

# Organization of Insect Societies

FROM GENOME TO SOCIOCOMPLEXITY



*Edited by*

Jürgen Gadau and Jennifer Fewell

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## CHAPTER SEVEN



# The Evolution of Communal Behavior in Bees and Wasps: An Alternative to Eusociality

WILLIAM T. WCISLO

SIMON M. TIERNEY

BEGINNING WITH DARWIN (1859), a fundamental question for research on social insects has concerned the evolution of divergent phenotypes among already-sterile individuals (Linksvayer and Wade 2005). As reviewed in this volume, the caste-based (eusocial) societies of termites (Isoptera), and ants, wasps, and bees (Hymenoptera), have been extensively studied. A second question concerns the evolutionary *origins* of group life, for which appropriate foci are societies in which group members share a nest but work is not organized by caste differences (i.e., cooperative breeders and communal nesters). Unlike cooperatively breeding vertebrates (see Brockmann 1997; Hayes 2000; de Waal and Tyack 2003; Ekman and Ericson 2006) and eusocial invertebrates (see Cole, this volume), much less is known about the behavior and evolution of communal, casteless societies and the ecological contexts in which they occur.

Despite arguments for and against revising social terminology (see references in Costa and Fitzgerald 2005; Wcislo 2005), we use Michener's (1974) definition of *communal behavior*: cohabiting females that share a nest but build, provision, and oviposit in their own cells. Theoretically it is important to distinguish such associations from quasisocial ones in which reproductively competent females jointly build and provision cells. In practice, however, it is difficult to distinguish between communal and quasisocial associations because of the difficulties in observing behavior within nests. As Michener (1974, 2007) and others have pointed out, for many

taxa these social terms apply to individual colonies or nests, but not to entire species, unless there is no intraspecific variation. Thus, although we sometimes refer to a particular species as having communal behavior, this is shorthand and we intend to refer to the particular nests studied in a given population. Conversely, many species are regarded as "solitary" even though some nests occasionally contain communal females.

A body of largely anecdotal evidence shows that communal behavior is widespread within the aculeate Hymenoptera. It evolved repeatedly and is stable over evolutionary time. Communal social groups are often described as egalitarian, or being comprised of reproductive equals, but in most cases this is an untested assertion. As West-Eberhard (1978) argued, in most group-living bees and wasps it is difficult to imagine that there are *no* reproductive inequalities, due to differences in age, genetic make-up, and nutritional status. It is more likely that female reproductive opportunities and output vary considerably, and that rudimentary dominant and subordinate behaviors are widespread (West-Eberhard 1978; Shimizu 2004; Jeanson, Kukuk, and Fewell 2005).

Perspectives on the evolution of communal behavior have shifted since early work by Wheeler (1923) and others. Communal societies of insects were thought to represent an intermediate stage in an evolutionary transition from solitary to eusocial behavior, with a step-wise increment in social complexity, such that solitary species first evolved communal behavior and then, via subsequent steps, the communal species gave rise to eusocial ones (Wheeler 1923; Evans 1958; Wilson 1971; West-Eberhard 1978). Studies of intraspecific variation in social behavior, coupled with a renewed emphasis on the importance of taking historical (phylogenetic) patterns into account, have suggested that this step-wise view of behavioral evolution is usually not supported by available data (Michener 1985; Carpenter 1989; Schwarz et al. 2003; Schwarz et al. 2007). Michener (1985, 2007) and others (e.g., West-Eberhard 2003) have argued that in some lineages behavior is so flexible that social organization may evolve without a series of intervening species, and that social behavior may be gained and lost so frequently that the phylogenetic signal in the behavioral data is unreliable. Indeed, Michener (2007, p. 15) suggests that the perennial question of the number of times eusociality has arisen during bee evolution is "both unknowable and useless. It is the wrong question." As discussed below, a phylogenetic question in need of more attention is why communal societies and caste-based ones appear to be evolutionary alternatives in different lineages.

In this chapter, we briefly summarize the occurrence of communal behavior in bees and wasps, and review studies showing that nestmates are often not kin, and that there is little evidence that females discriminate between familiar and unfamiliar individuals. Consequently, any potential benefits from indirect (inclusive) fitness benefits (*sensu* Hamilton 1964) are likely to be minimal. We discuss environmental conditions that might favor communal organization *vis-à-vis* solitary or eusocial behavior due to direct fitness benefits. Recognizing that successful organisms “solve” environmental “problems” (Wcislo 1989; Odling-Smee, Laland, and Eldman 2003), we consider whether communal social organization is an alternative solution to tackle the same environmental problems that were solved by the repeated evolution of caste-based social organizations. We also draw attention to critical questions for which data are almost totally lacking, and thus emphasize at the outset that any conclusions are necessarily tentative.

### Phyletic Distribution of Communal Behavior

We restrict our discussion to the nest-building Aculeata (Hymenoptera), excluding ants (i.e., Apoidea including both Apiformes and Spheciformes [Michener 2007]; Vespidae; and Pompilidae). We do not intend to provide an exhaustive survey, but cite reviews and representative examples. In some taxa, communal social organization occurs as an ontogenetic phase (e.g., co-founding gynes of many eusocial ants, see Heinze and Foitzik, this volume; Fefferman and Traniello, this volume) or as a temporary condition, while in others communal organization is maintained throughout the life of a colony. In many “solitary” bees and wasps, some nests are occupied by two or rarely more females. Such species are critical for understanding the evolution of tolerance (Reeve 1989; Moynihan 1998), which is a fundamental prerequisite for any kind of social organization. Opportunistic communal associations are frequently reported for species in which nests are spatially clustered in large aggregations (Eickwort 1981; West-Eberhard 1978; Cowan 1991; Matthews 1991; O’Neill 2001); however, these species are inherently more likely to attract the attention of interested biologists, and little is known of the relative frequency of opportunistic associations in species that nest in isolation relative to those that aggregate nests. In other species, females frequently switch nests and transient communal associations occur when two females overlap in the same nest (Wcislo, Low, and Karr 1985; O’Neill 2001).

Regular communal associations are known in many of the major lineages of bees, including Colletidae (Sakagami and Zucchi 1978; Spessa, Schwarz, and Adams, 2000; *contra* Michener 2007: p. 133, who stated that "all colletids are solitary"); Andrenidae (Paxton, Kukuk, and Tengo 1999; Paxton et al. 1996; Danforth 1989, 1991); Halictinae, especially the agapostemon sweat bees (Roberts 1969; Abrams and Eickwort 1981; Kukuk 1992; Richards, von Wettberg, and Rogers 2003); Nomiinae (Wcislo and Engel 1996); Megachilinae (Garófalo et al. 1992); Xylocopinae (Camillo and Garófalo 1989); and Apinae (Rozen 1984; Soucy, Giray, and Roubik 2003; Cameron 2004). Among wasps, these associations are known for Pompilidae (Wcislo, West-Eberhard, and Eberhard 1988; Evans and Shimizu 1996), Sphecidae (Evans and Hook 1986), and Eumeninae (Cowan 1991). For general reviews, see Michener (1974), Wilson (1975), Iwata (1976), West-Eberhard (1978), Eickwort (1981), Cowan (1991), Matthews (1991), and O'Neill (2001).

A striking fact about the phyletic distribution of communal behavior in aculeate Hymenoptera is that it typically occurs in clades in which there are no examples of caste-based societies (Eickwort 1981; Kukuk and Eickwort 1987; Danforth, Neff, and Baretto-Ko 1996). For example, most (28 of 39) species of nest-sharing wasps discussed by West-Eberhard (1978) are from clades where worker castes have never evolved. One exception to this phyletic pattern involves an intraspecific polyphenism in the sweat bee *Halictus sexcinctus* (Richards et al. 2003), in which both communal and eusocial nests are known from a single locality; an analysis of mitochondrial DNA sequences suggests that the two forms do not represent cryptic species. A second exception is known in a spheciforme wasp taxon (Pempredonini), in which communal species and the eusocial *Microstigmus* co-occur (see references in Matthews 1991; Wcislo 1992).

### Possible Evolutionary Transitions Involving Communal Behavior

West-Eberhard (1978) proposed that nest-sharing, casteless social groups would give rise quickly to polygynous family groups because of inclusive fitness benefits derived from associating with kin. She also hypothesized that once family groups evolve, then they are more likely to persist because kin selection will dampen the disruptive effects of intraspecific parasitic behaviors (e.g., cell and prey usurpation: Eberhard 1972; Eickwort 1975;

Ward and Kukuk 1998). Although she did not discuss them, two phylogenetic predictions follow from West-Eberhard's hypothesis. First, in lineages in which females do not live in family groups, such as communal *Perdita* or *Andrena* bees (e.g., Danforth, Neff, and Barretto-Ko 1996; Paxton et al. 1996), group-living should be evolutionarily labile and species should repeatedly switch from solitary to communal life histories. Phylogenetic studies show that some lineages with caste-based social family groups contain species with secondarily solitary behavior (Wcislo and Danforth 1997; Danforth, Conway, and Ji 2003), though there may be a "point of no return" where it is impossible to lose social behavior (Wcislo and Danforth 1997; Wilson and Hölldobler 2005) without going extinct or becoming an obligate social parasite (but see Chenoweth et al. 2007). In contrast, for lineages of bees and wasps with communal behavior there is no evidence for secondary reversions to solitary behavior, unlike birds in which communal roosting has been lost repeatedly (Beauchamp 1999; Ekman and Ericson 2006).

A second prediction following West-Eberhard (1978) is that obligate brood and social parasites that attack related heterospecifics should evolve more frequently in lineages with females living in nest-sharing, nonfamily groups. The behavioral antecedents to obligate brood parasitism (i.e., opportunistic cheating or robbing) are widespread and occur in species with communal nesting behavior (Wcislo 1987; Field 1992). Lineages that contain many communal species (e.g., andrenid and nomiine bees, *Cerceris* wasps) have not generated any known obligate brood parasites, although communal species serve as hosts for some obligate brood parasites (reviewed in Wcislo 1987).

### Costs of Communal Social Organization

The relative costs and benefits of communal living have been discussed repeatedly (Lin and Michener 1972; Eickwort 1981; Cowan 1991; Kukuk 1992), although the empirical data are scant (see summary in Table 7.1). Potential costs fall into two general classes: one associated with increased competition for resources, and one with increased risk of losing those resources to conspecific cheaters.

#### Resource Competition

As with all social groups, there is likely to be increased competition for resources because conspecifics by definition are the closest competitors

for the same resources (Alexander 1974; Dittus 1988). Different females in a communal nest use the same set of floral resources, or the same set of prey resources (Wcislo et al. 1988, Wcislo 1993), so there is potential for competition. There are no studies, however, that assess the impact of resource limitations on the foraging efficiency of communal females, nor are there studies that indicate that any information transfer takes place among them. Indeed, a study of the facultatively communal bee, *Perdita coreopsisidis* (Andrenidae), showed that there are no differences between solitary and communal females with respect to duration of foraging trips; time spent within nests between trips; time of day spent foraging; number of trips needed to provision a cell; or the number of cells provisioned per day (Danforth 1989).

### Usurpation and Intraspecific Parasitism

The second potential cost for communal females is associated with increased probabilities of nest (or cell) usurpation and intraspecific brood parasitism. Although it is routinely claimed that group-living is associated with such increased risks (e.g., Eickwort 1981; Cowan 1991), few empirical studies have demonstrated that *intraspecific* parasitism and usurpation are more likely among communal nesters than among solitary ones (e.g., Eberhard 1972; Eickwort 1975; Wcislo 1987; Field 1992). Nevertheless, anecdotal evidence suggests that the claim is valid. The spider wasp *Auplopus semialatus* (Pompilidae), for example, regularly lives in small communal groups with fewer than eight females; cohabiting females vigorously contest the use of empty brood cells and captured spiders, and repeatedly usurp prey from nestmates (Wcislo, West-Eberhard, and Eberhard 1988). In most species of communal bees and wasps, however, it is extremely difficult to assess true rates of intraspecific parasitism for two reasons. First, many species nest in the soil, which makes it impractical to record behavioral observations without the use of observation nests (e.g., Danforth 1991), and thus it is difficult to observe usurpation. Secondly, genetic markers are not particularly informative in assessing whether cells have been usurped, unless they are coupled with behavioral observations, since they will otherwise show that multiple females are reproducing within a given nest.

Table 7.1. Overview of proposed costs and benefits associated with communal societies, in comparison with an assessment of those costs and benefits associated with caste-based societies. An assessment of available empirical evidence for communal nesting is also given.

Cost/benefit to communal organization	Comparison with caste-based societies	Empirical evidence from communal bees and wasps
<b>Proposed costs</b>		
<i>Competition</i>		
Intense competition within nests for resources needed for brood rearing	Less intense competition among principal egg layers	Anecdotal
<i>Conspecific cheating</i>		
<i>Increased nest parasitism and cell usurpation</i>	Equivalent risk of intraspecific parasitism among foundresses; some worker reproduction but not phylogenetically widespread	Largely anecdotal
<i>Temporal costs due to extra time spent protecting nests and cells from intraspecific parasites</i>	Lower costs associated with guarding against intraspecific parasites	Largely anecdotal
<b>Proposed benefits</b>		
<i>Improved defense</i>		
<i>Passive defense against interspecific parasites and predators</i>	Equivalent	Few studies inconclusive as to whether conspecific solitary nests are worse off than communal ones



*Active defense* (nest guarding)

Equivalent

Few studies inconclusive as to whether conspecific solitary nests are worse off than communal ones

*Energetic savings*

*Nest site limitations* make it advantageous to join rather than initiate a nest

Equivalent savings

None

Shared cost of general *nest construction*

Equivalent for cofounders and swarm founders

True for some arid zone taxa but not widespread among all communal vs. solitary comparisons

Increased foraging efficiency via *information transfer* amongst nestmates

Equivalent for species with communication among foragers

None

### Temporal Constraints

Another potential cost associated with intraspecific parasitism is the loss of time that could be spent on foraging and other tasks rather than guarding cells or nests. A communal spider wasp *Auplopus semialatus*, for example, required up to 120 minutes to seal a brood cell before it was safe from marauding nestmates, suggesting there is a cost to defending a cell (but see Soucy, Giray and Roubik 2003 for a counterexample). In general, however, we lack detailed time budgets for solitary and communal bees and wasps, which are needed to assess how much time is actually lost in guarding a nest or brood cells.

### Benefits of Communal Social Organization

Potential benefits associated with group-living in bees and wasps also fall into two general classes: one associated with improved defense, and one associated with energetic savings from shared nest construction and maintenance (see Table 7.1). Benefits associated with improved defense may be passive or active.

#### Passive Defense

Enhanced passive defenses arise from a dilution effect associated with increasing group size, analogous to Hamilton's (1971) "selfish-herd" arguments. If a parasite or predator attacks a brood cell at random, then the probability that any given cell is attacked is  $1/N$ , where  $N$  is the number of cohabiting females. Establishing nests in soil versus twigs may also shape relative rates of parasitism, if the relative complexity of environmental space (roughly two- versus three-dimensional, respectively) influences the success rate for searching parasites (Matthews 1991; Weislo 1996). 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 (Weislo 1996). If this conclusion is sustained, then group-living should evolve more frequently among soil-dwelling lineages rather than among stick- or mud-nesters (Michener 1985).

Improved defense may also arise as an incidental by-product of

increased activity at the nest entrance. In many cases it is difficult to ascertain whether individuals are behaving as functional guards or are merely standing near the nest entrance, which effectively guards it as a by-product of some other behavior. Both solitary and group-nesting females of an orchid bee spent approximately the same amount of time in their nests, but as a result of staggered foraging trips multi-female nests were unoccupied only 1.7% of the time, while solitary nests were unoccupied 30.1% of the time (Soucy, Giray, and Roubik 2003). Satellite flies (*Leucophora*) that entered a bee host nest (*Andrena agilissima*) remained within the nest for shorter periods of time if another host female returned to the nest, suggesting activity *per se* effectively guards a nest (Polidori et al. 2005). In contrast, anecdotal evidence for the facultatively communal bee, *Perdita coreopsidis*, showed that the most populous nest also had the highest rate of cell parasitism (Danforth 1989), implying that more individuals do not translate into better defense, and in fact may render the nest more attractive to parasites and predators.

#### Active Defense and Nest Guarding

Wilson and Hölldobler (2005) argued that a prime driving force behind the evolution of eusociality are advantages associated with improved defense (also, e.g., Lin and Michener 1972; West-Eberhard 1978). They argued that small groups are better defenders than are solitary individuals, and larger groups are better than smaller groups. The same argument applies to communal nests (Lin and Michener 1972; West-Eberhard 1978; Forbes et al. 2002). Interspecific comparisons are confounded by the fact that the suite of natural enemies which attack solitary or social forms are not always the same; macroparasites and predators may have greater impact on solitary females, while microparasites (e.g., bacteria) may have greater impact on social ones (Wcislo 1997; Schmid-Hempel 1998). Conclusive tests of the idea that groups are more effective defenders than singletons are relatively scarce because they require comparisons of solitary and group-living individuals of the same species in the same location. Furthermore, from a defensive perspective, there is no reason to expect fundamental differences between communal and eusocial groups unless the latter have specialized defender morphs ("soldiers"), which are unknown in bees and wasps.

Active defenses may be associated with increased guarding behavior.

Most nests of the sweat bee *Agapostemon virescens*, for example, were occupied by communally nesting females, and one bee was continuously present at the nest entrance when bees were foraging (Abrams and Eickwort 1981). Communal nests were not attacked by cleptoparasitic bees (*Nomada articulata*), whereas the parasites entered the only solitary nest in the study when the occupant was out foraging. Likewise, a nest of a communal spider wasp, *Auplopus semialatus*, was unattended for less than a minute during more than 42 hours of observation, and in that brief time an obligate cleptoparasitic wasp, *Irenangelus eberhardi*, successfully oviposited in an open brood cell (Wcislo, West-Eberhard, and Eberhard 1988; for other examples, McCorquodale 1989a; Garófalo et al. 1992; Spessa, Schwarz, and Adams 2000). In contrast, females of the obligately communal bee, *Perdita portalis* (Andrenidae), were never observed guarding nests, suggesting that improved nest defense is unlikely to be associated with the maintenance of communal behavior in this species (Danforth 1991).

#### Nest Site Limitations

It may be advantageous to share a nest with others if nest sites are rare or nests are difficult to establish (Michener 1974; McCorquodale 1989a, 1989b). The availability of nesting substrata helps shape the community-level composition of Mediterranean bee communities (Potts et al. 2005), suggesting that nest site availability may be a limiting resource (Schwarz, Bull, and Hogendoorn 1998; Langer, Hogendoorn, and Keller 2004 for eusocial bees). It is not clear, however, whether suitable nesting substrata are more limiting for communal versus solitary species.

#### Sharing the Costs of Nest Construction

Various researchers have noted that communal nesting seems to be especially common in Australian halictine bees and sphecoid wasps (e.g., Knerer and Schwarz 1976; Evans and Hook 1986), and andrenid bees in the southwest deserts of North America and Mexico (e.g., Danforth 1991), where they frequently nest in very hard and compact soil. In such regions nests tend to be initiated following rains when the soil is soft (McCorquodale 1989b). Although there are no studies to ascertain the relative costs associated with establishing nests in wood or soil, or in relatively hard versus soft soil, causal links between substrate hardness and nest sharing have

been proposed repeatedly (Evans and Hook 1986; McCorquodale 1989a, 1989b; Wcislo, Fernandez-Marin, and di Trani 2004). In communal *Perdita* bees, for example, Danforth (1991) suggested that nest sharing may be advantageous due to the energetic and temporal costs associated with solitary nest excavation. Danforth also noted that if the period of resource availability is relatively brief, there may be temporal factors that select against solitary nesting, assuming that it takes a solitary individual more time to dig a nest relative to joining an already established one. In sphecoid wasps, however, spatial patterns of soil hardness were not associated consistently with patterns of nest provisioning behavior (see Wcislo, Low, and Karr 1985; McCorquodale 1989b, and references therein).

### Information Transfer

In birds, increased foraging efficiency is hypothesized to be one of the prime advantages associated with communal roosting (Ward and Zahavi 1973; Beauchamp 1999), assuming that roosts act as centers for information transfer whereby unsuccessful foragers can follow successful ones to a feeding site. To date there are no behavioral studies showing that communal bees and wasps use cues from foraging nestmates to reduce search time, as is well-known for numerous eusocial insects.

### Nest Productivity and Communal Behavior

Measures of per capita productivity imply that there are either benefits or costs to group nesting, depending on whether productivity is an increasing or decreasing function of group size (Michener 1974). In many taxa with behavioral castes there is an overall decrease in per capita productivity with increasing group size (Michener 1974; Karsai and Wenzel 1998), while in other taxa, especially in eusocial allodapine bees, there is increased productivity with initial increases in group size (Schwarz, Bull, and Hogendoorn 1998; Tierney, Schwarz, and Adams 1997; Tierney et al. 2002). In a communal colletid bee, *Amphylaeus morosus*, per capita productivity was not significantly different for communal or solitary nests (Spessa et al. 2000; also e.g., Danforth 1989). Published estimates of productivity may be biased, however, if solitary nests or those with fewer females suffer higher rates of nest failure than those with more females, or if brood development is not followed through to the adult stage.

### Kinship and Recognition Systems in Communal Societies

An ability to recognize and discriminate between nestmates and non-nestmates (frequently kin versus non-kin) is widespread in caste-based social insect groups (Fletcher and Michener 1987). West-Eberhard (1978) reviewed early literature on nest-sharing wasps and argued that about half of the 29 species she tabulated lived in groups that were comprised of relatives, based on behavioral inferences (e.g., frequent re-use of cells, low rates of dispersal) and on theoretical grounds: if group living is advantageous, then family-based group living will be favored because of additional indirect fitness benefits that accrue via kin selection, and genes that enable associations with relatives will be shared by those relatives (Hamilton 1964; Wilson and Hölldobler 2005). More recent studies using genetic markers are inconsistent with her arguments, and instead have shown that nest-sharing, casteless groups often are comprised of nonrelatives (Kukuk and Sage 1994; Danforth, Neff, and Barretto-Ko 1996; Paxton et al. 1996; Spessa, Schwarz, and Adams 2000; Kukuk, Bitney, and Forbes 2005; but see McCorquodale 1988 and Pfennig and Reeve 1993 for examples of kin associations).

Few studies are available that assess recognition capabilities in communal species for comparison with caste-based societies, or in solitary species that occasionally share nests (e.g., Pfennig and Reeve 1989). Kukuk and co-workers studied patterns of food exchange in a communal Australian bee (*Lasioglossum hemichalceum*; Halictidae) and found no tendency to preferentially direct food toward familiar individuals or nestmates (Kukuk and Crozier 1990; Kukuk 1992). Furthermore, females from distant nests can be introduced into another nest without evidence of fighting, and they begin to provision cells in the new nest (Ward and Kukuk 1998; Wcislo, personal observation), again suggesting the lack of any discrimination. A lack of discrimination between familiar and unfamiliar females was also observed during staged encounters for two species of communal andrenid bees (*Andrena* and *Panurgus*) (Paxton, Kukuk, and Tengo 1999). Females have been reported to join nests in other communal bees and wasps with no signs of aggression or guarding by the resident females (Danforth 1991; Abrams and Eickwort 1981), implying that communal nests generally are relatively open societies.

The occurrence of open societies raises the question of whether group members are incapable of recognizing familiar individuals. There is a

biased phyletic distribution of caste-based societies among bees and spheciforme wasps (Apoidea) (Wcislo 1992), in that eusociality has evolved repeatedly in the former, while it is extremely rare in the latter. Wcislo (1992) hypothesized that this pattern was associated with the phyletic distribution of chemically-mediated individual nest recognition as an evolutionary antecedent for kin recognition mechanisms. If valid, this hypothesis in turn suggests that studies are needed to assess such nest recognition capabilities (or lack thereof) in communal lineages of bees and wasps, which might help explain why lineages with communal behavior rarely generate eusocial species.

### Conclusions and Future Directions

Theory and limited empirical evidence suggest that the main advantage derived from group living is improved defense against predators and parasites. The evolution of communal nesting as a stable state is therefore paradoxical in that if individuals benefit from group nesting, they would then further benefit from doing so with relatives (West-Eberhard 1978; Wilson and Hölldobler 2005). Yet, as mentioned above, studies using genetic markers indicate that communal nest-sharing females often are not relatives. On the other hand, if individuals benefit from cooperating with non-relatives, then they would further benefit by cheating and exploiting the cooperative behavior of those non-relatives (Eberhard 1972; Eickwort 1975; Axelrod 1984). A major unresolved empirical question, therefore, is what limits or constrains cheating in such communal societies of non-relatives?

Aviles (2002) developed a model in which tendencies to cooperate and to form groups dynamically co-evolve, and she showed that the problem of cheaters ("freeloaders") is resolved if there are significant group-size effects on fitness. That is, cheaters will increase in frequency when rare, but then decrease in frequency when they are common because groups that contain excessive cheaters will have lower per capita productivity. Aviles' model shows that per capita productivity increases up to a certain group size (~8), and then decreases. Empirical data on per capita productivity for different size social groups varies considerably (see section Nest Productivity and Communal Behavior). The effect of freeloading on per capita productivity is empirically unknown. In a social sphecid wasp, *Trigonopsis cameronii*, females occasionally robbed prey from nestmates, especially

when their own hunting success was poor, which raises the possibility that freeloading in these wasps may actually enhance productivity (Eberhard 1972), but additional studies are needed.

If group living is beneficial, then what constellation of genetic and environmental factors helps explain tendencies to evolve communal- versus caste-based societies? Many examples of caste-based societies involve mother-daughter associations (i.e., matrilineal eusocial groups). These associations form during a window of opportunity determined by egg-to-adult developmental times, adult longevity, and the length of the local growing season (Wcislo and Danforth 1997). For example, if larval development is too slow relative to adult longevity, or relative to the length of the growing season, then overlap of generations will be precluded. We speculate that communal behavior is an alternative form of social organization especially suited to environments with short growing seasons or where the length of the growing season is relatively unpredictable. This hypothesis is consistent with the observation that arid regions tend to be especially rich in species with communal behavior, though quantitative data are lacking.

Nearly 50 years ago Evans (1958) synthesized available information and theory concerning the evolution of group living in wasps, and he pointed out that "speculation on the origin of social life seems to have outstripped the observational data (p. 457)." Twenty years later, in a like-minded pursuit, West-Eberhard (1978, p. 853) wrote that data were still so scarce that Evans' sentence "is now a model of understatement." More recently, in reviews of primitively social wasps, Cowan (1991, p. 73) lamented how "much of the information about these insects consists of the barest anecdotes," while Matthews (1991, p. 601) listed critical factors for understanding social evolution and he noted that data "are virtually nonexistent." Similar concerns hold true for bees (Wcislo and Engel 1996). In a book dedicated to Bert Hölldobler, who has done so much to advance our understanding of the origins and evolution of social behavior in insects, one would like to end in a positive manner. Unfortunately, our review ends on a note that echoes Evans, West-Eberhard, Cowan, and Matthews, because empirical studies of solitary and communal nest-sharing bees and wasps continue to lag behind the rest of the field, despite their critical position for understanding the origins of social behavior.

Ironically, the most fitting tribute to one who has so eloquently argued for making a "journey to the ants" is to veer away from ants and their



highly eusocial counterparts among the bees and wasps, and turn instead to the bees and wasps that have made but a short journey in the realm of sociality.

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