

Social Biology of the Polistine
Wasp *Mischocyttarus labiatus*:
Survival in a Colombian
Rain Forest

MARCIA LITTE

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ABSTRACT

Litte, Marcia. Social Biology of the Polistine Wasp *Mischocyttarus labiatus*: Survival in a Colombian Rain Forest. *Smithsonian Contributions to Zoology*, number 327, 27 pages, 5 figures, 15 tables, 1981.—The Neotropical polistine wasp *Mischocyttarus labiatus* (Fabricius) was studied in montane rain forest at Anchicayá, Colombia. The social behavior of the species and some environmental factors that affect it were investigated. Nests of *M. labiatus* were founded by one or more females (foundresses). Each colony with more than two females contained one queen (primary egg-layer), one or more cofoundresses that rarely foraged and had well-developed ovaries, and one or more cofoundresses that were active foragers and showed little ovarian development. Most daughters emerging in their nests became active foragers. Males began to emerge early in the colony cycle. They remained with their natal nest throughout their lives, but mating occurred away from nests. Males flew regular patrol routes in sites away from nests.

By removing specific types of females from colonies and by observing natural situations of queen and cofoundress disappearance, the flexibility of the behavioral roles of remaining females could be determined. Multifoundress group queens were capable of nesting alone, cofoundresses and daughters could become queens, nonforaging cofoundresses could become foragers, and foragers could become nonforaging cofoundresses.

Nest productivity varied with foundress group size. Adult survivorship was low during the period between nest initiation and emergence of adult daughters (pre-daughter phase). Forty-four percent of queens and 40% of nonforaging cofoundresses survived, but only 27% of foragers and 20% of lone-nesting females. During the seven-week predaughter phase, nest survivorship was low (20%); over shorter periods of time it varied with foundress group size. Nest parasites (Diptera: Phoridae: *Magaselia* (*M.*) sp. near *scalaria*) were responsible for the greatest proportion (32%) of the failures. Many parasite attacks, particularly on multifoundress nests, were followed by brood eating, nest cutting (removing comb from petiole) and renesting by wasps.

Some cofoundresses and daughters initiated their own nests following failure of the original nests. In general the success and growth rates of these nests were similar to those of other nests in the general population.

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Social Biology of the Polistine Wasp *Mischocyttarus labiatus*: Survival in a Colombian Rain Forest

Marcia Litte

Introduction

Theories of sociobiology in general, and of the evolution of social behavior in particular, are applicable to a wide variety of animal species, yet the impetus for their formulation and the subject matter for their testing have largely been eusocial insects (West Eberhard 1967; Hamilton, 1964, 1972; Wilson, 1971, 1975; Alexander, 1974; West Eberhard, 1975; Metcalf, 1975; Trivers and Hare, 1976). In eusocial species colonies are composed of nest foundresses and emergent daughters, with a reproductive division of labor among conesters. Primary egg-layers are termed queens; secondary or non-egg-layers are termed helpers or, more specifically, cofoundresses or daughters. Few of the many species of social insects, however, have been studied in detail and the basic biologies of most species are completely unknown. This, for example, is apparent among the polistine wasps (Vespidae: Polistine): only approximately 15 (2%) of the estimated 700 species have been studied in some detail (see Wilson, 1971, and Richards, 1971, for references). Among these species great diversity has been found in colony size, structure,

method of initiation, and division of labor. Thus, the number of studied species representing each type of biology is small and perhaps some types have not yet been discovered. The paucity of data makes the formulation and testing of theories difficult, and further theorizing will probably not be fruitful until more basic field work has been completed.

I studied the polistine wasp *Mischocyttarus labiatus* (Fabricius) to investigate the social biology of the species and to gather data necessary for the testing of present theories. *Mischocyttarus*, the largest genus in the Vespidae, is largely Neotropical in distribution (Richards, 1971). The social biologies of only two species have been studied, *M. drewseni* in Brazil (Jeanne, 1972) and *M. mexicanus* in Florida (Litte, 1976, 1977), though several field investigations are presently being conducted on other species.

Mischocyttarus labiatus is distributed from Panama south to Paraguay (Bequaert, 1944; Richards, 1945). Despite the extensive range of this species and its apparent abundance in some areas (e.g., Trinidad: Fitzgerald, 1938), no studies have been conducted on its biology. Rau (1933) describes nests from Panama, as does Fitzgerald (1938) from Trinidad.

Field work with *M. labiatus* was designed to

Marcia Litte, Mountain Lake Biological Station, Pembroke, Virginia, 24136, and Smithsonian Tropical Research Institute, P. O. Box 2072, Balboa, Panama.

determine (1) the basic social biology of one population of the species, including the colony cycle, the behavioral characteristics and role flexibility of colonial females, and the behavior of males, and (2) population characteristics, including colony productivity and survivorship as it varied with the number of nest foundresses, causes of nest failures, frequencies of renesting after nest failure, and adult survivorship. Renesting by surviving colonymates (queens, cofoundresses, or daughters) allowed for a comparison of the nesting success of different types of females, and in conjunction with artificial or natural removal of various types of females from colonies, served to determine how surviving females adjusted to stresses placed on colonies.

In this paper I will report the results of this field work and, in an attempt to delineate some of the environmental parameters that affect social behavior, will compare *M. labiatus* with the tropical species *M. drewseni* (Jeanne, 1972) and *M. mexicanus* (Litte, 1976, 1977), and also with *Polistes canadensis* (West Eberhard, 1969), a tropical species similar in many respects to species of *Mischocyttarus*.

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Methods

This study was conducted at Anchicayá, Colombia (3°42'N, 76°48'W), in a montane rain

forest habitat at 400 m elevation. In this habitat mean temperature was 24°C and mean annual rainfall was 2000 mm. The climate was basically aseasonal in terms of temperature and precipitation. Wasp colonies were abundant and 126 nests (including 46 renestings) were observed during the three-month study (September–November 1976). Nests were initiated throughout the tenure of the field study. Fifty-eight nests (31 single-foundress and 27 multifoundress) were observed from the time of initiation; these nests were followed up to 10 weeks and were used for determination of nest survivorship rates during specified time intervals (58 nests for 30 days following initiation and 39 nests for 50 days following initiation; the latter period corresponded to the brood development period and thus the predaughter, foundress association phase of nests). These nests were not observed synchronously over a common period of time but, as environmental conditions (temperature and precipitation) at Anchicayá were aseasonal, this asynchrony would probably not bias survivorship rates in any way. Causes of nest failures were noted where possible. Nest parasites were common in this habitat. I reared parasites from 25 parasitized nests in order to determine the duration of the immature period of the parasites.

The same population of nests was used for analysis of productivity. Indices of productivity were made in terms of the number of cells (and pupae where appropriate) present at specified points in colony development (when the first egg hatched, when the first larva pupated, and when the first daughter eclosed) and the emergence rate of pupae and daughters in these nests. Productivities of single-foundress and multi-foundress nests were compared as were those of individuals and colonies in first nesting and renesting situations.

To facilitate behavioral observations, wasps were individually marked with Testors enamel. I made 100-minute observations on 23 nests for periods of 2 to 50 days per nest. Egg-laying, egg-eating, foraging, nest construction and other duties, nest defense, and interactions (biting and

solicitation of food) among nestmates were observed and quantified.

Female wasps with known behavioral roles were dissected for determinations of ovarian development, spermathecal contents, extent of fat layer, and for size measurements (head width and wing length). Ovarian development was scored on the basis of maximum ovariole width, and females were divided into four classes with the following ovariole widths: class 1 = 1.6–2.0 mm; class 2 = 1.1–1.5 mm; class 3 = 0.5–1.0 mm; class 4 = 0.1–0.4 mm.

The females of those nests that were observed from the time of initiation were used to determine the adult survivorship rate. Wasps were assumed to be dead if they were not seen at original or new nests for a period of at least one week.

In order to quantify the degree of behavioral flexibility of nest foundresses (queens and cofoundresses) and of daughters, I removed or witnessed the natural disappearances of females with specific roles from nine colonies and added a newly emerged female to one colony. These nests were then observed for 10 to 30 days to determine responses of remaining females to the altered nesting situations.

Finally, for observations of male reproductive behavior (patrolling of nest site areas), males were marked either in their patrolling sites or on their nests. The frequency of male-male interactions was quantified at patrolling sites, as was the nature of the patrolling behavior. Male-female interactions on the nests were observed.

TERMINOLOGY

Foundress: Female that initiates a nest either alone or with a group.

Queen: Primary egg-laying foundress in a colony.

Dominant cofoundress: Secondary or non-egg-laying foundress in a colony; rarely forages and frequently aggressive.

Foraging cofoundress: non-egg-laying foundress that frequently forages and is rarely aggressive.

Predaughter nesting phase (pre-emergence phase): Period between nest initiation and emergence of first adult daughter.

Postdaughter nesting phase (emergence phase): Period between the emergence of the first adult daughter and colony termination.

Social Biology

COLONY CYCLE

NEST INITIATION AND THE PREDAUGHTER NESTING PHASE.—The open-comb paper nests of *Mischocyttarus labiatus* were almost exclusively located in small crevices on rocks cliffs, generally surrounded by small ferns, lichens and vines (Figure 1). The cliffs, located at the rain forest edges, overlooked either a road or a river, and thus were well exposed. Herbaceous and woody flowering plants were abundant along both the top and the bottom of the cliffs. Nest petioles (4–7 cm long) were suspended vertically either from the rocky crevice roofs or from stems or rootlets. Due to their location, their brown or gray color, and their



FIGURE 1.—Predaughter phase nest of *Mischocyttarus labiatus* located in cliff crevice (oviposition by queen).

small size (largest combs 6 cm in diameter), nests were fairly cryptic.

Nests were initiated by from one to nine females (foundresses). In the total population of nests 42.9% were multifoundress nests. However, failure rates were higher for single-foundress than for multifoundress nests and the frequency of renesting after failure was higher for multifoundress groups than for lone foundresses (see "Nest Survivorship"). Thus the frequency of multifoundress nests in the population at any given time was markedly different from the frequency of nests observed being initiated by groups. Of the 18 nests observed from the time of initiation and thought to be first nestings, 4 (22.2%) had multiple foundresses.

The number of egg-layers or females with maximally developed ovaries in foundress groups varied with group size (Table 1). Two-foundress nests all had only 1 egg-layer; the other foundress was never observed to lay eggs and had undeveloped ovaries. Colonies with 3 or more foundresses contained 1 or more females with developed ovaries. In these colonies 1 of these females (queen or primary egg-layer) laid eggs at a much higher rate than the other. All of the secondary or non-egg-layers are referred to as cofoundresses. Those cofoundresses with developed ovaries are called "dominant cofoundresses" whereas those with poorly or undeveloped ovaries are called "foraging cofoundresses" (see "Behavior of Females on the Nest"). Dominant cofoundresses rarely foraged, and, if so, mainly for plant fiber used in nest construction; they thus resembled queens in spending relatively little time away from their

nests. Foraging cofoundresses sought nectar and arthropods (both fed to nestmates and larvae) and to some extent plant fiber, and spent considerably more time away from their nests.

The composition of colonies was fairly stable, for though females disappeared from the groups (presumed dead) or renested apart from the original groups, I observed only 2 cases in which females joined a foreign colony. One female joined a queen that was renesting. Another joined the same colony after her own nest was destroyed. Both behaved as foraging cofoundresses on their original nests and on their new nests. Queens actively defended their nests against foreign conspecifics, this presumably preventing frequent joining behavior.

Colonies grew at rates that varied with group size. However, growth patterns were similar among the single- and multi-foundress groups: cell building and oviposition rates were initially high (Table 2), but decreased after approximately 10 days and then decreased considerably more after the first egg hatched. They tended to remain low until shortly before larvae began to pupate (Figure 2). This slackening of growth rates during the larval period was most marked in single-foundress nests; it appears to be a trend common to several species of *Polistes* and both *M. drewseni* and *M. mexicanus* (see review in Litte, 1976). Because the egg and pupal periods were similar in duration (see below), the result of the pattern was that eggs laid when the first larvae pupated hatched when those pupae eclosed as adults. These larvae were then cared for by the newly emerged daughters. In addition, since oviposition rate declined during the latter part of the all-egg stage, there were relatively few larvae present in these nests when the pupae appeared.

After their first eggs hatched, lone-nesting females began to forage for arthropods and foraged more frequently for nectar. Though they added few new cells to their nests they continued to forage for plant fiber used in heightening the cell walls. Foraging cofoundresses in multi-foundress groups occasionally brought arthropod loads, and frequently nectar loads, to their nests when only

TABLE 1.—Mean number of females with ovarian development of class 1 or class 2 in multi-foundress nests

Mean number of females	Number of foundresses	Number of nests
1.0	2	6
2.0	3	5
2.0	4	1
2.5	5	2
2.0	6	1
3.0	9	1

TABLE 2.—Productivity (mean number of cells or pupae) of single- or multi-foundress nests at four stages in colony cycle (number of nests in parentheses, range in brackets)

Stage	Number of foundresses						
	1	2	3	4	5	8	9
1. Number of cells 5 days after nest initiated	4.1 (10) [2-5]	4.4 (5) [3-5]	6.2 (5) [6-7]	8.0 (3) [5-11]	9.0 (2) [9-9]		
2. Number of cells when first egg hatched	8.4 (11) [4-11]	7.5 (2) [6-9]	10.7 (6) [9-12]	12.0 (2) [10-14]	17.0 (2) [17-17]	12.0 (1)	11.0 (1)
3. Number of cells when first larva pupated	10.3 (9) [9-14]	10.0 (3) [10-10]	17.0 (1)	18.3 (3) [13-21]		31.0 (1)	
4. Number of cells when first daughter emerged	11.8 (6) [10-14]	28.7 (3) [27-30]	41.0 (2) [34-48]	34.0 (1)	46.0 (1)		
Number of pupae when first daughter emerged	1.2 (6) [0-2]	3.0 (3) [2-4]	4.5 (2) [3-6]		4.0 (1)		
Pupation rate (new pupae/day)	0.3 (5)	1.1 (2)	1.3 (2)	1.1 (1)			

eggs were present. These loads were solicited by and fed to queens (Figure 3). However, after eggs hatched these females actively foraged to feed the larvae as well. Foragers searched for arthropods (immature lepidopterans, orthopterans, and hemipterans) and nectar (*Hyptis capitata*, Compositae; *Kohleria spicata*, Gesneriaceae; *Cavendishia laurifolia*, Ericaceae) among vegetation within approximately a 100 m radius of their nests. Plant fibers (bark and dry leaves) were generally gathered near the nests (as close as 3 cm). Foraging trips for fiber were thus significantly shorter than for food (plant fiber: \bar{X} =4.7 minutes, N=78; arthropods: \bar{X} =26.1 minutes, N=20; nectar: \bar{X} =35.7 minutes, N=70, P=0.01, Mann-Whitney U-test). Thus females that predominantly foraged for fiber (lone-nesting females after pupae and daughters began to appear and queens and dominant cofoundress in multi-foundress groups) spent relatively little time away from their nests (see "Behavior of Females on the Nest").

POSTDAUGHTER NESTING PLACE.—The duration of the immature stage of wasps averaged 48.5 days, the egg, larval, and pupal stages all being of similar length (egg: \bar{X} =16.1 days, range = 14-19 days, N=19; larva: \bar{X} =16.1 days, range = 15-18 days, N=10; pupa: \bar{X} =16.3 days, range = 13-18 days, N=11).

After daughters emerged as adults they remained relatively inactive for 10 days before they began to forage. While on the nests they frequently solicited returning foragers and distributed food to larvae. Due to high rates of nest failure, very few nests actually survived to produce adult offspring and thus observations of behavior during the postdaughter phase were made on only three nests.

In 1 large nest (Eb) in which daughters emerged at a high rate (1 per 1.5 days), 2 (the first and seventh to emerge) foraged only for plant fiber. They were dominant individuals on the nest, frequently soliciting foragers, biting nest-mates, and sparring with each other. Sparring behavior (Figure 4) consisted of 2 wasps facing each other, head to head, alert antennae forward, and immobile, each spar lasting about 5 seconds and ending as 1 wasp turned away. These wasps on Eb never bit each other and appeared to be of equal status in dominance. All other daughters emerging during the 46 postdaughter-phase days that this nest survived foraged for both nectar and arthropods. In other nests in which daughters emerged at a slower rate, all daughters foraged for both nectar and arthropods, with no indication of specialization for either. In all of these

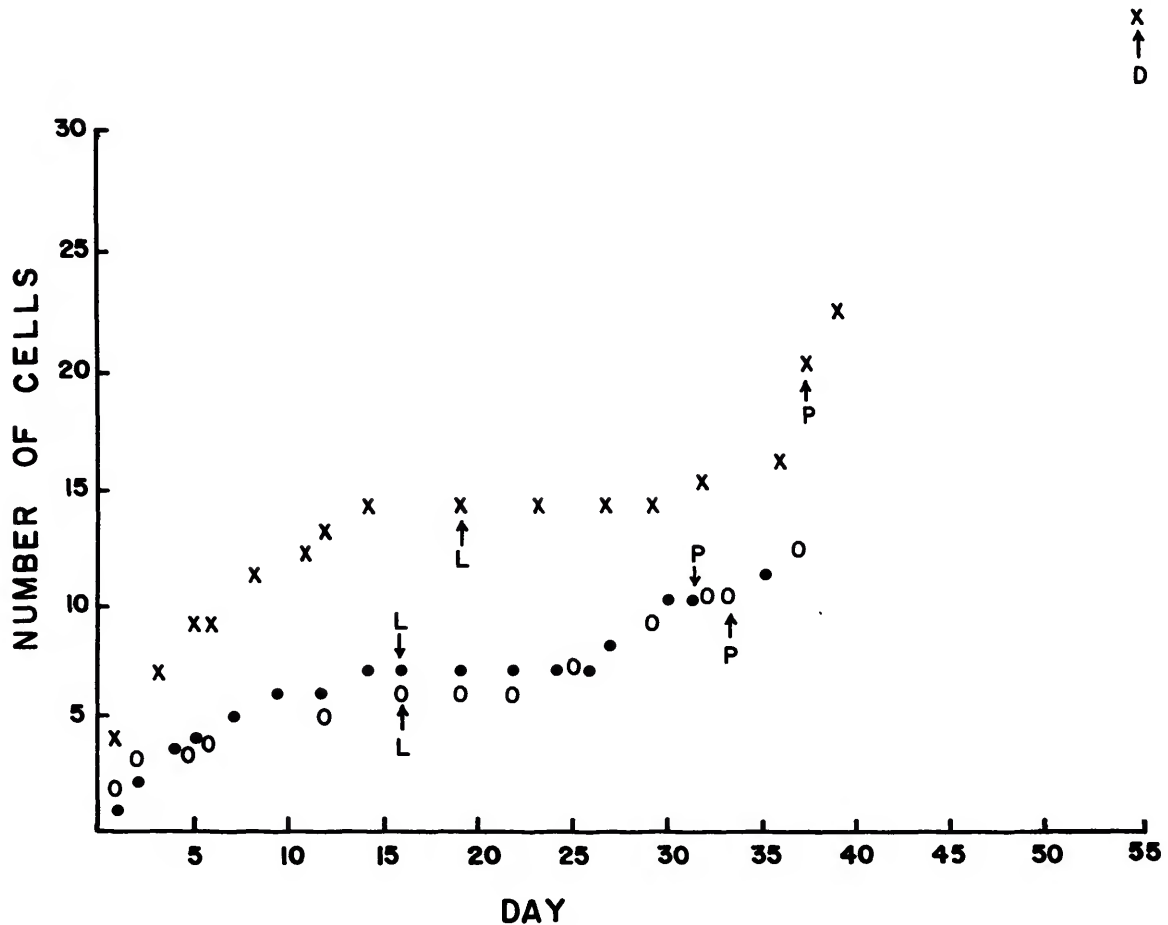


FIGURE 2.—Growth of three nests of *Mischocyttarus labiatus* during the predaughter phases of the colony cycles (solid circle = 1-foundress nest; open circle = 2-foundress nest; X = 4-foundress nest; L = first larva; P = first pupa; D = first adult daughter).

nests, queen mothers foraged for plant fibers only, and behaved similarly to queens in predaughter phase, multifoundress groups. The foraging behavior of lone-nesting foundresses thus changed markedly after daughters began foraging. During the predaughter phases they spent a mean of 35.9% of their time away from their nests; during the postdaughter phase this value was 7.1%.

I saw no daughters that correspond to the nonworkers of *Polistes canadensis* (West Eberhard, 1969) and *M. drewseni* (Jeanne, 1972). Whether nonworkers were produced in colonies of *M. labia-*

tus that survived to have long postdaughter phases is not known. The nonworkers in the above-cited species are potential future reproductives. In *M. drewseni* these females begin to appear about 30 days after the first daughter. They may replace original queens or initiate new nests, depending on the time of their emergence in the colony cycles. *Polistes canadensis* differs in that some of the first emerging daughters may be nonworkers. These females can become replacement queens if given the opportunity (queen removal or death) or may found their own nests. First-emerging



FIGURE 3.—Queen and dominant cofoundress of colony of *Mischoctytarus labiatus* chewing arthropod loads solicited from forager.

daughters of *M. labiatus* colonies were capable of initiating their own nests and thus must be considered as potential future reproductives even though they worked on their natal nests.

PRODUCTION AND BEHAVIOR OF MALES ON THE NEST.—Males were abundant on flowers and in the nesting sites. Clearly there were more colonies in the postdaughter phase than I was able to find. My observations of male behavior on nests is limited to nest Eb. The first male emerged only 15 days after the first daughter. During the 46 days of the postdaughter phase, 24 daughters and 7 sons emerged. Males remained with their natal nest for what was assumed to be their entire lives (15 to 30 days). At approximately 10 days of age they began to leave their nests for several hours each day when they joined other males in patrolling distant nests sites (see "Behavior of Males at Patrol Sites"). The tenure of individual males at



FIGURE 4.—Sparring behavior of two dominant daughters of colony of *Mischoctytarus labiatus*.

patrolling sites was 2 to 25 days and thus the mean time on the nest (20.7 days) was probably an accurate estimate of male life expectancy.

While on their natal nest the males frequently solicited returning foragers for nectar and arthropod loads and were almost always fed. Though the queen-mother generally ignored her sons, the 2 dominant daughters on nest Eb frequently bit and chased these males, and I occasionally saw them grab the males' legs in their mandibles and pull them about the nest. Males fled but rarely left the nest when so treated. After nest Eb was knocked down, 1 of the dominant daughters initiated a new nest; her mother and dominant sister disappeared but she was joined by 5 sisters and 2 brothers. She often repelled the males as they tried to land on the nest. The frequency with which she bit 1 brother, relative to her total time in contact with him (4.0 times/100 wasp-min.), was almost twice as great as the frequency with which she bit her sisters (2.2 times/100 wasp-min.).

In *M. drewseni* (Jeanne, 1972) and *P. canadensis* (West Eberhard, 1969) first males emerge on nests

approximately 40 and 30 days, respectively, after the first daughters. If 15 days is a typical first-emergence time for *M. labiatus*, then males in this species are produced considerably earlier than in *M. drewseni* and *P. canadensis*.

BEHAVIOR OF FEMALES ON THE NEST

I grouped females of *Mischocyttarus labiatus* into 3 types according to several criteria, including foraging behavior, ovarian development, and frequency of biting and solicitation of nestmates. Foraging behavior was measured as percent of time away from nests and as number of foraging trips per 100 minutes. Biting and solicitation frequencies were calculated in terms of the number of bites or solicitations made by each wasp relative to the time in contact with all other wasps.

NEST FOUNDRASSES.—Tables 3 and 4 show the percent of eggs laid on the nest, mean percent of time away from the nest, mean number of foraging trips/100 minutes, percent of nest construction behavior that was cell initiation, biting and solicitation frequencies, number of times/wasp-minute bitten by the most frequent biter, and designated behavioral type of 26 wasps (foundresses) from 7 of the colonies studied.

In all of the colonies observed, parallels among the various categories listed above were clear. Of 22 egg-laying foundress females, 19 spent less than 10% of their time away from their nests, and foraged mainly for plant fibers; 18 of these were the most frequent biters and solicitors of other nestmates.

In this group of egg-laying females, wasps were of 2 types: those that laid most of the eggs on a given nest and those that laid relatively few. The former are termed queens and the latter dominant cofoundresses. Of 14 colonies with 3 or more females, 5 contained 2 egg-layers. Queens and dominant cofoundresses in these 14 colonies were responsible for 83.0% and 17.0% respectively of the 53 eggs laid; in the 5 colonies with the 2 egg-layers each, they were accountable for 68.2% and 31.8% respectively of the 28 eggs laid.

Dominant cofoundresses always laid their eggs in the presence of the queens (and indeed the mean duration of queens' plant fiber foraging trips, 4.7 minutes, was less than the mean duration of oviposition, 6.9 minutes, and thus cofoundresses could rarely oviposit in the absence of the queens). Though the queens remained quiet during the process, in the 9 cases I observed, queens within 90 minutes of the egg-laying moved slowly across the nest, inspected cells, and antennated the cofoundresses' eggs. They then removed the eggs, ate them, and in some cases oviposited in those or different cells. Cofoundresses were often present, remaining quiet, during the egg-eating. All of the eggs I observed laid by cofoundresses were so eaten. All females antennated their own eggs immediately after oviposition; the cues used by a queen to detect a foreign egg may have been olfactory in nature.

Four of the 22 egg-laying females mentioned above were dominant cofoundresses. They rarely foraged other than for fiber, all were the second most frequent biters and solicitors of nestmates, and all were the most frequently bitten wasps on the nests. Queens, the most frequent biters, were rarely bitten by nestmates.

Some females were never observed laying eggs, but upon dissection showed ovarian development of class 1 or 2. Of 4 such females in 4 different colonies, 3 were active foragers, though they were more frequently bitten than were nestmates of ovarian development classes 3 or 4, and all were more frequent biters and solicitors of nestmates than were their class 3 and 4 nestmates. They are designated dominant cofoundresses.

There was at least 1 dominant cofoundress on each nest with 3 or more wasps. Since they were needed for behavioral experimentation I did not dissect many of these. Correlations were thus made between measures of foraging activity and frequency of biting and solicitation. Of 9 wasps (non-egg-layers, on nine colonies) that were away from their nests less than 40% of the time or never returned with food, 6 were the second most frequent biters and solicitors and were the most frequently bitten wasps on the nests. In the other

TABLE 3.—Characteristics of queens, dominant cofoundresses, and foraging cofoundresses of six predaughter phase colonies (number of observation minutes in parentheses; F = fiber, N = nectar, A = arthropods, Q = queen, DCf = dominant cofoundress, FCf = foraging cofoundress)

Nest	Wasp no.	Role	% all eggs laid in nest	Mean % observation time away from nest	Mean number of foraging trips per 100 min.			% nest constructions that were initiations	Mean number of bites per 100 wasp-min.	Mean number of solicitations per 100 wasp-min.	Mean number of times bitten per 100 wasp-min.
					F	N	A				
Ra (1600)	1	Q	100	4.6	1.00	0	0	14	2.00	1.00	0
	2	DCf	0	36.1	1.00	0	0	0	0	1.34	2.41
	3	FCf	0	86.0	0.43	1.43	0.43	33	0	0	0.99
Xg (800)	4	Q	100	4.5	0.63	0	0	17	1.74	1.26	0
	5	DCf	0	45.0	0.13	0	0	0	0.58	1.57	2.79
	6	FCf	0	96.2	0	1.00	0.25	0	0	0	0.99
Qa (600)	7	Q	100	8.0	1.0	0	0	20	2.68	5.94	0
	8	DCf	0	67.4	0	0.20	0	0	0.99	3.36	4.00
	9	FCf	0	81.1	0	1.80	0	0	0	0	2.08
Z0' (800)	10	Q	100	8.6	1.13	0	0	44	3.00	2.67	0
	11	DCf	0	64.7	0.25	0	0	0	0	1.54	3.20
	12	FCf	0	96.0	0	1.25	0	0	0	0	2.00
ZM1 (400)	13	Q	100	4.5	1.00	0	0	0	0	12.96	0
	14	DCf ¹	0	90.0	1.00	0.50	0.50	0	0	3.33	0
	15	FCf ²	0	81.5	0	2.50	0.50	0	0	0	0
	16	FCf	0	98.5	0	2.50	0	0	0	0	0
MC1' (900)	17	Q	100	3.3	1.10	0	0	29	2.96	1.61	0
	18	FCf	0	85.8	0	1.78	0.67	0	0	0	1.83

¹ Fully developed ovaries, inseminated.

² Undeveloped ovaries, inseminated.

3 colonies these nonforagers were never bitten and did not bite nestmates. Because of the coincidence of extensive ovarian development and low levels of foraging activity found in the 8 previously discussed females, the latter 9 nonforagers were assumed to have developed ovaries and are thus considered dominant cofoundresses.

While on the nests both queens and cofoundresses performed nest duties of cell initiation, cell enlargement, petiole-strengthening (an application of an oral secretion), petiole-rubbing (an application of an abdominal secretion), distribution of food to larvae, thermoregulatory wing fanning, and nest defense. Queens and dominant cofoundresses spent means of only 9.3% (N = 15) and 6.6% (N = 15), respectively, of their on-the-nest time performing such duties, the queens working significantly more than the dominant cofoundresses (P = 0.05, Mann-Whitney U-test).

Of 21 foundress females never seen to lay eggs and later found to be of ovarian development classes 3 or 4, 20 were away from their nests more than 60% of the time; these females foraged mainly for nectar and arthropods. Twenty of them were the least frequently bitten and least frequent biters and solicitors of nestmates. They are here designated foraging cofoundresses. Foraging cofoundresses were present on all multi-foundress nests. Two-foundress nests were each composed of a queen and a foraging cofoundress. The ovaries of the latter (N = 6) were all of class 4. These females were rarely bitten by queens and were very active foragers (mean of 84.5% of observation time spent away from the nest).

Considering the total population of females observed, queens and dominant cofoundresses rarely foraged, and then mainly for plant fiber (Table 3). They spent means of 4.8% (N = 29)

TABLE 4.—Sequence of nest failures and renestings of members (eight foundresses) of colony Mb and roles played by each member (number of observation minutes in parentheses; F = fiber, N = nectar, A = arthropods, Q = queen, DCf = dominant cofoundress, FCf = foraging cofoundress)

Nest	Date initiated	Days survived	Cause of failure	Wasp no.	Role	% all eggs laid in nest	Mean % observation time away from nest	Mean number of foraging trips per 100 min.			Mean number of bites per 100 wasp-min.	Mean number of solicitations per 100 wasp-min.	Mean number times bitten per 100 wasp-min.
								F	N	A			
Mb1 (700)	9-15	12	rain	19	Q	100	7.1	0.57	0	0	0.72	1.44	0
				20 ^a	DCf	0	26.0	0.29	0	0	0.21	0.74	0.96
				21	DCf	0	60.1	0	0	0	0.79	0.79	0.41
				22	FCf	0	96.1	0	0.29	0	0	0	0
				23	FCf	0	90.1	0	0.71	0	0	0	0
				24	FCf	0	97.7	0	0.43	0	0	0	0
Mb2 (800)	9-15	3	abandoned	25	FCf	0	99.8	0	0.14	0	0	0	0
				20	Q	100							
Mb3 (800)	9-27	23	parasite	19	Q	50	0.5	0.13	0	0	1.21	1.01	0
				21	DCf	0	19.6	0.25	0.13	0	0.11	0.66	1.55
				22	DCf	50	69.5	0	0.63	0	0.21	0	1.67
				23	FCf	0	84.4	0.25	0.38	0	0	0	0
Mb2' (500)	10-3	13	destroyed	24	FCf	0	95.1	0	0.14	0	0	0	0
				20	Q	100	5.0	0.25	0	0	0	4.00	0
Mb5 (1400)	10-10	>45	parasite	25	FCf	0	93.8	0	0.25	0	0	0	0
				26	Q	100							
Mb4 (1400)	10-20	35	parasite	19	Q	43	3.2	0.64	0	0	1.45	1.33	0
				21	DCf	57	36.0	0.43	0.14	0.14	0	0.43	1.56
				22	FCf	0	76.8	0.08	0.33	0	0	0	1.09
				24	FCf	0	99.5	0.14	0.71	0.07	0	0	1.00
Mb6 (400)	11-24	>10		19 ^b	Q	100	4.3	1.00	0	0	0.76	0.28	0
				21 ^c	DCf	0	27.5	0.25	0.25	0	0	0	0.76
				24 ^d	FCf	0	75.5	0.25	0	0	0	0	0

^a Joined after abandoning nest Mb2.

^b Ovarian development class 1, inseminated (see page 00 for class size).

^c Ovarian development class 1, inseminated.

^d Ovarian development class 4, uninseminated.

and 26.7% (N = 16) of observation time away from their nests. Foraging cofoundresses and daughters brought nectar and arthropods back to their nests, spending considerably more time away (mean = 89.0%, N = 40, P = 0.001, Mann-Whitney *U*-test). Lone-nesting females foraged for fiber, nectar, and arthropods, but the durations of their nectar- and arthropod-hunting trips (11.7 min., N = 37, and 8.7 min., N = 6) were considerably shorter than those of foraging cofoundresses (35.7 min., N = 70, and 26.1 min., N = 20, P = 0.01, Mann-Whitney *U*-test). They

were away from their nests a mean of only 35.9% of observation time. Foraging cofoundresses frequently fed on nectar in the vicinity of their nests before leaving on their trips, this in part contributing to the length of those trips.

Queens not only bit and solicited nestmates with higher frequencies than did other foundresses, but were rewarded relatively more often (Table 5; nectar: P = 0.001, χ^2 test). Perhaps as a correlation with aggression on the nest, queens were markedly more prone to defend nests against foreign conspecifics than were cofoundresses. For

TABLE 5.—Percentage of solicitations by queens and cofoundresses that result in nectar or arthropod donation (number of solicitations in parentheses)

Role	Nectar	Arthropod
Queen	100 (182)	78.3 (23)
Cofoundress	84.1 (88)	66.7 (6)

example, during a one-month period the queen in one colony was observed defending 16 times more frequently (per time on the nest) than other cofoundresses.

Both queens and cofoundresses initiated cells during both pre- and postdaughter phases, though the former did so with a higher frequency ($P = 0.05$, X^2 test); of 144 acts of nest construction by queens, 21.5% were cell initiations, whereas of 80 such acts by cofoundresses 12.7% were initiations.

All 12 queens and dominant cofoundresses that I dissected while fresh were inseminated. One of 4 foraging cofoundresses was not. In 4 of 4 cases, queens were larger in body size than both dominant and foraging cofoundresses.

In summary, queens were the primary but not the sole egg-layers and were the only egg-eaters on nests, and were frequent biters and solicitors of nestmates. They rarely foraged and then only for plant fiber. Dominant cofoundresses had well-developed ovaries, some laying eggs; most rarely foraged, and then mostly for fiber. They were generally the most frequently bitten wasps, and the second most frequent biters and solicitors. Foraging cofoundresses had little if any ovarian development, were active foragers, were rarely bitten by queens, and rarely bit or solicited nestmates. The differential survivorship of these types of females will be discussed in "Adult Survivorship."

DAUGHTERS.—I dissected only 4 daughters on normal colonies. All were active foragers, uninseminated, and were considerably smaller than their mothers. They were of ovarian development class 3 or 4, and are called foraging daughters. Two daughters (nest Eb) that rarely foraged and frequently bit and solicited nestmates were not

dissected while they were members of their natal nest, but they presumably had well-developed ovaries, since 1 began laying eggs on a new nest 3 days after the original was destroyed. They are called dominant daughters.

Foundress associations of *Polistes canadensis*, once stabilized, contain 1 queen, several nonaggressive foragers, and several passive nonworking individuals that were previous contenders for the queenship (West Eberhard, 1969). In *M. drewseni* 1 female lays most of the eggs in each predaughter phase nest; the other egg-layers, similar to the queen, precipitate more dominance interactions and appear to forage less than do the non-egg-layers (Jeanne, 1972). In contrast, foundress groups of *M. mexicanus* during 1 part of the year contain 1 egg-layer each, and 1 or more nonaggressive foragers. Colonies with 3 or more cofoundresses contain at least 1 aggressive female that rarely forages but has little ovarian development (Litte, 1977). Thus, similar to *M. labiatus*, colonies of *M. mexicanus* and perhaps *M. drewseni* are composed of queens, dominant cofoundresses, and foraging cofoundresses.

FLEXIBILITY OF BEHAVIORAL ROLES OF FEMALES.—The ability of wasps to change their behavioral patterns when stresses or changed nesting situations are imposed upon them is a measure of their role flexibility. The behavioral change may result in a partial restoration of the previous nesting situation and may thus serve to maintain colony integrity and productivity. In order to test the flexibility of females and to determine the effects of this flexibility on colony development I made or took advantage of 4 types of manipulations on well-studied colonies and then observed closely the resultant behavior of the wasps. In 3 cases I observed behavior of multifoundress queens after their cofoundresses were removed or disappeared; in 3 cases queens were removed or disappeared from nests, leaving daughters or cofoundresses; in 3 cases I removed all foraging cofoundresses from colonies, leaving 1 queen and 1 dominant cofoundress per colony; in one case I performed the latter and later added a foraging female. As usual, individual wasps

were observed as to their oviposition, foraging, and biting and solicitation behaviors.

Cofoundress Removal (nests Qb', Qa', ZC1'; Table 6): All cofoundresses were removed from 3 nests at the time the first egg hatched. Within a day of cofoundress removal, lone queens began to leave their nests frequently on brief plant fiber and nectar foraging trips. Within 5 to 7 days they began foraging for arthropods. Thus, during the period following cofoundress removal, 3 queens in 3 nests were away from the nest a mean of 47.3% of the observation time. This value was greater than that for normally lone-nesting females ($\bar{X} = 35.9\%$, $P = 0.05$, Mann-Whitney *U*-test). The frequency with which the lone, experimental queens foraged also tended toward that of normally lone-nesting females (Table 6). Nest growth ceased after cofoundress removal, however; the queens adding no new cells or eggs to nests until after larvae began to pupate. This decline in growth rates was more extensive than that normally observed in single- or multi-foundress nests during the larval periods, and resulted in lowered productivity as compared to that of

normal multi-foundress nests and in slower growth rates than single-foundress nests of similar age (Table 6). Though 4 larvae were reared in each of 2 nests, larval development times were relatively long in these nests (21 and 24 days versus 16 days in normal nests). Two of the experimental queens ate eggs soon after cofoundress removal; brood eating, however, was not unusual among lone-nesting females.

Thus, multi-foundress group queens, when deprived of nestmates, can assume the behavior of a lone-nesting female and can work, though perhaps less efficiently than normally lone-nesting females, to ensure the production of offspring. In several cases, queens abandoned their nests after cofoundresses disappeared. Unfortunately, I do not know the circumstances involved in the abandonments.

Queen Removal (nests Qa, Ua'; Table 7): On the same day that a queen disappeared from her nest (Qa, at the time the first egg hatched) the previous dominant cofoundress laid an egg and ate another; she was never observed ovipositing previous to this. She rarely left the nest on that or

TABLE 6.—Behavioral role flexibility: cofoundress removal (number of cofoundresses before removal in brackets; number of observation minutes in parentheses; number of cells added since previous stage in parentheses and underlined; F = fiber, N = nectar, A = arthropods)

Nest	% observation time away from nest	Mean number of foraging trips per 100 min.			Number of cells when first egg hatched	Number of cells when first larva pupated	Number of cells when first daughter emerged
		F	N	A			
Qb' [3]							
Before removal	1.6 (300)	0	0	0	9	—	—
After removal	41.7 (1000)	0.50	2.67	0.33	—	9 (0)	9 (0)
Qa' [2]							
Before removal	8.8 (400)	1.00	0	0	7	—	—
After removal	55.0 (600)	0.33	2.33	0.33	—	7 (0)	—
ZC1' [2]							
Before removal	2.5 (1100)	0.27	0	0	—	—	—
After removal	45.3 (300)	0.33	1.67	0.33	—	—	—
Control nests							
1-foundress, Qc	29.7 (400)	1.00	2.00	0.25	8	9 (1)	10 (1)
2-foundress					7.5	10.0 (2.5)	28.7 (18.7)
3-foundress					10.7	17.0 (6.3)	41.0 (24.0)
1-foundress					8.4	10.3 (1.9)	11.8 (1.5)

any subsequent day, her mean percent of time away from the nest declining rapidly to 8.8%, a value similar to that of multifoundress queens in general (4.8%) and to her superceded queen in particular (8.0%). As a cofoundress she had rarely foraged, though spending considerable time from the nest; after queen removal, she foraged only for plant fiber (Table 7). This cofoundress had been more frequently bitten by the queen than had been the foraging cofoundress on the nest. She in turn had bitten and solicited, though less frequently than the queen, the foraging cofoundress. After queen removal, this female never bit the forager although she frequently solicited the latter. The forager's behavior did not change with queen removal; she continued to forage and donate loads upon solicitation. Only 1 cell was constructed in the nest during the larval period, so that productivity was low relative to normal 3-foundress nests, and the growth rate was slow relative to normal 2-foundress nests (Table 7). Larval development time was normal, however, presumably due to the continued activity of the forager.

In 1 other case in which a queen disappeared from her nest, a dominant cofoundress replaced her almost immediately as queen. Thus, deprived of their queens, cofoundresses appear to be capable of rapidly transforming into queens. The dominant cofoundresses that are likely to su-

percede are those individuals that had developed ovaries in the presence of the previous queen. The 3-foundress nest is converted into a functional 2-foundress nest.

First emerging daughters of colonies of *M. labiatus* were also capable of becoming queens. In 1 case (2-female nest Ua') a daughter oviposited 5 days (age 25 days) after queen removal and in another case (Rb') 8 days (age 15 days) after removal. In the former, early nest growth rate was similar to that of most 1-foundress nests (Table 7).

Foraging Cofoundress Removal (nests ZC1', Zh3, O; Table 8): Within a day of removal of foraging cofoundresses (6 days after nest initiation of ZC1', previous to nest initiation in Zh3, and at the time the first egg hatched in nest O) dominant cofoundresses began to spend considerably more time away from their nests ($P = 0.05$, Mann-Whitney *U*-test) and were vigorously solicited by queens upon returning. These cofoundresses that had been frequently bitten, though never solicited, by queens before forager removal, were frequently solicited, but less frequently bitten, after removal (Table 8). Though none had foraged for more than plant fiber as dominant cofoundresses, all 3 began foraging for nectar within a day of forager removal and for arthropods within 7 to 10 days; the frequency of fiber foraging of 2 cofoundresses declined during this period (Table 8). One of the

TABLE 7.—Behavioral role flexibility: queen removal (number of observation minutes in parentheses; number of cells added since the previous stage in parentheses and underlined; F = fiber, N = nectar, A = arthropods)

Nest	% observation time away from nest	Mean number of foraging trips per 100 min.			Number of cells after first 5 days	Number of cells when first egg hatched	Number of cells when first larva pupated
		F	N	A			
Qa							
Before removal	67.4 (500)	0	0.20	0	—	13	
After removal	8.8 (900)	1.00	0	0		14 (<u>1</u>)	
Ua'					4	7 (<u>3</u>)	
Control nests							
3-foundress						10.7	
2-foundress						7.5	
1-foundress					4.1	10.0 (<u>2.5</u>)	
						8.4 (<u>4.3</u>)	

TABLE 8.—Behavioral role flexibility: foraging cofoundress removal (number of foundresses before removal in brackets; number of observation minutes in parentheses; number of cells added since previous stage in parentheses and underlined; F = fiber, N = nectar, A = arthropods)

Nest	% of observation time away from nest	Mean number of foraging trips per 100 min.			Times bitten per wasp-min. by queen	Times solicited per wasp-min. by queen	Bites per 100 wasp-min. by cofoundress	Solicitations per 100 wasp-min. by cofoundress	Cells after first five days	Cells when first egg hatched	Cells when first larvae pupated	Cells when first adult emerged
		F	N	A								
ZC1' [5]												
Before	33.5(1400)	0.25	0	0	2.53	0	1.77	1.48	10			
After	85.2(1100)	0.09	0.91	0.25	0.82	5.71	0	0		12(2)		
Zh3 [3]												
Before	22.0(600)	0.25	0	0	4.51	0	0	0				
After	86.5(1400)	0.33	1.53	0.13	1.67	10.00	0	0	4	7(3)	10(3)	
0 [9]												
Before	2.0(500)	0.20	0	0	1.52	0	0.92	0.74		13		
After ¹	87.1(1300)	0	1.41	0.50	1.58	17.46	0	0			13(0)	
After ²	37.9(1100)	0	0.71	0.21	2.76	6.08	1.34	0.85				18(5)
Control nests												
5-foundress									9	17(8)		
8-foundress										12	31(19)	
2-foundress									4.4	7.5(3.1)	10(2.5)	28.7(18.7)

¹ After removal of foraging cofoundresses.

² After addition of forager.

3 dominant cofoundresses was observed ovipositing before forager removal. None did so after removal. One of these (from nest Zh3) was dissected 50 days after forager removal; she was of ovarian development class 4, rather than the class 1 or 2 expected of a dominant cofoundress.

In 2 of the nests (O and ZC1') growth ceased or declined after forager removal, not increasing until near the time of the first pupation (Table 8). Larval development time was very long in 1 (30 days, nest 0). The third nest (Zh3) was parasitized shortly after forager removal. The queen and cofoundress initiated a new nest that grew at a rate normal for 2-foundress nests (of similar age, Table 8) and in which larval development time was normal (13 days).

Thus dominant cofoundresses, those individuals most prone to replace queens when given the

opportunity, are also capable of assuming the behavior of foragers when necessary for the maintenance of the nest.

Foraging Cofoundress Addition (nest 0; Table 8): After foraging cofoundresses were removed from 1 of the above-discussed colonies (nest 0) and the dominant cofoundress was observed over a 25-day period to assume the behavior of a forager, a newly emerged adult from another nest was placed on nest 0 (at the time the first larva pupated). Here she was readily accepted by the 2 females present, and was fed, upon solicitation, by the forager. She began to forage for nectar and arthropods at the ages of 12 and 15 days, respectively. During the period after the added wasp began foraging, the previous forager began to leave the nest less frequently, and the nature of her foraging trips changed with a reduction in

arthropod and nectar foraging. She bit and solicited the new forager more frequently than she had other foragers while she was a dominant cofoundress, and she was bitten even more frequently by the queen than she had been as a dominant cofoundress. Before the new forager was added she refused the solicitations of the queen less frequently than she did after the new forager was added (5% versus 20% of solicitations, respectively).

When dissected 10 days after forager addition, this cofoundress was found to be of ovarian development class 3 and was inseminated. This degree of ovarian development was more than would be expected for a normal forager (class 4) but less than that expected for a dominant cofoundress (1 or 2). Her degree of ovarian development reflected her midway position between a dominant and foraging cofoundress. Her ovaries were probably enlarging, as they were clearly different in appearance from the stringy ovaries (class 4) of the cofoundress of nest Zh3 that changed from a dominant to a foraging role.

Thus, a foraging cofoundress, when relieved of the pressures of foraging to feed the queen and brood, can become a more dominant individual in the colony. An analogous situation to forager addition is the emergence of daughters in multifoundress colonies. Foraging cofoundresses in 2-foundress nests may be expected to become more dominant after daughters begin foraging. In one nest (Id'; Table 9) a female that had foraged actively while a cofoundress, spent much less time

away when daughters began foraging, and then foraged exclusively for fiber. Though rarely bitten as a forager, she was frequently bitten by the queen during the postdaughter phase, and during the latter time she solicited, though rarely bit, returning foragers. In 1 other nest (ZN; Table 9), a foraging cofoundress remained as such during the postdaughter phase when daughters were actively foraging. What determines whether a cofoundress will maintain or alter her behavior after daughter emergence is not clear. Nest ZN was larger than Id' and perhaps the demands of the brood on this nest were enough to maintain the foraging activity of the cofoundress.

The foraging behavior of lone-nesting females changed, after daughters began foraging, more markedly than did that of the cofoundresses on nests 0 and Id'. They became similar to queens of multifoundress groups.

Behavioral flexibility of cofoundresses was also apparent in *M. mexicanus* (Litte, 1976). In this species, dominant cofoundresses or daughters replaced queens that were removed from colonies. Here, however, though future replacement queens rapidly became queenlike in terms of foraging and biting behavior, they did not begin ovipositing until 10 to 14 days after queen removal. This reflected the low degree of ovarian development of dominant cofoundresses of this species.

BEHAVIOR OF MALES AT PATROL SITES

Males of *Mischocyttarus labiatus* patrolled regular flight routes during their hours away from their

TABLE 9.—Behavioral role flexibility: cofoundress addition (number of observation minutes in parentheses; F = fiber, N = nectar, A = arthropods)

Nest	% observation time away from nest	Mean number of foraging trips per 100 min.			Number of bites per 100 wasp-min. by queen
		F	N	A	
Id'					
Before emergence	97.5(500)	0	2.00	0	0
After emergence	29.8(1300)	0.17	0	0	2.45
ZN					
Before emergence	98.5(300)	0	3.50	0	0
After emergence	99.0(300)	0	2.50	0	0

natal nests. Though in 20 hours of observation I never saw mating occur along these routes, the presumed function of these flights was reproduction (mating was never observed on post- or predaughter phase nests). Males older than 10 days of age spent about 4 hours each day (1000–1400 hours) flying in their patrol sites. These sites generally encompassed 1 or more wasp nests and numerous flowers upon which males and females fed. Males from 1 nest that I observed patrolled in sites away (at least 100 m) from their natal nest. At the same time, the natal nest area of these males was the patrol site of other foreign males. Within the sites males flew along fixed flight paths or circuits, frequently landing on leaves where they either perched briefly, dragged their abdomens over the leaf surface, presumably spreading a secretion, or antennated spots that had previously been visited by other males.

I concentrated most of my observations on one patrol site, a cliff face extending 18 m along the road, including 11 males over a 35-day period. During this study several tendencies became apparent.

Pathways of individual males within a patrol site converged through time so that within 2 or 3 days of a new male's entrance into the site his pathway was essentially identical to that of the other males already present. I demonstrated that this convergence was a male-male phenomenon, rather than the reaction of each male to certain features of the rocks and vegetation, by removing patrolling males and 2 days later introducing several foreign males. One of these remained and assumed a patrol route different from that of the previous males.

The duration of the consecutive trips of an individual male decreased throughout the day's patrolling period, in correspondence with the decrease in number of stops made on vegetation in the flight path. For example, on 1 day, 1 male's first flights were 20, 13, 12, and 10 minutes long, whereas all of his later flights were less than 6 minutes. During his first 3 consecutive 30 minute periods of patrolling he abdomen-dragged 25, 10, and 3 times.

The mean duration of flight circuits for any given male varied considerably among days (e.g., 5.0–16.3 min. for one male). However, there was a strong correlation ($r = 0.71$, $P = 0.01$) between the mean path durations of any given pair of males on any given day. This, in addition to path convergence, was also indicative of some type of male-male interaction.

Such interactions could be mediated visually and/or chemically. During 30 male-male contact hours, I observed only 2 in-flight encounters between 2 males. After these encounters males merely flew apart and resumed patrolling. However, the coincidences of abdomen-dragging on common leaves were frequent. Seventy-two (91.1%) of 79 drags of males were made on leaves they had already dragged on that or a previous day; 56 (62.9%) of 89 drags were made on leaves other males had dragged on that or a previous day; and 41 (24.4%) of 168 drags were made on leaves other males had dragged that same day. I frequently observed males making small variations in their flight paths to include circles around leaves that they or other males marked that day.

The patrolling and abdomen-dragging behavior of these males was clearly not territorial, as males converged upon, rather than excluded each other from, flight paths. Whether the male secretion was attractive to females is unknown, as conditions did not permit me to make the appropriate experiments. If it was, then the next obvious question is whether males converged upon each other for opportunistic reasons or because group signalling was more effective than individual signalling in attracting females (i.e., a form of mutualism).

Patrolling behavior by polistine wasps has not yet been reported. In *P. canadensis* (West Eberhard, 1969) and *M. mexicanus* (Litte, 1976) males converge on nest initiation locations and on flowers, respectively, sites in which receptive females are abundant.

Population Biology

NEST PRODUCTIVITY

Nest productivity (mean number of cells when the first egg hatched and the first larva pupated,

and mean number of cells and pupae as the first adult daughter emerged) was correlated with the size of the foundress group (Table 2, $P = 0.05$, Spearman Rank Correlation test). Once the first pupae appeared in nests, their rates of appearance were greater in multi- than in single-foundress nests (Table 2, Mann-Whitney U -test). The four-fold difference in appearance rate between single- and multi-foundress nests appeared to depend on the different durations of the larval periods. Larval development time depends on feeding rates in social insects (Wilson, 1971). Lone foundresses tended to concentrate their feeding efforts on one larva at a time; this larva thus pupated considerably earlier than the others present in the nests. In multi-foundress nests, several larvae were fed at fairly equitable rates (though older larvae were always given priority to the younger larvae present). Lone-nesting females appeared to place a premium on the rapid emergence of their first daughter rather than the closely spaced emergence of several daughters.

During the predaughter phases of colonies of *M. drewseni* the mean duration of the first larvae that appear is less than that of later-appearing larvae (Jeanne, 1972), suggesting that in this species, also, feeding efforts are concentrated on the first emerging larvae.

ADULT SURVIVORSHIP

Survivorship of adult females of *M. labiatus* varies with their behavioral roles. Queens of

multi-foundress groups and dominant cofoundresses had similar survivorship rates, both of which were considerably higher than those of foraging cofoundresses and foraging daughters during 50- and 30-day periods, respectively (Table 10, $P = 0.05$, X^2 test). Survivorship of lone-nesting females was as low or lower than that of foraging cofoundresses (Table 10).

NEST SURVIVORSHIP

SURVIVORSHIP RATES.—Survivorship of nests of *Mischocyttarus labiatus* was low. During the 30 days following nest initiation, survivorship of multi-foundress nests was greater than that of single-foundress nests (Table 11, $P = 0.05$, X^2 test). However, similar proportions of multifoundress nests and single-foundress nests survived for 50 days after initiation (corresponding to the time of the emergence of the first daughters in surviving nests; Table 11).

CAUSES OF NEST FAILURE.—There were 3 general causes of nest failure. In the total population nest parasites, *Megaselia* (*M.*) species near *scalaris* (Diptera: Phoridae) accounted for the largest proportion of failures; they caused a higher proportion of the multi-foundress nest failures than of the single-foundress nest failures (Table 12, $P = 0.001$, X^2 test). The parasitization rate of multi-foundress nests was greater than that of single-foundress nests (Table 12, $P = 0.001$). Phorid flies presumably searched for nests, using visual and/or olfactory cues, and the larger size of multi-

TABLE 10.—Percentage of adult survivorship, following nest initiation, for two species of *Mischocyttarus* (Litte, 1977) (initial number of wasps in parentheses)

Role	<i>M. labiatus</i>		<i>M. mexicanus</i> 8 weeks
	30 days	50 days	
Queens			
Single-foundress nests	44.4(27)	20.0(15)	77.6(76)
Multi-foundress nests	68.2(22)	43.8(16)	95.1(41)
Cofoundresses			
Dominant	75.0(8)	40.0(5)	84.0(75)
Foraging	62.5(40)	27.3(22)	
Daughters	11.1(10)	—	

TABLE 11.—Percentage of nest survivorship for two species of *Mischocyttarus* (Litte, 1977) (initial number of nests in parentheses)

Type of nest	<i>M. labiatus</i>		<i>M. mexicanus</i> 8 weeks
	30 days	50 days	
Single-foundress	38.7(31)	20.0(20)	62(76)
Multi-foundress	62.9(27)	21.1(19)	78(41)

TABLE 12.—Frequencies of three types of nest failures and proportions of failures for single and multi-foundress nests (N = total nests)

Nest/failure	No. failed nests	% total nests	% failed nests
Single foundress (N = 72)			
Parasitization	9	12.5	15.0
Destruction	14	19.4	23.3
Abandonment	37	51.4	61.7
Multi-foundress (N = 54)			
Parasitization	24	44.4	57.1
Destruction	10	18.5	23.8
Abandonment	8	14.8	19.1

foundress nests may have made these more obvious.

In other cases, nests were partially destroyed, leaving only a stem and a few torn cells (Table 12). Though predation was not observed, lizards were very common on the cliffs; many of these are known insectivores. Predation by birds was less likely as they were never seen foraging on the cliff faces and as wasp nests were located in small crevices that were probably inaccessible to the large wrens and tanagers common in the habitat.

Predation of active wasp nests by ants was observed only once, and this by army ants against which the nest owner was no match. Lone-foraging ants, however, were common in the cliff crevices and I often observed ants walking among the vegetation near the nests, clearly trying to climb onto the nests. Upon seeing the ants, wasps assumed alert postures, with antennae forward and forelegs up. They leaned over the nest edges and bit at the ants as the latter approached. If the ants persisted, the wasps vigorously rapped

their abdomens against the nest surfaces, this perhaps acting as warning signals to nestmates. In no case did I see ants successfully mount the nest combs. In addition to active defense, wasps also rubbed the long nest petioles with the venters of their abdomens, presumably smearing a chemical repellent as does *M. drewseni* (Jeanne, 1970). Upon contact, ants did not appear to be disturbed by the petioles but the ants never climbed down them to the combs. In addition, females trimmed the vegetation surrounding their nests in such a way that ants could not reach the comb directly.

The importance of ant predation, however, cannot be overlooked in its possible effects on social behavior. In several 2-female nests, queens and cofoundresses tended to leave their nests to forage only when the other was present. For example, in nest Qa' (Table 13) the queen and cofoundress alternated their paper and nectar or arthropod trips 5 times during a 100-min. observation period, so that at no time was the nest left vacated. In 6 nests, queens made 39.1% of their departures (fiber trips) when cofoundresses were present; the latter never left their nests while the queens were away. As cofoundresses were present an average of only 16% of the observation time, this would indicate that queens deliberately left their nests when other wasps were present. The significance of this in terms of nest defense was clear: nests were rarely left vacated and as single

TABLE 13.—Time and alternation of foraging trips by queen and cofoundress in 2-foundress nest Qa'

Hour	Departure	Return
1050		queen
1050	cofoundress	
1103		cofoundress
1107	cofoundress	
1124		cofoundress
1125	queen	
1131		queen
1131	cofoundress	
1201		cofoundress
1202	queen	
1208		queen
1210	cofoundress	
1220		cofoundress

females were capable of repelling lone-foraging ants from their nest sites, nests of multi-foundress groups were adequately defended. Whether wasps as single individuals or as groups could repel or impede phorid flies is not known. Durations of foraging trips of lone-nesting females were less than those of cofoundresses; the amount of time that single-foundress nests were unattended was thus relatively small.

I found similarly in *M. mexicanus* in Florida that multi-foundress nests were rarely left unattended. Here also the duration of foraging trips of lone-nesting females was short, generally less than the time in which foraging ants (common predators) found and raided unguarded prey items (Litte, 1977).

In numerous cases seemingly intact nests were abandoned; they sometimes contained brood when they were first found abandoned. Though occasionally nest owners were later found re-nesting, they were generally never found again and were assumed to have died. Abandonment was the most common cause of failure of single-foundress nests, and a larger proportion of single-foundress than of multi-foundress nests was abandoned (Table 12, $P = 0.001$, X^2 test). In 3 cases cofoundresses from multi-foundress nests disappeared and queens from these nests then abandoned within 5 days.

Nest and adult survivorship rates during the predaughter periods were considerably higher in *M. mexicanus* than in *M. labiatus* (Tables 10, 11). In Florida, *M. mexicanus* colonies were attacked by birds, but no parasites were reared from nests.

NEST PARASITIZATION.—The behavior of the nest parasites, *Megaselia* species, and the proximate responses of *M. labiatus* females appeared to be very stereotyped, at least the latter indicating an evolutionary history of parasitization. This species of nest parasite was not specific to *M. labiatus*, however, as it was observed in the nests of one other species of *Mischocyttarus* and of a species of *Polybia*. Once a female phorid located a wasp nest (nests of all developmental stages were attacked), she flew rapidly onto the surface, darting and running among the cells, ovipositing

in cells with brood and probably in empty cells as well. After detecting the fly, the immediate response of wasps on the nest was to rapidly chase and dart after it, making frequent biting and wing-buzzing motions. However, in none of the nests in which I observed the parasitization process did wasps appear to be effective in deterring the parasites from laying at least some eggs. Defense by wasps may have limited the number of eggs laid by single phorids, however, for of 25 nests from which parasites were reared (and observed to be attacked by only 1 female each) the number of adult flies ranged from 3 to 124. Nevertheless, in view of the subsequent behavior of the wasps, nest parasitization was an all-or-nothing phenomenon.

Wasps on a newly parasitized nest remained hyperactive for up to 30 minutes after the fly had left the area. Foragers returning during this time at first attempted to distribute their food about the nest, but soon assumed the active behavior of their nestmates. As early as 10 minutes after the initial attack by the fly, wasps began to discard larvae from cells. During the immediate post-attack period, small brood were removed, chewed, and fed to older larvae (Figure 5). In the following 1 or 2 days, pupae were similarly treated; the few remaining larvae were then removed and eaten, as were the eggs. As the nest became freer of brood, wasps spent more time away; many of these nests already had numerous tiny phorid larvae crawling among the cells searching for nondiscarded brood. Adult wasps appeared to be oblivious to these larvae.

In some cases of nest parasitization, the queen then began the prolonged task (which I observed twice in its entirety) of cutting her nest comb from its petiole. During the first 2 hours of this process she did nothing more than occasionally land on the top of the comb and mouth the joint between the comb and petiole. Any nectar foragers returning to the nest at this time were actively solicited by the queen. After numerous of these mounting bouts, the wasp began to walk in a circle around the base of the comb, placing stress on the joint and forcing an oblique angle



FIGURE 5.—Brood-eating by queen of colony of *Mischocyttarus labiatus* following nest parasitization.

between the comb and petiole. When the joint was loosened she bit it with her mandibles, thus cutting the comb free. The fallen comb was ignored by the wasps, and any remaining wasp or fly brood were soon devoured by ants.

In cases where wasps renested in the same site, reusing the same petiole, the queen within several hours of comb-cutting began to construct her first new cell. She performed all of the labor in building this and generally the second cell, though nestmates occasionally returned with nectar and were vigorously solicited by the queen. Other nestmates (females that were dominant cofoundresses on the original nests) joined in the construction of the later cells. During the early stages of nest growth, before all nestmates could fit on

the nest, wasps took turns in their construction activities. Nestmates that foraged during the day often did not spend the night either on or near the nest.

The frequency of brood-eating after parasitization was higher than the frequency of renesting, for lone- and group-nesting females generally discarded at least some brood whether they renested or not. Multi-foundress groups renested after 18 (75.0%) of 24 failures due to parasites; single females renested after only 2 (22.2%) of 9 failures. Fourteen of the 18 multifemale groups and 1 of the 2 lone-nesting females that renested comb-cut and reused the original site. Comb-cutting thus occurred more frequently in multi-female nests (after 58.3% of failures due to parasites) than in single-female nests (after 11.1% of such failures).

The effect of brood-eating and comb-cutting was far-reaching. None of the nests so treated produced live flies. Instead of comb-cutting one multi-foundress group abandoned its nest, after eating most of the brood, and renested 3.5 m away. I reared 124 adult flies from their original nest. Wasps that cut off their combs may have effectively decreased the local parasite population. Parasites clearly migrated into the nest sites, however, for the second nests of several colonies were parasitized.

Despite the comb-cutting behavior, phorids were abundant in the habitat, presumably due to the presence of alternate hosts, the fecundity of females, and the short developmental time of the immature parasites (egg through larva: \bar{X} =5.2 days; pupa: \bar{X} =8.3 days), the latter ensuring that some abandoned parasitized nests produced adult flies before they were raided by ants. The parasitization rate of single-foundress nests was lower than that of multi-foundress nests, yet the former were probably responsible for most of the surviving flies as they were more frequently abandoned. Lone foundresses tended to renest further from original nest sites than did multi-foundress groups, but the new nests of the lone foundresses were often located in the neighborhood of other multi-foundress groups and thus lone-nesters were probably not avoiding parasites by dispersing.

One advantage of multi-foundress groups re-nesting in the same site may be that in this way females from the group are not lost in the re-nesting process. Lone-nesting females would not be so constrained. However, only 1 of 16 females, from 4 multi-foundress groups that re-nested more than 2 m away from their original sites, was unable to find the new nest.

The efficiency of nest relocation was perhaps enhanced by a distinctive behavior of queens. These females, when leaving or returning to their newly initiated nests, walked, dragging their abdomens, over leaves and stems in the area between the original and the new nests. They behaved as though spreading a secretion. Nestmates flying in this area landed on the marked sites, which they then antennated. Due to the low frequency of foragers returning to these small nests, I did not attempt to quantify or experiment with this behavior. Queens were also seen abdomen-dragging around their nests when their cofoundresses disappeared or were removed.

Though such abdomen-dragging in relation to nest relocation has not been reported in other species of *Mischocyttarus* or *Polistes*, Nauman (1975) observed that after army ant raids on nests of several polybiine species, females dragged their abdomens over structures in a trail between old and new nest sites, perhaps spreading a secretion. Dragged structures were antennated by other wasps, and appeared to be functional in the directional and cohesive movement of the colony.

Fitzgerald (1938) indicated that phorid larvae (species not specified) were found frequently in nests of *M. labiatus* in Trinidad. There was no evidence of nest parasitization in either *M. drewseni* or *M. mexicanus*. West Eberhard (1969) described a darting and wing-buzzing behavior performed by females of *P. canadensis* in response to an ichneumonid parasite, but gave no indication that parasitization caused the termination of nests. Survivorship of colonies of these species was not as severely limited as it was in *M. labiatus*.

STRUCTURE REUTILIZATION AND NEST USURPATION.—The tendency of wasps to reutilize previously existing structures (as in reuse of original

petioles after comb-cutting) was apparent in several other circumstances. In 3 cases re-nesting wasps appropriated nests abandoned by other wasps, cutting off the old combs and reusing the petioles. In 4 other cases I observed single females reutilizing abandoned nests, 1 of which was empty at the time. Females laid eggs in these nests after eating some of the brood present.

Nest reutilization behavior graded into attempted nest usurpation. One of the females that first appropriated an unattended nest later flew to an active nest that contained 3 wasps (2 newly emerged daughters and the queen that was away when the foreigner appeared), landed on the nest, and was vigorously attacked upon the return of the queen. After grappling on the ground with the queen, the potential usurper flew off and landed on the vegetation 3 m from the nest. At her next attempt to land on the nest she was again attacked, driven off by the queen, and subsequently not seen again.

I observed only one case of nest usurpation in which a foreign female appropriated the queen role of another individual. This latter wasp then became a foraging cofoundress.

Both nest or petiole reutilization and nest usurpation appeared to be methods of increasing nesting efficiency, in the former case the appropriating wasps earning part of the nest structure, and in the latter case earning an existing or potential work force.

RENESTING RATES.—Because wasps frequently re-nested after their previous nests failed, colony survivorship was considerably higher than nest survivorship. Renesting rates were higher for multi-foundress groups (after 25 (60.2%) of 42 nest failures) than for single-female nests (after 19 (31.7%) of 60 nest failures, $P = 0.001$, X^2 test). Single females began new nests with more delay than groups (3.9 days versus 0.8 days, $P = 0.001$, Mann-Whitney U -test) and at greater distances (9.0 m versus 0.3 m, $P = 0.01$). Nineteen (70%) of the re-nesting multi-foundress groups remained in their nest sites, using their previous nest stems after cutting off the old combs. Because re-nestings would be more difficult to find at greater dis-

tances, the renesting frequency of lone foundresses may have been underestimated.

Many colonies of *M. labiatus* performed multiple renestings (Table 14). In the total population the survivorship of second nestings was similar to that of first observed nestings. An example of multiple renesting by one colony is outlined in Table 4.

Despite the high failure rate of nests, the renesting rate was also high and the density of nests in the study site did not markedly vary. For example, during a 30-day period, 29 nests failed while 28 (including renestings) were initiated.

COMPARATIVE NESTING SUCCESS OF DIFFERENT TYPES OF FEMALES

Colony renesting, precipitated mainly by nest parasitization, served in several cases as natural experiments in comparing the reproductive success of different types of females. Of 30 multi-female nest failures after which at least 1 member of the original colony renested, the queen disappeared in only three. Queens thus remained queens in 90% of the renestings. In the 3 cases where the queens were lost, a cofoundress renested alone in 1, a daughter renested alone in the

second, and a daughter renested with a group of sisters in the third.

Queens renested alone in 3 of the 30 renestings. Two achieved nest growth rates similar to that of the average single-foundress nest (Table 15, nests ZC1" and MC2). The egg-laying rate of 1 female (4 eggs/5 days) was less than her rate during the analogous period in her previous five-foundress nest (7 eggs/5 days) suggesting that the oviposition rate was limited by the cell construction rate.

There were 27 cases of the 30 renestings in which queens initiated the renestings. At the same time that the queens initiated new nests, cofoundresses from 6 of the original colonies left and initiated their own. Five of these nested alone; 1 renested with a nestmate from the original colony. These cofoundresses that became queens were dominant cofoundresses on original nests in all cases but 1 involving a foraging cofoundress.

Mb was an 8-foundress nest that was broken from its support. The queen and 5 cofoundresses renested in the same site (nest Mb1, Table 4); the dominant cofoundress renested alone 7 m from the original nest (nest Mb2). After 3 days, during which she occasionally flew near the queen's nest, this cofoundress rejoined the group, having laid 3 eggs in her own nest. Though initially repulsed by the queen, she persisted in her attempts to join and was eventually successful. In the group she behaved as a dominant cofoundress (Table 4). The wasps of nest Mb1 renested again after their nest was deluged with rainwater in a particularly violent storm. The queen and 4 cofoundresses moved 10 m to their next nest site (Mb3). At the same time the same cofoundress that had previously tried to nest alone did so again, this time taking 1 of the original cofoundresses with her to the same site she had previously used. They worked on this nest (MB2') for 13 days before it was destroyed, the original dominant cofoundress acting as queen and the original foraging cofoundress remaining a forager. The early growth rate of this nest was similar to that of other two-cofoundress nests (Table 15).

After Mb was broken 1 of the original cofoundresses was repulsed on every attempt to land on

TABLE 14.—Number of nestings, failures, and renestings for single- and multi-foundress nests of *Mischocyttarus labiatus* (frequencies shown in parentheses)

Nesting phase	Single-foundress nests	Multi-foundress nests
First nestings	53	29
First nesting failures	45 (84.9)	24 (82.7)
Renestings	14 (31.1)	18 (75.0)
Renesting failures	12 (85.5)	13 (72.2)
Second renestings	3 (25.0)	4 (30.8)
Second renesting failures	2 (66.7)	4 (100)
Third renestings	1	2
Third renesting failures	1	1
Fourth renestings	1	1
Fourth renesting failures	1	0

TABLE 15.—Productivity and growth of ten nests of queens, cofoundresses, and daughters that nest apart from their original colonies (number of cells added since previous stage in parentheses; Q = queen, DCf = dominant cofoundress, FCf = foraging cofoundress, D = preforaging-age daughter, DD = dominant daughter, FD = foraging daughter)

Nest	Number of foundresses	Wasp no.	Role on original nest	Role on new nest	Cells after first five days	Cells when first egg hatched	Cells when first larva pupated	Cells when first adult emerged
ZC1''	1	27	Q, 5→2-foundress nest	Q	5	9 (4)	end of observations	
MC2''	1	28	Q, 2-foundress nest	Q	5	abandoned		
Lb	1	29	Q, 2-foundress nest	Q	3	destroyed		
Mb2'	2	20	DCf, 8-foundress nest	Q	5	destroyed		
		25	FCf, 8-foundress nest	FCf				
Mb5	1	26	DCf, 8-foundress nest	Q		8	8 (0)	10 (2)
Ma'	1	30	FCf, 3-foundress nest	Q		4	6 (2)	10 (4)
Qa'	2	8	DCf, 3-foundress nest					
		9	→ Q, 2-foundress nest	Q	5	7 (2)	FCf death	
			FCf, 3→2-foundress nest	FCf				
Mf'	1	31	D, first to emerge	Q		7	abandoned	
Eb'	6	32	DD, 7th to emerge	Q	6	17 (11)	20 (3)	end of observations
		33	FD, 17th to emerge	FCf				
		34	D, 20th to emerge	DCf				
		35	D, 21st to emerge	FCf				
		36	D, 22nd to emerge	FCf				
		37	D, 23rd to emerge	FCf				
Rb''	1	38	D, first to emerge	Q	4	destroyed		
Control nests								
1-foundress					4.1	8.4 (4.3)	10.3 (1.9)	11.8 (1.5)
2-foundress					4.4	7.5 (3.1)	10.0 (2.5)	28.7 (18.7)
5-foundress					9.0	17.0 (8.0)	25.0 (8)	46.0 (21)

nest Mb1, Mb3, and Mb2. This cofoundress began her own nest (Mb5, Table 4) 25 days after Mb was destroyed, and this was 1 of the few nests in the entire population that produced daughters. The growth rate of this nest was only slightly slower than that of other single-foundress nests (Table 15).

In 2 other situations dominant cofoundresses split from their original groups after nest failures and initiated their own nests while the queens initiated nests with the remainder of the groups. While working on these nests the two cofoundresses frequently flew near the queen's nests and frequently dragged their abdomens over structures in the area between original and new nests (distances of 2 m) presumably trying to gather

recruits. Both cofoundresses abandoned their attempts after laying only 1 egg each, and joined their former groups. Here they maintained roles of dominant cofoundresses (e.g., nest Z0', Table 3).

Females abandoned 3-foundress nest Ma after it was parasitized. Only the foraging cofoundress was found reneesting, this nest initiated 9 days later, 90 m from the original site. This nest was another of the few that successfully produced daughters; its initial growth rate was slightly slower than that of other single-foundress nests (Table 15).

In another situation a cofoundress that had become a replacement queen (nest Qa) initiated a new nest (Qa') with a foraging cofoundress after

the original was parasitized. The early growth rate of this nest was similar to that of normal 2-foundress nests (Table 15).

Of the 30 renestings following nest failures, 2 were initiated by daughters. In one case the first emerging daughter was 4 days old when her nest was destroyed and her mother disappeared. She initiated a nest (Mf') 15 days later, and the early growth rate was similar to that of other single-foundress nests (Table 15). In the other case a dominant daughter initiated a new nest after the original (Eb) was knocked down. She was the seventh daughter to emerge on her nest, and was 40 days old when she assumed the queenship. Her mother and dominant sister disappeared, but 5 sisters remained with her. According to all criteria she behaved as a queen on a multi-female nest. The growth rate of this nest was similar or only slightly lower than that of 5-foundress nests (Table 15).

In the final case, a first emerging daughter replaced her mother as queen on her natal nest. This was later parasitized and she then initiated her own nest (Rb''), Table 15). The nest growth rate during the first 5 days was the same as that of her mother's nest during its first 5 days.

The above cases of renestings demonstrated that all types of females are capable of initiating their own nests; though some appear to achieve slower growth rates than the average, at least some are clearly capable of producing adult offspring.

Discussion

The phorid parasites of the nests of *Mischocyttarus labiatus* may have had 3 evolutionary effects, in addition to the brood-eating response, on the social biology of the wasps. First, the mean larval developmental period was relatively short (16.1 days) as compared to 26.6 days in *P. canadensis* (West Eberhard, 1969), 20.2 days in *M. drewseni* (Jeanne, 1972), and 24.8 days in *M. mexicanus* (Little, 1976). This serves to reduce the time that brood are susceptible to parasites. Second, the first male was produced early (15 days after the

first daughter) in at least 1 *M. labiatus* nest. In *P. canadensis* and *M. drewseni*, first males were produced 30 days and 40 days respectively after the first daughter. Frequencies of renesting were greater for groups than for single females in *M. labiatus*. However, perhaps above a certain group size renesting probabilities did not increase. Thus males could be produced early in the colony cycle without detracting from the colony's probability of renesting. Finally, all types of females of *M. labiatus* (multi-foundress group or lone-nesting queens, dominant or foraging cofoundresses, and first emerging, dominant, or foraging daughters) were capable of renesting (initiating nests) either alone or in groups. This was demonstrated where wasps, after nest parasitization or destruction, renested as complete groups, as splinter groups, or as lone individuals. All types of females were potential reproductives. Queens in colonies of *P. canadensis*, *M. drewseni*, and *M. mexicanus* can be superceded by cofoundresses or daughters. However, whether these latter types of females can act as queens and can initiate nests (as opposed to inheriting nests) in these species is not known. In the study site at Anchicayá, in which nest failure rates were extremely high, yet in which the wasp nest density did not vary markedly, the population was perhaps maintained due to the rapid production of future reproductives by the three methods discussed above.

The early production of males by colonies of *M. labiatus*, if indeed a general phenomenon, may be an evolutionary response both to the high rate of nest failure due to parasitization and to the fact that in this aseasonal habitat where colony cycles were asynchronous, mating could occur year-round. Remaining on the natal nest (though mating away from it) may increase the survivorship of males, an advantage to females as well as males. Toleration of males in colonies of *M. labiatus* (the mean tenure of males on nests of *M. drewseni* is only 4.8 days) may be indicative of a relatively close genetic relatedness of sisters and brothers in this species or of a strategy of male production in which much energy is invested in a few males, i.e., feeding of adult males in the

nest by females is an extension of feeding male larvae.

Survivorship of nests and adults of *M. labiatus* was low, this perhaps explaining several of the reproductive characteristics of co-nesting females, and perhaps helping to answer the question of why cofoundresses joined and remained with the queens in founding nests.

At least 1 cofoundress in colonies of 3 or more females had well-developed ovaries and rarely foraged. Such females could hope to produce their own offspring by laying eggs in their queen's presence, by inheriting a nest from a dead queen, or by inheriting a work force in a renesting situation.

Cofoundresses were responsible for 17% of the eggs laid in nests, but due to differential egg-eating by the queens they appeared to produce no adult offspring. Of 54 multifemale nests queens died and were replaced by cofoundresses in only 2 (3.7%) cases. Survivorship of queens was very similar to that of dominant cofoundresses, explaining the low frequency of nest inheritance by cofoundresses. Of 36 renestings after failures of multifemale nests, 6 (16.7%) were initiated by cofoundresses. Two (33%) of these were successful in producing adult daughters; this value, though representing a small sample size, was actually higher than that for nests in the general population (20% or five producing adult daughters). In 1 of the 6 renestings the dominant cofoundress successfully recruited 1 member of the original nest.

Thus, cofoundresses had little if any chance of producing offspring in their queen's presence, had a small chance of inheriting a nest from a queen, and had a small chance of acquiring part of the original work force while renesting. The high frequencies of adult mortality, nest failures, and renesting perhaps made the maintenance by some cofoundresses of active reproductive systems advantageous. Ovarian development can be maintained only at the expense of foraging behavior. Nonforaging cofoundresses had a higher survivorship rate than did foragers, suggesting that dominant cofoundresses promoted their chances of

producing offspring by being ready at any opportunity to lay eggs and by prolonging the period of time (their longevity) over which they could oviposit.

Only about 17% of the cofoundresses were dominant cofoundresses. Foragers laid no eggs in the presence of queens and did not inherit nests or work forces from queens. As foraging cofoundresses they produced no offspring. However, the flexibility of these females suggested that given the opportunity they were capable of becoming dominant cofoundresses, thereby increasing their likelihood of producing offspring. It thus appeared that females would primarily serve their selfish interests (production of own offspring) if given the opportunity.

Cofoundresses, of course, worked on their queens' nests; they thereby promoted their own interests, as well as those of the queens', by virtue of their genetic relatedness to the queens. Foraging cofoundresses contributed much to the maintenance of the colonies. Dominant cofoundresses, on the other hand, contributed little. They foraged infrequently, and the proportion of their on-the-nest time that they worked was very small. It seems unlikely that they represented an important element, as compared to the queens and foraging cofoundresses, in the welfare of the nests unless they contributed to defense of the nests or unless stresses, such as disappearances of queens or foragers, were applied to the colonies. In these latter situations, dominant cofoundresses could replace queens or foragers, thus crucially contributing to the survival of the colony.

The readiness of dominant cofoundresses to assume the role of forager was not necessarily a large sacrifice of selfish interests. Such females, once deprived of all foraging nestmates, would not have had work forces to inherit even if they did reneest. They gave up minimal chances of producing surviving eggs. Thus their only sacrifices came in decreasing the possibility of inheriting nests from queens. Survival of brood and thus the production of a future work force became the cofoundresses' prime function. The interests of these females were ambivalent even in these

situations, however; they worked to produce offspring that were related to them and that would in turn work for them if they (the cofoundresses) reverted to their roles as dominant cofoundresses.

Survivorship of adults and nests of *M. mexicanus* was considerably greater than that of *M. labiatus* (Litte, 1977). In the former species, colonies each contained 1 queen, 1 or more cofoundresses that, though having little ovarian development, did relatively little foraging, and 1 or more foraging cofoundresses. Survivorship of queens was greater than that of cofoundresses. Nest failures were infrequent enough to make renesting rare. Thus, cofoundresses had little chance of producing their own offspring. Maintenance of developed reproductive systems by these females would have been of little advantage.

Survivorship rates in *P. canadensis* and *M. drewseni* are not known. However, in *P. canadensis* (West Eberhard, 1969) reproductive females during the early stages of colony development compete for the queenship, and thus some stand to inherit nests and work forces from defeated contenders. In *M. drewseni* (Jeanne, 1972) some cofoundresses lay eggs and may thereby produce a few of their own offspring.

Low survivorship of single-foundress nests and of lone-nesting females may also help to answer why many females of *M. labiatus* joined and remained in groups with queens. Over 30-day periods, survivorship of multi-foundress nests was greater than that of single-foundress nests, perhaps due to better defense against ants, and possibly parasites, and to the greater chances of the nests surviving the death of one foundress. However, survivorship of multi-foundress nests was similar to that of single-foundress nests over 50-day periods. Multi-foundress nests were more likely to be parasitized than single-foundress nests and this difference may have been most prevalent during the 30- to 50-day periods when multi-foundress nests were larger than single-foundress nests. However, as probability of renesting was

greater for groups than for single females, the average longevity of colonial females would be expected to be greater than that of lone-nesting females. Survivorship of lone-nesting females, similar to that of foraging cofoundresses, was considerably lower than that of dominant cofoundresses. Many lone females initiated nests and then disappeared within a few days, leaving intact nests. Of the 7 nests I observed initiated by lone cofoundresses or daughters, only 2 were successful in producing adult offspring. Three were abandoned by cofoundresses that then rejoined their original groups. Clearly some females were incapable or unwilling to nest alone; they perhaps served their interests more by helping relatives, and by waiting for opportunities to produce their own offspring within a group, than by nesting alone.

Lone-nesting females perhaps adjusted their nesting behavior and subsequent nest growth patterns to minimize their mortality rates. Adult mortality rates varied with the time spent away from the nest (a measure of foraging activity). Lone-nesting females that rarely foraged after larvae began pupating and whose nests grew very slowly after eggs began hatching perhaps profited in this pattern of nest growth by increasing their survivorship at the cost of producing fewer offspring early in the colony cycle.

All females of *M. labiatus* behaved, though to varying degrees, so as to serve both selfish and familial interests. In an analysis of the evolution of social behavior, selection at the levels of individual and kin must be considered. Wasps from multi-foundress nests renested as groups whether their original nests failed during the predaughter or the postdaughter phase. Renesting foundress groups thus consisted of females of a variety of familial relations, e.g., mother-daughter(s); mother, her sisters and her daughters; sisters; aunts-nieces. Because nest foundresses are often less closely related than siblings, in this species the importance of individual selection may be relatively great.

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