A new model for caste development in social wasps

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Key words: nutritional switch, caste, eusociality, social wasps, evolution, development, vibrations

Abbreviations: W/L, worker-to-larva ratio; JH, juvenile hormone; IIS, insulin/insulin-like signaling pathways

The most fundamental specialization of the eusocial insects is the division of colony members into two castes, workers (functionally sterile individuals) and reproductives.1 Understanding the proximal mechanisms leading to differentiation among individuals is therefore central to an understanding of the evolution of eusociality itself.2 Because the wasp family Vespidae includes species representing a range of degrees of sociality from solitary to swarm-founding, the wasps can provide clues about what the early evolutionary steps toward caste-determining mechanisms might have been.3-6

Specialization into reproductive and non-reproductive castes is one of the defining traits of eusocial insects. Knowledge of the proximal causes of caste differentiation is therefore central to achieving an understanding of the evolution of eusociality. Castes are an example of a polyphenism, multiple, discrete phenotypes arising from a single genotype in response to differencing environmental conditions. Here we focus on recent work in the social wasps to provide insight into how environmental conditions may trigger the development of caste across a range from independent- to swarm-founding social species. The amount of food larvae receive has long been recognized as a key input factor in the determination of caste, but that alone is insufficient to account for the range of combinations of size, development time and caste among the female offspring of Polistes, an independent-founding wasp. Recent experimental work on P. fuscatus has shown that vibrations that are associated with the feeding of larvae are another essential environmental input in the determination of caste. We present a model of how vibrational signaling in the context of feeding larvae could interact with nutritional input to account for the developmental patterns seen in these wasps. Mapping the distribution of vibrational signaling onto a phylogeny of the social wasps suggests that this trait characterized the common ancestor of the subfamilies Vespinae + Polistinae, diversified in the independent-founding species.15-19 Conversely, under-feeding produces smaller offspring.19 Workers, which are reared by the queen early in the colony cycle, are said to be the result of poor larval nutrition due to a low worker-to-larva (W/L) ratio at that time. The gynes, produced later, are the result of improved nutrition due to an increasing W/L ratio.5,13,20,21 Despite these pre-adult biasing effects, adults retain some behavioral and physiological plasticity to respond to the social context they find themselves in.7
Possible Role for Vibrational Signals

It has recently been suggested that vibrational signaling provides a second source of input that may modulate the effect of nutrition quantity.\(^\text{22}\) Vibrational signals are especially conspicuous in the genera Polistes, Mischocyttarus, Ropalidia and Belonogaster. Females produce these signals either by rapidly shaking the body while standing on the nest, or by striking some part of the body against the nest. The movements are typically vigorous enough to produce audible sound and to cause the whole nest to shake orvibrate.\(^\text{29,30}\) Some categories of these signals are performed primarily by the dominant females while feeding the larvae. The best-known example is antennal drumming in Polistes, which is performed at the highest frequencies early in the colony cycle, when workers are being reared, and at much reduced rates later, when gynes are being reared.\(^\text{31,32}\) Recent experimental evidence for Polistes fuscatus has shown that larvae in nests subjected to simulated antennal drumming (pulses at 17 Hz) develop into adults with significantly less fat body than larvae given random-frequency vibration of the same intensity.\(^\text{33}\) Low body fat is a worker-like trait, whereas high body fat is a characteristic of gynes.\(^\text{34,35}\) That vibrational signals can have this effect is not surprising. Mechanical stressors are known to have dramatic biochemical and developmental effects on insects and other animals.\(^\text{22}\)

Limits of the Nutritional-Switch Hypothesis

A mechanism based strictly on the amount of food received by larvae appears to be too simplistic, even for Polistes. This single-dimensional variable is insufficient to account for the multi-variate patterns of development seen in this and other independent-founding polistines.\(^\text{22}\) First, the rate of larval development, in insects generally positively correlated with resource availability,\(^\text{9}\) does not correlate well with size or caste. In Polistes, Mischocyttarus and Ropalidia, larval development times are shortest for the first few (worker) offspring, rise rapidly to a maximum for later-emerging workers, then gradually decline to intermediate durations for the remainder of the colony cycle, when gynes are produced.\(^\text{23-27}\) Second, the first-produced workers not only develop more rapidly than any subsequently produced females, but paradoxically they are also the smallest.\(^\text{24,26}\) Mead\(^\text{16}\) and Kudo\(^\text{28}\) concluded that the rapid growth of the first larvae in Polistes is due to more intensive feeding, but this is contradicted by studies providing supplemental feeding of larvae, which leads to both more rapid larval development and growth to larger, not smaller, adult size.\(^\text{22}\) Furthermore, the larger females produced later in the colony cycle include workers that do not differ measurably in size from gynes.\(^\text{21,24}\) In other words, size, development rate and caste vary semi-independently of one another to produce more combinations than can be explained by the single input variable of food quantity.
phenotype. Workers continue to emerge, albeit in decreasing numbers, possibly due to uneven distribution of food along with individual differences in exposure to and sensitivity to vibrational stimuli.

### Taxonomic Distribution of Vibrational Signaling

Mapping the taxonomic distribution of vibrational behavior in the context of feeding the larvae onto a phylogeny of the social Vespidae highlights its co-occurrence with independent-founding genera. These genera are characterized by small colony sizes (typically well under 100 individuals) and absence of morphologically distinct castes. Whether vibrational signals in these other genera play a caste-biasing role similar to that reported in Polistes remains to be investigated, but the principle of parsimony suggests that they do. Wasps in the less-derived subfamily Stenogastrinae form even smaller societies, lack reproductive and worker castes, and also lack any evidence of vibrational signaling directed at the larvae.

The Vespinae present a more diverse picture. Most form large colonies and show pronounced queen-worker dimorphism. The clearest account of vibrational signaling directed at the larvae is for *Vespa tropica*. When a founding queen returns to the nest with food for the larvae, she engages in prolonged tapping of the hind legs on the nest. This species is unusual in that colonies are among the smallest in the subfamily, with 5–15 workers at maturity, and gyne and worker are not morphologically different, although as in Polistes the gynes have...
much more fat body than workers, indicating caste differentiation originating in the immature stages. The more derived genera Vespuca and Dolichovespula (Fig. 2) are the most dimorphic of the social wasps, with gyne up to 40% larger and morphologically and physiologically distinct from workers. Colonies are large and gyne are reared in specially constructed large cells, opening the possibility that workers could be cued to feed different amounts or qualities of food by the size of the cell a larva is in. Thus, a strictly nutritional switch could be acting, although pheromones are also suspected to play a role. Interestingly, vibrational signals have been reported for a number of species. Workers of Vespuca consobrina occasionally drum their abdomens (gasters) vigorously on the nest during rounds of brood-cell inspection. This species also forms small colonies, with worker numbers of less than 100. Gaster drumming by founding queens or founding queens and workers has also been reported for Dolichovespula spp. and in young colonies of Vespuca spp., although it is not clear whether it is associated with feeding the larvae.

The four taxa that initiate colonies by means of swarms of queens and workers (Fig. 2) are also diverse, ranging from species with small colony size and lacking any queen-worker dimorphism or size difference to those with very large colonies and queens more than 20% larger than workers in some dimensions. Vibrational signaling directed at larvae has not been reported for any of the several hundred species in these groups, although most have not been studied at all. Queen-worker dimorphism in these species appears not to be derived from size-based allometry. In Apoica, for example, queens and workers overlap completely in body size, yet differ in body proportions. This means that the caste-differentiating mechanism cannot be triggered by a simple nutritional switch based on amount of food the larvae receive. Again, pheromones or oral secretions may be involved.

**Evolutionary History of Mechanisms of Caste Differentiation**

These patterns of occurrence begin to illuminate the evolution of environmental triggers of caste-determining developmental pathways. Vibrational signals appear to be a behaviorally applied mode of caste biasing that may be effective only in small colonies. They may have originated as un specialized forms of mechanical stress, perhaps applied directly to the larvae. The more specialized signals characterizing extant species may be ritualized forms of this early behavior. One scenario is that vibrational caste-biasing characterized the common ancestor of the clade Vespinae + Polistinae (Fig. 2A), diversified in form and function among the independent founders, then was superseded in the more derived taxa by other mechanisms, such as pheromones or differences in food quality. These may well be more effective mechanisms of caste biasing, able to affect hundreds or thousands of larvae, rather than a few tens. These mechanisms, which have evolved independently in several social vespid lineages, may have been instrumental in enabling the evolution of the larger colony sizes seen in the more derived vespies and in the several clades of swarm founders (Fig. 2).

**Acknowledgments**

We are grateful to B.J. Taylor, T. Schueller and A. Toth for critically reading the manuscript. Research supported by the College of Agricultural and Life Sciences, University of Wisconsin-Madison.

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