

Evolution of Swarm Communication in Eusocial Wasps (Hymenoptera: Vespidae)

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Eusocial paper wasps, yellowjackets, and hornets (Vespidae) exhibit two modes of colony foundation, primitively eusocial independent founders and advanced eusocial swarm founders. Unlike independent founders, swarm-founding wasps require a means of social communication to coordinate the movement of colony members between nest sites. We employed a phylogeny of paper wasps, yellowjackets, and hornets to test for patterns of correlated evolution between the mode of colony foundation and the presence of sternal exocrine glands. We also reviewed data on worker actions during swarming to determine whether swarm communication behavior was dependent upon gland possession and whether communicative behavior was shared among swarm-founding species. We did not find evidence for an association of sternal glands with swarm founding. Although sternal gland presence differed among swarm-founding species, worker behavior during swarming showed little variation. Workers of nearly all swarm-founding species rub their gasters on objects along swarm routes, independently of the occurrence of sternal glands. Widespread gastral rubbing indicates the use of swarm emigration trail pheromones from a diversity of glandular sources. Transitions from independent to swarm founding have been achieved via diverse pheromonal mechanisms in the Vespidae, while worker communicative behavior is either highly conserved or convergent.

KEY WORDS: correlated evolution; independent founding; social behavior; swarm founding; sternal glands.

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INTRODUCTION

Eusocial Vespidae (paper wasps, yellowjackets, and hornets) exhibit two discrete grades of social structure. Solitary reproductive females initiate new colonies in the independent-founding species, while coordinated groups of workers and reproductives initiate new colonies in the swarm founders (Jeanne, 1991). Cladistic analysis suggests that swarm-founding taxa evolved four times from independent-founding ancestors in the Vespidae (Wenzel and Carpenter, 1994). The transition from independent founding to swarm founding is often associated with fundamental changes in colony structure, including increases in colony size and in the complexity of nest architecture (Jeanne, 1991; Karsai and Wenzel, 1998; Bourke, 1999). Coordinating the swarm's movement to new nest sites requires a means of communication. In all taxa where swarm coordination has been observed directly, communication is apparently mediated by pheromones (Jeanne, 1980; Hunt *et al.*, 1995; Turillazzi, personal communication). The glandular sources and chemical components of swarming trail pheromones have been identified for some eusocial Vespidae (Jeanne, 1980; Downing, 1991; Clarke *et al.*, 1999). Experiments by Jeanne (1981) revealed that the swarm-founding wasp *Polybia sericea* (Olivier) communicates the location of new nests by rubbing a trail pheromone on objects between the old and the new nest sites. In *P. sericea*, the trail pheromone is produced by Richards' gland, an exocrine gland located on the underside of the abdomen, associated with the fifth (penultimate) gastral sternite.

Jeanne *et al.* (1983) surveyed the gland morphology and nest-founding behavior of 62 species of eusocial Polistinae (paper wasps), representing 24 of the then 27 polistine genera. They predicted that swarm founding would be associated with the presence of Richards' gland. However, all but 4 of the 47 swarm-founding species surveyed by Jeanne *et al.* (1983) belong to a single clade, the Neotropical tribe Epiponini. Thus, it was difficult to distinguish between traits that are generally characteristic of swarm founders and those characteristic of the epiponine lineage. We performed a test of Jeanne and co-workers' prediction by expanding the number of paper wasp taxa surveyed and analyzing the distribution of sternal glands and mode of colony founding in a phylogenetic framework.

For our comparative analysis (Martins and Hansen, 1996), we employed a generic-level phylogeny of eusocial Vespidae and their sister taxon, the Stenogastrinae (hover wasps) (Carpenter, 1991; Wenzel and Carpenter, 1994). We determined the gland morphology for most of the polistine genera that were not included in the survey by Jeanne *et al.* (1983) and broadened the scope of the survey to include the subfamilies Vespinae (yellowjackets and hornets) and Stenogastrinae. We tested whether swarm founding was

associated with possession of Richards' gland against the alternative that swarming evolved convergently in taxa that employ different pheromonal mechanisms. The specific predictions tested were that (1) swarm founding was more likely to evolve in lineages with Richards' gland (the source of trail pheromone in *Polybia* species) than in lineages without it, and (2) evolutionary losses of Richards' gland would be rare in swarm-founding clades. Because it has been proposed as a potential alternate trail pheromone source (Jeanne *et al.*, 1983), we include data from a previous study on the presence or absence of van der Vecht's gland (Smith *et al.*, 2001), an exocrine gland located on the sixth sternite and used by some species to produce an ant repellent. We also reviewed data on the actions of workers during swarming to assess whether swarm-coordination behavior was consistent among swarm-founding taxa.

MATERIALS AND METHODS

Histology

We obtained wasp specimens from colleagues and from our own collections. Adult female workers were collected from nests or by netting foragers. Wasps were placed directly into fixative or preservative in the field (Kahle's solution, 70% ethanol:formalin:glacial acetic acid, 18:1:1 volume mixture; or 70% ethanol).

For each wasp, we dissected the fifth sternite (the location of Richards' gland) away from the body and embedded it in resin (Spurr, 1969). We cut thin sections (2 μ m) along the sagittal plane with a glass knife on a Leica Ultracut R microtome, mounted the sections on gelatin-coated slides, and stained with toluidine blue. We examined the stained sections with a light microscope at 100–1000x magnification, depending on the size of the sternite. One to three specimens were examined for each species. Intraspecific variation in gland presence has not been noted in previous studies (Jeanne *et al.*, 1983; Smith *et al.*, 2001). Each species was scored as to whether the fifth sternal gland was present or absent, based on whether gland cells were associated with the anterior margins of the sternites (Hermann and Dirks, 1974; Noirot and Quennedey, 1974, 1991; Jeanne and Post, 1982; Jeanne *et al.*, 1983; Keeping, 1990; Downing, 1991; Raposo-Filho *et al.*, 1994). Nine of the 31 vespidae genera and species groups in our study were represented by histologically sectioned specimens of only one species (the genus *Protonectarina* is monotypic). We were unable to obtain specimens of the epiponine genera *Asteloeca* and *Marimbonda* and of the *Vespula* species-group *koreensis*. In a previous study we collected similar data on the species distribution of sixth sternal (van der Vecht's) glands (Smith *et al.*, 2001).



Fig. 1. Richards' gland (fifth sternite) of *Charterginus fulvus* Fox. AR, anterior ridge of sternite; 5th, fifth gastral sternite cuticle; GC, class III gland cells. Original magnification, $\times 400$.

Phylogenetic Relationships and Analyses

All phylogenetic analyses were based on a fully resolved cladogram of genera of Vespidae (Wenzel and Carpenter, 1994) with some modifications (Carpenter *et al.*, 1996; Smith *et al.*, 2001; Kojima, personal communication). When cladograms were available that resolved species at finer taxonomic groupings than genera (e.g., species groups within *Vespula* and *Ropalidia*), we used the highest taxonomic resolution available.

We included data from two of the six genera of the subfamily Stenogastrinae (hover wasps [Carpenter, 1988]) to infer the ancestral states of characters for the Vespinae - Polistinae. We follow Carpenter's (1991) placement of Stenogastrinae as the sister subfamily to Vespinae + Polistinae (Vespidae), although recent molecular evidence (Schmitz and Moritz, 1998) suggests that stenogastrines may be more distantly related to Vespinae + Polistinae. In either case, stenogastrines are informative about possible ancestral states of sternal glands in the eusocial Vespidae.

Character states were mapped onto the cladogram, and ancestral states were inferred, using unordered parsimony implemented by MacClade version 3.1 (Maddison and Maddison, 1992). Similar patterns of evolutionary transitions for two characters across independent lineages were taken as evidence of an evolutionary association between the characters (Felsenstein, 1985; Harvey and Pagel, 1991). We employed the concentrated changes test (Maddison, 1990) to test whether evolutionary changes in gland presence were significantly concentrated in lineages with different modes of colony founding, given the most parsimonious reconstruction of both characters' evolution. The concentrated changes test was performed using the "exact count" option in MacClade (Maddison and Maddison, 1992).

The concentrated changes test cannot be used to analyze unresolved nodes (polytomies [Maddison, 1990]), so our analysis included no more than two species for the highest-resolved clade (genus or species group). The concentrated changes test requires characters with binary states and yields best results with a complete and fully resolved phylogeny (Maddison, 1990; Martins and Hansen 1996). All characters we tested were binary, and we have nearly complete sampling of the vespidae phylogeny (genera or species groups). For clarity of presentation, only genera or species groups are shown in our figures. However, unless otherwise noted, all analyses were based on the highest possible phylogenetic resolution: two representative species of each clade.

Behavioral Data

We combined our observations of worker behavior during swarm movement with previously published accounts. Our aim was to determine whether gaster-rubbing and trail-following behaviors are unique to swarm founders and whether these behavioral traits are always expressed by swarm founders. We also sought to determine whether the presence of sternal glands is associated with behavior exhibited during swarm movements.

RESULTS

Presence of Richards' Gland and Swarm Founding

Gland presence/absence never varied among species within the most highly resolved taxa (genus, subgenus, or species group). Richards' gland was present in approximately half (12 of the 21) of the swarm-founding genera or species groups in our analysis (Fig. 1 and Fig. 2). This gland was

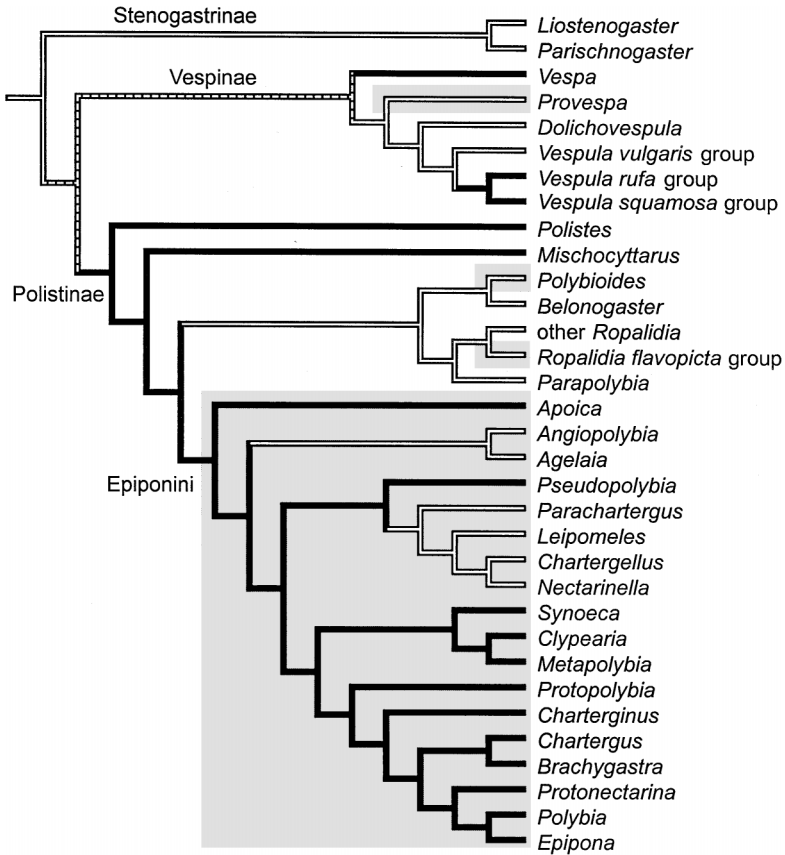


Fig. 2. Evolution of Richards' gland and colony founding behavior plotted on a phylogeny of the Vespinae + Polistinae (Wenzel and Carpenter, 1994). Richards' gland presence is represented by black, absence by white, and uncertainty by striped branches. Swarm-founding lineages are on a shaded background. Only once has swarm founding evolved in a lineage possessing Richards' gland.

also present in half (5 of 10) of the independent-founding genera or species groups. The lack of Richards' gland in stenogastrines suggests that the gland first evolved in the eusocial Vespidae (Vespinae + Polistinae). The most parsimonious reconstruction is that Richards' gland appeared two or three times and that all of these origins occurred in independent-founding paper wasp lineages. Swarm founding evolved only once in a lineage with Richards' gland (Epiponini) and three times in lineages without the gland (in the genera *Provespa* and *Polybioides* and in part of *Ropalidia*). Parsimonious reconstruction suggests that Richards' gland was lost three times, once

in a lineage containing both independent- and swarm-founding species (the Old World tropical Ropalidiini) and twice among the Neotropical swarm-founding Epiponini. There was no statistical support for an evolutionary association between swarm founding and the presence of Richards' gland (Fig. 2; concentrated changes test, $P = 0.96$).

Behavior of Wasps During Internest Movements

Off-nest gastral rubbing behavior has been observed in two species of the independent-founding genus *Mischocyttarus* (Table 1). Workers of swarm-founding species that have been observed during colony movement exhibited behavior consistent with the following of a chemical trail, including use of a common travel path and inspection of previously visited and putatively chemically marked objects along the flight path. The only apparent exception is *Apoica pallens* (Fabricius), which may employ aerially released pheromones in swarm coordination (Hunt *et al.*, 1995; Howard *et al.*, in press). Nearly all swarm-founding species have also been observed rubbing their gastral sternites on objects during swarm movement, either along the route between nests, at clusters of swarming wasps along the route, or at nest sites (Table 1). Exceptions include *A. pallens* and *Polybia* colonies that were moving short distances (<20 m [West-Eberhard, 1982]). There was no association between the presence of sternal glands and gastral rubbing by swarming workers. Gastral rubbing has been observed during internest movements in species with either fifth or sixth sternal glands and in species possessing neither gland (Table 1).

DISCUSSION

Evolution of Swarm Communication and Mode of Colony Founding

Our analysis revealed that occurrence of Richards' gland was not associated with the evolution of swarm founding in eusocial Vespidae. Richards' gland evolved (either once or twice) in independent-founding eusocial Vespidae. The function of Richards' gland in the independent founders is apparently variable. Dani *et al.* (1995, 1996) provided chemical and behavioral evidence for *Polistes dominulus* (Christ) and *P. sulcifer* Zimmermann that both Richards' and van der Vecht's glands produce ant-repellent compounds. On the other hand, behavioral assays done on *P. myersi* Bequaert showed that only van der Vecht's gland had ant-repellent properties (London and Jeanne, 2000). Swarm founding apparently evolved four times in the

Table 1. Summary of Observations of Worker Behavior and Sternal Gland Presence Associated with Swarm Founding of Colonies in Eusocial Vespidae^a

	Swarm-Founding	Trail following observed	Rubbing observed	Possesses 5th gland	Possesses 6th gland	No. colonies observed	Reference(s)
Independent-Founding							
<i>Mischocyttarus immarginatus</i>	Richards	No	Near new nest	Yes	Yes	1	O'Donnell (1992)
<i>Mischocyttarus tabiatus</i> (Fabricius)	Between nests	Possibly	Between nests	Yes	Yes	4	Litte (1981)
<i>Polybioides tabidus</i> (Fabricius)	Between nests	Yes	Between nests	No	No	2	Francescato <i>et al.</i> (1993); Dani <i>et al.</i> (1997)
<i>Ropalidia romandi</i> (Le Guillou)	Between nests	Yes	Between nests	No	No	5	Kojima (1994)
<i>Angiopolybia pallens</i> (Lepeletier)	Between nests	Yes	Between nests	No	No	"Several"	Naumann (1975); Chadab and Rettenmeyer (1979)
<i>Apoica pallens</i> (Fabricius)	No	No	No	No	No	3	Hunt <i>et al.</i> (1995); Howard <i>et al.</i> (unpubl. data)
<i>Leipomeles dorsata</i> (Fabricius)	Between nests	Yes	Between nests	No	No	1	Naumann (1975)
<i>Nectarinella championi</i> (Dover)	At swarm clusters	Yes	At swarm clusters	No	No	NR	Jeanne & Keeping (pers. obs.)
<i>Parachartergus apicalis</i> (Fabricius)	Between nests	Yes	Between nests	No	No	At least 2	West-Eberhard (1982)
<i>Parachartergus colobopterus</i> (Lichtenstein)	Between nests	Yes	Between nests	No	No	3	Jeanne & Keeping (pers. obs.)
<i>Parachartergus fraternus</i> (Gribodo)	Between nests	Yes	Between nests	No	No	NR	Jeanne & Bouwma (pers. obs.)
<i>Agelata</i> (near <i>hamiltoni</i> Richards)	Between nests	Yes	Between nests	No	Yes	NR	West-Eberhard (1982)
<i>Agelata areata</i> (Say)	Between nests	Yes	Between nests	No	Yes	NR	Jeanne (1975); West-Eberhard (1982)
<i>Agelata myrmecophila</i> (Ducke)	Between nests	Yes	Between nests	No	Yes	1	Naumann (1975)
<i>Agelata pallipes</i> (Olivier)	Between nests	Yes	Between nests	No	Yes	NR	Jeanne (pers. obs.)
<i>Agelata testacea</i> (de Saussure)	Between nests	Yes	Between nests	No	Yes	NR	Jeanne (pers. obs.)
<i>Brachygastra lecheguana</i> (Latreille)	Between nests	Yes	Between nests	Yes	No	NR	Landolt & Reed (pers. comm.)
<i>Metapolybia aztecoides</i> Richards	NR	Yes	NR	Yes	No	NR	West-Eberhard (1982)
<i>Polybia bistriata</i> (Fabricius)	Between nests	Yes	Between nests	Yes	No	1	Naumann (1975)
<i>Polybia catillifex</i> Moebius	Between nests	Yes	Between nests	Yes	No	"Several"	Naumann (1975); Chadab and Rettenmeyer (1979)

<i>Polybia occidentalis</i> (Olivier)	Between nests	Yes	Yes	No	> 100	Forsyth (1978, 1981); Jeanne (pers. obs.)
<i>Polybia rufi</i> Bequaert	No	Yes	Yes	No	2	West-Eberhard (1982)
<i>Polybia scrobalis</i> Richards	At old nest	No	Yes	No	1	Chadab and Rettenmeyer (1979)
<i>Polybia sericea</i> (Olivier)	Between nests	Yes	Yes	No	7	Jeanne (1981)
<i>Polybia velutina</i> Ducke	No	No	Yes	No	1	Chadab and Rettenmeyer (1979)
<i>Protopolybia exigua</i> (de Saussure)	Between nests	No	Yes	No	1	Chadab and Rettenmeyer (1979)
<i>Synoecca surinamensis</i> (Linnaeus)	Between nests	Yes	Yes	No	At least 2	West-Eberhard (1982); Jeanne <i>et al.</i> (1983)
<i>Synoecca virginea</i> (Fabricius)	Between nests	Yes	Yes	No	NR	Jeanne (pers. obs.)

^aFor each species for which worker behavior during swarming has been observed, we indicate whether and where gastral rubbing was observed and where the workers rubbed along the swarm route, whether trail following was observed, whether the species possesses fifth sternite (Richards') or sixth sternite (van der Vecht's) gastral glands, and the sample size (number of colonies observed). NR—not reported, throughout.

Vespididae (in *Provespa*, *Polybioides*, part of *Ropalidia*, and the Epiponini). Only in the tribe Epiponini did swarm founding evolve in a lineage already possessing Richards' gland. Even within this clade, which includes species that use Richards' gland secretion as a trail pheromone during swarming (below), our analysis suggests that Richards' gland has been lost twice (in *Angiopolybia* + *Agelaia* and in *Parachartergus* + *Leipomeles* + *Nectarinella* + *Chartergellus*).

In contrast to the presence of sternal glands, worker behavior along swarm routes is remarkably consistent among swarm-founding species, including representatives of three of the four independently evolved swarm-founding taxa (excepting *Apoica*). No behavioral data are available on worker communicative behavior during swarming in *Provespa* (Matsuura, 1999). Workers of all species observed to date rub their gasters on prominent objects along the route, making remarkably stereotyped movements of the gaster (Naumann, 1975; Kojima, 1994; Jeanne, personal observation). Nestmates examine rubbed objects, and wasps in some species have been attracted to glandular secretions experimentally applied to these objects (Jeanne, 1981). *Apoica*, the basal genus of the swarm-founding Epiponini, has Richards' gland but apparently does not employ it during swarming. *Apoica pallens* appears to orient during swarming using an airborne pheromone released from the lower side of the abdomen (gastral sternites [Howard *et al.*, in press]). Workers of *Polybioides tabidus* (Fabricius), *Ropalidia romandi* (Le Guillou), and several genera of epiponines lack Richards' gland (and in some cases lack van der Vecht's gland as well) but still display gastral-rubbing and trail-following behavior. In addition to gastral rubbing, *Synoeca septentrionalis* Richards workers have been observed chewing and licking leaves along swarm routes (Jeanne *et al.*, 1983).

These observations suggest that wasps use a diversity of pheromones and glandular sources to coordinate swarming. Gastral glands are implicated in most cases by the workers' behavior, although the glands' identity has not been confirmed in most cases. Based on several observations of gaster dragging in *Agelaia* swarms, Jeanne *et al.* (1983) speculated that van der Vecht's gland is the source of the trail pheromone. According to S. Turillazzi (personal communication), the Paleotropical genus *Polybioides*, which has no sternal glands, may use Dufour's gland (*P. tabidus*) and the venom gland (*P. raphigastra* [de Saussure]) as sources of trail pheromone.

Swarm founding is a major transition in the evolution of eusociality. It enables much larger, longer-lived colonies with better-developed division of labor relative to independent founding (Jeanne, 1991; Karsai and Wenzel, 1998; Bourke, 1999). Swarm-founding species are ecologically dominant over independent founders where they coexist in the New World,

Asian, and Australian tropics (Heithaus, 1979; Jeanne, 1991; Kojima and van Achterberg, 1997) but not in the Congo Basin (Carpenter and Wenzel, 1999). Our results support the hypothesis that strong selective pressures favor swarm founding and associated social structure in tropical habitats (Jeanne, 1991). In the tropics, seasonal restrictions on the timing of colony foundation are relaxed (O'Donnell and Joyce, 2001). Colony foundation by lone, overwintered queens is unnecessary, permitting swarms that reduce the risks of nest initiation and permit more rapid colony growth (Jeanne, 1991).

Selective pressures favoring swarming have led to the evolution of swarm communication via a variety of pheromonal mechanisms. Swarm founding, and the accompanying changes in colony structure, can be viewed as an adaptation to the wasps' tropical habitats, rather than being constrained by historical factors such as the presence of Richards' gland (Maddison, 1990; Harvey and Pagel, 1991; Jeanne, 1991). Our analysis further suggests that communicative mechanisms that enable the transition from independent to swarm founding are evolutionarily labile, as has been predicted for social communicative displays in general (West-Eberhard, 1983).

The behavioral distinction between swarm and independent founding may not be absolute. Independent-founding species of the polistine genera *Mischocyttarus*, *Polistes*, and *Ropalidia* sometimes exhibit aspects of behavior similar to swarm founders, such as gastral rubbing near nest sites (Litte, 1981; West-Eberhard, 1982; Itô, 1992; O'Donnell, 1992). Some *Polistes* species, in which workers from a destroyed nest follow the queen to a new nest site, may exhibit "quasi-swarming" behavior (West-Eberhard, 1982). Furthermore, two temperate species of *Vespa* (Vespinae; typically classified as independent founders) relocate their colonies after outgrowing the small cavities in which they first nest (Matsuura, 1991). These species present an opportunity to identify the ecological and social factors that favor swarming and may prove informative as to how current mechanisms of communication originated in ancestral swarm founders.

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REFERENCES

- Bourke, A. F. G. (1999). Colony size, social complexity and reproductive conflict in social insects. *J. Evol. Biol.* **12**: 245–257.
- Carpenter, J. M. (1988). The phylogenetic system of the Stenogastrinae (Hymenoptera: Vespidae). *J. N. Y. Entomol. Soc.* **96**: 140–175.
- Carpenter, J. M. (1991). Phylogenetic relationships and the origin of social behavior in the Vespidae. In Ross, K. G., and Mathews, R. W. (eds.), *The Social Biology of Wasps*, Cornell University Press, Ithaca, NY, pp. 7–32.
- Carpenter, J. M., and Wenzel, J. W. (1999). The relative abundance of swarm-founding social wasps in the Congo Basin (Insecta: Hymenoptera; Vespidae, Polistinae). *Nat. Hist. Bull. Ibaraki Univ.* **3**: 9–14.
- Carpenter, J. M., Wenzel, J. W., and Kojima, J. (1996). Synonymy of the genus *Occipitalia* Richards, 1978, with *Clypearia* de Saussure, 1854 (Hymenoptera: Vespidae: Polistinae, Epiponini). *J. Hym. Res.* **5**: 157–165.
- Chadab, R., and Rettenmeyer, C. W. (1979). Observations on swarm emigrations and dragging behavior by social wasps (Hymenoptera, Vespidae). *Psyche* **86**: 347–352.
- Clarke, S. R., Dani, F. R., Jones, G. R., Morgan, E. D., and Turillazzi, S. (1999). Chemical analysis of the swarming trail pheromone of the social wasp *Polybia sericea* (Hymenoptera: Vespidae). *J. Insect Physiol.* **45**: 877–883.
- Dani, F. R., Morgan, E. D., and Turillazzi, S. (1995). Chemical analysis of sternal gland secretion of paper wasp *Polistes dominulus* (Christ) and its social parasite *Polistes sulcifer* (Zimmermann) (Hymenoptera: Vespidae). *J. Chem. Ecol.* **21**: 1709–1718.
- Dani, F. R., Cannoni, S., Turillazzi, S., and Morgan, E. D. (1996). Ant repellent effect of the sternal gland secretion of *Polistes dominulus* (Christ) and *P. sulcifer* (Zimmermann). (Hymenoptera: Vespidae). *J. Chem. Ecol.* **22**: 37–48.
- Dani, F. R., Clarke, S. R., Jones G. R., Morgan, D. E., and Dejean, A. (1997). Search for a trail pheromone in a social swarming wasp of the Old World (*Polybioides tabidus*; Hymenoptera: Vespidae). *Proceeding of the C.N.R.S. Jacques Monod Conference "Chemical Communication in Vertebrates and Invertebrates,"* p. 41.
- Downing, H. A. (1991). The function and evolution of exocrine glands. In Ross, K. G., and Mathews, R. W. (eds.), *The Social Biology of Wasps*, Cornell University Press, Ithaca, NY, pp. 540–569.
- Felsenstein, J. (1985). Phylogenies and the comparative method. *Am. Nat.* **126**: 1–25.
- Forsyth, A. B. (1978). *Studies on the Behavioral Ecology of Polygynous Social Wasps*, Ph.D. dissertation, Harvard University, Cambridge, MA.
- Forsyth, A. B. (1981). Swarming activity of polybiine social wasps (Hymenoptera: Vespidae: Polybiini). *Biotropica* **13**: 93–99.
- Francescato, E., Turillazzi, S., and Dejean, A. (1993). Swarming behaviour in *Polybioides tabida* (Hymenoptera: Vespidae). *Actes Coll. Insectes Soc.* **8**: 121–126.
- Harvey, P. H., and Pagel, M. (1991). *The Comparative Method in Evolutionary Biology*, Oxford University Press, Oxford.
- Heithaus, E. R. (1979). Community structure of Neotropical flower visiting bees and wasps: Diversity and phenology. *Ecology* **60**: 190–202.
- Hermann, H. R., and Dirks, T. F. (1974). Sternal glands in polistine wasps: morphology and associated behavior. *J. Ga. Entomol. Soc.* **9**: 1–8.
- Howard, K. J., Smith, A. R., O'Donnell, S., and Jeanne, R. L. (In Press.) Novel method of swarm emigration by the epiponine wasp, *Apoica pallens* (Hymenoptera Vespidae). *Ethol, Ecol, Evol.*

- Hunt, J. H., Jeanne, R. L., and Keeping, M. G. (1995). Observations on *Apoica pallens*, a nocturnal Neotropical social wasp (Hymenoptera: Vespidae, Polistinae, Epiponini). *Insectes Soc.* **42**: 223–236.
- Itô, Y. (1992). Relocation of nests by swarms and nest reconstruction in late autumn in the primitively eusocial wasp, *Ropalidia fasciata*, with discussions on the role of swarming. *J. Ethol.* **10**: 109–117.
- Jeanne, R. L. (1975). Behavior during swarm movement in *Stelopolybia areata* (Hymenoptera: Vespidae). *Psyche* **82**: 259–264.
- Jeanne, R. L. (1980). Evolution of social behavior in the Vespidae. *Annu. Rev. Entomol.* **25**: 371–396.
- Jeanne, R. L. (1981). Chemical communication during swarm emigration in the social wasp *Polybia sericea* (Olivier). *Anim. Behav.* **29**: 102–113.
- Jeanne, R. L. (1991). The swarm-founding Polistinae. In Ross, K. G., and Matthews, R. W. (eds.), *The Social Biology of Wasps*, Cornell University Press, Ithaca, NY, pp. 191–231.
- Jeanne, R. L., and Post, D. C. (1982). Richards' gland and associated cuticular modifications in social wasps of the genus *Polybia* Lepeletier (Hymenoptera: Vespidae: Polistinae: Polybiini). *Insectes Soc.* **29**: 280–294.
- Jeanne, R. L., Downing, H. A., and Post, D. C. (1983). Morphology and function of sternal glands in polistine wasps (Hymenoptera: Vespidae). *Zoomorphology* **103**: 149–164.
- Karsai, I., and Wenzel, J. W. (1998). Productivity, individual-level and colony-level flexibility, and organization of work as consequences of colony size. *Proc. Natl. Acad. Sci. USA* **95**: 8665–8669.
- Keeping, M. G. (1990). Rubbing behavior and morphology of van der Vecht's gland in *Belonogaster petiolata* (Hymenoptera: Vespidae). *J. Insect Behav.* **3**: 85–104.
- Kojima, J. (1994). Behavior during artificially induced swarm emigration in an Old World polistine wasp, *Ropalidia romandi* (Hymenoptera: Vespidae). *J. Ethol.* **12**: 1–8.
- Kojima, J., and van Achterberg, K. (1997). Social wasps collected by Malaise trapping in Southeast Asia, with a note on relative abundance of swarm-founding species (Insecta: Hymenoptera: Vespidae). *Nat. Hist. Bull. Ibaraki Univ.* **1**: 1–13.
- Litte, M. (1981). Social biology of the polistine wasp *Mischocyttarus labiatus*: Survival in a Colombian rain forest. *Smithson. Contrib. Zool.* **327**: 1–27.
- London, K. B., and Jeanne, R. L. (2000). The interaction between mode of colony founding, nest architecture and ant defense in polistine wasps. *Ethol. Ecol. Evol.* **12**: 13–25.
- Maddison, W. P. (1990). A method for testing the correlated evolution of two binary characters: Are gains or losses concentrated on certain branches of a phylogenetic tree? *Evolution* **44**: 539–557.
- Maddison, W. P., and Maddison, D. R. (1992). *MacClade: Analysis of Phylogeny and Character Evolution*, Sinauer and Associates, Sunderland, MA.
- Martins, E. P., and Hansen, T. F. (1996). The statistical analysis of interspecific data: A review and evaluation of phylogenetic comparative methods. In Martins, E. P. (ed.), *Phylogenies and the Comparative Method in Animal Behavior*, Oxford University Press, Oxford, pp. 22–75.
- Matsuura, M. (1991). *Vespa* and *Provespa*. In Ross, K. G., and Matthews, R. W. (eds.), *The Social Biology of Wasps*, Cornell University Press, Ithaca, NY, pp. 232–262.
- Matsuura, M. (1999). Size and composition of swarming colonies in *Provespa anomala* (Hymenoptera, Vespidae), a nocturnal social wasp. *Insectes Soc.* **46**: 219–223.
- Naumann, M. G. (1975). Swarming behavior: Evidence for communication in social wasps. *Science* **189**: 642–644.
- Noirot, C., and Quenenedey, A. (1974). Fine structure of insect epidermal glands. *Annu. Rev. Entomol.* **19**: 61–80.
- Noirot, C., and Quenenedey, A. (1991). Glands, gland cells, glandular units: Some comments on terminology and classification. *Ann. Soc. Entomol. Fr. (N.S.)* **27**: 123–128.
- O'Donnell, S. (1992). Off-nest gastral rubbing observed in *Mischocyttarus immarginatus* (Hymenoptera: Vespidae) in Costa Rica. *Sphecos* **23**: 5.

- O'Donnell, S., and Joyce, F. J. (2001). Seasonality and colony composition in the tropical eusocial wasp *Mischocyttarus mastigophorus* Richards (Hymenoptera: Vespidae). *Biotropica* **33**: 468–473.
- Raposo-Filho, J. R., Calloni, C., and Delfino, G. (1994). Structural and ultrastructural features of the glands in the VI and VII gastral sternites of female *Mischocyttarus (Kappa) atramentarius* Zikán 1949 (Hymenoptera Vespidae). *Ethol. Ecol. Evol. Special Issue* **3**: 47–52.
- Schmitz, J., and Moritz, R. F. A. (1998). Molecular phylogeny of Vespidae (Hymenoptera) and the evolution of sociality in wasps. *Mol. Phylogenet. Evol.* **9**: 183–191.
- Smith, A., O'Donnell, S., and Jeanne, R. L. (2001). Correlated evolution of colony defense and social structure: A comparative analysis in eusocial wasps (Hymenoptera: Vespidae). *Evol. Ecol. Res.* **3**: 331–344.
- Spurr, A. R. (1969). A low viscosity epoxy resin embedding medium for electron microscopy. *J. Ultrastruct. Res.* **26**: 31–43.
- Wenzel, J. W., and Carpenter, J. M. (1994). Comparing methods: Adaptive traits and tests of adaptation. In Eggleton, P., and Vane-Wright, R. I. (eds.), *Phylogenetics and Ecology*, Academic Press, London, pp. 79–101.
- West-Eberhard, M. J. (1982). The nature and evolution of swarming in tropical social wasps (Vespidae, Polistinae, Polybiini). In Jaisson, P. (ed.), *Social Insects in the Tropics, Vol. 1*, Universite de Paris-Nord, Paris, pp. 97–128.
- West-Eberhard, M. J. (1983). Sexual selection, social competition, and speciation. *Q. Rev. Biol.* **58**: 155–183.