# Chapter 2
# The Evolution of Swarm Founding in the Wasps: Possible Scenarios

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**Abstract** Independent- and swarm-founding wasps represent two discrete social syndromes, differing from each other in a number of traits that include colony size, level of social complexity, queen number, division of labor among workers, nest architecture, body size, and ecological dominance. Swarm founding evolved independently at least four times in the Vespidae. While much attention in recent decades has been paid to unraveling the steps leading to eusociality in the vespids, virtually none has been devoted to understanding how swarm founding evolved from its ancestral independent-founding state. Here I suggest possible scenarios by which the transition could have occurred. I argue that the key initial step was the evolution of pheromonal queen signaling, which enabled the evolution of larger colonies. Larger colonies in turn led to the decentralization of colony control away from a dominant queen and onto the workers. Other traits of the swarm founders, including polygyny, nest envelopes, nocturnality (in *Apoica* and *Provespa*), and small body size, probably evolved later. Swarm founding appears to be an inevitable outcome of the evolution of larger colony size among tropical vespids.

**Keywords** Social complexity · Decentralization · Colony size · Major transitions · Queen signaling

## 2.1 Introduction

The eusocial wasps comprise some 1000 species worldwide and encompass a tremendous range of colony size and degrees of social complexity (Jeanne 1991). This diversity is especially evident in the subfamily Polistinae, by far the largest and most widely distributed of the three subfamilies of social vespids. Species of

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Vespidae fall into two conspicuously different behavioral groups, based on their mode of colony founding (Hölldobler and Wilson 1977; Jeanne 1980). In the *independent founders (IF)*, new colonies are initiated by one or a few inseminated females, without the aid of workers. In contrast, s*warm founders (SF)* initiate new colonies by means of a group comprising many workers and a smaller number of inseminated females (queens). Although the independent-founding species (including the Polistinae and the Vespinae) outnumber the swarm founders by roughly 3 to 1 (J.M. Carpenter, pers. comm.), the SF are the more ecologically dominant (Wilson 1990) group in the tropics, especially in the Neotropics (Jeanne 1991; Kojima and Van Achterberg 1997; Carpenter and Wenzel 1999).

IF and SF appear to comprise largely discrete behavioral syndromes, with remarkably little overlap between them (Jeanne 2003) (see also (Bourke 1999). The most discrete trait appears to be the mode of founding itself. We know of no intermediates between independent founding and swarm founding, and in fact it is hard to imagine what such an intermediate would look like. In addition to mode of founding, each group is characterized by a set of associated traits (Table 2.1). In column 3 of the table, I have given most of these traits an estimated degree-of-overlap score. A few of these associated traits appear to be almost as discrete as the mode of founding itself—most notably worker control and queen number—although deeper research on little-studied SF genera may challenge this assessment. Most of the other traits characterizing the two groups show greater or lesser degrees of overlap.

The two groups also represent two discrete levels of social complexity (Jeanne 2003). IF species can be characterized as having simple societies. Colonies in this group are small, comprising less than 100 adults and often many fewer. Colony members engage in conflict over access to direct reproduction. Colony control—regulation of the colony's activity level (Jeanne 2003)—is centralized in the queen, who maintains her position as top reproductive via dominance interactions with her subordinate co-foundresses and worker offspring (Reeve 1991). Division of labor among workers is minimal or non-existent. Selection at the individual level appears to play the dominant role in maintaining sociality in this group.

In contrast, SF species form complex societies. Colonies are typically large enough that workers have little chance of direct reproduction, leading to the convergence of their self-interests with those of the queens (Bourke 1999; Jeanne 2003). Consequently, colony control is decentralized onto the workers. Interactions among colony members give rise to self-organizing processes that in turn lead to adaptive patterns of behavior at the colony level. Age polyethism among workers is strongly developed, and some species have evolved queen-worker dimorphism. Selection on these colony-level traits predominates over selection on individual-level traits (Jeanne 2003). Drawing an analogy between these two levels of social organization and solitary animals, we could say that the IF are roughly analogous to the Parazoa (sponges) and the SF to the Eumetazoa.

**Table 2.1** Comparison of traits of IF vs. SF social wasps

| IF traits | SF traits | IF-SF overlap |
|---|---|---|
| *Colony founding* | | |
| Propagules are individual gynes | Propagules are swarms comprising workers and gynes or queens | None |
| Founding female/queen searches for and selects nest site | Workers search for and select nest site | None |
| Associate foundresses ("helpers") join founding female hours or days later [Apparent exception: *Parapolybia varia* (Yamane 1985)] | Scout workers recruit swarm (queens + workers) to new nest site via mechanical(?) and chemical signals and queens and workers emigrate together to the new site | None? |
| *Queen signaling* | | |
| Queen physically dominates subordinates, inducing them to take up worker roles. Evidence for queen pheromone in some species (Landolt et al. 1998), but apparently absent in others (Gadagkar 2001) | Queens are passive; hypothesized queen pheromone signals reproductive status | Much |
| *Queen-* vs. *worker-control of colony activity* | | |
| Queen domination of workers stimulates colony activity. Exceptions in some *Polistes* (Jha et al. 2006), *Ropalidia* (Bruyndonckx et al. 2006) | Workers regulate colony activity, stimulate activity via biting attacks | Some |
| *Division of labor* | | |
| Founding female/queen initiates nest | Workers initiate nest | None |
| Founding female/queen initiates new nest cells | Workers initiate new nest cells. Exception: *Chartergellus golfitensis*: (Chavarria-Pizarro and West-Eberhard 2010) | Some |
| Founding female/queen forages for nest material for cell initiation. Exceptions in some species: *Mischocyttarus drewseni* (Jeanne 1972) | Workers forage for all nest material and do all nest construction | Some |
| *Colony size* | | |
| Colonies are small, rarely exceeding 100 adults (range: $10^0$–$10^2$) | Colony sizes large, exceeding one million workers (range: $10^1$–$10^6$) | Some |
| *Queen number* | | |
| Short-term monogyny: typically one egg-laying queen. Exceptions: *Ropalidia rufoplagiata* (Gadagkar 2001); *R. revolutionalis* (Henshaw et al. 2004, 2015) | Long-term polygyny: multiple egg-laying queens cycling down to several or even one during colony development. Exception: *Provespa* is monogynous (Matsuura 1999) | Some |

(continued)

**Table 2.1** (continued)

| IF traits | SF traits | IF-SF overlap |
|---|---|---|
| *Queen competition* | | |
| Founding females engage in contest competition among themselves for the right to be the sole egg-layer, establishing a dominance hierarchy with the egg-layer in the alpha position. Exception: *Ropalidia marginata* (Gadagkar 2001) | Queens do not act aggressively toward one another; by constructing cells faster than queens can fill them with eggs (in newly founded nests), workers create the condition in which queens engage in scramble competition via egg-laying | None |
| *Nest architecture and construction* | | |
| Nest growth gradual and continuous, responds to demand for oviposition sites; controlled by queen | Nest construction/expansion explosive/episodic, construction of new cells exceeds demand for oviposition sites; controlled by workers Abundance of empty cells may create context for queen-queen competition. Exceptions exist (Jeanne and Bouwma 2004) | Some |
| No nest envelopes (except in Vespinae) | Nest envelopes in most species. Exceptions: *Apoica*; most *Agelaia* spp. | Some |
| Nests of single combs, or if multiple combs, separately attached to the substrate | Nests of single or multiple combs | Some |
| *Behavioral specialization* | | |
| Little or no specialization among workers | Age polyethism. Task partitioning: foraging and nest work performed by different individuals Exception: *Chartergellus golfitensis* (Chavarria-Pizarro and West-Eberhard 2010) | Some |
| *Life history traits* | | |
| Egg-to-adult development times longer: 38–87 days | Egg-to-adult development times shorter: 28–30 days | None? |
| Worker lifespans longer | Worker lifespans shorter | ? |
| *Colony survival* | | |
| Low rates of colony survival | High rates of colony survival | None? |
| *Defense* | | |
| Chemical defense of nest against scouting-and-recruiting ants | Active defense of nest against scouting-and-recruiting ants. Exceptions: *Nectarinella* and *Leipomeles* employ sticky traps | Some |

Traits are generalized and are focused primarily on the Polistinae. Examples of exceptions, if known, are indicated. The column headed “IF-SF overlap” provides a subjective estimate of the degree of overlap between the two groups for each trait: none, some, and much. Note that some of these are tentative and with more research will likely need to be revised

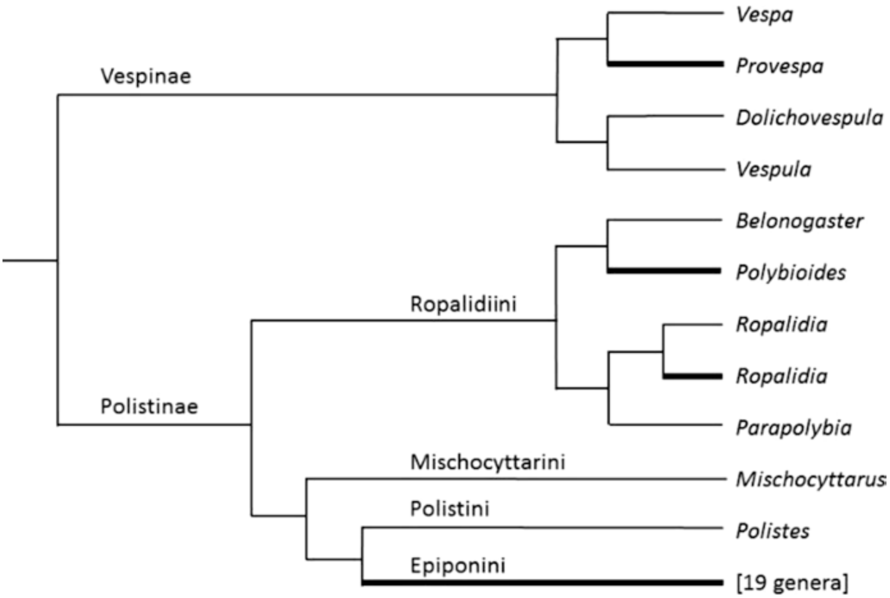

**Fig. 2.1** Phylogenetic tree of the social vespids (*Stenogastrinae not shown*), showing the subfamily Vespinae and the four tribes of Polistinae. Heavy lines indicate lineages in which swarm-founding evolved. Note that *Ropalidia* contains both IF and SF species. Phylogeny based on Pickett and Carpenter (2010) and J. M. Carpenter, pers. comm.

Swarm founding evolved independently at least four times in the Vespidae (Carpenter 1991), in each case from an independent-founding ancestor (Fig. 2.1). Compared with the origin of eusociality itself from solitary ancestors, the transition from IF to SF has been little-addressed (but see West-Eberhard (1982) and Henshaw et al. (2004)). Yet it can be argued that the IF-to-SF transition was the more difficult of the two, because it represents a more significant shift from individual-level selection to selection at the level of the group, the colony (Szathmáry and Maynard Smith 1995). My aim here is to explore how this transition may have happened by examining the steps required to evolve swarm founding. My main focus will be on the Polistinae and its three origins of SF, although references to the Vespinae will be made when informative.

Howard Evans was able to identify a series of steps from solitary to eusocial wasps, with most steps represented by extant species (Evans 1958). In contrast, species representing intermediate steps along the path from IF to SF appear to be nonexistent. That is, the two groups appear to occupy discrete adaptive peaks separated by a fairly deep valley. This suggests that intermediate conditions are not evolutionarily stable, i.e., that the whole suite of SF traits had to evolve more or less together. Nevertheless, it may be possible to identify a key trait, or traits, that may have been a first step enabling the shift from IF to SF (Fig. 2.2). What clues do we have as to what that critical step might have been? I emphasize that the ideas expressed below are speculative, and others may argue for different evolutionary pathways.

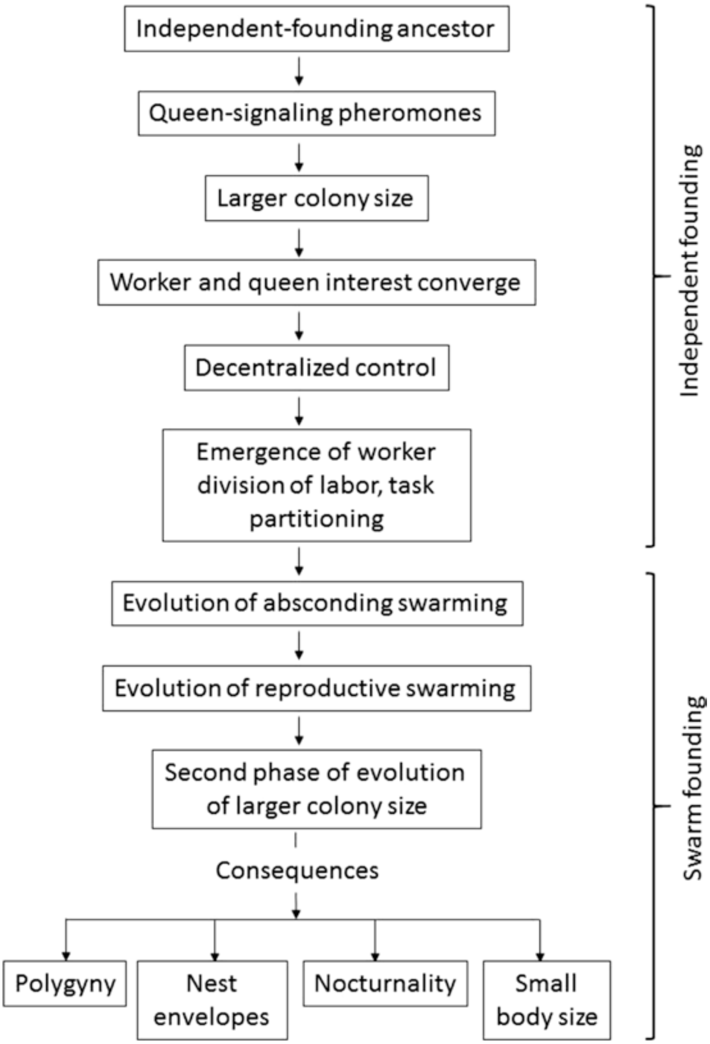

**Fig. 2.2** Diagram of hypothesized steps in evolving swarm founding from an independent-founding ancestor

## 2.2 Decentralized Control of Colony Activity

I have argued elsewhere that the most essential underlying difference between the two groups is decentralized (worker) control over colony activity in the SF vs. centralized (queen) control in the IF (Jeanne 2003). In the typical IF species, the queen is the pacemaker of the colony, stimulating worker activity via physical dominance (Reeve and Gamboa 1983; Bruyndonckx et al. 2006). Furthermore, queens engage in certain non-reproductive tasks, such as foraging for nest material and the initiation of new cells. In contrast, in the SF the workers take over all or most non-reproductive tasks, while the queens are largely limited to oviposition and are generally behaviorally passive. This derives, at least in part, from large colony size, wherein any single individual has a small chance of becoming the egg layer (Bourke 1999). Thus, workers are shut out of direct reproduction, leading to the convergence of their self-interests with those of the queen(s) (Bourke 1999; Jeanne 2003).

How does this decentralized control come about? As just argued, the shift from queen to worker control requires large colony size. Colony size in the IF appears to be constrained to a few dozen adults by the limited reach of the behavioral means used by the queen to signal her status to the workers. In this group, queen signaling is primarily via physical dominance attacks on subordinates and workers (Spradbery 1991) and vibrational signaling to developing larvae (Jeanne and Suryanarayanan 2011; Suryanarayanan et al. 2011). In *Mischocyttarus drewseni*, for example, virtually every female offspring is physically dominated by the queen during its first few days as an adult (Jeanne 1972). This requires repeated, close physical contact, which limits the number of offspring over which this kind of signaling can be effective. Two factors lead to the breakdown of this form of colony control. First, the rate of emergence of young females increases during the ergonomic stage, and second, the absolute rate of domination by the queen decreases as she ages. Both lead to an increasing likelihood that some young females do not receive enough of this signal during their first few days as adults to shift them into worker roles. Some of these become non-working potential gynes and some may go on to challenge and supersede the reigning queen, leading to serial polygyny (Jeanne 1972). This puts the colony into the reproductive stage, producing not only these non-working females, but males, at the expense of additional workers and continued growth of the size of the colony. The resulting increase in mouths to feed, coupled with the decreasing number of workers to feed them, leads to the decline of the colony after 5–8 months from founding. Colonies of *Polistes*, *Ropalidia*, *Belonogaster*, and other IF polistines appear to be size-limited for similar reasons (Owen 1962; West-Eberhard 1996).

## 2.3 Queen-Signaling Pheromone

This suggests that the necessary first step enabling the escape from the limits of behavioral queen signaling on colony size was very likely the evolution of effective queen pheromones. In the SF there is little or no direct physical aggression by queens toward workers, strongly suggesting that queen signaling is by chemical means, i.e., via queen pheromones (West-Eberhard 1978b; Spradbery 1991; Kelstrup et al. 2014). On the other hand, in some SF aggression and displays by workers toward females appear to be a means of biasing the development of emerging females into becoming queens (Platt et al. 2004; Kelstrup et al. 2014). Effective queen pheromones enable the evolution of larger colony size, which in turn is essential for the convergence of worker and queen interests. Queen pheromones have not as yet been chemically characterized for any SF species, nor is it known how queen pheromones are delivered to all the members of the colony. Possibilities include direct contact with the queens, airborne dispersal of volatile compounds, substrate-borne contact pheromones via the nest carton, and surface hydrocarbons on queen-laid eggs (Endler et al. 2004; Oi et al. 2015).

Intermediate stages in the transition from physical to chemical signaling are apparently stable, as suggested by the variation in intensity of domination behavior among species of IF. The assumption here is that decreasing intensity of dominance behavior across taxa reflects an increasing role for chemical signaling. The degree of reliance on physical signals ranges from the despotic and violent domination seen in *Polistes canadensis* and *Belonogaster grisea* to mild or non-existent interactions, as in *P. instabilis, P. versicolor, Mischocyttarus angulatus*, and *Ropalidia revolutionalis* (Spradbery 1991; Ito 1993; de Souza and Prezoto 2012)). *R. marginata*, an IF species, establishes linear dominance hierarchies, but they are not headed by the queen (Gadagkar 2001). Instead, the queen is docile, rarely engaging in physical attacks on nestmates. This suggests that she maintains her monopoly on egg-laying via pheromones, and indeed there is evidence that one source is the Dufour's gland and that she applies the pheromone to the nest surface (Mitra and Gadagkar 2011; Mitra et al. 2011; Saha et al. 2012). If the effectiveness of the pheromone is experimentally reduced, queens resort to aggression toward workers to maintain their status (Saha et al. 2012). *Polistes gallicus* has also been shown to produce a queen-signaling pheromone, in this case via the van der Vecht's gland (Dapporto et al. 2007).

A similar variability is seen in the Vespinae. In small-colony vespines, both physical dominance and presumed queen pheromones are utilized, whereas in species forming larger colonies (*Vespula vulgaris* group), there is apparently complete reliance on chemical signaling, with no sign of residual physical signals (Spradbery 1991). Two compounds, n-C29 and 3-MeC29, have been shown to be queen pheromone components in both *Vespula vulgaris* and *Dolichovespula saxonica* (Oi et al. 2016).

Among SF species we also see variation in the degree of queen-worker interactions. Aggressive dominance displays in which queens bend the gaster laterally (the "bending display") toward approaching workers or other queens was first described for *Metapolybia aztecoides* by West-Eberhard (1978b). Similar displays and even aggression by queens have since been reported for *Chartergellus* spp., *Synoeca* sp., *Protopolybia acutiscutis*, *Leipomeles*, *Asteloeca ujhelyii*, and *Parachartergus fraternus*, but are apparently absent in *Protopolybia fuscatus*, *Parachartergus colobopterus*, and *Nectarinella championi* (reviewed in Chavarria-Pizarro and West-Eberhard 2010). Older workers of *Parachartergus colobopterus* are aggressive toward younger ones, but queens are not involved in these encounters (Platt et al. 2004). These displays and acts of aggression by queens and workers suggest an incomplete reliance on queen pheromones to signal queen status.

Both physical and chemical queen control over reproduction by workers appear to be reliable ("honest") signals (Mitra and Gadagkar 2012). Although in the proximate sense the signals have physiological effects on the receivers, at the level of ultimate causation, the receivers extract honest information about the sender that they respond to so as to obtain a fitness benefit for themselves (Peso et al. 2015). This view is supported by the recent finding that cuticular hydrocarbons, specifically saturated hydrocarbons, act as a conserved class of queen pheromones, inhibiting worker reproduction across all three groups of eusocial Hymenoptera (Mitra and Gadagkar 2012; Van Oystaeyen et al. 2014). If queen pheromones were detrimental to workers' fitness— that is, if queens were manipulating workers against their personal interests—selection would act on workers to evolve resistance and in turn on queens to overcome that resistance. The path of the resulting evolutionary arms race would result in rapid change in the composition of queen pheromones in each lineage, leading to species-specific differences among them (Peso et al. 2015).

## 2.4 Larger Colony Size

An IF ancestor that evolved an effective queen pheromone would be able to evolve larger colony size. The simplest route would be through the lengthening of the ergonomic phase, i.e., by enabling the continued increase in worker numbers before switching to the reproductive phase. Such colonies could still look much like those of *Polistes* or *Mischocyttarus*, i.e., they would retain independent founding, except that the colony cycle would be longer and colonies would grow larger. The combination of relatively large colony size and strong and effective queen-signaling pheromones would move the colony well along the road to the convergence of workers' interests with those of the queen and thus toward worker control of colony activities. Among existing species, this stage may be most closely represented by the Vespinae, for which there is good evidence for queen-signaling pheromones (Oi et al. 2016). However, no known IF polistine has these characteristics, suggesting that ancestral tropical IF that evolved along this path went on to evolve swarm founding.

## 2.5 Evolution of Swarm Founding Itself

Among tropical polistines, the next step was probably the evolution of swarm founding itself. Here I characterize a true "swarm" as worker-controlled, to distinguish it from associations of independent-founding females. In some temperate-zone *Polistes*, satellite nests are sometimes founded by groups of workers in mid-summer (Strassmann 1981; Page et al. 1989) in a process that has been likened to swarming (Rau 1941), but there is little evidence that it is any closer to true swarming than is ordinary springtime independent founding in these species.

It seems certain that worker control had to be in place before swarming could evolve, as it is the workers that scout out a suitable nest site and coordinate the eventual move to it by the rest of the swarm (Forsyth 1981). How the transition could have occurred is less evident than the steps enabling the evolution of larger colony size. One possibility is that the swarm as the colony-founding unit first evolved in the context of loss of the brood to a predator; that is, the absconding swarm (Jeanne 1991) was the first step. In the Neotropics, mass-foraging ants (e.g., *Eciton* spp.) are important predators of social wasps, and most wasp species have no effective defense against them. Most of the adults usually escape and can renest, starting the colony cycle over. In many parts of the tropics, nesting is possible year-round, so there is no seasonal constraint on this. Colonies ought to be at an advantage if the adults can stay together and renest as a single, large group, rather than dispersing to form small independent-founding groups of one or a few individuals. One advantage is seen in today's SF wasps: the ability to quickly build a nest and stock it with a large number of eggs. Another is a reduction in the risk of failure during the founding stage. A founding swarm of many individuals not only vastly reduces the risk of failure by attrition due to predation on individual group members (West-Eberhard 1982), but it increases the likelihood that it will successfully defend the brood against natural enemies. This step may not have been hard to take. It would require that the workers scout out and reach consensus on a nearby site for renesting. One hurdle to achieving this step is the need to evolve some mechanism by which the numerous scouts arrive at a consensus on a single site. Recruiting the swarm members to the new site may require only a modest ability to communicate location, e.g., by chemical marking of the chosen site itself. If the distance between the old and new sites is short, members of the group should be able to arrive at the new site by detecting the airborne volatiles emitted from it. Several SF species have been observed to scent-mark the new site, but omit the chemical trail when the distance to the new site is less than 20 m or so (West-Eberhard 1982). This suggests that the laying of a chemical trail could have been a secondary step, enabling emigration over greater distances. On the other hand, behavior similar to that seen in the epiponines sometimes occurs among the IF. Queens of *Mischocyttarus labiatus* scent-mark (drag the gaster) on leaves between the old and new nest sites shortly after nest initiation (Litte 1981), suggesting that scent trails could have preceded the evolution of swarming. But in this case, it is presumably inseminated foundress females, not workers, that lay down the scent marks.

Once such absconding swarming was in place, the swarm as the reproductive propagule would have to secondarily evolve. This may have been a more difficult step: absconding swarming is simple—the entire adult population (except males in some species (Bouwma et al. 2000)) makes the move, whereas reproductive swarming requires decisions about when to emit a swarm, what proportion of the colony to bud off into each swarm, and which workers will go with which queens. This added complexity is another reason that absconding swarming may have led the way.

The move to swarm founding appears to have been an all-or-none transition. As far as known, existing polistine species unambiguously fall into either the IF or the SF category. Indeed, it is hard to imagine what an intermediate IF-SF stage might look like. The absence of large colonies (>100 adults) among the ~750 species of IF polistines suggests that the transition to swarm founding was an inevitable endpoint of the sequence "queen pheromone → large colony size → worker control →

swarm founding," at least in the tropics. Alternatively, there may be other, possibly ecological, limits on colony size for tropical IF. There are no known reversals of the swarming habit within the Epiponini, despite that numerous species have secondarily evolved colony sizes that are well within the range of those of independent founders (Pickett and Wenzel 2007), suggesting that swarming is a "point of no-return" (Hölldobler and Wilson 2009) and that the swarm-founding wasps occupy a high peak in the adaptive landscape.

There are variants of the paradigm exemplified by *Polybia* of rapid regrouping following absconding, with scouts reaching consensus on a new site and guiding swarm members to it via a chemical trail (Jeanne 1981; Sonnentag and Jeanne 2009). *Apoica,* for example, apparently does not deploy scouts and does not lay scent trails. Instead, volatiles are wafted into the air after the swarm is airborne (Howard et al. 2002). Some species of *Agelaia* do not emigrate to a new nest site in a single event, but spread the move from the old to the new nest over several days (Jeanne 1975b). Exploring species in these and other genera in more detail may shed some light on the evolutionary steps taken.

Once swarm founding had evolved, the evolution of much larger colony size could have followed relatively quickly. There is no known theoretical limit to the size of a reproductive swarm. Colonies of some species of *Agelaia* attain sizes of $10^4$–$10^6$ adults (Jeanne 1991; Zucchi et al. 1995) and doubtless send out proportionately large swarms. Smaller colony size could also have evolved. A number of extant epiponine species have mature colony sizes of well under 100 adults (Jeanne 1991; Jeanne 2003; Pickett and Wenzel 2007).

## 2.6 Consequences and Correlates of Swarm Founding

Among the SF polistines are several other traits that seem clearly to have evolved after swarm founding was achieved. Because they are not known in the IF polistines, I call them consequences, or correlates, of swarm founding. For the same reason, they are worth calling attention to, in that they may help provide insight into why the swarm founders have become so ecologically dominant.

### *2.6.1 Polygyny*

As far as is known, long-term polygyny characterizes all species in the three groups of polistine swarm founders, although this remains unconfirmed for many species and even for entire genera. West-Eberhard postulated that polygyny was either directly derived in the wasps from the polygyny of presocial groups or was secondarily derived from the short-term monogyny characterizing the IF (West-Eberhard 1978a). A phylogenetic test between these two hypotheses comes down in favor of the latter (Carpenter 1991). The same path was evidently taken in the ants, where polygyny is strongly correlated with large colony size (Boulay et al. 2014). That colonies of *Provespa* are monogynous (Matsuura 1999) indicates that polygyny is not a necessary concomitant of swarm founding and suggests instead that we look for extrinsic causes. A source of selection favoring polygyny may come from natural enemies. One advantage of spreading the egg-laying function among multiple queens instead of a single physogastric individual is the retention of mobility in the event of an attack on the colony (Richards and Richards 1951). The type of predator may also matter. In the Neotropics, army ants, particularly those in the genus *Eciton*, are major predators of social wasps. Their primary prey are the larvae and pupae in the nest, but they also will take any adult that fails to evacuate the nest quickly. In 2013 at the Reserva Florestal Adolpho Ducke north of Manaus, I witnessed an attack by *E. hamatum* on a nest of *Chartergellus jeannei.* Although most of the adults managed to flee, less than a minute after the first ant reached the nest, ants blocked the entrance, trapping significant numbers of wasps inside the nest and thereby subjecting them to capture (Fig. 2.3). Since in many wasp species the queens are the last to leave the nest in event of threat (Richards and Richards 1951), some of those killed may well have been queens. By spreading egg-laying capacity among many reproductives, the absconding swarm would likely still have enough queens to quickly stock its new nest with enough eggs for rapid growth.

In the Old World tropics, on the other hand, driver ants are apparently less important predators on social wasps than are army ants in the Neotropics (Yamane 1996). Instead, certain *Vespa* species appear to be the more important threat (Matsuura and

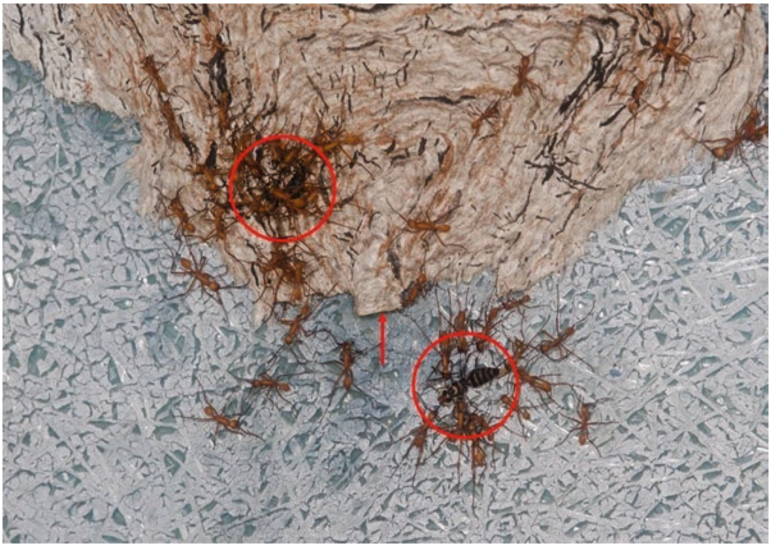

**Fig. 2.3** Raid of a nest of *Chartergellus jeannei* by *Eciton hamatum* at Reserva Florestal Adolpho Ducke, Manaus, Amazonas, Brazil. Two adult wasps are shown being captured (red circles). Nest entrance is shown by the arrow. Photo was taken barely 2 minutes after the first ant reached the nest. Substrate is the outer wall of a fiberglass water tank

Yamane 1990). These hornets present a different kind of predation on colonies. *Vespa* workers are much larger than are those of most of their social wasp prey, and their raids involve just one or a few workers acting with impunity to carry off the brood over several days (Jeanne and Hunt 1992). In the face of such a predator, the defending adults are at comparatively little risk, and a single queen would have a high chance of surviving these attacks and eventually emigrating with the workers to start a new nest. This may in part explain the monogyny of *Provespa* in that region. On the other hand, swarm-founding *Ropalidia* in the same habitats are polygynous (Kojima and Jeanne 1986; Spradbery and Kojima 1989; Kojima 1996); R. L. Jeanne, unpublished data), so intrinsic factors may have played some role in the evolution of polygyny in the *Ropalidia*.

As far as we know, the rule in SF polistines is long-term polygyny with periodic reduction to one or a few queens (cyclical oligogyny) (Ross and Carpenter 1991). In contrast, colonies of most IF polistines are monogynous. Seeming exceptions include *Ropalidia revolutionalis*, an IF species in which some colonies have multiple co-occurring egg-layers (Henshaw et al. 2004). There are also several reports of polygynous colonies of *Polistes* spp., especially when old nests are reused (Liebert et al. 2008). Based on such observations, Henshaw and colleagues have suggested that the evolution of polygyny may have preceded swarm founding in some lineages and that the evolution of cyclical oligogyny was preceded and enabled by worker manipulations that helped preserve high relatedness under multiple queens (Henshaw et al. 2004).

### *2.6.2 Nest Envelopes*

Nest envelopes are another trait of interest in this context. The IF polistines are noteworthy for their universal lack of nest envelopes. Why this is so is an interesting question in itself, but is beyond the scope of this chapter. In contrast, the vespines universally have them, as do the great majority of SF polistines. The fact that all *Apoica* and most *Agelaia*, both basal epiponine genera, lack envelopes suggests that the first species to cross the threshold to swarm founding also lacked an envelope. Similarly, the common ancestors of the clade *Belonogaster* (no envelopes) + *Polybioides* (envelopes) and of the clade *Parapolybia* (no envelopes) + *Ropalidia* (envelopes in some SF species) very likely also built naked nests. Envelopes appear to have evolved at least six times independently in the polistine and vespine wasps: once each in *Polybioides*, *Ropalidia*, and *Provespa*, at least twice in *Agelaia,* and once (or more) in the clade representing the remaining epiponine genera (Wenzel 1991). *Agelaia* is the most basal epiponine genus to have evolved envelopes. In the two species that build them (*A. areata, A. flavipennis*), the envelope is an extension of the petiolate comb, and so is little-removed from the IF nest type, whereas envelopes in the other genera differ fundamentally from this and may well have evolved independently of *Agelaia* and even of each other. In fact, given the tremendous diversity of epiponine nest architecture (Jeanne 1975a; Wenzel

1991), it seems plausible to hypothesize that envelopes had multiple origins in that clade. In other words, even if swarm founding evolved only once in the Epiponini, there could have been an adaptive radiation of envelope design, with many independent attempts, most successful enough to have been universally adopted. It has been argued that envelopes were secondarily lost in the SF *Ropalidia* that moved to cavity nesting (Kojima and Jeanne 1986); the same argument could be raised in the case of *Agelaia* (Wenzel 1991). However, that line of reasoning seems weak in light of the fact that vespine species that have made the same move retain at least rudimentary envelopes. Nevertheless, the question of which is the apomorphic state—naked nests or envelopes—in these lineages is an interesting and unresolved one.

The thick, air-filled envelope of the vespines is almost certainly an adaptation that insulates the nest against low temperatures, enhancing homeostatic control of the temperature around the brood (Himmer 1931; Schmolz et al. 2000). But why have the SF polistines, in their tropical habitats, evolved envelopes several times? I suggest that it ultimately has to do with the novel selection pressures faced by larger colonies and the larger nests they require. Nests of many SF species comprise more than one comb, arranged in a large diversity of architectural forms (Jeanne 1975a; Kojima and Jeanne 1986; Wenzel 1991) to accommodate the added weight while maintaining expandability. With the exception of *Apoica*, SF either enclose their nests in an envelope (typically carton, but in some cases cemented-together leaves) or nest in cavities Richards 1978a) (Wenzel 1991). The basal epiponine genus *Apoica* (Pickett and Wenzel 2007) builds a single naked comb [see (Pickett et al. 2009)], and the multi-combed nests of most species of *Agelaia*, sister group to the remaining Epiponini, are naked, but all remaining genera of epiponine wasps construct nests with envelopes. The selective advantages of covered nests probably involve both homeostatic control of physical conditions and protection from rain and natural enemies, as well as escape from the limitations of finding suitable cavities to nest in. Whereas the small, single-combed nests of IF polistines are often built under leaves of understory plants, which provide at least some shelter from the elements, larger nests are heavier and require sturdier substrates such as trunks, branches, and twigs, which provide little shelter. Envelopes effectively prevent rain from reaching the brood in the combs.

Perhaps an equally important function is to restrict access to the brood by arthropod enemies. Envelopes limit access by scouting-and-recruiting ants to the narrow entrance and increase the likelihood that the workers can detect approaching scout ants on the envelope and remove them (Jeanne 1975a). The universal occurrence among the IF polistines of tough nest pedicels made up mostly of chitin-like oral secretion and their coating of ant-repellent glandular secretion stands in stark contrast to the apparent complete absence of these adaptations among the SF species (London and Jeanne 2000; Makino 2010) and supports the notion that envelopes evolved as a more effective means of defense against ants than is a chemically defended pedicel.

Envelopes may be even more effective in preventing parasitoids from reaching the brood. The brood of IF species are subject to attack by four to five times as many species as are swarm founders (Makino 1985; Yamane 1996). In contrast to the large diversity of lepidopteran species reported to attack brood of IF, none have as yet been recorded from SF and are rarely found in vespine nests (Yamane 1996). It has been experimentally shown for *Polybia occidentalis* that the envelope significantly reduces access to the brood by phorid flies (London and Jeanne 1998). This wasp also responds facultatively to high numbers of phorids flying near the nest by reducing the size of the entrance (London and Jeanne 1998). In addition, species lacking envelopes appear to be more likely to suffer colony failure from heavy infestation than are SF species (Schremmer 1972; Jeanne 1979; Litte 1981; Schmid-Hempel 1998) (but see (Simões et al. 1996)). Envelopes have also been cited for reducing the infestation of vespine nests by parasitoid moths (Matsuura and Yamane 1990).

Wasps in the genus *Apoica* are unique among epiponines in that they neither construct an envelope nor nest in cavities. In nine of the ten species (exception, *A. arborea* de Saussure; see below), the single comb is provided with a thick (25 mm in *A. flavissima* (Yamane et al. 2009) felt-like mat of plant hairs above the brood cells. Two explanations of the function of this feature have been proposed (Yamane et al. 2009). One is that it serves to strengthen the attachment of the combs to the substrate. This seems unlikely, given that the thickening tapers to the outer margins of the comb and does not occur just at the point of attachment. The second explanation is that it insulates the brood cells from fluctuations in temperature. This also seems unlikely, in that temperature fluctuations in a central cell in an active nest of *A. flavissima* have been shown to be much less than those measured in an empty nest (Yamane et al. 2009), indicating that the adults and brood have a much greater effect on moderating temperature than does the nest structure. A third possibility is that the thick felt functions to prevent parasitoids such as ichneumonids from reaching the backs of the brood cells with their ovipositors, as does *Pachysomoides*, for example, in parasitizing *Polistes* (West-Eberhard 1969). It is noteworthy that the cell openings on the face of the comb are protected during the day by the multiple layers of closely packed adults, which are likely very effective in preventing access to the brood from that direction. No such clustering occurs on top of the comb. Although records are few, the rate of parasitization suffered by *Apoica* appears to be exceptionally low. Other than the unusual case of heavy infestation by phorids in a nest of *A. pallens* (Schremmer 1972) [cited by Schremmer as *A. pallida* (Richards 1978b)], the only brood parasitoid ever recorded for the genus (two species) is the hymenopteran *Seminota marginata* (Westwood) (Bertoni 1911; Trindade et al. 2012; Santos and Noll 2013). This trigonalid may get around the defensive curtain of adults by making its way into the nest indirectly, either via a primary host (caterpillar) brought to the nest as food or by laying its eggs on plants utilized as nesting material by this wasp (Santos and Noll 2013). Interestingly, the adult/brood-cell ratio in the genus is much higher than in other swarm founders—close to 1.0, compared to well under 1.0 for other epiponines (Richards 1978b) (Jeanne, unpublished data). Such a high ratio of workers to nest cells may be an adaptation to maintaining the large number of adults required by this form of defense. An alternative nest architecture is seen in *A. arborea*, whose nest is a long, narrow comb comprising entirely sessile cells built under a branch (Pickett et al. 2009). The supporting branch may provide the same barrier to probing parasitoids as does the felt-like thickening of the comb-back of its congeners.

### 2.6.3 Nocturnality

Nocturnality has evolved twice in swarm-founding wasps—in *Apoica* and *Provespa*—but apparently never in the IF. We can only speculate as to the selective forces favoring this form of specialization, but escape from natural enemies may have played a role here as well. Having the entire adult population forming an inactive, tightly packed mass covering the face of the comb maximizes their effectiveness in physically blocking parasitoids from reaching the brood during the day, when most parasitoids presumably are active. While escape from parasitoids has also been proposed for nocturnality in certain bees, escape from competition for food resources is an alternative explanation (Wcislo et al. 2004; Warrant 2008). An interesting difference between the two genera is that while *Provespa* swarms emigrate at night (Matsuura 1999), *Apoica* emigrates during the day (Hunt et al. 1995).

### 2.6.4 Small Body Size

The adults of most New World IF wasps are medium (~1 cm) to large (2+ cm) in size. Most SF species tend to be smaller, with a number of species very small indeed. Analysis (Fig. 2.4) shows that *Polistes* spp. are on average the largest polistine wasps and are significantly larger than *Mischocyttarus* ($t$ = 14.4; $p$ < 0.001). *Mischocyttarus* spp. in turn are significantly larger than the epiponines ($t$ = −7.35; $p$ < 0.001). In fact, 98% of *Mischocyttarus* species are smaller than the average-sized *Polistes*, and 78% of the epiponine species are smaller than the average *Mischocyttarus*. Thus it is clear that in the New World the SF polistines are significantly smaller than are the IF species. Karsai and Wenzel (1998) came to the same conclusion based on head widths and suggested that small body size may have evolved repeatedly in different epiponine lineages.

What factors might favor smaller body size in the SF than in the IF? Several possible explanations come to mind.

1. *More workers per unit of resource*. Smaller worker size allows more workers to be produced from a given amount of resources, enabling in turn a greater increase in colony size (Karsai and Wenzel 1998; Bourke 1999).
2. *Escape from competition for food*. Another hypothesis is that small body size evolved in response to competition with larger-bodied independent founders by enabling the exploitation of smaller prey. If this is true, it begs the question of how the move to swarm founding enabled this.

   Neither of these hypotheses explain why IF species have not also evolved smaller body size.

   The following explanations avoid this shortcoming.
3. *Mode of defense against natural enemies*. It may be that for the modest-sized colonies of the IF, large body size is maintained by the need for an effective stinging defense against vertebrates. In contrast, the larger colonies of the SF can

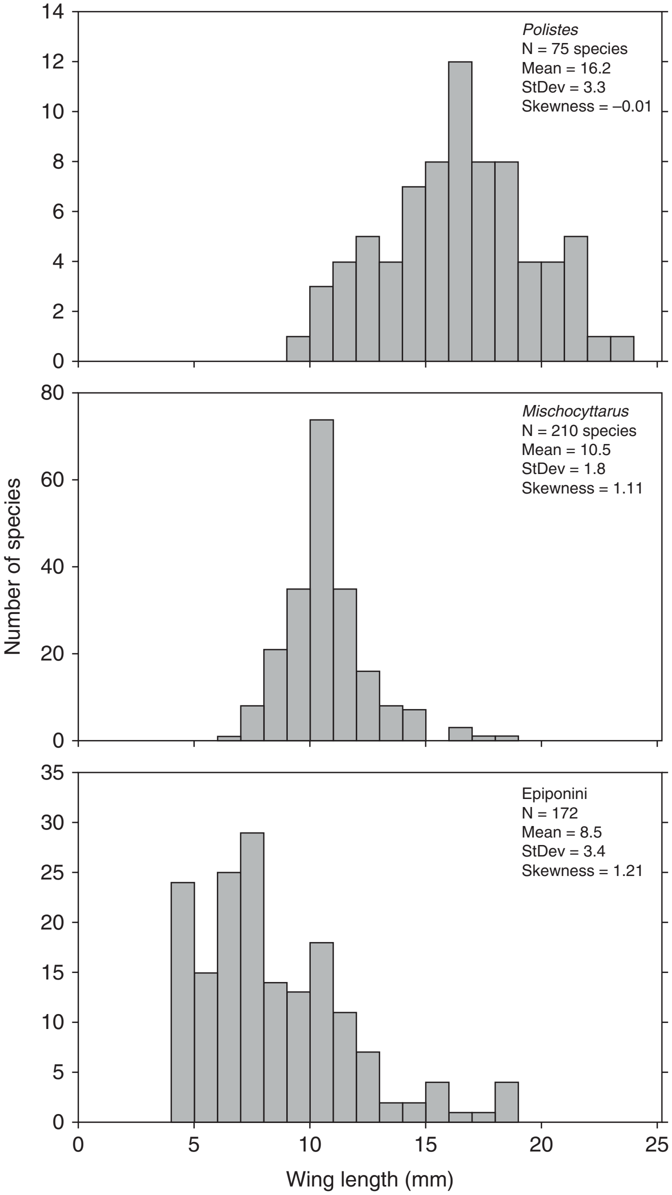

**Fig. 2.4** Wing lengths of New World polistine wasps. Shown are the frequency distributions of wing length for each of the three taxa. Where data were available for two or more subspecies, only one entry was made for the species. Where a range was given, the middle value was used. (Data from: (Zavattari 1906, Bequaert 1938, Bequaert 1943, Bequaert 1944, Araujo 1945, Richards 1945, Araujo 1946, Araujo 1949, Richards and Richards 1951, Willink 1959, Naumann 1968, Richards 1978b, Cooper 1993, Silveira and Carpenter 1995, Mateus and Noll 1997, Cooper 1999, Raw 1999, Cooper 2000, Cooper 2001, Carpenter and Kojima 2002, Pickett 2003, Carpenter et al. 2004, Pickett and Wenzel 2007, West-Eberhard et al. 2010, dos Santos et al. 2015, Grandinete et al. 2015))

sting in larger numbers, making up for the reduced deterrent effect of individual stings by their smaller workers. Arguing against this scenario, on the other hand, is the fact that many small-bodied SF have quite small colonies (e.g., *Leipomeles*, some *Protopolybia*).

4. *Co-evolution with increased task complexity*. Small body size may have evolved in SF under selection for higher tempo of interaction and greater task complexity in larger colonies (Karsai and Wenzel 1998). Greater task complexity in large-colony species has been demonstrated (Karsai and Wenzel 1998; Jeanne 2003), but tempo has yet to be measured in a social wasp species.

One of the striking features of Fig. 2.4 is the increase in skewness in going from *Polistes* to the Epiponini, culminating in the strongly truncated size-frequency distribution shown in the latter group. Twenty-four species have wing lengths of 4 mm, but no species in the dataset is smaller than that. This suggests, first, strong selection for small size and, second, that 4 mm is a strict lower limit. What might impose such a limit? One possibility is that wasps smaller than this lack the size and mandible strength to collect and manipulate vegetable fibers into a nest. Whatever it may be, the sphecid genus *Microstigmus* appears to have escaped it. *Microstigmus comes,* for example, has a wing length of just 2.4 mm (Matthews 1968).

## 2.7 Conclusions

It can be argued that the IF and SF represent two discrete social syndromes, each characterized by a set of mutually stable traits (Bourke 1999; Jeanne 2003). This is especially the case for the mode of founding itself; no intermediates are known. Yet several of the other traits do not cleanly sort into one or the other of the groups, as the examples in Table 2.1 show. As more species in both groups are investigated with regard to such traits, we will begin to discern patterns in how they correlate with colony size, life-history traits, and phylogeny, and these in turn will lead to better explanations of how the SF may have evolved from their IF ancestors. There is a need for such studies of more species of SF, particularly those in the lesser-known genera and those with colony sizes overlapping those of the IF. *Ropalidia* deserves special attention, because it is the only genus containing members of both groups, suggesting that the key to how the transition was made may be more apparent than in the Epiponini (Henshaw et al. 2004; Henshaw et al. 2015).

In addition to colony size and body size, the IF and SF differ in certain life history traits. One example is the significant negative correlation across all social wasps between mean worker lifespan and colony size (Toth et al. 2016). Another is the ratio of worker lifespan to egg-to-adult development time for workers, a strong determinant of the rate of colony growth (Richards and Richards 1951). Both appear to be significantly lower in the SF than in the IF. As an aside, it is striking that in the few species we have data on, development time exceeds the mean worker longevity, refuting the Richardses' assertion that the length of life of workers must exceed the average developmental period, or true social life is not possible (Richards and

Richards 1951) (p. 120). This dictum may apply to the crossing of the threshold from solitary to eusocial life, but not to workers in eusocial colonies, where the more relevant requirement is that a worker's contribution to the colony during her lifetime must be sufficient to rear the equivalent of her replacement; anything above that, and the colony will grow in size. Unfortunately, we have data on these and other life-history traits for too few species to know how they correlate with colony size, body size, or the swarm-founding habit. Data on these and other aspects of life history for both IF and SF species would be very useful, as would comparative analyses of rates of work and per-worker lifetime contributions to colony productivity for both groups.

The solution to such multi-faceted puzzles will depend on the creative thinking of future vespidologists to refine and expand these ideas and others into testable hypotheses.

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