COMMUNICATION IN SOCIAL WASPS: PREDICTED AND
OBSERVED PATTERNS, WITH A NOTE ON THE SIGNIFICANCE
OF BEHAVIORAL AND ONTOGENETIC FLEXIBILITY FOR
THEORIES OF WORKER " ALTRUISM "

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SUMMARY

    Communication is a transfer of information, recognized by the fact
that some behavior or other characteristic ("signal") of one individual
leads to a consistent or predictable change in the behavior of another.
Communication in social wasps is reviewed. Darwinian theory predicts di-
versity in ritualized dominance signals due to strong selection on these
traits as critical determinants of reproductive success. Such diversity
occurs in the dominance rituals of wasps *Polistes* and stingless bees
Meliponini. Helping behavior of workers may have originated without self-
sacrifice (" altruism"), as a profitable alternative allowing ontogeneti-
cally or behaviorally suppressed females to reproduce indirectly, via
aid to relatives.The study of social insects may be at a turning point
where a developmental approach and an evolutionary approach will be fruit
fully combined.

RÉSUMÉ

La communication est un transfert d'information. On reconnaît ce
transfert en observant qu'un certain comportement ou une caractéristique
("signal") d'un individu amène un changement visible ou prévisible du com-
portement d'un autre. Chez les guêpes sociales (Vespidae), on oberve diffé
rents types de communication à l'occasion de la trophallaxis entre larves
et adultes, du comportement de dominance, de l'offre et de la sollicita-
tion de nourriture entre adultes, de la reconnaissance de la reine, de
l'alarme, de l'essaimage, de la construction du nid, de la reconnaissance
entre individus de la même société, des éxanges phéromonaux chez les mâles
et de la communication intersexuelle par les phéromones. Nous effectuons
ici une révision des travaux publiés à ce jour sur ces thèmes en y ajou-
tant des observations sur les espèces tropicales. Pour le moment, nous
ne savons pas encore s'il existe une communication par une butineuse des
informations permettant aus autres ouvrières de localiser une source de
nourriture. Il existe une hypothèse fondée sur la théorie de la selection
naturelle, qui prédit la diversité des signaux de dominance ritualisée
pour les raisons suivantes: la dominance pourrait beaucoup influencer
l'accès aux ressources, l'exposition aux risques, et la capacité des indi-
vidus d'un groupe, de se reproduire. Ces caractères, qui ont une influence
tellement importante sur la survie et sur le succès de la reproduction,
sont soumis à une sélection particulièrement intense. Et des caractères
soumis à une sélection intense pourraient évoluer plus rapidement.

Par conséquent, parmi des populations séparées mais apparentées (e.g.
les sous-espèces de la même espèce ou les espèces du même genre) ces carac
tères-ci pourraient diverger rapidement. Il y apparaîtrait alors une diver
sité peu commune,parmi ces traits. La diversité prévue de la dominance ri
tualisée est observée chez les guêpes (Polistes) et chez les abeilles
sans dard (Meliponini). Les conduites distinctives des espèces de Polistes
sont décrites ici pour la première fois. La souplesse phénotypique des in-
sectes sociaux, mise en évidence par leur système de communication, leur
déterminisme des castes et leur capacité d'apprendre, est négligée dans
beaucoup de discussions théoriques de "l'altruisme" de l'ouvrière. Le com-
portement de l' ouvrière , des individus dominés ou mal nourris,
aurait pu se développer sans aucun gène spécial pour l'altruisme,
étant donné 1) la capacité de soigner le couvain par les reproducteurs

avant l'évolution d'une caste ouvrière, 2) les conditions responsables de la suppression de l'oviposition (la reproduction) chez certains individus (manipulation de la nourriture des larves, effets saisonniers, rivalités entre compagnons du nid) et 3) la permanence du soin au couvain (e.g. du couvain produit par les parents) par les individus handicapés ou supprimés phénotypiquement comme une alternative profitable et facultative. Ici, il ne s'agit pas d'abnégation dans cette série d'évènements. Il est possible que l'étude des insectes sociaux soit arrivée à un point décisif où l'on mariera d'une manière fructueuse l'étude ontogénétique avec l'étude évolutionniste.

Communication -- the theme of this colloquium -- can be defined simply as a transfer of information. In practice, we recognize communication by the fact that some behavior or characteristic ("signal") of one individual leads to a consistent or predictable change in the behavior of another. In this paper I shall review briefly the kinds of communication known to occur in social wasps (*Vespidae*) I shall then make a prediction regarding communication in general, based on evolutionary theory, and examine the extent to which it holds for the social wasps. Finally, I shall conclude with a " postscript " containing some additional points I wish I had included in my inaugural address, inspired by what I learned from attending this excellent meeting and from conversation with its participants.

COMMUNICATION IN SOCIAL WASPS

The study of communication in social wasps is still mainly in the descriptive stage. The following kinds of communication are known:

Larva-adult Communication. In *Polistes* the feeding of larva by an adult is often preceded by audible drumming of the antennae or gaster against the nest (see Jeanne, 1980). In *Ropalidia cincta* and *R.marginata marginata* (Lepeletier) (Darchen, 1976a; pers.obs., in India) suc vi-

sits are proceded by a brisk fanning of the wings, and in *R.cyathiformis*
(Fabricius) (pers.obs) by a rapid shudder and antennal tapping. These vi-
brations of the nest at least sometimes cause the larva to expand its bo-
dy, bringing the head toward the mouth of the cell. And in *R.cincta* they
stimulate similar wing-vibrating behavior by other food-laden females (Dar
chen, 1976 a). I have stimulated larval feeding responses by sharply pric-
king the edge of the larval cell with a pin in *Polistes* and in *Parachar-
tergus*. In the *Vespinae*, non-swarming *Polistinae*, and possibly other so-
cial wasps, adults regularly imbibe the larval saliva (references in
(Jeanne,1980). This "oecotrophobiose" (Roubaud, 1916), later called
" trophallaxis" by Wheeler (1918), was among the first modes of wasp com-
munication described. Its nature and possible significance are reviewed
by Hunt (1982).

Morimoto (1960) observed that in *Polistes chinenesis antennalis* Pérez,
large larvae receive food before smaller larvae. He hypothesized that lar-
vae produce some signal which is performed more strongly by large larvae.
The sound produced by hungry *Vespa orientalis* larvae (Ishay and Schwartz
1973), raise the possibility that such larvae may call attending adults.
Other evidence that signals may originate with the larvae comes from the
fact that adults neglect large larvae about to form the silken cap to the
cell prior to pupation , indicating that they distinguish such non-fee-
ding larvae from others (pers.obs.of *Polistes*).

Dominance communication. Adult wasps communicate dominance and subor
dinance, or relative aggressiveness, with a wide variety of stereotyped
postures and behaviors (e.g., see Darchen, 1976 a; Jeanne, 1972; Marino
and Pardi, 1970; Morimoto, 1961; and West-Eberhard, 1969, 1978a and be-
low). In at least some species pheromonal signals of dominance are suspec
ted (see West-Eberhard, 1977, 1982). In effect, these signals are threats
which function to establish rank or territory among individuals with only
occasional direct aggression.

Offering and Solicitation among Adults. Both solid foods (e.g.,the
meat of caterpillars) and regurgitated liquids are transferred among adult

wasps. In a wide variety of genera I have observed (e.g. *Polistes*, *Meta-polybia*, *Synoeca*, *Polybia* there is asymmetry in the antennal movements of interactants, with the "solicitor" actively moving its antenae against the face and mouthparts of the "donor", as described by Montagner (1966) for *Vespa*. Often the aggressive state or dominance rank of the individuals involved can be ascertained by observing such interactions, in which relatively subordinant individuals are more often donors (see West-Eberhard, 1969).

In some species (e.g., *Polistes major major* Palisot de Beauvoir, *Metapolybia aztecoides* Richards, and *Synoeca surinama*) the donors, espe-cially heavily-laden returning foragers, occasionally perform a rapid si-de-to-side movement of the body, with antennae held to the side and head thrust forward. In *Metapolybia*, *Synoeca* and *Polybia scrobalis* Richards this same movement is regularly performed by workers when they closely fa ce queens. During periods of intense competition among *Metapolybia* queens this " queen dance" of the workers is performed very vigorously, and in the case of relatively subordinant queens sometimes turns to a violent attack (see West-Eberhard, 1978).

Queen Recognition. The "queen dance" of workers indicates a capaci-ty for queen recognition by nestmates. The mechanism by which queens are recognized is not known. It may be identical or related to behavioral or pheromonal dominance signals (see West-Eberhard, 1977, for a review). The unidentified signal is very quickly manifested by new queens: when a monogynous queen was removed from a colony of *M. aztecoides*, wor-kers performed the queen dance to her successors within 24 hours, even though they had not been treated as queens prior to queen removal.

In some tropical polybiini, e.g., *Parachartergus colobopterus* (Lichtenstein), *Pseudochartergus chartergoides* morph *cinctellus* (Fox), and *Nectarinella championi* (Dover), I was not able to distinguish known queens by any behavior other than oviposition, nor by any behavior of workers toward them, even after several hours of close observation. Although I may have missed some critical detail of behavior I suspect that in these species queen recognition is pheromonal.

Alarm communication (1) Response to parasitoids. Upon detection insect parasitoids of the brood, e.g., flies (*Phoridae*, *Sarcophagidae*) and parasitic Hymenoptera (Ichneumonidae - see Demolin, 1982), female social wasps of several genera (below) begin a characteristic rapid running about the nest, often accompanied by rhythmic wing-buzzing, darting at nestmates, and inspection of cells. This behavior, while it may be basically vigilance or search, can also involve true communication, since it often causes other individuals to do the same even when they have not perceived the parasitoid themselves (West-Eberhard, 1969). This form of "parasitoid alarm" behavior occurs in *Polistes* (numerous species), *Metapolybia aztecoides*, *Polybia diguetana* R.du Buysson, *Polybia emaciata* Lucas, and *Synoeca septentrionalis* Richards; and in *Protopolybia acutiscutis* (Cameron) (Naumann,1970). In *Polybia scrobalis* Richards a contagious parasite alarm occasionally involved rhytmic wing fanning without running. And in *Pseudochartergus chartergoides* (Gribodo) the parasite alarm was a long fast non-jerky run with continuous rather than rhytmic wing fanning.

(2) Other alarm signals. Some social wasp species have special coordinated defensive reactions to disturbances near the nest which imply communication among colony members. Perhaps the most spectacular is the "drumming" alarm of *Synoeca* (*S.septentrionalis*, pers.obs.; *S.virginea* (F.), Chadab, 1979) and *Angiopolybia pallens* (Lepeletier) (Chadab,1979). In *Synoeca* wasps on the inside and outside surfaces of the broadly domed, corrugated nest envelope raise and lower their wings in unison while producing a synchronous vibration of the resonant envelope carton. The fearsome "drumming" or "marching" (Chadab, 1979) is audible many meters away from the nest, and the synchronized flashing of the iridescent blue-black wings of these large wasps adds to its effectiveness as a warning. The drumming noise is produced primarily by an abrupt biting or scraping of the nest envelope with the mandibles (unpublished observations of *Synoeca*), perhaps also accompanied in some species by a stroke with the gaster,which is moved sharply downward at the same time (Chadab, 1979). The drumming alarm seems to be a generalized reaction to disturbance, being performed in response to human provocation, army ants (see Chadab, 1979), and even

to parasitoids (pers.obs.of *S.septentrionalis* female's reaction to a phorid fly).

There is abundant observational evidence of alarm pheromones in social wasps. For example, sudden simultaneous disturbance of more than 100 *Synoeca surinama* females on a nest caused release of a pheromone sufficient to produce an allergic reaction in a hypersensitive observer about 30 cm. from the nest (see West-Eberhard, 1982). When alarmed, several species raise the abdomen and extrude the sting (Naumann, 1970, on *Protopolybia acutis cutis;* pers.obs. of *Polistes canadensis canadensis*, and *Synoeca septentrionalis* in Colombia). Jeanne (1981,1982) has shown experimentally that in *Polybia occidentalis occidentalis* (Olivier) and in a Brazilian population of *Polistes canadensis* (L.) the odor of venom elicits alarm, lowers the threshold for (but does not release) attack, and attracts aroused wasps to the site of release. A similar reaction to venom may account for my observation that aroused *Stelopolybia hamiltoni* Richards attacked an insect net containing a stinging female. Maschwitz (1964) cites work by Pavan showing that alarmed *Vespa* females raise the abdomen and shoot venom for several centimeters in the direction of the disturbance. An ether-soluble substance mixed with the venom causes workers to run out from the nest and attack nearby objects.

Chadab (1979) studied reactions to army ants (*Eciton*) of a large number of neotropical vespids. Many performed " general fanning" of the wings, a sometimes contagious (communicated) alarm behavior not directed at the disturbance. In *Polybia exigua* (de Saussure) general fanning caused wasps to come out of the nest, and those outside to disperse over the surface of the envelope.

Swarming Communication. As far as known, all of the Polistinae (Ropalidiini, Polistini, and Polybiini) found their colonies in swarms containing many workers and, usually, many queens except in the case of species (e.g., of *Polistes, Belonogaster, Mischocyttarus*, and *Ropalidia*) which build nests without envelopes. The only departures from this rule known to me are the genera *Stelopolybia* (*Gymnopolybia*), which builds nests in natural cavities and has secondarily lost the nest envelope, yet

founds nests in swarms; and *Apoica*, which builds unenveloped nests and swarms. Even in the usually non-swarming, non-envelope-building genus *Ropalidia*, a species (*R. timida* van der Vecht) having an enveloped nest evidently founded a colony with a swarm (Pagden, 1976). (Add this reference and Darchen, 1976 b, on *Polybioides tabidus* Fab. to references in West-Eberhard ,1982, for a complete bibliography on swarming in social wasps.) In most swarming species whose movement to a new nest site has been observed, the swarm moves diffusely along a scent trail made by scouts who rub their abdomens on prominent leaves and other substrates at 3-10 m. intervals along the route. The swarm-trail pheromone is produced by the " Richards organ" of the fifth gastral sternite. Species forming " clumped swarms" move slowly from one cluster to another along the swarm route and seem to rely less on scent trails (see West-Eberhard, 1982).

Food-source Communication. The existence of coordinated movement to new nest sites raises the question of whether or not polybiine wasps can communicate regarding the location of food sites. So far there is no indication that they can. *Stelopolybia* wasps frequently appear in large numbers at food sites, but a systematic search for site communication in these and other neotropical wasps yielded negative results (Lindauer, 1961; Forsyth, 1978). Their aggregation on food is evidently due to common orientation to odors (especially, of rotting meat, or flowers), and the fact that they have very large colonies (e.g. see Jeanne,1975 a) and therefore large numbers of foragers in a given region. In some species foragers are preferentially attracted to sites being visited by other foragers (Forsyth, 1978, on *Stelopolybia pallipes*; Free, 1970, on *Paravespula* spp).

In *Polistes fuscatus* I observed that the return of a forager often caused a burst of activity among the wasps on the nest, which in turn often led to departure of foragers (see also Spieth, 1948; Jeanne,1972). Foraging success might by this means lead to increased foraging activity, but there is no indication that information on either the nature or location of the foraged material is transmitted to the subsequent foragers, which often do not even contact the newly returned individual. In

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Protopolybia acutiscutis the behavior of successful foragers about to lea
ve the nest seems to be ritualized as a " departure dance ", a rapid,
erratic running around on the comb with high speed wagging and occasional
contact of nestmates (Naumann, 1970).

Coordination of Nest-building (stigmergie). Social wasps, especia-
lly the tropical Polybiini, are notable for building a great variety of
kinds of complex nests, many of them with a stereotyped and species-
distinctive form (see Jeanne, 1975b). Since large numbers of workers
participate in nest construction, each one adding only a small amount
of subsequently unmalleable pulp at a time, it would be very interesting
to know how their behavior is guided by the cues provided by the pre-
existent structure. Films of building behavior indicate that the ante-
nnae guide the formation of regular arcs forming cylinders, and, bet-
ween adjacent cells, straight walls forming hexagons (West-Eberhard,
1969). During envelope construction the antennae are moved against the
two sides of the surface being built (Naumann, 1970, on *Protopolybia*
acutiscutis. Montagner (1966) reviews some experimental work on control
of building in the Vespinae.

Nestmate Recognition. Wasps, like other social insects, usually vi-
gorously attack"foreign" individuals (non-nestmates) which attempt to
land on the nest. They also associate preferentially with females from
the same natal nest when founding new nests, even in species (e.g., of
Polistes) lacking coordinated (swarm) orientation to the new site
(West-Eberhard, 1969). Nestmate recognition is evidently archieved by
numerous cues. Mode of approach to the nest is important, as demonstra-
ted by the fact that heavily laden returning foragers which make a hesi-
tating, clumsy approach are attacked as if foreign (West-Eberhard,1969).
Orientation mistakes (West-Eberhard, 1969; Kasuya, 1981) and new nest lo-
cations indicate that learned nest-finding cues play a role in bringing
and keeping nestmates together. In a pioneer experimental study of nest-
mate recognition in *Vespa* (*Paravespula*) Montagner (1966) showed that it
could be affected by adult diet, with foreign individuals fed on the

same diet treating each other more like nestmates than did nestmates fed different foods. More recent experimental studies show that temperate zo ne *Polistes* foundresses can distinguish between overwintered females which originated on the same nest in the previous autumn even without nest-loca- tion cues or distinctive diets(Ross, and Gamboa, 1981; Pfennig et al,1982; Pratte,1982; Shellman and Gamboa, 1982). The cues are evidently learned,do not depend on association during hibernation, and require the presence of a nest (Shellman and Gamboa, 1982).

Pheromonal Communication by Males. In many species of social waps ma- les are either territorial or patrol a regular route along with other ma- les. In several species (reviewed in West-Eberhard, 1982, pp.123-124, see also Turillazzi and Cervo, 1981) males evidently scent-mark the places whe re they sit or land by rubbing these sites with the abdomen, which is known to contain many secretory organs (see West-Eberhard, 1982; to the marking and patrolling species listed there can now be added *Synoeca septentriona- lis* Richards). In addition, Kasuya (1981) observed that territorial and sexually active males of *Polistes jadwigae* Dalla Torre sit with the abdo- men raised, evidently releasing a scent; and in a Mexican population of *Polistes major* males mark substrates with a secretion from the mandibles (J.W. Wenzel, pers. Communication of unpublished research). It is not yet known whether these marks function in communication among males, or to attract females, or both. That males can detect these marks is indicated by the fact that in *Mischocyttarus* species and *Polybia sericea* patrolling males repeatedly visit the same (marked) leaves.

Sex Pheromones of Females. An observation (Sandemann, 1938) that ma- les aggregate near females in *Dolichovespula sylvestris* suggests that the female produces an attractant scent, but this possibility has never been further investigated. Post and Jeanne (1982) report that in *Polistes fuscatus* the contents of the female's venom gland and sac act as a sex pheromone releasing male copulatory behavior. This fits well with the ob- servation that in filmed mating sequences grasping of the female's abdo- men with the male parameres coincides with sting extrusion by the female (West-Eberhard, 1969).

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EXPECTED PATTERNS IN THE EVOLUTION OF COMMUNICATION

Some characters of organisms are more important than others in deter mining the survival and reproductive success of their bearers. I shall re fer to such characters as being under relatively " strong" selection.

Insofar as characters are influenced by genetic inheritance, the ra te of spread of genes influencing them depends importantly on the strength of selection. Another way of saying this is: the greater the difference in survival or reproductive success between a possessor and a non-possessor of a particular genetic allele, the faster that allele should change in frequency and the faster the affected phenotype can evolve (change in form).

One consequence of this is that in isolated populations or species of related organisms, strongly selected characters may show marked diver gence (due to their rapid evolutionary change). If this is true, then com parative study of related populations (e.g., subspecies of the same spe cies, or species of the same genus) should reveal that the strongly selec ted characters are those which most vary between the populations compared.

The social insects offer many opportunities to test this idea.There are great differences in the reproductive success of different members of colonies, e.g., of queens vs. workers, and of non-laying workers vs. la ying workers. In all social insects, these " caste " differences depend to a large degree on non-genetic differences in conditions: larval feeding, seasonally changing parameters during development (Deleurance, 1952), age (West-Eberhard, 1978 a, 1981), and social circumstances (West-Eberhard, 1978a). In addition, caste determination and " queen control" in social insects often involve the use of certain stereotyped behaviors, e.g., the dominance behavior of *Polistes*, and the oviposition rituals of stingless bees, as well as pheromonal signals of dominance (e.g., those of honeybee queens - Velthuis, 1976 a). The difference in reproductive success between an egg-layer and a non-egg-layer is so very great that if these behaviors have an important effect on likelihood of oviposition they may be conside red "strong" selection. In honeybees, for example, a worker which even briefly escapes queen control and lays just one male-producing egg has a genetic contribution to the next generation which is an estimated 25 times

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greater than that of a worker which lays no eggs (West-Eberhard, 1981*).
By the reasoning given above, dominance rituals and pheromones involved
in queen control should thus often diverge rapidly and show striking spe-
cies-to-species variation. (Additional factors expected to contribute to
the rapid divergence of socially important traits are discussed in Wes-
Eberhard, " in press" *Quart.Rev.Biol.*

Among the wasps, one obvious place to expect such an effect is in
the genus *Polistes*, where the aggressive threat and attack behavior of
females affects their access to food and empty cells in which to lay eggs
(West-Eberhard, 1969 and references therein). Do the aggressive displays
of *Polistes* species show the predicted diversity ? In the species whose
dominance behavior has been observed they do:

In P. *fuscatus fuscatus* (Michigan, USA) " dominant" behavior invol-
ves strong antennal solicitation, as well as "mouthing" -- chewing or
licking the body of the subordinant, especially the head and wings, while
maintaining a higher posture. The immobile subordinant characteristically
crouches low near the nest surface. If the object of these behaviors res-
ponds actively, rather than passively or with regurgitation, the interac-
tion may escalate into a biting attack. The dominance behavior of P. *fusca
tus* can be described as generalized. Antennal language and mouthing or
"mauling" occur in other species of *Polistes* (e.g., P.*gallicus* Pardi,
1946) as well as in the Vespinae (Montagner, 1966; Akre et al, 1976).

In P.*erythrocephalus* (Cali, Colombia) ritualized aggression takes
the form of exaggerated abdomen wagging (the"lateral vibrations" of Gam-
boa and Dew, 1981). Milder abdomen wagging or rubbing against the nest sur
face is associated with dominance in many *Polistes* species (references
in West-Eberhard, 1982). However,in P.*erythrocephalus* it is much stron-
ger, and produces a loud vibration of the nest.

* The data and calculations on which this estimate is based are in an
  Appendix in West-Eberhard, 1981. That appendix omits an important sec
  tion due to an editor's error. I can provide the correct version to
  any interested reader.

P.canadensis canadensis (Meta, Colombia) has the simplest aggressive behavior observed. In this species the queen is territorial: she threatens females not engaged in building or brood care, causing them to move off the face of the nest and, especially, away from the new regions of the comb where egg-laying is most frequent. The threat behavior of *P.canadensis* is simply a slow approach with antennae forward. This causes nest mates to move away. Non-queens in the pre-emergence colony observed did not have aggressive or threat interactions, so a hierarchy was not evident.

P.major major (San Antonio de Escazu, Costa Rica) has three distinctive aggressive displays not yet observed in any other *Polistes* species. All three are conspicuous and dramatic. The most common is a "wagging run ": when approached by another individual aggressive females perform a violent shaking of the body while running a variable (usually short) distance on the comb, with the head held low. This produces an audible vibration of the nest. It is probably derived from the dominance-associated abdomen wagging so common in *Polistes* (above). When two aggressive females approach each other they sometimes perform " lateral bending" similar to that observed in *Metapolybia* (West-Eberhard, 1978a) and *Synoeca*, or a "sting threat" with the tip of the abdomen bent forward beneath the body as if to sting.

Polistes carnifex carnifex (Cali, Colombia), like *P.major*, also has highly ritualized aggressive behavior, but instead of being violent and exaggerated the movements involved are slow and attenuated. Aggressive females perform "slow solicitation" toward other females. moving toward them very slowly with antennae outstretched, then move the antennae very slowly against the approached female's face. The a proached female often responds to prolonged slow solicitation with a single sharp jerk backward, followed by a swift return to position. This interaction, undoubtendly derived from the normal solicitation behavior so common in social wasps (above), gives an impression of great tension. Indeed, if the females respond with more rapid movements it can escalate into a ferocious biting and stinging fight, and I once observed a female killed as a result.

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A special offering behavior is associated with the slow-solicitation aggressive display in P.carnifex.Offering females present food with the antennae strikingly raised like the horns of a goat. Thus unusually clear antennal signal of intention to offer food may function to avoid any possibility of confusion with the agressive antennal movements which can lead to such violent attacks.

An unidentified Polistes species (probably P.pacificus modestus) observed in Guanacaste (Palo Verde), Costa Rica, performed still another distinctive dominance behavior. A worker (one of 12 females on a nest from which offspring adults had already begun to emerge) repeatedly performed the following stereotyped behavior: she mouthed a newly emerged (less than one day old) female from head to tip of the gaster, then turned, and walked over the top of her while rubbing her gaster over the young female's body (Raveret and Richter, 1980). This behavior seems likely to represent dominance since (1) it is common in social wasps for newly emerged females to be the object of dominance interactions importantly affecting their subsequent rank (Montagner, 1966; Pardi, 1946; West-Eberhard, 1977, 1978a). (2) in some species it is the young females who become queens if the queen is removed (West-Eberhard, 1978 a), and (3) this stereotyped behavior involved mouthing as well as abdomen stroking, both activities associated with dominance in Polistes (above).

I must emphasize that there exists no systematic study of dominance variation in Polistes. The behaviors described here happened to be noticed by observors during general studies. A systematic description of ritualized aggressive behavior in different species of Polistes, encompassing the entire colony cycle and utilizing standard descriptive terminology, is needed to reveal the full extent of overlap, intergradation, and distinctiveness (species specificity) of displays. However, these preliminary data do indicate that (1) there are several distinctive variants of agrressive behavior within the genus Polistes, and (2) different species have different display repertoires. This supports the hypothesis predicting diversity in agressive displays.

One group of social insects in which there has been a systematic comparative study of dominance rituals is the stingless bees (Meliponini).Observers agree that the complex and stereotyped provisioning and oviposi-

tion rituals represent " comportement de dominance ritualisé" (Sommeijer, 1981, p.1; see also Sakagami et al, 1965, 1973; Velthuis, 1976b). *Melipona* shows a high degree of ritualization, whereas in *Plebeia* and *Friesella*, considered to resemble the ancestral genera of *Melipona*, there is a greater proportion of direct aggression in these interactions (Sommeijer, 1981) Furthermore, in accord with the present prediction, these rituals show "extreme diversity" among the several congeneric species studied (Zucchi and Sakagami, 1982, p.223; see review in Sakagami,1982).

In conclusion, comparative study of these two groups of social insects (*Polistes*, and stingless bees) supports the hypothesis of diversity in aggressive communication. Of course striking diversity sometimes occurs in signals not involved in intraspecific competitive communication, for example, in the defensive pheromones of termites (Parton et al, 1981). If these pheromones prove to be under very strong selection (e.g., predation is a critical determinant of colony, and queen, success), such diversity would conform to the same fundamental prediction of an association between strong selection and rapid evolutionary change. A more complete discussion of this hypothesis, with illustrative examples from a wide variety of organisms, is given in a recent review (West-Eberhard,"in press").

Postscript: The Significance of Behavioral and Ontogenetic Flexibility for
Theories of Worker " Altruism"

Communication implies flexibility. Although we usually identify "communication" with short-term behavioral changes it can lead to long-term or even permanent changes,as in the case of dominance signals and pheromones involved in queen control and caste determination. Thus, what we call "communication" in fact forms a continuum with the kinds of information transfer and flexibility which occur (e.g., via hormonal and environmental "signals") during ontogeny.

Even this brief review of communication in the social wasps gives abundant evidence of the flexibility of social insects; and the huge literature on caste determination in wasps, ants, bees and termites constitutes one of the most thorough documentations of ontogenetic flexibility in organisms (e.g.,see Nijhout and Wheeler, 1982).

Learning is also important in the development of crucial behavior patterns, including those of nestmate recognition (above) and brood care (Jaisson,1975).There can be no doubt in the mind of any student of social insects that behavioral and ontogenetic flexibility plays an important role in their lives.It must also have played an important role in their

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evolution:

The facultative determination of caste in virtually all social insects (for recent review see Brian, 1979; and Nijhout and Wheeler, 1982) calls for a reevaluation of recent genetic theories of the origin of worker behavior. Although early versions of these theories (for example, Hamilton, 1964) focussed on the situations in which helping would be advantageous in terms of individual reproductive success ("inclusive fitness"), more recent population-genetics models have focussed on the conditions under which a gene for "altruism" would spread in a population (see references in Crozier, 1982). The first approach accommodated facultative worker behavior (e.g., as applied to workers among *Polistes* foundresses, West-Eberhard, 1968; and caste determination in tropical Polybiini, West-Eberhard, 1981). By this approach helping would occur only if and when an individual's circumstances or ontogeny made such behavior likely to be more productive than any other available alternative (e.g., idleness). The second approach is concerned with the problem of explaining the spread of alleles causing a reduction in the personal reproduction of bearers (" altruism"- see Crozier, 1979). It tends to overlook the fact that the expression of helper phenotypes is situation dependent and may not involve self-sacrifice of the kind implied by the term " altruism".

An altruistic allele may never have been involved in the evolution of insects sociality. Workers are generally products of flexible ontogenies. They are commonly starved (or at least differently nourished) and or other wise suppressed or dominated individuals. Such worker behavior could have originated without a special allele for altruism, given (1) the brood-care capacity of reproductive individuals prior to the evolution of a worker caste; (2) group living (an ecological situation in which solitary reproductives are at a great disadvantage); (3) conditions (manipulation of lar val diet, seasonal effects, or competition with nestmates) by which reproduction became suppressed in some members of the group; and (4) continued brood care (e.g., of brood produced by relatives) by the phenotypically handicapped or suppressed individuals as a profitable facultative alternative (not an act of self-sacrifice).

In this scheme workers are " losers" who simply do the best they can by helping rear nestmates (which happen to be relatives). This fits well with what is known about social organization in the relatively primitively social bees (Michener and Brothers, 1974) and wasps (West-Eberhard,

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1978b), and with the ubiquity of caste-flexibility in the social insects. If the original workers were, as virtually all are today, suppressed or socially handicapped individuals, then models attempting to explain the difficult spread of an allele for worker altruism are unnecessary, unrealistic, and irrelevant.

This interpretation also removes the much discussed " difficulty" of explaining why males do not work in the social Hymenoptera (discussed by Crozier, 1982): If worker behavior is basically the normal sexual reproductive behavior with oviposition curtailed, then one would not expect it in males, whose normal reproductive behavior does not usually include brood care (see Alexander, 1974). (In contrast, in the cockroaches supposed to resemble the ancestors of the termites, brood care can involve adults of both sexes - Nalepa, 1982).

Taking into account development and phenotypic flexibility (which, like other characteristics of organisms must be a product of genetic evolution) would remove many of the serious and justifiable objections to the seemingly overly genetic-deterministic theories of " sociobiology" (e.g., see Pratte and Gervet, 1980). This might clear the way for more students of social insects to begin to use ideas from modern natural selection theory in their research. One of the main points of my lecture was to show how Darwinian selection theory can make scientifically useful predictions about social insects in an area other than the evolution of altruism. By "scientifically useful" I mean " revealing facts or patterns in nature which were not seen or understood before." I dit not perceive diversity in the dominance displays of *Polistes* or see their similarity with those of the meliponine bees - until aided by natural selection theory. More importantly, I could have done better research on dominance communication had I realized earlier by any reasonable logic that such variation might occur.

I believe that we are at a turning point in the study of the behavior, physiology, and evolution of the social insects. It is a point when two strong traditions, one more experimental and developmental, the other more Darwinian, can be combined fruitfully. Evolutionary interpretations are sometimes judged too speculative to be of interrest. I offer the ideas presented here in the spirit of the following passage from J-B. Lamarck's " Physique terrestre" (Museum National d'Histoire Naturelle,MS

756, 1st cahier, p.3; Burkhardt, 1977, p. 230):

> " Pour moi je pense qu'il peut etre maintenant utile de rassem-
> bler les faits recueillis, et de s'efforcer à les considerer
> dans leur ensemble, afin d'en obtenir les résultats généraux
> les plus probables. Celui qui concluerait que dans l'étude de
> la nature, nous devons toujours nos borner à amasser des faits,
> ressemblerait à un architecte qui conseillerait toujours de
> tailler des pierres, de préparer des mortiers, des bois, des
> ferrures, etc., et qui n'oserait jamais employer ces matériaux
> pour construire un édifice."

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