

# Expanded Food Choice as a Possible Factor in the Evolution of Sociality of Vespidae (Hymenoptera)

by

Eliani Rodrigues da Silva<sup>1</sup> & Klaus Jaffe<sup>2</sup>

## ABSTRACT

A recent theory suggests that economic considerations are more important than genetic ones in the emergence and maintenance of social behavior. Evolution of social behavior in wasps, thus, could be based on the development of worker castes, which increase the efficiency of brood care and energy use of the colony. If so, social wasps should collect a larger range of prey, favoring polyethism, as social behavior should increase the adaptive value of social species among wasps by increasing the range of prey accessible. We explored the literature and showed that the Eumeninae, which are mostly solitary, draw prey from significantly fewer orders of arthropods than wasps in the subfamily Vespinae and Polistinae, which are mainly social, supporting the hypothesis that social behavior may have emerged as a more efficient way to feed and care for the young by opening a wider range of food sources, increasing the amount of food and quality of care provided to the young. Two alternative explanations of this data are also discussed.

**Key words:** Evolution, social behavior, prey, generalist and specialists, economic efficiency.

## INTRODUCTION

Social behavior has to be adaptive in order to emerge and be maintained in evolutionary history, and factors other than genetic relatedness may be important in the evolution of eusociality, at least among wasps (Arathi & Gadagkar 1998). Yet what are the specific adaptive advantages conferred by social behavior? This question may have different answers for different taxa, yet little is known about the subject. Computer simulations suggest that social behavior is unstable unless it provides important economic benefits as well as fitness gains to the individuals involved (Jaffe 2001). In this respect, we know that social behavior favors energetic efficiency (Fonk & Jaffe 1996; Cabrera

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<sup>1</sup>UNESP, Instituto de Biociências, Departamento de Zoologia, C.P. 199, Rio Claro, Brazil  
email: ersilva@rc.unesp.br

<sup>2</sup>Departamento de Biología de Organismos, Universidad Simón Bolívar, Apartado 89000, Caracas 1080, Venezuela email: kjaffe@usb.ve

& Jaffe 1998; Muradian *et al.* 1999), but it might have many other advantages. Another support of the importance of economic considerations in the evolution of behavior comes from the interactions between Lycaenid lepidoptera larvae and ants. Here, economically mutually beneficial cooperation is much more common than exploitation (Osborn & Jaffe 1997)

Among allodaptine bees, the advantages of group living seem to be increased protection of the brood as some females guard while others forage and feed brood (Schwartz *et al.* 1998); and by enhanced brood production by increasing rearing efficiency, for example, through task specialization minimizing travelling times or learning costs (Jeanne 1986). Among carpenter bees, social behavior may be a response to strong constraints on solitary nesting (Hogendoorn & Velthuis 1999). Evolution of social behavior in wasps is thought to be based on the development of worker castes, which increase the efficiency of brood care (West-Eberhard 1978). Here we want to explore if increased efficiency in food retrieval may be favored by social behavior among the wasps. For example, Steiner (1986) suggested that social wasps use their sting only for defense, whereas in solitary wasps the sting is used for capture, immobilization and conservation of the prey, where each species produces its own specific toxins. These adaptations are clearly related to the type of prey the wasp collects. Oster & Wilson (1978) suggest that four factors may determine the evolution of castes in social insects: the distribution of food items in space and time, the size distribution of the items, the resistance of the items to recovery (including the effectiveness of their antipredator defenses) and the abundance and ecology of competitors and predators. Thus again, type and range of prey may favor polyethism and social behavior may increase the adaptive value of social wasp species by increasing the range of prey accessible.

Cowan (1991) defined the social levels among wasps as varying between solitary (females build nests individually, they do not interact with their offspring and provide food to their offspring massively), to eusocial (several females cooperate in nest building, they maintain a division of labor which correlates with reproductive output, several generations overlap in the same nest, and food provisioning is progressive), with a range of variations between those two extremes, according to the behavior of each species. The family Vespidae (Aculeata: ovipositor is modified forming a sting which allows the inoculation of venom) has, following Carpenter (1991), approximately 4000 species grouped in 6 subfamilies. Three of the subfamilies have only solitary species: Euparagiinae with only one genus and nine species; Massarine with 19

genera and 250 species and Eumeninae with 184 genera and 3000 species. The other subfamilies include, with a few exceptions, social species: Stenogastrinae with 50 species and six genera; Polistinae with 800 species and 29 genera; and Vespinae with 60 species and four genera.

### **Euparagiinae**

The subfamily Euparagiinae is distributed in the southwest of USA and Mexico (Richards 1962). The workers fill the nest cells with curculionid larvae (Williams 1927; Clement & Grissell 1968; Cowan 1991). Their feeding habits can thus be considered to be very specialized as their prey is restricted to one family of Coleoptera.

### **Massarinae**

The Massarinae are cosmopolitan, inhabiting mainly in hot climates and differ from other wasps in that they fill the nest cells exclusively with pollen and nectar (Cowan 1991). Thus, these wasps are highly specialized and do not feed on other arthropods.

### **Eumeninae**

The majority of wasp species are in the cosmopolitan subfamily Eumeninae (Cowan 1991). The Eumeninae larvae are entomophagous. Females leave whole insects in excavated nests in the soil or in aerial mud chambers. The cells is a reference point for the activity of the wasps who fly from tree to tree looking for prey, exploring the vegetation, and storing mainly larvae of Tortricidae and Geometricidae which have been previously paralyzed by injecting venom into the thorax or first gastric segments of the prey (Spradbery 1973).

Evans & Eberhard (1970) classified the steps used for nest construction and food provisioning in order to rebuild a putative evolutionary path to sociality in wasps. They describe the behavior of the Eumeninae, which lay eggs suspended from fine filaments in mud cells so as to distance the egg from the humid substrate. They conclude that an interesting characteristic of most solitary wasps is the specificity of the prey captured so that each species can specialize in capturing techniques, paralyzation and manipulation of the prey from species from the same genus or from closely related genera. In contrast social species show little prey specificity and seem to collect whatever is common in their environment.

Most eumenines are solitary (Carpenter 1993), but several group-living (nest sharing) eumenines are known (West-Eberhard 1978).

### **Stenogastrinae**

The subfamily Stenogastrinae occurs south of India up to New

Guinea and some researchers consider some of its species to be solitary, based on the number of individuals encountered in a nest (Turillazzi 1991). Spradbery (1973) suggest that these wasps inhabit tropical forests and generally build their delicate nests near water sources and can be considered as among the most primitive wasps, intermediate between the Eumeninae and the eusocial wasps.

### **Polistinae**

The largest group of social wasps, the Polistinae or paper wasps, are found in tropical areas, especially in South America. Most species are in the cosmopolitan genus *Polistes* (Carpenter 1993) and have highly developed social behavior but with rather small colonies compared to those of other Vespidae (Edwards 1980). Polistinae feed mostly on arthropods.

### **Vespinae**

The subfamily Vespinae includes four genera: *Vespa*, *Provespa*, *Dolichovespula* and *Vespula*. The species in the first two genera show specialized habits and are oriental in origin. *Provespa* contains three endemic species of the tropical east of Asia and *Vespa* has 23 species distributed all over East Asia, including some species in the South Pacific and New Guinea (Matsura 1991). *Dolichovespula* and *Vespula* yellowjackets are very diverse in their social biology and are widely distributed in the Northern Hemisphere (Greene 1991). The colonies have annual cycles and between 700 and 5000 workers, depending on the species. A characteristic of the group is its capacity to attack and predate bee nests (*Apis mellifera*, *A. dorsata*, *A. cerana*, *A. florea* and *Bombus*) feeding on eggs, larvae, pupae and adult bees (Akre & Mayer 1994).

## METHODS

Thus, from what is known about the foraging habits of wasps, it seems that sociality and generalist predatory habits are correlated. At the moment, the relationship between social behavior and food choice among wasps is summarized in Table 1. Based on this relationship, we might postulate that social behavior favors more efficient foraging, allowing the wasps to draw on a much broader source of potential prey. The species in the non-social subfamilies of wasps Euparagiinae, Massarinae are clearly specialized to prey on a very restricted range of food. Little is known about the feeding habits of few species in the subfamily Stenogastrinae. To test the consistency and strength of the correlation between social behavior with polyphagy, we reviewed the literature for data on feeding habits of species in the most species rich

Table 1. Known foraging habits and social behavior of wasp species in the various subfamilies.

| Sub-family            | Foraging habits     | Social behavior |
|-----------------------|---------------------|-----------------|
| <b>Euparagiinae</b>   | Specialist Solitary |                 |
| <b>Massarinae</b>     | Specialist Solitary |                 |
| <b>Eumeninae</b>      | Specialist?         | Solitary        |
| <b>Stenogastrinae</b> | Generalist?         | Social          |
| <b>Polistinae</b>     | Generalist?         | Social          |
| <b>Vespiniae</b>      | Generalist?         | Social          |

non-social subfamily, the Eumeninae, and the subfamilies Vespine and Polistinae, which have high diversity of social species. The hypothesis being that solitary wasp species are specialized in the type of prey they capture, whereas social species are more generalists in their feeding preferences of their offspring.

One problem of course is how to define specialization. It can mean hunting only one species, one family (many sizes and habits of prey), or it can mean hunting a taxonomic variety by a specialized cue (e.g., only rotten meat — thought the meat can be of a large range of taxa). Here we take a broad cut-point between generalist and specialists by counting the number of orders the prey of a wasp species comes from. More refined studies should be undertaken in the future when, hopefully, more information will be available. The survey in the literature can be considered as a random sampling of species in the subfamilies studied, because any potential bias by researchers publishing these works in choosing species, is unlikely to differ between the subfamilies.

## RESULTS

The data from the literature regarding information about prey for species of the subfamilies Eumeninae, Vespiniae and Polistinae is summarized in Tables 2, 3 and 4. Among the Eumeninae wasps, all of the 29 species except two collect lepidoptera larvae. The two exceptions plus two other species collect coleoptera prey. In contrast, of the 10 species listed among Vespiniae, only three species forage on prey from two or fewer orders of arthropods, whereas the other seven species forage on prey from more than four different orders. A Mann Whitney U test comparing the two subfamilies with comparable sample size, shows significant differences in the number of orders the wasps draw they prey from ( $z = 4.1$ ,  $p < 0.0001$ ). Data from Polistinae show that the report with the smallest number of prey orders is three, with one species

Table 2. Prey species of Eumeninae wasps.

| WASP SPECIES                   | PREY  | REFERENCE                  | ORDER  |
|--------------------------------|---|----------------------------|--|
| <i>Pachodynerus nasidens</i>   | Pyralidae<br>Olethreutidae<br>Alucitidae<br>Thyrididae  | Jayasingh & Taffe 1982     | Lep.<br>Lep.<br>Lep.<br>Lep.                 |
| <i>Ancistrocerus adiabatus</i> | <i>Choristoneura fumiferana</i><br>Tortricidae  | Collins & Jennings 1987    | Lep.<br>Lep.                                 |
| <i>Ancistrocerus antilope</i>  | <i>Choristoneura fumiferana</i>   | Collins & Jennings 1987    | Lep.   |
| <i>Euodynerus leucomelas</i>   | <i>Choristoneura fumiferana</i><br><i>Acleris</i> sp 1<br><i>Acleris</i> sp 2<br><i>Archips rosana</i><br><i>Sparganothis reticulatana</i>                      | Collins & Jennings 1987    | Lep.<br>Lep.<br>Lep.<br>Lep.<br>Lep.         |
| <i>Leucodynerus russatus</i>   | Psychidae<br>Gelechiidae<br>Gelechioidea-<br>Cosmopterygidae<br><i>Cicindela lemnicata</i>  | Knisely 1985               | Lep.<br>Lep.<br>Lep.<br>Lep.<br>Col.         |
| <i>Ancistrocerus adiabatus</i> | <i>Acleris variata</i>  | Jennings & Houseweart 1984 | Lep.   |
| <i>Ancistrocerus antilope</i>  | <i>Nephoteryx</i> sp  | Jennings & Houseweart 1984 | Lep.   |
| <i>Ancistrocerus catskill</i>  | <i>Nephoteryx</i> sp<br><i>Trichotaphe</i> sp<br><i>Acleris variata</i><br><i>Choristoneura fumiferana</i><br><i>Rheumaptera hastata</i><br><i>Chionodes</i> sp | Jennings & Houseweart 1984 | Lep.<br>Lep.<br>Lep.<br>Lep.<br>Lep.<br>Lep. |
| <i>Euodynerus leucomelas</i>   | <i>Nephoteryx</i> sp<br><i>Reumaptera hastata</i><br><i>Choristoneura fumiferana</i><br><i>Trichotaphe</i> sp   | Jennings & Houseweart 1984 | Lep.<br>Lep.<br>Lep.<br>Lep.                 |
| <i>Odynerus erythrogaster</i>  | Lepidoptera<br><i>Filatima</i> (Gelechiidae)  | Parker 1984                | Lep.<br>Lep.                                 |
| <i>Odynerus cinnabarinus</i>   | Lepidoptera<br><i>Filatima</i> (Gelechiidae)  | Parker 1984                | Lep.<br>Lep.                                 |

Table 2. continued

|                                 |  |                     |                      |
|---------------------------------|--|---------------------|----------------------|
| <i>Ancistrocerus gazella</i>    | Lepidoptera  | Gathman et al. 1994 | Lep.                 |
| <i>Odynerus papagorum</i>       | <i>Helianthus</i> sp<br><i>Gaillardia lutea</i><br><i>Brauneria purpurea</i> | Isely 1913          | Lep.<br>Lep.<br>Lep. |
| <i>Odynerus arvensis</i>        | Pyralidae<br>Noctuidae   | Isely 1913          | Lep.<br>Lep.<br>Lep. |
| <i>Odynerus annulatus</i>       | <i>Loxostege sticticalis</i>   | Isely 1913          | Lep.                 |
| <i>Odynerus dorsalis</i>        | <i>Pyrius tessellata</i>   | Isely 1913          | Lep.                 |
|                                 | <i>Philosara catullus</i><br><i>Callirhoe involucrata</i>                    |                     | Lep.<br>Lep.         |
| <i>Pterochilus 5-faciatus</i>   | Noctuidae- <i>Chenopodium</i>  | Isely 1913          | Lep.                 |
| <i>Odynerus hildage</i>         | <i>Helianthus</i> sp<br><i>Gaillardia lutea</i><br><i>Brauneria purpurea</i> | Isely 1913          | Lep.<br>Lep.<br>Lep. |
| <i>Eumenes</i> spp.             | Geometridae  | Spradbery 1973      | Lep.                 |
|                                 | Tortricidae<br>Noctuidae   |                     | Lep.<br>Lep.         |
| <i>Eumenes pedunculatus</i>     | 30 species Lepidoptera   | Spradbery 1973      | Lep.                 |
| <i>Pseudepipona herrichii</i>   | Tortricidae  | Spradbery 1973      | Lep.                 |
| <i>Odynerus spinipes</i>        | <i>Phytonomus</i> sp & <i>Hyperbaa</i>                                       | Spradbery 1973      | Lep. & Col.          |
| <i>Odynerus reniformis</i>      | <i>Phytonomus</i> sp   | Spradbery 1973      | Lep.                 |
| <i>Ancistrocerus oviventris</i> | Microlepidoptera   | Spradbery 1973      | Lep.                 |
| <i>Gymnomerus laevipes</i>      | <i>Hyperba</i> sp  | Spradbery 1973      | Col.                 |
| <i>Ancistrocerus antilope</i>   | Gelechioidea   | Spradbery 1973      | Lep.                 |
|                                 | Pyralidae  |                     | Lep.                 |
| <i>Symmorphus crassicornis</i>  | <i>Chrysomela populi</i>   | Spradbery 1973      | Col.                 |

Table 3. Prey species of Vespinae wasps.

| WASP SPECIES                    | PREY   | REFERENCE      |
|---------------------------------|--|----------------|
| <i>Vespa simillima</i>          | Insecta: Orthoptera<br>Mantodea<br>Odonata<br>Hemiptera<br>Lepidoptera<br>Coleoptera<br>Hymenoptera<br>Diptera<br>Arachnida: Araneae | Matsuura 1984  |
| <i>Vespa analis</i>             | Insecta: Orthoptera<br>Mantodea<br>Odonata<br>Hemiptera  | Matsuura 1984  |
| <i>Vespa analis</i>             | Insecta: Lepidoptera<br>Coleoptera<br>Hymenoptera<br>Diptera<br>Arachnida: Araneae   | Matsuura 1984  |
| <i>Vespa crabro</i>             | Insecta: Orthoptera<br>Odonata<br>Hemiptera<br>Hymenoptera   | Matsuura 1984  |
| <i>Vespa mandarina</i>          | Insecta: Mantodea<br>Lepidoptera<br>Coleoptera<br>Hymenoptera<br>Arachnida: Araneae  | Matsuura 1984  |
| <i>Vespa tropica</i>            | Insecta: Hymenoptera   | Matsuura 1984  |
| <i>Provespa vulgaris</i>        | Insecta: Dermaptera<br>Orthoptera<br>Hemiptera<br>Lepidoptera<br>Coleoptera<br>Diptera   | Spradbery 1973 |
| <i>Vespula</i> sp               | Insecta: Orthoptera<br>Odonata<br>Lepidoptera<br>Coleoptera<br>Hymenoptera<br>Diptera  | Spradbery 1973 |
| <i>Provespa germanica</i>       | Insecta: Hemiptera<br>Hymenoptera  | Spradbery 1973 |
| <i>Dolichovespula silvestre</i> | Insecta: Hymenoptera<br>Diptera  | Spradbery 1973 |

foraging on prey from over 10 different orders. Thus, the data is congruent with the hypothesis that social behavior has emerged as a more efficient way to feed the young, opening a wider range of food

Table 4. Prey species of Polistinae wasps.

| WASP SPECIES                | PREY   | REFERENCE            |
|-----------------------------|--|----------------------|
| <i>Polybia occidentalis</i> | Insecta: Orthoptera<br>Neuroptera<br>Psocoptera<br>Phthiraptera<br>Mecoptera<br>Hemiptera<br>Lepidoptera<br>Coleoptera<br>Hymenoptera<br>Diptera<br>Arachnida: | Gobbi et al. 1984    |
| <i>Polybia paulista</i>     | Insecta: Lepidoptera<br>Hymenoptera<br>Diptera<br>Coleoptera<br>Hemiptera  | Gobb i& Machado 1985 |
| <i>Polybia ignobilis</i>    | Insecta: Lepidoptera<br>Coleoptera<br>Hymenoptera<br>Diptera   | Gobbi & Machado 1986 |
| <i>Agelaia pallipes</i>     | Insecta: Heteroptera<br>Diptera<br>Orthoptera<br>Lepidoptera<br>Coleoptera<br>Hymenoptera<br>Arachnida: Araneae<br>Acarina                                     | Machado et al. 1987  |
| <i>Polybia sericea</i>      | Insecta: Hymenoptera<br>Lepdoptera<br>Diptera<br>Hemiptera<br>Collembola<br>Odonata<br>Arachnida: Acarina  | Machado et al. 1988  |
| <i>Polistes simillimus</i>  | Insecta: Lepidoptera<br>Diptera<br>Homoptera   | Prezoto et al. 1994  |

sources, and increasing the amount of food and quality of care provided to the young.

## DISCUSSION

The literature thus supports the view that a relationship between polyphagy and social behavior exists, eliminating three interrogation signs in Table 1, and leaving only the case of the Stenogastrinae open

for further study. However, at least two alternative explanation for the correlation found are possible:

1. The evolution of social behavior is driven by other evolutionary forces and that once sociality has been achieved, a greater need for food drives social species to broaden their food supply. In order to discard this alternatives, we have to demonstrate that expanded food choice is important in the original spread of worker phenotype (i.e. the primary innovative difference between solitary and eusocial insects) by looking into the factor in transitional forms - "primitively" social ones - which live in groups and show variance in female fertility. The Stenogastrinae should be especially interesting in this respect.

2. The relationship between sociality and polyphagy is homologous and not necessarily correlated in other taxa. This argument is not likely to hold the test of time, as the pattern of sociality and polyphagy among bees seem to resemble that found among wasps here (Michener 2000, personal communication)

Social evolution may be driven, at least partially (i.e. relatedness, predation, a certain hormonal preadaptation to social life, capacity for egg resorption in suppressed females, nest building, nest sharing etc. may also be involved), by the advantages social cooperation provides in allowing species to broaden and making their foraging habits flexible. This work suggests that looking for economic factors for understanding social behavior in other taxa may prove fruitful in improving our understanding of the evolution of social behavior.

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