THE EVOLUTIONARY ORIGIN AND ELABORATION OF SOCIALITY IN THE ACULEATE HYMENOPTERA: MATERNAL EFFECTS, SIB-SOCIAL EFFECTS, AND HETEROCHRONY

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abstract

We discuss the evolutionary origin and elaboration of sociality using an indirect genetic effects perspective. Indirect genetic effects models simultaneously consider zygotic genes, genes expressed in social partners (especially mothers and siblings), and the interactions between them. Incorporation of these diverse genetic effects should lead to more realistic models of social evolution. We first review haplodiploidy as a factor that promotes the evolution of eusociality. Social insect biologists have doubted the importance of relatedness asymmetry caused by haplodiploidy and focused on other predisposing factors such as maternal care. However, indirect effects theory shows that maternal care evolves more readily in haplodiploids, especially with inbreeding and despite multiple mating. Because extended maternal care is believed to be a precondition for the evolution of eusociality, the evolutionary bias towards maternal care in haplodiploids may result in a further bias towards eusociality in these groups. Next, we compare kin selection and parental manipulation and then briefly review additional hypotheses for the evolutionary origin of eusociality. We present a verbal model for the evolutionary origin and elaboration of sib-social care from maternal care based on the modification of the timing of expression of maternal care behaviors. Specifically, heterochrony genes cause maternal care behaviors to be expressed prereproductively towards siblings instead of postreproductively towards offspring. Our review demonstrates that both maternal effect genes (expressed in a parental manipulation manner) and direct effect zygotic genes (expressed in an offspring control manner) are likely involved in the evolution of eusociality. We conclude by describing theoretical and empirical advances with indirect genetic effects and sociogenomics, and we provide specific quantitative genetic and genomic predictions from our heterochrony model for the evolutionary origin and elaboration of eusociality.

THE NATURE and amount of parental investment varies widely across taxa. In some species, gamete size appears to be reduced to a minimum, indicating minimal investment, while in others, parents expend many resources on large gametes and/or postnatal parental care (Trivers 1972; Clutton-Brock 1991). Brood defense and provisioning are forms of parental investment found in a wide variety of animals, such as some crustaceans, spiders, mites, scorpions, millipedes, insects, and vertebrates (Wilson 1971). Social systems characterized by these types of parental care are described as being "subsocial" (sensu Wheeler 1923; Wilson 1971; Alexander et al. 1991). Although behaviorally similar to parental care, alloparental or sib-social care has a more restricted taxonomic distribution. By "sib-social" care, we mean those instances in which young adults remain for some time in their natal nest to help rear siblings, as is found in some birds, mammals, and insects (Wilson 1975). Finally, in some taxa described as being "eusocial," sib-social helpers remain at their natal nest more or less permanently, and there is a reproductive division of labor, overlapping of adult generations, and cooperative brood care (Michener 1969; Wilson 1971). Traditionally, only the ants and some bees and wasps (all found in the insect order Hymenoptera) and the termites were considered to be eusocial. More recently, eusociality has been discovered in naked mole rats (Jarvis 1981), aphids (Aoki 1982; Itô 1989), an ambrosia beetle (Kent and Simpson 1992), thrips (Crespi 1992), and snapping shrimp (Duffy 1996). There has been discussion about broadening the definition of eusociality to also include taxa with helpers that provide sib-social care only temporarily (e.g., Gadagkar 1994; Crespi and Yanega 1995; Sherman et al. 1995).

The evolution of parental care is often understood as maximizing the direct fitness of the parents (i.e., individual-level selection) (e.g., Alexander 1974; Clutton-Brock 1991). However, indirect genetic effect models reveal that assigning components of offspring fitness, such as early survival, to parents can lead to incorrect evolutionary inferences (Wolf and Wade 2001). The evolution of sib-social care is more complex because the beneficiaries of care are not offspring of the caregivers but rather kin to them with varying degrees of relatedness. Darwin (1859) suggested that selection at the family level could result in the evolution of sterile helpers, as found in eusocial insects. Hamilton (1963, 1964a,b, 1972) formalized these ideas in his theory of inclusive fitness and showed that altruistic behaviors evolve when the genetic relatedness (r) between social partners is greater than the ratio of fitness costs (c) to the performer over the fitness benefits (b) to the recipient: $r > c/b$. This relationship, known as Hamilton's Rule, is the foundation of inclusive fitness or kin selection theory. Wade (1979, 1980, 1982b, 1985) and others have shown that kin selection is a combination of two levels of selection, namely selection among individuals within kin groups and selection among kin groups. In this theoretical context, Hamilton's Rule specifies the conditions under which selection among kin groups is stronger than opposing selection within kin groups.

In this paper, we discuss the evolutionary origin and elaboration of social behaviors in the aculeate Hymenoptera and offer maternal effects and indirect genetic effects theory as a complement to existing models of social evolution. Individual and colony phenotypes of social insects are influenced by genes expressed zygotically as well as by genes expressed in social partners (i.e., mother, sibling brood, sibling workers) (Figure 1). These direct and indirect genetic effects and interactions among them are likely to strongly influence the evolutionary dynamics of social insect traits (e.g., Cheverud 1984, 2003; Wolf et al. 1998), and we believe that incorporating these various effects will lead to more comprehensive and realistic models of social evolution.

Several authors have discriminated between the evolutionary origin, maintenance, and elaboration of eusociality, emphasizing that the selection pressures involved in the evolutionary origin may be very different than those involved in the maintenance or elaboration of eusociality (e.g., Crespi 1996; Michener 2000). We focus largely on the evolutionary origin of eusociality, specifically the
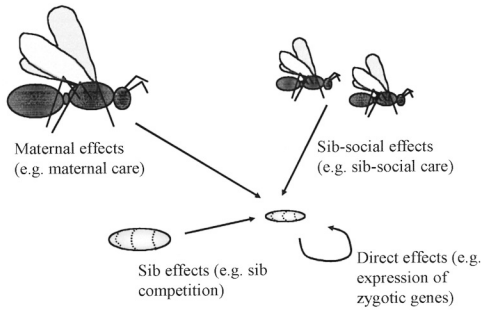
FIGURE 1.   DIRECT AND INDIRECT EFFECTS ON A
LARVAL PHENOTYPE

Social insect phenotypes are influenced by a variety of direct and indirect effects. These different influences on a focal larva's phenotype are shown by the arrows. Siblings expressing sib-social care are shown to be smaller than the mother to indicate that only individuals in poor condition express sib-social care.

genetic and developmental basis of sib-social care. We also discuss the evolutionary elaboration of eusociality (e.g., queen-worker phenotypic divergence), but stress that the genetic and developmental machinery underlying the origin of eusociality is also likely to be involved in the elaboration of eusociality.

First we review the role of haplodiploidy in the evolution of maternal and sib-social care, because this genetic system facilitates the evolution of maternal effect genes just as it sometimes does altruism genes through kin selection. Second, we introduce parental manipulation, a traditionally recognized alternative to kin selection for the evolution of eusociality, and review the differences between kin selection genes and parental manipulation genes. We then review more proximate, mechanistic hypotheses and present a scenario for the evolutionary origin and elaboration of eusociality based on heterochrony genes that modify the timing of expression of maternal care. Finally, we discuss how quantitative genetic and sociogenomic approaches can be used to study the evolution of eusociality. Although we focus primarily on the social aculeate Hymenoptera, we believe that our remarks are applicable to the evolution of sociality in all taxa in which sib-social care is derived from maternal care.

HAPLODIPLOIDY AND THE EVOLUTIONARY ORIGIN OF EUSOCIALITY

THE "HAPLODIPLOID HYPOTHESIS"

For much of the past century, social insect biologists believed that eusociality arose more than ten times in the order Hymenoptera (wasps, bees, and ants) but only once in nonhymenopteran insects (termites) (e.g., Wheeler 1923; Wilson 1971). As a corollary to kin selection theory, termed the "haplodiploid hypothesis" by West-Eberhard (1975), Hamilton (1964b) suggested that a sterile female caste had more frequently evolved in the haplodiploid Hymenoptera because of the asymmetry of genetic relatedness that exists between haplodiploid females and their relatives. Full sib haplodiploid females are more closely related to one another ($r = 0.75$) than they are to their brothers ($r = 0.25$) or to their own sons and daughters ($r = 0.5$). In contrast, diplodiploid male and female siblings are equally related to one another and to their offspring ($r = 0.5$). Thus, alleles causing haplodiploid females to care for their sisters instead of their own offspring spread more easily than such alleles in diplodiploids.

Although the haplodiploid hypothesis was initially embraced (e.g., Wilson 1971, 1975; Trivers and Hare 1976), it is now doubted by most social insect biologists (reviewed by Andersson 1984; Bourke and Franks 1995; Crozier and Pamilo 1996; Queller and Strassmann 1998). Because haplodiploid sisters are less closely related to their brothers than diplodiploids, female haplodiploid helpers must invest more resources in rearing sisters than brothers to capitalize on the high relatedness (Trivers and Hare 1976; Wade 1979). Furthermore, colonies with helpers must bias resource investment towards females to a greater degree than the rest of the population so that female-biased investment and helping behavior become associated (e.g., Charlesworth 1978; Charnov 1978b; Iwasa 1981; Grafen 1986). While several authors have proposed models by which this may occur (e.g., Seger 1983; Grafen 1986; Godfray and Grafen 1988; Frank and Crespi 1989), the conditions that favor the evolution of eusociality in haplodiploids are not as easily met as initially proposed by Hamilton (1964b).

In addition, multiple queens (polygyny) and multiple mating (polyandry) are common in the eusocial Hymenoptera (reviewed by Bourke and Franks 1995; Crozier and Pamilo 1996), and both reduce the relatedness among female siblings (Hamilton 1972; Wade 1982a). These phenomena often reduce relatedness to values lower than that expected between parents and offspring or between diplodiploid siblings so that the theoretical benefit of haplodiploidy disappears or is greatly mitigated (e.g., Gadagkar 1991). This has been taken as evidence refuting the haplodiploid hypothesis, although conditions found in highly eusocial populations likely do not reflect conditions in populations at the evolutionary origin of eusociality (Crespi 1996).

The phylogenetic association between haplodiploidy and eusociality also seems to be weaker than it was once perceived. Although all Hymenoptera are haplodiploid, only four aculeate hymenopteran clades contain eusocial species (Hunt 1999). Several other large taxonomic groups are haplodiploid but do not have eusocial members (e.g., some mites, scale insects, whiteflies, and beetles) (Normark 2003), and eusociality occurs in several diplodiploid groups, including termites, naked mole rats, aphids, snapping shrimp, and an ambrosia beetle (Gadagkar 2001).

OTHER PREDISPOSING TRAITS FOR THE EVOLUTION OF EUSOCIALITY

Other characteristics besides the relatedness asymmetry caused by haplodiploidy may explain the prevalence of eusociality in the Hymenoptera. For example, Hamilton (1972:206) stated, "Male haploidy is certainly not the only prerequisite for evolving a sterile caste. Perhaps the preadaptations of solitary nesting Hymenoptera as porters and builders are equally important." Similarly, a variety of other traits may be predispositions, for example, maternal care, nest building, mandibulate mouthparts, the female sting, above average chromosome numbers, short lifespan of adults relative to juvenile development time, and protogyny enabled by haplodiploidy (Wilson 1971; Sherman 1979; Andersson 1984; Starr 1985; Queller 1989; Alexander et

al. 1991; Crespi 1996; Hunt 1999). Some authors stress the uniqueness of each lineage in which eusociality has arisen and the complexity of factors influencing the evolutionary origin of eusociality, such that searching for a small number of common factors underlying the evolutionary origin of eusociality is not likely to be successful, and may even be misleading (Crespi 1996; Hunt 1999). Nevertheless, Alexander et al. (1991) argued that parental care is a universal and necessary precondition for the evolution of eusociality and noted that maternal care is found more commonly in the Hymenoptera than in any other arthropod group.

MATERNAL CARE, PROTECTED INVASION THEORY, AND MATERNAL EFFECTS THEORY

Despite the difficulties described above for the haplodiploid hypothesis to explain the distribution of eusociality, "some crusaders still search among the rubble of haplodiploidy" (Hunt 1991:426–427). With the discovery of eusociality in some species of haplodiploid thrips (Crespi 1992), Reeve (1993) reassessed the importance of haplodiploidy in the evolution of eusociality. "Protected invasion theory" indicates that dominant maternal care and female alloparental care alleles are less likely to be lost by drift when rare, and are more likely to fix by selection relative to paternal and male alloparental care alleles in haplodiploids or parental or alloparental care alleles in diplodiploids (Reeve 1993; Reeve and Shellman-Reeve 1997).

Using a maternal effects model, Wade (2001) similarly showed that maternal effect alleles (including alleles for maternal care) fix more readily in haplodiploids relative to diplodiploids. In addition, multiple mating does not restrict the evolution of maternal effect genes as it does kin selection genes (Wade 2001). Furthermore, Wade (2001) found that, unlike under kin selection, inbreeding differentially facilitates the evolution of maternal care in haplodiploids relative to diplodiploids. Inbreeding theoretically has strong effects on the probability of complex sociality evolving (Wade and Breden 1981; Breden and Wade 1991) and may be

involved in the evolution of sociality in a number of groups such as naked mole rats, spiders, termites, and ambrosia beetles (reviewed in Choe and Crespi 1997). Thus, genetic system and mating system affect the probability of sociality evolving, and both protected invasion theory and maternal effects theory predict that maternal care should evolve more readily in haplodiploid relative to diplodiploid populations.

THE ASSOCIATION OF HAPLODIPLOIDY WITH SUBSOCIALITY AND EUSOCIALITY

An association between subsociality and haplodiploidy has long been noted (Borgia 1980; Andersson 1984; Alexander et al. 1991). "Indeed, in arthropods, haplodiploidy seems more closely correlated with subsociality than with eusociality" (Alexander et al. 1991:18). For example, subsociality in mites and ticks (subclass Acari) is only found in haplodiploid species (Saito 1997). Subsociality and haplodiploidy also co-occur in some thrips (Thysanoptera, Crespi and Mound 1997), bees and wasps (aculeate Hymenoptera), and ambrosia beetles (Coleoptera: Xyleborini, Kirkendall 1993).

It is commonly accepted that subsociality is a precondition for the evolution of eusociality (e.g., West-Eberhard 1987; Alexander et al. 1991; Hunt 1994). If subsociality is more likely to evolve in haplodiploid populations (Reeve 1993; Wade 2001), and eusociality is derived from subsociality, then eusociality is also more likely to be found in haplodiploid populations. Despite the difficulties discussed above for the haplodiploid hypothesis, there are still strong theoretical reasons to expect an association between haplodiploidy and eusociality. Below we review models for the evolutionary origin of eusociality and then describe a new model for the evolutionary origin of eusociality from subsociality.

PARENTAL MANIPULATION AS AN ALTERNATIVE TO KIN SELECTION

Two hypotheses, mutualism and parental manipulation, are traditionally presented as alternatives to kin selection for the evolutionary origin of eusociality. The mutualism hypothesis suggests that eusociality evolves through mutualistic group living (e.g., Michener 1958; Lin and Michener 1972; West-Eberhard 1978; Itô 1993), wherein individuals live together and reciprocally assist one another in procuring food and defending a common nesting site. Many authors (e.g., Hamilton 1972; Andersson 1984; Bourke and Franks 1995; Crozier and Pamilo 1996) have argued that mutualism alone cannot lead to eusociality, however, and thus we do not discuss the mutualism hypothesis further. As a second alternative to kin selection, Alexander (1974) and Michener and Brothers (1974) suggested that eusociality evolves through parental manipulation, wherein mothers restrict the reproductive options of some offspring so that they assist in the rearing of additional fully-fertile offspring. Reviews have emphasized that such parental manipulation is not a mutually exclusive alternative to kin selection (Michod 1982; Andersson 1984; Bourke and Franks 1995; Crozier and Pamilo 1996), and each may operate sequentially or in concert (Craig 1979). Furthermore, parental manipulation requires interactions between kin (parents and offspring), and need not be considered distinct from kin selection theory (Michod 1982; Andersson 1984; Bourke and Franks 1995; Crozier and Pamilo 1996). The spread of parental manipulation alleles is driven by among-family selection (i.e., among kin group selection, or "kin selection"), just like kin selected altruism alleles.

In theory, however, there are expected differences between the evolutionary dynamics of alleles that cause parental manipulation and kin selection alleles that cause worker altruism (e.g., Charnov 1978a; Craig 1979; Crespi and Ragsdale 2000; Wade 2001). The primary difference lies in the nature of the genetic underpinnings of the evolving behaviors. In most kin selection models, the altruistic genes are located in and expressed in the genomes of the caregiving relatives. This can be considered "offspring control" in the case of the evolution of eusociality, because whether an offspring helps raise its sibs directly depends on its own genotype (Michod 1982). In parental manipulation models, the genes in question are located in and expressed in the maternal genome,

although there may also be genes in the zygotic genome that direct offspring response to parental manipulation (Craig 1979).

Because of these differences in the location of genes underlying the behaviors, the benefit to cost ratio necessary for alleles to spread by parental manipulation is often less than kin selection (Charnov 1978a; Craig 1979; Wade 1998, 2001; Crespi and Ragsdale 2000). For example, in many models, the benefit to cost ratio necessary for parental manipulation alleles is half that of kin selection alleles, so parental manipulation alleles spread more easily (Michod 1982). In addition, a new parental manipulation mutation will have an initial advantage relative to a kin selection mutation expressed zygotically (Alexander 1974; Seger 1991). When a new parental manipulation mutation is expressed in a mother, it causes some portion of her offspring to express sib-social care (assuming the offspring already possess the capability to express sib-social care, see Charlesworth 1978; Craig 1979; Crespi and Ragsdale 2000), benefiting the remaining fully-fertile offspring, half of which carry the new mutation. Alternatively, when a new kin selection mutation is expressed, the individual bearing the mutation expresses sib-social care and bears a cost, but the sibling beneficiaries likely do not carry the mutation (just as with mutations causing aposematism, see Brodie and Agrawal 2001).

Throughout this paper, we consider "offspring control alleles" to be zygotic alleles that, when expressed, cause an individual to behave "altruistically" and provide care to fully-fertile siblings at the expense of its own reproduction (alleles with a negative direct effect and a positive sib-social effect). "Parental manipulation alleles," in contrast, are maternal effect alleles that cause a female to manipulate some of her offspring to help rear additional, fully-fertile siblings (alleles with a negative maternal effect and a positive sib-social effect).

Additional Models for the Evolutionary Origin of Eusociality

Because kin selection theory provides no insight into the developmental, physiological, or ecological basis of eusociality (Alexander 1974; Michener and Brothers 1974; West-Eberhard 1987; Hunt 1999), several authors have searched for more proximate, mechanistic explanations for the evolution of eusociality. In this sense, parental manipulation theory is appealing because it provides a specific underlying behavioral mechanism for sib-social care, namely, "mom made me do it" (Alexander 1974; Michener and Brothers 1974). Scenarios for the evolutionary origin of eusociality, such as the subfertility hypothesis (West-Eberhard 1975; Craig 1983) and especially the nutritional scenario (Hunt 1991, 1994, 1999), provide further explicit ecological and behavioral mechanistic details. West-Eberhard's (1996) "ovarian groundplan" scenario has a developmental focus and describes how queen and worker phenotypes diverge based on an ancestral developmental program (see also Gadagkar 1997, 2001).

Other authors have attempted to identify particular selection pressures that might favor offspring that stay at their natal nest and help rear sibs (reviewed by Queller 1996), such as defense of nests against parasites and predators (Lin and Michener 1972), the potential to inherit proven nest sites (Andersson 1984; Alexander et al. 1991), and various demographic factors (Queller 1989, 1996; Gadagkar 2001). Another approach, reproductive skew modeling, uses phenotypic optimization to build upon Hamilton's Rule (Hamilton 1963, 1964a,b, 1972), identifying the expected reproductive decisions and the distribution of reproduction based on relatedness among social group members, constraints to solitary breeding, and benefits to group living (e.g., Keller and Reeve 1994; Emlen 1995; Jeon and Choe 2003).

It has been difficult to empirically study the various hypotheses and factors described above for the origin of eusociality. For example, studies of sex allocation are described as providing strong support for kin selection theory (e.g., Queller and Strassmann 1998; Chapuisat and Keller 1999), but do not provide evidence for the existence of kin-selected altruism alleles causing sib-social care (Alonso and Schuck-Paim 2002). One difficulty in studying the origin of eusociality is

finding the right study system: most highly eusocial lineages with sterile workers and large societies (e.g., many ants, honey bees, stingless bees) are highly derived and have been eusocial for millions of years (Danforth 2002). The selection pressures and traits of these taxa are likely to be very different than those of taxa at or closer to the origin of eusociality. Other lineages, such as xylocopine bees (Michener 1985, 2003), halictid bees (Danforth 2002), and vespid wasps (Hunt 1999), contain genera, species, and sometimes populations within species that range from subsocial to eusocial and have traits and selection pressures more relevant to understanding the origin of eusociality (Danforth 2002). Phylogenetic study of these lineages suggests that eusociality is frequently lost and study of taxa, once eusocial or trapped at the threshold, may shed light on the necessary traits and selection pressures for the maintenance of eusociality (Wcislo and Danforth 1997). For example, Michener and Brothers (1974) attempted to distinguish between worker altruism and parental manipulation using behavioral observations of a halictid bee. Recently, Langer et al. (2004) tested assumptions of skew theory in a halictid, and several authors used phylogenetic approaches to study factors important in the evolution of eusociality (e.g., in vespids, Carpenter 1991; Hunt 1999; in halictids, Danforth 2002; in xylocopines, Schwarz et al. 2003; Cronin 2004).

It is important to note that the hypotheses, scenarios, or factors discussed above for the origin of eusociality are not mutually exclusive. Each explains different aspects of the origin of eusociality. For example, among-family selection provides an evolutionary mechanism for the evolution of sib-social care and sterile castes, while the specific benefits to group living provide the possible underlying causes of among-family selection. Scenarios for particular lineages, such as the nutritional scenario for social vespids, provide more mechanistic, physiological, developmental, and life historical details for how a specific case(s) of sociality evolved. A unique feature of our heterochrony model (below) is that it provides details of the genetic and developmental basis of sib-social care behaviors (cf.

ovarian groundplan scenario, West-Eberhard 1996).

The Model: The Evolution of Sib-Social Care from Maternal Care with Heterochrony

Our model for the evolutionary origin of eusociality from subsociality is based on the premise that sib-social care behaviors are developmentally homologous with and evolutionarily derived from maternal care behaviors (see Dawkins 1979; West-Eberhard 1987, 1996; Alexander et al. 1991; Hunt 1994; Bourke and Franks 1995). More specifically, we propose that prereproductive sib-social care is caused by the early expression of genes for maternal care. In the ancestral condition, maternal care behaviors are expressed as one of the final steps in a coordinated series of physiological and behavioral changes that occur through reproductive development (West-Eberhard 1996). Thus, ancestrally, maternal care genes are expressed only after mating and other steps of reproductive development. In the derived condition, aspects of the reproductive developmental program are co-opted so that maternal care behaviors are expressed prereproductively towards siblings instead of offspring (see West-Eberhard 1996). That is, genes for maternal care are expressed prereproductively in female helpers in the derived condition. This is a case of behavioral heterochrony, modification of the expression of genes regulating behavioral development that causes a change in the timing of expression of behaviors. Behavioral heterochrony is thought to be important in a wide variety of animal groups (West-Eberhard 2003), and has been explicitly invoked in the evolution of eusociality in termites (Nalepa and Bandi 2000; West-Eberhard 2003) and the evolution of helping behavior in birds (Jamieson 1989). In our model, genetic variation underlies variation in the timing of the expression of maternal care behaviors (for discussion of whether genetic variation must underlie the evolution of eusociality, see West-Eberhard 1987, 1992b; Crozier 1992; Bourke and Franks 1995). In this view, sib-social care is an evolutionarily derived trait, and the evolution of the capacity for females

to provide care prereproductively towards their sibs is a first step in the evolutionary origin of eusociality from subsociality.

The key point of our model is that sib-social care is based on the altered expression of maternal care genes and that the origin and elaboration of eusociality involves the evolution and regulation of this altered expression so that sib-social care is expressed when it is adaptive. We stress heterochrony and sib-social care as the prereproductive expression of maternal care genes above, however, the exact nature of altered expression of maternal care genes is dependent on life history. In most extant aculeate Hymenoptera, mating and dispersal occur at about the same time, followed by nest foundation and the expression of brood care behaviors (Hölldobler and Wilson 1990; Ross and Matthews 1991; Michener 2000; O'Neill 2001). In this case, opportunities for sib-rearing only exist before mating and dispersal so that sib-social care must be expressed prereproductively. In other cases, mating and dispersal are not so closely linked, and, for example, mated offspring overwinter in the natal nest (e.g., Michener 2000). In these cases, opportunities for sib-rearing exist after mating. Sib-social care then could be expressed postreproductively, similar to the ancestral condition. Finally, in some cases, mated offspring females may lay eggs in their natal nest. Then, care behaviors are expressed toward a combination of their own offspring and their siblings (or nieces and nephews as in semisocial models, e.g., Michener 1958; West-Eberhard 1978; Itô 1993). In all of these cases, sib-social care behaviors are based on the expression of maternal care genes, and the evolutionary elaboration of sib-social care involves the regulation of expression of these genes.

THE DEVELOPMENTAL BASIS OF SIB-SOCIAL CARE

The expression of sib-social care must be conditional such that both helper and normal reproductive phenotypes can be produced by a single genotype. Discrete alternative phenotypes, or polyphenisms (e.g., alternative horn morphs in male dung beetles, alternative castes in female social insects), are typically induced by environmental stimuli such as photoperiod, crowding, and nutrition level (reviewed by Nijhout 2003). Caste in the eusocial Hymenoptera is determined primarily by nutritional signals received during larval development (reviewed by Wheeler 1986; Hartfelder and Engels 1998; O'Donnell 1998). However, in some taxa, caste determination seems to occur primarily in the adult stage, and dominant, egg-laying females suppress the ovarian development of underdominants through behavioral interactions or pheromones (Wheeler 1986; O'Donnell 1998; Gadagkar 2001). Nutrition and behavioral dominance are environmental cues mediated by endocrine mechanisms, such as hormone titer with a threshold, which initiate alternative developmental pathways into reproductive females or workers (Nijhout and Wheeler 1982; Wheeler 1986; West-Eberhard 1996; Robinson and Vargo 1997; Hartfelder and Engels 1998; Nijhout 2003). Polyphenisms are thought to be derived from phenotypically plastic traits, using preexisting physiological and endocrine developmental mechanisms (Nijhout 2003). Thus, the evolution of discrete castes in the eusocial Hymenoptera involves the elaboration and regulation of preexisting endocrine and developmental mechanisms sensitive to environmental conditions (Wheeler 1986; West-Eberhard 1987, 1996; Nijhout 2003).

In our model, the behavioral switch between normal and precocious maternal care via the heterochronic expression of maternal care genes is also largely determined by the social environment mediated by the endocrine system. The sensitivity of the behavioral switch to environmental signals and the endocrine response is affected by genes expressed zygotically during development (West-Eberhard 1987, 1996). As stressed by indirect genetic effects theory (e.g., Moore et al. 1997; Cheverud 2003), the social environment is affected by genes expressed in social partners such as the mother, other sibling brood, and sibling adults. Thus, both zygotic genes (direct genetic effects) and genes expressed in the mother and other social partners (indirect genetic effects) affect the expression of sib-social care

(Figure 2B). The evolution of sib-social care may proceed as a series of sequential maternal and zygotic evolutionary events or the simultaneous coevolution of integrated maternal-zygotic behaviors (see Craig 1979).

The evolutionary origin of sib-social care in our model is based on preexisting behavioral traits, with the regulation of the expression of sib-social care based on preexisting physiological and endocrine machinery (Dawkins 1979; West-Eberhard 1992a, 1996). We suggest that there may often be a small number of genes underlying this behavioral heterochrony, permitting rapid social evolution once the appropriate mutations arise (see Michener 1985). These may be rare or, alternatively, they may be common in subsocial populations, but only rarely adaptive (see Michener 1985).

THE EXPRESSION OF SIB-SOCIAL CARE IN SOCIALLY POLYMORPHIC SPECIES

It is possible that the first step in the evolution of eusociality, the expression of sib-social care, could occur long before the evolution of a permanent sterile caste and in a wide range of subsocial taxa where opportunities for sib-rearing exist. This appears to be the case in some bee lineages, such as Apidae: Xylocopinae. Michener (1985:303; see also Tierney et al. 2002) states, "The existence of a minority of nests containing colonies, some of them with castes (i.e., semisocial and eusocial), in various species of *Ceratina,* in most allodapines, and perhaps also in *Xylocopa,* suggests that this polymorphism or at least a potential for it arose in a remote common ancestor of the modern species and has persisted, without ever proceeding to fixation." Alternatively, alleles enabling sib-social care (i.e., heterochrony alleles in our model) may be fixed, but the sib-social behaviors are expressed only under certain conditions (indeed, alleles causing sib-social care must be conditionally expressed, but in some populations the necessary environmental conditions may never occur so that sib-social care is never expressed) (Soucy and Danforth 2002). That is, the social polymorphism may be environmentally determined. Parental manipula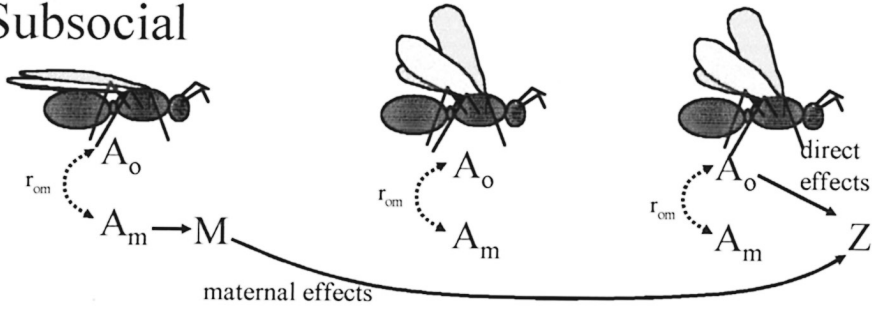tion requires that the manipulated offspring already possess the ability to provide sib-social care (Charlesworth 1978; Craig 1979; Crespi and Ragsdale 2000). Experimental manipulation of colonies can confirm the capacity of prereproductive adults to provide sib-social care under certain ecological conditions, and induction of eusociality has been shown for some normally subsocial bees in the genus *Ceratina* (Sakagami and Maeta 1982; Michener 1985).

Environmental conditions related to altitude, latitude, and day length are known to be important in the expression of sociality in some socially polymorphic halictid bees (Wcislo 1997; Yanega 1997). Plateaux-Quénu et al. (2000) transplanted foundress females from eusocial and noneusocial populations of the halictid *Lasioglossum* [*Evylaeus*] *albipes* into conditions simulating those normally experienced by the alternate social form (see also Cronin 2001). In general, changing rearing conditions did not change the expression of worker behavior, which suggests that it may have a genetic basis (Plateaux-Quénu et al. 2000). Soucy and Danforth (2002) studied the phylogeography of a socially polymorphic halictid, *Halictus rubicundus,* and found that populations expressing eusociality belonged to different genetic lineages than noneusocial populations, a finding also consistent with a genetic basis to sociality (see also Zayed and Packer 2002). Transplant or common garden experiments are a useful first step in distinguishing genetic from environmental causes of sociality and complement correlational findings from phylogenetic studies. As described in the next section, a quantitative genetics approach provides techniques to further study the relative environmental and genetic contributions to the expression of sociality.

THE QUANTITATIVE GENETIC BASIS OF SIB-SOCIAL CARE

Standard social evolution models use an optimality approach to predict evolutionary outcomes based only on assumed selective pressures. Selection does not equal evolution (Fisher 1958; Arnold and Wade 1984; Moore and Kukuk 2002), however. Something of the genetic architecture underlying traits must be
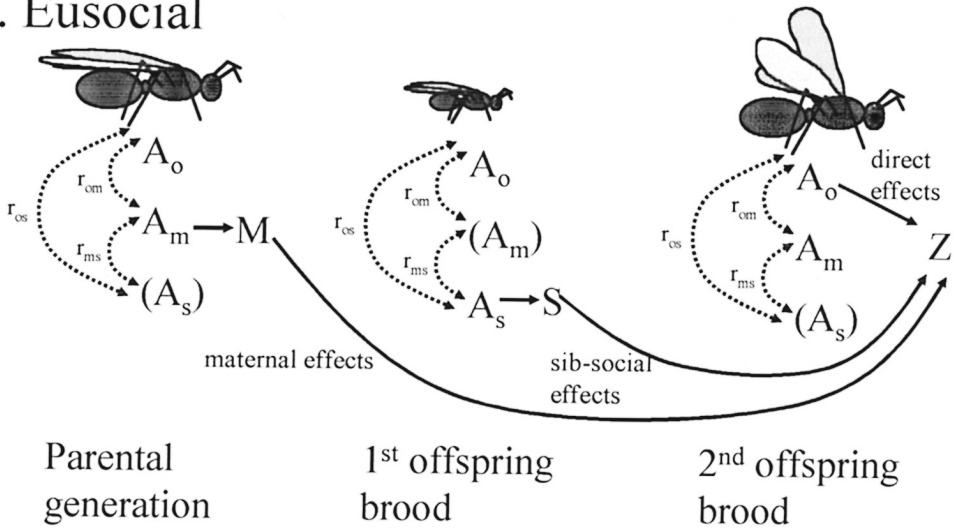
Figure 2.   Path Diagram for Influences of Direct and Indirect Additive Genetic Effects on a
          Phenotype of a Second Brood Offspring

A mother with folded wings is shown on the left, and her first and second brood female offspring are in the center and right, respectively. Panel A shows a subsocial colony in which offspring of both broods reproduce, disperse (hence the extended wings), and express maternal care genes toward their own offspring (not shown). Panel B shows a eusocial colony in which first brood offspring remain at the natal nest (hence folded wings) and express sib-social genes toward their sibs (second brood dispersing offspring with extended wings) instead of reproducing, dispersing, and expressing maternal care genes toward their own offspring. The first brood offspring is smaller than the other individuals to indicate that it is in poor condition and cannot successfully reproduce on its own. The symbol, A_o, is for direct additive genetic effects that influence the phenotype of the individual in which they are expressed, while A_m represents maternal additive genetic effects that influence offspring phenotypes through their effect on maternal performance, M. The A_s represents sib-social additive genetic effects that influence sibling phenotypes through their effect on sib-social performance, S. Genetic effects in parentheses are not expressed (i.e., the eusocial mother and her second brood offspring express maternal care genes but do not express sib-social care genes, while smaller first brood offspring express sib-social care genes but do not express maternal care genes). Solid arrows represent influences on a phenotype Z of the second brood offspring. Doubleheaded dotted arrows represent genetic correlations between additive genetic effects due to pleiotropy: (1) r_{om} is the direct maternal additive genetic correlation; (2) r_{os} is the direct sib-social additive genetic correlation; and, (3) r_{ms} is the maternal sib-social additive genetic correlation. In panel A, phenotype Z of the second brood offspring is influenced by maternal and direct effects. In panel B, phenotype Z of the second brood offspring is influenced by maternal and direct effects, as well as by sib-social effects from the first brood offspring. Note that sib-social care initially is merely the pleiotropic expression of maternal care genes, so that at least initially, $r_{os} = r_{om}$ and $r_{ms} = 1$. For clarity, no environmental effects, paternal effects, or effects due to competition among sibs are shown. Paths for the transmission of additive genetic effects from mother to offspring weighted by maternal-offspring relatedness (1/2) are also not shown nor is the genetic relatedness between sibs (3/4 in haplodiploids with a singly-mated mother) shown, although relatedness among social partners is accounted for in indirect genetic effect models.

understood before the response to selection can be reliably predicted. A quantitative genetic approach compares phenotypes among individuals of known relatedness to estimate components of the genetic architecture underlying traits, such as the additive genetic variance for a trait (usually described as a proportion of the total phenotypic variance, or heritability) and the genetic covariance between traits (usually presented as a genetic correlation) (Falconer and MacKay 1996; Roff 1997; for discussion of application of a basic quantitative genetic approach to social insects, see Moritz 1986; Owen and Harder 1995; Moore and Kukuk 2002). Even if there is genetic variance for a trait, it may not respond to selection as expected if the trait genetically covaries with other traits. Genetic covariance between traits can act as an evolutionary constraint because correlated traits do not evolve independently (Falconer and MacKay 1996; Roff 1997).

When the social environment affects the expression of a trait, genes expressed in social partners (indirect genetic effects) as well as zygotic genes (direct genetic effects) affect a phenotype (Figure 1, 2). In social insects, the social environment is clearly important in the expression of individual and colony phenotypes (West-Eberhard 1996; Wcislo 1997) so that indirect genetic effects likely play a major role in determining the evolutionary dynamics of these traits. However, traditional social evolution models do not include both direct and indirect genetic effects (e.g., Cheverud 1984, 2003). Additionally, if genes have pleiotropic effects on traits expressed by different life stages (e.g., larval traits and maternal traits), then the traits will be genetically correlated (Figure 2), potentially causing evolutionary constraints analogous to constraints caused by genetic correlations among traits expressed within a single individual. Optimality approaches ignore these evolutionary constraints even though they potentially have important impacts on evolutionary dynamics (Cheverud 1984; Lynch 1987; Cheverud and Moore 1994; Wolf et al. 1998; Cheverud 2003; Wolf 2003). For example, when genetic correlations between direct and indirect effects are considered, Hamilton's Rule must be altered to include a genetic correlation term,

which may often dominate the inequality (Cheverud 1984, 2003; Cheverud and Moore 1994; Wolf et al. 1998). We have highlighted the potential importance of both direct and indirect effects in our heterochrony model. It is also clear under our model that there will be a genetic correlation between maternal and sib-social care (Figure 2).

It is possible to experimentally dissect the relative contributions of direct, maternal, and sib-social effects, and the interactions among them. Cross-fostering offspring between unrelated foster mothers is a powerful approach to estimate direct and maternal effects on a phenotype (Cheverud and Moore 1994; Roff 1997; Lynch and Walsh 1998). If a full factorial design is used, such that mothers rear some of their own offspring and some unrelated offspring, the phenotypic variance due to direct effects, maternal effects, and the direct-maternal interaction can be estimated. This approach has recently been used to study the evolution of maternal care in several natural systems, including burying beetles (Rauter and Moore 2002), dung beetles (Hunt and Simmons 2002), burrower bugs (Agrawal et al. 2001a), and a passerine bird (Kölliker et al. 2000). Alternatively, in social insects, a series of manipulations (e.g., mixing larvae among colonies, mixing workers among colonies, and removing queens) can be used to estimate the relative magnitude of among-colony variance due to direct effects, maternal effects, sib-social effects, queen by larval interaction, worker by larval interaction, and queen by worker interaction.

The experimental designs described so far estimate the relative importance of direct and indirect effects to the evolutionary dynamics of traits within populations. Analogous cross-fostering manipulations between populations or species would estimate the relative importance of direct and indirect effects in the fixed differences between populations or species. Cross-fostering between a subsocial population or species and a eusocial population or species would be especially insightful in understanding the fixed genetic differences between them underlying the expression of sociality. For example, if subsocial offspring reared by eusocial mothers express sib-social care, and eusocial offspring reared

by subsocial mothers do not express sib-social care, then maternal effect, "parental manipulation" genes are important. If subsocial offspring reared by eusocial mothers do not express sib-social care, and eusocial offspring reared by subsocial mothers do express sib-social care, then direct effect, "offspring control" genes are important. Ideally, a full factorial design could be used in which mothers from eusocial and subsocial populations rear offspring from their own population as well as all other populations. This design enables the estimation of variance due to direct effects, maternal effects, and direct-maternal interaction. If maternal and direct effect genes evolve in concert, then only certain combinations of maternal and zygotic genotypes may result in offspring expressing sib-social care, which suggests that the coadaptation of maternal and zygotic traits are important (Wade 1998; Wolf and Brodie 1998; Wolf 2000a,b).

Genetic Constraints to the Evolutionary Divergence of Maternal and Sib-social Care

Under our model, maternal care and sib-social care are both the pleiotropic expression of the same set of maternal care genes, so as sib-social care spreads through a population, there will be a strong positive genetic correlation between sib-social care and maternal care (r_{ms} in Figure 2B). Allelic variation affecting maternal care will similarly affect sib-social care. Genotypes that produce good mothers will also produce good sib helpers. This positive genetic correlation between maternal and sib-social care means that selection on one trait will cause a correlated response to selection on the second trait. At first glance, this seems unimportant because, initially, maternal and sib-social care can be thought of as a single trait. However, when alleles affecting brood care behaviors are expressed in helpers as well as in mothers, the total fitness effects of these alleles are changed. For example, if there is a synergistic effect between maternal and sib-social care, such that colonies that add on helpers produce more fully-fertile adults than colonies without helpers (e.g., West-Eberhard 1975;

Oster and Wilson 1978; Queller 1989, 1996), then alleles causing increased levels of brood care may be favored.

Subsequent to the initial spread of sib-social care, mutations that affect one trait (e.g., sib-social care) positively and the other trait (e.g., maternal care) negatively may arise and will spread if the sum of the two effects on fitness is positive. The genetic correlation between maternal and sib-social care may then diminish and permit maternal and sib-social care to diverge to some extent and specialize as separate traits. In this way, some alleles could produce good "queens" and other alleles could produce good "workers." In addition, gene duplication, such that each caste has a separate set of genes, can further enable the divergence of queen and worker phenotypes. More simply, caste-specific gene expression can evolve (West-Eberhard 1996; Gadagkar 1997, 2001). However, genes that have pleiotropic expression in both queens and workers might not be able to be optimized for both queen and worker phenotypes, and the divergence of queen and worker phenotypes may be constrained to some degree.

The evolutionary elaboration of queen-worker dimorphism may be constrained in many eusocial species because each queen founds a colony independently and must provide care for the first brood, just as workers provide care for subsequent broods. Thus, though queens and workers in these species are divergent in many morphological, physiological, and behavioral traits, there are times in the colony cycle that each must perform similar brood care behaviors. Alleles affecting brood care are then likely to have pleiotropic effects on both maternal care and sib-social care, and sustain a genetic correlation between maternal and sib-social care.

Only antagonistically pleiotropic alleles affecting one trait positively and another trait negatively are likely to remain segregating in the population because alleles that affect both traits positively or negatively will quickly fix or be lost (Falconer and MacKay 1996; Roff 1997). Segregating antagonistically pleiotropic alleles may cause a negative genetic correlation between maternal and sib-social care. This could result in a genetic constraint

to the further divergence of maternal and sib-social care. Similarly, negative genetic correlations between male and female fitness have been found in fruit flies, showing strong evidence for antagonistic pleiotropy ("intralocus conflict") between the sexes (Chippindale et al. 2001). These negative genetic correlations are thought to be important constraints to the divergence of male and female traits and the evolution of sexual dimorphism (Rice and Chippindale 2001; Badyaev 2002), just as we suggest that negative genetic correlations between maternal and sib-social care may be a constraint to the divergence of maternal and sib-social care and the evolution of queen-worker dimorphism.

Obligate swarm-founding bees, wasps, and ants, as well as socially parasitic species, do not found colonies independently (reviewed by Peeters and Ito 2001). Queens are never without workers and they never have to perform brood care behaviors (Jeanne 1991; Peeters and Ito 2001). Pleiotropy for genes affecting brood care may be less of a constraint to queen-worker divergence for some phenotypes in these species. Obligate swarm-founding species, such as honey bees (*Apis* spp.), stingless bees (e.g., *Melipona* spp.), army ants (e.g., *Eciton* spp.), and driver ants (e.g., *Dorylus* spp.) often have highly divergent queen and worker phenotypes, with high queen egg-laying rates and large colony size (Hölldobler and Wilson 1990; Bourke and Franks 1995; Bourke 1999; Michener 2000).

SOCIOGENOMICS AND THE MOLECULAR BASIS OF EUSOCIALITY

A quantitative genetic approach will provide insight into the genetic architecture of social traits (i.e., sib-social care), and this should lead to increasingly realistic models of social evolution. A sociogenomic approach (sensu Robinson 1999) will identify specific genes underlying the social traits and will elucidate the molecular basis of these traits (Krieger and Ross 2002). Our heterochrony model for the evolution of eusociality makes explicit predictions regarding patterns of gene expression for the expression of sib-social care. In our model, sib-social care first

appears as the heterochronic expression of maternal care genes. We predict that many of the same genes will be expressed in adults performing sib-social care behaviors as in adults performing maternal care behaviors. This will be especially true in populations of incipiently eusocial species but less so in those with an advanced degree of eusociality, where more genes are expected to have caste-limited expression due to selection for the elaboration of queen-worker divergence (see West-Eberhard 1996; Gadagkar 1997; 2001). However, because the evolutionary elaboration of sib-social care behaviors and queen-worker phenotypic differences is likely based upon simple modification of preexisting physiological, behavioral, and genetic machinery, queen and worker traits, even in highly eusocial species, are expected to have a common molecular basis. We further suggest that some of the key genes involved in the evolution of sib-social care are genes that regulate the timing of expression of maternal care behavior genes.

Social insect biologists have been successful in identifying regions of the genome involved in social traits in two model systems, the honey bee, *Apis mellifera,* and the imported red fire ant, *Solenopsis invicta,* both of which have a highly derived degree of eusociality (Robinson 1999). Ross and Keller and collaborators have demonstrated that the locus *Gp-9* affects male and female size, colony queen number, and overall social organization of *S. invicta* (Keller and Ross 1995; Ross and Keller 1998; Keller and Parker 2002; Krieger and Ross 2002). A sociogenomic approach has been used to study the molecular basis of caste differentiation in *A. mellifera*. Screening for differential gene expression in queen- and worker-destined honeybee larvae reveals that many genes are indeed expressed differentially (Corona et al. 1999; Evans and Wheeler 1999, 2001; Hepperle and Hartfelder 2001).

Robinson and colleagues have also been successful in elucidating the molecular basis of worker behavioral development in *A. mellifera*. In honeybee colonies, division of labor from hive work to foraging is associated with an age-related transition of workers that involves changes in brain chemistry and

structure, endocrine activity, and gene expression (reviewed by Robinson 2002). Specific genes involved in this age-related behavioral transition have been identified (Toma et al. 2000; Ben-Shahar et al. 2002), and these genes can be considered behavioral heterochrony genes. In addition, genes underlying this transition have pleiotropic effects on genes involved in the sequential expression of phases in the reproductive cycle (Amdam et al. 2004). Thus, worker behavioral development and maternal reproductive development have a common genetic basis, and genes regulating worker behavioral development seem to be derived from genes that regulate maternal reproductive development (Amdam et al. 2004). These results are consistent with the predictions of our model above, as well as West-Eberhard's (1996) ovarian groundplan scenario. Furthermore, Robinson and Ben-Shahar (2002) used a comparative genomics approach to ask whether social evolution, in a general sense, in model organisms (including *A. mellifera*) usually involves gene diversification or changes in gene regulation that influences spatial or temporal patterns of gene expression. As predicted under our model, it seems that new gene regulation is often involved in the evolution of social behaviors (Robinson and Ben-Shahar 2002).

The honeybee genome sequencing project should help to further elucidate the molecular bases of social behavior and caste determination (Robinson and Ben-Shahar 2002). Once genes involved in caste differentiation and social behaviors have been identified in honeybees, probes can be developed to search for homologues in nonmodel social Hymenoptera. It would be particularly interesting to determine if these genes are conserved across social taxa.

Although most sociogenomic study has concentrated on genes expressed during zygotic development (i.e., direct effect genes) (but see Ross and Keller 2002), we emphasize that indirect effect genes expressed in social partners are also likely to be involved in the expression of social traits, such as sib-social care. Identification of the specific ways that individual genes influence the expression of social traits will enable biologists to explicitly study the roles and interplay between direct effect (e.g., offspring control) and indirect effect (e.g., parental manipulation) genes.

SUMMARY AND CONCLUSIONS

We make five main points: (1) The role for haplodiploidy in the evolution of eusociality has been downplayed, and other predisposing factors, such as maternal care, have been highlighted. However, maternal care genes evolve more readily in haplodiploids relative to diplodiploids, as shown by protected invasion theory (Reeve 1993) and maternal effects theory (Wade 2001). It is widely accepted that eusociality is evolutionarily derived from subsociality, so the prevalence of subsociality in haplodiploids (such as the aculeate Hymenoptera) may make the evolution of eusociality in these groups more likely. (2) Although both offspring control and parental manipulation genes evolve through among-family selection, there are expected evolutionary differences in the dynamics of these genes due to their different genomic locations (i.e., zygotic versus maternal). (3) We propose that the evolutionary origin of sib-social care involves heterochrony, by the condition-dependent, prereproductive expression of maternal care behaviors in females towards their siblings instead of their offspring. The expression and regulation of sib-social care behaviors are likely to be based on the modification of existing developmental, physiological, and endocrine mechanisms. Genes expressed in both the zygotic genome and the genomes of social partners (e.g., maternal genome) are likely to affect the expression of sib-social care. (4) Quantitative genetic approaches, especially using indirect genetic effect models, enable the separation of direct and indirect environmental and genetic effects on social traits, and may be particularly insightful when applied to socially polymorphic species. Because sib-social care arises from maternal care in our model, there will be a genetic correlation due to pleiotropy between maternal care and sib-social care, which may constrain the divergence of these two traits. We predict that this genetic correlation will be strongly positive in incipiently eusocial populations,

and it will be more negative in more advanced eusocial species. (5) The emerging field of sociogenomics will yield insight into the molecular basis of sib-social care behaviors, and we predict that many of the genes involved in the expression of sib-social care behaviors are also involved in the expression of maternal care behaviors. Recent study of the genetic basis of worker behavioral development in the honeybee *Apis mellifera* supports these predictions (Amdam et al. 2004). Identification of the specific genes involved in the expression of sib-social care may further elucidate the roles of direct effect, zygotic genes and indirect effect genes expressed in social partners in the evolutionary origin and elaboration of eusociality.

Throughout this paper, we used the evolutionary perspective of indirect genetic effects. Indirect genetic effects theory makes unique predictions about social evolution relative to traditional optimality model approaches (see Roff 1994) because it explicitly considers both direct and indirect genetic effects as well as interactions between the two (Cheverud 1984, 2003; Cheverud and Moore 1994; Wolf et al. 1998; Agrawal et al. 2001b). We believe that modeling social evolution using an indirect genetic effects framework will allow social insect biologists to develop more realistic models. Importantly, quantitative genetics provides techniques to empirically study the assumptions of optimality models and the predictions of indirect genetic effects models (see Kölliker et al. 2000; Agrawal et al. 2001a; Kölliker and Richner 2001; Rauter and Moore 2002; Wolf 2003). Ideally, this top-down phenotypic, quantitative genetics approach can be used in concert with a bottom-up molecular, sociogenomics approach. We suggest that quantitative genetic and sociogenomics approaches should be used to build upon existing social evolution models, such as kin selection, parental manipulation, and skew models (see Roff 1994).

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