic S., Johnson B. R., Harpur B. A., Kent C. F., Zayed A., Anderson K. E., Linksvayer T. A. 2015. The transcriptomic and evolutionary signature of social interactions regulating honey bee caste development. *Ecology and Evolution* 5:4795–4807.

Volny V. P., Gordon D. M. 2002. Genetic basis for queen-worker dimorphism in a social insect. *Proceedings of the National Academy of Sciences of the United States of America* 99:6108–6111.

Wagner D., Gordon D. M. 1999. Colony age, neighborhood density and reproductive potential in harvester ants. *Oecologia* 119:175–182.

Walsh J. P., Tschinkel W. R. 1974. Brood recognition by contact pheromone in the red imported fire ant, *Solenopsis invicta. Animal Behaviour* 22:695–704.

Wang Q., Goodger J. Q. D., Woodrow I. E., Elgar M. A. 2016. Location-specific cuticular hydrocarbon signals in a social insect. *Proceedings of the Royal Society B: Biological Sciences* 283:20160310.

Warner M. R., Kovaka K., Linksvayer T. A. 2016. Late-instar ant worker larvae play a prominent role in colony-level caste regulation. *Insectes Sociaux* 63:575–583.

Watkins J. F. H., Cole T. W. 1966. The attraction of army ant workers to secretions of their queens. *Texas Journal of Science* 18:254–265.

Wenseleers T., Ratnieks F. L. W. 2004. Tragedy of the commons in *Melipona* bees. *Proceedings of the Royal Society B: Biological Sciences* 271:S310–S312.

Wenseleers T., Ratnieks F. L. W. 2006a. Enforced altruism in insect societies. *Nature* 444:50.

Wenseleers T., Ratnieks F. L. W. 2006b. Comparative analysis of worker reproduction and policing in eusocial Hymenoptera supports relatedness theory. *American Naturalist* 168:E163–E179.

Wenseleers T., Ratnieks F. L. W., Billen J. 2003. Caste fate conflict in swarm-founding social Hymenoptera: an inclusive fitness analysis. *Journal of Evolutionary Biology* 16:647–658.

Wenseleers T., Hart A. G., Ratnieks F. L. W., Quezada-Euán J. G. 2004a. Queen execution and caste conflict in the stingless bee *Melipona beecheii. Ethology* 110:725–736.

Wenseleers T., Helanterä H., Hart A., Ratnieks F. L. W. 2004b. Worker reproduction and policing in insect societies: an ESS analysis. *Journal of Evolutionary Biology* 17:1035–1047.

Wenseleers T., Ratnieks F. L. W., Ribeiro M. de F., Alves D. de A., Imperatriz-Fonseca V.-L. 2005. Working-class royalty: bees beat the caste system. *Biology Letters* 1:125–128.

Wenseleers T., Helanterä H., Alves D. A., Dueñez-Guzmán E., Pamilo P. 2013. Towards greater realism in inclusive fitness models: the case of worker reproduction in insect societies. *Biology Letters* 9:20130334.

Went F. W., Wheeler J., Wheeler G. C. 1972. Feeding and digestion in some ants (*Veromessor* and *Manica*). *BioScience* 22:82–88.

West-Eberhard M. J. 2003. *Developmental Plasticity and Evolution.* Oxford (United Kingdom): Oxford University Press.

Wheeler D. E. 1986. Developmental and physiological determinants of caste in social Hymenoptera: evolutionary implications. *American Naturalist* 128:13–34.

Wheeler D. E. 1991. The development basis of worker caste polymorphism in ants. *American Naturalist* 138:1218–1238.

Wheeler D. E. 1994. Nourishment in ants: patterns in individuals and societies. Pages 245–278 in *Nourishment and Evolution in Insect Societies,* edited by J. H. Hunt and C. A. Nalepa. Boulder (Colorado): Westview Press.

Wheeler D. E., Buck N., Evans J. D. 2006. Expression of insulin pathway genes during the period of caste determination in the honey bee, *Apis mellifera. Insect Molecular Biology* 15:597–602.

Wheeler D. E., Buck N. A., Evans J. D. 2014. Expression of insulin/insulin-like signalling and TOR pathway genes in honey bee caste determination. *Insect Molecular Biology* 23:113–121.

Wheeler G. C., Wheeler J. 1953. The ant larvae of the subfamily Formicinae. *Annals of the Entomological Society of America* 46:126–171.

Wheeler G. C., Wheeler J. 1976. Ant larve: review and synthesis. *Memoirs of the Entomological Society of Washington* 7:1–108.

Wheeler W. M. 1910. *Ants: Their Structure, Development and Behavior.* New York: Columbia University Press.

Wheeler W. M. 1918. A study of some ant larvae, with a consideration of the origin and meaning of the social habit among insects. *Proceedings of the American Philosophical Society* 57:293–343.

Wheeler W. M., Bailey I. W. 1920. The feeding habits of Pseudomyrmine and other ants. *Transactions of the American Philosophical Society* 22:235–279.

Wiernasz D. C., Cole B. J. 2003. Queen size mediates queen survival and colony fitness in harvester ants. *Evolution* 57:2179–2183.

Wiernasz D. C., Yencharis J., Cole B. J. 1995. Size and mating success in males of the western harvester ant, *Pogonomyrmex occidentalis* (Hymenoptera: Formicidae). *Journal of Insect Behavior* 8:523–531.

Wiernasz D. C., Sater A. K., Abell A. J., Cole B. J. 2001. Male size, sperm transfer, and colony fitness in the western harvester ant, *Pogonomyrmex occidentalis. Evolution* 55:324–329.

Wilson E. O. 1953. The origin and evolution of polymorphism in ants. *Quarterly Review of Biology* 28:136–156.

Wilson E. O. 1958. The beginnings of nomadic and group-predatory behavior in the ponerine ants. *Evolution* 12:24–31.

Wilson E. O. 1971. *The Insect Societies.* Cambridge (Massachusetts): Belknap Press of Harvard University Press.

Wilson E. O. 1974. Aversive behavior and competition within colonies of the ant *Leptothorax curvispinosus. Annals of the Entomological Society of America* 67:777–780.

Wilson E. O., Hölldobler B. 1980. Sex differences in cooperative silk-spinning by weaver ant larvae. *Proceedings of the National Academy of Sciences of the United States of America* 77:2343–2347.

Wolf J. I., Seppä P. 2016. Queen size dimorphism in social insects. *Insectes Sociaux* 63:25–38.

Wolschin F., Mutti N. S., Amdam G. V. 2011. Insulin receptor substrate influences female caste development in honeybees. *Biology Letters* 7:112–115.

Wong J. W. Y., Meunier J., Kölliker M. 2013. The evolution of parental care in insects: the roles of ecology, life history and the social environment. *Ecological Entomology* 38:123–137.

Woyke J. 1977. Cannibalism and brood-rearing efficiency in the honeybee. *Journal of Apicultural Research* 16:84–94.

Zube C., Kleineidam C. J., Kirschner S., Neef J., Rössler W. 2008. Organization of the olfactory pathway and odor processing in the antennal lobe of the ant *Camponotus floridanus. Journal of Comparative Neurology* 506:425–441.