



DECONSTRUCTING THE SUPERORGANISM: SOCIAL PHYSIOLOGY, GROUNDPLANS, AND SOCIOGENOMICS

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ABSTRACT

Our understanding of insect societies is rapidly expanding due to an emphasis on integrative approaches. Emerging tools enabling the molecular dissection of social behavior, together with novel hypotheses for the evolution of eusociality, are emblematic of this progress. However, an obstacle to a truly integrative approach remains, as social physiology—the basis of group-level coordination—has generally been neglected by geneticists. In this paper, we begin a synthesis of these fields by first reviewing three classes of social insect organization that mark major transitions in increasing social complexity. We then develop an expansion of the superorganism concept in order to place eusociality into a broad evolutionary context, and we also interpret current molecular and genetic work on the evolution of eusociality. The groundplan hypothesis proposes that eusociality arose via simple changes in the regulation of ancestral gene sets affecting reproductive physiology and behavior, and we argue that this hypothesis is explanatory for the evolution of division of labor (social anatomy) but not for the regulatory systems that ensure group-level coordination of action (social physiology), which we propose is dependent on previously unrelated traits that are brought together into novel genetic networks. We conclude with a review of recent work in sociogenomics that supports our hypotheses.

INSECT SOCIETIES are often described well into the millions and are characterized by as the pinnacles of social evolution. The elaborate systems of morphological and most complex insect societies have colony sizes physiological division of labor (reviewed in

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Hölldobler and Wilson 1990; Seeley 1995). Dense networks of communication overlay this division of labor to ensure that societies act with a unity of purpose (Seeley 1995). Such organizational sophistication is thought to be the basis for the great ecological success of these groups, which can account for the majority of animal biomass in some habitats (Wilson 1987; Wilson and Hölldobler 2005). Moreover, the evolution of these societies has long been of special interest to evolutionary biologists, as they represent the most elaborate cases of reproductive altruism (Hamilton 1964; Trivers and Hare 1976).

Social insects have the potential to be exceptional models for integrative biology as they are the focus of intensive study at a range of levels, from the molecular to the behavioral (Calderone 1993; Seeley 1995; Page et al. 2000; Tautz et al. 2001; Chittka 2004; Robinson et al. 2005; Franks and Richardson 2006; Gotzek and Ross 2007; Le Conte and Hefetz 2008). Advances in genomics, in particular, have recently led to major progress in decoding the genetic and molecular bases of social behavior (Robinson et al. 2005; Fitzpatrick et al. 2005; Grozinger et al. 2003, 2007; Whitfield et al. 2003, 2006; Hummon et al. 2006; Wheeler et al. 2006). Furthermore, novel “groundplan” hypotheses, which propose that the evolution of sociality occurs by the simple modification of conserved gene networks that underlie reproductive physiology and behavior, are increasingly supported (West-Eberhard 1996; Linksvayer and Wade 2005; Amdam et al. 2004, 2006; Hunt et al. 2007). Concurrent with these advances at the molecular level, our understanding of insect societies at the behavioral and physiological levels has also grown in recent years (Seeley 1989, 1995, 1998; Jeanne 1999; Dornhaus and Chittka 1999; Franks et al. 2002; O’Donnell 1998, 2001; Fewell 2003; Couzin and Franks 2003; Pratt and Sumpter 2006; Slessor et al. 2005). The concept of self-organization, for example, has created unprecedented interest in distributive processes (Deneubourg and Goss 1989; Franks et al. 2002; Camazine et al. 2001) and has greatly increased our understanding of group-level decision mak-

ing and task allocation (Franks et al. 2002; Seeley et al. 2006; Pratt and Sumpter 2006).

Research across so many fields of biology should allow for a deeply integrative approach to the study of insect societies, but this has yet to occur. Researchers studying the proximate basis of division of labor, social physiology, and collective decision making at the organismal level, and researchers studying the molecular and genetic bases of the same phenomena, have largely moved along independent trajectories. Here we present a synthesis of these fields. First, we present a brief synopsis of the key results of the organismal (purely behavioral) approaches. We then use this synopsis as background material for interpreting the genetic basis of both division of labor and social physiology. In general, our goal is to encourage those researchers working at the molecular level to pay greater attention to social physiology, as its genetic basis may be considerably more complex than current models acknowledge. Although research on the genetic basis of conflict within societies—especially the search for anarchy genes—is important and complementary to our discussion (Crozier and Pamilo 1996; Queller and Strassman 1998; Oldroyd and Osborne 1999; Thompson et al. 2006), it exceeds the parameters of our article; therefore, we leave this topic for future work and focus on those adaptations that evolved in the context of cooperation and honest signaling. We begin by briefly reviewing the range of social organization found in social insects, highlighting important innovations associated with evolutionary transitions to increasingly complex societies. Next, we describe social physiology—the mechanisms by which colonies achieve unity of purpose, and a branch of social biology that has heretofore been largely overlooked in recent discussions about the evolution and proximate basis of eusociality. We then describe the reproductive groundplan paradigm, highlighting its strengths and limitations for explaining the evolutionary elaboration of sociality. We review sociogenomics, arguing that the evolution of the complex communication systems (social physiology) associated with advanced eusociality may have proceeded

via the evolution of novel genetic networks. Finally, we review recent sociogenomic studies on honeybees and fire ants that support many of our hypotheses.

THE MAJOR ORGANIZATIONAL PATTERNS AND TRANSITIONS

Traditionally, social insects are put into three groups based on social complexity: incipiently eusocial, primitively eusocial, and advanced eusocial (Michener 1969, 1974; Wilson 1971). Incipiently eusocial species are characterized by a colony size of two to six individuals, in which one individual is an egg layer and the others are foragers. All individuals are totipotent, in that each can act as a solitary insect (reviewed in Michener 1974; Wcislo and Danforth 1997; Neville et al. 1998; Schwarz et al. 2007). Primitively eusocial species have colony sizes of several hundred at maturity and are composed of two distinct behavioral castes: queens and workers (Bourke 1999; Hunt 2007). Dominance hierarchies are common in these societies, along with derived forms of chemical and acoustic signaling (O'Donnell 2001; Dornhaus and Chittka 1999, 2001; Le Conte and Hefetz 2007; Molet et al. 2008). Workers are flexible and can usually perform any task (other than reproduction) at a given time (reviewed in Michener 1974 and Jeanne 1999). Finally, advanced eusocial species have colony sizes ranging from the thousands to the millions, and are characterized by both morphologically distinct queen and worker castes and often by temporal and physical castes among the workers (reviewed in Hölldobler and Wilson 1990; Bourke and Franks 1995; Seeley 1995; Bourke 1999). As Jeanne (1986, 1996, 1999) has shown, the organization of work in advanced eusocial societies is fundamentally distinct from that in smaller primitively eusocial societies, as per capita work output is nonlinear in large societies rather than linear as in small societies. The transition to nonlinear work output is brought about by the benefits of specialization and complex organization, which are beyond the capacity of most primitively eusocial societies as they require a large colony size (see Figure 1). For simplicity, we will refer to the organizational principles illustrated

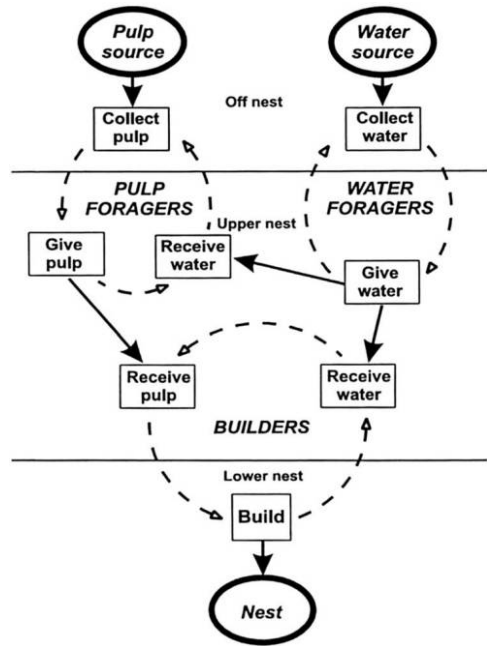


FIGURE 1. ASSEMBLY LINE DYNAMICS IN *POLYBIA OCCIDENTALIS*, A SWARM-FOUNDING PAPER WASP

Wasps specialize in one of three tasks: building, water collecting, or pulp collecting (Jeanne 1986b, 1996, 1999). Each task is a subroutine of the larger task of building. Each worker requires the help of those involved in the other tasks to complete its subroutine. A builder must receive pulp and water to make building materials, pulp receivers must receive water and pass on their pulp to builders, and water receivers must unload their water. Therefore, a time delay in the production of work in any subroutine slows down the entire process. The simplest way to prevent time delays is to have a sufficiently large work force, such that queuing delays are minimized by mass action. Jeanne (1999) found that it requires at least 50 workers for this system to function effectively. In other words, at least 50 workers are required for the benefits of specialization to outweigh the costs of queuing delays (each worker is better able to do its task when it does not also have to do the others). Fifty workers are not many for a permanently large society like *Polybia*, but, for *Polistes*, it can be more than half the work force—an untenable situation given that building is a small portion of the total work to be done. Assembly line dynamics thus require a large colony size and represent a novel organizational structure not possible in the ancestral context of small colony size. (Figure reproduced from Jeanne 1999, with permission from Birkhauser.)

in Figure 1 as “assembly line dynamics.” Dominance hierarchies are rare or absent altogether in advanced societies, and workers, even in temporal castes, have a limited ability to perform tasks outside their caste-specific task repertoire (Huang and Robinson 1992; Robinson 2002; Johnson 2003, 2005, 2008; Wegener et al. 2009). Finally, communication is pervasive in advanced eusocial colonies, with large numbers of pheromonal and acoustical signals providing the basis for task allocation (Wilson and Hölldobler 1988; Hölldobler 1995; Tschinkel 1998; Seeley 1995; Pankiw 2004).

Although there is a considerable overlap or grey area in organization among the three traditional categories of social insects, there are also clear adaptations that differentiate them from one another (Figure 2). The first is the transition from a solitary lifestyle to incipient eusociality and alternative reproductive strategies (Sherman et al. 1995). This transition led to division of labor, but not to extensive communication in relation to task allocation, perhaps because colony size is very small and selection is still primarily at the individual level. Therefore, it required the evolution of behavioral or physiological switches that allow individuals to transition between reproductive and nonreproductive behavioral states (Gadagkar 1997; West-Eberhard 2002). The second transition, to a primitively eusocial society, is characterized by the evolution of division of labor complex enough to require extensive signaling to ensure group-level coordination of action. Although primitively eusocial societies are relatively simple in organization, the individual insects that comprise them can exhibit complex communication mechanisms that are absent in more advanced societies (Tibbetts 2002; Franks and Richardson 2006). This is perhaps because task allocation in these species depends in part on independent decision making processes rather than extensive task partitioning (reviewed in Jeanne 1999). These societies thus resemble more a sports team made up of slightly different individuals. For this reason, we will refer to such societies as “team-like” (our use of the term “team” is not related to previous usage of the term by Anderson and Franks 2001). Func-

tionally, team-like societies meet the challenges of an unpredictable environment with flexible workers and, to a lesser extent, with sophisticated organization. It is likely that both individual-level and group-level selection shape team-like societies. The final transition to the advanced eusocial stage is associated with the evolution of assembly line dynamics dependent on large colony size. In advanced insect societies, selection is primarily at the group level and most problem solving is collective in nature (Franks 1989; Deneubourg and Goss 1989; Seeley 1995; Gordon 1996; Fewell 2003). Complex wasp and bee societies are composed of monomorphic individuals arranged into elaborate assembly lines reminiscent of factories (reviewed in Seeley 1995; Jeanne 1999; Anderson and Ratnieks 1999a,b). The most complex ant societies, in contrast, are arranged around a permanent division of labor based on morphologically specialized workers (reviewed in Oster and Wilson 1978). This evokes a system analogous to a complex machine with dissimilar parts. For these reasons, we will refer to these groups as either factory-like (monomorphic workers) or machine-like (physical castes). It is only through dense webs of communication within and between functionally discrete groups that colonies of both types are able to function as a cohesive whole (Wilson and Hölldobler 1988; Seeley 1995). Factory- or machine-like societies meet the challenges of an unpredictable environment with sophisticated organization and communication, and, only to a lesser extent, with flexible workers.

SOCIAL PHYSIOLOGY

Social physiology refers to the communication systems, dependent on cues and signals, that facilitate the coordination of group-level activity (Wilson and Hölldobler 1988; Seeley 1995; Pankiw 2004). A cue is any aspect of the environment, biological or otherwise, that provides reliable information, but that has not been shaped by natural selection for that purpose (Bradbury and Vehrencamp 1998; Seeley 1998). Typically, cues are unintentional byproducts of the activities of other organisms or information-

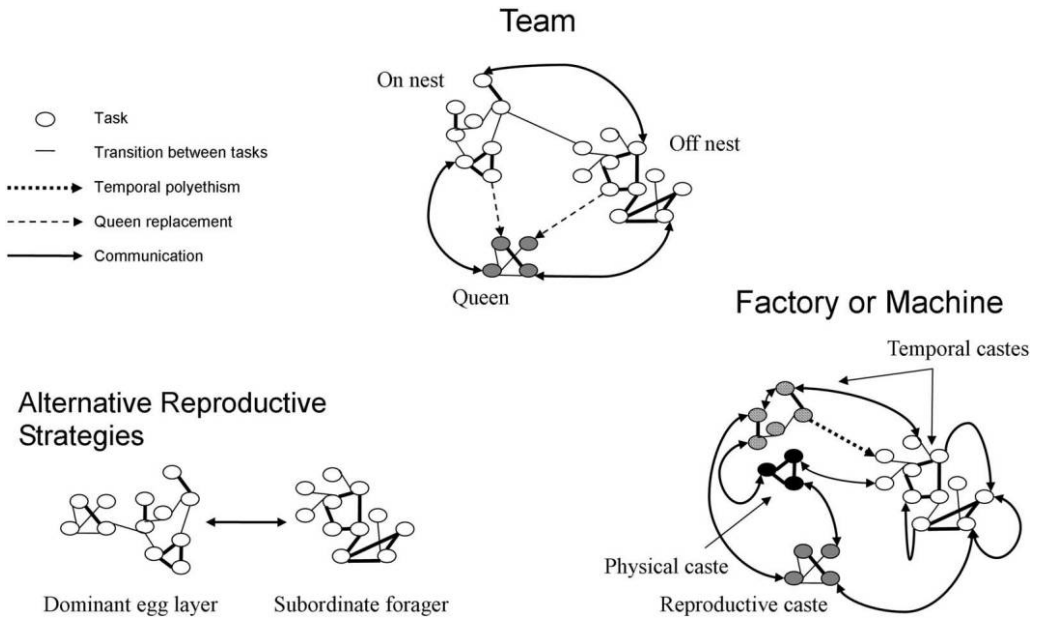


FIGURE 2. ORGANIZATION OF WORK AMONG SOCIAL INSECTS

Colony-level ethograms showing patterns of organization of work among social insects. As in classic ethograms, the nodes represent tasks, and the links between them represent switching from one task to another. The thickness of the links indicates the likelihood of switching. Different shading or color coding of tasks indicates that physiological or morphological specialization underlies task performance. This figure (and the others like it) thus represent patterns of task switching and degrees of totipotency. (Left) Individuals in incipiently eusocial species have two alternative reproductive strategies: they can found their own nest, or stay with their mother (dominant) and become a helper (subordinate). If they become a subordinate, they engage in tasks other than reproduction. Dominants typically refrain from working outside the nest and focus on reproduction and guarding the nest. Subordinates are often mated and can quickly switch between the two states. (Top) The organization of a team-like society (primitive eusociality). Hundreds of individuals within a mature colony work in parallel, with division of labor between the queen and workers. Work output from activities on and off the nest have the potential to become out of sync. To prevent this, colonies have evolved communicative abilities such that the output from each task set provides feedback to the others. Functionally, the team meets the challenges of an unpredictable environment primarily with flexible workers and, to a lesser extent, with sophisticated organization. (Right) Organization of a factory- or machine-like society. Many thousands to millions of individuals work in parallel, and workers are members of either a distinct physical or temporal caste. Scores of cues and signals maintain colony-level coordination. In addition, assembly line dynamics—either within or between castes—require advanced communication. Factories and machines largely meet the challenges of an unpredictable environment with sophisticated organization and communication and, only to a lesser extent, with flexible workers.

rich features of the environment, such as the position of the sun. A worker, for example, may smell like the flower she just left, allowing the other bees in the nest who encounter her to know that said flower type is producing nectar (Seeley 1995). In general, anything that provides accurate information could be a useful cue. Thus, any sensory modality might be involved in the information gathering phase of any social behavior.

A signal has both a message intended by the sender and a meaning interpreted by the receiver (Bradbury and Vehrencamp 1998). Signals are essentially cues that have been shaped by natural selection. In cases of honest communication, both the sender's mechanism of producing the signal and the receiver's ability to receive it have been altered by natural selection in order to increase the signal's information content and the reliabil-

ity of reception. In bumblebees, for example, returning workers conduct a buzzing run through the nest, which communicates to the other bees that food is available in the field (Dornhaus and Chittka 1999, 2001). The ancestral cue may have been a higher rate of movement and agitation in successful versus unsuccessful foragers after a dearth of nectar in the field, with a higher probability of commencing foraging after being jostled. Selection likely worked on variation in cue production and reception to increase the length of time a worker spends buzzing (such that it communicates to the entire nest) and the probability that a jostled bee will commence foraging. Most social insect signals are chemical in nature, but substrate vibration signals are also quite pervasive (Hölldobler and Wilson 1990; Seeley 1995; Le Conte and Hefetz 2008).

Although the fixed genetic attributes of workers can affect their probability of task performance leading to division of labor (Calderone and Page 1988; Robinson and Page 1988; Calderone et al. 1989; Oldroyd et al. 1993; Pankiw and Page 2000; Fewell and Page 2000; Jeanson and Fewell 2008), social physiology is fundamental to colony-level task allocation, because societies require mechanisms that rapidly alter a worker's probability of task performance (response thresholds) in accordance with critical changes in the environment and the colony demography (Huang and Robinson 1992; Seeley 1995; Gordon 1996; Chittka and Müller 2009). As the honeybee has been the subject of the most research with regard to this topic, we will focus on one of its social physiology processes. Figure 3 shows a simplified diagram of the regulation of nectar collection (reviewed in Seeley 1995). There are several coordination problems that must be simultaneously addressed at the colony level: (1) how much labor to devote to the four types of foraging (nectar, pollen, water, and propolis), (2) how to best allocate the foragers to the different locations in the field where these commodities are available, and (3) how to ensure that the proper ratio of foraging, to nectar receiving, to comb building is maintained. A review of one of these

coordination problems (Problem 3) will be sufficient to illustrate the basic principles.

Nectar collection and storage is distributed between two castes (Seeley 1992; Seeley and Tovey 1994). Foragers collect nectar in the field and transfer it to the middle-aged bees near the nest entrance. The middle-aged bees then process the nectar into honey and store it at the top of nest. Middle-aged bees also pace their comb-building activities such that they do not run out of storage space (Pratt 1999). Tight coordination between the two castes is vital, and a mismatch between the efforts of the two groups will lead to a disruption of nectar collection (Seeley 1992; Seeley and Tovey 1994; Anderson and Ratnieks 1999a,b). Coordination is the result of information acquisition via cues perceived on the dance floor and in the field by foragers, and by signals sent by the foragers to the middle-aged bees. The shaking or vibration signal is a message sent by the foragers to all the bees within the nest (Nieh 1998; Schneider et al. 2001). It increases the activity rate of recipients (Lewis et al. 2002; Schneider and Lewis 2004) and is produced at a rate proportional to the total amount of foraging. Essentially, it provides a mechanism for activating foragers in the morning and for informing middle-aged bees of forager activity rates throughout the day. The communication of activity rate via this mechanism works well to ensure coordination between foragers and middle-aged bees if no strong change in nectar availability occurs, but it can fail if the amount of nectar coming into the nest suddenly increases (reviewed in Seeley 1995). In such cases, which are common in nature, the middle-aged bees must rapidly increase nectar processing. The mechanism used to accomplish this brings together cues and signals in the following manner: nectar foragers use the time it takes them to find a nectar receiver as a measure of the current match between incoming nectar and the current processing capabilities of the colony (i.e., number of receivers). Short times indicate a good match, while long times indicate too many foragers and not enough receivers (Seeley and Tovey 1994; Ratnieks and Anderson 1999). After experiencing long wait times, foragers stop foraging, shut down recruitment of more foragers, which would only make the mismatch worse, and sig-

Social Physiology of Nectar Collection in *Apis mellifera*

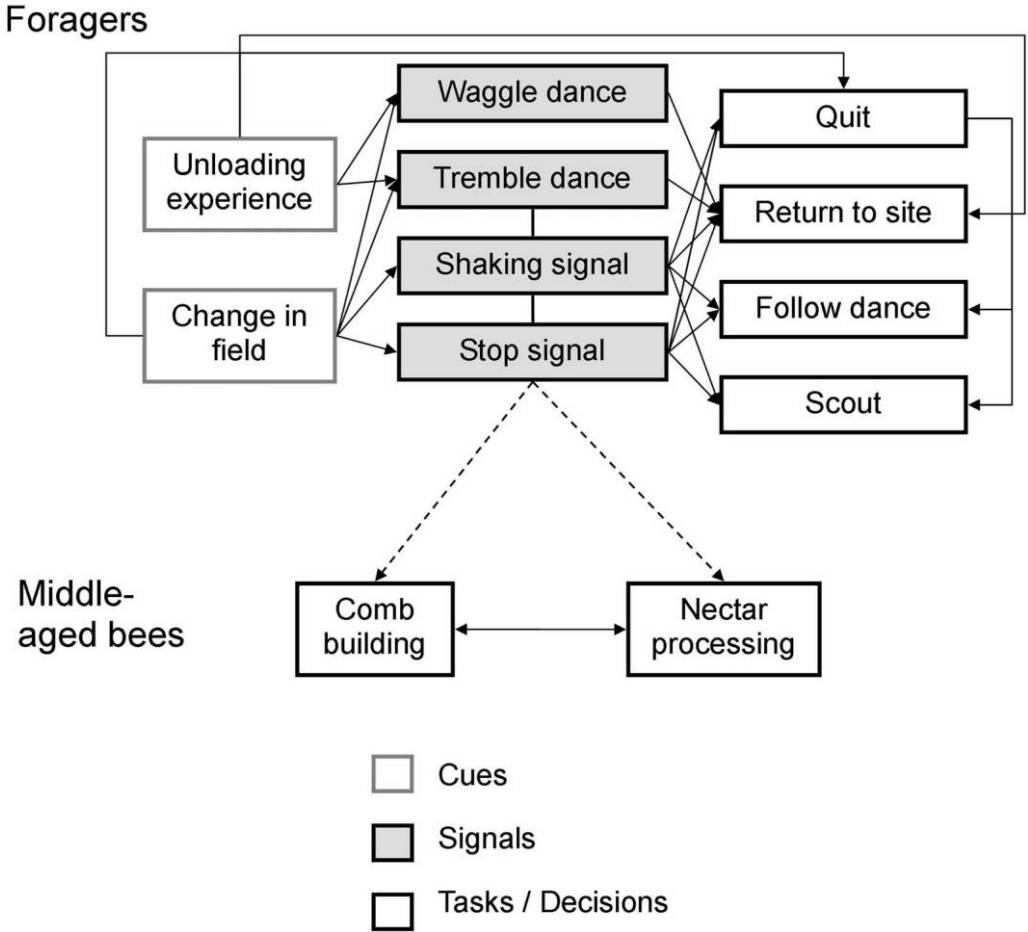


FIGURE 3. FLOW DIAGRAM OF THE SOCIAL PHYSIOLOGY OF NECTAR COLLECTION IN *APIS MELLIFERA*

Example of a complex social physiology process in a factory-like society. Honey production is partitioned between two castes of bees—the foragers, who collect nectar, and the middle-aged bees, who build comb and process nectar into honey. Disruption of the work output in either group disrupts the whole process because foragers cannot unload nectar if there are insufficient receivers or if there is no storage space in the nest. This figure illustrates how cues and signals are used by foragers to coordinate the decision making of both groups of bees. Lines from boxes relating to forager behavior indicate steps in the decision making process (i.e., information collection via cues and information transmission or reception via signals) or task decisions (boxes on the right). Lines from the foragers to the middle-aged bee task boxes indicate the transfer of information via signals that modulate middle-aged bee behavior. Foragers determine the current state of the colony based on cues they perceive on the dance floor and signals they receive from other bees while there. They then integrate this information with the cue-based information that they collected in the field to make a decision to either continue foraging or produce one of four signals used to modulate the activities of the other foragers and middle-aged bees. Signals that are sent to the middle-aged bees are noted in the grey shaded boxes and are connected with vertical lines. These include the shaking signal, which modulates activity rate; the tremble dance, which informs the middle-aged bees that more nectar receiving is necessary; and the stop signal, the meaning of which is still unknown for middle-aged bees. Signals to other foragers include the waggle dance, which recruits more foragers to a particular food source, and the stop signal, which causes recipient foragers to stop waggle dancing. (For a more detailed discussion, see Seeley 1995 and Devries & Biesmeijer 1998).

nal to the middle-aged bees that more receivers are necessary. The two signals used in this situation are the tremble dance, which informs middle-aged bees to act as receivers (Seeley 1992; Seeley and Tovey 1994), and the stop signal, which shuts down waggle dancing (i.e., the forager recruitment signal) (Nieh 1993). Once middle-aged bees have increased their rate of nectar receiving, wait times decrease and foragers again begin to produce waggle dances to advertise food sources. Many aspects of this process (not covered here) are still poorly understood, but the work to-date illustrates the complexity of social physiology in advanced eusocial species.

EXPANDED SUPERORGANISM CONCEPT

In this final section on organismal approaches to the evolution and elaboration of eusociality, we expand on the superorganism concept in order to illustrate the fundamental similarity of the organizational problems facing insect societies and multicellular organisms (Wilson 1971, 1985; Seeley 1989b; Seeley 1997; Moritz and Fuchs 1998; Hölldobler and Wilson 2008). In both cases, what were once solitary organisms are joined together into one cohesive whole (Bell and Mooers 1997; Smith and Szathmari 1997; Bonner 2001). This is accomplished first by specializing individuals—cells or organisms—for limited roles, and, second, by developing the group-level coordinating mechanisms necessary to achieve a unified behavior from the specialized units (Figure 4). In multicellular organisms, specialization is achieved via a complex developmental process underlying the construction of anatomy. Coordinating mechanisms, termed “physiology,” take the forms of the endocrine and nervous systems. In social insects, specialization, in its most derived state, takes the form of castes and the complex developmental processes by which they are created, which we now term “social anatomy,” while coordination takes the form of what Seeley (1995) has already termed “social physiology.” Coordination problems are the same for the two groups, but with logistical differences. In the case of multicellular organisms, all the units are physically joined. In this context, when a message needs to be conveyed to the whole collective, the signal—a hormone, for example—can be released into the blood-

stream and quickly sent everywhere. Likewise, when a faster and more directed signal needs to be sent, it can be accomplished by physical connections between specialized cells (neurons). For the social insect colony, which is composed of disconnected units, the problem is the same, but the solution is modified to fit the situation. For general messages, a pheromone with a high volatility is often used. For messages that need more precise transmission, mechanical signals in which one worker grabs another or produces a complex acoustic signal are typically used (reviewed in Seeley 1995, 1998). In both cases, the function is the same as for the endocrine or nervous system: a general message is sent broadly to the collective, or a more information rich and faster signal is sent to particular members. Thus, we have the elucidation of a social anatomy and physiology. These basic superorganism concepts apply to team-like, factory-like, and machine-like societies. The only differences have to do with the sophistication of the relevant social anatomy and physiology.

GROUNDPLAN HYPOTHESES: EUSOCIAL EVOLUTION VIA SIMPLE MODIFICATION OF ANCESTRAL GENETIC NETWORKS

Solitary insects transition and sometimes cycle between life history phases associated with foraging and reproduction. Transitions between these phases are thought to be mediated by changes in hormonal titers that are associated with changes in the expression of multiple sets of pleiotropically-linked genes (reviewed in West-Eberhard 1996; Hunt 2007). West-Eberhard (1987, 1996, 2003) proposed that changes to this “groundplan” could account for many aspects of eusocial evolution (see also Michener and Brothers 1974; Charnov 1978; Gadagkar 1997). In particular, she proposed that the evolutionary dissociation of the full solitary hymenopteran task repertoire into distinct reproductive (i.e., queen) and foraging (i.e., worker) components in eusocial lineages could arise via simple modification of ancient behavioral regulatory processes. Linksvayer and Wade (2005) proposed that changes in the timing of expression of maternal care genes from post- to pre-reproduction underlie the origin of sib-care behaviors—a first step in the evolution of

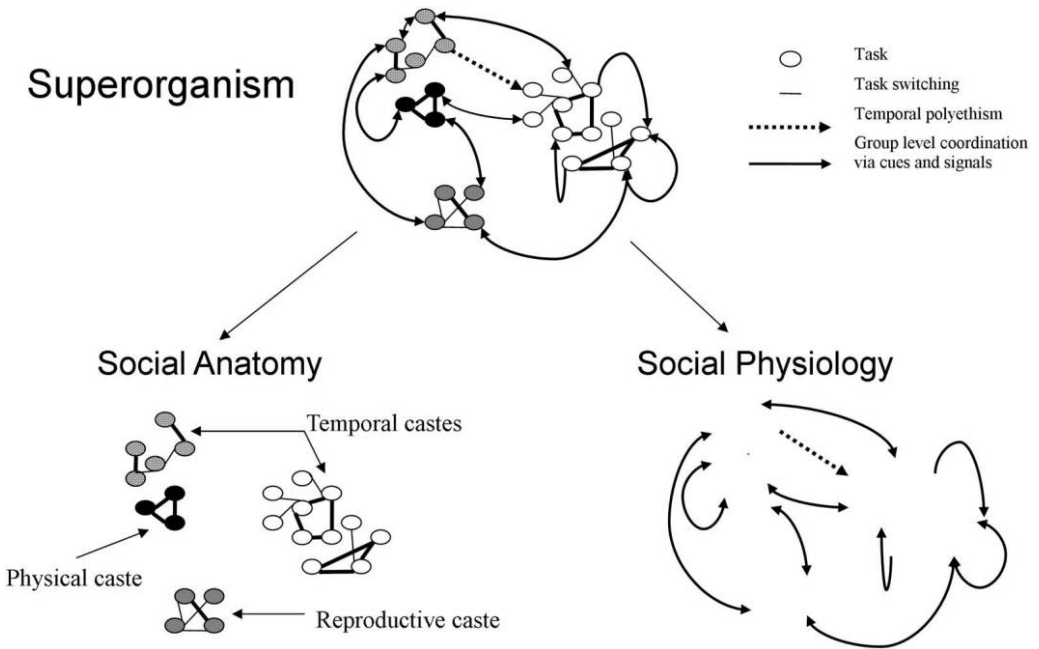


FIGURE 4. SUPERORGANISM CONCEPT EXPANDED INTO SOCIAL ANATOMY, DEVELOPMENT, AND PHYSIOLOGY COMPONENTS

This figure shows a colony-level ethogram for a factory- or machine-like society (the most sophisticated superorganisms). Different shading or fill patterns indicate that a particular physiological or morphological specialization is required for the performance of the task. Thus, caste repertoires are composed of tasks with similar shading or fill patterns. Unlike in traditional ethograms, communication mechanisms are included in the schematic (as curved or rounded arrows representing the flow of information via cues and signals). We argue that the same functional problems define eusociality and multicellularity. Specialization of the units of systems provide for both anatomy and social anatomy, both of which allow for the benefits of specialization. Developmental processes, either at the cellular or social levels, facilitate the construction and maintenance of the anatomical systems. Finally, coordinating the actions of the specialized units takes the form of either physiology or social physiology, both of which are dependent on either broadcasting signals to the entire group or transferring more complex and directed messages between particular units. The endocrine system handles broadcasting signals in multicellular organisms, while pheromones often play the same role in social insects. The nervous system facilitates the fast exchange of complex information in multicellular organisms, whereas mechanical and acoustic signals, such as the waggle dance, play the same role in social insects.

eusociality. Further dissociation of queen and worker components could arise through the elaboration of caste-specific gene expression or the evolution of caste-specific genes (see also Gadagkar 1997). West-Eberhard (1987) also proposed that the evolution of temporal polyethism could be explained by sequential expression of different components of the ancestral groundplan. Thus, the fundamental proposal of the groundplan hypothesis is that the patterns of labor division found in complex societies are built upon simple changes in the regulation of con-

served ancestral gene sets underlying the expression of tasks found in solitary insects.

Broadly speaking, a range of data supports the general assertion that hypothetical conserved genes and physiological mechanisms important to life history regulation in solitary insects are also involved in the organization of work in social insects. There are differences in gene expression, hormonal titers, and reproductive proteins in queen- versus worker-destined larvae, or reproductive and non-reproductive individuals, in a variety of taxa (e.g., Evans and Wheeler 1999; Hunt

et al. 2007; Hoffman and Goodisman 2007; Toth et al. 2007). Changes in gene expression, hormonal titers, and reproductive proteins also correlate with behavioral transitions between worker age groups (Robinson 1992; Whitfield et al. 2003; Amdam et al. 2004; Nelson et al. 2007). Thus, the caste and current behavioral state of a social insect individual is influenced by the expression of sets of genes, many of which likely have similar functions in solitary ancestors. Furthermore, specific gene pathways in solitary insects, such as those for insulin-signaling as well as related pathways that mediate physiological responses to nutritional state and reproductive development (Tatar et al. 2003; Flatt et al. 2008), have been found to have upstream effects in reproductive caste determination (Patel et al. 2007; Wheeler et al. 2006), and also to affect worker behavioral transitions in honeybees (Ament et al. 2008).

There is also evidence that associations between reproductive traits and behavior exist in worker honeybees, in accordance with a stricter interpretation of West-Eberhard's ovarian groundplan hypothesis (also called the reproductive groundplan hypothesis) (Amdam et al. 2003, 2004, 2006). For example, Amdam et al. (2006) found that the probability of honeybee foragers collecting pollen versus nectar and their age at first foraging are influenced by ovariole number—a static reproductive trait determined during the larval stage—such that foragers with larger ovaries tend to forage earlier and collect pollen versus nectar. The authors proposed that pollen foragers express ancestral genes associated with reproduction, and that ovariole number differences between foragers contribute to colony-level foraging patterns (Amdam et al. 2006). However, experiments designed to test this hypothesis using a line of honeybees artificially selected for increased reproductive potential failed to support it (Oldroyd and Beekman 2007; see also Amdam and Page 2008, Tsuruda et al. 2008).

INTEGRATING GROUNDPLANS WITH SOCIAL ANATOMY

The full set of gene pathways common to both solitary and social insects and funda-

mental to physiological processes, endocrine signaling, and development can be considered components of a broadly defined insect “groundplan.” Furthermore, as a large portion of the social anatomy phenotype is present in the solitary ancestor as a behavioral or life history phase, it is feasible for the evolution of social anatomy to have proceeded via changes in the expression of relatively intact, conserved gene sets. As we reviewed, there is evidence to support this hypothesis. Thus, broadly defined “groundplan genes” play an important role in the evolution and expression of the caste phenotypes that form the basis of social anatomy (Figure 5A).

There are two major complications that have yet to be adequately addressed with respect to the groundplan hypothesis and social anatomy and development. First, we need an explanation for the expansion of task repertoire in social versus solitary insects, and second, though it is an active field of research, the regulatory aspects of social anatomy are still poorly understood (see Smith et al. 2008 for a review of progress). With respect to task expansion, an advanced social insect colony has a task repertoire approximately twice that of a solitary insect (Oster and Wilson 1978; Hölldobler and Wilson 1990). Furthermore, although some simple group-level processes, such as division of labor between a guard and a forager, can arise spontaneously via self-organization (Page and Mitchell 1998; Cahan and Fewell 2004), many highly derived caste-specific traits have no correlates in solitary wasps or bees. The advanced brood care behaviors of honeybees, for instance, provide a clear example of a highly derived eusocial behavior without an obvious antecedent in solitary bees (reviewed in Winston 1987).

The second point missing from approaches that argue that social insect castes are rearrangements of solitary insect behaviors (Page and Amdam 2007) is that colony-level regulatory processes control the expression of caste-generating gene sets. In short, whether a larva develops into a queen or a worker depends on social environmental factors—such as nutrition—that are regulated by the colony (Wheeler 1986; there is also growing evidence of genetic influences on caste, re-

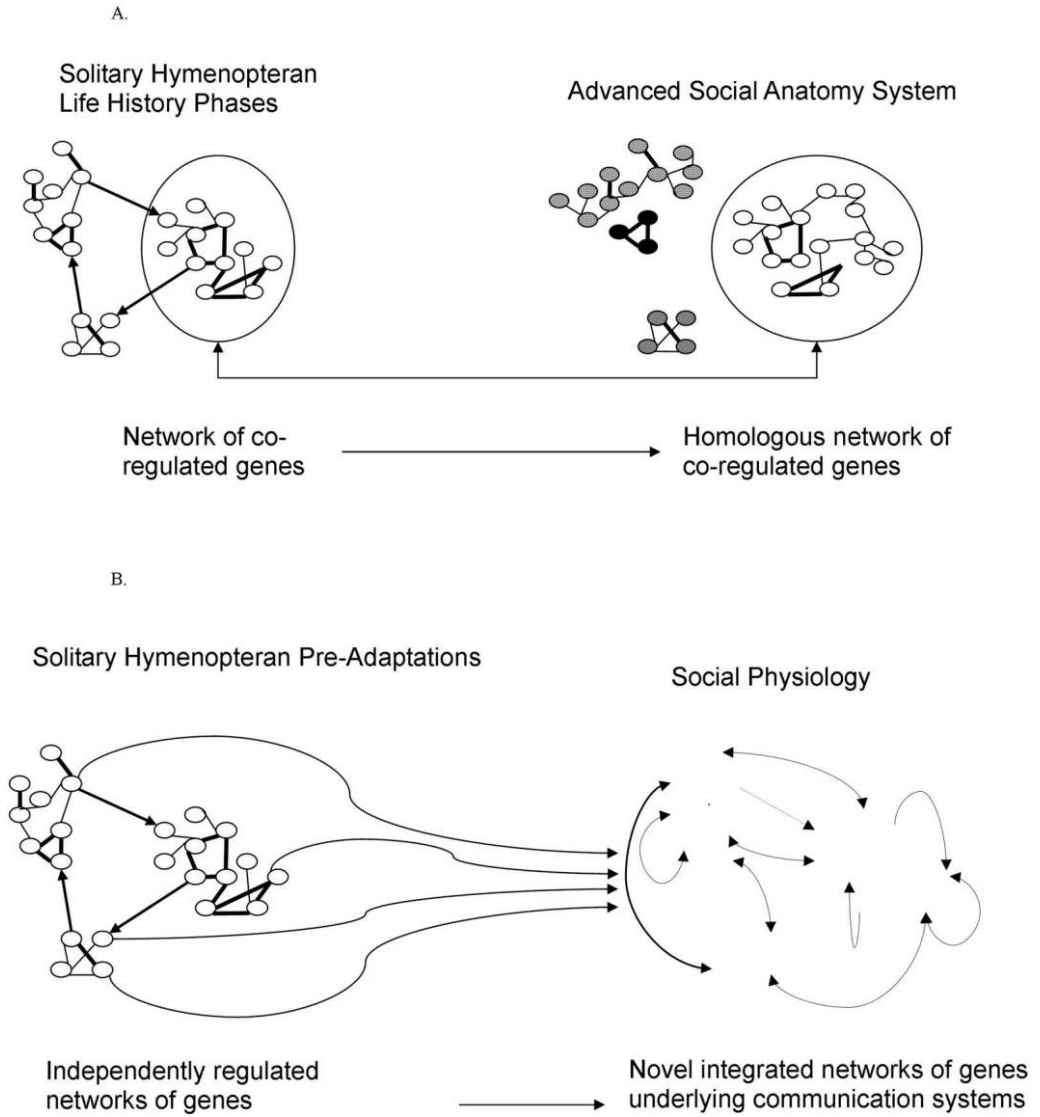


FIGURE 5. SYNTHESIS OF THE GROUNDPLAN HYPOTHESIS AND SOCIAL ANATOMY AND PHYSIOLOGY

Illustration of the proposed evolutionary relationship between solitary hymenopteran traits and social anatomy and physiology in eusocial insects. The text above the schematic describes the behavior, while the text below describes its proposed genetic basis. (A.) Left side shows the behavioral/life history phases of a solitary hymenopteran. Social anatomy and development are hypothesized to be based on changes in the regulation of the ancestral genetic networks underlying these behavioral phases. Two unresolved questions, however, revolve around the genetic basis of novel tasks performed by social insects (shown as a large increase in task repertoire) and caste specific physiological adaptations (shown with shading/patterning of tasks). (B.) Hypothesis for the genetic basis of social physiology. In advanced eusocial species, tasks are often partitioned between groups of individuals in different castes. Coordinating the actions of these individuals is based on the transfer of information via multiple sensory modalities. This is not a problem faced by solitary species, and no intact genetic network can be co-opted for this function. We hypothesize that novel networks are constructed de novo in response to this selective pressure from a toolkit of formerly independent sensory processes (illustrated with arrows from the ancestral behavioral repertoire flowing to a network of social physiology processes). The expansive nature of these social physiology processes suggests that a large scale reorganization of the genome may have occurred during the evolution of advanced eusocial colonies.

viewed by Anderson et al. 2008). Similarly, the dynamic behavioral and physiological state of individual workers also depends on the social environment (Huang and Robinson 1992, 1996). In this way, caste-specific expression of groundplan genes is controlled by social feedback loops—that is, social physiology. For example, the proportion of different castes produced in colonies across a variety of social insect taxa has been shown to be mediated by social physiological networks (Johnson and Wilson 1985; Porter and Tschinkel 1985; Robinson 1987; Hölldobler and Wilson 1990; Huang and Robinson 1992; Kaspari and Byrne 1995). Groundplan genes determine the physiological responses of individuals to the social environment. Genes expressed in nestmates determine how the social environment is regulated at the colony level (i.e., social physiology). The effects of these two types of genes must be integrated so that colonies produce distinct caste phenotypes (Linksvayer 2006, 2007; Linksvayer et al. 2009). Thus, the evolution, development, and expression of caste phenotypes (social anatomy) depends critically on the integration of genes affecting social physiology with broadly defined groundplan genes.

More generally, all individual-level traits in insect societies are influenced by the composite “socio-genome” of the colony (Linksvayer et al. 2009). That is, the genetic basis of individual-level traits includes networks of genes expressed within focal individuals—for example, determining physiological responses to environmental factors—but these environmental factors are regulated via colony-level feedback loops and also have a genetic basis. These genetic components of the social environment (i.e., indirect genetic effects) can be studied by using an interacting phenotype approach (Moore et al. 1997; Linksvayer and Wade 2005; Linksvayer 2006, 2007).

GROUNDPLANS AND SOCIAL PHYSIOLOGY

Conserved groundplans are important for the evolution of social anatomy, but can the groundplan hypothesis be extended to account for social physiology? That is, does social physiology evolve via the simple modification of conserved gene networks common to all insects? We believe

the answer is a complex “yes” and “no.” To explain, we must first consider the phenotype in question. In the case of the evolution of social anatomy, we agree that intact networks of genes can be co-opted because the task sets that define castes are largely present in the solitary ancestors; the problem is, thus, to freeze an individual in a particular behavioral phase. For instance, the construction of a nursing caste only requires changing the timing of the expression of maternal care genes from post- to pre-reproduction (Linksvayer and Wade 2005). Social physiology is of a fundamentally different nature, however. In this case, the ancestor does not exhibit the phenotype (group-level coordination of action) as it is solitary and has no need to send or receive coordinating messages in the context of task allocation. Thus, the co-option of a large, intact pleiotropically-linked gene set is highly unlikely. However, what the solitary species does possess is a toolkit of sensory abilities used in a variety of functionally independent contexts. Solitary bees, like most insects, have the ability to sense substrate vibrations and near-field sound, as well as a huge variety of odors useful for the avoidance of predators and the identification of foodstuffs (reviewed in Yack 2004; Hallem et al 2006). They also communicate in the context of mating with pheromones (reviewed in Ayasse et al. 2001).

The heart of our proposal is that the genes that underlie these disconnected sensory abilities in solitary ancestors are brought together into novel genetic networks that form the basis for social physiology in eusocial descendants (Figure 5B). In honeybee nectar collection, for example, the subgenual organs, which facilitate the reception of substrate vibrations, are critical for all four signals shown in Figure 3 (Kilpinen and Storm 1997; Nieh and Tautz 2000). In contrast, the subgenual organs are not used as a basis for regulating foraging in solitary bees who rely on their individual hunger and their assessment, via time-keeping mechanisms, of whether food is available in the field. Thus, a collective decision-making process, such as the regulation of nectar collection, is based on a number of for-

merly independent sensory processes. The genetic bases of these sensory processes are hypothesized to be integrated with ancestral groundplan networks, such as those that control foraging, to form novel genetic networks that underlie social physiology.

THE GENETIC BASIS OF COLONY-LEVEL
ADAPTATIONS (COLLECTIVE DECISION
MAKING)

In the preceding section, we hypothesized that the evolution of social physiology may be based on a major reorganization of the genome, or the construction of novel gene networks. Here we elaborate further by exploring the consequences of collective decision making at the genomic level. First, we consider the ancestral state. A solitary wasp can only do one thing at a time. Thus, only portions of its genome associated with a particular task are expressed at any given time. The expression of alternative networks of genes that control different patterns of adult behavior must therefore be regulated at the genomic level. Now consider an advanced insect colony. There are thousands or millions of individuals specialized for many distinct roles, all working in parallel. Thus, at the colony level, all of the gene networks in the genome underlying almost all adult behaviors are expressed simultaneously. Furthermore, as we saw with nectar foraging in honeybees, it is necessary that the activities of each caste be integrated with those of the others. Hence, for a eusocial colony, the problem at the genomic level is to co-regulate the expression of all of the networks of genes that control various adult behaviors. We therefore predict that collective decision making should be dependent on highly integrated genetic networks that control the regulation and expression of multiple behaviors by individuals in multiple castes.

We now return to the superorganism concept to place the hypotheses explored thus far into a broader evolutionary perspective. We outlined how two problems, the origin of eusociality and the origin of multicellularity, are functionally similar at the phenotypic level. We now argue that at the genomic

level, in contrast, the problems are very different. This is because a single-celled organism has few preadaptations that can be used as the basis for group-level coordination in a multicellular organism. This may be a cause for the expansion in gene number between single-celled and multicellular organisms (Vellai and Vida 1999; Taft et al 2007; but see Lynch 2007). In the case of the evolution of eusociality, however, the units are whole organisms with complex genomes. Many of the genes necessary to construct a superorganism may already be present in the genome, but the problem resides in the rearrangement of these genes into novel networks. We thus have a case of evolution solving similar problems at the phenotypic level with different mechanisms at the genetic level.

SOCIOGENOMICS: THE GENETIC AND
MOLECULAR BASES OF SOCIAL TRAITS

A key goal of sociogenomics is to determine how genes and patterns of gene expression change with the shift from solitary to social life (Robinson et al. 2005). Consider Figure 5A. Many of the nodes representing tasks remain the same, as a large number of the tasks are similar in solitary and social species. For example, a solitary bee must recognize flowers via their visual and olfactory characteristics and then extract either pollen, nectar, or both. Such tasks do not vary much between solitary and social bees, and they likely use the same physiological machinery and have the same genetic basis. Furthermore, when we look deeper into basic developmental and physiological processes, it is obvious that social insects not only have much in common with their solitary hymenopteran ancestors, but with all insects as well (Robinson et al. 2005). These facts provide several challenges to biologists attempting to elucidate the molecular basis of social traits. We identify three categories of genes with effects on behavior that are of interest with respect to the evolution of sociality. First, many genes influence behaviors that are common to solitary and social species, such as flower recognition behaviors. These behaviors likely did not play a role in the evolution of sociality, therefore identifying the underlying genes is

irrelevant to our understanding of the genetic basis of sociality. Second, some genes affecting behavior have altered expression patterns but retain similar functions. For example, sibling care and maternal care behaviors are similar and likely have a similar genetic basis, but sib-care genes are expressed in unmated offspring, whereas maternal care genes are expressed in mated mothers (Linksvayer and Wade 2005). Third, some genes have gained new functions during the course of social evolution. Gene duplication, followed by functional divergence of the copies, may be a particularly important mechanism in endowing these genes with novel functions (Gadagkar 1997).

In this final section, we review two case histories that illustrate how these categories of change at the genetic level contribute to the evolution of eusociality. Case Study 1 focuses on honeybee social anatomy, reviewing work that supports the groundplan hypothesis, but emphasizing that novelty at the genetic level may strongly contribute to the evolution of caste specific traits unique to the eusocial lifestyle. Case Study 2 reviews research on fire ants relevant to our hypotheses for the genetic basis of social physiology, and particularly relevant to our hypothesis that genes underlying social physiology should have pleiotropic effects on many aspects of organization of work (social anatomy and physiology), as the same sensory systems underlie multiple mechanisms of colony-level coordination of action.

CASE STUDY 1: SOCIAL ANATOMY AND DEVELOPMENT IN *APIS MELLIFERA*

As we argued in the section on groundplans, there are many caste-dependent physiological specializations that facilitate the performance of tasks (reviewed in Oster and Wilson 1978; Winston 1987; Hölldobler and Wilson 1990). Honeybee nurses, for example, are highly specialized in terms of physiology and behavior, with a narrow task repertoire focused on brood care. Their physiology is primed for this role and changes drastically when they leave this caste to become middle-aged bees (Winston 1987; Johnson 2003, 2008; Wegener et al. 2008). The evolution of their caste characteristics provides an

interesting example of how the three categories of change at the genetic level (as aforementioned in the previous section) contribute to the evolution of advanced eusocial behavior.

Nurses are the protein source for all the larval and adult bees in the nest (Crailsheim 1991, 1992). To play this role, nurses consume large quantities of pollen and convert it into a proteinacious secretion—brood food (reviewed in Winston 1987). We will focus on two factors that are physiologically central to this process: high titers of vitellogenin (Vg) and the production of brood food. Vg is an insect egg yolk protein that is associated with reproduction in insects (reviewed in Tufail and Takeda 2008). Consequently, in solitary species, it reaches its highest concentration after mating, relatively late in life (Tufail and Takeda 2008). In the honeybee, however, Vg has taken on several new roles. First, it reaches its highest level early in a worker's life, when it serves as a general storage protein that is converted to brood food in nurses' hypopharyngeal glands (Amdam et al. 2003). Second, Vg plays a role in social development by interacting with the juvenile hormone, which is associated with worker maturation (Pinto et al. 2000; Guidugli et al. 2005). In summary, Vg, a gene important to the reproduction of all insects, has changed in its timing of expression (Category 2) and has taken on new functions (Category 3) in the evolution of the honeybee nursing caste.

The production of a specialized brood food is a novel adaptation in the honeybee; solitary bees as well as eusocial bees simply feed pollen to their young (reviewed in Michener 1974). Within this context, major royal jelly proteins (MRJPs) serve vital roles (Schimdtzova et al. 1998; Albert et al. 1999). These proteins, thus far found only in the honeybee, form much of the basis for the glandular secretions fed by nurses to developing larvae and are also central to controlling the production of sexuals versus workers (reviewed in Wheeler 1986). The nine MRJPs are thought to have evolved via tandem duplication of one of the many yellow protein genes (Drapeau et al. 2006). This particular yellow protein (yellow-e3) is expressed strongly in the hypopharyngeal glands—the site of brood food production—and is

adjacent to the cluster of MRJP genes (Drapeau et al 2006). Furthermore, since all MRJPs are expressed in hypopharyngeal glands (Schidtzova et al. 1998; Santos et al. 2005), Drapeau et al. (2006) concluded that these genes evolved specifically for their role in brood feeding. Some of the MRJPs, however, have subsequently come to play other physiological roles in tissues throughout the body (Drapeau et al. 2006). Novel genes (MRJPs), therefore, play a vital part in generating the caste specific physiology of nurses.

CASE STUDY 2: SOCIAL ANATOMY AND PHYSIOLOGY IN *SOLENOPSIS INVICTA*

Fire ants display an extreme machine-type organization, making them among the most complex social insects (Tschinkel 1993, 2006). Fire ant workers, for example, are completely sterile with vestigial ovaries not capable of producing eggs (Tschinkel 2006). The workers are also organized into complex temporal and physical castes, the actions of which are coordinated by a rich system of communication (Cassill et al. 2002; Cassill 2003). Recent years have seen the growth of a fascinating body of work on fire ant genetics (reviewed in Gotzek and Ross 2007; Wang et al 2008), and, in this section, we review how this work supports our hypotheses for the genetic basis of social physiology.

A key prediction of our hypotheses is that the disruption of a communication process should have multiple effects on colony organization and behavior. The subgenual organs, for example, are involved in the reception of all four signals shown in Figure 3 and should, as a result, be central to all those processes mediated by these signals. Therefore, if we could alter the function of the subgenual organs in honeybees, we would expect strong effects on foraging decisions, the rate of incoming nectar, the amount of comb built, and the overall activity rate of the colony, with the partially common genetic basis of all of these processes serving as the basis for this phenomenon. Unfortunately, we currently have no way of knocking out or altering sensory structures such as the subgenual organs. However, nature has provided us with a natural experiment of a similar

process in fire ants, but, in this case, the disruption is to the mechanics of chemical communication.

Many social physiology processes are almost wholly dependent on chemical communication via pheromones (reviewed in Le Conte and Hefetz 2007). It has long been known, for example, that foraging dynamics in ants are strongly dependent on complex trail pheromones (reviewed in Hölldobler and Wilson 1990; Morgan 2009), but signaling between reproductive and nonreproductive castes is also primarily chemical in nature (reviewed in Slessor et al. 2005; Le Conte and Hefetz 2008). Queen fertility in many species, for instance, is signaled by a pheromone (Endler et al. 2004; Endler et al. 2006; reviewed in Le Conte and Hefetz 2007). When the fertility signal wanes, the workers rear a new queen—who produces a strong signal—and kill the old one. Simple negative feedback mechanisms such as this likely govern many aspects of colony-level behavior, as the queen's position as egg layer is central to setting colony-level activity rates (LeConte and Hefetz 2008). It is thus not surprising that queens produce a large number of highly complex pheromone blends that modulate worker behavior in a variety of contexts (Vargo and Hulsey 2000; Pankiw 2004; Le Conte and Hefetz 2008).

Fire ants, *Solenopsis invicta*, are characterized by two alternative life histories (reviewed in Tschinkel 1998). Monogynous colonies are characterized by a single, large fecund queen who founds a nest independently, while polygynous colonies are characterized by multiple smaller queens and colony reproduction via budding. Monogynous colonies are highly territorial, while polygynous colonies are far less so. Monogynous colonies are consequently somewhat dispersed in space, whereas polygynous colonies are more strongly clumped together (Ross and Fletcher 1985; Ross et al. 1997; Vandermeer and Alonso 2002). These differences in behavior, ecology, and life history have been traced to one segregating Mendelian factor, Gp-9, which has been shown to be an Odorant Binding Protein (OBP) (reviewed in Gotzek and Ross 2007).

Monogynous colonies are always headed by a queen with a BB genotype at the Gp-9 locus, while polygynous colonies are headed by queens of genotype Bb. The b allele has a mutation leading to a charge-altering substitution at a location on the protein thought to be associated with binding ligands (Krieger 2005; Gotzek and Ross 2007). This OBP, therefore, has either strongly changed in function or is nonfunctional. It is not known whether the protein is involved in the production of pheromones or in their reception, but, in either case, this mutation represents a strong change to the chemical communication system. As per our prediction, this alteration has resulted in changes to multiple social anatomy and physiology processes. Interestingly, queen number is regulated by workers, and the presence of as few as 5–10% of workers with the b allele results in the acceptance of multiple queens into the colony (Ross and Keller 2002). Furthermore, the gene expression profiles of workers are affected more strongly by the genetic composition of the social environment (i.e., through indirect genetic effects) than by the direct effect of their own Gp-9 genotype (Wang et al. 2008). These results demonstrate that the expression of the polygyne phenotype is dependent on the composite genotype of the colony, which is as expected if social feedback loops (i.e., social physiology) regulate the expression of individual-level and colony-level phenotypes. Thus, the presence of the b allele, or of a handful of alleles in a non-recombining inversion adjacent to GP-9, within colonies leads to major changes in social anatomy (queen number, mass, and behavior with respect to colony foundation) and social behavior (worker aggression towards non-nestmates).

In summary, numerous studies suggest that fire ant traits such as toleration of multiple queens, territorial behavior, queen nest-founding behavior, and morphology are functionally related via the coordinating actions of a common pheromonal social physiology mechanism dependent on variation at the Gp-9 locus. The organization of work (social anatomy and physiology) in the fire ant is thus integrated to the extent that a strong change in one essential sensory process has effects on many aspects of colony behavior. To propose a

hypothesis for the genetic basis of these results, it is useful to use an interactive network approach (Lee et al. 2002; Alon 2003; Fewell 2003). In recent years, successful applications of network approaches have been used to elucidate the genetic basis of complex traits, including behavior (Anholt 2004; Dequeant et al. 2006; Long et al. 2008; Renn et al. 2008; Ayroles et al. 2009). In short, one constructs a network with each gene represented as a node. Connections between nodes represent functional relationships or interactions between genes. In other words, genes connected by lines in the network underlie or influence the same trait. A common method of showing a functional relationship for a gene is to knock it out or alter its function using a variety of techniques, and to then record the effect(s) on different phenotypes (reviewed in Hammond et al. 2001). Based on previous studies, every composite trait can be expected to have a complex genetic basis, represented by a densely interconnected network of genes (reviewed in Barron and Robinson 2008). To return to the case of fire ants, disruption of Gp-9, which nature has done for us, causes changes in a host of traits including queen number, worker territorial behavior, and queen morphology. Therefore, Gp-9 is a member of each of the networks of genes underlying these traits. Furthermore, all of the networks underlying those traits affected by Gp-9 are likely part of one network, with genes (such as Gp-9) underlying social physiology processes as hubs. Hubs—nodes with very large numbers of connections—often play key roles in the function and evolution of biological systems (Levy and Siegal 2008; Zotenko et al. 2008; Bullmore and Sporns 2009). As social physiology mechanisms serve to integrate the activities of workers in different behavioral states (and, accordingly, the expression of different networks of genes in those workers), it is reasonable to propose that pheromones and other social physiology traits may be hubs in the genetic networks of social insects.

SUMMARY AND CONCLUSIONS

Following Wilson (1971) and Seeley (1995), we argued that the primary problem of insect sociality is coordination of activity at the group

level. This is not an issue for solitary insects and is, hence, a novel problem posed by the eusocial lifestyle. In short, as a worker's task repertoire decreases in size, colony-level communication mechanisms must proportionally increase to allow for coordination at the group level (Jeanne 1986). While this pressure is minimal in incipiently eusocial species, it becomes important with the transition to a team-like society. The problem becomes acute with the transition to factory- or machine-like societies dependent on inflexible division of labor and assembly line dynamics. As Jeanne (1999) elegantly showed, assembly line organizational systems are beyond the means of small societies, thus indicating that there are strong qualitative differences in organization between team-like and factory- or machine-like societies. At the extreme, societies such as driver and leaf cutter ants are characterized by a complex social anatomy of inflexible castes governed by elaborate systems of communication (social physiology) that facilitate collective decision making in every domain of colony life.

We used this synopsis of social insect behavior to interpret recent work on the proximate basis of eusociality. The groundplan and its associated hypotheses propose that division of labor arises via simple changes in the regulation of ancestral pleiotropically-linked genes that affect reproductive physiology and behavior. As we reviewed, however, decreasing a

worker's task repertoire (division of labor) leads to the novel and pressing problem of then ensuring that the disconnected task sets continue to be performed in appropriate ratios to one another. To date, this communication cornerstone of the eusocial lifestyle has been neglected by the groundplan approach, which is focused on conserved gene networks. Furthermore, as we illustrated, the groundplan approach cannot be extended to the study of social physiology, as the communication networks that characterize social physiology have no direct antecedents in the solitary Hymenoptera. We proposed that social physiology, in contrast to the minor alteration of intact genetic networks, is dependent on many formerly independent sensory processes being integrated together into novel gene networks. These novel gene networks then facilitate the coordination of action necessary for collective problem solving. We concluded by arguing that the evolution of eusociality involves a complex mix of changes in gene expression, genes with modified functions, and novel genes. We reviewed data from honeybee and fire ants that support this notion and our hypothesis for the genetic basis of social physiology.

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