TRAIT MAPPING AND SALIENCE IN THE EVOLUTION OF EUSOCIAL VESPID WASPS

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Abstract.—The multiple independent origins of eusociality in the insect order Hymenoptera are clustered in only four of more than 80 families, and those four families are two pairs of closely related taxa in a single part of the order. Therefore, although ordinal-level characteristics can contribute to hymenopteran eusocial evolution, more important roles have been played by traits of infraordinal taxa that contain the eusocial forms. Many factors have been proposed and discussed, but assessments of traits’ salience to eusocial evolution have heretofore not been joined to phylogenetics. In the present analysis, cladograms of superfamilies and families of Hymenoptera and of the family Vespidae are used to ordinate the appearance of traits that play roles in vespid eusociality. Proximity of traits’ first appearance to the origin of eusocial Vespidae is taken as one measure of traits’ salience to vespid eusocial evolution. Traits that subvert only eusocial taxa and that are uniquely associated with eusociality have foundations in more general traits that subvert more inclusive taxa. No single trait is uniquely causative of vespid eusocial evolution. High-salience traits that closely subvert vespid eusociality include nesting, oviposition into an empty nest cell, progressive provisioning of larvae, adult nourishment during larval provision malaxation, and inequitable food distribution among nestmates. The threshold characteristic of Polistes-grade eusociality is life-long alloparental brood care by first female offspring who remain, adult nourishment during larval provision malaxation, and inequitable food distribution among nestmates. The threshold uniseminated, at their natal nest. Traits directly associated with occurrence of such workers are larva-adult trophallaxis, which can foster relatively low larval nourishment early in a colony cycle, and protogyny and direct larval development, which combine to yield restricted mating opportunities for female offspring that are the first to emerge in the colony cycle. Trait mapping suggests no role for asymmetry of relatedness due to haplodiploidy, but it suggests high salience for haplodiploidy as a mechanism enabling the production of all-female clutches of first offspring.

Key words.—Caste, character ordination, haplodiploidy, Hymenoptera, Vespidae.

Although there are more than 80 families of Hymenoptera (Goulet and Huber 1993), eusociality is found in only four of these: Vespidae, Formicidae, Sphecidae s.l., and Apidae s.l. The vast majority of hymenopterans, therefore, are not eusocial. Crozier and Pamilo (1996, p.78) address a conceptual relationship between the solitary and eusocial forms: “Rather than assume that [noneusocial hymenopterans] are on the way to eusociality, it is reasonable to assert that time has been sufficient and therefore to ask the question ‘what has prevented the evolution of eusocial behavior?’ in those cases. These extant [noneusocial] species should be seen as ones possessing features preventing the evolution of eusociality.” To survey the order Hymenoptera and extract a coherent picture of traits that constrain the full diversity of hymenopteran eusociality and helper behavior. In one such attempt, Evans (1958; Evans and West-Eberhard 1970) linked features of reproductive behavior with grades of hymenopteran social organization. In another, Malyshev (1968) linked traits of life history and development in a broad overview of the evolution of major life-history patterns in Hymenoptera. However, these studies preceded phylogenetic analysis of Hymenoptera, and neither figures prominently in current discussions.

Cladistic relationships among organisms can serve as a framework to sequence the appearance of characters, including ones not used in constructing the cladograms. Such an ordination of traits’ first occurrences can then can be used to hypothesize evolutionary pathways for derived states. Such post hoc exercises cannot test the phylogenetic hypothesis expressed by the cladogram; instead, the cladogram becomes a framework to infer the history of changes in character states among related taxa. Such an approach has been used, for example, to enlighten foundations of the mutualism between yuccas (Yucca spp.) and yucca moths (Tegeticula spp.; Pellmyr and Thompson 1992; Pellmyr et al. 1996), of body sizes and ecomorphs of Caribbean Anolis lizards (Losos 1992), and of the origins of insect biodiversity (Grandcolas 1997).

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Cladograms now exist for the major infraordinal taxa of Hymenoptera. Among the independent origins of eusocial hymenopterans, however, only one taxon, Vespidae, presently has a cladistic ordering of living taxa that span the range from solitary to highly eusocial. Therefore, I propose to first survey the order Hymenoptera and characterize life history and morphology of taxa in which eusocial forms occur. I then will use previously published cladograms to sequence the first appearance of traits germane to eusocial evolution in Vespidae. I will not argue that any single character is the essential trait on which vespid eusociality is based; instead, I propose as an operating principle that salience of a character to vespid eusocial evolution is proportional to proximity of the first appearance of that trait to the appearance of vespid eusociality. This proposition is based on the precept that although traits that subtend both solitary and eusocial forms can be components of eusociality, those traits that subtend exclusively eusocial taxa are more likely to be directly linked to the eusociality itself. Therefore an ordination of traits beginning with those that subtend the entire order Hymenoptera and leading to those that subtend exclusively eusocial Vespidae can constitute one measure of traits’ salience to vespid eusocial evolution.

**Review of the Order Hymenoptera**

The order Hymenoptera has great variety in life history and morphology, with over 100,000 species described (Goulet and Huber 1993) from a possible total of from 300,000 (Goulet and Huber 1993) to a number of species informally estimated by some hymenopteran systematists to rival that of Coleoptera. Hymenoptera are holometabolous insects that are distinguished from other orders by membranous wings (with fore- and hind-wings typically coupled by tiny hooks called hamuli; Basibuyuk and Quicke 1997), haplodiploidy (with its associated asymmetry of relatedness among male and female full sibs), and an ovipositor formed from modified vestiges of appendages on the eighth and ninth abdominal segments (lepismatid form of Scudder 1961). Mandibles (chewing mouthparts) are found in several other orders, but they are usually also given, in combination with the other features, as a distinguishing characteristic of Hymenoptera in contrast to other holometabolous insects such as flies (Diptera) or moths and butterflies (Lepidoptera). The order is traditionally divided into two suborders, Symphyta and Apocrita, with the latter commonly divided into Parasitica and Aculeata. These widely used names usefully organize life-history patterns and will be employed in the following discussion, although both Symphyta (Whitfield 1998) and Parasitica (Gauld and Bolton 1988) are paraphyletic. The focal taxa in the following discussion (Hymenoptera, Apocrita, Aculeata, Vespidae) are monophyletic. Figure I shows infraordinal phylogenetic relationships of Hymenoptera and indicates the four families that contain eusocial species.

**Symphyta**

Adult Symphyta typically feed on nectar or honeydew; some also eat pollen, flower parts, or small insects (Gauld and Bolton 1988). Most symphytans use their ovipositor to make ovipositional slits or borings in plant tissue. Glands associated with the ovipositor probably first produced lubricants, but modification of gland products to alter the oviposition site (e.g., gall formation) appeared early in symphytan evolution (Gauld and Bolton 1988). Most larval Symphyta have three pairs of thoracic legs and some have caterpillar-like abdominal prolegs. Most symphytan larvae feed on green plant tissue; larvae of Siricoidea feed mostly on wood that has been softened and made more nutritious by certain fungi. Carnivory in larval Hymenoptera is postulated to have occurred when stem-boring symphytan larvae encountered and consumed other insect larvae in the plant tissue (Handlirsch 1907 in Gauld and Bolton 1988). Support for this proposition comes from the Orussoidea, which are the phylogenetic intermediate between the wood-feeding Siricoidea and the carnivorous Apocrita and which have larvae that feed on the larvae of wood-feeding beetles (e.g., Vilhelmsen 1997). Apocrita

Adult Apocrita possess an extreme constriction between the first and second abdominal segments. The first abdominal segment (the propodeum) is broadly fused with the thorax and is superficially indistinguishable from it. The constriction (the “thread waist” or petiole) precedes the remainder of the abdomen (the gaster). Larvae of Apocrita are legless and carnivorous, except for secondary phytophagy in such groups as Cynipidae (gall wasps) and Agaonidae (fig wasps) and pollen-feeding in Apidae s.l. (bees) and Masarinae (pollen wasps).

**Parasitica**

Parasitica (reviewed by Gauld and Bolton 1988; Godfray 1994; Quicke 1997) have two basic life-history patterns (Askew and Shaw 1986). An “idiobiont” adult female uses her ovipositor to sting an arthropod and anesthetize or kill it. She then lays a single egg near, on, or rarely within the motionless host. The larva feeds, typically as an ectoparasitoid, on the provision item as its only food and then pupates. A “koinobiont” female uses her ovipositor to place an egg on or, more commonly, to inject an egg into an immature arthropod host. Not anesthetized, the host generally completes its own larval growth before the hymenopteran larva begins to feed on it, typically as an endoparasitoid, eventually killing it. Most Parasitica larvae, including probably all endoparasitic ones, have hindguts that do not open until the larva is ready to pupate. Endoparasitic larvae thus do not void feces as they grow and therefore do not toxify their host or despoil their own source of nourishment.

Koinobiont life-history features include small to very small (alecithal) ova and egg maturation in the ovaries shortly after adult emergence (pro-ovigenesis of Flanders 1950). Gauld and Bolton (1988, p. 19) note that pro-ovigenic females “often need only carbohydrate food in order to live long enough to lay their usually relatively small and more numerous eggs.” The majority of Parasitica are koinobiont and pro-ovigenic, and the life history is derived from the idiobiont pattern, which is retained in the basal lineages of many groups (J. B. Whitfield, pers. comm.).

Idiobiont life histories include large and yolky (lecithal)
ova, maturation of only a few ova at a time (synovigenesis of Flanders 1950), and relatively long adult lifetimes with continuous ovigenesis. Although some idiobionts may produce their first eggs without feeding, production of relatively large eggs continuously over a relatively long lifetime requires that the adult female ingest protein. The thread waist constrains such feeding to liquids or liquid suspensions (Hunt 1982, 1991). Like most adult hymenopterans, idiobiont females may feed on nectar or honeydew, which contain primarily carbohydrates (Maurizio 1975). Free amino acids also occur in both nectars (Baker and Baker 1973) and honeydews (e.g., Sasaki et al. 1990), but in low quantities. It is not surprising, then, that idiobiont females commonly feed on hemolymph oozing from the sting wound of the arthropod that they have stung; Jervis and Kidd (1986) give an extensive review of host feeding by adult parasitoids. Feeding on host hemolymph, without oviposition, is a common life-history feature of some parasitoids and can cause higher mortality of herbivorous insects than does parasitoidism (Jervis and Kidd 1986). Females of the parasitoid family Ichneumonidae will feed on any insect carcass they find in a wet state in captivity (P. W. Price, pers. comm.), and such behavior seems likely to occur in nature.

Once an idiobiont adult female has located a host (Vinson 1976), that host must be suitable not only in nutritional quality (Vinson and Iwantsch 1980), but also in quantity. Large idiobionts require correspondingly large hosts, and if stinging immobilizes the host, then that host is at risk of desiccation, being taken by ants, etc. Apparent adaptations may minimize such risks: the large, yolky egg engenders large body size at larval eclosion, which can foster rapid attainment of large final size, and selected hosts are often in relatively concealed
locations (Gauld and Bolton 1988). Gender of parasitoid offspring has been shown to vary as a function of host size (King 1987), host age (e.g., Ueno 1997), sequential ovipositions into a single host (“superparasitism”; Holmes 1972; Werren 1980), and presence (King 1996) and local density (Werren 1983) of conspecific adults.

Aculeata

Aculeata are unified and distinguished by repositioning of the oviduct ventral to and separate from the ovipositor. The ovipositor retains its morphology and role in stinging, but no longer functions in oviposition. The most likely sister group to Aculeata is Ichneumonoidea (Rasnytsin 1988; Whitfield 1992, 1998), the basal lineages of which are idiobiont Parasitica. Female Scoliidae and Tiphidae, for example, search subterranean burrows for a beetle larva, sting and paralyze it, lay an egg on it, and depart. Similar life histories, with some behavioral sophistication, occur in Mutillidae, some Chrysididae, and some Pompilidae. Increased complexity is found in many Pompilidae and a great number of Sphexidae: a stung and anesthetized host is transported to a preexisting crevice or cavity, hidden away, and an egg is laid on it. In some species a nest chamber is excavated at the site where the host lies after anesthetization, or in still further elaboration the host is transported by dragging or flight to a previously constructed nest chamber (reviewed by Evans 1958; Evans and West-Eberhard 1970).

There is a close relationship between the size of the wasp and the size of the single host. The very large tarantula hawks in genus Pepsis, subgenus Dinopenis, do indeed provision their nest with a full-grown tarantula that is stung and then dragged across the ground. One apparent adaptive trend in Aculeata that fly with their larval host is increased wing loading (Gauld and Bolton 1988; see Danforth 1989). Within the size range of suitable hosts, solitary aculeate wasps tend to lay female eggs on larger hosts and male eggs on smaller hosts (e.g., Pompilidae: Evans and West-Eberhard 1970). The cicada killer, Sphecius speciosus, lays female eggs in nest cells containing two cicadas and male eggs in nest cells containing only one; females are consequently about twice the size of males (Dow 1942).

The linkage between wasp size and host size is broken by a common aculeate life-history elaboration—capture of wasps that are individually smaller than adequate for growth of a larval wasp and transport of multiple such hosts to a preexisting cavity. Often larger cavities are used to rear females and smaller cavities to rear males (Krombein 1961), and some nest-building species preferentially lay female eggs on larger provision masses (e.g., Brockmann and Grafen 1992; Molumby 1997). Capture of insects as a source of adult food rather than larval provision has been noted on a few occasions (e.g., Lin 1978).

Eusociality has evolved within Aculeata once in Formicidae (or possibly twice: Wilson 1971; Hölldobler and Wilson 1990), at least once in Sphexidae s.l. (Matthews 1991), numerous times in Apidae s.l. (Michener 1974), and once in Vespidae (Carpenter 1982). All instances of hymenopteran eusocial evolution are in taxa that build nests and provision larvae with foods gathered on repeated foraging trips. The four families containing eusocial species are the only families of Hymenoptera for which nesting is a family-level trait.

Vespidae

Vespidae is an assemblage of mostly robust, medium to large wasps. Most have a longitudinal fold of the wings when at rest (Danforth and Michener 1988). Cladistic analysis reveals monophyly of six living subfamilies (Carpenter 1982, 1991; Fig. 2).

Euparagiinae

Euparagaunes are solitary. They nest in soil, where a cell is constructed and an egg laid in it before foraging for multiple weevil larvae; the nest cell is mass provisioned and sealed before the wasp larva ecloses from the egg.

Masarinae

Masarinae provision their larvae with pollen, which foraging female wasps carry internally in the crop. Brood-cell provisioning in Masarinae is equivalent to mass provisioning (Gess 1996). Although most masarines are solitary, Zucchi et al. (1976) report that Trimeria howardii in subtropical Brazil has nest sharing by several females; it may have progressive provisioning of larvae as well as direct (uninterrupted) development of some larvae and diapause of others.

Eumeninae

Cowan (1991) reviews biology of Eumeninae, the most diverse vespid subfamily, with some 3000 described species in over 180 genera (Carpenter 1986). Some eumenines nest in pre-formed cavities; some excavate nests in soil; still others construct nests from mud or masticated plant material. Mud nest construction generally involves drinking water into

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**Fig. 2.** Cladogram of subfamilies of living Vespidae from Carpenter (1982). Eusociality occurs in the two subfamilies marked with an asterisk; all species of Polistinae and Vespinae are eusocial. The traits at each numbered node are: (5) nesting, oviposition preceding provisioning, mass provisioning with small provision items via central-place foraging; (6) pollen ingestion (?); (7) provisions captured with mandibles instead of sting, provision malaxation with concomitant adult nourishment, simultaneous progressive provisioning of multiple larvae, multiple adults per nest, interadult trophallaxis, absence of larval diapause, protogyny; (8) petiolate paper nests, larva-adult trophallaxis, lifelong sterile workers, painful antivertebrate venom; (9) queen-worker brood-cell size difference.
the crop and regurgitating it to mix with soil. Saliva may be added to the soil and water mixture (Isely 1913). Eumenines that nest in pre-formed cavities typically lay male eggs in the first several nest cells that they provision (Krombein 1967). Provision items (generally caterpillars) are stung and anesthetized, then transported to a nest cell that in most cases already contains the wasp’s egg. Unlike most solitary wasps, eumenines “often knead [the caterpillar] by chewing it with their mandibles, working from one end of the caterpillar to the other without breaking its skin” (Cowan 1991, pp. 46–47). Cowan notes that mass-provisioning eumenines apparently only lightly paralyze provision items, but “prey brought to nests by progressive provisioners are flaccid and completely immobile, as though severely kneaded” (Cowan 1991, p. 50). At least some eumenines do still more: Calligaster cyanoptera bites the head off its provision items (Williams 1919) and Synagris cornuta chews an item into unrecognizable paste before feeding it directly to its larva (Roubault 1911). Such wasps likely take hemolymph from the provision item into their crop. One, Oreumenes decoratus, apparently also regurgitates ingested hemolymph to moisten mud for nest construction (Iwata 1953). In many progressive-provisioning species the adult female may remain at or in the nest between foraging trips, and in some (e.g., Synagris), progressive provisioning incorporates direct contact between an adult female and her larva. Zethus minutus can have 15 or more females per nest with complex behavioral interactions among them (West-Eberhard 1978, 1987a).

Stenogastrinae

Stenogastrinae (reviewed by Turillazzi 1991) make architecturally diverse nests of mud, chewed plant material, or mixtures of these (Wenzel 1991). Foraging wasps malaxate (chew) provision items with their mandibles, imbibe the hemolymph, and transport the remains in their mandibles to the nest. There, malaxed solids and regurgitated liquids are placed near small larvae, which then feed on them, or on the ventral surface of larger larvae, which have a coiled posture. At times other than provisioning, adults have been observed to lick a clear liquid from the ventral surface of larger larvae. Multiple nest cells, with larvae of varied ages and sizes, are open and provisioned simultaneously. Cofoundresses (if any) and emerged daughters participate in foraging, construction, and larval provisioning at the same time as does the egg-laying foundress. Adult nestmates share food among themselves by regurgitation. Females of some species form a dominance hierarchy in which food sharing plays a role, but in other species no such hierarchy has been found. Turillazzi (1985) notes that from three to five female Parischnogaster nigricans serrei emerge before the first male offspring emerges. Females apparently mate when they are 20 to 50 days of age (Turillazzi 1985, 1991), thus un inseminated females in a colony may be only young females. To date there is no unequivocal evidence of females functioning as life-long workers and never becoming inseminated.

Polistinae

Polistinae (reviewed in Ross and Matthews 1991; Turillazzi and West-Eberhard 1996) are characterized by presence at nests of life-long uninseminated worker females during at least part of the colony cycle. The subfamily contains 28 genera in four tribes (Carpenter 1993). Basal genera (Polistes, Mischoctyntus, Belonogaster, Parapolybia, and part of Ropalidia) use wood pulp paper to build open-comb nests suspended from a stalk or petiole. One or several inseminated females found a nest from which offspring, including first-generation workers, are reared. Thus, this “independent-founding” life history characteristically includes a period in which no offspring are present at newly founded nests. Founds (and, later, workers) forage for arthropods (mostly caterpillars) that they subdue with their mandibles; the sting is used exclusively in defense of the nest and colony. Provisions for larvae are extensively malaxed, and the malaxated adult imbibes and derives nourishment from the provision hemolymph (Hunt and Noonan 1979; Hunt 1984). Adults of a colony transfer ingested hemolymph among individuals (interadult trophallaxis of Hunt 1982); net movement of nourishment up a dominance hierarchy occurs in both foundress associations (Pardi 1948) and among workers (O’Donnell 1995). Malaxed provision items and regurgitated hemolymph are fed directly to larvae. Larvae produce a nutritional saliva (Hunt et al. 1982, 1987) that adults actively solicit and drink (Roubault 1916). Surrender of the saliva by larvae (larva-adult trophallaxis of Hunt 1982) may vary as a function of level of colony nourishment (Hunt 1988), which is low in foundress nests and higher in nests with offspring workers (e.g., West-Eberhard 1969). In temperate zone Polistes, some species produce “early” males (e.g., Strassmann 1981; Page et al. 1989), but males and reproductive females are typically produced only after emergence of an exclusively female brood (e.g., West-Eberhard 1969), most but not all of whom work (Page et al. 1989; Hunt 1991). Although males might be present in the environment at any time in humid tropics (S. O’Donnell, pers. comm.), West-Eberhard’s (1969, p. 71) observation that in Polistes erythrocephalus in Colombia “male production . . . followed a period of female emergence” is typical of colonies of the vast majority of tropical polistines (J. W. Wenzel, pers. comm.). About half of newly emerged females isolated from colonies of Ropalidia marginata engage in nest construction and about half do not (Gadagkar et al. 1988, 1990a); correlates of nest-founding ability include level of larval nourishment and amount of food consumed by the isolated adult (Gadagkar et al. 1990b).

Polybioiodes, part of Ropalidia, and all 22 genera of the Neotropical Epiponini have “swarm-founding” life histories, in which multiple inseminated queens accompanied by numerous sterile workers move en masse to initiate a new colony (reviewed by Jeanne 1991). There is never a solitary or reproductive-only life-cycle phase; offspring workers are always present. Queen and worker females can be dimorphic in shape (e.g., Jeanne et al. 1995) and size (e.g., Hunt et al. 1996), and evidence strongly suggests that caste differentiation occurs during larval development (O’Donnell 1998; see also West-Eberhard 1996).

Vespinae

Vespinae, the yellowjackets and hornets, have life history, nest construction, and behavioral biology similar to inde-
pendent-founding Polistinae (reviewed by Spradbery 1973; Matsuura and Yamane 1990; Greene 1991; Matsuura 1991). Colonies of Vespinae are founded at the start of an annual active season by solitary, inseminated young queens (except in the swarm-founding, nocturnal *Provespa*). Vespinae have large queens and small workers, which are determined by differential larval nourishment as a correlate of size of the nest cell in which a larva is reared (Spradbery 1973).

**Trait Mapping**

Relationships of major divisions of Hymenoptera (Fig. 1) and of subfamilies of Vespidae (Fig. 2) are shown together with the placement of traits, numbered and described below, on branches where they appropriately subtend distal taxa. Traits are ordinated by successive branches, but sequencing of traits on any single branch is generally not possible. Traits that are synapomorphies are given below in boldface type; those that are symplesiomorphies are italicized. Other traits are at least characteristic of the taxon they subtend. Branch 1 includes two traits that are part of the starting groundplan.

**Branch 1: Hymenoptera**

1a. Mandibles (groundplan trait). Arguments for a significant role for mandibles in eusocial evolution indirectly address higher salience traits. Most importantly, mandibles enable nest construction. Many (but not all) nesting hymenopterans also use their mandibles to transport larval provisions. Some Eumeninae and all Stenogastrinae, Polistinae, and Vespinae use mandibles to malaxate larval provisions.

1b. Lepismatid ovipositor (groundplan trait). This sclerotized, rigid structure is present in some of the earliest (Devonian) wingless insects, but among Holometabola it is retained only by Hymenoptera. Apocrita are the only stinging insects. In Aculeata, the ovipositor is used exclusively for stinging.

1c. Membranous wings coupled by hamuli. The ability to carry heavy loads in flight suggests a remote, yet potentially significant, role for hamuli.

1d. Haplodiplody with relatedness asymmetry of male and female full-sibs. Haplodiplody characterizes both Hymenoptera and Thysanoptera (thrips) as well as a variety of other arthropod taxa (Bull 1983). In all, about one-fifth of known animal species have haploid males (Crozier and Pamilo 1996).

**Branch 2: [Orussoidea + Apocrita]**

2. Larvae carnivorous. Carnivory by larval Orussoidea and Apocrita was presaged by the tendency of larval phytophagous Symphyta to opportunistically utilize foods more nourishing than plant mesophyll (Gauld and Bolton 1988). Larvae of Siricoidea, the sister group to [Orussoidea + Apocrita], feed on wood, whereas larvae of Orussoidea feed on larvae of wood-boring beetles.

**Branch 3: Apocrita**

3a. Larvae legless. Leglessness in larvae whose food habits do not require locomotion could reflect either adaptive developmental economy or selective neutrality accompanied by degenerative mutation fixed by genetic drift (see Fong et al. 1995). (Vermiform locomotion has evolved secondarily in some parasitic bee larvae [Wcislo 1987], and novel leglike structures stabilize larvae of allodapine bees that are reared in open nest chambers [Michener 1974].)

3b. Closed larval hindgut. Found in most Parasitica and Aculeata (the trait is reversed in the bee genus *Xylocopa*, e.g., J. W. Wenzel, pers. comm.), the closed proctodeal opening enables the subsequent evolution of nesting (Evans and West-Eberhard 1970) because larvae do not despoil their growth surroundings.

3c. Petiolate abdomen. It is often stated that the thread waist of Apocrita facilitates precision in oviposition. However, Symphyta lack the petiole yet have precise oviposition, albeit into plant tissue rather than a living insect. For example, some sawflies in the genus *Euiura* are incredibly accurate, placing a large egg in a tiny, newly formed bud, which is followed by gall formation (P. W. Price, pers. comm.). Furthermore, many basal lineages of Apocrita do not oviposit into their hosts, although they do sting and anesthetize them (J. B. Whitfield, pers. comm.). Character ordination suggests no scenario for origin of the petiolate abdomen of Apocrita, but presence of the petiole imposes a constraint that affects the activities of every adult apocritan: nourishment can only be obtained from liquids (Spradbery 1973; Hunt 1982).

**Branch 4: Aculeata**

4a. Repositioned oviduct. Relocation of the oviduct enables selection to act on morphology of the sclerotized, rigid ovipositor for stinging only. Simultaneously, selection is freed to act on products of glands associated with the ovipositor as venom and pheromone rather than for ovipositional roles such as lubrication.

4b. Lecithal ova; synovigenesis; adult feeding on host hemolymph. The idiobiont traits of large, sequentially matured ova necessitate proteinaceous adult nourishment, but the thread-waisted abdomen restricts such nourishment to liquids or liquid suspensions. Feeding on hemolymph oozing from sting wounds presages feeding on hemolymph during malaxation of larval provisions.

4c. Host anesthetization; selection of concealed hosts. These foraging components of the idiobiont character suite presage nesting (Evans 1958; Evans and West-Eberhard 1970).

**Branch 5: Vespidae**

5a. Larvae reared in a constructed nest. Nesting, a sophisticated mode of brood concealment, involves excavations in soil as the basal condition in Euparagiinae and Masarinae. Use of preexisting cavities by some Eumeninae is derived, as is nest construction from modified materials in some Eumeninae and in all Stenogastrinae, Polistinae, and Vespinae. Independently evolved nesting in Formicidae and in [Speccidae + Apidae] supports eusociality in those families in the same way as in Vespidae: nesting establishes the essential conditions for central-place foraging with repeated provisioning trips and for interspecific encounters other than courtship and mating.

5b. Oviposition into an empty cell. This basal trait for
Vespidae enables selection to act on brood gender sequence and sex ratio independently of constraint on an ovipositing female to assess provision mass before fertilizing or not fertilizing her egg. The trait is lost in a few Eumeninae but retained in [Stenogastrinae + Polistinae + Vespinae].

5c. Provision items too small to support development of a full-size adult. Nesting and central-place foraging allow dissociation of prey size and size of the adult wasp. Most species of the basal genera in Polistinae are individually large in size, yet they are able to rear numerous offspring without the constraint of finding and transporting one prey item per offspring that is large enough for each offspring’s full development. Reduction in prey size enables foraging efficiencies that can lead to both higher offspring numbers and higher population densities (Hunt 1991).

5d. Mass provisioning of brood cells. This basal trait of Vespidae is a corollary of the trait of repeated foraging trips per nest cell and is widespread in nesting solitary Aculeata that provision with prey smaller than the adult wasp.

Branch 6: [Masarinae + Eumeninae + Stenogastrinae + Polistinae + Vespinae]

6. Pollen ingestion (?). Data on this point (Hunt et al. 1992) are inadequate for a firm conclusion, but ingestion of pollen—either actively or passively while gathering nectar—may be a source of dietary nitrogen for most nectar-feeding adult Vespidae.

Branch 7: [Stenogastrinae + Polistinae + Vespinae]

7a. Capture of prey with mandibles. Mandibular capture of larval provisions frees the sting from selection on provision anesthetization, and it opens a gateway to foraging efficiencies by linking brood provisioning with adult self-nourishment during provision malaxation (Hunt 1984, 1991).

7b. Provision malaxation. Provision malaxation occurs in some progressively provisioning Eumeninae and is characteristic of all Stenogastrinae, Polistinae, and Vespinae. Malaxation of larval provisions accompanied by hemolymph ingestion provides the basic proteinaceous nourishment to support adult longevity accompanied by sustained synovigenic oogenesis at levels greater than those that can be achieved by solitary Aculeata and that are necessary to achieve the longevities and brood production levels characteristic of eusocial Hymenoptera (Hunt 1991).

7c. Simultaneous progressive provisioning of multiple larvae. Simultaneous progressive provisioning is enabled by nest architecture of multiple open brood cells that brings not only the provisioning adult and larvae into contact, but that fosters direct contact among nest-sharing adults or between foundress(es) and the first offspring to emerge from an uneven-aged brood.

7d. Multiple adults per nest. Solitary foundresses occur in all three subfamilies subtended by this trait; therefore the focal multiple adults in this case are the colony foundress and her female offspring. Sociality in [Stenogastrinae + Polistinae + Vespinae] is matrifilial regardless of whether a foundress is solitary or part of a foundress group.

7e. Interadult trophallaxis. Presence of multiple adults at a nest opens opportunities for dominance interactions. Although Pardi’s (1948) focus was on foundress associations, behaviors similar to dominance interactions occur between solitary foundresses and their daughters (e.g., Reeve and Gamboa 1987), among offspring workers (e.g., O’Donnell 1995), and among nestmates of swarm-founding species (e.g., Hunt et al. 1987). Dominance interactions incorporate inequitable distribution of food via interadult trophallaxis as an inherent component (Pardi 1948). The origin of interadult trophallaxis, whether between cofoundresses or between a foundress and her daughters, may lie in appeasement behaviors during potentially aggressive encounters. Regurgitation of crop contents in interadult trophallaxis was presaged by regurgitation for nest construction in some Eumeninae.

7f. Absence of larval diapause. Diapause, the passing of an unfavorable season as an immature in developmental arrest, necessitates emergence of both males and females at the start of the following favorable season to ensure females’ insemination. Direct (uninterrupted) development, with the ensuing unfavorable season being passed by adults in quiescence, enables reproduction to be begun the following favorable season by previously inseminated females alone. Although male paper wasps may enter quiescence (Hunt et al. 1999), no activity by males that have passed through quiescence from a previous season has been reported at the start of a colony cycle. The absence of parental-generation males eliminates a mating opportunity for first female offspring of the following generation. Absence of larval diapause is a life-history trait found in all eusocial Vespidae and Halictini (sweat bees; Matthews 1991).

7g. Protopgyny. The means by which proximate cues affect fertilization versus nonfertilization in ovipositing Hymenoptera are poorly known. Nonetheless, existence of a mechanism on which selection can act is clearly indicated by the ability of parasitoids to match offspring gender with host size or age and of solitary aculeates to match offspring gender with host size, nest-cell size, or nest-cell provision mass. Most solitary nesting Aculeata are protandrous (Gauld and Bolton 1988); all eusocial Hymenoptera are protogynous. This life-history transition is enabled by oviposition into empty nest cells of uniform size, which unlinks fertilization versus nonfertilization from assessment of cell size or larval provision mass.

Branch 8: [Polistinae + Vespinae]

8a. Petiolate paper nests. Use of wood fibers mixed with saliva enables construction, virtually any time and anywhere, of nests that can be tough, durable, and large (Jeanne 1975; Wenzel 1991) and that can be the locus of social interactions that foster eusociality (Starr 1991; Hansell 1996). The nest petiole may be coated with a glandular secretion that provides protection of the brood against marauding ants (Jeanne 1970).

8b. Larva-adult trophallaxis. This trait was presaged by the lapping of clear liquid, which is probably saliva, from the ventral surface of larval Stenogastrinae. In Polistinae and Vespinae, the saliva serves as nourishment to the adults that drink it (Spradbery 1973). Selection for survival of brood cannibalism via salivary appeasement has probably fostered both nutritional richness of the saliva (Hunt et al. 1982, 1987)
and traits of trophallaxis-avoidance behavior and morphology in larvae (Hunt 1988).

8c. Life-long sterile workers. Presence at the nest of life-long nonreproductive worker offspring is the hallmark of eusociality in [Polistinae + Vespinae]. First-brood female larvae of independent-founding Polistinae develop under conditions of low rates of incoming foraged provisions and high rates of larva-adult trophallaxis, and in most cases no males are present when they emerge. These females, then, are the offspring that exhibit context-dependent facultative alloparental brood care (West-Eberhard 1987a,b) and are workers at their natal nest. Offspring workers occur independently of considerations of single versus multiple foundresses.

8d. Painful antivertebrate venom. The evolutionary significance of protecting nest and brood against vertebrates via painful stings (Starr 1985, 1989) has been questioned (Kukuk et al. 1989; Hunt 1994), but character ordination underscores correspondence of defensive stinging and Polistes-level eusociality.

Branch 9: Vespinae

9. Queen-worker brood-cell size difference. Vespine queens construct small cells from which workers emerge; workers construct additional worker cells but also the larger cells, generally in a separate nest comb, from which queens are reared. Construction by a queen of nest cells too small to foster full development of reproducitively competent females interacts with protogyny to yield not merely first-generation worker offspring, but large numbers of them, all without dominance interactions or other per-individual means to suppress daughters’ ovarian development.

**Discussion**

Trait mapping illustrates that eusocial evolution in Vespidae rests on concatenation of serially evolved traits. That is, many traits are necessary and no single trait is sufficient for vespid eusocial evolution, and relevant traits did not arise as a unified suite. The trait mapping also shows that relevant traits that subdivide both solitary and eusocial taxa reflect constraints or adaptations that did not impinge on eusociality at their origin. For example, nesting behavior is demonstrably sine qua non for eusocial evolution in Hymenoptera, but nesting rests on a foundation of antecedent traits for provision concealment (Evans 1958; Evans and West-Eberhard 1970).

The serial ordering of relevant traits can be interpreted as one measure of traits’ salience to eusocial evolution. It might be argued that all of the discussed traits are equally important for vespid eusocial evolution, because eusociality in Vespidae requires the integration of all of the discussed traits. However, traits that subdivide both solitary and social taxa often lack specificity with regard to sociality. For example, although nesting is essential for hymenopteran eusociality, not all nesting behaviors and architectures will suffice for hymenopteran eusocial evolution; only nesting that enables direct contact between nestmates can foster eusociality. In contrast, traits that subdivide primarily or exclusively eusocial taxa are more immediately linked to eusociality. For example, interactions among nestmates, both larva-adult and interadult, open the door to unequal distribution of nourishment, which underlies differences in fecundity among female nestmates. Thus, although vespid eusociality requires both nesting and unequal distribution of nourishment, the latter trait is more immediately linked to eusociality and therefore can be ascribed higher salience.

The adaptive origin of oviposition into an empty nest cell is unknown for Vespidae (for solitary sand wasps, Evans [1966] suggests selection to circumvent egg predation by milktommamine fly larvae borne on a wasp’s initial prey item). The consequence of such oviposition, however, is that it unlinks the association found in solitary aculeates between provision mass and offspring gender. It is in this context that the trait mapping highlights a very significant role in vespid eusocial evolution for haplodiploidy—it is a mechanism that can enable protogyny. Selection favoring ovipositional protogyny reflects two points: only female hymenopterans work, and the vast majority of females that work at their natal nest are un inseminated. Hunt (1994) therefore argues negative selective value of “early” males in Polistes. Because neither males nor inseminated female offspring work at their natal nest, “early” males can reduce the possible workforce at a critical stage of colony development in two ways, by consuming scarce resources in the early stages of colony development without a work payoff upon emergence and by inhibiting the work of any newly emerged females they may inseminate. Scarcity of offspring males due to protogyny is exacerbated by absence of parental-generation males following quiescence of adults that develop without larval diapause in seasonal environments, which doubly restricts mating opportunities for first female offspring and sets the stage for alloparental brood care by these unmated females. A significant role in hymenopteran eusocial evolution for haplodiploidy as a mechanism that can enable protogyny has been argued from life-history perspectives by Brian (1965), Richards (1965), Alexander (1974), Gauld and Bolton (1988), and Hunt (1991, 1994).

Seger’s (1983) “halictine” model of split sex ratio approaches the scenario revealed by the character ordination for Vespidae. Although Seger ascribes significance to haplodiploidy different from that proposed here, support for the significance of haplodiploidy-enabled protogyny can be drawn from Seger’s example of the bee Halictus ligatus. In Trinidad, where colony cycles are continuous and males are active year-round, H. ligatus is solitary; in New York and Ontario, where colony cycles are annual and males are absent in spring, H. ligatus is eusocial (Michener and Bennett 1977). Yanega (1988, 1989) documented the mechanistic basis of such eusociality in Halictus rubicundus in New York: female offspring that are inseminated soon after emergence become founndress reproductives (after overwinter quiescence), whereas female offspring that go unmated in their first few days after emergence remain as workers at their natal nest. A similar scenario probably exists in the independent-founding polistine wasp Ropalidia formosa, which produces males as early as the second or third offspring and is “nearly solitary,” having the smallest nest sizes and numbers of resident adults per nest (approximately one) of any Polistinae (Wenzel 1987).

William Morton Wheeler (1923, 1928) listed independent
origins of insect sociality and inspired similar enumerations at the dawn of the sociobiology era (Wilson 1971, 1975) that focused attention on eusociality evolving “at least eleven times in the Hymenoptera” (Wilson 1971). Emphasis on “Hymenoptera” rather than “nest-making Aculeata” lent credence to study of asymmetry of relatedness due to haplodiploidy, a characteristic of the order Hymenoptera, as contributory to eusocial evolution (Hamilton 1964a). However, extensive empirical studies of intracolony relatedness have shown that “The genetic asymmetry potentially created by haplodiploidy is insufficient by itself to promote the origin or the maintenance of eusociality” (Gadagkar 1991, p. 20). Trait mapping graphically illustrates one reason why this assertion should not be surprising; this trait subdents approximately 80 families of exclusively solitary Hymenoptera in addition to the four families containing eusocial forms.

Current support for a role of asymmetry of relatedness comes from split sex ratio theory (Grafen 1986; Boomsma and Grafen 1990, 1991) that addresses the problem of population sex ratio imbalance (Fisher 1958) that would ensue if workers in all colonies reared primarily sisters (Maynard Smith and Szathmáry 1995). Indeed, Maynard Smith and Szathmáry (1995, p. 267) note, “it is hard to see how a causal connection between haplodiploidy and sociality could arise except through split sex ratios.” However, no consistent pattern of empirical support can be drawn from an extensive number of sex ratio studies (Crozier and Pamilo 1996). Furthermore, split sex ratio theory focuses on sex ratio of reproductive (not worker) offspring. This focus is analogous to propositions that eusocial Polistinae are protandrous (e.g., Strassmann and Hughes 1986). Such arguments can be made only if one ignores nonreproductive worker offspring, but because only female hymenopterans work (notwithstanding Hunt and Noonan 1979; Cameron 1985, 1986; O’Donnell 1995), gender of first-brood offspring is critical to development of a eusocial colony of hymenopterans and cannot be ignored in theoretical explorations of the origin of their eusociality. Indeed, at the threshold of eusociality the distinction between reproductive and worker offspring is often context dependent. No aspect of the character ordination indicates a role for asymmetry of relatedness in vespid eusocial evolution.

Assertions such as that by Queller (1996, p. 218) that “many individuals give up their own reproduction in order to help rear the offspring of relatives” draw no support from the analysis presented here. Propositions that offspring workers reflect outcomes of variable development in response to environmental (i.e., nourishment) variations (West-Eberhard 1987a,b, 1988, 1989, 1996) are supported by this analysis. Indeed, the trait mapping and consequent ordination ascribes highest salience in vespid eusocial evolution to various traits involving nourishment. The high salience for hymenopteran eusociality of provision malaxation as a source of adult nourishment, higher among nestmates is the foundation for Darwin’s (1858) oft-quoted assertion that “selection may be applied to the family, as well as to the individual, and may thus gain the desired end” of selecting traits of morphology and behavior in non-reproductive female workers that differ from those of female reproducitives. Family(colony)-level selection will occur, however, in diplo-diploids (e.g., Isoptera) as well as haplo-
diploids, and it will occur regardless of whether individuals can assess their relatedness to nestmates or global conditions of their colony.

An emerging body of theory and empiricism is showing that even though individual members of a colony respond only to stimuli of their immediate surroundings, the sum of individual stimulus-response behaviors is self-organization (Pasteels and Deneubourg 1987; Bonabeau et al. 1997) of a colony that represents a new, supraindividual level of selection (Wilson and Sober 1989). In such a system, inclusive fitness (Hamilton 1964b) is an inherent property through which selection acts on colony-level reproductive consequences of colony members’ individual traits and behaviors. In such a colony-level selective environment, intracolony reproductive contests and their selective ramifications may not be entirely inconsequential, but they are of far less consequence than selection at the level of the colony in an ecological arena of competing colony-level units (Buss 1987; Corning 1997).

W. D. Hamilton (1966, p. 108) has said, “The real difficulty is explaining why the juveniles develop the altruistic trait.” Ordination of characters via trait mapping does not address an adaptationist scenario of why vespid workers evolved, but it very informatively addresses a mechanistic scenario of how the integrated structural components of vespid eusociality evolved via sequential appearance of traits individually shaped and collectively interlinked by natural selection.

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