

Enabling Mechanisms in the Origin of Sociality in the Hymenoptera—The Sting's the Thing

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ABSTRACT Group living carries a special cost in added parasite and predator pressure because of clumping of individuals. In insects, such pressure comes primarily from larger, vertebrate predators. At the earliest social stages, social defense measures have not yet evolved, so that predators must be resisted with devices existing in solitary individuals. In the absence of these, predator pressure is an obstacle to the evolution of sociality. The aculeate Hymenoptera have such a device in the sting, unique in its power against very large enemies. The view is developed here that this has allowed the Aculeata to surmount the large-predator obstacle and facilitated the origin of sociality. A corollary to this view is that restriction of the sting to females is sufficient to account for the worker caste being female in all species.

OUR THINKING about insect social evolution has been inspired and directed by two simple observations: 1) Eusociality (the condition of living in colonies with cooperative brood care, reproductive castes, and overlap of adult generations) is confined to two taxa making up about 5% of known living insect species: the termites and aculeate Hymenoptera. 2) Most independent origins of eusociality have evidently been in the Aculeata. Conservative estimates are that it has arisen 12 times in the aculeates; just once in termites (Wilson 1971: chap. 17). From this comes the working consensus that there is something exceptional in the Aculeata to facilitate social evolution, and the search for these special features (enabling mechanism, Hinton 1977).

What's So Special About the Aculeata?

Early attempts to find such a key centered around complexes of physical and ecological features, none of them unique. For example, Wheeler's (1923) survey of insect social behavior had as its main theme the evolution of brood care as a precondition for cooperative nesting. Michener and Michener (1951) suggested that a nervous system capable of complex responses and an apparatus for manipulating food and nesting material distinguish the termites and aculeates in a preadapting fashion.

Hamilton's (1964, 1972) radically different answer to this question was based on the observation that, because of the haplo-diploid sex-determination mechanism of the Hymenoptera and very few other taxa, some classes of kin have greater genetic

identity than they would if males were diploid. Given the primitive scenario in which a daughter wasp chooses between nesting on her own (solitarily) or subordinating her personal reproduction to assist her mother (the key step in the origin of eusociality), haplo-diploidy increases the chance that the second option will maximize her inclusive fitness.

Relatedness is only one of the key variables in comparing fitness, though, and within the spectrum of insect ecology the "all other things being equal" formulation has limited meaning. It may be fruitful to consider additional features that make it more likely that sociality will evolve in one or both of these groups and not in others (for a similar view, see Craig 1980). Here I try to show that living in groups carries an important cost that is often overlooked and that a special feature of the Aculeata militating against this cost is to be found in the name itself—they sting. The core of this simple argument is not new. I have found it hinted at (Michener and Michener 1951, Zikán 1951, Michener 1974, Schmidt 1982) and at least once directly stated (Kugler 1978), in each case in one or a very few sentences. For an alternative view of the stinger's main function, see Evans (1975).²

What's Wrong with Sociality?

One advantage of sociality lies in the potential for joint defenses against natural enemies. Lin (1964), Lin and Michener (1972), and Michener (1974) have developed the idea that pressure from arthropod parasites and predators is a key factor

² "[Possibly] too much has been made of the sting as a defense against vertebrate enemies, and too little made of the sting as a means of repelling foreign queens."

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favoring hymenopteran sociality. Zikán (1951) pointed out that the differentiation of soldiers from workers is found only in species with very large colonies and concluded that only with such large colony size is it possible to have specialized soldiers. Visscher (1980) has described defense mechanisms against microbial growth in honey bee colonies.

Let us stand the views of Lin, Michener, and Zikán on their heads and consider, first, that sociality, far from being a general solution to parasite and predator pressure, is an invitation to increased pressure; and second, that the evolution of very large colonies makes a soldier caste necessary for the first time.

Such novel pressures must be countered by new survival devices. In flying insects this does not so much concern self-defense by adults, which retain the ability to escape, as the protection by a small number of adults of often larger numbers of brood. These latter tend to be slow-moving, soft-bodied, and edible. Maximal body mass in insects is commonly reached as larvae just before pupation (Endopterygota) or final apolysis to adulthood (Exopterygota).

I suggest that pressures against the maintenance of sociality are less to be expected from invertebrates and microbes than from much larger, usually vertebrate predators. The key distinction is one of size, between small organisms that can exploit just one insect at a time, no matter how they are dispersed, and larger ones that can consume many insects at once. From the larger organisms' point of view, sociality organizes insects from a multitude of insignificant morsels into a new edible critical mass. From the insects' point of view, sociality selects for the appearance of a new class of predation.

A few examples will suffice to show that social insects do, in fact, attract special attention from vertebrates. In parts of North America, blue jays, *Cyanocitta cristata*, and summer tanagers, *Piranga rubra*, are frequent predators of *Polistes* wasps, which appear to be for them a significant diet component (D. L. Gibo and J. W. Krispyn, personal communications). Similarly, bird predation is the main cause of mortality in *Polistes exclamans* Viereck in Texas (Strassmann 1981). Preiss (1967) has shown that in Delaware the striped skunk, *Mephitis mephitis*, preys heavily on eastern yellowjackets, *Vespula maculifrons* (Buysson). In the neotropics, monkeys have at least once been seen to attack *Pseudopolybia compressa* (Saussure) wasps and eat their brood (D. C. Meyer, personal communication). Jeanne (1975) gave further pertinent examples for social wasps. And if ants and termites were suddenly to become solitary, every anteater, aardvark, and pangolin in the wild would starve. The point here is that most insects would be little able to withstand such predation attempts. If this is not clear, imagine how group-living crickets or moths, for example, would fare against a

single crow or rat. Such vulnerability must be a sufficient obstacle to the evolution of sizeable groups. This does not suggest that defensibility promotes sociality, merely that it may permit it. This is analogous to Alexander's (1974) point about dispersed food resources as an obstacle to sociality.

These last two paragraphs introduce a key logical problem. The best way to show that social insects attract vertebrate predators is to show that vertebrates eat them, yet if this is so how can it be maintained that the sting has special antivertebrate power? This is a familiar paradox in the study of defensive strategies: the more completely effective a tactic is, the less necessary it appears to be, or vice versa. Two types of evidence can lead out of this apparent impasse. First, an experimental removal of the putative defense should increase mortality. I know of no rigorous test of this type, but a common crude one, the removal of adults from an accessible wasp colony while leaving the brood in place, gives the expected result. Second, colony defense is not completely effective and shows some instructive shortcomings. Given the evidently considerable edible biomass of social insects in most communities, it is striking that so few vertebrates are reported to prey significantly on them. Jeanne's (1975) list for social wasps, for example, is very short, and I can add little to it. Only a small number seems able to circumvent the colonies' defenses to a worthwhile extent. In the cases of a few specialists on ants and termites (anteaters, etc.), it is well known how this is done. What is curious is that a majority of species on Jeanne's or any other such list (of honey-bee predators, for example) are rather generalist feeders. Very little is known of how they do what so many other generalists apparently cannot.

Among large diverse taxa, then, sociality is more expected where there are preadaptations to repel or collectively evade large predators. I shall review some widely used antivertebrate tactics of insects, with a view to examining their applicability to colony defense and showing the uniqueness of the hymenopteran stinger. I use "stinger" to refer to the venom-injection apparatus, and "sting" to refer to the event or symptoms. Following Edmunds (1974), primary defenses are those that operate regardless of whether there is immediate danger, while secondary defenses are brought into play only when danger is perceived.

Primary Defense

Anachoresis. Edmunds (1974) defined anachoresis as the habit of living in holes or crevices. This is common in social insects, and may have been important in the repeated evolution of sociality among halictine bees. By nesting usually in the ground with brood cells dispersed, halictines appear to set a high cost on digging them out and eating them (C. D. Michener, personal communication; Batra 1984). At the same time, this cost

is not infinitely high, and it seems that if halictine colonies did not have such small biomass they would come under much greater predation pressure. A corollary to this is the hypothesis that predation threat is sufficient to keep halictine colonies small.

Anachoresis would, then, seem capable of giving only a limited general reprieve unless an impenetrable nesting cavity can be found or built. Natural crevices, such as tree hollows with an appropriately small passageway, are uncommon. Although many social insects build nests with a hard outer shell (e.g., mud-nesting *Polybia* wasps, many *Crematogaster* and *Azteca* ants, nasute and fungus-gardening termites), rarely is this so hard that it cannot be breached by many vertebrates (personal observations). Similarly, while I have never seen evidence that birds break open the mud nests of *Trypargilum* or *Sceliphron* solitary wasps, almost certainly most medium-sized birds could do so if it were sufficiently rewarding.

The social sphecid *Microstigmus comes* Krombein also nests so that its brood is inaccessible or unworkable to eat, but it does so in quite a different way. The small, baglike nests are built on the broad leaf under-surface of the palm *Cryosophila guagara* Allen (Matthews and Starr 1984). Nests are easy to see, but to both crawling and flying vertebrates they must be nearly impossible to reach. They are made from the palm's surface pubescence, and I have found them to be tasteless and in no way noxious to eat. They form such a bulky cocoonlike covering for a miniscule biomass, though, that *Microstigmus* must be free from any engulfing predation. It is out of the question that this wasp, 4 mm long, has the stinging power to repel any vertebrate. As with halictines, it seems that predation threat is enough to preclude the evolution of large colonies in *Microstigmus*.

Inedibility. Many insects are not good food; they are unpalatable, poisonous, too tough, or spiny. Except in ants, though, none of these features is common in adult social insects, and I doubt that any is found in social insect larvae. Over the years I have tasted larvae of many social wasps and some ants, termites, and social bees and found them all quite palatable. The least edible insect larvae are probably in the Lepidoptera, which have species with poisonous flesh (in at least five families) and with venomous setae (in at least 13 families [Pesce and Delgado 1971]). Why are social insect larvae not similarly inedible? There are two hypotheses: a) the diet of most species is not suitable for sequestering or synthesizing poisons, or b) social insects have a relatively short larval period, so that it is not worthwhile to invest in such protection.

Mimicry or Crypsis. Sociality undermines the effectiveness of each of these. Social crypsis, especially, is very nearly a contradiction in terms. The wasps *Mischocyttarus melanarius* (Cameron) and *Parischnogaster depressigaster* (Rohwer) build nests closely resembling a dead leaf and a twig,

respectively, but in each case colonies are small and the cryptic resemblance is weakened with nest growth (personal observations). In each of these the sting is reasonably painful, though almost never used against humans (personal observations).

Secondary Defense

Flight. Aculeates fly well, although not outstandingly so. Only for schooling fish (Shaw 1962, 1978) and some birds (e.g., Tinbergen 1951, Humphries and Driver 1971) has it been shown that social flight from a predator can be superior to individual flight. And as indicated earlier, most insect larvae are little able to move quickly.

Stinging. Several animal taxa have evolved apparatuses that can actively inject painful or paralyzing venom through vertebrate skin. In insects, such ability is known in some predaceous heteroptera (especially reduviids and notonectids), to a certain extent in predaceous flies, and in aculeates. The uniqueness of such stingers is that they are compact, require no gross alteration of body plan (e.g., there is little external difference between bees and ants with stingers and those without), yet can have a powerful impact. Combined with undiminished flying ability, they provide a great defensive advantage. The stinger is the insect analog of gunpowder. As such, it represents a revolution in defensive capability and a key enabling mechanism for a revolution in social behavior.

On the Nature of Stings

Most large animals can be pursued and stung by flying aculeates with unreduced stingers. Except by becoming somewhat armored, it should be exceptionally hard to evolve defenses against the effects of stings. The reasoning behind this hypothesis is the following: 1) Pain is the body's alarm system but, as de Réaumur (1722) may have been the first to say³, the hymenopteran sting is a lie. Except in cases of massive envenomization or allergic response, insect stings seem to induce pain disproportionate to real damage. This makes it feasible to repel some predators even when it would be to their advantage, in food gain against real physical damage, to stay and eat the brood. Unfortunately, we still have no rigorous way to measure sting pain (Starr, unpublished data), so our estimation of the relative importance of damage and pain remains crude. Nonetheless, I believe that anyone who has been stung by different species will agree that there is this disproportion. 2) Like other forms of alarm, sharp sudden pain is a relatively nonspecific message and does not lend itself to fine discrimination. There is no reason to believe that pain tolerance is not subject to natural selec-

³"It is well known that the pain from wasp stings results not so much from the wound made by so sharp a needle as the venomous fluid which the needle injects into the wound."

tion, but an evolved indifference to stings would carry with it an indifference to other, "undeceitful" types of pain.

It is not yet clear how variation in stings among aculeates correlates with the distribution of social habits. More specifically, what is the relationship of each of sting pain and toxicity with primitive eusociality? Evans and West-Eberhard (1970) hypothesized that the switch in wasps from feeding on whole prey to macerated prey removed the need for precise, nonfatal stings and set the sting free to become more toxic or painful, and, thus, a powerful defensive organ. Blum (1981) and Janzen (1981) made similar points. There is no simple correlation for humans between the toxicity and painfulness of arthropod stings (Schmidt 1985; Starr, unpublished data), so that for defense the emphasis should be on pain.

The relationship between sociality and sting pain is well worth investigating, but departures from simple correlation are already apparent. For example, while the Eumenidae and *Eustenogaster* spp., solitary relatives of the social wasps, and the primitive ponerine and myrmecine ants, usually have painful stings, similar-sized solitary bees and solitary sphecids wasps, related to bees, rarely do (Brown 1954, Stumper 1960, Evans 1963; Starr, unpublished data). And the universally solitary Mutillidae and Pompilidae are noted for their very painful stings (personal observations and numerous personal communications). We may finally have to be satisfied with the conclusion that a certain medium level of painfulness is needed to repel vertebrates, but that higher levels give little added advantage. A failure to find consistent chemical differences between the venoms of most solitary wasps (rarely used for defense) and of mutillids and social wasps (rarely used except for defense) would corroborate this.

Why Are Workers Never Male?

Most social aculeates are female. Males tend to be short-lived and when present in the colony rarely contribute more than their gametes. Hamilton (1964, 1972) accounted for this with a genetic peculiarity: unlike females, males have no extraordinary relatedness to their sisters, so that kin selection has no special scope for favoring male worker-like altruism. However, this merely predicts that males will be less inclined than females to work where there is a significant cost, not their near-universal nonworking (Charlesworth 1978), so that it is necessary to look to other factors. An extrinsic factor adduced for this is that in the solitary state males lack the behavioral structures for nesting (West-Eberhard 1975, Charlesworth 1978). When defense is taken into account, it is clear that males are also physically unfit to be workers, as they have no stinger. It is curious that Crozier (1979) noted exactly this fact, while giving it the

opposite emphasis.⁴ Unfortunately, the view of males presented here is consistent both with Hamilton's kin-selection theory of the origin of worker habits and Alexander's (1974) competing parental-manipulation theory. At the same time, it presents a ready reply to Hamilton's (1975) pointed challenge to parental-manipulation theory to explain why manipulative queens do not cause their sons, all of whose genes come from their mothers, to work: Good workers can only be made from females.

Concluding Remarks

The argument has been made that the ability to sting is a key enabling mechanism in hymenopteran early social evolution, permitting group living in at least some of those lineages where it persists. The sting's universal importance is not established, though, and in some groups it may well be insignificant in this regard. Specifically, the stings of halictine bees and *Microstigmus comes* seem largely ineffective against vertebrate predators. In that case, these groups must have pursued a different strategy from larger, more aggressive social insects, in which small colony mass removed them from the purview of vertebrate predation. At the same time, the continued threat of predation must severely limit their nesting options and colony size. Progress on this question awaits more comparative sting-pain data. The social halictines and *M. comes* represent a majority of independent origins of eusociality (Wilson 1971; chap. 17), but a small minority of eusocial species.

Emphasis here has been on early social evolution. With much larger colony size there arise other, social ways of defending the colony against vertebrates, so that stinging need not be the key tactic. A majority of ant species and most advanced eusocial bees have lost the stinger. It is important to note that all these are in the more socially complex lineages, usually with very large colonies, unlike primitively social groups. There is little indication how termites survived the crucial early stages, but it may have been a combination of inaccessibility and greater age. The antiquity of termite sociality is only vaguely known (Burnham 1978, Carpenter and Hermann 1979), but they may already have evolved large colonies and the soldier caste before vertebrate predators became a serious threat.

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⁴"The only worker acts that male wasps would seem unable to perform are prey capture and nest defense (because they lack stings)."

Others who have read it critically are Dennis F. Howard, Charles Kugler, Charles D. Michener, and Justin O. Schmidt. Roberto J. Montilla taught me to use the word processor for an earlier version.

References Cited

- Alexander, R. D.** 1974. The evolution of social behavior. *Annu. Rev. Ecol. Syst.* 5: 325-383.
- Batra, S. W. T.** 1984. Solitary bees. *Sci. Am.* 250: 120-127.
- Blum, M. S.** 1981. Chemical defenses of arthropods. Academic Press, New York.
- Brown, W. L.** 1954. Remarks on the internal phylogeny and subfamily classification of the family Formicidae. *Insectes Soc.* 1: 21-31.
- Burnham, L.** 1978. Survey of social insects in the fossil record. *Psyche* 85: 85-133.
- Carpenter, F. M., and H. R. Hermann.** 1979. Antiquity of sociality in insects, pp. 81-89. *In* H. R. Hermann [ed.], Social insects, vol. 1. Academic Press, New York.
- Charlesworth, B.** 1978. Some models of the evolution of altruistic behaviour between siblings. *J. Theor. Biol.* 72: 297-320.
- Craig, R.** 1980. Sex ratio changes and the evolution of eusociality in the Hymenoptera: simulation and games theory studies. *J. Theor. Biol.* 87: 55-70.
- Crozier, R. H.** 1979. Genetics of sociality, pp. 233-276. *In* H. R. Hermann [ed.], Social insects, vol. 1. Academic Press, New York.
- de Réaumur, R. A. F.** 1722. Histoire des guêpes. *Mém. Acad. R. Sci., Paris* (1719) 21: 302-364.
- Edmunds, M.** 1974. Defense in animals. Longman, Harlow, Essex.
- Evans, H. E.** 1963. Wasp farm. Natural History Press, New York.
1975. Social parasitism of a common yellowjacket. *Insect World Dig.* 2: 6-13.
- Evans, H. E., and M. J. West-Eberhard.** 1970. The wasps. University of Michigan Press, Ann Arbor.
- Hamilton, W. D.** 1964. The genetical evolution of social behaviour. Part II. *J. Theor. Biol.* 7: 17-52.
1972. Altruism and related phenomena: mainly in social insects. *Annu. Rev. Ecol. Syst.* 3: 193-232.
1975. Gamblers since life began: barnacles, aphids, elms. *Q. Rev. Biol.* 50: 175-180.
- Hinton, H. E.** 1977. Enabling mechanisms, pp. 71-73. *In* Proc. XV Int. Congr. Entomol., Washington, D.C., 1976.
- Humphries, D. A., and P. M. Driver.** 1971. Protean defense by prey animals. *Oecologia* (Berlin) 5: 285-302.
- Janzen, D. H.** 1981. Evolutionary physiology of personal defense, pp. 145-164. *In* C. R. Townsend and P. Calow [eds.], Physiological ecology: an evolutionary approach to resource use. Blackwell Scientific, Oxford.
- Jeanne, R. L.** 1975. The adaptiveness of social wasp nest architecture. *Q. Rev. Biol.* 50: 267-287.
- Kugler, C.** 1978. A comparative study of the myrmicine sting apparatus (Hymenoptera, Formicidae). *Stud. Entomol.* 20: 413-548.
- Lin, N.** 1964. Increased parasitic pressure as a major factor in the evolution of social behavior in halictine bees. *Insectes Soc.* 11: 187-192.
- Lin, N., and C. D. Michener.** 1972. Evolution of sociality in insects. *Q. Rev. Biol.* 46: 131-159.
- Matthews, R. W., and C. K. Starr.** 1984. *Microstigmus comes* wasps have a method of nest construction unique among social insects. *Biotropica* 16: 55-58.
- Michener, C. D.** 1974. The social behavior of the bees. Harvard University Press, Cambridge, Mass.
- Michener, C. D., and M. H. Michener.** 1951. American social insects. Van Nostrand, New York.
- Pesce, H., and A. Delgado.** 1971. Poisoning from adult moths and caterpillars, pp. 119-156. *In* W. Bücherl and E. E. Buckley [eds.], Venomous animals and their venoms, vol. 3. Venomous invertebrates. Academic Press, New York.
- Preiss, F. J.** 1967. Nest site selection, microenvironment and predation of yellowjacket wasps, *Vespula maculifrons* (Buysson), (Hymenoptera, Vespidae) in a deciduous Delaware woodlot. M.S. thesis, University of Delaware, Newark.
- Schmidt, J. O.** 1982. Biochemistry of insect venoms. *Annu. Rev. Entomol.* 27: 339-368.
1985. Chemistry, pharmacology, and chemical ecology of ant venoms. *In* T. Piek [ed.], Venoms of the Hymenoptera. Academic Press, New York (in press).
- Shaw, L.** 1962. The schooling of fishes. *Sci. Am.* 206: 128-138.
1978. Schooling fishes. *Am. Sci.* 66: 166-175.
- Strassman, J. E.** 1981. Parasitoids, predators and group size in the paper wasp, *Polistes exclamans*. *Ecology* 62: 1225-1233.
- Stumper, K.** 1960. Die Giftsekretionen der Ameisen. *Naturwissenschaften* 47: 457-463.
- Tinbergen, N.** 1951. The study of instinct. Clarendon Press, Oxford.
- Visscher, P. K.** 1980. Adaptations of honey bees (*Apis mellifera*) to problems of nest hygiene. *Sociobiology* 5: 249-260.
- West-Eberhard, M. J.** 1975. The evolution of social behavior by kin selection. *Q. Rev. Biol.* 50: 1-34.
- Wheeler, W. M.** 1923. Social life among the insects. Harcourt, Brace, New York.
- Wilson, E. O.** 1971. The insect societies. Harvard University Press, Cambridge, Mass.
- Zikán, J. F.** 1951. Polymorphisms and Ethologie der sozialen Faltenwespen (Vespidae Diptoptera). *Acta Zool. Lilloana* 11: 5-51.

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Importance of the Sting in the Evolution of Sociality in the Hymenoptera

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ABSTRACT We argue that the sting has minimal importance as a preadaptation facilitating the evolution of eusociality in the Hymenoptera. Rather, the origins of eusociality occurred in the context of small colonies occupying small nests. Subsequent increased colony size was accompanied by attraction of vertebrate predators and by the evolution of colony defense strategies, some of which involved the use of the sting. Furthermore, the sting is not an important factor contributing to the lack of male workers in the Hymenoptera.

KEY WORDS Insecta, preadaptation, defense, eusociality

IN A PAPER concerning the evolution of eusociality, it was stated that a major cost of group living may be added parasite and predator pressure (Starr 1985). However, several additional assertions also were made that warrant further consideration—predation pressure on group-living Hymenoptera occurs primarily by vertebrate predators attacking brood; vertebrate predation pressure is a barrier to the evolution of eusociality; Hymenoptera, by possessing a sting, are able to surmount this barrier, thus facilitating the evolution of eusociality (a point also made by Darlington [1981]); and male Hymenoptera would make poor workers because they do not possess a sting. We argue that these assertions are not correct and that the possession of a single attribute, the sting, does not explain the evolution of eusociality in the aculeate Hymenoptera (see also Stubblefield & Charnov 1986).

Predation on brood of most group-living Hymenoptera is not primarily by vertebrates. Arthropod predation may be more important for most ants, wasps, and bees (see Table 1).

Ants are typically the most important predators of other ants. For example, the alarm-defense communication system of the formicine ant *Pheidole dentata* Mayr is most strongly triggered by ants of the genus *Solenopsis* (Wilson 1976). Slave-making ants such as the *Formica sanguinea* group, *Leptothorax duloticus* Wesson, and others are important predators of their host species (see Wilson 1971, Table 19-1). Further, army ants also commonly prey on other ant species (Rettenmeyer 1963; see Wilson 1971, Table 4-6).

Ants are the major brood predators on tropical social wasps (Richards & Richards 1951; Jeanne

1970, 1975, 1979) that reside in aerial carton nests or occasionally inside cavities. It is generally agreed that eusociality in wasps originated in tropical areas (Evans & West-Eberhard 1970, Carpenter 1982); this is where the majority of social wasp species presently occur (Jeanne 1975). Ant species richness and overall predation rates are also greatest in the tropics (Jeanne 1979), and the threat of ant predation may well have had a major influence on the evolution of life cycle, nest architecture, and social organization of social wasps (Richards & Richards 1951; Jeanne 1970, 1975; Post & Jeanne 1981). For example, Ito (1986) reports that 80% of *Ropalidia fasciata* (Fabricius) nests in Okinawa were abandoned because of attacks by ants, heavy parasitism by ichneumon wasps, or destruction by typhoons. Many ants recruit groups of foragers to a food source and can quickly and efficiently dispose of a large amount of food. The small size of individual ants does not, as Starr (1985) asserts, limit group-foraging invertebrates such as ants to exploiting "just one insect at a time."

Many social wasps have evolved responses to ant predation. For example, *Mischocyttarus drewseni* Saussure coats the slender petiole on which its nest is suspended with a secretion that is highly repellent to most ants; *Polistes* and possibly *Belonogaster*, *Parapolybia*, and *Ropalidia* similarly protect their petiolate nests from ant predation (Jeanne 1970, 1975). Jeanne (1975) suggests that the decisive advantage of the carton that encloses the nests of many tropical Vespidae is that it physically restricts ant access to brood within the nest.

There are instances in which vertebrate predation (principally by birds and bats) is an important mortality factor in social wasp nests, especially in the temperate zone on *Polistes* (e.g., Gibo 1974, Gibo & Metcalf 1978, Strassmann 1981) but also in the tropics on various polistine genera (e.g.,

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Table 1. Reports indicating that predation on brood of most group-living Hymenoptera is not primarily by vertebrates

Taxon	Reference
Vespidae	Richards & Richards 1951; Jeanne 1970, 1975, 1979
<i>Ropalidia</i>	Ito 1986
<i>Mischocyttarus</i>	
<i>Polistes</i>	Jeanne 1970, Gibo 1974, Jeanne 1975, Gibo & Metcalf 1978, Strassmann 1981
<i>Belonogaster</i>	
<i>Parapolybia</i>	
<i>Metapolybia</i>	Forsyth 1978
<i>Polybia</i>	Windsor 1976, Forsyth 1978
Formicidae	
<i>Pheidole</i>	Wilson 1976
<i>Leptothorax</i>	Wilson 1971
<i>Formica</i>	
Army ants	Rettenmeyer 1963, Wilson 1971
Apoidea	
Halictidae	Batra 1965, Michener 1974
Apidae	
<i>Bombus</i>	Hobbs 1965a,b, 1966a,b, 1967, 1968; Alford 1975; Richards 1978; Fisher 1984, 1985
<i>Trigona</i>	Carroll & Janzen 1973, Michener 1974
<i>Melipona</i>	
<i>Apis</i>	Morse 1978, Seeley et al. 1982, Nickerson & Harris 1985

Metapolybia [Forsyth 1978], *Polybia* [Windsor 1976, Forsyth 1978]). Especially in tropical regions, the effects of brood parasites and predatory ants are usually of greater consequence to social wasps. Stinging is not an effective defense against bird and bat predators. The "strategy" of initiating satellite nests to reduce the impact of bird predation suggested by Strassmann (1981) also is used against infestation by tineid moths in the absence of vertebrate predation (Jeanne 1978). There is no evidence from their behavioral patterns that vertebrate predation has shaped the evolution of sociality in wasps.

Ants are also important predators of social bees. *Camponotus abdominalis floridanus* (Buckley) preys on honey bee nests in Florida (Nickerson & Harris 1985). Important predators of honey bees, as listed by Morse (1978), include ecitonine and doryline army ants; the ants *Iridomyrmex humilis* (Mayr), *Formica integra* Nylander, *F. rufa* L., *Camponotus* spp.; as well as hornets in the genus *Vespa*, particularly *V. orientalis* L. and *V. mandarina* Smith. In addition, the sphecid wasp *Phylanthus triangulum* F. is an important predator of honey bee adults. Seeley et al. (1982) pointed out that *Apis florea* F. coats the twig upon which its nest is built with a sticky resin to repel ants. Carroll & Janzen (1973) reported that the only conspicuous social insects free of nest predation by ants are bees in the genera *Trigona* and *Melipona*. Some members of these groups protect their nests with tree resins, thereby preventing ants from entering (Michener 1974). However, stingless bees of the

genus *Lestrimellita* are important pests of other meliponine bees and may destroy colonies by repeated robbing (Michener 1974).

Vertebrate predation is frequently important in nests of the highly social Apidae, and many of the defensive measures cited by Michener (1974) can be viewed as being especially effective against such large predators as bears and humans (see Morse 1978). This predation may be directed as much against the stored provisions (honey) as against the brood itself and is a consequence of the large colony size and specialized food storage behavior now exhibited by honey bees and stingless bees. Consequently, vertebrate predation was probably not as important in the early stages of social evolution in the Apinae and Meliponinae. Bumble bees (Bombinae) have smaller, more primitive societies. The clustering of brood and stored provisions in a compact nest within a cavity is attractive to small mammal predators such as skunks (Alford 1975), and defensive measures by worker bumble bees (including stinging) are directed against vertebrates that attempt to excavate bumble bee nests (Michener 1974). Nevertheless, arthropod predation and parasitism and especially attacks by social parasites (*Psithyrus*) (Fisher 1984, 1985) and usurping congenics (e.g., Richards 1978) are more important mortality factors in *Bombus* nests than are attacks by mammals (Hobbs 1965a,b, 1966a,b, 1967, 1968).

The sweat bees (Halictidae) and carpenter bees (Allodapini) exhibit the initial stages of social behavior and are therefore especially important in estimating the importance of predation on the evolution of eusociality. Nests of these bees are frequently parasitized or invaded by predators, and guarding behavior by workers may be evident, including constricting the nest entrance, consistent guarding at the entrance, biting at intruders with mandibles, and blocking the entrance with the abdominal dorsum. Nest enemies are always other arthropods, including velvet wasps, flies, cleptoparasitic bees, and conspecific usurpers. Ants may be important brood predators, but the attacks presumably occur underground and are difficult to observe. Mandibular gland allomones may be more important in repelling ants and many other arthropod enemies in solitary bees and in allodapines (Cane 1986), although not in sweat bees, which lack well-developed mandibular glands. There are no observations of vertebrate predation on the brood of halictid bees despite thousands of hours of field observation made on dozens of eusocial species. In addition, numerous solitary and communal bees and wasps typically aggregate their subterranean nests, providing a concentration of brood (reviewed in Eickwort [1981]), but vertebrate predation on brood has not been observed to be a significant mortality factor in these noneusocial species.

From these data, we conclude that predation pressure by vertebrates may be a barrier to the evolution of large colony size but is not a barrier to the evolution of eusociality. Eusociality evolved more than four times in halictine bees, and at least

once in the allodapine bees (Michener 1974). Recent work has shown that primitive eusociality can evolve in a single step from a solitary ancestor (Michener 1985). Thus, the threshold of eusociality was almost certainly crossed in very small colonies; such small colonies of bees are not subject to brood predation by vertebrates. We believe the same was true for the small colonies within which eusociality originated in the Vespidae and Formicidae.

The sting is significant as a defense against vertebrate predators of brood only in some advanced eusocial Hymenoptera. In solitary and presocial bees and wasps, the sting is used as a personal defense and to defend the nest against some arthropod invaders such as mutillid wasps and cuckoo bees (Michener 1974). Workers in small colonies of primitively eusocial bees and some wasps do not attack vertebrates at the nest site. Students of halictine bees can excavate even the largest colonies without being attacked (P.F.K. & G.C.E., unpublished data).

Only in large colonies in which there is an "expedient" worker force do bees, wasps, and ants aggressively attack a potential or actual vertebrate predator. This transition may occur seasonally in the same colony, as in yellow jackets (Akre et al. 1980), hornets, and bumble bees, where young, small nests are not defended as are older nests with a large worker force.

The sting becomes an effective nest defense against vertebrate brood predators in advanced eusocial insects in conjunction with a communication system (probably involving pheromones) that recruits workers to mount a mass defense. This type of defense occurs in some honey bees (Seeley et al. 1982) and some advanced vespine and polistine wasps (Jeanne 1975, 1980).

However, injecting venom with a sting is not essential for colony defense in advanced eusocial Hymenoptera. A large group of tropical eusocial bees, the Meliponinae (Apidae), do not possess stings. Instead, masses of biting bees mount an effective colony defense (see review in Michener [1974]). Many ants, the Formicinae and Dolichoderinae in particular, do not inject venom with a sting for colony defense and in fact lack a sting. Instead, they use their mandibles to inject defensive allomones.

As Starr himself (1985) suggested, vertebrate predation pressure may not always select for large colony size. Forsyth (1978) suggested that vertebrate predation on tropical wasps can select for large colony size or for colony size small enough for nests to be cryptic to vertebrates. Jeanne (1975, 1978) has described the colony defense strategies of species that build small, cryptic colonies versus those that build large, conspicuous, aggressively defended colonies. The contrast is also evident in honey bees; *Apis florea* F. in the Old World tropics builds small, cryptic nests and does not rely on direct colony defense. Its congener, *A. dorsata* F., builds large, conspicuous nests and is known for its pugnacious colony defense (Seeley et al. 1982).

In summary, we offer an alternative interpretation concerning the importance of the sting in the evolution of eusociality. We believe that eusociality most likely evolved in the context of small colonies occupying small nests. In some groups the combined efforts of many individuals permitted the evolution of large colony size and large nests. Increased size was accompanied by attraction of vertebrate predators and the evolution of colony defense strategies, some of which involve the use of the sting.

Most importantly, the threshold of eusociality was crossed in the context of small colonies, and it is within this context that the importance of the sting to the evolution of eusociality must be examined. In this context (small nests of halictine bees or polistine wasps) the sting is used in contests for dominance among females residing in the same nest and in colony defense against both intraspecific intruders (potential usurpers or intraspecific cleptoparasites) and some arthropod parasites. Only arthropod brood parasites that challenge the adult nest occupants directly, such as cuckoo bees, elicit a defense involving the use of the sting. Such brood parasites account for only a fraction of the total brood parasitism found in halictine bees (e.g., Batra 1965). Thus, the sting is effective against only some arthropod brood parasites.

From these arguments it follows that the possession of a sting may not be a primary factor determining why workers in the social Hymenoptera are female.

The sting is an important adaptation for prey capture in solitary aculeate wasps; this may help explain why provisioning is solely a female trait in these wasps (Eickwort 1981). However, prey capture by social vespids does not involve the sting; insect prey are subdued with the mandibles and cut up and masticated before transport to the nest. Similarly, ant workers may not sting their prey. Therefore, the lack of a sting would not appear to preclude male wasps and ants from participating in brood care. Eusociality arose many times in the bees (at least seven [Michener 1974]). The tasks of bee workers include gathering pollen and nectar, feeding brood, incubating brood (in Apidae), constructing nests, and guarding. None of these tasks requires that a worker possess a sting. Male brood care has been reported in primitively eusocial polistine wasps and in the bumble bee *Bombus griseocollis* (DeGeer) (Cameron 1985, 1986). In the solitary wasp genera *Oxybelus* and *Trypoxylon*, male nest guarding reduces brood parasitism (Peckham 1977, Brockmann 1980). Moreover, morphological variation involving increased overall size and a syndrome of changes, including enlargement of the head and mandibles that would allow males to be both effective competitors for mates and guards, has arisen repeatedly in the halictine and andrenid bees (cf. Kukuk & Schwarz in press). Thus, although instances of male helping behavior are rare, the evidence indicates that there is no convincing phylogenetic constraint on male

behavior or morphology prohibiting hymenopteran males from becoming effective workers.

The argument that male Hymenoptera are preadapted to be inefficient workers in comparison with females is not convincing. Theoretical arguments (see Pamilo 1984) indicate that sex-ratio bias and worker-produced males are important in the evolution of female worker behavior in male-haploid insects and these factors differentiate male-haploid from male-diploid insects. However, there is no barrier, theoretically speaking, to the evolution of male workers in the Hymenoptera. Why, then, is male helping behavior rare and why do we see both male and female workers in diplo-diploid species? Are hymenopteran females better preadapted for parenting than are "proto-termites" females because they possess a sting?

The answer to such a query is clearly no. Alternative hypotheses can be generated by considering the life history patterns of solitary Hymenoptera and the orthopteroid orders. There are several relevant life history differences that could be involved. For example, in nonsocial Orthoptera (sensu lato), males contribute vital resources to the females, and male parental investment is often considerable (e.g., Schal & Bell 1982, Gwynne & Morris 1983). On the other hand, with few exceptions hymenopteran males contribute only sperm and have a minimal parental investment (Alcock et al. 1978, Eickwort & Ginsberg 1980).

Parental investment is of major importance in influencing sexual selection (Trivers 1972). Males in the group from which the termites arose were evolutionarily committed to parental investment and thus preadapted to remain with their mates and "protect" their investment. Hymenopteran males, on the other hand, responded to sexual selection for high levels of mate searching activity during the limited period of time during which females are receptive, and each male maximizes his fitness by inseminating as many females as possible (Eickwort & Ginsberg 1980, Thornhill & Alcock 1983). Thus, in the evolution of termite social behavior, the forces of sexual selection and kin selection may have worked in harmony to promote the evolution of male workers, whereas the evolution of male altruism in the Hymenoptera was opposed by the forces of sexual selection. Solitary, nest-building hymenopteran females possess all the requisite behaviors of brood care, whereas males do not. However, the reasons for this large difference in life history between the sexes are of importance when considering the evolution of all-female altruism.

There are also developmental differences between the two insect taxa; the orthopteroid orders are hemimetabolous (paurometabolous) and the Hymenoptera are holometabolous. In eusocial Hymenoptera, only adults are capable of providing brood care, while termite workers are initially immature forms. Investigation of the selective forces acting on these and other life history differences

between these two taxa is likely to be more productive than the simple tautology that there are no male workers in the Hymenoptera because they would make poor ones.

In addition, worker production of males is an important factor in the evolution of workers in male-haploid species (Pamilo 1984). Electrophoretic evidence indicates that workers in colonies of the primitively eusocial halictine bee *Dialictus zephyrus* (Smith) produce sons (Kukuk & May in press). Thus, the fitness of a female worker can be enhanced directly or by kin selection if she stays in the nest. For a male, an increase in personal fitness could be obtained only by leaving the nest and investing time in searching for mates (intranidal mating is rare in bees; see Kukuk & Schwarz [in press]).

In summary, the rarity of male workers in eusocial Hymenoptera may be caused by life history factors including the effects of sexual selection on the behavior and morphology of males, not simply because females are morphologically preadapted to evolve as workers by possessing a sting and males are not.

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References Cited

- Akre, R. D., A. Greene, J. F. MacDonald, P. J. Landolt & H. G. Davis. 1980. Yellow jackets of America north of Mexico. USDA, Agriculture Handbook 552.
- Alcock, J. E., E. M. Barrows, G. Gordh, L. J. Hubbard, L. L. Kirkendall, D. Pyle, T. L. Ponder & F. G. Zalom. 1978. The ecology and evolution of male reproductive behaviour in the bees and wasps. *Zool. J. Linn. Soc. Lond.* 64: 293-326.
- Alford, D. V. 1975. Bumblebees. Davis-Poynter, London.
- Batra, S. W. T. 1965. Organisms associated with *Lasiglossum zephyrum* (Hymenoptera: Halictidae). *J. Kans. Entomol. Soc.* 38: 367-389.
- Brockmann, H. J. 1980. Diversity in the nesting behavior of mud-daubers (*Trypoxylon politum* Say: Sphecidae). *Fla. Entomol.* 63: 53-64.
- Cameron, S. A. 1985. Brood care by male bumble bees. *Proc. Natl. Acad. Sci. U.S.A.* 82: 6371-6373.
1986. Brood care by males of *Polistes major* (Hymenoptera: Vespidae). *J. Kans. Entomol. Soc.* 59: 183-185.
- Cane, J. H. 1986. Predator deterrence by mandibular gland secretions of bees (Hymenoptera: Apoidea). *J. Chem. Ecol.* 12: 1295-1309.
- Carpenter, J. M. 1982. The phylogenetic relationships and natural classification of the Vespoidea (Hymenoptera). *Syst. Entomol.* 7: 11-38.
- Carroll, C. R. & D. H. Janzen. 1973. Ecology of foraging by ants. *Annu. Rev. Ecol. Syst.* 4: 231-259.
- Darlington, P. J., Jr. 1981. Genes, individuals, and kin selection. *Proceedings of the National Academy of Sciences* 78: 4440-4443.

- Eickwort, G. C.** 1981. Presocial insects, pp. 199–280. In H. R. Hermann [ed.], *Social insects*, vol. 2. Academic, New York.
- Eickwort, G. C. & H. Ginsberg.** 1980. Foraging and mating behavior in Apoidea. *Annu. Rev. Entomol.* 25: 421–446.
- Evans, H. E. & M. J. West-Eberhard.** 1970. *The wasps*. University of Michigan, Ann Arbor.
- Fisher, R. M.** 1984. Evolution and host specificity: a study of the invasion success of a specialized bumblebee social parasite. *Can. J. Zool.* 62: 1641–1644.
1985. Evolution and host specificity: dichotomous invasion success of *Psithyrus citrinus* (Hymenoptera: Apidae), a bumblebee social parasite in colonies of its two hosts. *Can. J. Zool.* 63: 977–981.
- Forsyth, A. B.** 1978. Studies on the behavioral ecology of polygynous social wasps. Ph.D. dissertation, Harvard University, Cambridge, Mass.
- Gibo, D. L.** 1974. The selective advantage of foundress associations in *Polistes fuscatus* (Hymenoptera: Vespidae): a field study of the effects of predation on productivity. *Can. Entomol.* 110: 519–540.
- Gibo, D. L. & R. A. Metcalf.** 1978. Early survival of *Polistes apachus* (Hymenoptera: Vespidae) colonies in California: a field study of an introduced species. *Can. Entomol.* 110: 1339–1343.
- Gwynne, D. T. & G. K. Morris.** 1983. Orthopteran mating systems. Westview, Boulder, Colo.
- Hobbs, G. A.** 1965a. Ecology of species of *Bombus* Latr. (Hymenoptera: Apidae) in southern Alberta. II. Subgenus *Bombias* Robt. *Can. Entomol.* 97: 120–128.
- 1965b. Ecology of species of *Bombus* Latr. (Hymenoptera: Apidae) in southern Alberta. III. Subgenus *Cullumanobombus* Vogt. *Can. Entomol.* 97: 1293–1302.
- 1966a. Ecology of species of *Bombus* Latr. (Hymenoptera: Apidae) in southern Alberta. IV. Subgenus *Fervidobombus* Skorikov. *Can. Entomol.* 98: 33–39.
- 1966b. Ecology of species of *Bombus* Latr. (Hymenoptera: Apidae) in southern Alberta. V. Subgenus *Subterraneobombus* Vogt. *Can. Entomol.* 98: 288–294.
1967. Ecology of species of *Bombus* (Hymenoptera: Apidae) in southern Alberta. VI. Subgenus *Pyrobombus*. *Can. Entomol.* 99: 1271–1292.
1968. Ecology of species of *Bombus* (Hymenoptera: Apidae) in southern Alberta. VII. Subgenus *Bombus*. *Can. Entomol.* 100: 156–164.
- Ito, Y.** 1986. Social behaviour of *Ropalidia fasciata* (Hymenoptera: Vespidae) females on satellite nests and on a nest with multiple combs. *J. Ethol.* 4: 73–80.
- Jeanne, R. L.** 1970. Chemical defense of brood by a social wasp. *Science* 168: 1465–1466.
1975. The adaptiveness of social wasp nest architecture. *Quart. Rev. Biol.* 50: 267–287.
1978. Construction and utilization of multiple combs in *Polistes canadensis* in relation to the biology of a predacious moth. *Behav. Ecol. Sociobiol.* 4: 293–310.
1979. A latitudinal gradient in rates of ant predation. *Ecology* 60: 1211–1224.
1980. Evolution of social behavior in the Vespidae. *Annu. Rev. Entomol.* 25: 371–396.
- Kukuk, P. F. & B. P. May.** In press. Dominance hierarchy in the primitively eusocial bee *Lastoglossum (Dialictus) zephyrum*: is genealogical relationship important? *Anim. Behav.*
- Kukuk, P. F. & M. Schwarz.** In press. Macrocephalic male bees as functional reproductives and probable guards. *Pan-Pac. Entomol.*
- Michener, C. D.** 1974. *The social behavior of the bees*. Harvard University, Cambridge, Mass.
1985. From solitary to eusocial: need there be a series of intervening species?, pp. 293–305. In B. Hölldobler & M. Lindauer [eds.], *Experimental behavioral ecology and sociobiology*. G. Fischer, Stuttgart.
- Morse, R. A. [ed.].** 1978. *Honey bee pests, predators and disease*. Cornell University, Ithaca, N. Y.
- Nickerson, J. C. & D. L. Harris.** 1985. *The Florida carpenter ant*. Florida Department of Agriculture and Consumer Services Entomology Circular 269.
- Pamilo, P.** 1984. Genetic relatedness and the evolution of insect sociality. *Behav. Ecol. Sociobiol.* 15: 241–248.
- Peckham, D. J.** 1977. Reduction of miltogramine cleptoparasitism by male *Oxybelus sublatus* (Hymenoptera: Sphecidae). *Ann. Entomol. Soc. Am.* 70: 823–828.
- Post, D. C. & R. L. Jeanne.** 1981. Colony defense against ants by *Polistes fuscatus* (Hymenoptera: Vespidae) in Wisconsin. *J. Kans. Entomol. Soc.* 54: 599–615.
- Rettenmeyer, C. W.** 1963. Behavioral studies of army ants. *Univ. Kans. Sci. Bull.* 44: 281–465.
- Richards, K. W.** 1978. Nest site selection by bumble bees (Hymenoptera: Apidae) in southern Alberta. *Can. Entomol.* 110: 301–318.
- Richards, O. W. & M. J. Richards.** 1951. Observations on the social wasps of South America (Hymenoptera: Vespidae). *Trans. Roy. Entomol. Soc. Lond.* 102: 1–170.
- Schal, C. & W. J. Bell.** 1982. Ecological correlates of parental investment of urates in a tropical cockroach. *Science* 218: 170–173.
- Seeley, T. D., R. H. Seeley & P. Akranakul.** 1982. Colony defense strategies of the honeybees in Thailand. *Ecol. Monogr.* 52: 43–63.
- Starr, C. K.** 1985. Enabling mechanism in the origin of sociality in the Hymenoptera—the sting's the thing. *Ann. Entomol. Soc. Am.* 78: 836–840.
- Strassmann, J. F.** 1981. Parasitoids, predators, and group size in the paper wasp *Polistes exclamans*. *Ecology* 62: 1225–1233.
- Stubblefield, J. W. & E. L. Charnov.** 1986. Some conceptual issues in the origin of eusociality. *Heredity* 57: 181–187.
- Thornhill, R. & J. Alcock.** 1983. *The evolution of insect mating systems*. Harvard University, Cambridge, Mass.
- Trivers, R. L.** 1972. Parental investment and sexual selection, pp. 136–173. In B. Campbell [ed.], *Sexual selection and the descent of man*. Aldine, Chicago, Ill.
- Wilson, E. O.** 1971. *The insect societies*. Harvard University, Cambridge, Mass.
1976. The organization of colony defense in the ant *Pheidole dentata* Mayr (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.* 1: 63–81.
- Windsor, D.** 1976. Birds as predators on the brood of *Polybia* wasps (Hymenoptera: Vespidae: Polistinae) in a Costa Rican deciduous forest. *Biotropica* 8: 111–116.

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In Reply, Is the Sting the Thing?

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I suggest that pressures against the *maintenance of sociality* are less to be expected from invertebrates and microbes than from much larger, usually vertebrate, predators (Starr 1985b; emphasis added here).

Most importantly, the threshold of eusociality was crossed in the context of small colonies, and it is within this context that the importance of the sting to the evolution of eusociality must be examined (Kukuk et al. 1989).

KUKUK ET AL. (1988) summarize my line of reasoning that stinging ability has been an important enabling mechanism in the multiple origins of eusociality in the aculeate Hymenoptera (Starr 1985b) and then dispute it on several grounds. Their summary is fair and pertinent but contains one important misunderstanding. As exemplified in the first quotation above, I do not suggest that vertebrates are the main enemies of social insects but that they are a key element militating against the transition from solitary to social life. A selective factor with a large impact is one that discriminates sharply between genotypes, not necessarily one that culls or inhibits a great number of organisms. Kukuk et al. show good reason to consider ants the premier enemies of most social insects, including other ants, but this does not exactly address the question. My argument rests on the hypothesis that ants exert about equal pressure on solitary and primitively social species, whereas vertebrate predators are preferentially attracted to the latter.

Despite the misunderstanding, Kukuk et al. implicitly call this hypothesis into question by pointing to the recruitment systems that allow colonies of many ants to exploit sizable food sources quickly. The ants they mention as important enemies of social insects are all from advanced genera (*Camponotus*, *Eciton*, *Formica*, *Iridomyrmex*, *Leptothorax*, *Oecophylla* [implied], *Pheidole*, and *Solenopsis*) characterized by relatively large colonies and usually efficient recruitment. This is relevant if eusociality arose in environments similarly rich in recruiting ants and such recruitment draws ants to exploit the clumped brood of primitively social insects more thoroughly than that of solitary insects.

The first proposition is evidently partly true. The fossil record of social hymenoptera (Burnham 1978, Carpenter & Hermann 1979) is fairly good but does little to resolve this point. First, it gives minimum ages for bumble bees, honey bees, stingless bees, and apparent social wasps similar to those for an array of advanced ants, including some of the genera just named, so that we must reserve judgment

on which came first. Second, there is no need to ask whether primitively social ants were faced with such enemies, unless it is proposed that eusociality is polyphyletic in ants. The statement that "ants are typically the most important predators of other ants" is thus as irrelevant as it is true. And for primitively social halictine and anthophorid bees, the question is moot in a different way, as members of these groups evidently continue to cross the eusociality threshold (Michener 1985). On the other hand, unless some lineages of social hymenoptera are much older than is now believed, it cannot be doubted that they were all faced from the beginning with larva-loving predaceous vertebrates.

The second proposition is true of some *Eciton* (among others) but I know of no evidence that it is generally true. It is certainly testable.

Kukuk et al.'s other criticisms are largely independent of the misunderstanding mentioned above (which may be more my fault than theirs), so that a hard core of disagreement between our respective views remains. This concerns the selective factors that preserve the stinger as a defensive device. Its utility in defense can hardly be doubted, because it remains well-developed even in groups that no longer use it in food-gathering (the secondary loss of the stinger in many advanced social ants and bees is not relevant here). As Kukuk et al. indicate, solitary wasps and bees sting in self-defense and to defend brood against arthropod intruders, whereas none is known to attack vertebrate intruders. They conclude that this remains much the same in primitively social groups, and this is where our views diverge.

There is a simple a priori reason to expect females of primitively social hymenoptera often to defend aggressively against vertebrates by stinging. The stings of many solitary wasps and bees are painful to even such extraordinarily large animals as ourselves (Starr 1985a), so that it seems that one or a few of them could put a vertebrate to flight. It is not problematic that they do not try, as they almost never have sizable clumps of vulnerable brood that would justify the risk of attacking a large animal. Social wasps and bees, on the other hand, often do have more brood to lose, and many of them will attack. If Kukuk et al. mean to imply

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that primitively social wasps rarely attack a human intruder, I insist that this is not accurate. I have had the pleasure to be attacked and stung by several species of *Mischocyttarus*, independent-founding *Ropalidia*, and especially *Polistes*. My nerve endings doubt that "stinging is not an effective defense against bird and bat predators [of polistine wasps]," unless this simply means that it is ineffective where we see afterward that it has been ineffective.

Nonetheless, it is certainly true that many primitively social hymenoptera cannot be provoked to sting us. Kukuk et al. point in particular to halictine bees, which never attack when their nests are excavated, and the few that I have forced to sting me were not impressive. As I originally stated (Starr 1985b), the main protection of these insects is evidently their burrow-nesting habit, which would appear to facilitate and necessitate a diffuse arrangement of the brood. Kukuk et al. maintain that the aggregated colonies of many burrowing wasps and bees provide "a concentration of brood," but in what meaningful way is this true? To a predator, such brood—only relatively closer together within a predominant matrix of earth—are surely not comparable to the compact mass in a regular brood-comb.

Even distinguishing this other way of eluding predation, it is inescapable that many primitively social hymenoptera are not nearly as pugnacious as the sting hypothesis would lead us to expect. A case in point are the stenogastrine wasps. These usually nest in accessible places, some can deliver a painful sting (unpublished data), and aggregated colonies of some species raise the concentrated numbers of brood and adult females to the levels of many polistine wasps, yet I have never heard of an attack on a human intruder. Furthermore, it should not be implied that *Polistes* and similar wasps can be relied upon to attack when provoked, especially early in the colony cycle. Significantly often they flee, abandoning healthy brood when it would appear cost-effective to defend. Possibly human beings are just so massive, compared with natural vertebrate enemies, that we sometimes disrupt their evolved defensive responses. The following experiment suggests itself: Use a simulated rat or animal of similar size to threaten early colonies (up to 10 adult females and at least 5 large larvae) of an independent-founding polistine and record the wasps' responses until most have either attacked or fled. If they do not attack fairly reliably, this would be inconsistent with the sting hypothesis and consistent with the view of Kukuk et al. I propose that we do this experiment jointly in the early summer of 1989 in Ithaca, N.Y., using *Polistes fuscatus* (F.).

Although "it is generally agreed that eusociality in wasps originated in tropical areas," it is not clear what importance Kukuk et al. give to this factor in weighing the evidence. They go from this statement directly to cite data from Okinawa, and the bulk of their facts on primitively social species are

taken from even more northerly localities. This implies that data from the temperate zones are comparably applicable in this question to those from the subtropics and tropics. I see no reason to disagree.

Let me call attention to the second quotation above, which is a key point of common ground. It seems to me that where Kukuk et al. introduce extraneous facts (e.g., the impact of social parasites on advanced social species), it is from a failure to keep this point in mind. At the same time, it introduces an area of possible disagreement, or at least of confusion. I do not propose that vertebrate predation pressure is an obstacle to the origin of eusociality per se but to the greater concentration of individuals that almost always accompanies group living. At minimum, a eusocial unit can comprise just two adult females and a few brood, and it is out of the question that such a colony would especially attract the attention of larger predators. I am not concerned here with the structure of a society, only its togetherness, and I recognize that the two are not necessarily coupled. My working conception of early eusociality includes a peak colony size of perhaps 15–20 adult females and a 10-fold increase in brood mass over the solitary condition. That is to say, I assume that any lineage that crosses the eusociality threshold should face no organizational barrier to achieving colonies of at least this size almost immediately. If Kukuk et al. have in mind no more than about three or four females and their brood (in speaking of "small colonies") and consider 50–100 adults as already approaching "large colony size," then much of our apparent disagreement may be only in the words.

Kukuk et al. correctly point out that if the main argument of the sting hypothesis is mistaken, the idea of male nonworkerness as a necessary result of stinglessness also fails. In this context, their enumeration of workerlike acts occasionally performed by males is entirely irrelevant. Their discussion of alternative bases for male nonworkerness is interesting, and I hope to see it further developed elsewhere, but it does not speak to the question of whether the lack of a stinger is a sufficient reason why workers are not male.

Is the selective basis for similar social systems the same in different lineages? It is an article of parsimony within sociobiology that it is, at least among similar organisms. In that case, is it appropriate to seek a single peculiarity of the Aculeata as the decisive factor in their disproportionate tendency toward eusociality? The history of our search indicates that many consider this a good way to begin. It may well turn out that, in fact, eusociality results from the confluence of several independent factors, rather like the origin of life on Earth. What I have tried to do in the sting hypothesis is to examine one factor closely enough to suggest its role (for an analogous treatment of the problem of the origin of endopterygote insects, see Downes [1987]). Possibly the stinger in itself contributes

nothing substantial to an understanding of why and how so many hymenoptera are social. But I cannot concede that this has yet been demonstrated.

References Cited

- Burnham, L. 1978.** Survey of social insects in the fossil record. *Psyche* 85: 85-133.
- Carpenter, F. M. & H. R. Hermann. 1979.** Antiquity of social insects, pp. 81-89. *In* H. R. Hermann [ed.], *Social insects*, vol. 1. Academic, New York.
- Downes, W. L. 1987.** The impact of vertebrate predators on early arthropod evolution. *Proc. Entomol. Soc. Wash.* 89: 389-406.
- Kukuk, P. F., B. Alexander, G. C. Eickwort, R. Gibson, R. A. Morse, F. Ratnieks & M. Raveret-Richter. 1989.** The importance of the sting in the evolution of sociality in the Hymenoptera. *Ann. Entomol. Soc. Am.* 82(1): 1-5.
- Michener, C. D. 1985.** From solitary to eusocial: need there be a series of intervening species?, pp. 293-305. *In* B. Hölldobler & M. Lindauer [eds.], *Experimental behavioral ecology and sociobiology*. G. Fischer, Stuttgart.
- Starr, C. K. 1985a.** A simple pain scale for field comparison of hymenopteran stings. *J. Entomol. Sci.* 20: 225-232.
- 1985b.** Enabling mechanisms in the origin of sociality in the Hymenoptera—the sting's the thing. *Ann. Entomol. Soc. Am.* 78: 836-840.

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