THE NATURE AND EVOLUTION OF SWARMING IN TROPICAL SOCIAL WASPS (VESPIDAE, POLISTINAE, POLYBIINI)

M.J. WEST-EBERHARD

Smithsonian Tropical Research Institute, Balboa, Panamá
(Mail : Escuela de Biología, Universidad de Costa Rica,
Ciudad Universitaria, Costa Rica, Central América)

SUMMARY

Absconding (evacuating) swarms of social wasps following damage to nest or brood are more likely when the brood is young. Reproductive (fissioning) swarms in *Metapolybia aztecoides* occur during periods of much competition among queens. When a well-developed queen or group of queens is present nest enlargement rather than swarming may follow peaks of female production. In times of worker shortage neither nest enlargement nor swarming occurs. Seasonal swarming is reported in some species from 5° - 20° N. latitude, and from 12° - 35° S. latitude. Preparations for swarming include regrouping, cessation of nest building, unusual readiness to fly when disturbed, buzzing runs, trail marking, and, sometimes, brood cannibalism, aggressive begging, new nest initiation, and temporary aggregation along the swarm route. Old workers serve as scouts. Swarming individuals independently search for scent marks, with efficiency probably improved by use of prominent landmarks, conservation of direction and altitude between marks, and close spacing of marks at turns. Two possibly intergrading modes of trail following distinguish «diffuse» and «clumped» swarms. The trail pheromone is probably derived from sternal gland secretions originally important in dominance and territoriality, and subsequently used as «assembly» pheromones, orientation cues, recruitment signals, and (finally) markers guiding long migrations. There may be some co-evolution of pheromonal trail marking by swarming females and that of conspecific males. Honeybee swarming, like wasp swarming, is associated with periods of marked intracolony reproductive competition, whose onset is timed via regulation of queen rearing.

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RESUMEN

La naturaleza y evolución del enjambrazón en las avispas sociales (Vespidae, Polistinae, Polybiini)

En las avispas sociales los enjambres de abandono del nido después de algún daño al nido o a su cría son más frecuentes cuando la cría está joven. Los enjambres reproductivos (fisión de la colonia) en *Metapolybia aztecoides* ocurren cuando haya much a competencia entre las reinas. En el caso que hayan presentes una o varias reinas bien desarolladas, la extensión del nido en vez de la enjambrazón puede seguir la producción de un grupo grande de hembras adultas. Durante las épocas de escasez de obreras no ocurre ni formación de enjambres ni extensión del nido. Enjambres estacionales se han descrito en algunas especies entre las latitudes 5° N. y 20° N., y 12° S. y 35° S. Los preparativos para enjambrar incluyen reagrupamiento sobre o cerca del nido ; paro de construcción ; tendencia al vuelo con poco estímulo ; carreras cortas y rápidas sobre el nido ; establecimiento de un camino marcado con feromonas ; y, a veces, canibalismo de la cría, solicitación agresiva de alimentos, comienzo de construcción del nido nuevo, y agrupación en la ruta establecida para guiar el enjambre. Las obreras viejas toman el papel de guias. Cada individuo sigue la ruta buscando las pistas químicas, con mejor resultado por el uso de puntos sobresalientes, por conservar la misma altura y el mismo sentido entre puntos marcados, y por la aplicación de marcas adicionales donde voltea la ruta. Existen dos modos de seguir la ruta (con posibles formas intermedias) : enjambres difusos, y enjambres agrupados. La feromona utilizada para guiar enjambres es probablemente derivada de sustancias producidas por glándulas esternales originalmente importantes en comportamiento de dominancia y territorio, y después usadas como feromonas de agrupamiento, como pistas de orientación, como atrayentes a nidos nuevos, y, finalmente, para marcar la ruta de migraciones largas. Puede haber co-evolución de feromonas de enjambrar con las usadas por machos de las mismas especies para marcar rutas de patrullaje. Los enjambres de abejas son en muchos detalles semejantes a los de avispas, siendo también asociados con competencia reproductiva marcada, cuyo comienzo se coordina por regular la producción de reinas.

INTRODUCTION

One of the most distinctive behavioral characteristics of the large-colony tropical social polybiine wasps is the ability to found nests by swarming. That is, movements between old and new nest sites are effected by the coordinated synchronous migration of large numbers of individuals including both workers and queens. Among the social insects only the tropical polybiine wasps and the highly eusocial bees (*Apis* species and stingless bees,

Meliponini) are said to swarm, although the fissioning and migration of certain ant colonies (e.g., army ants) are parallel phenomena. Among the 35 currently recognized genera of social wasps (see Richards, 1978) all except seven are known or believed likely (as Polybiini) to found nests in swarms. The seven non-swarming genera include the Vespinae (yellow jackets and hornets), *Polistes*, and four primarily tropical Polybiine genera similar to *Polistes* in usually building unenveloped combs : *Ropalidia, Parapolybia* and *Belonogaster* in the Old World ; and the primarily neotropical genus *Mischocyttarus*. In these genera nests are sometimes initiated by groups of females which, especially if a former nest was located near the site, may be quite large and loosely referred to as a «swarm» (see below). However, there is so far no unequivocal evidence for swarming (synchronous, coordinated migration) in any of these «non-swarming» genera.

The swarming behavior of wasps has only recently attracted the attention of investigators. Naumann (1975) was the first to describe the abdominal «dragging» behavior along the route followed by swarms, and Jeanne (1975a, 1981) has experimentally confirmed Naumann's conclusion that the swarming wasps follow a scent trail made by applying the secretion of an abdominal gland to «dragged» (rubbed) surfaces. Two kinds of swarms have long been distinguished (e.g., see Richards and Richards, 1951) : *absconding* (secondary, or evacuating) swarms, produced when the nest is abandoned following some catastrophe (such as predation or other damage to the nest) ; and *reproductive* (primary, or fissioning) swarms, produced when a part of the adult population of a colony leaves to begin a new nest. Although the two kinds of swarming entail much similar behavior (e.g., chemical trail marking by scouts, and coordinated leaving of the original site), there may be important differences between them (e.g., with regard to migration distance, preparations for swarming, and swarm composition). The majority of observations so far available deal with either induced or naturally absconding swarms, or with migrating or recently settled swarms of unknown origin. *Seasonal* swarms occur in some species, and can involve both absconding (nest abondonment) (see Naumann, 1970) and budding (departure of only a portion of the colony adults) (Richards, 1978, after Rodrigues, 1968).

This report is based on the few published reports of swarms and swarming behavior, as well as on my own observations of swarming and related biology in 15 Polybiine species (Table I).

Table I – Species observed, and localities

Tabla I – Especies observadas y localidades

Species	Locality
Brachygastra augusti (de Saussure)	Cali, Colombia
Leipomeles dorsata (F.)	Panama, Barro Colorado Island
Metapolybia aztecoides Richards *	Cali, Colombia
Parachartergus apicalis (F.) *	Near San Jose, Costa Rica
Parachartergus colobopterus (Lichtenstein)	Gaira, Madgalena, Colombia
Polybia diguetana R. du Buysson	San Antonio de Escazu, Costa Rica
Polybia ignobilis (Haliday)*	Cali, Colombia
Polybia liliacea (F.)	Puerto Viejo, Meta, Colombia
Polybia raui raui Bequaert*	San Antonio de Escazu, Costa Rica, & Chiriqui, Panama
Polybia scrobalis pronotalis Richards	Cali, Colombia
Polybia sericea (Olivier)	Puerto Viejo, Meta, Colombia
Stelopolybia areata (Say) *	San Antonio de Escazu, Costa Rica
Stelopolybia hamiltoni Richards *	San Antonio de Escazu, Costa Rica
Synoeca surinama (L.) *	Puerto Viejo, Meta, Columbia

* Species in which swarm movement observed by the author. Colonies of other species listed observed either while preparing to swarm, after nest initiation, or performing other swarm-related behavior in the text. Specimens identified by O.W. Richards and deposited in the British Museum of Natural History, London.

* Especies en las cuales el autor observó el movimiento de enjambrazón. Colonias de las otras especies citadas observadas ya sea cuando se preparaban a enjambrar, despuès de la iniciación del nido, o desarollando comportamiento discutido en el texto.

THE DECISION TO SWARM : CONDITIONS PRECEDING SWARMING

Absconding swarms, with nest abandonment, can follow a variety of kinds of catastrophes which befall colonies. Those observed include predation by army ants (Richards and Richards, 1951 ; Naumann, 1975 ; Chadab, 1979, pers. obs. of *Metapolybia aztecoides*) ; predation by animals capable of damaging the nest envelope (e.g. bats : Jeanne, 1970 ; pers. obs. of damage by an unknown predator of *Synoeca surinama* in Meta, Colombia) ; invasion by insect parasitoids (e.g., phorid filies – see Schremmer, 1972) ; overheating (pers. obs. of *Metapolybia aztecoides*) ; severe damage to a nest due to a landslide provoked by heavy rainfall (pers. obs. of *Polybia raui*) ; etc. A recently abandoned nest of *Polybia liliacea* contained termites in the nest carton near its attachment to the supporting branch and no other obvious sign of damage or predation. In short, many kinds of damage are associated with nest abandonment. But little is known about how the wasps decide to migrate rather than wait or repair damage. Evidently the odor (or presence of only a few individuals) of army ants is sometimes sufficient to induce nest abandonment (Chadab, 1979). On the other, Jeanne (1970) observed that

large colonies of *Polybia sericea* would calmly repair damage by predatory bats, abandoning the nest only when attacked on more than one successive night. I have repeatedly removed large sections of nest envelope from observation nests of *Metapolybia* and *Synoeca* without provoking swarming. One variable which seems to affect readiness to abscond is the composition of the brood. I have noticed that colonies with few pupae and large larvae (a large proportion of eggs and small larvae) seem more likely to abandon manipulated nests. For example, the sudden shining of bright light for only a few seconds on a newly founded comb of *Synoeca surinama* caused the wasps to immediately stop building and begin swarm preparations. They abandoned the nest (which contained eggs and a half-completed envelope) two days later. Chadab (1979) also noted an unusual readiness to abscond in an *Apoica* colony whose brood consisted primarily of eggs in recently vacated cells. Forsyth (1978) documented this tendency in a study of *Metapolybia azteca* in Costa Rica : seven of 41 colonies absconded within a day after the capture of all adults for marking and subsequent release. All seven nests contained few or no larvae, although the colonies were in different stages of development (three were newly founded ; three were mature, male-producing colonies ; and one lacked brood following dry-season cannibalism). This effect of brood composition on readiness to swarm makes sense in terms of natural selection : there is less to be gained by short-term adherence to a nest which is empty or contains only brood which would require many days to rear, whereas staying with a large nearly mature brood for even a day might pay off in the form of many additional young adults. Furthermore, the presence of only very young brood or many empty cells often reflects reproductive periodicity which can affect the advantage of swarming in other ways : a young brood often follows a large emergence of adults, and the presence of a large proportion of young individuals in a swarm enhances the likelihood that it will survive the long period (4-6 weeks) before additional workers can be produced. High worker mortality often produces a crisis during this period (see West-Eberhard, 1981), and repeated absconding at short intervals (or just preceding a large emergence of adults when reproduction is pulsed) could lead to colony extinction. It is therefore of interest that Naumann (1970) observed what he believes to be «enforced» reproductive periodicity in seasonally swarming tropical species, with adults cannibalizing intermediate-aged brood so that imagoes are produced synchronously. Swarms then follow soon after large emergences.

Reproductive swarming conditions are difficult to document, because it is difficult to predict when colony fission is likely to occur. Even in seasonally swarming species, not all colonies produce swarms, and knowing that a swarm has departed requires either direct observation, or extensive marking and censusing of individuals. Seasonal reproductive swarming in *Metapolybia*

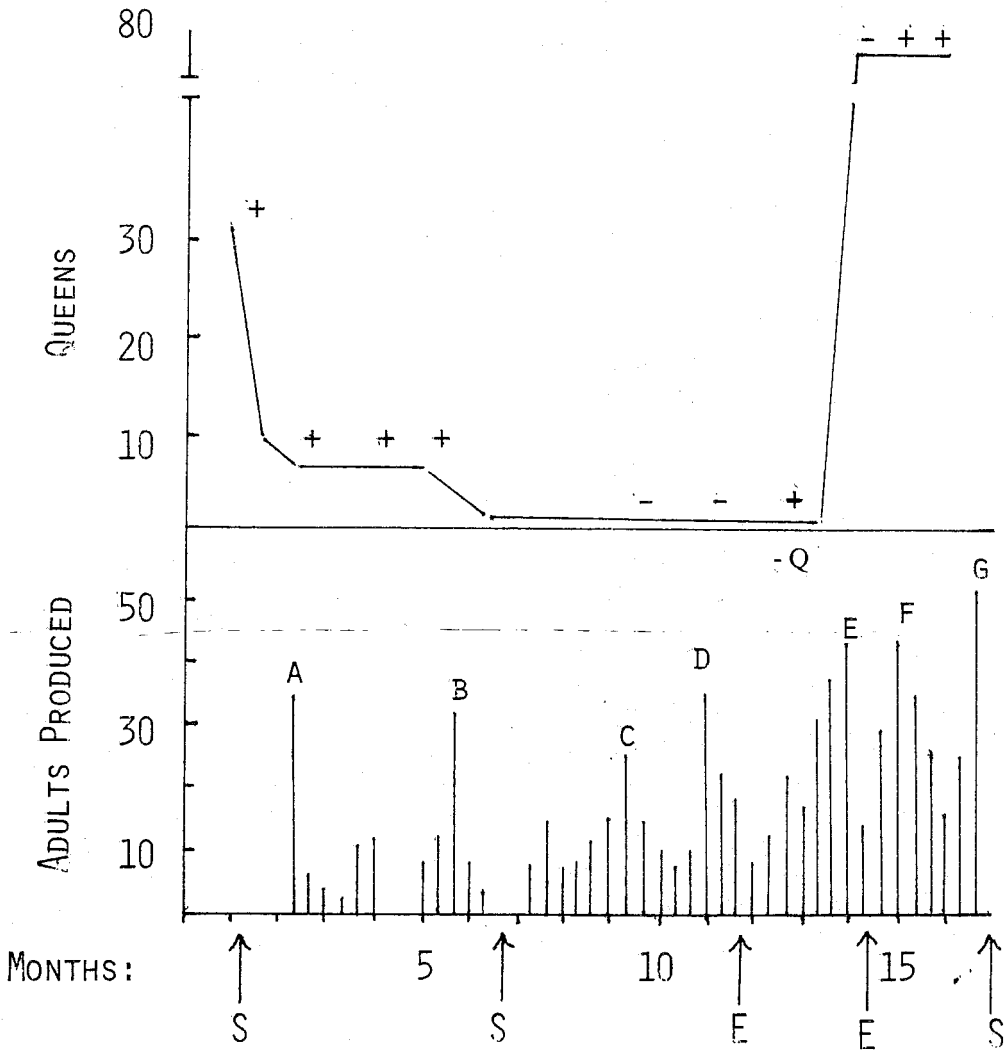

Fig. 1 – Timing of reproductive swarm emission in relation to adult emergence and queen agressiveness in a colony of *Metapolybia aztecoides*. Letters denote peaks (a-g) of production of adult females, swarm production (S), nest enlargement (E), and date of disappearance of single queen (-Q). Symbols + and - denote presence (+) and absence (-) of marked aggressiveness among queens.

Fig. 1 – Tiempo de emisión de reproductoras durante la enjambrazón en relación à la emergencia del adulto y la agresividad de la reina en una colonia de *Metapolybia aztecoides*. Las letras denotan picos (a-g) de producción de hembras adultas, producción de enjambre (s), agrandamiento del nido (E), y fecha de desaparición de la única reina (-Q). Símbolos + y - denotan la presencia (+) y ausencia (-) de agresividad marcada entre las reinas.

azteca Araujo and *Polybia occidentalis* (Olivier) in a markedly seasonal region of Costa Rica is associated with other seasonally synchronized events such as male production, aging of established queens, brood cannibalism, and aggression among young queens (Forsyth, 1978). The precise order in which these events occur, and the nature of and non-swarm-producing colonies, are not known. It is therefore of interest to examine the pattern of reproductive swarming observed in a colony of *Metapolybia aztecoides* whose history I followed closely for 18 months. In Cali, Colombia (4° N latitude) *M. aztecoides* shows no obvious reproductive seasonality. Furthermore, no males were produced by this colony or its observed descendents during the 18 month observation period. However, 905 females were produced and marked. Colony fission (swarming with division of the colony into more than one group) occurred three times :

1. Nine days after colony foundation, 17 of the 35 founding queens left with an unknown number of workers. When pre-swarming activity (see below) was first observed, along with intensive fanning (cooling) activity, I placed a palm leaf on a roof above the nest to provide shade. When next observed, both swarming preparations and fanning had stopped among the remaining wasps, but a swarm had already departed. Thus colony fission apparently occurred in response to temporarily unfavorable conditions (overheating), with some wasps leaving and others staying.
2. Five months after colony foundation, half (3) of the remaining six foundress queens left with a large number of workers (110 had been produced), leading to a severe shortage of workers (only nine present prior to the next synchronous emergence). Swarming occurred 10-15 days after the peak of a large emergence, when the population of adults was the highest it had been since nest initiation.
3. Sixteen months after nest foundation, during the second of two major peaks of female production following a nest enlargement (see Fig. 1), two swarms, containing 200-250 and 92 individuals, abandoned the original nest and founded new nests less than 30 m. away.

Although the first swarm may have been an abortive absconding swarm (including only part of the colony because the nest was shaded), aggressiveness among queens was occurring and may have contributed to their readiness to fission. This nest was not obviously damaged until after the adults had absconded, when it quickly deteriorated as if chewed by a mouse. Just prior to swarming the envelope removed (routinely) to facilitate observation was not repaired by the wasps. It is possible that envelope removal, although not causing swarming during the previous 16 months, triggered swarming at this time of unprecedented population size and, also, brood immaturity following massive emergences (Fig. 1). It is also possible that the two swarms left

independently of each other, the first as a «reproductive» swarm and the second for some reason «absconding». (I was not present when the two swarms left). All three swarming events were preceded by brood cannibalism (eating of larvae) and marked aggressiveness among queens (bending threats, and vigorous «dancing» by workers – see West-Eberhard, 1978). Both instances of swarming in the mature colony followed massive emergences of adults (Fig. 1). The colony at those times was composed of unusually large numbers of adult females and unusually small numbers of large larvae and pupae. Pulsed, or cyclic, adult production is a common characteristic of swarm-founded colonies, especially in small-colony species. Adult emergence peaks occur because rapid comb construction and egg-laying by a swarm leads to synchronized emergence of adults followed by another round of (synchronous) egg laying. This cycle can persist for many months (see Fig. 1).

Although swarming in this colony followed peaks of adult production, not all peaks were followed by swarming. Analysis of the adult-production peaks *not* followed by swarming helps to further define the conditions leading to colony fission. Two peaks (d en a, Fig. 1) were followed by nest enlargement rather than swarming. In both these cases there was a notable absence of aggression among queens, following peak d because there was only a single well-developed (unchallenged) queen present, and following peak e because the large number of queens present were young, relatively undeveloped (having small ovaries), and not yet strongly competing (see West-Eberhard, 1981). The timing of events is also revealing : both swarming and nest enlargement occurred 10-15 days after emergence peaks, which corresponds to the time required for newly emerged females to show slight ovary development. If a dominant queen (s) is not present at that time, newly emerged *Metapolybia* females begin to lay eggs (see West-Eberhard, 1978).

These observations indicate that emergence peaks lead to colony fission indirectly, by causing a rise in the number of competing females (potential egg layers) on the nest. That is, reproductive swarming in *Metapolybia* is a product of reproductive competition involving newly emerged females rather than a simple consequence of crowding. When emergence peaks lead to nest enlargement rather than reproductive swarming, the young females (potential queens) play a disproportionately large role in enlarging the nest. Although 15-25 day-old females represented only 39 % of the adult population present following emergence peak d (Fig. 1) they made up 56 % of the females observed building the new comb. These females obtained pulp by tearing down the old envelope rather than foraging, and sometimes acted aggressive toward the monogynous queen when she visited the new comb. Building without foraging is a characteristical activity of young, somewhat ovary-developed, females and recently suppressed former queens (see West-Eberhard,

1981). Thus the activity of a newly-emerged female can be channelled either toward reproduction (and sometimes swarming) or toward enlarging the parental colony, depending upon the social circumstances in the colony soon after she emerges.

Some emergence peaks (a, c, and f) led to neither swarming nor nest enlargement. The newly emerged females simply became workers. In all these cases an established mature queen (c) or group of queens (a and f) was present, and the population of workers was low relative to the size of the colony. Following peak a there was can acute worker shortage due to the long delay in female production following nest founding, and all foraging was being performed by former queens. At peak c the crisis was less severe, but the adult population was low following a long period of low productivity after a swarm (Fig. 1). And at the time of peak f many would-be workers had become queens and were thus consuming foraged food rather than obtaining it. So emergence peaks in the presence of dominant queen(s) and worker scarcity lead to the production of workers without swarming or nest enlargement. This suggests that colony fission requires an abundant worker population in addition to reproductive competition among females. As already noted, swarming is associated with low populations of large larvae. Colony fission may prove predictable when peaks in the functional-worker/larva ratio coincide with peaks in reproductive competition among females.

Seasonal swarming occurs in many Polybiine wasps at intermediate latitudes (Table 2). So far little is known about the nesting cycles of these species. It is impossible to state whether extrinsic cues such as changes in daylength or humidity affect swarming, or whether synchrony is simply a consequence of marked seasonality in food availability and activity times leading to synchrony of brood production and (hence) swarming propensity. Seasonal swarming is not closely synchronized, but, at least in some regions, occurs during a 3-4 month period (e.g., see Machado, 1977).

PRE-SWARMING BEHAVIOR

Swarming is preceded by marked changes in the behavior of wasps at the nest. They are described below in approximate order of their occurence.

Pre-swarming pheromone release. The original stimulus to begin swarm preparations, at least in the case of absconding swarms, may be the release of a chemical alarm signal by disturbed individuals. This was suggested by a peculiar combination of circumstances while observing a large newly founded colony of *Synoeca surinama*. Directing very bright reflected sunlight on the comb (in order to film behavior) provoked synchronous strong alarm behavior.

Table II – Seasonal swarming in tropical social wasps (Polybiini)

Tabla II – Enjambrazón estacional en las avispas sociales tropicales (Polybiini)

Species	Months	Season	Place	Latitude	Source
Brachygastra lecheguana (Latr.)		early dry	Jalisco, Mexico	16° - 20° N	Buysson, 1905
Polybia occidentalis (Olivier)	Nov.-Jan. May-Aug.	mid rainy, early dry rainy	Guanacaste, Costa Rica	10°40' N	Forsyth, 1978
Metapolybia azteca	Oct.-Dec.-Jan. May-June	late rainy, early dry rainy	Guanacaste, Costa Rica	10°40'	Forsyth, 1978
Metapolybia pediculata Sauss.	Aug.-Sept.		Panama	9°10'N	Rau, 1933
Protopolybia acutiscutis (Cameron)	May-June	late dry	Panama	9°10'N	Naumann, 1970
Epipona tatua (Cuv.)	late Dec. mid June	early dry	Cayenne, Fr. Guiana	5°N	Lacordaire, 1838
Polybia ruficeps Schrottky	Sept.-Oct.	dry	Mato Grosso, Brazil	12°50'S	Richards, 1978
Polybia occidentalis (Olivier)	May-June Sept.-Oct.	dry	Rio Claro, Brazil	22°25'S	Machado, 1977
Parachartergus apicalis (F.)	April-May	winter	Alto Parana, Paraguay	24° - 25° S	Bertoni, 1912
Polybia occidentalis		late summer	Mercedes, Uruguay	33°S	Brethes, 1903
Polybia scutellaris (White)	Oct. Nov.-Dec.	early summer late dry	Argentina Rio Claro, Brazil	34°55'S 22°25'S	Bruch, 1936 Rodrigues, 1968

Several individuals immediately began performing buzzing runs and loop flights (see below) which were taken up by others within a short time, and all building activity ceased. My face was close to the nest when this occurred (protected by a head net) and I soon felt a stinging irritation in both eyes which became watery and swollen. This sensation (an allergic reaction) was relieved when I moved away from the nest. Although close inspection of alarmed individuals revealed no special postures or extruded stings suggesting pheromone release, I believe that a diffusable alarm substance was being produced which I (being hypersensitive to wasp tissues and venoms) was able to detect. Naumann (1970) also believes that a pre-swarming alarm substance may be released by buzzing runners in *Protopolybia* and has noticed that they sometimes hold the abdomen high «extended and noticeably recurved or decurved as if releasing a substance» (p. 122).

Regrouping. If the nest has been destroyed or attacked (e.g., by army ants) the resident adults quickly abandon the nest and then form a cluster close to the nest site. I have observed this in an absconding colony of *Polybia raui* whose nest was severely damaged when rain caused a landslide in the roadbank where it was attached to a root ; and it is common when nests are destroyed by man. Chadab (1979) observed regrouping following 19 army ant raids on a variety of neotropical polybiines, and found that regrouping was completed an average of 72 minutes after nest abondonment (range 21-190 minutes). Jeanne (1981) saw profuse abdominal «dragging» (scent marking) of the regrouping site in *Polybia sericea*. Dragging ceased once the temporary cluster was formed, then began again during trail marking (see below).

Buzzing runs (called «breaking behavior» by Naumann, 1975). Excited running by a few to many individuals is the most characteristic and widespread pre-swarming behavior noted by observers (e.g. Bruch, 1936 ; Naumann, 1970 ; Jeanne, 1975a ; Forsyth, 1978). It is this behavior on the nest that is the first definite cue that swarming is likely to occur. When absconding swarms are provoked by a sudden event (such as the shining of a bright light on the nest) buzzing runs are an immediate reaction which continues with increasing intensity until the wasps leave. They were first mentioned by Bruch (1936), who saw wasps running and turning («volteando») in a colony of *Polybia scutellaris* before it swarmed. Some wasps (probably scouts) returning to the nest run erratically about, occasionally engaging in brief mouthpart contact with encountered nestmates, then suddenly take flight. Sometimes the wings are raised, and at high intensity the wings are buzzed, and the running wasp seems to tumble about crazily bumping into other. In *Synoeca surinama* workers performing buzzing runs showed typical «offering» behavior (mandibles raised, antennae motionless) accompagnied by rapid lateral shaking and followed by mounthpart contact with encountered nestmates.

At low intensity this behavior seems to cause no reaction in the wasps on the nest, but at high intensity it sometimes causes clusters to break up and activity to rise, with an increasing number of wasps performing similar runs.

Buzzing runs are similar in apperance and function to several other kinds of behavior in social wasps. The «parasite alarm» of *Polistes* (West-Eberhard, 1969) and many other genera (observed by me in *Polybia emaciata, Polybia diguetana, Metapolybia aztecoides,* and *Synoeca surinama* ; and by Naumann, 1970, in *Protopolybia acutiscutis*) resembles pre-swarming buzzing runs in that the performer moves erratively around the comb jerking near nestmates, and often flipping the wings, sometimes causing others to do the same. The parasite alarm movements are more rhythmic than the buzzing runs, and can almost always be associated with the presence of some brood parasite, such as an ichneumon wasp or phorid fly. However, the behaviors are so similar that they are sometimes confused until the context of the behavior can be ascertained. If foraging continues and there is little change in intensity or numbers performing buzzing runs they probably represent anti-parasitoid behavior. As noted by Naumann (1970, p. 122) buzzing runs sometimes occur in response to severe disturbance (such as seizing an individual with forceps) without leading to swarming. It is unknown how many individuals (or which ones) must be stimulated to provoke swarming. Buzzing runs are remarkably similar to the «Schwirrlaufen» performed by swarming honeybee scouts (Lindauer, 1955 ; Seeley et al., 1979), which similarly rise in frequency prior to swarm liftoff (Seeley et al., 1979). All of these behaviors incorporate either fast runs, wing buzzing, bumping nestmates, rapid shaking, or brief mouthpart contact or some combination of these elements. And all seem to stimulate movement and/or flight in nestmates.

Because this behavior is at first performed by a few individuals who repeatedly leave the nest and return loadless, it seems likely that these are the individuals («scouts») active in choosing a new nest site and/or marking the trail followed by the swarm. The suspicion that this is the case is reinforced by the observation that in *Metapolybia* a disproportionate number of females performing buzzing runs and repeated trips away from the nest are old foragers – the females most familiar with the surrounding area and most prone to searching activities away from the nest. During the hour just prior to swarming in a colony of *M. aztecoides* only 15 (16.7 %) of the 92 females present performed buzzing runs. Nearly one third of these females were known foragers more than two months old, even though this age class made up only 10 % of the population present. The remainder were younger females of unknown foraging history. None was a queen. Similarly, during two hours of observation on the first day of swarming preparations following predation on a nest of *Synoeca surinama*, only eight (7,6 %) of the 105 females present

performed buzzing runs. All were old (72 days or more) members of the swarm which had founded the nest nine weeks before. None of the 77 younger offspring of that colony (females 1-21 days old) performed buzzing runs. Forsyth (1978) likewise found that marked wasps performing buzzing runs prior to swarming in *Polybia occidentalis* were known foragers. He also observed that these individuals were active in initiation and construction of the new nest, althought they sometimes switched to other (non-foraging) roles once the nest was established.

Unusual readiness to fly when disturbed. Once buzzing runs have runs have started, events, (such as envelope removal or marking of individuals with paint) usually causing no reaction, lead instead to flying off the nest (observed in *Synoeca surinama* and *Metapolybia aztecoides*). Increased alertness and readiness to fly may be a consequence of the buzzing runs, which (as just described) resemble other kinds of alarm behavior perhaps leading to readiness to attack or chase an intruder.

Loop flights. During the pre-swarming period many individuals take flight briefly, then return to the nest where they perform buzzing runs or simply land. Forsyth (1978, p. 139) has described these short «loop flights» in *P. occidentalis* as follow : «relatively slow flights of circular motion with the wasp usually facing the nest and looping in a radius of 0.5 to 2 meters». As the wasp hovers near the nest during a loop flight nestmates in that region often take flight and begin performing loop flights themselves.

Hovering near the nest has been observed to stimulate flight in several contexts other than swarming. For example, in *Polybia diguetana* R. du Buysson females performed loop flights near the nest entrance for more than an hour while a phorid fly (a common brood parasitoid) was on the nest. Their behavior, which also included buzzing runs, was distinguishable from pre-swarming behavior only because normal foraging and building continued, and individuals returning to the nest from long flights never participated (as would swarm «scouts»). Individuals on the nest sometimes walked forward or flex when approached by a hovering nestmate. Machado (pers. comm.) reports that loop flights occur in *Polybia paulista* when flying aggregations of «lambe-olho» flies (Diptera, Chloropidae) occur near the nest.

In *Metapolybia aztecoides* loop flights occur without relation to either distance and hover facing the nest, causing others near them to take flight and perform similar flights until all individuals present (including the usually passive queens) have left the nest. Some fly about the area as if searching ; and although they appear aggressive and alarmed they do not sting even objects within a few centimeters of the nest. Eventually all return, and normal activity is resumed. False swarming creates a frightening airborne mass of wasps near the nest, and migh function to intimidate some predators. However,

it is not clearly associated with any threat to the nest, and I believe it may sometimes be initiated by the slow hovering approach of heavily laden foragers. (A small false swarm occured in *Parachartergus apicalis* when a strong wind forced approaching wasps to hover before the entrance, causing others to take flight as in the false swarming of *Metapolybia*). Whatever the adaptive significance (if any) of false swarming, just as in true swarming, hovering loop flights seem to stimulate leaving the nest even by normally non-flying individuals (queens, and newly emerged females). Loop flights observed in *Polybia raui* increased dramatically just prior to liftoff of the swarm (Fig. 2). Forsyth (1978), p. 140) believes that leaving the nest is «relatively directional» and «appears to be guided by the looping activity of scouts». I have noticed marked changes in the shapes and positions of clustered wasps prior to liftoff in *P. raui* and *P. liliacea*, which appear to be directional in nature (e.g., rotation from one side of the nest to another ; and increased compactness of a regrouped cluster accompanied by a bulging in the side toward the new nest site). The possibility that loop flights function in the initial orientation of the swarm merits further investigation.

Clustering on the surface of the nest. Naumann (1970) photographed this phenomenon in *Protopolybia acutiscutis* (Cameron) (Naumann's specimens were recently identified by O.W. Richards according to Jeanne, pers. comm. ; called *P. pumila* by Naumann, 1970) and I have observed it in an absconding colony of *Polybia liliacea* attacked by termites. In the latter case the clusters persisted throughout the day prior to swarming, sometimes changing position. At noon the day before swarming occurred (at 7:05 a.m.) the wasps were concentrated on the windward side of the large nest while dispersed on the opposite side, but 1.5 hours later the cluster had shifted to the opposite side although the wind direction had not changed. I attempted to see if the location of the rotating cluster could be used to predict the direction of the swarming, but could not discern the path of the trail at the time the swarm left. The nest was about 10 m high in a tree and the thousands of circling wasps were soon lost to my view (see «liftoff, below).

Building arrest. Even if the wasps have not left the nest, one sign that it will soon be abandoned is the marked reduction or cessation of pulp foraging and additions to envelope and comb. I have noted this in *Metapolybia azracoides, Polybia liliacea, Polybia sericea,* and *Synoeca surinama.*

Brood cannibalism and aggressive begging. Eating of large larvae and pupae (but not eggs and small larvae) by workers occurred prior to both absconding and reproductive swarms in *Metapolybia aztecoides*, prior to absconding in *Synoeca surinama* (reproductive swarms were not observed in that species), and prior to swarming in *Protopolybia acutiscutis* (Naumann, 1970). Recently abandoned nests of *Polybia sericea* and *P. liliacea* contained

eggs and small larvae, but no large larvae or pupae. In a pre-swarming colony of *S. surinama* all brood abortion was performed by old workers ; young (1-21 days old) females did not participate, and showed no interest in eating larvae seized by the others (there were no females of intermediate age present). Although building activity stopped during pre-swarming activities as already described, foraging for food continues. In *Polybia sericea* I once observed strikingly aggressive solicitation by nest wasps of returning foragers during the four days prior to absconding. Returnees were literally mobbed and violently attacked by up to ten nestmates at a time. Wasps waiting on the envelope sometimes attacked slowly approaching foragers in the air and once desperately solicited from each other in fruitless frenzy when unable to locate a returning forager that had landed on a nearby leaf. Two attacked workers that were captured and dissected proved to be old (dark apodemes – see West-Eberhard, 1975) mated females with discolored spermathecae and signs of former ovary development. Two dissected attackers were both unmated young (light apodemes) females with undeveloped ovaries. The dissected individuals provide a possible explanation for the aggressiveness of solicitation observed : the attacked workers were «reserve» foragers – former queens that probably became workers during a shortage of workers as is known to occur in other species (see West-Eberhard, 1981). And the solicitors were very young females, perhaps too young (less than 10-15 days) to have begun foraging. Thus this colony may only recently have produced offspring females after absconding from a previous site leading to an acute shortage of foragers and inability to quickly enough bring food to meet the pre-swarming demands of non-foraging adults. This demand did seem associated with preparations to swarm : the same colony observed six days later at the new nest no longer showed aggressive solicitation of returnees although a large cluster of idle wasps was present. Aggressive begging was not observed in other pre-swarm colonies, perhaps because enough workers were present to supply the apparently increased demands of nestmates prior to swarming.

Trail marking. The «dragging» behavior, or rubbing of the ventral surface of the gaster on substrates at intervals between new and old nest sites, has been well-described by Naumann (1975) and Jeanne (1975a). So far it has been seen in six of the 23 genera of «swarming» polybiine wasps, namely, in *Angiopolybia* (Naumann, 1975 ; Chadab & Rettenmeyer, 1979), *Leipomeles* (Naumann, 1975), *Stelopolybia* (Naumann, 1975 ; Jeanne, 1975a ; pers. obs. of *S. areata* and *S. hamiltoni*), *Synoeca* (pers. obs.), *Parachartergus* (pers. obs.), and in several species of *Polybia* (Naumann, 1975 ; Jeanne, 1981 ; Forsyth, 1978 ; pers. obs.). It presumably occurs in all swarming genera ; at least none have been known to coordinate swarm movement by any other means. The Richard's organ associated with production of the trail pheromone

is present in 16 of the 18 genera examined (Richards, 1978 ; see also Landolt and Akre, 1979 ; Jeanne and Post, in press). Of the two species (*Angiopolybia pallens* and *Leipomeles dorsata*) in which glands were lacking, one (*L. dorsata*) is known to perform abdomen dragging along the swarm trail (Naumann, 1975).

Jeanne (1981) reports that movies of dragging behavior in *Polybia sericea* show that the fifth gastral sternite is applied to the rubbed surface during dragging. He was able to induce swarming wasps to follow an artificial trail made by rubbing the glandular («Richards'organ») region of that segment on pieces of filter paper that were in turn placed along a row of stakes in the field. He (but not his assistant) can smell the Richards'gland secretion on leaves, and finds that it has a distinctive leatherlike odor.

Scent trails are apparently not used in very short (less than 20 m.) absconding swarms (Forsyth, 1978 ; Chadab, 1979 ; Chadab & Rettenmeyer, 1979 ; pers. obs. of *P. raui*), although the new nest site itself may be heavily marked. This is not surprising since wasps marking and following scent trails regularly fly several meters between marks. In Jeanne's experiment scent marks were placed four meters apart. Trails are sometimes diffuse in that different scouts mark different routes to the same site. (pers. obs. of *S. surinama*). Jeanne (1975a) has observed wasps dragging as far apart as 10 m. along a line perpendicular to the direction of swarm movement. Although previous reports do not state whether dragging occurred during incoming or outgoing trips to (or from) the old nest, or both, my observations of trail marking in *S. surinama* revealed that early in trail marking dragging occurred only on incoming trips. During that period outgoing wasps only followed trails, pressing the tips of their antennae against landing surfaces as described by Naumann (1970), Jeanne (1975), and Forsyth (1978). However, within an hour of liftoff I noticed that wasps were marking on outgoing trips as well.

Jeanne (1981) reports that in colonies that have not recently swarmed females have thick deposits of brownish viscous secretion over the Richards' gland. In recently migrated colonies, on the other hand, this substance is depleted, especially in older individuals. Richards (1978) states that in some collected colonies queens can be distinguished from workers by the greater accumulation of secretion over their Richards'gland, which he therefore believed might be a «queen substance» involved in maintenance of reproductive dominance within the colony (see below). Whatever its functions, the accumulation may simply be due to the often greater age of queens, and the fact that they do not participate in swarm trail marking (allowing for a greater accumulation of secretion) (see Jeanne, 1981).

Temporary aggregations along the swarming route prior to liftoff. Forsyth (1978) observed that *Polybia occidentalis* scouts form small aggregations

near the nest along the trail being marked. The positions of these aggregations eventually become fixed, and the loop flights (see below) are made between the old nest and the nearest aggregation, giving a strong directionality to the flights and causing the aggregation to grow as the short flights increase in frequency (see below).

Nest initiation prior to swarm arrival. Some species (*Polybia velutina* – Chadab, 1979 ; *Polybia sericea* – Jeanne, 1981 ; *Apoica pallens* – Naumann, 1975) at least sometimes begin construction of the new nest before the swarm arrives. In other cases observers at a new nest site have noted swarm arrival without previous building (e.g., in a *Synoeca* species, probably *septentrionalis* Richards, observed by R. Matthews and C. Starr in Costa Rica and in *Polybia scutellaris* – Bruch, 1936). In *Synoeca surinama* I saw some individuals carrying pulp along a swarm trail during the time that the main body of the swarm was passing my observation place, suggesting that building had already begun. Unfortunately I was unable to pursue the wasps across an anaconda-infested swamp to the new site.

The pre-liftoff preparations described above occupy from five hours to four days in the case of absconding swarms (Chadab, 1979). The average for 20 swarms representing a wide variety of genera raided by army ants was 20.7 hours (Chadab, 1979). As pointed out by Chadab (1979), one factor affecting the time required for absconding preparations is probably the amount of time required to find a suitable new nest site. The longest preliftoff time she observed (four days) was for a colony of *Polybia rejecta*, a species usually nesting in trees containing large colonies of ants (*Azteca*). The long preparation time may have reflected the difficulty of finding such a site.

SWARM MOVEMENT

Liftoff. Following the sudden rise in frequency of loop flights (Fig. 2) the wasps begin to leave the vicinity of the nest rather than return to it. It is difficult to pinpoint the exact moment at which this change in behavior occurs, because the loop flights are accompanied by longer flights (of varying length) away from the nest, and the loop flights themselves may lengthen with time (I was unable to document this possibility). The observer is only sure that liftoff has occurred when it is over : wasps seem to fill the air, and the number on the nest or in the regrouped cluster declines. Then, within a few minutes, they are gone, leaving only a few stragglers on the nest or broadly circling nearby.

Trail following. In all seven species whose swarm movement I have observed (Table I) wasps seem to follow the trail to the new site as individuals.

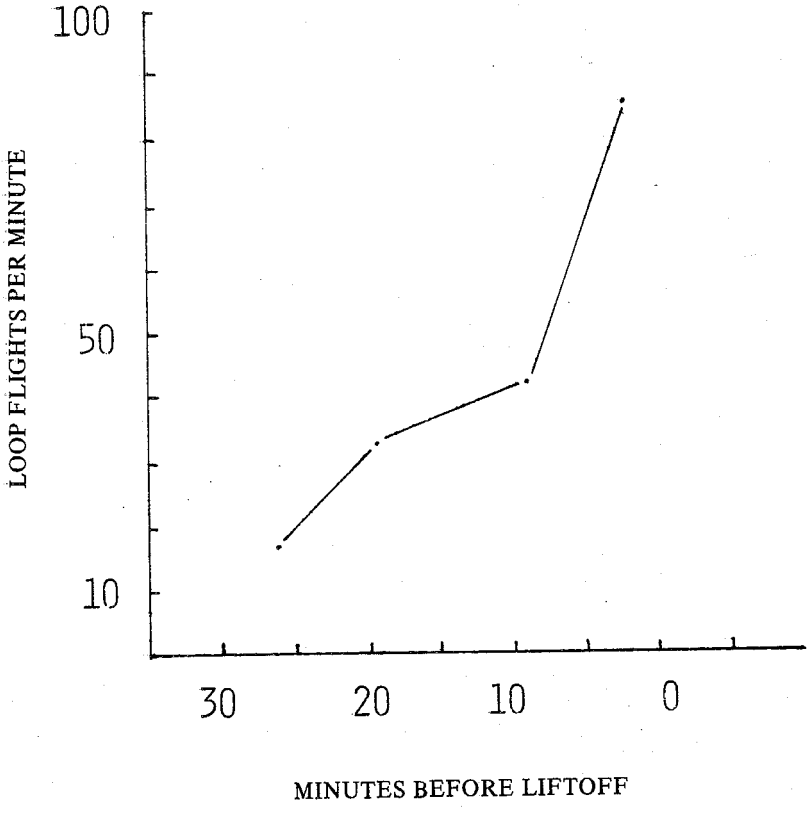

Fig. 2 – Frequency of loop flights prior to swarm liftoff in *Polybia raui*

Fig. 2 – Frecuencia de vuelos en forma de U anteriores a la elevación del enjambre en *Polybia raui*

That is, each female seeks landmarks one after another rather than following a straght line to the end ; and each wasp seems to fly and search for marked sites on her own, rather than in a group or in response to the movements of others. Although clusters may form along the route (see below) wasps do not form moving clusters in the air as do honeybees and the swarms of wasps are less compact. While a swarm of 10,000 honeybees occupies a «circular» volume about 10 m. in diameter and 3 m. high (Seeley et al., 1978) large diffuse swarms of wasps (e.g., *Stelopolybia* species) are commonly spread over an area up to 100 m long and 20-50 m wide. They sometimes take more than

more than 30 minutes to pass a given point, with stragglers visible for 30 additional minutes (pers. obs.).

The behavior of a trail-following wasp resembles that of a forager in that she visits and inspects vegetation and other objects somewhat erratically as she flies along. However, the following observed features of trail-marking and trail-following behavior probably help to facilitate directional movement :

1. Use of prominent landmarks. Scouts mark (and followers inspect) mainly conspicuous or protruding surfaces, e.g., the tops of shrubs, isolated plants in clearings, the apical leaf of a branch, or the top of a fencepost. An observer (and presumably a wasp) can predict which objects along a trail are likely to be used, and this consistency in choice must increase the efficiency of the trail.

2. Conservation of direction and altitude. Trail followers leaving a marked site tend to continue in the flight direction with which they approached it. If the next most prominent objects in an approximately straight line prove to be unmarked, the area soon fills with temporarily disoriented, searching wasps. As a result there is much disorientation and «piling up» of wasps at turns, whether they are to the side or vertical (e.g., up into the canopy of a tree, or down into a ravine). Turning disorientation is particularly obvious in very large swarms. A spectacularly large swarm of *Stelopolybia areata*, containing uncountable thousands of wasps (Jeanne, 1975b, estimated the adult population of a colony of this species at 21,800) occupied an area only 2-3 m wide when moving along a straight path. However, when forced to turn to move past a house, searching wasps were spread over an area 50 m wide. Disoriented individuals must sometimes be permanently lost. These two behaviors – use of prominant landmarks, and conservation of direction – mean that swarming wasps readily follow clear topographical features such as fencelines, trails, roadcuts, and the edges of clearings (noted by Jeanne, 1975a in *Stelopolybia areata* ; pers. obs. of *Synoeca surinama*).

3. Close spacing of marked sites at turns. The abdomen rubbing activities of scent-marking wasps are particularly frequent at turning points. This must serve to reorient searchers and «anchor» them to the point where the search for the next mark must begin, thus helping to reduce turning disorientation.

Clumped swarms. Some species (*Polybia ignobilis, P. raui*, and *Parachartergus apicalis*) at least sometimes form temporary, compact clusters at intervals along the the swarm route. Clusters are spaced about as far apart as the scent-marked sites of other species, and occupy similar kinds of sites. As the swarm progresses the forward-most clusters grow, while those behind dissolve. A clumped swarm of *P. raui* was remarkable for the absence of scent marking, at least during the two hours it was observed. Although many wasps searched vegetation between four clusters, none rubbed its abdomen on

objects between cluster sites. When I placed the plant abandoned by one cluster in the path of wasps moving between two others they paid no special attention to it. And when a second site was abandoned, passing wasps were not attracted to leaves which had been covered with swarm females only minutes before. Thus, if the leaves at these cluster sites are initially chemically marked, they are no longer attractive when the wasps leave. Similarly, scent marking was very infrequent (1-2 times/observation hour) in a clumped swarm of *Parachartergus apicalis* even on a «difficult» route between two clusters (more than 50 meters, circumnavigating a tall building). However, the moving wasps behaved as if following a scent trail, most taking the same route, searching vegetation, and showing disorientation at turns. By contrast, a small diffuse swarm of *P. apicalis** scent-marked frequently. When successive clusters are closely spaced and within sight of each other, as the were in the *Polybia raui* swarm, wasps may not employ scent marks. Cluster sites are conscicuous (to me) because constant loop flights (26/minute in a 50-wasp cluster of *Parachartergus apicalis*) surround them with a cloud of moving wasps. This may facilitate visual orientation. There was no obvious scenting behavior (abdomen dragging or raising) at the site of a newly initiated, growing cluster of *Parachartergus apicalis*. Clumped swarms appear to progress much more slowly than do diffuse swarms. The approximate center (densest portion) of the large swarm of *Stelopolybia areata* moved an estimated average 17.5 meters per minute (1.05 km per hour), even when the 200 m timed path included two difficult obstacles (a deep ravine, and a house). An observer must keep moving quickly to follow such a swarm, whereas the clumped swarms I have observed, while not precisely timed, require several minutes or even hours to advance by one cluster (with 20 m the maximum distance I have recorded between cluster sites). Dissolving clusters, while a relatively slow mode of movement, may have the advantage of reducing losses due to disorientation.

Small short-lived cluster sometimes occur in diffuse swarms, and along the route between large cluster, in *P. apicalis*. Searching females seem attracted to leaves where others are sitting. Such «piling up» during diffuse swarm movement may have been a precursor of clumped swarming. Future research should reveal whether these two swarming patterns – clumped, and diffuse – are strictly species specific or situation dependent, and whether or not pheromones are employed differently in the two modes.

* Two somewhat divergent populations (species ?) were identified by O.W. Richards as *P. apicalis* (see Richards, 1978) : one at 1350 m (San Antonio de Escazu, hills S.W. of San Jose) with diffuse swarms and a truncated conical nest entrance ; and another at 1200 m (San Pedro de Montes de Oca, east of San Jose), with clumped swarms and a tubular nest entrance. Specimens are deposited in the British Museum (Entomology).

Overnight resting clusters. Diffuse swarms sometimes rest in compact clusters at night en route to a new nest site. Rau (1933) observed that a cluster of *Polybia emaciata* Lucas remained for two days on a wire not resembling a nest site on Orchid Island (Gatun Lake, Panama). Jeanne (1975a) followed the movements of a diffuse swarm of *Stelopolybia areata* in Mexico, and found that it moved 70-100 meters per day, resting as a cluster on trees at night.

Length of migrations. As pointed out by Forsyth (1978) it would be of great interest in understanding the population structures of social wasps to know the migration distances of reproductive and absconding swarms. Unfortunately, such information is very difficult to obtain. I have repeatedly tried in vain to follow swarms of *Metapolybia aztecoides*, but have been frustated by their small size and the apparent diffuseness of their swarms. Even after two full days following the pre-swarming behavior of *Polybia liliacea*, a relatively large wasp, I was unable to follow the swarm, which diffused in a spectacular liftoff up into the canopy of a large tree and disappeared from view. It is sometimes possible to locate new nests of marked colonies after swarming. Two new nests of *Metapolybia aztecoides*, representing the entire population of an abandoned nest, were found within 20 m of the old site. An a marked colony of *Polybia sericea* relocated 250 m from its abandoned nest. Much longer migrations probably occur. The longest documented one I know of is 319 m in four days, by an absconding swarm of *Stelopolybia areata* (Jeanne, 1975a). The total migration may have been longer, as nest building had not begun when the observations ceased. It is quite common for absconding swarms to nest within a few meters of an abandoned site. Chadab (1979) lists the relocation distances for 17 colonies of seven polybiine species raided by army ants. All began construction only 0.3-2.0 m from the abandoned nest. Chadab notes that these values are likely to be somewhat unrepresentative because of the difficulty of finding more distant new sites. As suggested by Forsyth (1978) the upper limit for migration distance may be the foraging range of the foragers who act as scouts.

Behavior at the new site. I have only once observed the arrival of a swarm at a new nest site. In that case, a swarm of *Stelopolybia hamiltoni* moving into an enclosure (a cardboard box) many wasps were abdomen dragging the enclosure entrance as the swarm arrived, and many stood or walked nearby with abdomens raised and wings buzzing. These wasps were already aggressively defending the new site, in contrast to their passivity toward observers while en route.

The composition of swarms. Absconding swarms must often contain all of the adult female members of a colony. When this is the case, their age and caste composition would simply depend on that present when absconding

happens to occur. However, Forsyth (1978) reports that absconding by *Metapolybia azteca* following army ant raids sometimes leads to colony fission. The causes and consequences for colony composition of such splitting are unknown. Forsyth (1978) took advantage of the seasonal swarming habit of *Metapolybia azteca* and *Polybia occidentalis* in Costa Rica to estimate the composition of reproductive swarms. Since he observed predation destruction of nests to be low during swarming seasons, swarms collected at those times were presumed likely to be reproductive rather than absconding swarms. Ten dissected seasonal swarms of *M. azteca* contained 1-36 queens (mean = 11), and 16-174 workers (mean = 66.8). And ten dissected swarms of *Polybia occidentalis* contained 2-21 queens each (mean = 7.8), and from 69-350 workers (mean = 223.6). Males have never been observed to actually move along with a swarm, but there are several reports of males at very new nest sites. Ducke (1905) observed males in a nestless swarm of *Apoica pallida* ; and Richards (1978) found males with females from a very new nest of *Apoica flavissima* in the collection of the Museu Paulista (Sao Paulo, Brazil). He also cites Rodrigues (1969) as reporting males in a 45-day-old colony of *Polybia occidentalis* var. *scutellaris*, and speculates that they may have been present in the founding swarm. However, Machado (1977) has since found that the egg-to-adult developmental time in that species can be as short as 35 days, so it is possible that the males were produced there. I have observed males with a swarm of *Leipomeles dorsata* during the first day of nest construction, and at a pre-emergence nest of *Parachartergus coloboptera*, where their attempts to enter the nest resembled those of parasitic wasps and flies. Like parasitoids, these male were vigorously chased by attendant workers. In none of these cases is it known whether the males followed the swarm trail or arrived at the new site later.

THE EVOLUTION OF SWARMING IN WASPS

Explaining the origin of a complex coordinated activity like swarming can be approached via the comparative study of related forms. Fortunately, in the case of the social wasps there are several non-swarming genera (*Belonogaster, Ropalidia, Polistes, Mischocyttarus*, and *Parapolybia*) belonging to the same subfamily (Polistinae) as the swarming species. Observations of these genera offer a few clues regardind the possible origins of coordinated long-distance migration.

Functions of the sternal glands in non-swarming social wasps

The «Richards'gland» of the fifth abdominal sternite, source of the swarm trail pheromone, is the one morphological feature with which we can begin searching for homologies in non-swarming species. Examining the functions of the sternal gland secretions in these groups may provide clues as to the origin of trail marking. The Richards' gland is present in examined species of *Polistes* and *Mischocyttarus* (Hermann and Dirks, 1974 ; Landolt and Akre, 1979 ; Post and Jeanne, 1980 ; Richards, 1978 ; Turillazzi, 1979) while being absent or not easily distinguished in *Belonogaster* and *Ropalidia* (*Parapolybia* has apparently not been examined) (Richards, 1978). The function of the Richards'gland secretion in non-swarming species is unknown : it has never been isolated for identification or subjected to behavior experiments. However, in many non-swarming species the abdomen is frequently rubbed or wagged on the surface of the nest. One type of abdomen rubbing – stroking of the nest top and pedical by the terminal abdominal sternite – in *Mischocyttarus, Polistes,* and *Belonogaster* species, has been shown to involve application of an ant repellent substance produced by the van der Vecht's gland of the seventh abdominal sternite (Jeanne, 1972. See recent summaries in Jeanne, 1975c and Post and Jeanne, 1981). Some authors (e.g., Hermann and Dirks, 1974 ; Turilazzi, 1979 ; cf. Post and Jeanne, 1980) assume that the Richards'gland has the same function. However, two kinds of observations suggest another or additional function of abdomen rubbing and the associated glands : some species that rub the pedical with the abdomen are nonetheless readily invaved by ants (e.g., *Ropalidia cincta* – Darchen, 1976), and *R. cyathiformis* – Gadagkar and West-Eberhard, in prep) ; and abdomen rubbing occurs in situations that suggest an association with social dominance and territoriality rather than nest defense. For example, queens (but not workers) of *Ropalidia marginata* and *Polistes canadensis* stroke the nest surface with their abdomens as they move across the region containing eggs (at the bottom of the nest rather than near the pedical) ; and workers of an unidentified *Polistes* species abdomen stroked the bodies of newly emerged females (Raveret and Richter, 1980), a class of individuals often special objects of aggression and domination in social wasps (see West-Eberhard, 1978 ; Gadagkar and West-Eberhard, in prep.). Both abdomen wagging (a variable intensity side-to-side movement of the abdomen against the surface of the nest, often producing a soft or sharp rattling sound on the comb) and abdomen stroking (a sinuous rubbing of the abdomen on the nest surface by a walking female) are associated with dominance and/or territoriality in *Polistes, Ropalidia,* and *Vespula* species (Maher, 1976 ; Gamboa and Dew 1981 ; Jeanne, 1977 ; Greene et al., 1978, pers. obs. of *Ropalidia ciathiformis,*

Polistes canadensis canadensis, and *P. major* in which it is performed most frequently by egg-layers).

Behavior observations thus suggest that sternal gland secretions of non-swarming species may function widely as dominance signals and territorial scents, in addition to sometimes being anti-predator secretions. It is therefore reasonable to hypothesize that the Richards'gland secretion functioned in one or all of these contexts in the ancestors of swarming species, then came to be used to mark the route to new nest sites (see below). Since the abdomen stroking (and possible sternal gland pheromone production) of non-swarming species is so often dominance related, it is of interest to note that queens of some swarming species are distinguished from workers in having a conspicuous accumulation of waxy secretion over the Richards'gland (Richards, 1970, 1978 ; pers. obs. of *Stelopolybia areata* and *S. hamiltoni*). It would be of interest to investigate the possibility that the gaster-bending behavior of queens in a variety of Polybiine genera (see West-Eberhard, 1977, p. 226 ; Naumann, 1970) serves to expose the Richards'gland. (As pointed out by Spradbery, 1973, the greater distension of a developed queen's oocytefilled gaster separates the sternites, exposing the sternal glands even when the queen is at rest). If the Richards'gland secretion does serve a double function, as a queen-recognition pheromone within the nest, and a trail-marking pheromone during swarming, it would provide a striking parallel with the double function of the honeybee «queen substance» that, within the nest, contributes to reproductive suppression of nestmates, and outside the nest causes clustering by swarming bees (see Michener, 1974, pp. 135, 361).

Swarm-like behavior in non-swarming species

Polistinae. Quasi-swarming – movements of nestmates from an old to a new nest site with some at least rudimentary communication or coordination en route – has been observed in a few non-swarming species. A marked *P. erythrocephalus* queen and ten nestmates whose nest (nest V6, see West-Eberhard, 1969, p. 63) was destroyed by ants first regrouped about one meter from their original nest site. The queen remained there for a day, with from 2-8 nestmates clustered with her or nearby. She sometimes moved to join others, rather than the reverse – the queen was not necessarily the nucleus of the group. However, these wasps did not join the more than 40 others associated with five newly founded nests in the vicinity ; nor did foreign wasps join them. Thus nestmates apparently recognized each other. Four days later the entire group of 11 wasps permanently occuped a nest founded two days earlier by another female about two meters from their original nest site. Similar loosly coordinated short migrations were noted by Litte (1976) in

Florida populations of *Mischocyttarus mexicanus*. Marked wasps from three abandoned nests formed shifting aggregations of up to 34 nestmates on leaves within five meters of abandoned nets. Some persisted for 38 days following nest abandonment. Two of these groups initiated nests one and five meters from their respective natal nest sites.

A striking example of quasi-swarming behavior in non-swarming wasps was observed by Litte in Colombian *Mischocyttarus labiatus* (Litte, in press). The population studied was heavily parasitized by phorid flies, that provoked frequent nest abandonment and renesting. Queens, leaving or returning to their new nests, dragged their abdomens over leaves and stems in the area between the old and the new sites. Other wasps landed on and antennated these rubbed surfaces. Queens also «abdomen dragged» near nests when nestmates disappeared or were experimentally removed. And Litte twice saw subordinate females from abandoned nests «abdomen drag» between new nests started by themselves and new nests started by dominant queens, in an apparent attempt to recruit nestmates. This is the first report of apparent scent-marking, resembling that of swarm scouts, in a non-swarming polybiine wasp. It is of interest that it occurs in a species having an unusually high rate of parasitization and renesting (Litte, in press), and that it apparently involves either or both the sternal glands present in others species of this genus (Richards, 1978 ; Landolt and Akre, 1979) but not previously known to be used in the context of nest site location or recruitment.

Vespinae. Another phenomenon very much like swarming is the mid-season «translocation» of nests by *Vespa crabro flavofasciata* Cameron and *V. simillima* Smith in southern Japan (Edwards, 1980, after Matsuura, pers. comm.). When early nest sites become too small for the growing nest, 30-100 workers («scouts») search the surrounding area for new sites, and form aggretations away from the nest. At first they settle in several sites, eventually congregating in only one. Meanwhile, as in the case of pre-swarming behavior in tropical polybiines, enlargement of the original nest ceases, and the queen stops laying eggs. When the queen flies to the new site nest construction begins. Some workers continue to feed larvae and newly emerged adults at the old nest for about a month, but eventually it is abandoned. Since new nests can be as far as 180 m from the old nest it would be of great interest to know how the new site is located. As many as 60 % of *Vespa simillina* colonies translocate their nests in this manner.

Possible stages in the evolution of swarming in wasps

Observations of non-swarming and primitively-swarming wasps suggest the following series of hypothetical steps in the evolution of swarming in this group :

1. Application of a repellent scent or territorial marker to the nest surface, as commonly observed in non-swarming species (aboves).
2. Use of sternal gland scents as assembly pheromones. Such scents applied to temporary resting places or newly founded nests might serve to attract, or keep together nestmates that have left the parental nest, like the assembly pheromone postulated for *Vespa* and *Polistes* (called «building initiation pheromone» by Ishay and Perna, 1979).
3. Use of scents as orientation cues. Wasps might then begin to search for scents when moving from an old to a new nest site, making the assembly pheromone begin to function as an orientation cue.
4. Short, directional recruitment trails. Selection could then favor nest foundresses that attract or lead potential joiners to their new nests by applying scent marks in the region between nests, as in *Mischocyttarus labiatus* (Litte, in press).
5. Long migration trails. New nest sites a long distance from the old nest could then be located via a series of scent marks forming a trail, as in the swarming Polybiini.

The advantages of swarming

Swarming has two salient consequences : long-distance migration, and large foundress groups. Migration away from the location of a damaged nest must sometimes enable wasps to escape a region frequented by predators or parasites, or some other unfavorable aspect of an abandoned site. And it would tend to reduce competition among the offspring of fissioning mature colonies. However, nothing is known about comparative colony success following different lengths of migration, since even the latter datum is very rarely obtained except for very short migrations. There is more basis for speculation regarding the advantage of a large foundress group. In *Polistes* multi-foundress colonies have better survival rates (Gibo, 1974) and higher productivity (Gibo, 1978 ; Metcalf and Whitt, 1977 ; Gamboa, 1978) than single-foundress nests. And in *Ropalidia marginata* the probability of extinction of colonies correlates negatively with the size of the adult population (Gadagkar et al., 1978). Furthermore, the larger the foundress group the quicker the establishment of large brood comb (West-Eberhard, 1969). The importance of quickly rearing a new crop of adults is dramatized by the high mortality rate (short life expectancy) of workers compared to the time required to replace them. In a colony of the swarming polybiine wasp *Metapolybia aztecoides* the average time required to rear a female from egg to first foraging (55 days) exceeded the foraging lifespan of workers (7-52 days) (West-Eberhard, 1978). Thus a new colony is in danger of running out of

workers (and going extinct) before new workers can be produced. I have documented the near extinction of a swarm-founded colony of *Synoeca surinama* due to worker mortality (West-Eberhard, 1981). Obviously, the larger the group of workers and queens present in the swarm, the more likely is the colony to survive a pre-elergence decline in adult numbers. Strassmann (in press) reached a similar conclusion in a study of the effects of group size in *Polistes*. She found that reduced probability of orphaned brood (and colony extinction) is a more important consequence of large adult population than defense against parasitoids and predators. The ability to swarm must contribute of the Polybiini in the tropics (Richards, 1971) where this and other adaptations (Jeanne, 1975) seem to enable colonies to survive despite frequent predation, especially by ants (see Jeanne, 1975 ; Chadab, 1979).

A COMMENT ON THE EVOLUTION OF SWARMING IN RELATION TO MATING SYSTEMS OF SOCIAL WASPS

It is a striking fact that the very little known about the behavior of tropical polybiine males indicates that they, like the females, are capable of following, and in some species making, scent trails. In the llanos orientales of Colombia (Meta) I observed *Polybia sericea* males abdomen dragging on certain leaves in a small (560 m^2) area of pasture. Four marked males repeatedly visited the same 75 dragged (presumably marked) leaves day after day for 16 days. Although I did not see mating in ten hours of observation, and foragers of the same species did not seem to react to the leaves visited by males, it seems likely that virgin queens seek such areas and mate there. Males of this species (and some others, e.g., *Polybia liliacea*) have a conspicuous medial depression in the terminal gastral sternite that I found lacking in males of *Parachartergus colobopterus* known to engage in a reproductive tactic not involving trail marking (see above). Similarly, Litte observed male abdomen dragging and patrolling sites in *Mischocyttarus flavitarsis* (Litte, 1979) and in *M. labiatus* (Litte, in press) the same species in which females abdomen drag «recruitment trails» between new and old nest sites. I have observed dragging and patrolling by males of *M. melanarius* (Cameron) and *M. mexicanus* (form *sternalis*) in Costa Rica (cf. Jeanne and Castellon, 1980, who report patrolling without dragging by males of *M. drewseni*). In *M. mexicanus* form *sternalis*, males have very long brushlike hairs on the overlapped margin of the terminal three sternites (most developed on the penultimate sternite) (cf. Litte, 1979 on *M. flavitarsis*, in which males have glands and hairs on sternites 5 and 6). These males return to the same leaves even after a lapse without marking of

more than two months, suggesting that their scent marks are very long lasting (mate attractant scent marks of honeybees last up to seven years – Butler, 1970). This raises the question of whether there is a connection between the scent trails of males and those of females. It is possible that polybiine male pheromone originated as chemical mimics of already attractive scents used by females in swarming ; or that sexual attractants evolved first and are simulated by swarming pheromones. On the other hand, trail marking could have evolved independently in the two contexts, or could have originated independently and been followed by convergence in the scents used by the two sexes. Abdomen dragging by males near newly founded nests occurs in the non-swarming wasp *Polistes canadensis* (pers. obs.), and I have also seen it by solitary eumenid males (a *Zethus* species) near active nesting holes. This indicates that at least the glandular apparatus for producing scents could have been present in males prior to the evolution of swarming by females. It would be of interest to compare the chemical structures of male and female sternal gland secretions. The only possible indication I have that the two sexes may react to the same scents is the observation of males present at very recently initiated nests (see above), raising at least the possibility that they followed the scent trail of the founding swarm. Some co-evolution of male and females pheromones in social wasps seems possible from the fact that there is much evidence in bees (in which this is a better studied aspect of social biology) for contextflexibility (and, hence, evolutionary lability) in the functions (or «meanings») of pheromones (e.g., see Michener, 1974).

A POSSIBLE RELATION OF INTRA-COLONY COMPETITION AND SWARMING IN BEES

As in *Metapolybia* wasps, reproductive swarming in *Apis mellifera* is preceded by dramatically increased reproductive competition among females, associated with the emergence of young gynes. In the case of honeybees, the timing of gyne production is regulated by a complex of factors (see Michener, 1974) and coincides with times of high worker population and a diminution in the production of queen substance (and, hence, presumably decreased suppression of queenlike tendencies in nestmates). As in *Metapolybia*, worker honeybees participate in the activities surrounding reproductive competition among queens. During the pre-swarming period of reduced foraging and egg-laying the queen «is often disturbed by workers forming a ball around her or striking her» (Michener, 1974, p. 132). And the younger and/or smaller among newly matured gynes are distinguished by the workers and killed (see Michener, 1974, p. 209). The possibility that older, larger gynes more successfully meet

challenges of «testing» workers (as is suggested by the queen selecting process in *Metapolybia* – see West-Eberhard, 1978) has apparently not been investigated in honeybees. «Piping» of honeybee queens seems to me likely to play a role in competition among gynes : it occurs only at times when there are, or recently have been *multiple* mature queens in a colony (Otis, 1980) ; and once a mature gyne has begun piping those emerging later move silently to the bottom of the hive where they are ignored by resident queen and workers (summary in Otis, 1980). If this interpretation of the function of piping is correct, the facts that piping and swarming are associated in honeybees (Michener, 1974 ; Otis, 1980), and that piping can even lead to swarming in colonies lacking other preparations for swarming (Simpson and Cherry, 1969 ; Simpson and Greenwood, 1974), further indicates that reproductive swarming of honeybees is associated with intra-colony reproductive competition. In honeybees, colonies are able to regulate the onset of competition among gynes (and, hence, the timing of swarming) by restricting the timing of gyne production. Honeybee swarming (colony fission) may originally have occurred as a function of competition among gynes, and then selection may have favored making this event coincide with periods of ample provisions and/ or crowding and perhaps other conditions (see Winston an Taylor, 1981) enhancing the probability of success of new colonies.

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