CHAPTER SIXTEEN

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Social Life from Solitary Regulatory Networks: A Paradigm for Insect Sociality

ROBERT E. PAGE JR., TIMOTHY A. LINKSVAYER, AND
GRO V. AMDAM

HOW DO COMPLEX social systems evolve? What are the evolutionary and developmental building blocks of division of labor and specialization, the hallmarks of insect societies? In this chapter we describe research into the evolution and development of division of labor in the honeybee *(Apis mellifera).* In solitary insects, shifts during life history between reproductively active and inactive states are associated with widespread changes in physiological state. In honeybees, variation in the physiological state of workers is also associated with variation in behavior. We suggest that worker behavioral specialization and division of labor are based on the modification of regulatory networks underlying shifts in reproductive state.

We begin by describing how studies of the phenotypic and genetic architecture underlying pollen hoarding in honeybees led us to propose a link between worker behavioral specialization and reproductive state. Next we describe how hormonal pleiotropy underlies associations between reproductive state and behavior in solitary insects, and how evolutionary adoption of these pleiotropic regulators is a plausible foundation for honeybee worker behavior. This view is summarized in the reproductive ground plan hypothesis of social evolution, which explains the link between worker behavior and reproductive state. Finally, we broadly consider the evolution of eusociality to elucidate how adoption of ancestral genetic, developmental, and reproductive physiological machineries can be of general importance for emergence of advanced social behavior.

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The Evolution of Division of Labor in Honeybees

Division of labor among worker honeybees is based predominantly on age, with individuals progressing through a series of tasks from in-hive tasks to foraging (Robinson 1992). Further specialization occurs among foragers for pollen or nectar collection. The cumulative efforts of pollen and nectar foragers determine colony pollen and nectar stores. Page and Fondrk (1995) conducted two-way (bidirectional) selection for the amount of surplus pollen stored in the comb (pollen hoarding; see also Hellmich, Kulinceric, and Rothenbuhler 1985). After just three generations, colonies of the high pollen hoarding strain contained about six times more pollen, demonstrating a strong response to selection. With subsequent generations of selection, Page and coworkers studied individual behavioral and physiological traits that changed as a result of selection on the colony-level phenotype. This enabled them to look for mechanisms at different levels of biological organization that causally underlie the differences in the colony-level phenotype (Page and Erber 2002).

One dramatic change that arose was in the age at which bees initiated foraging behavior. High-strain bees (workers from the high pollen hoarding strain) initiate foraging about 10 days earlier in life than low-strain bees (Pankiw and Page 2001). High-strain bees are more likely to specialize on collecting pollen while low-strain bees are more likely to specialize on nectar (Page and Fondrk 1995; Fewell and Page 2000; Pankiw and Page 2001). High-strain bees are also more likely to collect water, and when they collect nectar, they accept nectar with lower sugar content than do bees of the low strain. Low-strain bees are also much more likely to return empty from foraging trips (Page, Erber, and Fondrk 1998).

Differences in forager pollen load sizes between strains arise through their dissimilar responses to pollen foraging stimuli. Fewell and Winston (1992) showed that colonies respond to changes in quantities of stored pollen by altering the allocation of foraging effort to pollen collection. When presented with additional stored pollen beyond what had already been stored, colonies responded with a reduction in the number of pollen foragers and the sizes of the pollen loads. The opposite effect on foraging behavior was observed when stored pollen was removed. Colonies, therefore, maintain the amount of stored pollen around a regulated set point. Studies by Dreller, Page, and Fondrk (1999) and Dreller and Tarpy (2000) demonstrated that foragers directly assess the amount of pollen stored in

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the combs and adjust their foraging behavior accordingly (also see Vaughan and Calderone 2002). The mechanism appears to involve the assessment of empty cells near the areas of the nest where larvae and pupae are located. Therefore, the regulatory mechanism underlying pollen storage involves individual assessment of stored pollen and individual "decisions" with respect to what to collect on a foraging trip (Fewell and Page 2000). High-strain colonies regulate set point centers around much larger quantities of stored pollen than do low-strain colonies. Therefore, high-strain bees have a threshold for stored pollen (or empty cells near the brood) that is different from low-strain bees. When co-fostered in an unselected wild-type colony, high-strain bees perceive the amount of stored pollen as being below their optimal set point while the low-strain bees perceive it as above theirs. As a result, high-strain bees are more likely to forage for pollen and low-strain bees are more likely to forage for nectar.

High- and low-strain bees also respond differently to changes in pollen and brood stimuli in colonies. Young larvae and hexane rinses of young larvae, which extract pheromones, stimulate pollen-specific foraging behavior, while stored pollen acts as an inhibitor (Pankiw, Page, and Fondrk 1998). Pankiw and Page (2001) co-fostered high- and low-strain bees in colonies with high- and low-pollen hoarding stimuli. High stimulus colonies were experimentally manipulated to contain less stored pollen and more larvae than the low stimulus colonies. Foragers in the high stimulus colonies were more likely to collect pollen, collected larger loads of pollen, and, consequently, collected smaller loads of nectar independent of whether they were of the high or low strain. High-strain bees, however, had a larger difference in foraging behavior between treatments, demonstrating a genotype-by-environment interaction, where high-strain bees were more sensitive to the foraging stimulus environment than the low-strain bees.

Such changes in foraging behavior are expected consequences of bidirectional selection on pollen hoarding. However, high-strain bees are also more likely to forage for water than are low-strain bees (Page, Erber, and Fondrk 1998), and when they collect nectar they accept nectar with lower sugar concentrations. There was no obvious physiological or behavioral mechanism to explain these relationships until Page and colleagues looked at the responses of pollen and nectar foragers to sucrose solutions. Bees respond reflexively to antennal stimulation with sucrose by extending the proboscis. Page et al. used a series of solutions with increasing sucrose

concentrations to determine the sucrose responses of wild-type pollen and nectar foragers. The results were surprising: pollen foragers were more likely than nectar foragers to respond to water and lower concentrations of sucrose.

The sucrose sensitivity of pollen and nectar foragers might be related to the physiological status of the bees. Pollen foragers could be comparatively depleted of blood sugars as a result of their foraging activity and, therefore, more responsive. However, sucrose sensitivity might also be a property of the neural states of the animals, which then in turn result in differences in foraging behavior. Thereby, sucrose sensitivity would be an indicator of potential foraging behavior. To distinguish between these two alternative hypotheses, high- and low-strain bees were tested for sucrose sensitivity when they were no more than a week old, before they initiated foraging (Page, Erber, and Fondrk 1998). High-strain bees were more responsive to sucrose solutions and water at this early age, suggesting that selection for pollen hoarding had changed a fundamental property of the sensory-response system with consequences at the level of foraging behavior. Subsequent studies have shown that differences in water and sucrose responses exist between the selected strains at adult emergence, 2 to 3 weeks before the bees initiate foraging (Pankiw and Page 1999).

If water and sucrose responses are indicators of differences in neural states related to nectar and pollen foraging, then it should be possible to also assay wild-type bees when they emerge as adults and predict their foraging behavior 2 to 3 weeks later. Pankiw and Page (2000) tested wild-type bees for their responses to water and sucrose when they were less than a week old. Bees were marked for individual identification, placed back into their colony, and returning foragers were collected and their foraging loads analyzed. Bees that were the most responsive to water and sucrose solutions when they were 5 days old were the most likely to collect water on a foraging trip. The next most responsive group collected pollen, followed by both pollen and nectar, nectar exclusively, and the least responsive group was most likely to return to the nest empty (Figure 16.1). Thus, responses to sucrose and water can be said to be reliable indicators of the neural states of bees and used to predict foraging behavior. This result has been confirmed in additional, independent studies by assaying newly emerged bees (Pankiw 2003; Pankiw et al. 2004).
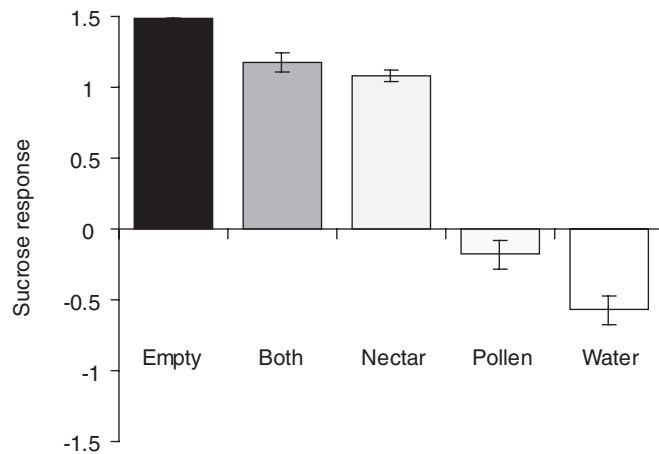
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Figure 16.1. Sucrose responses of 1-week-old bees predict their foraging behavior later in life. The *x*-axis shows the foraging material collected by the bees when they have reached foraging age. The y-axis shows the lowest sucrose concentrations (Log10) at which 1-week-old bees responded with proboscis extension. Bees with the highest sucrose responsiveness (i.e., the lowest threshold) at young age are more likely to later forage for water or pollen. Individuals with low sucrose responsiveness (i.e., a high threshold) are more likely to later collect nectar, nectar and pollen, or to return empty (data from Pankiw and Page 1999).

In general, bees with high responsiveness to sucrose, like the high strain bees and pollen foragers, learn faster and reach a higher asymptote of learning than bees with that are less responsive (Scheiner, Erber, and Page 1999; Scheiner, Page, and Erber 2001a, b, 2004; Scheiner et. al. 2001; Scheiner, Barnert, and Erber 2003. This is because learning performance is related to the evaluation of the sucrose stimuli used during conditioning, which can be measured as a response threshold to sucrose solution (Page, Erber, and Fondrk 1998; Pankiw and Page 2000; Scheiner, Erber, and Page 1999; Scheiner, Page, and Erber, 2001b; Scheiner, Barnert, and Erber 2003; Scheiner and Erber, this volume). In accordance with these findings, high-strain bees and pollen foraging wild-type bees perform better on tactile and olfactory associative learning tests than do low-strain bees and nectar foragers (Scheiner, Erber, and Page 1999; Scheiner, Page, and Erber 2001a, b).

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Responsiveness to sucrose also correlates with locomotor activity when bees first emerge as adults. Humphries, Fondrk, and Page (2005) tested locomotion in newly emerged wild-type bees by measuring their walking activity in an enclosed arena, and then determined their response to sucrose using the proboscis extension response protocols. The more active bees were also more responsive to sucrose. High-strain bees, furthermore, were more active than low-strain bees, consistent with the results from wild-type bees.

Sensory sensitivity and activity levels in response to stimuli associated with food, mating, and oviposition sites change through the reproductive cycle of solitary insects (reviewed by Amdam et al. 2004). Such associations motivated studies on correlations between the reproductive physiology and behavior of worker bees. Worker bees from the high strain group have larger ovaries (more ovarioles per ovary) than do workers from the low-strain group (Amdam et al. 2006). Wild-type workers that forage for pollen likewise have more ovarioles per ovary than do those
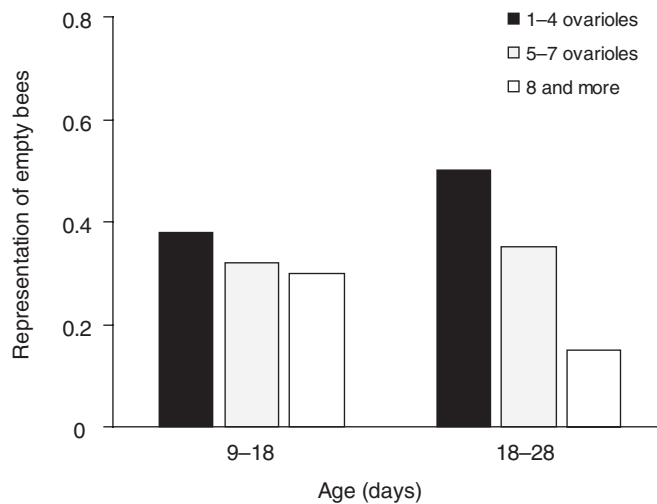

Figure 16.2. The relationship between ovariole number and the probability of returning empty to the nest from presumably the first foraging trip. Bees with the fewest ovarioles are more likely to return empty both in the group of young bees (9–18 days old) and in the group of older workers of more typical foraging age (18–28 days old). The difference is less apparent in the first group, probably because of a higher probability of randomly obtaining empty nonforagers when sampling from a population of workers younger than the typical foraging age of bees.

that collect nectar. Wild-type bees that return empty from foraging trips ("unsuccessful" foragers) have the fewest ovarioles (Figure 16.2), in accordance with abovementioned trait associations of the low-strain workers. Wild-type workers with larger ovaries forage earlier in life than those with smaller ovaries (Amdam et al. 2006). Wild-type workers with more ovarioles are more responsive to low concentration sucrose solutions than those with fewer ovarioles (J. Tsuruda, unpublished data), thus linking the whole suite of traits discussed above with ovary size and, thereby, the full phenotypic syndrome of high-strain bees. Ovariole number is determined during larval development, about 3 to 5 days after hatching. Therefore, events that take place during this period that result in variation in ovariole numbers in workers shape the subsequent behavior of worker honeybees. This is manifested in specialization and division of labor and, in the absence of the queen, oogenesis and oviposition.

Genetic Architecture of Pollen Hoarding

Genetic mapping studies have been used to elucidate the genetic basis of the phenotypic differences between the high and low pollen hoarding strains. These studies revealed four major quantitative trait loci (QTL) that explain a significant amount of the phenotypic variance for pollen hoarding and foraging behavior (Hunt et al. 1995; Page et al. 2006; Rueppell et al. 2004; Rueppell, Pankiw, and Page 2004). The genetic architecture of pollen hoarding and foraging behavior is complex (Figure 16.3). All QTL have pleiotropic effects on multiple traits associated with pollen and nectar foraging, thus providing an explanation for the correlative association of this set of traits. They are also richly epistatic, interacting with one another in complex ways. All individual QTL and most of their interactions affect pollen and nectar load sizes. All individual QTL also affect concentration of nectar collected. The *pln1* region is especially interesting because it has a demonstrated direct effect on all behavioral traits. The combination of these QTL studies and the completed honeybee genome sequence and annotation provide informed candidates for future studies of the genetic basis for variation in pollen hoarding and foraging behavior. A recent analysis proposed that positional candidate genes involved in endocrine signaling provide the most coherent explanation for the syndromes (Hunt et al. 2007).
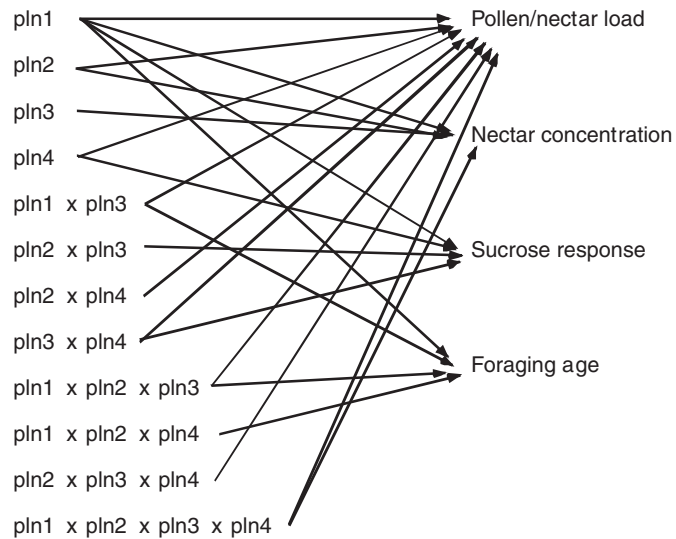
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Figure 16.3. Complex genetic architecture of traits associated with foraging behavioral differences between the high and low pollen-hoarding strains of Page and Fondrk (1995). Arrows indicate significant effects involving the four major Quantitative Trait Loci *(pln1–pln4)*. Interactions between QTL indicate epistasis and effects on multiple traits indicate pleiotropy.

Hormonal Signaling Cascades

The suite of traits that vary with foraging behavior include ovary size, temporal behavioral development, sensory modulation, and motor response systems. The genetic architecture of this set of traits suggests an interactive regulatory network that operates on biological systems at multiple levels of organization in a time scale of days and weeks, thus making hormonal signaling cascades prime causal candidates for modulating the differences between pollen and nectar foragers.

Classical Endocrine Factors

Ecdysone and juvenile hormone (JH) are key hormonal modulators of insect behavior (Hartfelder 2000). Ecdysone is produced by the prothoracic gland during larval and pupal development, and by the ovary during the adult stage. JH is a growth hormone produced by the *corpora allata* of

insects (Hagenguth and Rembold 1978). JH has been hypothesized to play an important role in honeybee division of labor by pacing age-related changes in behavior, especially the transition to foraging (Robinson 1992; Robinson and Vargo 1997). Many studies have demonstrated elevated blood titers of JH in foragers relative to bees that perform tasks in the nest (e.g., Robinson 1987; Huang and Robinson 1992; Huang, Robinson, and Borst 1994; Sullivan, Jassim, et al. 2000; Sullivan, Fahrbach, et al. 2003). Treatment with the JH analog methoprene results in bees initiating foraging behavior earlier in life (for review see Bloch, Sullivan, and Robinson 2002) and increases sucrose responsiveness in young bees (Pankiw and Page 2003), suggesting that JH plays a role in sensory modulation.

Overall, JH correlates with age-based changes in honeybee behavior and sensory sensitivity, but does it pace behavioral development? Sullivan et al. (2000, 2003) removed the *corpora allata* from newly emerged bees. The allatectomized workers initiated foraging at about the same time as the control bees, suggesting no effect on the transition to foraging. In another study, worker honeybees from the high and low pollen hoarding strains initiated foraging at different ages and also differed in JH titer at adult emergence; however, their JH titer was not different 12 days later, just prior to the initiation of foraging (Schulz et al. 2004). Thus, it is clear that JH is not necessary for behavioral development, but that treatments with JH and JH analog nonetheless have behavioral effects.

Endocrine Effects of Vitellogenin

Vitellogenin provides a possible alternative endocrine pathway for the development of pollen foraging. Vitellogenin is a major yolk precursor in many insects (Babin et al. 1999) and is also the most abundant hemolymph protein in worker bees that perform tasks in the nest prior to foraging (Engels and Fahrenhorst 1974; Fluri, Sabatini, et al. 1981; Fluri, Lüscher, 1982). Recent studies have shown that vitellogenin gene activity suppresses the JH titer of worker bees (Guidugli et al. 2005). Conversely, JH is known to suppress the synthesis of honeybee vitellogenin at onset of foraging (Pinto, Bitondi, and Simões 2000). These data suggest that the two proteins are linked in a positive feedback loop via a mutual ability to suppress each other. Amdam and Omholt (2003) hypothesized that foraging behavior is initiated when vitellogenin titer drops below a certain threshold level. The feedback action of JH on vitellogenin could be a reinforcing

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mechanism that causes workers to become behaviorally and physiologically locked into the forager stage.

In support of Amdam and Omholt's hypothesis, Nelson et al (2007) found that reduction of vitellogenin gene activity by RNA interference (RNAi) caused bees to forage earlier in life. Amdam et al. (2006) demonstrated that vitellogenin RNAi increases the sucrose responsiveness of worker bees, and suggested that honeybee vitellogenin modulated behavior and sensory sensitivity via a signaling pathway that includes JH as a downstream feedback element.

Honeybee vitellogenin is produced by the abdominal fat body, but evidence suggests that this protein triggers responses in other cell types (Guidugli et al. 2005), implying that vitellogenin itself can be classified as a hormone. The documented effects of JH and JH analog treatments, therefore, can be understood as results of suppressed vitellogenin action (Amdam et al. 2006).

Reproductive Ground Plan—A Synthesis

Associations between foraging behavior and traits such as vitellogenin level, ovary size, and rates of behavioral development suggest that division of labor and particularly foraging specialization in honeybees are derived from the reproductive regulatory networks of solitary ancestors. Amdam et al. (2004) proposed that the suite of traits associated with foraging behavior and their underlying genetic architecture were part of a reproductive regulatory network (see also West-Eberhard 1987b, 1996). In solitary insects, different stages of the female reproductive cycle (previtellogenesis, vitellogenesis, oviposition, and brood care) are linked and involve coupled physiological and behavioral changes (Finch and Rose 1995). JH and ecdysone are key hormones controlling vitellogenesis in many insect species (e.g., Socha et al. 1991; Hiremath and Jones 1992; Brownes 1994); in addition, they regulate behavioral transitions associated with changes in reproductive state, such as the shift from foraging for nectar in previtellogenic females to protein foraging in vitellogenic individuals, as occurs in the mosquito *Culex nigripalpus* (Hancock and Foster 2000). JH and ecdysone also modulate changes in sensory perception, locomotor activity, and reproductive physiology (Zera and Bottsford 2001)—traits that have been shown to be different in workers from the high and low pollen hoarding strains and in wild-type pollen and nectar foragers.

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In solitary insects, hormonal effects on reproductive traits typically act in mature adults following a pre-reproductive phase where the animals may enter diapause or aestivate and disperse (Hartfelder 2000). In honeybees, however, these hormonal signals seem to have shifted in time (Amdam et al. 2004), occurring in the late pupal stages where they activate the production of vitellogenin (Barchuk, Bitondi, and Simões 2002). Differential amplitude of JH titers are observed in newly emerged high and low pollen hoarding bees where high-strain workers have higher titers of JH (Schulz et al. 2004). This elevated titer correlates with a higher level of vitellogenin mRNA and a higher vitellogenin hormone titer in the blood (Amdam et al. 2004). Compared to the low-strain bees, workers of the high pollen hoarding strain have more ovarioles, which already show an active previtellogenic ovarian phenotype at adult emergence (Amdam et al. 2006). It has been proposed that if such documented markers of JH and
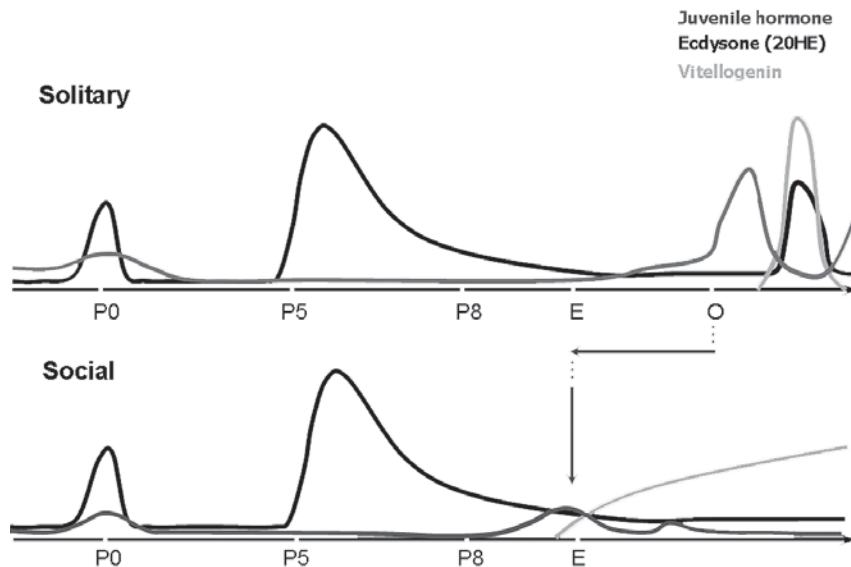

Figure 16.4 A time course of blood hormones and vitellogenin titers from early to late pupal stages (P0–P8) through emergence (E) and into mature adults with activated ovaries (O) in solitary insects (upper panel), compared to honey bee development (lower panel) (from Pinto et al. 2002; Barchuk et al. 2002). Amdam et al. (2004) hypothesized that the spikes of hormone titers linked to O in solitary insects has shifted in time in social insects and is homologous with the increases in titer observed at E in honey bee workers.

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ecdysone action are present early in honeybee adult life (Figure 16.4), then pleiotropic effects on behavior may have shifted from later life-stages as well (Amdam et al. 2004), as demonstrated by the differences in sensory responses and locomotor activity of high- and low-strain bees and the correlation of locomotor and sensory responses in wild-type workers.

The recent finding that ovariole number correlates with sensory responsiveness in wild-type bees (J. Tsuruda, unpublished data), and the known association between such sensory responses and foraging behavior 2 to 3 weeks later, suggest that gonotropic events in young bees have persistent effects on adult behavior. High-strain bees and pollen foragers seem to be similar to ancestral gono-active females, while low-strain bees and nectar foragers are like gono-inactive females. These insights have been summarized in the "reproductive ground plan" hypothesis of social evolution (West-Eberhard 1987b, 1996; Amdam et al. 2004). The hypothesis proposes that the genetic and hormonal networks that govern reproductive development, physiology, and behavior in solitary species represent a fundamental regulatory system with the capacity to serve as the basis for the evolution of social phenotypes. We discuss next how evolutionary modification of pre-existing developmental, endocrine, and behavioral building blocks can lead to the evolutionary origin and elaborate on the two traits fundamental to eusociality: sib-care and queen-worker caste dimorphism.

Evolution of Eusociality

Origin of Eusociality

It is commonly accepted that sib-care behavior expressed by helper females toward the sibling brood is homologous with and evolutionarily derived from maternal care behavior expressed toward offspring (West-Eberhard 1987a; Alexander, Noonan and Crespi 1991). In the heterochrony model for the origin of eusociality, sib-care behavior expressed in helpers is the result of the modified, early expression of genes for maternal care (Linksvayer and Wade 2005). In the ancestral condition, maternal care behavior is expressed as one of the final steps in a coordinated series of physiological and behavioral changes that occur through reproductive development (West-Eberhard 1996). In the derived condition, the timing of expression of maternal care behavior is altered so that this behavior is expressed pre-reproductively toward siblings instead of post-reproductively toward

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offspring. Under this model, the evolution of the capacity for females to provide care pre-reproductively toward their siblings is a first step in the evolutionary origin of eusociality from subsociality (Linksvayer and Wade 2005). The next step involves the regulation of the timing of expression of genes for maternal care behavior so that eusocial colonies produce both helper females and fully-reproductive females.

As discussed above, in both queen and worker honeybees there is a shift in the timing of hormonal signals involved in activating ovaries relative to solitary insects, from post- to pre-emergence (Amdam et al. 2004). Because behavior and gonotropic cycle are linked, this shift may be related to the heterochronous shift in behavior hypothesized for the origin of sib-care. That is, the evolution of the capacity of females to provide care pre-reproductively may be associated with a shift in the timing of hormonal signals in all females (i.e., both reproductive "queen" phenotypes and helper "worker" phenotypes) so that the hormonal shift observed in highly social honeybees may be the result of ancient evolutionary events. Early ovary activation and vitellogenesis may also increase the reproductive potential of young queens and provide young worker bees with a source of protein that can be converted into larval food (Amdam et al. 2003, 2004). Thus, timing of hormonal signals and the physiological and behavioral responses observed in highly social honeybees may be the result of evolutionary modification associated both with the origin of eusociality as well as more recent evolutionary elaboration associated with increased colony size and social complexity. Comparative studies using other eusocial, as well as subsocial, aculeate Hymenoptera will elucidate these hypotheses.

Elaboration of Eusociality

After the origin of eusociality, among-colony selection would likely favor the evolutionary divergence of helper and reproductive phenotypes, if the result was a more efficient division of labor. However, this divergence is initially constrained because of their common genetic basis; maternal care and sib-care are, theoretically, influenced by the same set of genes, so the two traits cannot evolve independently (Linksvayer and Wade 2005). Therefore, evolutionary modification of the genetic basis of maternal and sib-care through gene duplication (Gadagkar 1997), or more simply caste-specific gene expression, can enable these phenotypes to diverge. Yet,

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even in highly social taxa such as honeybees, many genes have pleiotropic effects on queen and worker phenotypes, which is expected given that these phenotypes are derived from common genetic, physiological, and behavioral building blocks (West-Eberhard 1996; Amdam et al. 2004, 2006; Linksvayer and Wade 2005).

Polyphenisms such as reproductive caste in social insects are thought to be derived from phenotypically plastic traits, using preexisting physiological and endocrine developmental mechanisms (Nijhout 2003). The evolution of discrete castes involves the elaboration and conversion of preexisting phenotypic plasticity to phenotypic differences between castes. This occurs in part through the evolutionary modification of endocrine and developmental mechanisms that are sensitive to environmental conditions (Wheeler 1986; West-Eberhard 1987a, 1996). Just as the timing of expression of maternal care behavior is affected by both intrinsic and extrinsic factors, so are traits associated with reproductive caste such as ovary size and body size. Larval genes affect developmental responses to environmental conditions (such as nutritional quality and quantity). For example, the sensitivity of the developmental switch of caste determination is influenced by genes affecting the endocrine response to nutritional signals (Wheeler 1986). Additionally, the environmental conditions of developing larvae are determined by the social milieu of the colony provided by nestmates, and this social environment is influenced by genes expressed in sibling brood, sibling helpers, and the queen (Linksvayer and Wade 2005; Linksvayer 2006). The evolution of distinct developmentally canalized queen and worker phenotypes then involves evolutionary fine-tuning of both the social environment and the developmental response.

In subsocial animals with extended maternal care, the evolution of maternal and brood phenotypes has been considered as a co-evolutionary process (Wolf and Brodie 1998; Agrawal, Brodie, and Brown 2001; Kölliker, Brodie, and Moore 2005). After the origin of eusociality, a third class of social partners, adult helper females, is added, so that social insect phenotypes are influenced by the genomes of three types of interacting social partners: brood, workers, and queens. The evolution of phenotypes in eusocial colonies (e.g., those associated with reproductive caste) can be considered as the co-evolution of queen, worker, and brood phenotypes (Linksvayer and Wade 2005; Linksvayer 2006).

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Conclusion

We suggest here that complex social behavior as found in eusocial insects is derived from reproductive regulatory networks common to all insects. Small changes in the timing of expression of maternal care behavior may be all that is needed to form reproductive and nonreproductive phenotypes, the basis of eusociality. Additional evolutionary fine-tuning of hormonal networks regulating development, reproduction, and maternal care, and tuning of the developmental environment through modification of the behavior of social partners, may produce the amazingly diverse and complex insect societies that we continue to admire.

Acknowledgments

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