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ENVIRONMENTAL HIERARCHY, BEHAVIORAL CONTEXTS, AND SOCIAL EVOLUTION IN INSECTS

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Resumo

Insetos sociais frequentemente são usados para investigar a importância do parentesco (relação genética) na evolução de sociedades complexas. Estes estudos genéticos geralmente minimizam o papel organizador do ambiente na moldagem do desenvolvimento e da expressão de características socialmente relevantes. Como notado por Hamilton (1964), na sua formulação original de abordagens "genéticas" para a compreensão da socialidade, o ambiente social desempenha papel fundamental na determinação de fenótipos de organismos sociais. Cada nível de organização biológica (i.e. genoma, célula, indivíduo, grupo social) tem seu próprio ambiente. Em níveis de organização biológica diferentes, fatores ambientais (i) atuam como gatilhos de processos desenvolvimentais; e (ii) definem processos seletivos naturais. Um foco explícito em fenótipos, em diferentes níveis de organização biológica com diferentes níveis de ambientes, gera um arcabouço para utilizar-se a evolução da socialidade em insetos como uma ferramenta para integrar estudos de desenvolvimento e evolução. Atenção especial é dada a áreas que necessitam de mais estudos, especialmente para espécies tropicais, para complementar a riqueza de estudos genéticos e informações sobre espécies da região temperada.

Abstract

Social insects are frequently used to investigate the importance of kinship (genetic relatedness) in the evolution of complex societies. These genetic studies often downplay the organizing roles of the environment in shaping the development and expression of socially-relevant traits. As noted by Hamilton (1964) in his original formulation of "genetical" approaches to understanding sociality, the social environment plays a major role in determining phenotypes of social organisms. Each level of biological organization (e.g. genome, cell, individual, social group) has its own environment. At different levels of biological organization, environmental factors (i) act as triggers for developmental processes; and (ii) define natural selective processes. An explicit focus on phenotypes, at different levels of biological organization with different levels of environments, provides a framework to use the evolution of insect sociality as a tool to integrate studies of development and evolution. Special attention is drawn to areas that need further study, especially for tropical species, to complement the wealth of genetic studies and information on temperate species.

Introduction

Darwin (1859) recognized that *intra*specific phenotypic diversification among already sterile individuals was a potentially fatal flaw for his evolutionary theory. He solved the problem by arguing that selection also occurs at the family level, which permits apparently altruistic behavior. Hamilton (1964 *et seq.*) later generalized the notion of selection acting on family (kin) to explain the evolution of altruism, placing considerable emphasis on genealogical relatedness. Hamilton recognized that the social environment plays a critical role in determining how labor is apportioned within societies. Yet his principle of inclusive fitness and kin selection deflected attention away from environmental considerations, and instead generated a wave of studies assessing genetic relatedness among social group members (reviewed in Gadagkar, 1991); mechanisms of kin discrimination (reviewed in Fletcher & Michener, 1987); and conditions under which alleles for "altruism" might become fixed within populations (reviewed in Crozier & Pamilo, 1996). From a "selfish-gene" perspective, the environment has no role other than defining the strength and direction of natural selection. Social phenotypes (e.g., worker or queen forms), however, are typically determined in large part, or exclusively, by environmental differences, not genetic ones. Thus, social environments play a role in both phenotype development and selection. There is growing recognition that our neglect of environmental and ecological processes ("extrinsic factors") has left us with an incomplete understanding of how social behavior develops, evolves, or is lost to give rise to parasitic and secondarily solitary species. A "selfish-gene" perspective oversimplifies the relationship between organisms (phenotypes) and their environments, including their social and sexual ones, and it downplays the importance of developmental processes in shaping social phenotypes and their evolution.

Modern evolutionary biology works with many concepts that can be traced to Darwin (1859). His insights on natural selection were made possible in part by separating conceptually *"the organism"* from *"the environment"* (Lewontin, 1983; Wcislo, 1989). Before Darwin (1859), two widespread assumptions were that (i) "organism" and "environment" were inextricably interconnected and (ii) environmental differences themselves caused changes in form and function (e.g., Lamarck, 1809). Roughly speaking, assumptions (i) and (ii) underlie the discredited idea of inheritance of acquired somatic characteristics. To show that such historical change is phylogenetic (descent with modification from a common ancestor), without asserting a causal role for environmental differences [(i.e., without assumption (ii)], Darwin broke the organism-environment interpenetration. In this view, "the environment" posed an external problem, to which organisms "responded" by adaptive evolution via

natural selection, or they died out. Darwin (1859) initially minimized any organizing role for the environment in development, and any role for the organisms in constructing their environments: "When a variation is of the slightest use to a being, we cannot tell how much of it to attribute to the accumulative action of natural selection, and how much to the conditions of life. (p. 133)" After discussing several examples, Darwin continued, "Such considerations...incline me to lay very little weight on the direct action of the conditions of life. Indirectly...they seem to play an important part in affecting the reproductive system, and in thus inducing variability (p. 134)," which can be shaped by natural selection.

Although Darwin (1868) later emphasized the importance of the "conditions of life" in shaping development, and thus in generating selectable variation, many evolutionists continue to work within the earlier framework of the *Origin* (Darwin, 1859). Williams (1966: p, 67), for example, argued that "[w]e can regard the ecological environment as the strategy employed by Nature against an organism, which, in turn, *replies* with a strategy of its own that is designed to win the highest probable score (number of successful offspring)" (emphasis added). Likewise, most current genetic models of social evolution insolate organisms from their environments by applying selection coefficients to alleles or genotypes, ignoring the developmental interlude between genes and observed phenotypes (West-Eberhard, 1996). These models are deficient because selection does not act on genes directly, but rather on phenotypes [Brandon, 1990; Mayr, 1997; and for a debate as applied to social insects, compare Crozier (1992) with West-Eberhard (1992b)].

In this essay I review recent studies from the following perspective. How can we use insect sociality as a tool to better understand the organizing role of the environment in shaping the evolution of phenotypes (cf. Waddington, 1949)? What are the evolutionary consequences of environmental changes that result from animals' behavior (cf. Wcislo, 1989)? How does the social environment influence the development of group members (cf. West-Eberhard, 1996)? Many social insects have sophisticated communication, language or learning abilities, but little attention has been given to how these cognitive skills might relate to the *origins* of sociality (cf. Bernays & Wcislo, 1994). Social insects are excellent subjects for these questions because they provide rich examples of a complex interplay between phenotypes and environments at varying levels of biological organization (e.g., cells, individuals, colonies).

A central problem of insect sociality involves the evolution of developmental mechanisms that produce phenotypic discontinuities (i.e., discrete queen and worker forms) from an initially continuous phenotypic distribution (e.g., Wheeler, 1986; Crespi & Yanega, 1995; West-Eberhard, 1996; Gadagkar, 1997a). Associated with this discontinuity is the question of how different indi-

viduals, with differing constellations of traits, adopt particular strategies of apportioning labor, reproduction, and defense, in order to maximize inclusive fitness. Because social roles are usually determined by environmental factors, an understanding of this problem requires an appreciation of the roles played by environments at different levels of biological organization (see Woodger, 1929). At the proximate level, variable environments provide different cues that trigger alternative developmental processes, which helps generate variation among individuals that is potentially subject to natural selection The resulting phenotype (ontogenetic stage) becomes a part of the environment that provides cues that trigger subsequent developmental processes, as discussed below for soldier ant production (also see Hogan & Bolhuis, 1994; Pigliucci, 1996). At an ultimate level, environments have a selective role: different environmental states set conditions for natural and social selection, and other evolutionary processes (Mayr, 1997). These selective environments vary *temporally* because they are partly determined by organisms' behavior or that of their social partners (nest-mates, mates) (Wcislo, 1989). Thus, proximate and ultimate factors may be more intertwined than usually believed (see West-Eberhard, 1996).

By emphasizing the strong link between organisms and environments we can build a framework for merging information on proximate mechanisms of phenotypic determination (development) with phylogenetic patterns of phenotypic evolution (cf. Meyer *et al.*, 1995). As emphasized in this essay, this framework requires strict attention to the level of biological organization (cellular, individual, social, etc.), because each level has its own environment, comprised of elements from lower levels.

Possible and actual environments and their hierarchical organization

At each level of biological organization different environmental features are important. An organism's "environment" is not static, but changes during development (ontogeny) because each gene product (phenotype) contributes to the environment in which subsequent developmental decisions are made. For example, gene expression controlling juvenile hormone (JH) production in ant larvae changes the cellular environment to which individual cells respond and differentiate (e.g., Nijhout, 1994). High JH titres lead to the production of a greater number of soldier ants, which changes the social environment. In turn, this change raises the threshold at which cells respond to JH, and serves to regulate soldier production (for a review of the effects of the social environment on JH-mediated behavioral development, see Robinson & Vargo, 1997).

The evolution of social life created a new level of biological organization, in the same way that the evolution of multicellular animals created a new level of organization relative to unicellular animals (Buss, 1987; Maynard Smith

& Szathmáry, 1995). The colony is a new unit of organization (the social group) that interacts with the external environment, and the colony serves as the environment for lower units (individuals), as just discussed for the regulation of soldier production in ants. Thus, the social environment becomes critical in determining the reproductive success of individuals within the group due to social competition (West-Eberhard, 1979), and it serves to buffer individuals against influences from the external environment (*sensu* Brandon, 1990).

The pervasive influence of different environmental factors at different levels of biological organization means that a shift in levels changes the reference point for environmental considerations (e.g., Allen & Star, 1982; Eldredge & Grene, 1992). Jacob (1982) argued for the importance of distinguishing between possible evolutionary outcomes and actual ones, as a way to better understand evolution. A similar argument can be made for distinguishing between possible and actual environments. The *possible environment* describes the entire range of developmental and natural selective factors that potentially affect phenotypes, across the geographic range of the species (cf. Russell, 1934; Williams, 1966: 57ff.; Brandon 1990). This *possible environment* can be partitioned in myriad ways, depending on the question of interest. For example, a *genetic environment* emphasizes how genic information interacts (Mayr, 1954; Peterson & Sapienza, 1993). Gene expression can be altered, for example, by a change in position on the chromosome (e.g., Henikoff, 1995), but such precise information on phenotypic determination is lacking for social insects. An individual's *somatic environment* describes interactions among genetic and external sources of information (Williams, 1957, 1966; Waddington, 1975; Brandon, 1990). Somatic environments play an important role in determining which phenotypic traits are expressed, and thereby exposed to natural selection (e.g., worker-queen differentiation: Bonetti, 1992; Engels, 1990; West-Eberhard, 1996; Nijhout, 1994). At a higher level, the *social environment* influences which phenotypic traits are expressed as a result of social competition, the age structure of the colony, and the genetic relatedness among nest-mates (e.g., Hamilton, 1972, 1987; West-Eberhard, 1979; Stark *et al.*, 1990). For example, workers of the ant *Solenopsis invicta* (Hymenoptera: Formicidae) execute queens of a specific genotype (allelomorph) in some social environments, but not others (Keller & Ross, 1993). The *ecological environment* denotes the conventional view of "the environment," which sets the "problems" that organisms must solve (e.g., avoiding parasites or locating food), and influences, for example, the probability of successful reproduction for solitary *versus* social nesters.

An organism's possible environment is always wider than its actual environment. Possibilities are eliminated, modified or created during ontogeny [e.g., Wcislo, 1989; Brandon 1990; Bateson 1991; Gottlieb 1992; Odling-Smee 1996; Laland *et al.*, 1996]. In a sweat bee, *Halictus rubicundus* (Hymenoptera:

Halictidae), for example, Yanega (1997) hypothesized that each newly eclosed female has the potential to be (a) a foundress capable of entering diapause and later establishing a new nest; (b) a replacement queen that is incapable of entering diapause; or (c) a worker. Based on correlations, Yanega further hypothesized that there is a critical period at which time a female becomes a foundress *if* she mates; if she does not mate, then option (a) is precluded and her developmental potential is reduced to being a worker or a replacement queen (for contrary evidence see Plateaux-Quénu & Packer (1998).

Changes in behavior can also expand organisms' possible environments, and thus facilitate or retard evolution of other phenotypic attributes (Wcislo, 1989; Komers, 1997). For example, non-parasitic solitary bees collect floral resources to store in nests (reviewed in Wcislo & Cane 1996). In the context of natural selection, relevant environmental (ecological) features for a solitary bee include phenological synchronization with pollen plants, abilities to select a nest site, locate food and return to a nest, and relative abundance of parasites and predators. Under some conditions a conspecific individual behaves as a facultative parasite, and enters a nest to lay an egg on the pollen stored by another individual (e.g., Wcislo 1987a; Field 1992; Cichon, 1996; Jang *et al.*, 1996). In this case, relevant environmental features also include the abundance of host nests, an ability to fight hosts or destroy host immatures, or an ability to memorize the location and development of potential host nests. The *possible* environment includes features associated with both parasitic and non-parasitic modes of life, but the actual environment depends on which behavioral alternatives are followed.

A consideration of the parallel hierarchical structure of biological organization and its environment highlights the importance of environmental cues in triggering developmental responses in determining phenotypes, followed by the environmental screening of these phenotypes by natural selection. The following sections first describe social behavior and its phyletic distribution, followed by a discussion of attributes that play important roles in the evolution of sociality. In these sections, emphasis is placed on environmental regulation of these attributes, demonstrating the extensive inter-connectedness of organism and environment.

What is social behavior?

Social organization varies widely among taxa. Traditionally, emphasis has been on societies with sterile castes, because of difficulties associated with explaining the evolution of sterility ("altruism") by natural selection. Recently the proper definition of "eusociality" has been debated extensively (Gadagkar, 1994; Crespi & Yanega 1995; and Sherman *et al.* 1995; reviewed in Wcislo,

1997b; Costa & Fitzgerald 1996). The *status quo* definition simultaneously uses three criteria to define eusocial behavior (Michener, 1974; Wilson, 1971): (i) are individuals of more than one generation present? (ii) is there reproductive division of labor into fertile and more or less sterile castes? and (iii) is there cooperative brood care? Eusocial societies have been further sub-divided into "primitively-" and "advanced-" eusocial groups. Kukuk (1994) suggested that these modifiers be eliminated because they have unwanted teleological connotations, and they can be misinterpreted as conveying phylogenetic information. Different combinations of the above criteria define other social organizations (e.g., communal, semisocial; reviewed in Costa & Fitzgerald, 1996).

The *status quo* has been criticized for several reasons. First, recent studies have discovered complex social behavior in taxa for which it is difficult to apply this categorization (see below for examples). Secondly, the criterion of "reproductive division of labor" is ambiguous because it can be interpreted as permanent or temporary, and absolute or statistical. Finally, the criterion of "overlap of generations" is probably a bias of temperate-zone biologists (Gadagkar, 1994).

Crespi & Yanega (1995) proposed new definitions of social groups to focus attention on the origin of caste differences. They narrowed the scope of eusociality to include only groups with workers and queens that are locked into an irreversible developmental trajectory (i.e., once a worker or queen phenotype is determined, the developmental decision cannot be reversed). They argued that in order to study the evolution of division of labor it is critical to know whether reproductive alternatives (i.e., sterile worker *versus* fertile queen) are facultative (i.e., expression of a given phenotype depends on local environmental conditions) or obligate (i.e., expression of a phenotype is invariant). Therefore, they restrict the term "eusocial" to describe cases in which the reproductive alternatives are obligate. In contrast, Gadagkar (1994) and Sherman *et al.* (1995) expanded the definition of eusociality to include societies with some individuals that do not reproduce at least temporarily at some point in their mature lives, and instead help nest-mates rear offspring. Sherman *et al.* (1995) argue that "eusociality" is an artificial construct, representing the tail of a distribution of "reproductive skew" among animals in which offspring help their parent(s) rear offspring; some individuals within a colony produce more (or all) offspring, while others produce fewer (or none) (see Keller & Vargo 1993).

The relative merits of these revisions are discussed elsewhere (see Costa & Fitzgerald, 1996; Wcislo, 1997b), but several points are worth emphasizing. One, a focus on terminology places emphasis on semantics, rather than on the evolutionary strategies used by different individuals to maximize their fitness. Secondly, we need operational definitions that can be used with limited information because frequently the data needed for the revised definitions are

not available. Different operational definitions allow us to ask different questions about social behavior and its evolution, or use new criteria to assemble data in novel ways (see Lee, 1994; Wcislo, 1997b). By analogy, anthropologists interested in food production might classify human societies as slash-and-burn, pastoralist, or agricultural, while those interested in religious beliefs might classify the same societies as animist, theist, etc.; neither classification is inherently better than the other. Finally, no matter which definition is used, individual colonies can be placed into social categories, but the categories are not applicable to species or more inclusive taxonomic groups, if there is *within-taxon* variation. A recent popular approach to studying social evolution involves mapping the distribution of phenotypic character states onto phylogenetic trees that are derived using other characters (e.g., Carpenter, 1989; Packer, 1991; Richards, 1994; Danforth & Eickwort, 1997; reviewed in Wcislo & Danforth, 1997) (for methods, see Brooks & McLennen, 1991; for criticisms of methods, see Kluge & Wolfe, 1993). Phylogenetic mapping assumes that data from one or a few populations (or nests) characterize the entire taxon, which downplays variation or dismisses it as uninteresting "noise" (see Wiens, 1996; Gittleman *et al.*, 1996).

Phyletic distribution of eusociality

Using the traditional definition, eusociality has evolved independently most frequently in Hymenoptera, although only in the Aculeata (suborder Apocrita) *sensu* Brothers & Carpenter (1993). Worldwide, thousands of species of ants (Formicidae), paper wasps [Polistinae + Vespinae], and termites (Isoptera) are eusocial, but this behavior probably arose once in the common ancestor of each clade (see respectively, Hölldobler & Wilson, 1990; Carpenter, 1989; Thorne & Carpenter, 1992). For paper wasps (Vespidae), however, molecular data contradict morphological data and suggest that social behavior has evolved twice in Vespidae, once in the common ancestor of Stenogastrinae, and once in the common ancestor of [Polistinae + Vespinae + Eumeninae] (Schmitz & Mortiz, 1998). Sociality has evolved repeatedly among bees (e.g., Michener, 1974; Chavarría & Carpenter, 1994), especially among Halictidae (Wcislo, 1997a) and Old World allodapine bees (Apidae) (e.g., Schwarz *et al.*, 1997) . Eusocial behavior is also known in snapping shrimp (Duffy, 1996), mole rats (Sherman *et al.*, 1991), aphids (Stern & Foster, 1996), a beetle (Kent & Simpson, 1992), & thrips (Thysanoptera) (Crespi, 1992), although recent work indicates that the soldier forms do reproduce & thus their defensive behavior may not be altruistic (Bejah & Schwarz, 1998). For general reviews of hymenopteran eusocial taxa, see Michener (1974) [bees, Apoidea]; Choe & Crespi (1997) [Arthropoda]; Ross & Matthews (1991) [wasps, Vespoidea & Sphecidae]; Zucchi (1993) [stingless bees, Hymenoptera: Meliponini]; Hölldobler & Wilson (1990) [ants,

Hymenoptera: Formicidae]; Bourke & Franks (1995) [ants]; and Turillazzi & West-Eberhard (1996) [paper wasps, Hymenoptera: Vespidae]. Phylogenetic studies show that social behavior can be lost to give rise to secondarily solitary species (e.g., halictine bees: Richards, 1994; Packer, 1991; reviewed in Wcislo & Danforth, 1997; Gadagkar, 1997b), or to species that are social parasites (see Wcislo, 1987a, 1997c; Petanidou *et al.*, 1995). Studies of the environmental conditions under which social behavior is lost or suppressed should provide insights into conditions that favor the evolution of sociality (e.g., Eickwort *et al.*, 1996; Gadagkar, 1997b; Wcislo, 1996b, 1997a; Wcislo & Danforth, 1997).

Most bees and wasps are solitary, but within some lineages there is a range of behavior from solitary to social. Bees and spheciforme wasps (Apoidea *sensu* Alexander, 1992), eumenine wasps (Vespidae—Ross & Matthews, 1991), thrips (Thysanoptera—Crespi, 1992), and aphids (Homoptera: Aphididae—Stern & Foster, 1996) are especially relevant for questions centered on evolutionary *origins* of sociality, and the evolutionary *loss* of sociality, because social taxa can be compared with phylogenetic relatives that are not social. Taxa in which females share nests, but social roles are not well-differentiated, are especially important for future studies (e.g., Sakagami & Zucchi, 1978; Camillo & Garófalo, 1989; Zucchi *et al.*, 1969; Melo, this volume). In the New World, Halictidae (Hymenoptera) are important in this context because they show considerable variation in social behavior within and among species (e.g., Packer, 1993; Danforth & Eickwort, 1997; Wcislo, 1997a; Michener 1974; 1990; Yanega, 1993, 1997), but the biology of most species has not been studied, especially tropical ones (e.g., Campos, 1980; Wcislo *et al.*, 1993). The diverse and interesting Brasilian insect fauna (e.g., Camargo & Mazucato, 1984; Moure & Hurd, 1987; Cure *et al.* 1993), coupled with the strong tradition of excellence in social insect biology (e.g., Kerr, 1969; references in Soares & De Jong, 1992), insures that Brasilian biologists will continue making important contributions to studies of insect social behavior.

Enabling factors for the evolution of eusociality

The following sections present an overview of phenotypic traits and environments that might facilitate the evolution of sociality, or maintain sociality once it has evolved [For discussions of the evolution of social parasitism, see West-Eberhard, 1986; Wcislo, 1987a, 1997c; Petanidou *et al.*, 1995; Cichon, 1996)]. I discuss the significance of each trait from the usual genetic perspective, and also show how each trait also modifies the developmental and selective environments at different levels.

Haplo-diploidy and relatedness asymmetries

Hymenoptera are haplo-diploid; unfertilized eggs develop into males and fertilized eggs developed into females (see Cruz-Landim, 1984; Crozier & Pamilo, 1996; Cook & Crozier, 1995). A haplo-diploid sex determination mechanism also occurs in other arthropods such as thrips, some beetles, or mites (e.g., Crozier, 1975; Andersson, 1984). Hamilton (1964, 1972) realized that haplo-diploidy results in an asymmetry in the genetic relatedness between mother and daughter (on average, sharing genes with a probability of 0.5), and between a daughter and a sister (on average, sharing genes with a probability of 0.75), if the mother mates once. If all else is equal, this relatedness asymmetry gives an inclusive fitness advantage to siblings that help rear other siblings, rather than producing their own offspring, if worker females can bias resource investment towards worker-sisters (Trivers & Hare, 1976; reviewed in Crozier & Pamilo, 1996; Rosenheim *et al.*, 1996). Mueller (1991) provides experimental evidence from *Augochlorella* (Halictidae) that workers can bias the sex ratio in their own interests. Haplo-diploidy also provides a mechanism that allows females to control the sex of their offspring, minimizing the costly production of males that usually make no contribution to the social welfare of the group.

Many researchers have focused exclusively on relatedness to explain the evolution of eusociality (see Introduction), even though Hamilton (1964, 1972) and others discussed potential problems with this "3/4-relatedness" hypothesis (e.g., Alexander *et al.*, 1991). First, the majority of Hymenoptera are not social, so factors other than haplo-diploidy must be important. Second, if females use sperm from more than one male, then this dilutes the relatedness between sisters. We need information on the frequency of multiple mating and paternity in solitary or weakly social species (see Garófalo, 1980; Wcislo & Buchmann, 1995). Third, colonies can have more than one reproductive (queen), again diluting relatedness (see Keller, 1993). Thus there are good reasons to doubt that the "3/4 -relatedness" hypothesis by itself accounts for the biased phyletic distribution of eusociality in Hymenoptera (e.g., Hamilton 1987; Alexander *et al.*, 1991). However, it is important to stress that the more general idea of kin selection is not in question (see Queller & Strassmann, 1998).

The evolution of haplo-diploidy permits the establishment of social environments characterized by relatedness asymmetries. To exploit these asymmetries, however, organisms require cues that mirror relatedness differences, and neuro-sensory mechanisms to perceive them in nest-mates (see "Nest Recognition and Discriminative Cognitive Abilities"). The phyletic distribution of these sensory traits is not well understood. Haplo-diploidy is also important for the evolution of sociality because it allows mothers to control the sex of their

offspring, which means females can manipulate the sex ratio of their brood to maximize their inclusive fitness, as discussed above.

Although haplo-diploidy is usually viewed as a genetic mechanism that *facilitates* social evolution, Roubik *et al.* (1996) document a high level of diploid males (which are sterile) in several genera of orchid bees (Hymenoptera: Apidae: Euglossini). They hypothesized that haplo-diploidy may *impede* social evolution because of costs associated with producing sterile, diploid males (see e.g., Camargo, 1982; Carvalho *et al.*, 1995).

Parental care

Wheeler (1928) emphasized that eusocial behavior originated in family groups comprised of one or both parents that regularly cared for offspring. This "subsocial route" (parent-offspring) to eusociality was contrasted with a "semi-social route" involving a cohort of same-generation adults (Lin & Michener, 1972; Carpenter, 1989; Wickler & Seibt, 1993). A distinction between sub- and semi-social routes focused attention on the relative importance of genetic relatedness among nest-mates (Gadagkar, 1991). Alexander *et al.* (1991), however, argued that these distinctions distract attention from a more fundamental pattern: parental care ("subsociality") may be a universal precursor to eusociality (e.g., Eickwort, 1981; Windsor & Choe, 1994; Halffter *et al.*, 1996). Effectively, subsociality is a mechanism that gives parents control over many aspects of their offsprings' environments. Parents can enhance the natal environment (e.g., by manipulating food quantity or quality), favoring some offspring and increasing their chances of successful independent life. Parents can also impoverish the natal environment and discriminate against other offspring, decreasing their chances and constraining them to stay at home as helpers (Alexander, 1974; Michener & Brothers, 1974).

Consequences of nest ownership and central place foraging

Parental care is frequently associated with food storage and construction of a nest (Vander Wall, 1990). A nest or web is the stage for the evolution of social behavior (see Wenzel 1991; Starr, 1991). Nest construction with food storage has evolved in some beetles (Coleoptera) (Halffter & Edmonds, 1982); crickets (Orthoptera) (e.g., Lockwood & Rentz, 1996); termites (Isoptera) (Shellman-Reeve, 1997); ants (Hölldobler & Wilson, 1990); and several lineages of aculeate Hymenoptera (Pompilidae, Vespidae, Apoidea including Sphecidae) (Evans & West-Eberhard, 1970; Michener, 1974; Wenzel, 1991; Wcislo & Engel, 1996; reviewed in Vander Wall, 1990). Defining a nest more generally,

this list could be extended to include spiders and their webs, tent-making caterpillars (Lepidoptera), caddisflies (Trichoptera), and gall-making aphids (Homoptera) and thrips (Thysanoptera) (refs. in Choe & Crespi, 1997).

Different facets of nest site selection point to abiotic (physical) and biotic (biological) factors that passively modify environments. The spatial relationships among nests varies greatly among species. Both social and solitary forms, as well as ground-nesting or twig-nesting forms, can be found nesting within aggregations or be spatially isolated (e.g., Wcislo & Cane, 1996; Schwarz *et al.* 1997). A tendency to aggregate nests influences the spatial associations of genotypes (e.g., Kukuk, 1989; Yanega, 1990; Blows & Schwarz, 1991; Wilson *et al.*, **1992;** Pfennig & Reeve, 1993). Aggregations create opportunities for positive or negative social interactions (e.g., Gadgil *et al.* 1983), which in turn may select for refined perceptual capabilities for recognition and assessment (see "Nest Recognition and Discriminatory Cognitive Abilities").

Proximate mechanisms used by solitary bees or wasps to select a nest site are not well understood (reviewed in Wcislo & Cane, 1996; for eusocial forms, see Roubik, 1989). Different soil-dwelling species prefer certain edaphic conditions (soil types), but within an area of suitable habitat there may be no obvious abiotic factors that correlate with the patchy distribution of nests (e.g., Martins & Figueira, 1992; reviewed in Wcislo & Cane 1996). Potts & Willmer (1997) show that biotic and abiotic factors interact in the sweat bee, *Halictus rubicundus* (Halictidae), such that preferences for particular soil types change as a function of nest density.

Probably many solitary and weakly social species have nests isolated one from another, but these nests are hard to find, and not much is known of their biology (e.g., Zucchi *et al.*, 1969; Roubik, 1989; Wcislo & Cane, 1996). There may be consistent differences among species in tendencies to aggregate nests, but this has not been rigorously examined; the development of relevant statistical tests now permits such studies (see Campbell, 1996; Syrjala, 1996). Anecdotal observations suggest that nests in some lineages may be more densely aggregated in temperate areas than tropical ones (e.g., pers. obs. on Halictidae, Sphecidae; Martins, pers. comm. on *Sphex*). Again, however, we need quantitative tests.

Nesting aggregations can last only one season or persist for at least 35 years (examples in Wcislo & Cane, 1996). In some cases, aggregations persist until the habitat becomes unsuitable (e.g., vegetation overgrowing the nest site; Yanega, 1990). Persistent aggregations hypothetically permit the build-up of larger parasite populations, which, in turn, potentially increases benefits associated with group-living (see below). In one study, Eickwort *et al.* (1996) found that overall cell mortality for solitary nests of *Halictus rubicundus* (Halictidae) within an aggregation was 15.5%, while for isolated nests the rate was 8.1%.

Long-term population studies of solitary and social insects, and their parasites, are needed (and see next section).

Nest densities at aggregations can range from a few nests per meter^2 to an estimated 300 nests/m^2 in *Centris caesalpiniae* (Hymenoptera: Apidae) (Rozen & Buchmann, 1990). Hamilton (1971a) developed the hypothesis of a "selfish herd" to explain why animals live in herds: the herd (group) conceals a particular individual (EGO) from enemies because EGO is surrounded by neighbors who will be attacked first. Wcislo (1984) hypothesized that nesting aggregations function as a selfish herd, and gave supporting evidence from *Crabro* wasps (Sphecidae). However, this hypothesis has not been tested for most taxa (reviewed in Rosenheim, 1990; Wcislo & Cane, 1996).

Nest-site selection may influence tendencies to evolve social behavior (Michener, 1985, 1990; Wcislo, 1996a; Alexander *et al.*, 1991). Alexander *et al.* (1991) argued that sociality in some lineages [e.g., termites (Isoptera) and naked mole rats (Bathyergidae)] is related to the fact that they live in safe habitats where their domicile can be easily defended and expanded, and where one individual can control access to sites of reproduction. There may be habitat-specific differences in exposure to natural enemies, which in turn would modify the benefits and costs of group-living. Michener (1985, 1990) hypothesized that parasites and predators are more likely to locate bees' nests in the ground, relative to twig nests, because it would be easier to locate nests distributed in two-dimensional versus three-dimensional space. In turn, social evolution may be more frequent among ground-nesting taxa than twig-nesting taxa, because of enhanced benefits associated with mutualistic nest defense in such a putatively hostile environment. Comparisons involving pairs of related sister taxa showed that ground-nesting species more frequently had higher rates of parasitism than did twig-nesting species of bees and wasps; however, confounding factors suggest that this conclusion should be accepted with caution (Wcislo, 1996a). Experimental studies on the search behavior of natural enemies will probably be more effective in testing Michener's hypothesis. Jeanne (1975) hypothesized that latitudinal gradients in ant predation influenced wasp (Polistinae) social behavior, but the possible relevance of such predation to variation in nesting and social behavior of other taxa needs to be studied.

The evolution of nesting behavior itself is an environmental change with an important consequence for understanding the evolution of eusociality. Nesting behavior is invariably associated with food-hoarding, which concentrates resources (pollen, prey, etc.) in one location (see Vander Wall, 1990). Inevitably, this concentration attracts predators and parasites, including thieving conspecifics (Hamilton, 1971b; Wcislo 1987a; Field 1992). Nest-building increases the reward that others gain by stealing, effectively creating a more hosti-

le environment (cf. Côté & Poulin, 1995). This new hostile environment, in turn, may select for several modes of defense (next section).

Group-living as a mode of defense

An abundance and diversity of parasites and predators can select against independent (solitary) nesting. Natural enemies of solitary and weakly social insects range from bacteria to parasitic fungi, nematodes, insects, and mites, to predatory insects, and arachnids (e.g., Wcislo & Cane, 1996; see Schmid-Hempel, 1995 for eusocial insects). Any given individual (or colony), however, is usually attacked by a subset of these enemies. Morbidity rates from different enemies are not known for many species (e.g., Packer *et al.*, 1989), but such information is crucial for understanding the role that natural enemies play in the evolution of sociality. Hypothetically, microparasites (e.g., bacteria) will select *against* sociality because a larger colony theoretically facilitates transmission of pathogens relative to a smaller-sized colony, especially among kin-groups if queens mate once (Hamilton 1987). Macroparasites, however, will select *for* group-living because behavioral defenses can exclude the enemies (see also Choe & Crespi, 1997). Although theoretically important (e.g., Lin & Michener, 1972; Alexander, 1974; Wcislo, 1984; Hamilton 1987; Côté & Poulin, 1995), the relative costs and benefits of group-living under varying parasite loads are not well documented (e.g., Edgerly, 1994; Garófalo *et al.*, 1992; Hogendoorn & Velthuis, 1995; for reviews, see Schwarz *et al.*, 1997; Wcislo, 1997a).

Nest recognition and discriminatory cognitive abilities

Some insects [e.g., some spider wasps (Pompilidae), burying beetles (Silphidae)] construct a nest *after* resources are gathered together, or resources are already localized (see Vander Wall, 1990). Most nest-makers, however, repeatedly forage away from the nest, and therefore require cognitive abilities to return from afield and, in some species, to discriminate their nests from others nearby (Wcislo, 1992b). Nest recognition provides a behavioral context in which natural selection favors those individuals with increasingly sophisticated cognitive skills; in turn, these skills then might be modified for use in social contexts [for general discussion of links among perception, learning, and evolution, see Beugnon *et al.* (1996) and Vancassel *et al.* (1996)].

Orientation abilities of solitary insects, especially bees and wasps, have been well-studied, and, vision is usually the most important sensory modality (reviewed in Menzel *et al.*, 1996; Zeil *et al.*, 1996). Olfactory or contact chemi-

cal cues are also important orientation cues or signals for most bees, pemphredonine speciforme wasps, an earwig (Dermaptera), a gryllacridid (Orthoptera), and a terrestrial isopod (refs. in Wcislo, 1992b; Lockwood & Rentz, 1996). Individuals mark structures with glandular secretions or feces, which they use to recognize and discriminate the structure from nearby, conspecific structures (reviewed in Wcislo, 1992b). Selection for refined discriminatory capabilities should be more intense as the distance between nearest neighbors becomes shorter (e.g., nesting within aggregations versus alone) (see Hefetz, 1987; Wcislo, 1992). Such a system can be evolutionarily co-opted for use in distinguishing kin (or familiar individuals) from non-kin (unfamiliar individuals), and provide capabilities to manipulate social information regarding dominance status and relatedness asymmetries (Alexander 1979: 112ff.; Ayasse *et al.*, 1995).

Recognition and discrimination capabilities of most solitary or weakly social species have been studied only in the behavioral context of nest guarding (refs. in Fletcher & Michener, 1987; Wcislo, 1997c) or, less frequently, mating behavior (e.g., Wcislo, 1987b). In some cases (e.g., *Lasioglossum hemichalceum*, Hymenoptera: Halictidae) individual females can be introduced into foreign nests, suggesting that bees are not discriminating against non-resident bees (P. Kukuk, pers. comm.; WTW, pers. obs.).

The modalities by which individuals assess the reproductive capabilities and social status of nest-mates in very weakly differentiated societies also need to be studied. In *Lasioglossum zephyrum* (Hymenoptera: Halictidae), for example, socially-dominant individuals had high levels of activity, which apparently inhibits worker ovarian development (see Michener, 1990). Topical application of synthetic Dufours' gland secretions to gynes of *L. malachurum* alters the intensity of aggressive behavior during social competition, suggesting that social status can be assessed by pheromones (Smith & Weller 1989; see Ayasse *et al.*, 1995, for *Bombus*, Hymenoptera: Apidae).

Two likely sources for origins of the perceptual capabilities for social recognition are nest recognition by females, or mate recognition by males or females (Hölldobler & Michener, 1980). There is still not enough evidence to eliminate either possibility (Wcislo, 1987b, 1992a,b). Indeed, nothing is known about female perceptual capabilities in the context of sexual behavior. The possibility that a male-derived cognitive trait can be evolutionarily transferred to females is enhanced by a recent finding in honey bees (*Apis*, Hymenoptera: Apidae). Benatar *et al.* (1995) showed that artificial selection on males for improved learning results in a corresponding improvement in learning abilities of worker female progeny. Prey or food recognition is yet another context for the origin of recognition capabilities (cf. Bernays & Wcislo, 1994), but little is known about how solitary bees or wasps recognize their prey or pollen source.

Seasonality and sociality

Mother-daughter interactions and, by extension, the possibility for mother-daughter societies, require two conditions. First, an overlap of generations requires that the egg-to-adult developmental time be sufficiently short so that mothers are still living when their daughters become adults, or adults are long-lived. For example, the development time of a largely solitary bee, *Lasioglossum figueresi* (Halictidae), is almost 80 days, and most mothers have already died when the brood emerges, effectively precluding mother-daughter interactions (Wcislo *et al.*, 1993). A delayed developmental rate may be a larval strategy to avoid maternal manipulation. Secondly, eusocial colonies by definition have at least one brood comprised mostly of worker females, prior to the production of the reproductives. Thus, generation time must be sufficiently short, and the period of foraging activity sufficiently long, that at least two broods can be produced within the growing season at a locality (e.g., Martins, 1993).

Studies at high latitudes and high altitudes in north temperate regions show that the matrifilial (mother-daughter) stage is shortened or eliminated at the colder limits of their distribution. For example, the Holarctic sweat bee *Halictus rubicundus* is distributed across Eurasia and northern North America, where it extends to the southern United States. Its nesting biology has been studied at various lower-elevation sites in Europe and North America where it typically lives in eusocial nests (Eickwort *et al.*, 1996; Yanega, 1997). At a high-elevation site (2850 m) in the western United States the growing season is too short to permit two generations having the developmental rate of *H. rubicundus*; consequently, all females are solitary.

The proximate mechanism used to determine "length of growing season" may be photoperiod, at least for temperate species. Yanega (1993, 1997) presents strong correlational evidence to show that more males are produced in a temperate halictine bee (*Halictus rubicundus*) under longer photoperiods, although this demographic effect can be altered by temperature. Furthermore, he shows a correlation between the percentage of males within the population and the percentage of females entering diapause, which is associated with different social structures. For temperate species, he hypothesized that there is an indirect relationship between abiotic environmental factors and social behavior, mediated by demography, which may explain the different social organizations bees exhibit in different areas. Experimental evidence to test these ideas, however, is lacking.

Solitary bees and wasps, contextual change, and the evolution of tolerance

Group-living entails an environmental change that may facilitate further social evolution. With group-living, the social environment becomes increasingly important due to competition over the control of resources (Alexander, 1974; West-Eberhard, 1979; Craig, 1983). Group-living has potential benefits other than improved defense, including increased efficiency in locating resources (e.g., Gordon, 1996) or acquiring information about their external environment with greater reliability (e.g., Seeley, 1995). Recently, Emlen (1994, 1995) elaborated a general framework for the evolution of family-based groups in which he showed that information on the following four parameters can predict whether families and extended families (kin groups) will form or disintegrate: (i) cost-benefit ratio of group-living, (ii) abilities of individuals to achieve social dominance, (iii) genetic relatedness among group members, and (iv) probable success of independent nesting. Emlen (1995) noted that family groups are inherently unstable, and tend to disintegrate unless the probability of breeding independently is low because of unfavorable environmental conditions (i.e., strong "ecological constraints" on solitary behavior). The evolutionary loss or suppression of social behavior supports this contention (e.g., Richards, 1994; Eickwort *et al.*, 1996; Gadagkar, 1997b; Wcislo & Danforth, 1997). Ecological constraints, however, are not static and must be defined in reference to the organisms involved. As noted above, for example, parents can manipulate their offspring's environment, and thereby change the threshold at which a given individual is ecologically constrained, but often the individual variability relevant to such changes is downplayed.

Most bees and wasps lead solitary lives and are intolerant of same-sex conspecifics, and regulation of this aggression is required for social evolution (e.g., Zucchi, 1973; Sakagami & Zucchi, 1977; Moynihan, 1998). An early stage of social integration involves mutual tolerance among conspecifics (e.g., Melo, this volume; Horel *et al.*, 1996; Robertson *et al.* 1998). However, information is scarce on individual variability in tolerance thresholds among solitary insects, or during the solitary phase for social species. Intraspecific tolerance has been demonstrated with laboratory studies of the otherwise solitary sweat bee, *Lasioglossum figueresi* (Hymenoptera: Halictidae) (Wcislo, 1997d), as well as other solitary halictids (e.g., Kukuk, 1992; McConnel & Kukuk, in press), and sphecid wasps (Pfennig & Reeve, 1989) (for other examples, see Melo, this volume). Field observations likewise indicate a degree of tolerance among conspecifics. A female wasp, *Editha magnifica* (Sphecidae), successfully entered a foreign nest but refrained from killing the resident larva, or usurping the nest (Martins, 1993). Solitary wasps (*Sphex*, Sphecidae) (Pfennig & Reeve, 1989) and halictid bees (refs. above) respond differently to related versus unrelated in-

dividuals, suggesting some components of kinship discrimination are already present in solitary species.

An environment in which tolerant individuals have repeated interactions occur is favorable for the establishment and spread of cooperative behavior because individuals have opportunities to reciprocally express cooperative behavior (Hamilton 1971b; Axelrod 1984; Trivers, 1985: 361ff.). Tolerance for social interactions can enhance or diminish social differences among individuals due to social competition (see Staw & Ross 1989). Group-living spider wasps (Hymenoptera: Pompilidae) are not socially differentiated, and were usually indifferent to one another, but were fiercely aggressive when prey was available (and hence there was an opportunity for reproduction) (Wcislo *et al.*, 1988; reviewed in Evans & Shimizu, 1996). Other communal insects (e.g., *Perdita portalis*, Hymenoptera: Andrenidae) show no aggressive behavior or intraspecific parasitism, and there is no differentiation of social roles (Danforth, 1991). In contrast, differentiated social structures *decrease* the possibility of physical violence by clearly establishing dominant and subordinant relationships via ritualized behavior. Excellent examples of ritualized behavior are well-studied in stingless bees oviposition behavior (Meliponinae) (e.g., Zucchi, 1993).

A submissive response to an aggressor can increase the likelihood of similar behavior by both individuals during subsequent interactions. These repeated interactions are known to lead to learned dominant-subordinant relationships in other animals (references in Wcislo, 1989). Spontaneous interactions can be reinforced by changes in hormonal titre (Leshner, 1983), and by learning (see Wcislo, 1997a). In some *Bombus*, for example, a queen's dominance behavior is initially established by physical aggression, but later the subordinate workers avoid the queen on the basis of olfactory cues and presumably associative learning, without direct aggression (Free, 1953). These interactions can serve as variation for the origins of novel social organizations via contextual shifts (West-Eberhard, 1987; Wcislo 1997a). All of these areas remain little studied for casteless group-living insects, even though they are probably essential for understanding how behavioral flexibility and learning relates to the origins of eusociality (West-Eberhard 1992a; Wcislo, 1997a).

Future directions

Considerable emphasis has been placed on kinship in studies of insect sociality, and the major advances in molecular biology will give us increasingly precise information on the genetics of insect social behavior, based on few species that are used as "model systems" (e.g., the honey bee, *Apis mellifera*) (see Robinson *et al.*, 1997). However, these advances may outpace our understanding of the ecological and behavioral contexts in which genes are expressed and

hence in which phenotypes develop. Moreover, species of *Apis* are far from being "typical" social bees and it is questionable that they really are "model" species. To complement a genetical approach, we need to systematically address environmental roles in organizing the development of social behaviors.

We need to obtain behavioral data on the numerous species that have not been studied, especially in the tropics, with an aim to document variation in solitary and social behavior, among and within populations. Such studies will help us better understand the environmental features that influence the expression of social behavior (e.g., Banschbach & Herbers, 1996). Such studies need to be viewed in light of phylogenetic information to determine the number of times *a capability to express social behavior* has arisen in different lineages.

In general, we need experiments to understand the developmental basis of social behaviors. For species that show geographic variation in social behavior, rearing individuals from "social" populations and those from "solitary" populations under the same environmental circumstances will help us determine the breadth of the reaction norm (i.e., the extent to which the expression of particular social traits differs under different environmental conditions). "Common garden" studies are complicated by the fact that they must be continued for at least 2 generations, in order to assess the importance of maternal (cytoplasmic) effects (see Roff, 1996).

Parasites and predators have been implicated repeatedly in the evolution of social behavior for many years, yet few quantitative data are available, and we know little about the relative importance of different species of natural enemies, especially in the tropics. Presumably there are trade-offs between increasing group size and enhanced nest defense against macro-parasites like flies, wasps, and beetles, versus ease of transmission of micro-parasites like bacteria and virus. But these possible trade-offs have not been investigated.

Our tendency to externalize "the environment" hinders an appreciation of environmental modifications induced by activities of animals themselves. A focus on environmental sources of information should improve our understanding of the essential links among development and evolution, and provide a more complete picture of insect social evolution.

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