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The Social Biology of Polistine Wasps

BY

MARY JANE WEST EBERHARD
Universidad del Valle, Cali, Colombia

ANN ARBOR
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN
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(Continued on back cover)

CORRECTION SHEET

p. 21, line 17—for “an average of 0.85 loads” read “an average of 0.79 loads”

p. 22, Table 1 revised as follows:

TABLE 1

INDIVIDUAL DIFFERENCES IN QUALITY AND QUANTITY OF FORAGING (*P. fuscatus*)¹

	Foraging Rate (loads/hour observed)	Per Cent of each load-type in total recorded loads		
		% Pulp	% Water	% Food
Queen	0.11	75	25	—
Other Foundresses				
1	0.64	50	14	36
2	1.05	39	41	20
3	1.16	22	56	22
Offspring				
1	1.57	25	65	10
2	0.75	44	33	22
3	0.72	9	76	15
4	0.60	25	—	75
5	0.86	21	44	35
6	0.35	14	50	36
7	0.41	45	12	43
8	1.33	10	30	60
9	0.69	14	68	18
10	0.35	34	55	11
11	1.25	10	70	20
12	0.65	7	35	58
13	0.70	—	—	100
14	0.84	10	25	65

¹ Summary of lifetime records of all colony B38 females which brought 10 or more foraged loads to the nest during 102 hours of observation, June–September 1964. Foraging rate is given in loads/hour observed during life as active forager (period between first and last observed foraging trip). Offspring females are listed in order of their emergence.

p. 25, Table 3—for “No. 13” in bottom line, read “No. 18”

p. 42, Table 8—the symbols “<” and “>” should be reversed

p. 67, line 13—for “p. 00” read “p. 40”

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That old and true method of natural history—observation—must ever have a large share in the study of living things. Observation, experiment and reflexion are three in one. Together they are omnipotent, disjoined they become impotent fetishes. The biology of today, as we are beginning to realize, has not too much laboratory, but too little of living nature.

C. O. Whitman (1902)

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INTRODUCTION

PAPER WASPS of the genus *Polistes* (Vespidae, Polistinae) are social insects. They live in colonies having one egg-laying female (queen) and a number of workers which care for the queen's brood but do not oviposit. Colonies are founded by one or a few females and rarely last more than a year, even in the tropics. There are no known consistent morphological differences between queens and workers like those found in various ants, bees and termites.

Polistine wasps are of special interest to students of behavioral evolution because they are uniquely well suited for comparative study likely to provide insights into the nature and origins of animal sociality in general. Wasps have the compact life cycles characteristic of most insects, and are therefore more amenable than are social vertebrates to comprehensive studies of behavior. Vespid wasps range in degree of sociality from the solitary Eumenidae to the highly social Vespinae (yellow jackets and hornets), providing ample comparative material within a single superfamily. Among the vespids, *Polistes* has been called a "key genus" for understanding the evolution of sociality (Evans, 1958). It is represented by more than 150 species living in both tropical and temperate zones and exhibiting varied forms of colony organization intermediate between those of subsocial species (in which one or both parents care for their own young) and highly social ones (having a morphologically distinct sterile caste). The small, open (unenveloped) nests of *Polistes* make it possible to view the entire society simultaneously and to mark individuals for identification without disruption of normal activity. No social vertebrate and few other social insects can be observed in nature with such convenience.

This report describes the nature and functions of social behavior in polistine wasps primarily by comparing a temperate zone species, *Polistes fuscatus* (Fabricius), the common brown paper wasp of North America, with a predominantly tropical relative, *Polistes canadensis* (Linnaeus). Colonies of both species were observed during all stages of the colony cycle from nest initiation to abandonment. Extensive marking made it possible to record the functions and interactions of particular individuals, and long-term observations of undisturbed colonies provided information on the sequence of changes in colony composition and behavior.

Although about two-thirds of the approximately 160 recognized *Polistes* species live in the tropics, only two or three tropical species have been studied biologically. Generalizations about polistine social life are based

chiefly on investigations of a European wasp, *Polistes gallicus* (Linnaeus), and four species observed by Rau (1929) in Missouri. The only previous long-continued, intensive study of marked wasps in nature was carried out by Pardi (1942), who watched five colonies of *P. gallicus* almost daily from time of nest initiation to emergence of the first brood. Recent experimental investigations have focused on particular aspects of polistine biology, including caste determination (Deleurance, 1952a), nest building (Deleurance, 1948a, 1957), brood abortion (Deleurance, 1955) and dominance interactions (Pardi, 1946-48a; Deleurance, 1950; Pardi and Cavalcanti, 1951), and control of oviposition (Gervet, 1964b).

The most extensive previous behavioral study of tropical *Polistes* was that of Rau (1933), who observed various tropical bees and wasps, including *P. canadensis* and *P. versicolor* Olivier, for five weeks in Panama. Fragmentary observations of tropical *Polistinae* are mentioned by Hamilton (1964b), Kirkpatrick (1957), Roubaud (1916), and Zikán (1951). Other non-taxonomic literature on tropical *Polistes* deals with nest form (e.g., Bertoni, 1912) and size and composition of collected colonies (Richards and Richards, 1951). Richards and Richards (1951) summarized the impression given by these studies: "Biologically, the S. American species of *Polistes* are not very different from those of temperate countries, except that colonies are often founded by swarms rather than by single fertilised females" (p. 3).

The observations reported here show that there are important behavioral differences between temperate-zone and tropical *Polistes* species. They also provide new data on (1) the nature and functions of interactions involving dominance, and (2) the individual histories, manners of determination, and reproductive roles of queens and workers. Emphasis is placed on information relating to the evolution of social life in wasps and of general interest to the study of animal societies.

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TAXONOMY AND DISTRIBUTION

The *Polistes fuscatus* of this study is the typical form, *P. fuscatus fuscatus* (Fabricius). *P. fuscatus* and allied species (the "fuscatus group" of Bohart, 1949) have the northernmost range of any American *Polistes*, ranging as far north as Chilcotin, British Columbia (52° N. latitude) and south to Honduras, but being absent from continental South America (Bequaert, 1940).

P. canadensis, on the other hand, has a range centered in the tropics, with its northernmost representatives in the southwestern United States (Bohart, 1949). The populations observed in this study were of two color varieties; they were identified by Karl V. Krombein, U.S. National Museum, Washington, D.C., as *P. canadensis erythrocephalus* Latreille, found in the highly cultivated Cauca River Valley near Cali, Colombia (called "dry tropical forest" by Espinal and Montenegro, 1963), and *P. canadensis infuscatus* Lepeletier, found at 400 meters elevation in the densely forested Cordillera Occidental of the Andes directly west of Cali (an area called "very humid tropical forest" by Espinal and Montenegro, 1963). When the taxonomy of the forms presently called *canadensis* is better understood these subspecies may prove to be distinct species, as did the North American "subspecies" *annularis* Linnaeus. In this connection it may prove of interest that the vertical, planar combs of *P. canadensis infuscatus* differed consistently from the combs of *P. canadensis erythrocephalus*, which were somewhat horizontal and had concave upper surfaces due to divergence of the cell sides.

Although there are few marked structural differences among *Polistes* species, *P. canadensis* and *P. fuscatus* represent contrasting forms within the genus. Bequaert (1940) placed them at opposite ends of his key to the four "structural species" of North American *Polistes*, now considered four species groups (Bohart, 1949). Earlier, Bequaert (1918) noted that *canadensis* and *fuscatus* represent extremes among *Polistes* of the world with regard to the general shape of the abdomen, a character which had been used by H. de Saussure to separate the species into natural groups. This suggests that the evolutionary lines represented by the two species of this study diverged relatively early in the history of the genus. Therefore, differences seemingly related to the contrasting climatic conditions in which the species are presently found might also be due to other factors in the different phylogenetic histories of the two species.

METHODS OF OBSERVATION

This report is based primarily on field observations of marked wasps on unmanipulated nests. Forty-seven colonies containing marked individuals were observed for a total of 435 hours. Of these hours, 385 were spent watching two or more colonies simultaneously. Additional field data were provided by hours devoted to photography, collecting, and observation of wasps away from the nests.

Colonies were observed at their natural sites, on man-made structures (including buildings, tombstones, and an abandoned mine entrance). Each observation colony is identified in the text by a letter denoting its

locality and a number distinguishing it from other colonies at that site. For example, B38 identifies colony 38 at locality B. I observed *P. fuscatus* at localities A through S, located near Ann Arbor in southeastern Michigan (42°N. latitude), and *P. canadensis* at localities T through Z, located near Cali in west central Colombia (4°N. latitude). *P. canadensis infuscatus* was found only at locality U (25 miles west of Cali), where *P. canadensis erythrocephalus* was absent. Precise locations of the sites are given by West, 1967a (Appendix).

The following classification of colony stages in terms of nest contents was used to indicate relative age and probable adult composition of observation colonies:

Pre-emergence. Period from nest initiation to emergence of the first adult. Nest has no vacated pupal cells.

Emergence-enlargement. Period from the emergence of the first adult to the beginning of brood decline. Nest has shallow peripheral (new) cells containing eggs, and vacated pupal cells containing second brood.

Post-enlargement. No further new cell addition, as indicated by the absence of shallow egg-containing peripheral cells. Vacated pupal cells remain empty. There is an increasing number of empty cells and few eggs.

The females of a colony will be designated as follows:

Queen. The primary (usually the only) egg-layer.

Worker. A female offspring of the queen which foraged during its recorded history on a nest.

Non-worker. An offspring female which did not forage during its recorded history on a nest.

“Forage” means “brings loads to the nest.”

Individuals were marked with model airplane paint without anaesthetization or removal from the nest, in order to minimize disruption of the colony. Movement of wasps as they were marked produced useful variety in the size and position of marks, and locomotion and grooming kept paint from adhering to joints. In a few cases, carbon dioxide was used as an anaesthetic for whole colonies, but colonies used for long-term observations were not anaesthetized.

Nest maps showing the position and contents of each cell on each observation day provided a record of nest growth and colony composition, as well as indicating the dates of hatching, pupation and emergence for individuals of the brood. In this study individuals are called “pupae” if they are within a cell capped by the top of the silken cocoon spun by a mature larva.

A continuously-recording Bristol humidothermograph monitored temperature and relative humidity within ten feet of observation colonies at localities B and W. "Mean daily temperatures" used in the text are averaged daily means recorded at a U.S. Weather Bureau station seven miles southeast of locality B. Lowest night-time temperatures (those least likely to be affected by differences in position and shelter of recording instruments) recorded 8 July–30 September at locality B showed a high correlation ($r = 0.99$; $N = 29$) with the station records.

Two sets of observations spanned the colony cycles of *P. fuscatus* and *P. canadensis* from nest initiation to abandonment:

1. Pre-emergence colonies were observed for *P. fuscatus* at locality B (11 colonies) during the period 8 May–25 June 1965, and for *P. canadensis* at locality V (12 colonies) during the period 6 March–4 April 1965.
2. Four colonies were observed at one to two day intervals from before adult emergence until natural colony decline as follows: colony B38 (*P. fuscatus*), 17 June–18 September 1964; colonies W2, W3, W5 (*P. canadensis*), 20 November 1964–26 April 1965. On each observation day colonies were watched for at least one hour. Nest maps were made, newly-emerged individuals marked, and all marked individuals and their activities listed.

In addition I have observed pre-nest-founding and nest-founding behavior of several *Polistes* species in the southwestern United States: *P. flavus* Cresson, *P. major* Beauvois, and *P. canadensis navajoe* Cresson near Portal, Arizona; and *P. annularis* Linnaeus, *P. exclamans* Viereck, *P. metricus* Say and *P. rubiginosus* Lepeletier near Willis, Oklahoma.

High-speed motion pictures and still photographs supplemented written field notes in the analysis of rapid movements such as those involved in mating and construction behavior. The photographs which accompany the text were taken with a 35 mm single-lens reflex camera fitted with bellows, 135 mm lens, and electronic ring-strobe.

All dissections were of freshly-killed specimens. Number of oocytes present in the ovary was estimated by counting the number of bulges visible in the ovarioles at a magnification of 19X. This number was then divided by two, every other "bulge" being a group of nurse cells (Imms, 1964).

SOCIAL INTERACTIONS AMONG POLISTINE FEMALES

INTERACTIONS INVOLVING DOMINANCE

DOMINANCE AND SUBORDINANCE.—Dominance behavior in both species of this study is like that described by Pardi (1948a) in the European wasp,

Polistes gallicus: Dominant individuals move toward subordinates, antennate them vigorously, sometimes bite along the thorax, abdomen and wings, and hold the head erect when offering drops of liquid. Subordinate individuals turn away from dominants or become immobile in their presence, and sometimes offer drops with the head held low.

Pardi (1946, 1948a) demonstrated that a linear dominance hierarchy forms among the foundresses (females present during the pre-emergence period) and, later, the workers of a colony, and that there is a correlation between dominance order and ovarian development: dominant individuals generally have larger ovaries than do females ranking below them in a hierarchy. This conclusion is supported by the work of Gervet (1962, 1964a) on *P. gallicus*. I have observed dominance hierarchies among foundresses in *P. fuscatus*, *P. canadensis*, *P. flavus* and *P. annularis*, as have Morimoto (1960, 1961a, 1961b) in *P. chinensis antennalis* Perez and Yoshikawa (1963a) in *P. fadwigae* Dalla Torre. The latter author noted that the most dominant worker becomes the primary egg-layer following queen removal. Similarly, I have observed in *P. canadensis* that the most aggressive contender among females on a nest following queen removal begins laying eggs; and in *P. fuscatus* that the highest ranking females in a hierarchy on a newly founded nest were the only egg-layers (see "Foundress Associations," p. 25). These observations indicate that Pardi's conclusions regarding dominance and ovary size in *P. gallicus* apply to other *Polistes* species.

It is possible to distinguish dominants from subordinates and to predict the outcome of encounters simply by comparing the postures of the two individuals: the higher is dominant (Figure 1). "Equals" rise simultaneously higher and higher from the substrate, with increasingly violent antennal clashing and, finally, biting and stinging. This sometimes results in a "falling fight" in which grappling females lose their foothold on the nest and fall to the ground.

Fighting seldom results in obvious injuries, but I once saw a female fatally injured in a fight. Although the nature of the injury was unknown, she lay on her back with legs twitching and was thereafter unable to walk or fly. Usually, however, one of the encountering individuals acts subordinate and the interaction ends without a fight.

Dominance relations affect the positions of females on the nest (Pardi, 1948a). On pre-emergence nest W4 (*P. canadensis*, 1 December 1964) the dominant female usually sat on the nest face, the second-ranking female on the top near the pedicel, and the third-ranking female off the nest. This spacing was maintained because each time a subordinate moved toward the nest face she was attacked by a higher-ranking female and retreated.



FIG. 1. Dominance and subordination (*P. fuscatus*). The posture of the wasp on the right—head, body and antennae low—characterizes subordinate behavior; the elevated position of the wasp on the left is characteristic of dominance. Leg biting (shown here) is a common form of strong dominance.

On mature nests the same phenomenon typically keeps workers spaced about the nest face and might thus increase the effectiveness of colony defense.

On *P. fuscatus* nest B38 I noted during August (after disappearance of the queen) that spacing was maintained not by direct dominance encounters but by some individuals darting at approaching nestmates from given positions on the nest. I first noticed this seemingly territorial behavior while photographing a worker on which I had focused so that her length filled the camera's field. The worker repeatedly made swift darts out of the field toward other wasps, then returned to the precise spot where she had been before. Further observation showed that workers do not occupy the same positions from day to day, and do not restrict their brood-care activities to any one region of the nest.

OFFERING AND SOLICITATION AMONG ADULTS.—When a laden forager returns to the nest she frequently shares her load of pulp, solid food, or nectar with one or more nestmates, who may in turn re-divide portions with other individuals. Transfer of regurgitated liquids (and, less often, solids) fre-

quently involves antennation by the solicitor, whose antennae stroke those of the laden wasp near the head, alternately from above and below. During the transfer the receiving wasp ("solicitor") usually behaves as a dominant (active and standing high from the nest surface) whereas the offering (laden) wasp acts subordinate (immobile and with relatively low posture). Pardi (1948a) noted that transfer of regurgitated fluids proceeds from subordinate to dominant individual in *P. gallicus*; Morimoto (1960) observed the same effect of dominance in transfer of solid food.

As noted by Morimoto (1960) solid-load transfer often occurs without bodily contact. The two individuals simply stand face-to-face chewing at the load from opposite sides until it is divided and they separate. In some cases the solicitor behaves aggressively and seizes the entire load.

Returning foragers may initiate load transfer rather than beginning to build or feed larvae when they reach the nest. They stand with head raised and the load held in the mouthparts, turning toward passing individuals. I have seen a *P. fuscatus* worker thrust a load of food material at an unresponding nestmate with such force that bits of the load stuck to the associate's face. In contrast to the posture of a laden wasp during transfer, which is that of a subordinate, an offering wasp raises its head and body to the height of the individual it is approaching. In this respect offering behavior resembles a dominance interaction between equals. Since equals interact more frequently than do individuals more widely separated in the dominance ranking (see Pardi, 1948a; Morimoto, 1961b), this posture may stimulate aggressive behavior (solicitation) in an approached individual.

The communicative significance of the posture and approach of a wasp returning to the nest is especially evident in post-enlargement colonies having a large population of idle adults and few foragers. Wasps (laden or unladen) which land in the middle of the nest are frequently mobbed by soliciting adults, whereas individuals which land on the side and/or remain low upon landing avoid interaction with nestmates. Males and unladen females sometimes scurry with head and body low to the nest top, thus avoiding contact with solicitors and conserving the contents of their crop.

ABDOMEN-WAGGING.—Abdomen-wagging is a movement performed most frequently and energetically by queens, and occasionally by other females ranking high in the dominance hierarchy. The abdomen is pressed against the nest surface and moved back and forth producing an audible vibration of the nest. This movement is particularly associated with the increases in aggressiveness, activity, and solicitation which often precedes egg laying. It is performed at different rates at different times from a sluggish stroking by the abdomen of a walking wasp to a strong, rapid, and violent shaking of the whole body by a wasp standing in one place. Strong abdomen-wagging

often follows an aggressive encounter between a queen and a high-ranking subordinate, e.g. another egg-laying co-foundress on a pre-emergence nest; and it sometimes evokes an abdomen-wagging "answer" from an associate. This signal is most conspicuous during the pre-emergence period or after queen disappearance—when there is dominance and/or egg-laying competition among females.

Abdomen-wagging occurs in every *Polistes* species I have observed at the nest—*fuscatus*, *canadensis*, *flavus*, *annularis*, and *exclamans*. In *P. annularis* it is very vigorous and produces a sharp nest vibration heard several feet away. In *P. fuscatus* and *P. flavus* abdomen-wagging is generally slower and the sound softer.

Morimoto (1961a) noted abdomen-wagging in dominant females of *P. chinensis* and also considered it a signal because subordinates avoid individuals doing it and "sometimes leave the nest in response" (p. 242).¹ He also saw an abdomen-lifting motion characteristic of the queen and speculated that it might be the means by which nestmates recognize queens. Pardi (1942, p. 27) noted that the cell inspections by *P. gallicus* workers dispensing food to larvae are accompanied by "scondinzolamento" (tail-wagging), and compared this to the abdomen-wagging in the "dance" performed by honeybee foragers upon return to the hive (Von Frisch, 1961).

Mr. Robert L. Jeanne has brought to my attention the observation of Van der Vecht (1965, p. 441) that "In many social wasps there is a more or less distinctly delimited nonsclerotized area at the anterior margin of the sixth gastral sternite which may be a scent-producing organ of importance to social life." Mr. Jeanne has examined sterna of various wasps, including *P. fuscatus* and *P. canadensis*, and finds a glandular structure in the region mentioned by Van der Vecht; similar sternal glands have been described for various Vespinae (Bordas, 1908; Hammad, 1966). It is possible that a secretion of this gland is applied to the nest surface during "abdomen-wagging," and thus that the motion has some chemical communicative function.

NESTMATE RECOGNITION.—Observations of marked adults indicate that colony residents identify non-resident wasps in at least two ways: by their manner of approach to the nest (noted by Hamilton, 1964b), and by their dominance behavior.

Resident wasps usually fly swiftly and directly to the nest. However, non-residents frequently approach slowly or hover nearby without landing. Resident wasps respond to a hesitating approach by coming to the edge of the nest where they face the intruder with raised (aggressive) posture,

¹ Dr. R. Matsuda kindly translated portions of this paper written in Japanese.

waving the front legs in the air in a characteristic pre-flight manner, and sometimes buzzing the wings. Sometimes an alert resident leaves the nest to attack a sluggish approacher.

Approach behavior is the recognition cue rather than some other characteristic of the individual, as shown by "recognition mistakes" involving the attack on known (marked) nestmates. Foragers returning to the nest with unusually large food loads or abdomens distended with water fly sluggishly and sometimes approach the nests several times before gaining the momentum necessary to maneuver while landing. An extreme example of this was a heavily-laden worker of colony V5 which flew in pendulum-like arcs toward and away from the nest, landing at various points on the wall near the nest before gaining enough speed in the proper direction to land. This and other observed such approaches by nestmates evoked the same kind of aggression as that directed at non-residents.

Resident females usually antennate or contact mouth-to-mouth females which land on the nest. If neither acts subordinate, a fight ensues which may result in one individual leaving the nest. Such fights are conspicuous in pre-emergence associations: females become residents only when dominance conflict is absent (see *Foundress Associations*, p. 25). One instance of conflict prior to joining involved a transient female (No. 18) and the most subordinate resident of nest B18 (No. 15). No. 18 repeatedly approached the nest and fought with No. 15 for more than a week before becoming resident there as a subordinate to the latter. There was no evidence of dominance conflict with the five other nest residents, presumably because No. 18 was subordinate to them (being similar in rank, and hence in conflict with, lowest ranking No. 15). Thus dominance relations with residents are a "recognition" factor in the decision to accept or repel an approacher.

Rau (1939) had the impression that there is nestmate recognition by colony odor, and Pardi (1947) hypothesized that odor plays a role in individual recognition among associates as well as in discrimination between nestmates and non-nestmates, since in both cases some differential reactions do not seem to involve dominance cues. I have noticed that returning foragers sometimes walk directly to the queen, bypassing other nestmates, and offer solid material without solicitation or obvious dominance behavior by the queen. However this observation and those cited by Pardi (1947) do not eliminate the possibility of individual recognition by learned visible characteristics.

CLUSTER FORMATION.—Idle females sometimes cluster on nests, and clustering off the nest is common in *P. fuscatus* during autumn and spring. Clusters can be induced by subjecting wasps to low temperatures (Rau, 1938) or by putting them with immobile individuals. On 24 April 1963, I placed three

females in each of 41 jars and refrigerated them overnight at 5°C. Eighteen of the jars contained only live wasps and 23 contained in addition a dead female glued to the wall of the jar. Of the 54 wasps in jars without a dead female, 20 (37 per cent) came to rest in contact with others but the majority (63 per cent) remained dispersed. In the jars containing a dead wasp, a larger proportion (64 per cent) clustered and 52 per cent of these were in clusters including a dead wasp.

Direct observations of cluster formation show that a wasp rests in contact with another only if the latter is or becomes immobile when touched. Thus subordinate individuals (which become immobile when they encounter a dominant wasp) and chilled or dead wasps served as cluster nuclei. Wasp-size decoys (small cylinders of wire screen) were less frequently antennated than dead or living wasps and never induced clustering.

ALARM SIGNALS

When a *Polistes* female is approached suddenly by any moving thing, she reacts aggressively, with elevated posture, lifted wings and raised front legs. When I approached a colony, large numbers of females sometimes came to the nest edge and adopted this alert posture; but there is no evidence that intra-specific communication stimulates their concerted action. Rather, it appears to be a result of simultaneous but independent individual reactions.

Sometimes, however, a single alerted female darted suddenly, causing an audible vibration of the nest, which then quickly bristled with aggressive wasps. Furthermore, when collecting live specimens at night, when all wasps are immobile on the nest, I could remove them with forceps one by one without disturbing the colony if I seized each wasp by one leg and waited for it to climb onto (attack) the forceps before taking it off the nest. If pulled away suddenly, the wasp's tarsi caught in the nest carton, making a sharp vibration and alerting the entire colony.

These observations suggest that substrate vibration is an important component of alarm signals in *Polistes*, many of which involve swift or jerking movements and audible nest vibrations.

Females sometimes react to the approach of an intruder, such as a large flying insect, by darting once or twice and flipping their wings. This reaction sometimes spreads to other individuals several seconds after the intruder has flown away. Workers occasionally dart at each other in this fashion on the nest face, and one sudden dart by a female on one part of the nest is sometimes followed immediately by a dart by a female on another part of the nest.

The most intense alarm signal I have observed in *P. fuscatus* is that stimulated by the presence of the ichneumonid parasite *Pachysomoides fulvus* (Cresson), which lays its eggs in cells containing developing *Polistes* pupae. The *Pachysomoides* female lands near a *Polistes* nest and sits absolutely immobile, initially several inches away. It remains immobile until there are no wasps near the edge of the nest, or until those present turn away. It then advances suddenly toward the nest, sometimes only a fraction of an inch. Unless chased away it alights on the nest and thrusts its ovipositor through a cell wall. When a *Polistes* female detects a *Pachysomoides* female on or near the nest, she darts at it, causing it to fly away, and begins hyperaggressively darting and wing-flipping about the nest, particularly on the periphery and sometimes even off the nest near its edge. This causes a general rise in activity and other females begin to dart and flip their wings, although with less intensity than the original alarmist. I have seen darting and wing-flipping continue for as long as ten minutes after the parasite has taken flight.

In the several times I have observed this behavior, I have never seen wing-flipping by many females in *P. fuscatus* without later finding a female *Pachysomoides* nearby. Sometimes I noticed the small ichneumonid's presence only because the nesting wasps had begun their aggressive display.

When pupal caps remain on abandoned nests, close inspection often reveals two or three small neat holes on the sides of the cell where the *Pachysomoides* adults have emerged, leaving a pale dried bit of *Polistes* pupa (usually only the head, thorax, and appendages) above the oblique planar caps of the parasite cocoons. Gaul (1940) and Rau (1941) state that eggs are placed on larvae but neither author observed oviposition. I have seen oviposition by *Pachysomoides* four times, always into pupal cells.

Apparently the wasps' only defense against this parasite is discovery and routing of the female before oviposition takes place. There is no evidence that the wasps selectively destroy parasitized pupae.

Females of *P. canadensis* show the same alarm behavior at the approach of a similar parasite, *Pachysomoides stupidus* (Cresson). Once when the "parasite alarm" began on nest W2 I watched for a *Pachysomoides* female. There appeared instead a fat, striped fly (Diptera). It sat facing the nest briefly, then moved onto the nest face where it crawled about for several seconds while all of the wasps on the nest flipped and buzzed their wings. The alarm continued for several minutes after the fly left. Meanwhile a worker returned to the nest and distributed a load of water. She was the only female present not showing alarm behavior, except for occasional wing flips when darted at by an alarmed nestmate. However, when she had

finished dispensing her load, she began moving about the nest like the others, darting and flipping her wings. This is evidence that the parasite alarm is communicated to nestmates which have not directly perceived the presence of a parasite.

I did not see the fly oviposit, and none of the cells contained evidence of parasitism when I collected the nest three months later. However, a number of abandoned nests collected at localities X and Y contained brown dipterous puparia about 1 cm long; and an inhabited post-enlargement nest at locality Z contained living pupae in the same type of puparium. Roubaud (1910) observed a dipterous (tachinid) parasite of *Belonogaster* (Polybiinae) in Africa.

Females of *P. canadensis* show a distinctive reaction to ants which approach the nest. They stand buzzing their wings near the pedicel, which is the only access to the nest for pedestrian predators, and peck sharply at the ants with their mandibles. This behavior has some of the qualities of a signal: the wing-buzz comes in short loud bursts separated by intermittent pecks, producing a sound pattern heard only in the presence of ants. However, this does not seem to lead to a change in the behavior of other individuals.

NATURE AND FUNCTIONS OF THE QUEEN

OVIPOSITION.—The primary division of labor in *Polistes* is reproductive, the queen usually being the sole egg-layer among the females of a colony. The other tasks of the colony—building and brood care—are shared by individuals of both castes (Steiner, 1932; Pardi, 1942, 1951; Owen, 1962).

DOMINANCE.—The queen is dominant in her interactions with nestmates, a characteristic associated with her developed ovaries (Pardi, 1946, 1948a).

One result of the queen's dominance is stimulation of foraging by associates. She frequently and vigorously solicits from other females, and I have seen workers leave the nest after aggressive mouthpart solicitation or chewing along the body and wings (Fig. 1) by the queen. These workers sometimes return with foraged loads.

CELL INITIATION.—In established colonies of both *P. canadensis* and *P. fuscatus* the queen is the primary initiator of new cells. Twenty-three of 26 recorded cell initiations in *P. canadensis* (localities V and W) were by queens, as were 22 of 28 in *P. fuscatus*.

A close temporal association between building behavior and oviposition by queens suggests that individuals having mature ovarian eggs are stimulated to build (Fig. 2). In *P. canadensis* queens usually apply pulp within the ten minutes preceding oviposition. They sometimes add pulp to one

cell, then oviposit in another; but the usual sequence was new cell construction followed immediately by brief antennation of the cell and oviposition. Queens frequently go from construction to egg-laying in an unbroken series of movements.

In *P. fuscatus* the temporal association of building and oviposition is more variable. Once the queen of colony B10 added a load of pulp to a peripheral cell, then immediately went to another cell and oviposited. But more commonly there was a delay of 10 to 60 minutes between pulp addition and oviposition by *P. fuscatus* queens.

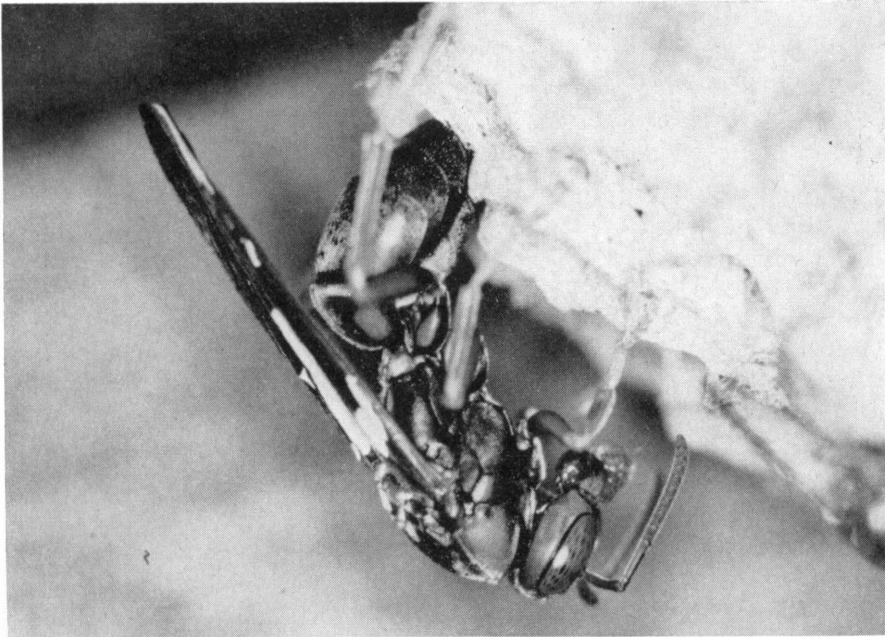


FIG. 2. Ovipositing queen with pulp. After several minutes of aggressive solicitation from nestmates the queen of colony A1 (*P. fuscatus*) obtained pulp from a worker, then began to oviposit in a peripheral cell before applying the pulp to the nest. Although building usually precedes egg-laying, this photograph illustrates the characteristic association between pulp acquisition and oviposition by *Polistes* queens.

Deleurance (1950) found that empty cells stimulate oviposition, and that subordinates lay eggs even in the presence of a queen if the eggs are removed from the nest leaving many empty cells. Therefore it could be argued that oviposition often follows construction activity simply because construction activity is likely to produce an oviposition stimulus in the

form of a new cell. However, oviposition is associated with construction activity even when new cell building is not involved. Sometimes a queen adds pulp to one cell, then oviposits in another. In *P. fuscatus*, building sometimes precedes oviposition even when empty cells are present and have been repeatedly antennated by the queen. The queen of colony A1 was photographed while ovipositing in such a cell after pulp acquisition but before beginning construction (Fig. 2).

Specialization of queens in cell initiation probably exists in other *Polistes* species. Morimoto (1959) observed that in *P. chinensis* oviposition often follows construction behavior "within a short time" (p. 113) and that the rate of new cell addition is similar to that of oviposition although "it is not evident whether the former is correlated with the latter" (1954, p. 522). Roubaud (1916) noted that in the African polybiine wasp *Belonogaster* workers (newly-emerged foragers) "ne paraissent pas prendre une part effective a la construction des nouveaux alveoles. Cette besogne est le propre des femelles fecondées, mûres sexuellement et prêtes a pondre" (p. 120).

Previous studies of the division of labor in *Polistes* seem to have failed to reveal the specialization in construction behavior noted above due to certain methodological peculiarities. Thus, although Steiner (1932) and Pardi (1942) studied individual differences in function among marked wasps, they lumped all building activity into one category—"construction"—and therefore would not have noticed different degrees of participation in cell addition and cell enlargement. On the other hand, Deleurance (1957) distinguished cell addition from cell enlargement, but did not record the activities of marked individuals. Even so, Pardi's data show that *P. gallicus* queens specialize in pulp foraging; and Deleurance (1957) noted a relationship between ovarian development and rate of new cell addition among foundresses: "la multiplication alvéolaire est en relation avec la physiologie de la ponte. Placées dans les mêmes conditions physiques, les femelles à forte fécondité construisent davantage de cellules que les autres. En outre, on observe un arrêt rapide de la multiplication alvéolaire chez Guêpes qui, après la fondation déposent un oeuf ou deux, puis cessent de pondre . . . les Guêpes pratiquement infécondes ne bâtissent presque pas de nouvelles cellules" (Deleurance, 1957, p. 128). He also discovered that queens ovariectomized five days after nest founding never built new cells (Deleurance, 1955). (An earlier paper [Deleurance, 1948a] entitled "Le comportement reproducteur est indépendant de la présence des ovaires chez *Polistes*" was written before Deleurance realized the importance of distinction between the two types of building.)

In spite of this compelling evidence of an association between construc-

tion activity and ovary development, Deleurance concluded that the females of a colony participate equally in cell initiation, and stated repeatedly and emphatically the opinion that "dans la société polygyne, en l'absence comme en la présence des ouvrières, le travail cartonier des femelles ne reflète pas la 'spécialisation' observée dans la ponte par l'une des Guêpes, et l'on ne peut prétendre qu'il y ait une division du travail" (1957, p. 195). Deleurance may have been led to an erroneous conclusion by the fact that his observations of individual differences were confined to pre-emergence colonies, in which the specialization does not exist (see Social Biology of *Polistes fuscatus*, below); his conclusion regarding colonies containing workers is based on a statistical correlation between numbers of females and rate of new cell building and the assumption that this indicates equal participation of all individuals in this activity. The observations of marked individuals described above indicate the invalidity of this assumption.

FORAGING.—Queens forage less than do workers. The queen of *P. fuscatus* colony B38 brought only 0.11 foraged loads to the nest per hour observed, compared to an average of 0.85 loads per hour for the workers (Table 1). Owen (1962), Steiner (1932) and Pardi (1942, 1951) found that the queen spends most of her active time on the nest where she "specializes" in tasks (e.g. guarding, cell inspection and oviposition) not involving absence from the nest.

The occasional foraging trips of queens are devoted to collection of materials (pulp and water) used in construction. Three of four loads (75 per cent) brought by the B38 queen were pulp, and the fourth was water. All workers carried a smaller proportion (7 to 50 per cent) of pulp (Table 1).

All of 17 recorded loads brought by *P. canadensis* queens to observation nests were pulp.

The data of Pardi (1951) show that *P. gallicus* queens also devote their few foraging trips to pulp collection and contribute nothing to food transport. However, Pardi evidently did not consider this significant "specialization."

A predominance of pulp in the foraged loads of queens is further evidence that construction activity is associated with developed ovaries.

Summarizing, *Polistes* queens have at least four distinctive behavioral characteristics: egg-laying, superior dominance, cell initiation, and specialization in pulp foraging. The present study suggests that cell initiation and pulp foraging by queens are characteristics directly associated with developed ovaries, as is dominance as shown by the experiments of Pardi (1946, 1948a).

TABLE 1
INDIVIDUAL DIFFERENCES IN QUALITY AND QUANTITY OF FORAGING (*P. fuscatus*)¹

	Foraging Rate (loads/hour observed)	Per Cent of each load-type in total recorded loads		
		% Pulp	% Water	% Food
Queen	0.11	75	25	—
Other Foundresses				
1	0.64	50	15	36
2	1.05	39	41	20
3	1.16	22	56	22
Offspring				
1	0.86	21	44	45
2	1.57	25	65	10
3	0.72	9	76	15
4	0.75	44	44	22
5	0.60	25	—	75
6	0.35	14	50	36
7	1.26	45	12	63
8	0.69	14	68	18
9	1.25	10	60	20
10	1.33	10	30	60
11	0.35	34	55	11
12	0.70	7	35	58
13	0.84	—	—	100
14	0.65	10	25	65

¹ Summary of lifetime records of all colony B38 females which brought 10 or more foraged loads to the nest during 102 hours of observation, June–September 1964. Foraging rate is given in loads/hour observed during life as active forager (period between first and last observed foraging trip). Offspring females are listed in order of their emergence.

SOCIAL BIOLOGY OF POLISTES FUSCATUS

EMERGENCE FROM HIBERNATION

Fecundated females overwinter in protected places (hibernacula), e.g., between the inner and outer walls of houses, under shingles and loose tarpaper, in cracks between boards, and (according to Bohart, 1942) beneath the loose bark of trees. During hibernation the ovaries contain few oocytes. Ovaries of 12 females taken from a hibernaculum at locality J in January and February (1963) contained an average of only 2.7 oocytes, compared to a mean of 23.7 for seven queens captured during July.

In spring the ovaries begin to develop several weeks before the onset of nest-building, which occurs in Michigan in early May. Three females taken from the locality J hibernaculum on 22 March 1964 contained 10 oocytes each; 15 females flying and walking sluggishly in the sun on 20 April 1963

had an average of 9.0 oocytes; and 23 netted 18–27 April 1964 averaged 10.6 oocytes per female. No spring-dissected female showed the lack of ovary development typical of summer workers and mid-winter hibernators, which often have no discernible oocytes.

Fat-body reduction accompanies oocyte growth. The fat-body was conspicuous in females collected in September prior to hibernation and in the 13 females taken from hibernacula in January and February, but very reduced in all but one of the 15 females with developed ovaries dissected on 20 April.

Spermathecae of all 28 dissected overwintering and overwintered females (potential foundresses) contained sperm.

The behavior of *P. fuscatus* females during the first warm days of spring is like that of *P. gallicus*, as described in detail by Pardi (1942). Females often aggregate in sunny places before beginning nests but such clusters disperse before nest-founding—they do not indicate future nest sites. Individual females eventually begin to sit alone on old nests and future nest sites, where they react aggressively toward other wasps. This heightened aggressiveness is probably associated with increased ovary development and contributes to the decreased frequency of cluster formation which, as shown above, depends on the presence of immobile (non-aggressive) individuals.

NEST INITIATION

Nests are usually initiated by a lone female (the “original foundress”) in *P. fuscatus*. Thirty-seven of 38 nests consisting of one to ten cells were attended by only one female; the one exception was colony B25, which had two foundresses when less than 24 hours old on 9 May 1965.

Most nests were initiated during the second week of May in 1963, 1964, and 1965. Twenty-nine (93 per cent) of the 31 nests present at locality B during summer 1965 were founded on 8 and 9 May; one more appeared on 12 May and another between 20–26 May. This synchrony of nest founding was probably due in part to a sudden warm spell which started on 7 May, when the temperature rose to 21°C. (mean daily temperature) after a week (1–6 May) in which the mean temperature had been 15.5°C. The fact that few nests appeared after 9 May indicates that most females which associate with nests after the first few days of construction activity join colonies initiated by other females rather than starting new ones of their own.

FOUNDRESS ASSOCIATIONS

By the time of the emergency of the first brood in late June, the majority of *P. fuscatus* colonies in the Ann Arbor region are attended by more than

one female. Of 46 nests examined at localities B and G in the evenings of 16 and 28 June 1965, 60 per cent had more than one resident female; and the majority (81 per cent) of the 97 nesting females were on multiple-foundress nests (Table 2).

TABLE 2
FOUNDRASS ASSOCIATIONS AT LOCALITIES B AND G, 16-28 JUNE 1965 (*P. fuscatus*)

Number Of Foundresses In Colony	Number Of Nests	Per Cent Total Nests	Number Of Females	Per Cent Total Females
1	18	39	18	19
2	16	35	32	33
3	7	15	21	22
4	2	4	8	8
5	1	2	5	5
6	1	2	6	6
7	1	2	7	7
Totals	46	99	97	100

The following description of foundress interactions is based primarily upon a study of ten colonies at locality B from the time of their initiation (8-9 May 1965) until they were destroyed by an unidentified foe on 21 June, just prior to the predicted emergence of the first adults. The colonies were located beneath the eaves of a low building, as indicated in Figure 3.

INTER-COLONY MOBILITY OF FOUNDRASSES.—During the four weeks following nest initiation there was much nest-to-nest movement of females. Histories of 38 marked foundresses at locality B show the following patterns of association with nests: 17 were transients, seen only once or twice on or in the vicinity of nests; 10 were "permanent residents", associated with a single nest for a prolonged period, and never seen on other nests; 3 attended one nest consistently for a time, then changed residence and consistently attended another; 2 were resident on one nest for a period and alternately attended more than one nest during another period; 2 attended more than one nest, never becoming resident on a particular one; and 2 were transients which became permanent residents on a particular nest.

Of the ten nest initiators, seven remained permanent residents and queens of the nests they initiated. Two others became workers on other nests and one began alternately to attend her original nest and another (nest B13) on which there was no permanently resident female. In general, then, there was little nest-to-nest movement by colony initiators compared to the rest of the foundress population; and most nest initiators became queens.

dominant individual, this indicates that the dominance rank of the B18 foundresses was in order of their joining the nest.

SIBLING ASSOCIATIONS.—There is indirect evidence that temperate zone *Polistes* females begin colonies near the site of the nest from which they emerged the summer before. Inhabited nests are often situated a few inches from nests built in previous seasons, and undisturbed sites often have clusters of abandoned nests indicating that the same place was used year after year (Davis, 1924; Pardi, 1942; Rau, 1929, 1931, 1940). One nest found at locality S was attached to the face of an older nest, and I have observed five cases in which nests were reused a second year.

When a whole colony is captured and killed, the site is sometimes not occupied the following year. A large locality L colony captured in August 1965 was one of a cluster including three abandoned nests, indicating that the site had been used repeatedly. No nest was built there in 1966 even though hundreds of overwintered wasps appeared in the vicinity during spring, and a new nest was founded adjacent to a similar cluster a few feet away on the same building.

Rau (unpublished manuscript) found a marked female hovering in April near the site of the nest where she had been queen the summer before. This female flew weakly, and died within a week after capture.

Direct evidence of sibling relationship among associated foundresses is given by Heldmann (1936a), who marked *P. gallicus* females in autumn on a nest where they presumably had emerged. Seven returned to the site the following spring, and four associated on a newly-founded nest.

During summer 1964 I marked 94 (76 per cent) of the estimated 124 female progeny of *P. fuscatus* colony B38 and 15 females of B36, 18 feet north of B38 (Fig. 3). Eighteen marked B38 females appeared at the locality B eaves (site of their parental nest) the following spring. Six individuals retained specifically identifiable marks applied between 25 August and 7 September 1964; the others bore fragmentary marks of colors used only on colony B38. Two additional females had equivocal marks which could have been applied on either B38 or B36.

After 10 June the composition of foundress groups did not change. On that date, 10 B38 offspring were nest residents, eight of them on nests B15 and B18—within four feet of the parental nest site (Fig. 3).

Fourteen of the 18 known progeny of B38 associated exclusively with nests founded by siblings during the pre-emergence period (Fig. 3). Two others became workers on nests founded by females of unknown origin. One foraged and oviposited on B24, a colony founded by an equivocally-marked female, then left after six days of residence there to become a

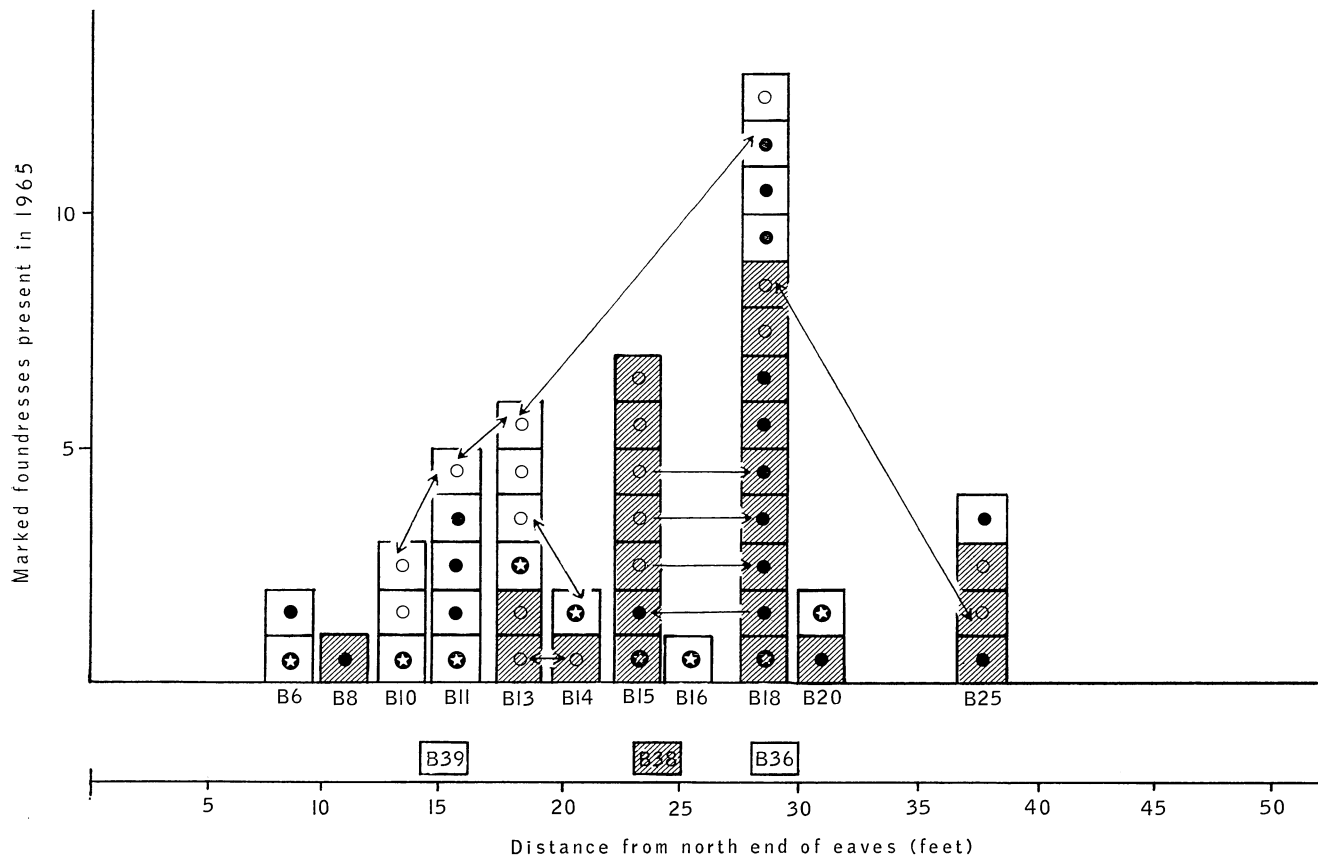


FIG. 3. Spatial distribution of nests and marked females at locality B eaves (*P. fuscatus*). Nests B36, B38, and B39 (in boxes, below) were inhabited in 1964, the others (above) in 1965. Each square of the histogram represents an individual seen on the indicated nest during 85 hours of observation, 8 May–21 June, 1965. Shaded squares represent females (siblings) marked on nest B38 in 1964. Open circles denote “transient” females sighted on nests but not resident there for more than one day in succession. Solid dots identify females present on more than one successive day. Stars identify nest initiators. Double-headed arrows show repeated movement between two nests; single-headed arrows indicate the direction of a change in residence.

worker on the nest (B15) of a sibling. Another female joined a sibling and an equivocally-marked female on a short-lived nest in the humidothermograph.

Probably few (if any) of the eight B38 progeny sighted near the eaves but not ultimately resident there built nests elsewhere. Sixty-seven females of 25 colonies located on other buildings at locality B were anaesthetized at night between 14–23 June. All were examined for previous marks and marked with colors not used at the eaves nests. None of them had been marked previously; nor did any ever appear at or near the eaves. This indicates that there was little (if any) movement of wasps between the eaves nests and those on nearby buildings.

The three colonies present at the eaves in 1964 were large enough to account for production of all the 36 females recorded there during spring 1965. Since an estimated 75 per cent of the total number of adults which emerged from B38 were marked, and 18 of those appeared at the eaves the following spring, four or five ($.25 \times 18$) of the unmarked spring females at the eaves were probably also from B38. B38 contained 247 cells and contributed 22–23 females (about one per 10 cells) to the spring foundress population. Therefore colonies B36 and B39, which consisted of 102 and 76 cells respectively, could together have contributed about 22–23 foundresses, assuming that (1) their brood size, average adult longevity, and numbers returning to the parental nest site were proportional to those of B38, and that (2) the number of recorded marks agree with the number of individuals actually marked, some unrecorded marks being possible due to movements of newly-marked individuals against unmarked females. The number (22–23) is near the number (18) of females of unknown origin actually observed at the eaves. Therefore all of the foundresses observed at the eaves in 1965 could have emerged there in 1964.

Two females marked in 1965 were found near the parental nest in mid-July 1966. One was the queen of a colony located less than an inch from the parental nest at locality L; the other was a subordinate female on a colony located two feet from her parental nest at locality A.

Orientation using common clues, perhaps those used the previous year in returning to the parental nest, may bring siblings together in spring. Two pairs of nests visited by the same females were in analogous positions with respect to surrounding structures. B18 was the newly-founded nest most frequented by B38 siblings, five of which became permanent residents there. The locations of B18 and B38 were analogous in at least two ways: both were in the southwest corner of enclosures formed by roof and rafters, and both were about 20 inches south of dark metal strips which contrasted with

the white eavestrough. Foragers of both colonies sometimes hovered directly facing the dark strips before landing on their respective nests, suggesting that the strips served as orientation cues. Nests B13 and B14 also occupied analogous positions, in the southwest corners of adjacent spaces beneath the eaves. They were alternately attended by foundresses No. 12 and No. 24, perhaps due to similarity in orientation cues associated with the two sites.

The destruction of the eaves nests on 20 June was a costly but informative experimental test of the hypothesis that nest-site selection is sometimes by orientation to previously-learned (parental) nest sites or their analogues. After disruption of the colonies, most of the marked wasps disappeared. Only queen No. 3 of colony B15 began to build a new nest: on 21 June she constructed a pedicel on precisely the spot where B18 had been. This suggests that the sites of B15 and B18 were so similar with regard to orientation cues that without colonies they were not distinguished by female No. 3 (an offspring of B38). Both sites had been occupied by colonies founded by B38 offspring; they were the sites most visited by B38 siblings; and four of the known siblings visited both sites, which had more visitors in common than any other two nest sites along the eaves (Fig. 3). These observations indicate that the sites of colonies B15 and B18 appeared similar to orienting offspring of B38. The basis of similarity may have been orientation cues analogous to those of the parental nest site, learned during the previous summer.

All newly founded nests visited by marked B38 offspring were in a section of the eaves about twenty feet long (Fig. 3). Within that range, proximity to the parental nest was apparently less important than analogous position in the formation of sibling associations. B16 was less than two feet from B38, yet no female marked on B38 appeared during 80 hours of observation during the pre-emergence period. B16 was in the northwest corner of a space beneath the eaves, whereas B38 was in the southwest portion of the same space.

QUEEN DETERMINATION

QUEEN-LIKE BEHAVIOR OF SUBORDINATE FOUNDRESSES.—In some respects the social organization of pre-emergence colonies is like that of colonies after the emergence of offspring workers: the dominant female forages less, receives more solicited material from associates, and lays more eggs than do subordinates (Table 4).

However, pre-emergence colonies differ from most post-emergence colonies in that (1) subordinates oviposit (see Pardi, 1942; Gervet, 1964a) and (2) most cells are initiated by subordinate females rather than by

TABLE 4
 ACTIVITIES OF B18 FOUNDRESS DURING THE PRE-EMERGENCE PERIOD (*P. fuscatus*).
 (BASED ON 26 HOURS OBSERVATION, 18 MAY-14 JUNE 1965)

Female	Dominance Rank	Eggs Laid	Eggs of Others Eaten	New Cells Started	Foraging Rate (Loads/Hour Observed)	Loads Received From Associates
No. 13	1	9	4	0	.08	25
No. 34	2	5	2	1	.50	20
No. 35	3	0	0	1	1.41	0
No. 28	4	0	0	2	1.56	5
No. 15	5	0	0	8	1.80	3
No. 6	6	0	0	0	1.22	1
No. 18	7	0	0	0	1.50	0

the queen. Subordinate foundresses oviposited on four of the ten 1965 locality B colonies (colonies 14, 15, 18 and 25). On nest B18 the second-ranking female (No. 34) oviposited, although less often than did the dominant foundress (No. 13); and all of the twelve cells initiated during 26 hours of observation were started by subordinates (Table 4). Foraging rate and number of cells initiated were inversely related to dominance rank among the five foundresses observed for more than ten hours (Table 4).

STANDING ASIDE.—Since violent fighting occurs between wasps of equal dominance rank, one might expect closely-ranked foundresses, such as ovipositing females No. 13 and No. 34 of B18 (Table 4), to be unusually aggressive toward each other. However, closely-ranked foundresses of *P. fuscatus* behave in ways which reduce the number of contacts between them. Females No. 13 and No. 34 usually rested, landed and applied pulp on opposite sides of the nest. During the period 9-15 May, when co-foundresses No. 7 and No. 11 were concurrently attending B25, each consistently stepped off the nest when the other returned from foraging. On 9 May No. 7 was adding pulp to the nest. No. 11 stood aside until she finished, then moved slowly onto the nest. No. 7 then stepped off and No. 11 added her load of pulp. The two wasps switched position in this fashion four times during an hour of observation. Each added a new cell (on opposite sides of the 7-cell nest) and oviposited in it. The only observed contact between the two wasps was when No. 11 came on the nest as No. 7 oviposited, antennated the egg layer briefly, then again moved off the nest.

Mutual standing aside also occurred on B15, when No. 3 and No. 25 (both egg layers) were present there on 9 May, and on B13 and B14 (21 May) where No. 28 and No. 24 consistently stepped off their respective nests

when No. 12 landed with a foraged load, then on again when she left or finished dispensing the load.

DIFFERENTIAL EGG-EATING.—On three nests (B1, B14 and B18) where I observed oviposition by the subordinates, the egg-laying females ate each other's eggs. Differential oophagy has been observed in *P. gallicus* by Heldmann (1936b) and Pardi (1942) and has been the subject of detailed study by Gervet (1964a).

Nine observed instances of differential egg eating in *P. fuscatus* had the following characteristics:

1. Only egg layers (No. 13, No. 24, No. 34 and two females of colony B1) ate eggs. Sterile females never ate eggs, even when they encountered and antennated eggs subsequently eaten by oophagic females.

2. Egg laying by the oophagic female usually occurred immediately after egg eating and was sometimes in a cell other than that formerly occupied by the eaten egg.

3. Oophagic females never ate their own eggs.

4. All eaten eggs were newly laid. The mean age of seven eggs for which times of oviposition and consumption are known was 11.4 minutes (range: 1–37 minutes); two eggs eaten by No. 13 had just been antennated by female No. 34 in a prolonged inspection like that which follows oviposition, suggesting that No. 34 had just laid the eggs. There was no oophagy of "old" eggs (eggs laid before observations began on a given day).

These observations suggest that an oophagic female may avoid eating her own eggs by recognizing newly laid eggs and eating them only when she has not herself recently laid an egg. Inspecting wasps may recognize newly-laid eggs by an adherent substance which becomes less detectable with time. Non-oophagic females No. 28 and No. 18 antennated newly-laid eggs longer than older ones. Once No. 18 stopped at a cell where oviposition and egg eating had occurred 40 minutes earlier, and vigorously antennated and bit at the side of the empty cell even though no trace of the eaten egg was visible to me. Perhaps inspecting wasps detect whatever substance (presumably a fluid, which would dry with time) makes the egg stick to the carton. If this is the case the long (up to 20 minute) post-oviposition egg inspection and heightened post-oviposition aggressiveness (abdomen-wagging, darting at associates and vigorous solicitation) of egg layers in *P. fuscatus* may function to reduce the likelihood that a fresh egg will be encountered and consumed by an oophagic associate.

Gervet (1964a) suggested that oophagic females of *P. gallicus* learn to discriminate the eggs of other females by "une qualité stimulante liée aux caracteres individuels des pondeuses" (p. 380). However, he noted that the

triggering of oophagy is directly linked to the age of the egg (p. 349), and many of his observations cited as evidence of a quality of eggs differing among individual egg layers could be attributed to newness alone.

Dominant female No. 13 of B18 always ate new eggs of No. 34 as soon as she contacted them. On the other hand, second-ranking female No. 34 sometimes antennated but did not eat eggs produced by No. 13 less than thirty minutes before. On each of four such occasions she (No. 34) had also oviposited in the preceding thirty minutes, although not always in the same cell. It is possible that oviposition by No. 34 temporarily depleted her supply of mature oocytes, rendering her temporarily non-oophagic. The dominant female produced 2–3 eggs per observation period (2–4 hours) on three different days, twice laying two eggs in less than ten minutes. The second-ranking female, however, never produced more than one egg per observation period. The more efficient oophagy by the dominant female (four out of five of her competitor's eggs destroyed compared with only two of her nine eggs lost to No. 34) may have been associated with her more constant supply of mature ova. This conclusion accords with the observations that only egg layers (females having mature oocytes) eat eggs (Table 4) and that oophagy and oviposition occur in close temporal association.

Oviposition by a subordinate foundress and differential oophagy continued on colony B1 until two weeks after emergence of the first female offspring. However other colonies observed after the pre-emergence period had only one ovipositing female. Pardi (1946, 1948a) and Pardi and Cavalcanti (1951) have shown that the ovaries of subordinates regress after a period of association with a dominant female, presumably due to expenditure of energy during foraging and through transfer of regurgitated food to soliciting nestmates.

SUMMARY AND CONCLUSIONS.—Foundress caste depends upon factors causing differential ovary development among siblings during the first days of spring nest building. Since dominance rank and (presumably) ovary size follow the order in which subordinates join a colony (B18), the caste of a particular female may depend on the time at which her reproductive physiology stimulates nesting (building) activity. Females with early-maturing ovaries initiate nests and are likely to become queens. However, judging by the paucity of nests initiated after the first days of building, and the apparent infrequency of usurpations, females with late-maturing ovaries are likely to become subordinates.

The mode of queen determination found in *P. fuscatus* appears to be the same as that described for *P. gallicus* by Pardi (1942–1948a), Deleurance (1950) and Gervet (1964a). Dominant foundresses become queens, and eat

the eggs of subordinates. Deleurance (1950) found that empty cells stimulate subordinates to oviposit and concluded that the removal of such stimuli by the oviposition of the queen is therefore important in queen control. However, he has introduced some confusion by maintaining that this information detracts from Pardi's (1946) discovery of the role of dominance relations in queen determination. Deleurance seems to be contradicting the idea that dominance is all-important in *Polistes* queen determination, a view which Pardi never espoused. Pardi and Cavalcanti (1951) responded to the criticisms of Deleurance with experiments reiterating what Pardi had already established—that subordination is accompanied by ovary regression.

Brian (1956) resolved this "controversy" by pointing out that queen control in *Polistes* (*P. gallicus*) appears to involve a "triple check" on reproduction by subordinates: oogenesis is suppressed by degeneration of the ovary during a period of nesting with a dominant female; oviposition is prevented because the dominant female keeps cells filled, hence removing oviposition stimuli; and embryogenesis is restricted by differential egg-eating.

Subordinate females resemble queens in being fertilized females with developed ovaries which initiate cells and (sometimes) lay eggs. They do most of the foraging and construction on nests during the pre-emergence period.

PRE-EMERGENCE GROWTH OF COLONIES

The mean number of cells per nest just prior to brood emergence (Table 5) was higher for colonies having a larger number of foundresses. However, as noted by Owen (1962), the production of cells per female was smaller in colonies having larger foundress groups.

The slope of the growth curve of B18 diverged from those of other locality B colonies as more females joined the foundress group (Fig. 4). The parallel changes in growth rate of the colonies reflect changes in mean daily temperature during the periods between cell counts (Fig. 4).

Colonies B16 and B20, first seen on 12 May (5 days after the other colonies were founded) were smaller at the end of the pre-emergence period than other colonies having the same number of foundresses.

BROOD PRODUCTION AND CASTE DETERMINATION

FACTORS AFFECTING BROOD DEVELOPMENT.—The mean duration of the egg, larval and pupal stages of the B38 brood was 13.0, 15.3 and 22.2 days respectively, with the total time from egg-laying to adult emergence averaging 47.8 days. The duration of the immature stages varied considerably

TABLE 5
 CELLS PER NEST AND PER FOUNDRESS PRODUCED DURING THE PRE-EMERGENCE PERIOD (*P. fuscatus*)

Foundresses Per Nest	Number of Nests			Mean Cells/Nest			Mean Cells/ ♀		
	1960-61 ¹	1965 ²	Total	1960-61 ¹	1965 ²	Mean	1960-61 ¹	1965 ²	Mean
1	29	11	40	23.9	24.3	24.0	23.9	24.3	24.0
2	14	11	25	36.9	48.9	42.2	18.5	24.5	21.1
3	6	4	10	47.5	50.0	48.5	15.8	16.6	16.2
4	6	2	8	69.0	54.5	65.3	17.3	13.6	16.3
5	4	0	4	60.5	—	60.5	10.1	—	10.2
6	1	1	2	61	82.0	71.5	10.2	13.6	11.9
7	1	1	2	130	111.0	120.5	18.6	15.9	17.2
N	61	30	91						

¹ 1960-61: colonies examined by Owen (1962) at locality S just before emergence of first workers.

² 1965: colonies examined at locality B just before first emergence of adults (16-21 June).

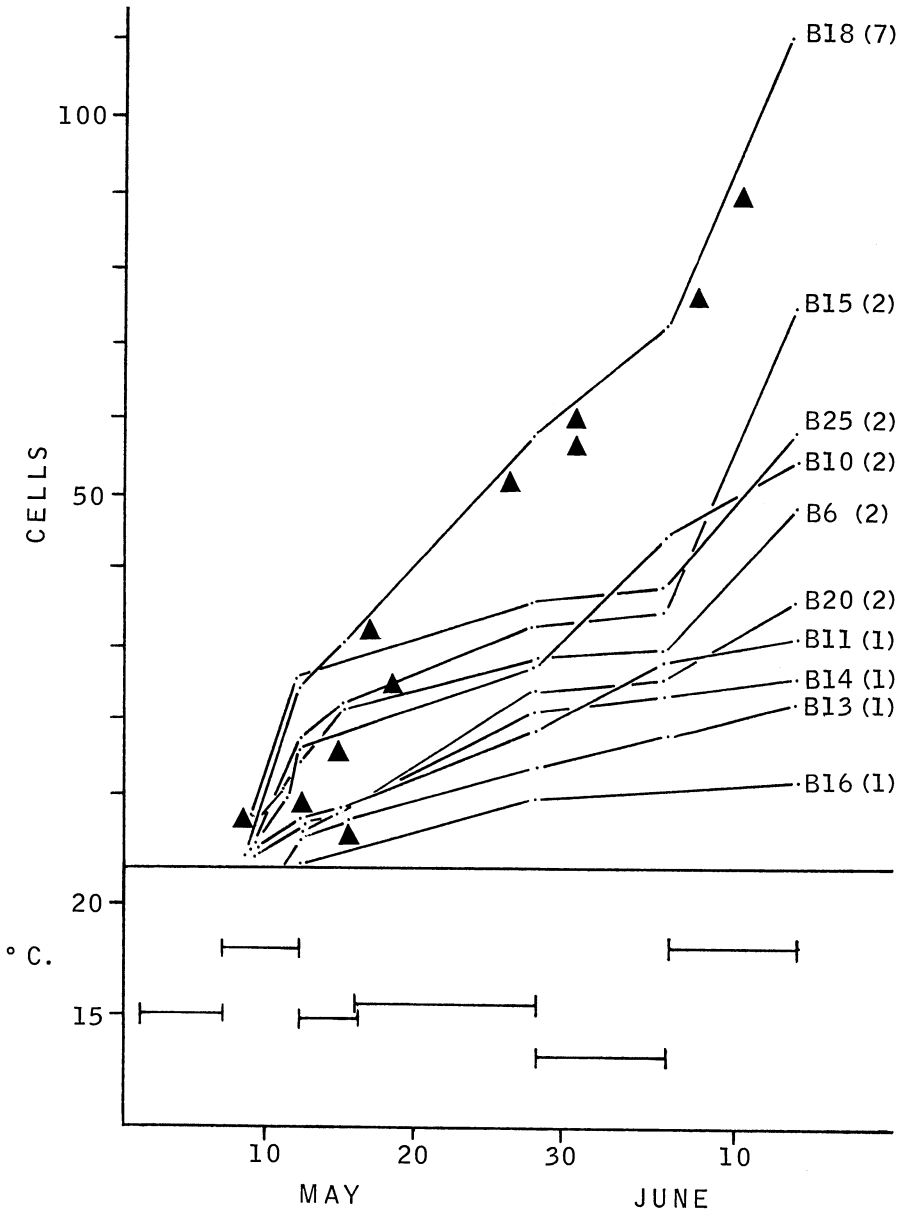


FIG. 4. Pre-emergence growth of nests at locality B, 8 May-14 June 1964 (*P. fuscatus*). Solid triangle indicates time of joining by a subordinate foundress; numbers in parentheses indicate number of foundresses present on 14 June. Horizontal lines below growth curves show mean daily temperature during the time between cell counts.

TABLE 6
DURATION OF DEVELOPMENT STAGES IN *P. fuscatus* (B38-1964)

Stage	N	Duration in days		
		Mean	S.D.	Range
egg	36	13.0	2.93	7-18
larva	58	15.3	3.42	9-23
pupa	124	22.2	4.85	9-33
total (egg to adult)	81	47.8	5.46	33-59
adult (worker)	32	22.8	10.71	2-30

among individuals, as indicated by the ranges and standard deviations of Table 6.

There was an inverse correlation between temperature and developmental time in the larval and pupal stages—larval and pupal periods are generally shorter at higher temperatures (Table 7).

The small positive coefficient of correlation of temperature and time in the egg stage ($r = +0.26$; 95 per cent confidence limits 0.07–0.53) probably does not reflect the general relationship of these parameters in *P. fuscatus*. Most of the individuals included in the egg sample occupied cells near the front of the nest which could be examined closely enough to distinguish eggs from newly hatched, egg-sized larvae. These cells were sometimes exposed to direct sunlight in the morning. Furthermore the shallow egg-containing cells offer little protection from temperature extremes compared to the insulation that must be afforded by the high walls and adjacent cells in the older and more central nest regions occupied by larvae and pupae.

Variations in total development time appear to be independent of mean temperature during development ($r = +0.08$), even though lengths of

TABLE 7
EFFECT OF TEMPERATURE ON DEVELOPMENT TIME OF *P. fuscatus* (B38-1964)

Stage	Egg	Larva	Pupa	Total
N	36	65	124	81
Range of developmental times (days)	7-18	9-31	9-33	33-59
Range of mean temperatures during each stage	18.5–26°C.	16–25.5°C.	16–25°C.	19.5–24.5°C.
Coefficient of correlation (r) of developmental time and mean temperature during development	+0.26	–0.50	–0.48	–0.08

both larval and pupal periods correlate negatively with temperature. The effect of temperature on development rate is masked in measures of total development time because the length of the pupal period of a given individual is an inverse function of the length of its larval period ($r = -0.68$; $n = 47$).

Larval nutrition apparently affected developmental rate. The cluster of squares labeled "A" in Fig. 5 is a group of pupae with unusually long pupal periods at relatively high temperatures; the large circles ("B") represent the opposite condition—unusually short pupal periods at low temperatures.

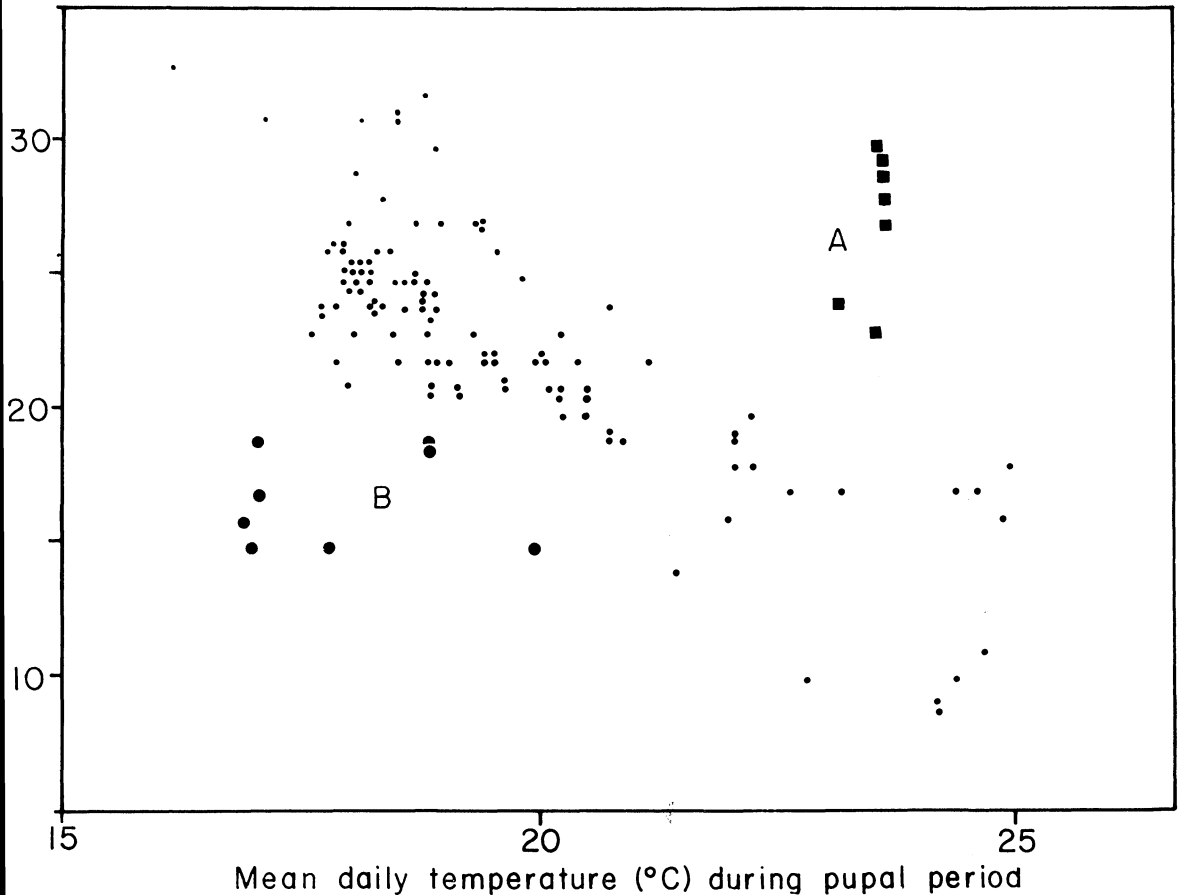


FIG. 5. Duration of pupal stage and mean daily temperature during pupal period. *Polistes fuscatus* colony B38. 8 June-4 October, 1964. Groups of pupae labeled A and B are discussed in the text above.

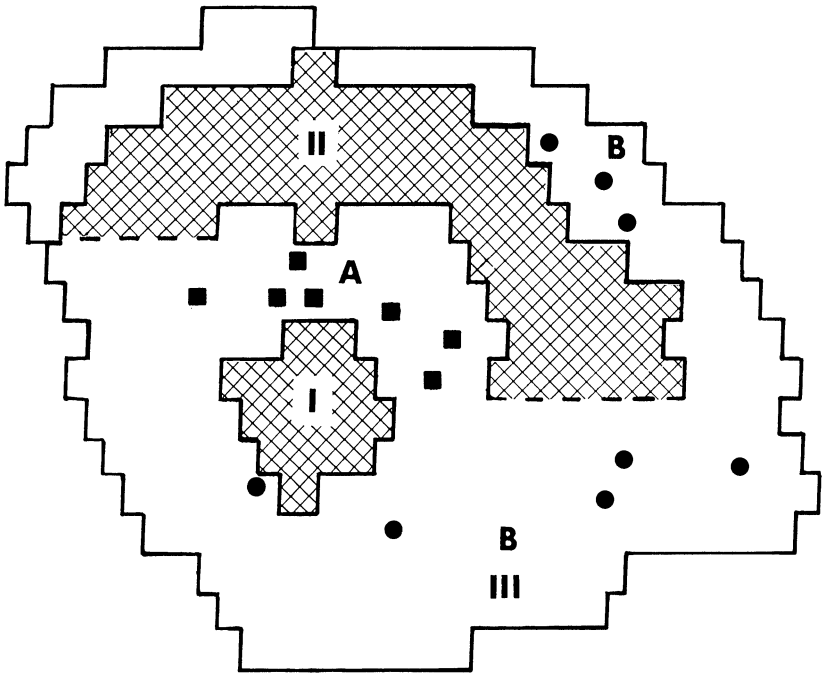


FIG. 6. Positions of cells containing individuals having extreme (long or short) pupal periods for the temperatures at which they developed (*P. fuscatus*, nest B38). "A" individuals (squares) had unusually long pupal periods at high temperatures; "B" individuals (circles) had unusually short pupal periods at low temperatures (see Figure 5). Hatched areas in center indicate nest regions containing pupae: I—during period when "A" individuals were larvae; II—during period when "B" individuals were larvae; III—area occupied by "B" individuals as larvae scattered among pupae.

The cells containing these individuals were located on B38 as shown in Fig. 6. The "A" individuals were near the nest center as larvae, the centermost cells at that time (late June and early July) being occupied by pupae as shown. The "B" individuals, on the other hand, were peripheral larvae in late July and early August, when the centermost cells contained larvae, and they were separated from the central larvae by a ring of capped pupal cells.

It is likely that females dispensing food center their activities in the nest region containing the most larvae. In a growing colony this region is always near the nest center. Cumber (1949) noted that bumblebee workers give more food to central larvae. Therefore it is possible that the long pupal periods of the "A" individuals were due to their better larval nutrition

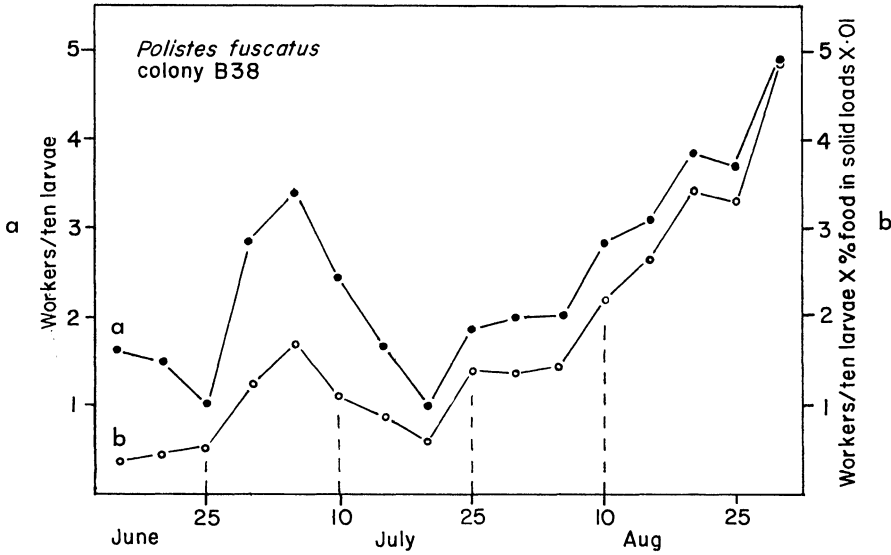


FIG. 7. Seasonal change in estimated amount of solid food available to larvae (*P. fuscatus* colony B38). Units on left axis (a) apply to solid circles (a on graph); units on right axis (b) apply to open circles (b on graph). The dotted lines divide the season into periods having different larval nutrition levels as follows: "low" larval nutrition—before 25 June and 10–25 July; "medium" larval nutrition—25 June–10 July; "high" larval nutrition—after 25 July.

and that the "B" individuals had shorter pupal periods because they were on the trophic periphery as larvae.

Figure 7b is an estimate of seasonal change in quantitative larval nutrition. A common estimate of this parameter appearing in discussions of caste determination in social insects is the worker/larva ratio (Figure 7a) or its inverse, the larva/worker ratio (e.g., Spradbery, 1965). Figure 7a is unique among published estimates of this ratio in that it is based on the unbroken history of a single colony (B38) in which the numbers of *functioning* workers and feeding larvae were known at all times. Furthermore, it was possible to test the rarely explicit assumption that the amount of food available to the larvae increased with the number of workers present: foraging records for the period 15 June–10 September indicate that on B38 the solid-load (food and pulp) foraging rate was directly proportional to the number of workers present ($r = +0.95$). In addition, the proportion of food in foraged loads increased as the season progressed (Figure 8). Figure 7b takes into account both change in the worker/larva ratio and the proportion of food

in solid loads. It is a reasonable estimate of quantitative larval nutrition provided that (1) the amount of nectar fed to larvae does not change with season or remains directly proportional to the amount of solid food in the diet, and (2) a constant proportion of food brought to the nest is given to larvae. The amount of nectar given to larvae is not taken into account here because it is difficult to distinguish between nectar and other fluids in transfers to and from larvae. The proportion of food given to larvae may decline during August, when there are many vigorously soliciting males and non-worker females present, competing with larvae for food brought by a relatively small number of workers (see Figure 9).

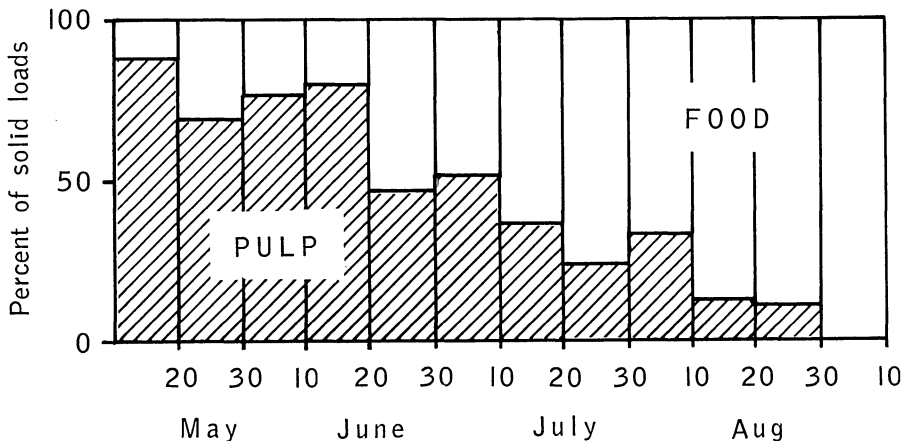


FIG. 8. Seasonal change in the proportions of food and pulp in loads brought to the nest (*P. fuscatus*). Data for 10 May–10 June 1965 are from simultaneous observations of colonies B13, B14, B15, B16, and B18. Data for 10 June–10 September are from observations of colony B38. Each bar indicates the composition of all solid loads observed during the 10 days spanned by the width of the bar.

Quantitative variations in nutrition indicated by Figure 7b seem to explain much of the variation in length of larval period not accounted for by temperature variation (Figure 10). If the B38 season is divided into high-, low- and medium-nutrition periods as indicated in Figure 7, individuals spending the majority (more than half) of their larval periods in each trophic condition fall together on the temperature vs. larval time scatter diagram (Fig. 10). Thus temperature and trophic differences account for much of the observed variation in length of larval period.

The apparent difference in slope of lines drawn (visually) through the high and low nutrition groups (Fig. 10) may indicate a greater sensitivity of

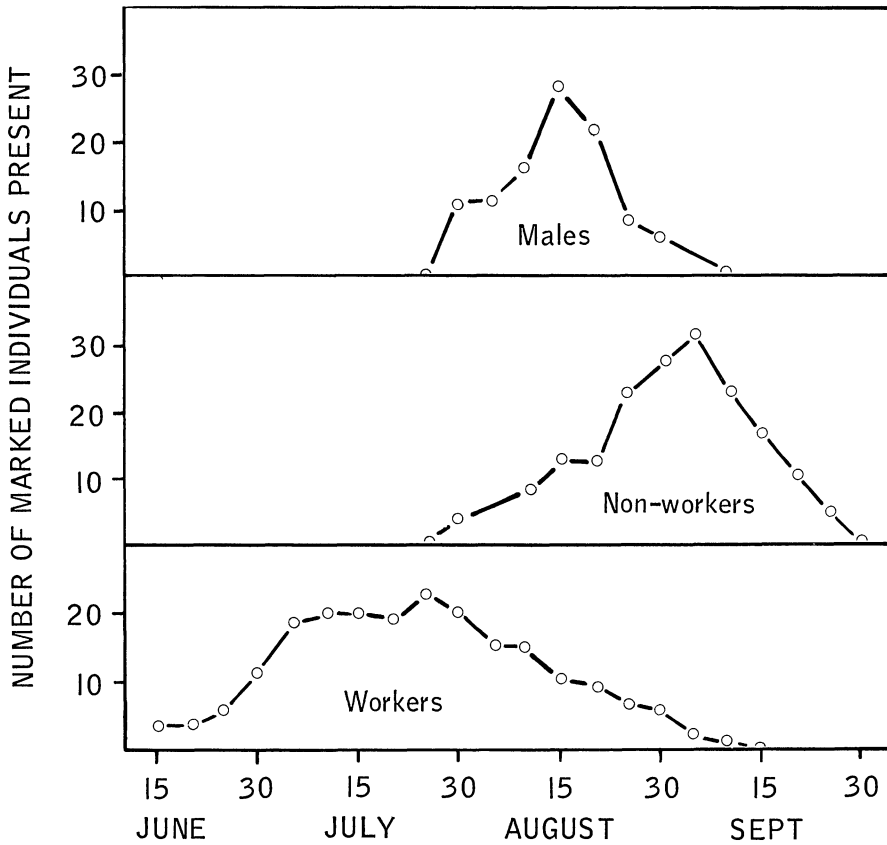


FIG. 9. Seasonal change in composition of adult population (*P. fuscatus* colony B38). Numbers are of marked adults of each category. Workers are females which foraged during their recorded histories on the nest.

low nutrition larvae to temperature differences; or it may be an artifactual consequence of the smaller and higher temperature range of the low nutrition sample.

Individuals which were pupae at relatively high temperatures (average temperature during pupal period greater than 21°C.) and were larvae during periods of low worker/larva ratio had shorter pupal periods than individuals in the other three combinations of high and low temperature and trophic conditions shown in Table 8. Conversely, individuals which were pupae at relatively low temperatures and had relatively high larval nutrition had long pupal periods (Table 8).

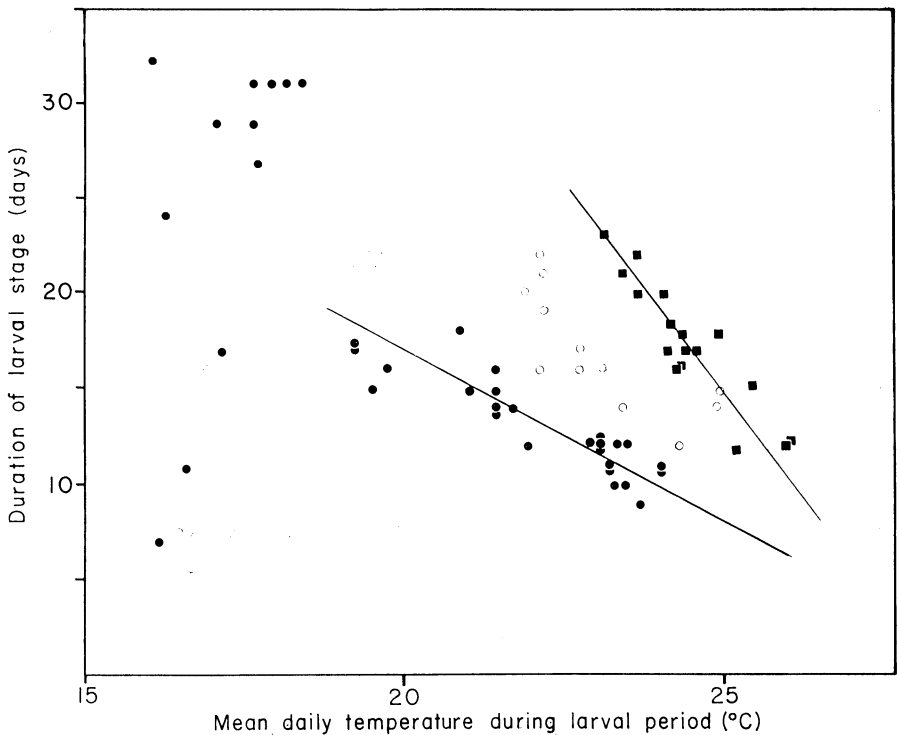


FIG. 10. Duration of larval stage and mean daily temperature during larval period (*P. fuscatus* colony B38). Symbols indicate nutritional period (Figure 8) during which the individual spent the majority of its larval stage: solid circles—"high" larval nutrition (larvae 24 July–18 August); open circles—"medium" larval nutrition (larvae 22 June–14 July); solid squares—"low" larval nutrition (larvae 3 July–31 July). Correlation coefficient of duration of larval stage and mean daily temperature: -0.50 .

TABLE 8
INTERACTION OF TEMPERATURE DURING PUPAL PERIOD AND LARVAL NUTRITION AS DETERMINANTS OF DURATION OF PUPAL PERIOD IN *P. fuscatus* (B38-1964)

Mean Temperature During Pupal Period	Larval Nutrition ¹	
	High (Duration of pupal period)	Low
<21°C.	18.5 days (6)	16.8 days (14)
>21°C.	23.6 days (10)	21.7 days (7)

¹ Larval nutrition levels ("high" and "low") are based on the zones of Figure 8. "High larval nutrition" pupae on 10–15 August (low pupal temperature) and 10–15 July (high pupal temperature). "Low larval nutrition" pupae pupated before 5 July (high pupal temperature) and between 22 and 26 July (low pupal temperature).

Of 30 individuals (22 males and 8 females) sexed as they emerged during the period when both sexes were emerging on B38, total development times are known for only 16. Ten males which emerged between 12 and 19 August had a mean total development time of 45.5 days (range: 41–48 days), which is slightly below the overall mean of 48 days for that period. Six females which emerged over a wider and later period (15 August–3 September) had a mean total development time of 48.2 days (range: 44–55 days).

The mean pupal time for 11 males which emerged 11–19 August was 20.1 days (range: 18–22 days), the same as the overall mean for that date. However, two-thirds of the individuals emerging during that period were males, so the comparison of the two figures does not prove an absence of sex differences in developmental times.

Mean pupal time for five females which emerged 19 August–3 September was 23.8 days (range: 19–27 days). During that period the average pupal time rose from 22 to 28 days, so the all-female sample fell within the values of the mixed sample.

This small sample of sexed individuals does not indicate any marked difference in developmental rate between males and females. Nor was there any bimodality evident in the developmental rates of any stage, or any suggestion of two classes of individuals with respect to any of the analyses of brood development presented above.

SEASONAL CHANGE IN SEX RATIO OF EMERGING BROOD.—All of the first thirty adult offspring of colony B38 were females (Fig. 11). The first male emerged on 27 July, and males and females emerged concurrently from that date until 10 September, after which no males were present on the nest and the few emerging adults were females.

All of these individuals were progeny of one female, the only observed egg layer on the nest until she disappeared on 30 July. Eggs produced after that date did not develop to adulthood.

The date of appearance of the first male, 27 July, is at the point of upward inflection of the curve describing adult emergence rate (Fig. 12B). Since the latter curve was parallel to that describing nest growth during the unextrapolated (directly observed) portions of the curves (Fig. 12B), and the queen lays one egg in each new cell soon after its initiation, the adult emergence rate reflects the oviposition rate of approximately 48 days (the mean total development time) before. This suggests that male-producing eggs were laid at a time of sudden increase in the oviposition rate of the queen. Furthermore the proportion of males among marked adults was directly proportional to the estimated oviposition rate when the eggs

producing them were laid (Fig. 13). Assuming that there was no sex bias in the marking procedure during the period of concurrent male and female emergence, and insofar as emergence rate reflects oviposition rate, there was a strong positive correlation between oviposition rate and the proportion of male eggs produced by the B38 queen.

This relationship of oviposition rate and sex ratio is like that found by Flanders (1946) in various parasitic wasps, which prompted him to

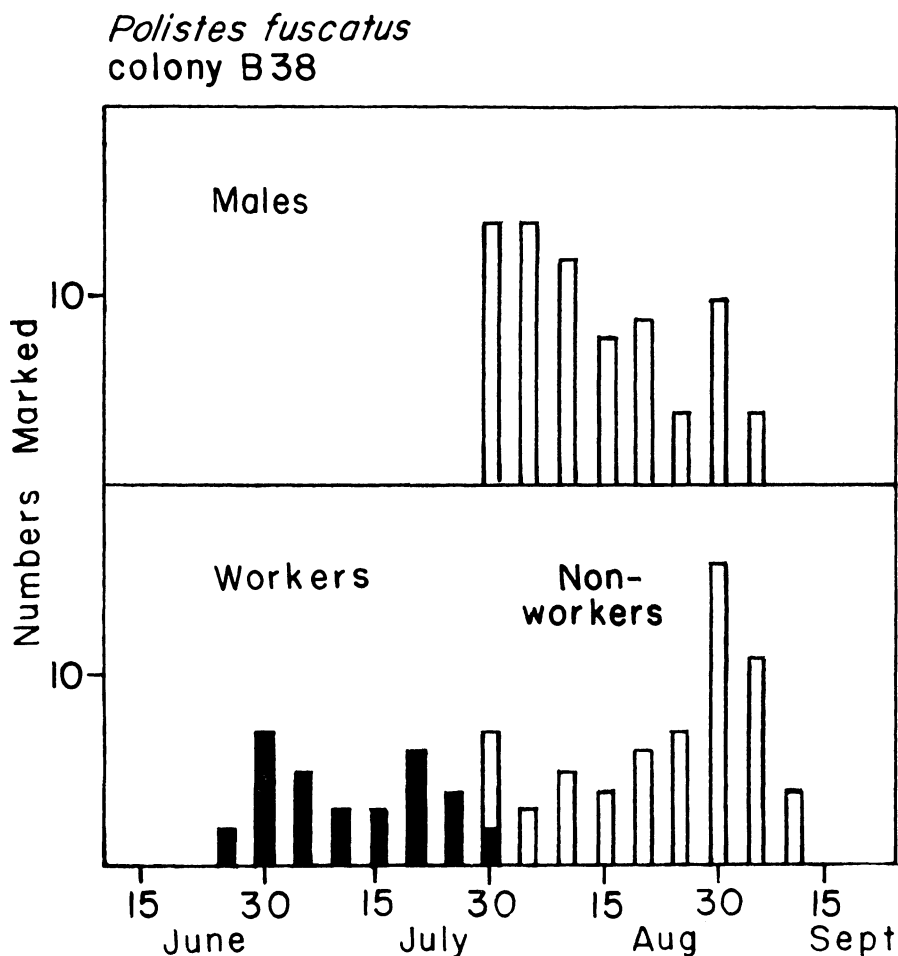


FIG. 11. Seasonal change in composition of emerging brood (*P. fuscatus* colony B38). Adults marked during preceding five-day period. "Workers" foraged during their recorded histories on the nest; "non-workers" did not.

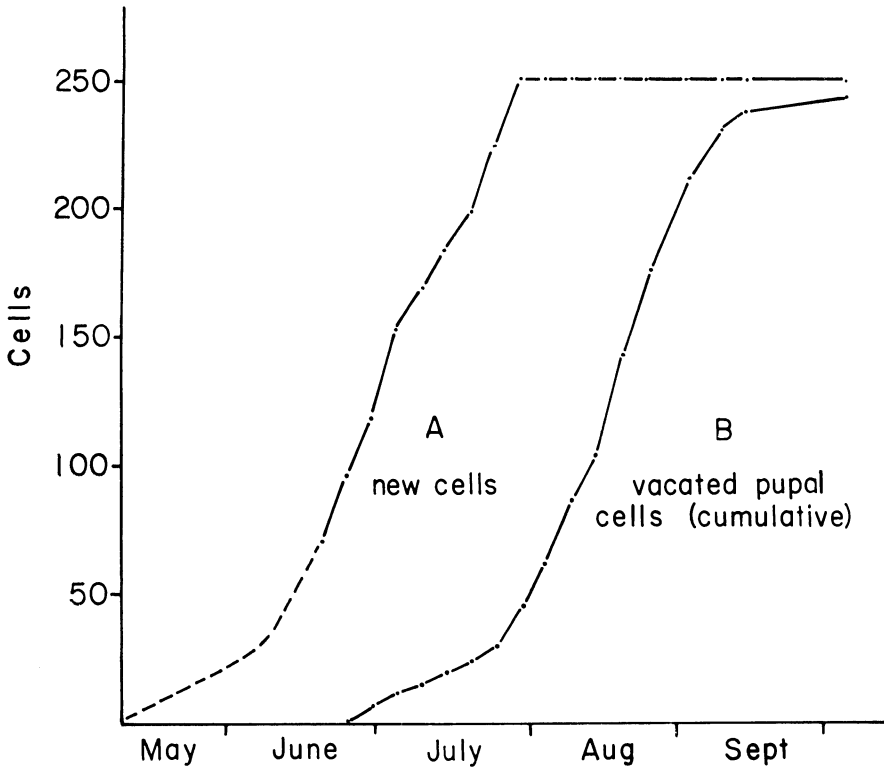


FIG. 12. Colony growth (*P. fuscatus* colony B38). "A" indicates rate of nest growth by cell addition; "B" is approximate brood emergence rate (see text, p. 43).

consider oviposition rate an important determinant of the sex ratio among Hymenoptera. He suggested that (haploid) males are produced at higher oviposition rates because the spermathecal gland may not secrete the sperm-activating fluid fast enough to enable sperm to contact every egg.

Spradbery (1965) reports that male production coincides with the peak in the oviposition rate in *Vespula* colonies but is not sure of the extent to which worker eggs contribute to male production.

SEASONAL CHANGE IN BEHAVIOR OF EMERGING FEMALES.—There are two behaviorally distinct groups among the adult female offspring of a *P. fuscatus* colony: workers, which are aggressive toward intruders, sit dispersed on the nest face even on cool nights, and bring foraged loads to the nest; and non-workers, which move away rather than attacking when approached, frequently sit in clusters on the nest top, and return unladen after trips from the nest.

All females marked 25 June–24 July were workers. On 26 and 27 July five females were marked: two foraged and three did not. After 27 July all marked females were non-workers throughout their recorded histories on the parental nest (Fig. 11).

The same behavioral difference between early- and late-emerged females was evident on three locality L colonies observed in 1966. All of the

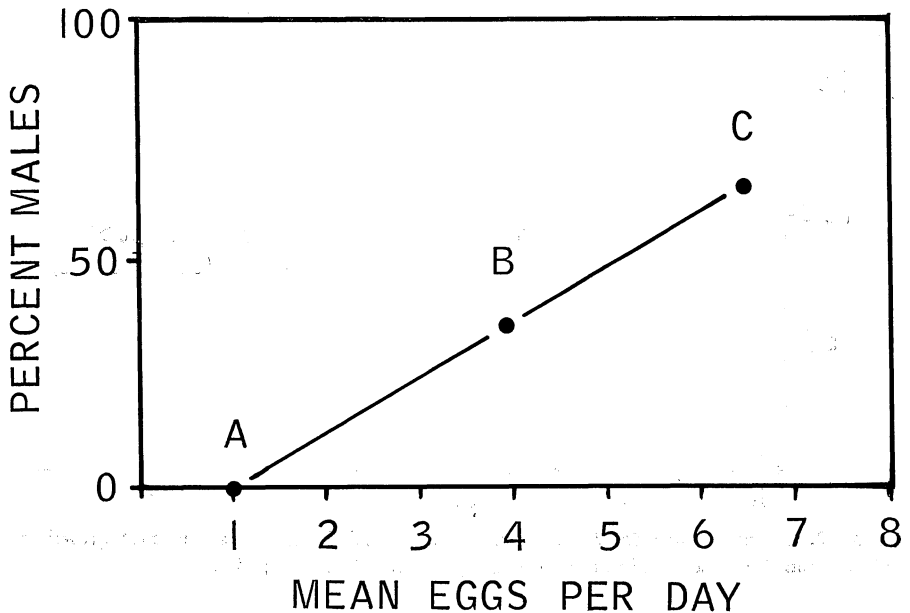


FIG. 13. Oviposition rate and sex ratio of progeny (*P. fuscatus* colony B38). Oviposition rate (eggs/day) "A" and "B" estimated by counting new cells and vacated pupal cells (empty cells generally receive one egg soon after being initiated or vacated). Oviposition rate "C" estimated using adult emergence rate (see text p. 43). Sex ratio estimated from numbers of males and females marked during a period 45 days (approximately one total development period) after oviposition period as follows: A—eggs laid 10 May–10 June (extrapolated from emergence dates), adults marked 25 June–25 July; B—eggs laid 20 June–5 July, adults marked 5–20 August; C—eggs laid 5 July–25 August, adults marked 20 August–5 September.

females present on 19 July were marked. When the nests were observed for two hours on 31 August there were 62 unmarked (probably most emerged after 19 July) females and only 13 marked individuals present. Yet all of the observed foraging was done by nine marked females and one small unmarked individual with battered wings (an old female, possibly missed

during marking or emerged soon after). The marked females were strikingly more active and aggressive than the unmarked ones, which rested on the nest top and in groups off the nest.

Deleurance (1949, 1952a) noted seasonal separation in *P. gallicus* of production of two kinds of females: workers, and "fondatrices-filles"—late-emerged, lethargic non-foragers which he considered to be in reproductive (ovarian) diapause during late summer. The behavioral differences between workers and non-workers are indeed of the kind which might be associated with differences in reproductive (ovarian or hormonal) physiology in *Polistes*: workers are aggressive and participate in building and brood care—they are more like queens than are non-workers, which are passive, subordinate and do not build or forage. Although workers have greatly reduced ovaries, usually completely devoid of visible oocytes, it is possible that they have active neurosecretory systems which affect their behavior even though ovarian development (yolk deposition) is repressed through work. Although worker honey bees (*Apis mellifera* Linnaeus) have greatly reduced ovaries, their corpora allata are as large as or larger than those of queens, and when brood cells are absent egg production by workers begins (Wigglesworth, 1954). Formigoni (1956) showed that worker honeybees have a neurosecretory cycle with behavioral correlates: neurosecretory product in the perikaryons of the pars intercerebralis (a site of secretions which act on the reproductive system) is low at the time of imaginal ecdysis, high in nurses and young foragers, intermediate in ventilator bees and wax workers, and absent in old inactive workers and at the onset of hibernation. *Polistes* workers sometimes go through a cycle of ovarian development and regression with age (Pardi, 1946), suggesting that they too may have such a neurosecretory cycle. The absence of such a cycle in non-workers may account for their inactivity.

Whether a female will be a worker or a non-worker must be determined either before emergence or shortly thereafter, since 13 of 14 workers present on B38 after 1 August foraged after that date even though none of the newly-emerged females did so.

Queen disappearance and the emergence of the first male coincided with the changeover from worker to non-worker emergence on B38 and may have caused or been associated with the cause of that change. These events occurred in the following sequence:

26 July—Emergence of first non-worker.

27 July—Emergence of last worker and first male.

29 July—Queen last seen (not present 30 July).

In view of the queen's role as a foraging stimulator, the aggressive solicitation of an active queen may induce newly-emerged females to begin

foraging, and it is possible that females do not begin foraging behavior if the queen is absent or inactive.

The concurrent emergence of males and non-worker females, and the relationship of oviposition rate and sex ratio on colony B38 (Fig. 13) fit Flanders' (1946, 1962) hypothesis that the rate of egg deposition may determine caste as well as sex ratio in social Hymenoptera. Flanders suggested that eggs deposited at a slow rate are subject to oosorption and may be deficient in the nutritive materials required for development into the fall-type female. Wilson (1955) criticized application of Flanders' hypothesis to ants on the grounds that in those insects polymorphism is generally a function of size, which can be altered greatly by varying the amount and kind of food given the larvae. However, this argument does not eliminate the possibility that *behavioral* caste characteristics are affected during the egg stage.

The behavioral difference between early and late emerging females is apparently not due to a quantitative difference in food given the two sets of larvae. Three of the 32 workers on B38 had larval periods entirely within the "medium" larval nutrition period (Fig. 7) and thus received amounts of food comparable to those of non-workers having all or part of their larval period in the "low" nutritional zone of 10–25 July (Fig. 7).

SEASONAL CHANGE IN CASTE-CORRELATED MORPHOLOGY.—During late June and July, when all emerging females are workers (Fig. 11), the queen is usually distinguished from the workers of a colony by her larger size and browner coloration. Furthermore, the non-workers resemble the queen in size and coloration.

In order to investigate the nature and amount of morphological difference between queens and workers, I examined the size and color of (1) overwintered females (potential queens) collected 22 March–17 June 1964 in hibernacula, in flight and on newly-founded nests at localities D, I, K and O, (2) unfertilized (probably worker) females collected 27 July 1965 on six emergence-enlargement stage nests at locality N, and (3) females which emerged in the laboratory during August from pupal cells present in the nests of group (2) (above) when they were collected.

I estimated body length by measuring wing length on the longest diagonal from tip to tegulum, which correlates ($r = +0.87$; $N = 45$) with body length—head plus longest part of lateral thorax plus sum of lengths of abdominal tergites. Coloration was expressed as a "color score" based on the color of 15 parts of the exoskeleton: clypeus, gena, frons, thoracic pleura, pronotum, scutum, scutellum, metanotum, propodeum, and the terga and sterna of the six abdominal segments. The value of the index for a given individual

TABLE 9
 SIZE AND COLOR OF FEMALES PRODUCED BY SEVEN NESTS IN EARLY AND MID-SUMMER
 (*P. fuscatus*)

Emergence Date	N	Mean Wing Length (mm.)	S.D.	Mean Color Score	S.D.
June-July	82	13.03	.67	-1.21	3.74
August	85	13.89	.73	+3.37	2.95
(Foundresses)	(97)	(14.30)	(.42)	(+2.44)	(4.30)

equals the number of brown-bearing parts minus the number of yellow-bearing parts. Thus a positive color score denotes an individual which is more brown than yellow, a negative score more yellow than brown.

The overwintered females had a greater mean wing-length and higher positive (brown) color score than did the early-emerged females (Table 9). The distributions overlapped broadly as shown by the standard deviations (Table 9) and Fig. 14.

The size and color differences of the two groups apparently represent a gradual seasonal change in the characteristics of the emerging brood. August emergences—group (3) above—had a mean wing length intermediate between those of their earlier-emerged sisters and the overwintered females (Table 9). The high color score of the August females (+3.37) compared

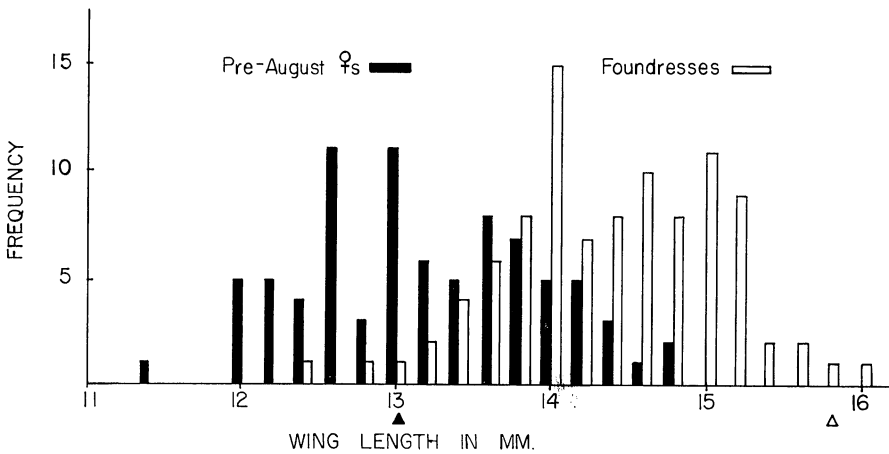


FIG. 14. Wing length of overwintered and early-summer females (*P. fuscatus*). Open triangle indicates wing length of the queen of colony N1, captured 27 July 1965; solid triangle indicates wing length of a worker of the same colony.

to that of the overwintered females (+2.44) is probably attributable to the relatively high mean score (+4.5; $n = 4$) of the parental queens of those females.

Figure 15 indicates the magnitude of the change within colonies. The distributions of color and size values within colonies are continuous and do not form temporally discrete groups.

Thus morphological differences between queens and workers are probably due to the fact that queens are generally (perhaps always) females produced late in the colony cycle, whereas workers are relatively early-emerged. That is, queens and workers in *P. fuscatus* probably represent two ends of a morphological continuum, only one of which survives the winter.

The seasonal increase in size of emerging females is probably due to seasonal increase in the amount of food given larvae like that described for colony B38 (Fig. 7). Quantitative seasonal change in larval nutrition causes caste-correlated variation in size of adult females in other social insects, e.g., bumblebees (Cumber, 1949; Free, 1955), vespine wasps (Spradbery, 1965) and halictine bees (Knerer and Atwood, 1966).

SIGNIFICANCE OF SEASONAL VARIATION IN SIZE AND BEHAVIOR OF EMERGING FEMALES.—Females which emerge late in summer are more likely to become next year's queens than are earlier-emerging females because (1) they are more likely to be non-workers, thus less likely to expend energy or receive injuries than are foragers in their frequent trips from the nest, and (2) they are on an average better nourished (larger in size) and therefore enter hibernation with greater energy reserves for winter survival and spring egg production. All of the six B38 progeny bearing individually distinctive marks when observed in foundress associations had been non-workers on the parental nest.

Some of the variation in ovary size and dominance noted among foundresses and crucial to queen determination on newly founded nests may be due to nutritional differences among siblings emerging at different times on the parental nest.

While seasonal changes in behavior and size may thus both affect caste, they appear to be independently determined, large size and lack of foraging behavior occurring together in late-emerging females due to the seasonal coincidence of these characteristics.

SIZE AND COMPOSITION OF ADULT BROOD PRODUCED BY COLONY B38.—On nest B38, 234 pupal cells were vacated from 25 June to 4 October (Fig. 12B). Adults sometimes remove cell caps and consume pupae. However, this was apparently infrequent on B38. Three observed instances left cell walls ragged and short where they were chewed by the cannibalizing females, and

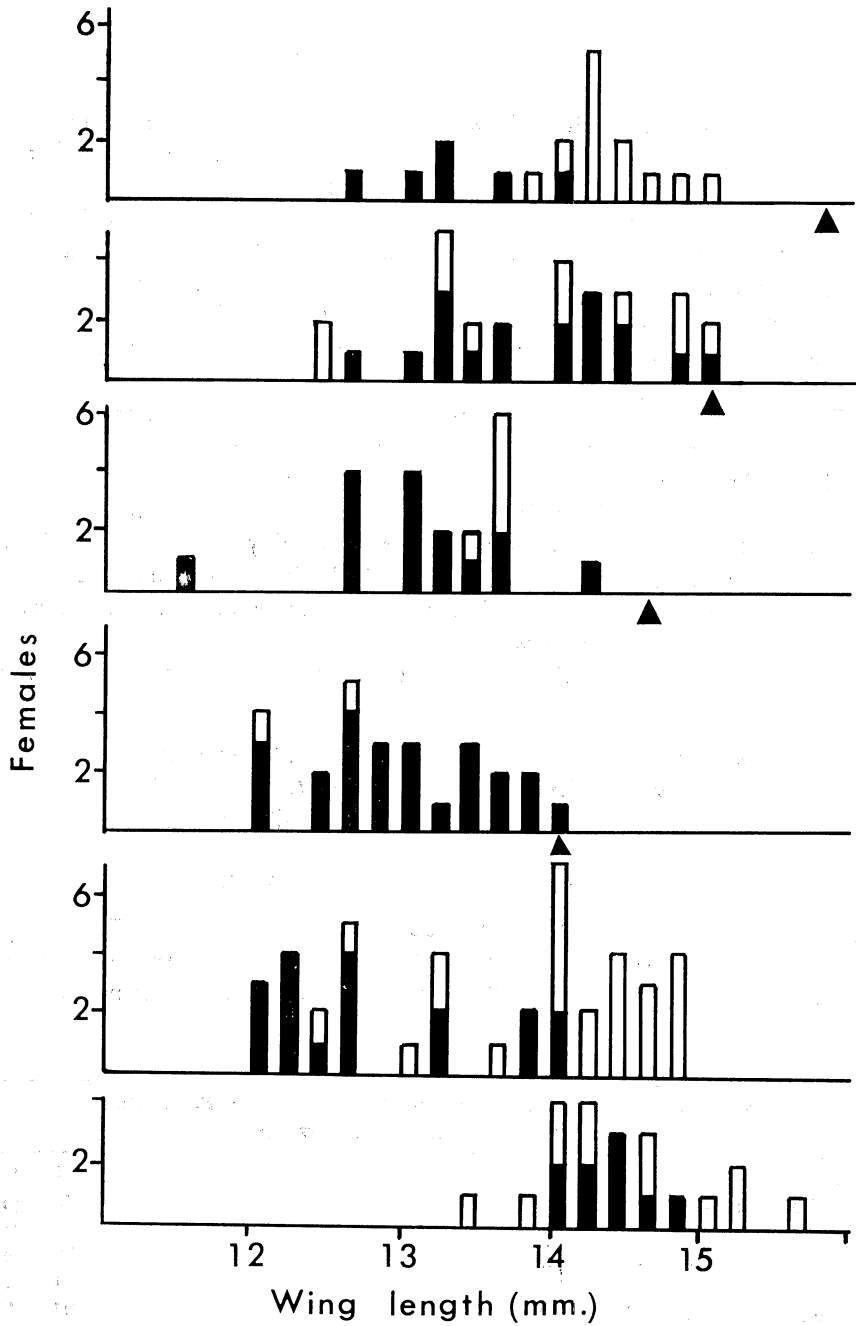


FIG. 15. Intra-colony variation in wing length of females emerging from six nests before and during August (*P. fuscatus*, locality N). Solid bars—unfertilized females on nest when collected on 27 July 1965. Open bars—pupae on 27 July, emerged in laboratory during August. Solid triangle—wing length of foundress queen (female containing mature oocytes, and sperm in spermatheca).

such chewing was not evident elsewhere on the nest. Therefore the recorded number of vacated pupal cells probably approximates the total number of adults produced by the colony. This number, 234, was near the number of cells (251) composing the nest when additions ceased on 31 July. Twenty-three of the nest's 251 cells produced two adults and 46 cells produced none.

All observed foragers were marked, and since the number of marked adults for the period of worker emergence tallies with the number of emergences (vacated pupal cells) for that period, the estimated size of the worker population (32) is probably quite accurate.

The number of non-foraging adults (males and females) marked is undoubtedly lower than the number produced because they emerged at a relatively high rate, often clustered out of sight on the nest top, and stayed on the nest a relatively short time (mean duration of stay on nest for marked workers = 22.8 days; non-worker females = 8.5 days; males = 4.7 days). However, the sex ratio of non-foraging marked adults probably reflects that of the emerging brood since the behavior of both sexes during the period of their concurrent emergence was similar.

The estimated composition of the adult brood of colony B38 was as follows (Table 10):

workers	32 (14 per cent)
non-worker females	92 (39 per cent)
males	110 (47 per cent)

TERMINATION OF THE COLONY CYCLE

EFFECTS OF CESSATION OF REPRODUCTION BY THE QUEEN.—The abrupt halt in growth of colony B38 (Fig. 12A) occurred on 30 July, the date of disappearance of the queen. Although two females, one a former worker

TABLE 10

PRODUCTION OF WORKERS, MALES AND NON-WORKERS IN <i>P. fuscatus</i> (COLONY B38, 25 JUNE-4 OCTOBER 1964)		
Estimated total adults (vacated pupal cells)	234	(a)
Marked adults: Workers	32	(b)
Non-workers	62	(c)
Males	75	(d)
Total	169	(e)
Male/Non-Worker ratio (marked adults)	1.2:1	(f)
Estimated total Males $(a - b) \times \frac{1.2}{2.2}$	110	(g)
Non-workers $(a - b - g)$	92	(h)
Overall ratio Males/total Females	0.88:1	(i)

marked on 27 June and the other a recently-emerged non-worker marked on 26 July, laid eggs on 11 and 13 August respectively, their activity did not regenerate colony growth.

Workers continued to attend larvae in the absence of the queen, and most eggs (18 of 30) laid during the last week of oviposition by the queen produced individuals which eventually pupated. However, the brood gradually declined as adults emerged and cells were left empty.

As observed by Pardi (1948b) in *P. gallicus*, nest growth sometimes continues, although at a reduced rate, following queen removal. An observed egg layer was taken from each of three nests (L1, L3, L4) on 18 July 1966. Dissection proved each to have developed ovaries and sperm in the spermatheca, indicating that all had been foundress queens. Forty-four days later (31 August) the nests had increased an average of 25 per cent above their size at queen removal, whereas four control nests (queens not removed) increased an average of 86 per cent during the same period (Fig. 16). Continued growth of experimental nests was evidently due to (1) establishment of substitute queens, observed ovipositing on nests L3 and L4 one week after queen removal, and (2) new cell initiation by workers, which would account for the addition of 12 eggless cells to nest L1.

Dissection of a substitute queen taken from L3 on 26 July revealed 36 oocytes and no sperm in the spermatheca. Following her removal, further new cells appeared on nest L3. Presumably other females began to oviposit and initiate new cells.

A substitute queen marked on nest L4 on 2 August was absent on 9 August; the nest did not grow subsequently.

New cell addition had ceased and the brood decline had begun on nest A1 on 29 August 1965 even though the queen was still present. However there were many empty cells on the nest indicating that she was no longer laying eggs. Dissection showed that she had large but degenerating ovaries, with five mature eggs having yellow spots and spotty opaque areas, in contrast to the homogeneous whiteness of the eggs of active queens.

These observations indicate that absence of a reproductively active female leads to cessation of new cell addition and eventual brood decline, suggesting that colony termination, like its initiation, is determined by the reproductive behavior of the queen.

All seven nests of Figure 16 grew very little after 9 August. Cold and rainy weather during the week 9–16 August probably accounted for some of the lack of building activity during that week. However none of the nests increased in size after 31 August. The evidently synchronous decline of these colonies suggests that there may be some extrinsic control of the timing of the reproductive death of *P. fuscatus* queens.

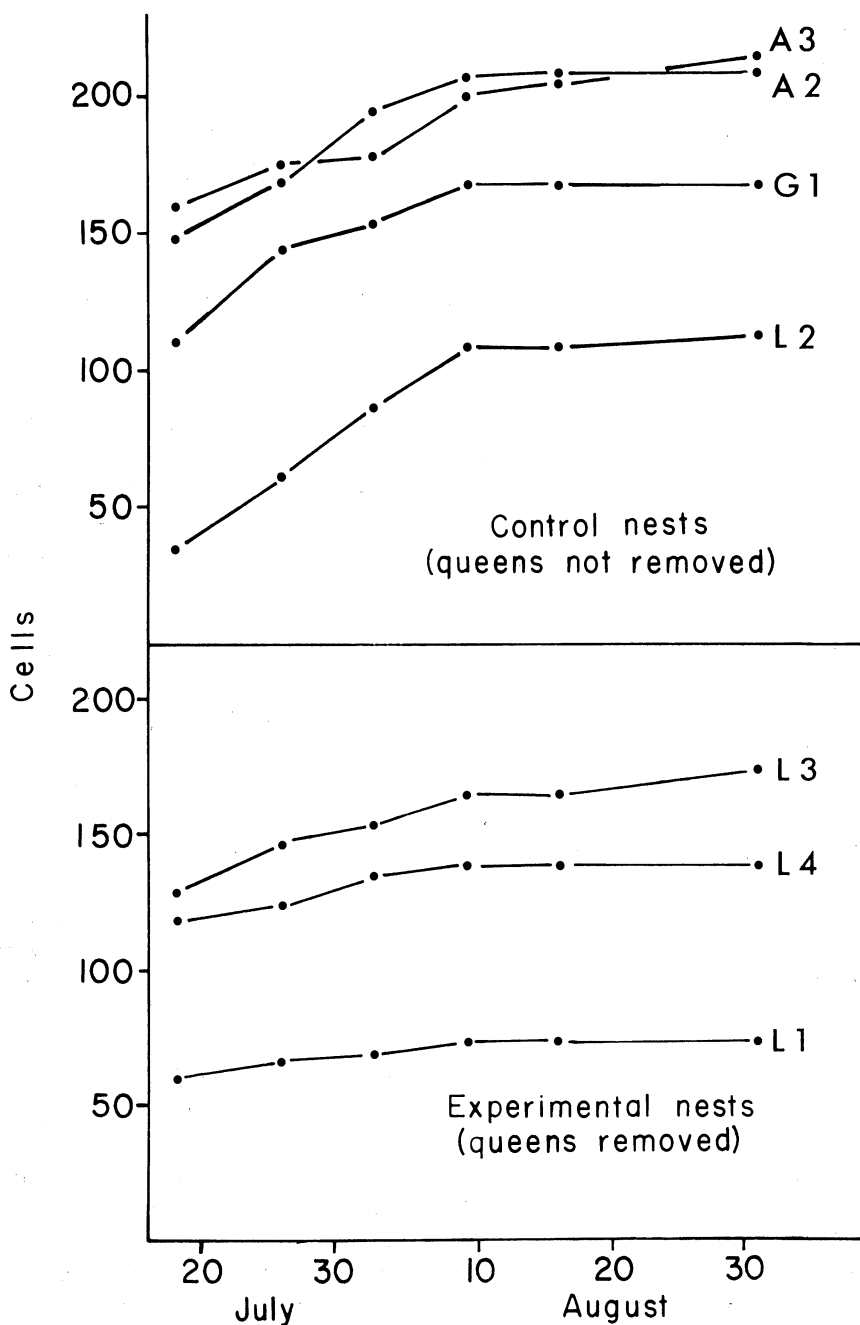


FIG. 16. Effect of queen removal on nest growth (*P. fuscatus*). An observed egg-layer was taken from each of the three experimental nests on 18 July 1966. Substitute queens were observed on nests L3 and L4 (see text p. 53).

BEHAVIOR OF MALES.—The behavior of males on the nest is in some respects like that of the non-worker females. They often sit low and immobile on the nest top or periphery, sometimes leaving the nest but returning loadless, and solicit and receive food and fluids (but not pulp) from associates. In addition they sometimes attempt copulation with both females and males, mounting, abdomen stroking, and sometimes even extruding the genitalia; but these encounters usually end with the wasp moving away and I have never seen copulation completed (genitalia firmly attached) on the nest in *P. fuscatus*. Males frequently fan their wings when it is hot, thus contributing to the cooling of the nest (Steiner, 1932). I once saw a *fuscatus* male dispensing a food load to larvae; and males regularly collect larval fluid.

During the mid-August peak of male abundance (Fig. 9), male-chasing is a conspicuous feature of behavior on the nest. The scurrying of males with workers in pursuit, often pulling at a male's hind leg clamped in their mandibles, gives the colony a disrupted appearance, although workers continue to forage and attend the brood. Male-chasing sometimes occurs off the nest. I once saw a female approach nest A1, then land near a crack where a male had been sitting for more than an hour. The female attacked the male until he left.

After a period of abundance there is a quite sudden absence of males. This occurred on colony B38 on 3 September 1964 (Fig. 9). On 29 August 1965 there were many males on both nests A1 and G2; but a week later (5 September) only two were visible on G2 and none on A1. After these dates only newly-emerged males, recognized by their slow movements and/or lack of a paint mark, were seen on the nests. Probably the "sudden" disappearance of the males was due to their leaving the nest soon after emergence, and a decrease in rate of male emergence (Fig. 11).

MOBBING OF RETURNED FORAGERS.—During the period of male and non-worker emergence the adult population on the nest grows at its fastest rate (Figs. 9 and 12), yet the forager population is steadily declining (Fig. 9) and therefore the ratio of soliciting non-foraging adults to workers rises. Perhaps due to the consequent scarcity of foraged food, returning workers are sometimes mobbed by soliciting adults on post-enlargement nests. In one such instance on nest A1 (4 September 1965) a single load of food material was shared by eight adult females, with none being fed to larvae. Mobbing of foragers is common on waning nests whereas during the period of nest enlargement most loads are divided among only two or three adults.

BROOD DESTRUCTION.—During the post-enlargement period females on nests G1 and B38 pulled larvae and pupae from cells ("abortive behavior")

and divided them among nestmates, fed bits to larvae, or dropped them off the nest. All of the four observed instances of abortive behavior occurred on or after 18 August, and after the cessation of oviposition by the foundress queens. One of the females which aborted a pupa on nest B38 was a former worker later observed ovipositing; the one abortion observed on nest G1 was by the foundress queen. One aborted individual was moribund or dead—discolored and unmoving. Others appeared normal and moved when pulled from their cells, while apparently similar individuals in adjacent cells were spared.

Deleurance (1948b, 1952b, 1955) has observed widespread abortive behavior in *P. gallicus* and considers it an important characteristic of waning colonies. He distinguishes two phases of brood production in *P. gallicus*: the early brood ("couvain normal") is composed of healthy individuals which develop normally; the second ("couvain abortif") contains individuals which usually develop abnormally, are subject to bacterial infections, and are removed from their cells and consumed by adults, the rare adults produced being generally abnormal. Deleurance considers the advent of the abortive brood, and the accompanying change in the behavior of adults (which begin to fight, destroy brood and eventually abandon the nest) important events in the natural decline of the colony.

I have not observed such phases in *P. fuscatus*. There was no large-scale brood destruction on colony B38 and no evidence of it on other nests observed during late summer. The only circumstance in which I have observed brood abortion on the scale described by Deleurance is on colonies brought into the laboratory, in which normal foraging and egg laying were consequently disrupted. However I have observed heightened aggressiveness among workers following queen removal in both *P. fuscatus* and *P. canadensis*, as did Morimoto (1961b) in *Polistes chinensis*; and in *P. canadensis* eggs and larvae shrivel and are removed following queen dysfunction or absence.

Deleurance does not mention having considered the presence or absence or reproductive condition of the queen at the onset of the couvain abortif, and this cannot be deduced from his descriptions of the condition of observation colonies, some of which (an unspecified proportion) were maintained in the laboratory.

Numerous attempts at explanation of the phenomenon (e.g., considerations of age of ovipositing female, quantitative and qualitative change in nutrition, changing secretions of aging workers, and microbial infections) have been inconclusive: "Quelle que soit l'origine du phénomène, l'existence du couvain abortif chez le Poliste s'oppose, notamment par ses séquelles, à la pérennité de la société" (Deleurance, 1955, p. 301).

DROP MAKING.—Males and females of waning colonies and in aggregations off the nest in autumn sometimes sit immobile with a drop of clear liquid on the mouthparts. The drop remains for as long as five minutes, then is slowly withdrawn. One female of colony A1 observed closely for thirty minutes on 23 September 1965 exuded and withdrew drops ten times, the average duration of a drop on the mouthparts being 108 seconds (range: 51–280 seconds). As a drop is withdrawn the mouthparts move in a chewing motion, and the wasp sometimes shifts position slightly; then it becomes immobile again, opens the mandibles and exudes another drop with a pumping motion of the abdomen.

Passing wasps do not seem to react to the presence of a drop on the mouthparts of another individual. When a drop-making individual is approached or bumped it immediately draws the drop into its mouth.

Deleurance (1952b) noticed that autumn females of *P. gallicus* are “forcibly crammed” with honey, which they regurgitate and swallow all day. The drops I have tasted are sweet, and drop making may serve to concentrate dissolved sugars by evaporation, thus increasing the energy/volume ratio of food held in the crop during a period of decreasing food availability. This behavior is similar to that of honeybees, which concentrate nectar by sucking it in and out over the surface of the tongue before storing it in a cell (Richards, 1961).

PRE-HIBERNATION AGGREGATIONS AND MATING

At night and on cool days during late summer and autumn most of the few adults on the face of the nest are workers. Non-worker females and males cluster on the nest top. On warm days the clusters are relatively dispersed and many adults sit on surfaces near the nest as well as on it.

Adults marked on observation colonies A1, B38, G1, and L1 and subsequently found in nearby clusters frequently reappeared on the parental nests where they sat and solicited from nestmates, then rejoined the off-nest clusters. Some marked wasps were found in the same clusters for several weeks and flew from and returned to them as they would to a nest.

Beginning in mid-August clusters appear away from the nest, often in cracks and on old abandoned nests. At first such clusters contain mostly males. Later both sexes begin to sit off the nest. In dark place the clusters persist even on warm days. On 17 September 1965 females remained clustered in a very warm (34°C.) but dark barn, and clusters also persist in cracks and above nests on warm days. This indicates that low temperature alone does not account for autumn clustering.

In *P. fuscatus* mating aggregations characteristically occur on and near

sunlit structures somewhat removed from and high with respect to surrounding objects, and near hibernation sites. One shed at locality S has been a mating site annually for four years (1962–1966). I have looked for nests each year in and on this shed but have found none; nor have I seen wasps there during summer. However during autumn many females crawl in and out of cracks near the roof; and in early spring 1961 large numbers of overwintered females came to a mercury vapor lamp placed in the doorway of the shed, indicating that they were concentrated in that area before building nests. At localities B, G and K mating activity occurred near crevices on the south sides of barns.

Sexually responsive males (males observed pursuing other individuals and attempting copulation) often sit near cracks through which females enter hibernacula. Unlike males on the nest, which are characteristically passive and unaggressive, they sit with body and wings raised, tilting their planar yellow faces at anything which moves nearby, and pursuing other individuals (males and females) in flight and on foot. Pairs of grappling wasps frequently fall to the ground, the male performing stroking movements with the abdomen and extruding the genitalia.

Females usually react aggressively to the copulatory attempts of males. They struggle violently until free, then fly away, whereupon the male usually returns directly to the sitting place where he had been before. In one instance when a female was relatively passive (walking slowly as the male mounted and performed the abdomen strokes) the abdomens of the two wasps seemed to be connected for about ten seconds. Usually, however, no such connection can be seen, and it was not possible to determine whether a particular grappling encounter resulted in copulation.

Mating sometimes occurs in hibernaculum-like cavities. At locality G I was able to look into a crevice entered by several females. Inside were six females and one male. A second male flew directly to the opening and entered the cavity. One of the females bit at him briefly, whereupon the male copulated with her. The genitalia were attached for several seconds and the male performed a series of rapid antennal vibrations while in copulo.

I saw mating activity in the same cavity several times between 5 and 28 September 1965. The males and females present on 5 September were marked and some remained there throughout this period. If *Polistes fuscatus* females mate more than once, persistence of such a mating group would tend to reduce the number of males inseminating a given female.

Marked males and females of the locality G mating cavity occasionally visited a large waning nest (G2) about three feet away, and may have

originated there. However, the larger mating aggregations are undoubtedly composed of more than one colony. I have seen marked B38 adults with many unmarked wasps of both sexes in an aggregation on the south window of a greenhouse about fifty yards from the parental nest.

In order to observe the movements involved in mating I partially immobilized a female captured at the locality S shed by fastening it to a stick with "tacky wax" (a mixture of paraffin, beeswax and yellow rosin) as shown in Fig. 17a. The female could move her legs, head, wings and abdomen, but could not fly. I pushed this female toward a male which had just fallen to the shed floor with a free female which quickly flew away. The male immediately grasped the captive female and copulated as shown in Fig. 17. A sequence of 25 still pictures of this copulation (duration: about 30 seconds) and high speed (64 ft/sec) motion pictures

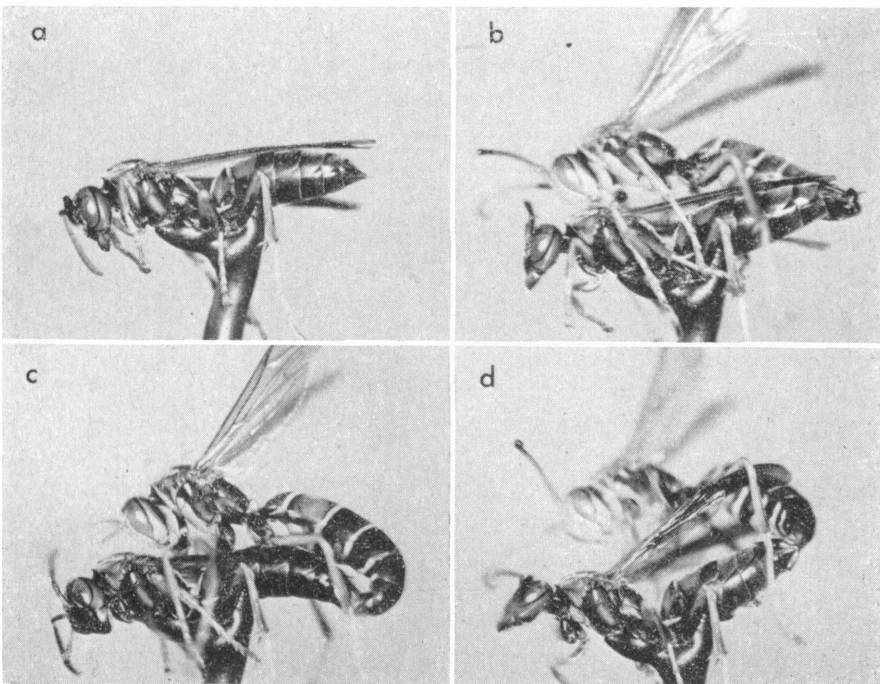


FIG. 17. Copulation of partially immobilized female and untethered male (*P. fuscatus*). *a*—Partially immobilized female can move head, abdomen, and appendages, but cannot fly. *b*—Initial grasping of female's abdomen with male's claspers. The sting of the female protrudes from the tip of her abdomen. *c*—Antenatal vibrations. The male's antennae occasionally move up and down in unison, with rapid vibrations on the downstroke. *d*—Position of male's parameres during copulation.

of another (duration: 20 seconds) showed the following movements by the male to be involved in copulation in *P. fuscatus*:

1. Abdomen-stroking. The male, mounted directly above the female and with head in line with hers, arches and flexes his abdomen up and down against both sides of the female's abdomen.

2. Extrusion of the genitalia.

3. Grasping of the female's abdomen with the claspers (parameres), after (or perhaps as) she extrudes her sting (Fig. 17b).

4. Rhythmic series of antennal vibrations, with both antennae moving simultaneously up and down in front of the female, vibrating very rapidly on the downstroke (Fig. 17c). Antennal vibrations occurred sporadically during the filmed copulation, and did not seem coordinated with any other particular movement of the pair.

5. Grasping of the female's antennae with the curved tips of the male's antennae.

The male sometimes held his antennae down in front of the female and antennal grasping occurred when they contacted those of the female, to which he responded by curling and lifting his antennae against hers. Weyrauch (1928) observed that in the courtship of *P. dubius* Kohl and *P. opinabilis* Kohl (= *P. biglumis* Fabricius) the male's antennae beat on the tops of the female's antennae, and that the "rings" formed by his terminal antennal segments encircle the female's antennae and are pulled along them from base to tip. A similar description is given by Yoshikawa (1963b) for *P. fadwigae* and *P. yokahamae* Radoszkowsky. This use of the antennae by *Polistes* males may be homologous with the antennal grasping observed in *Odynerus spinipes* Linnaeus (Eumenidae) by Chapman (1870): the male's antennae "are directed straight forwards, their curled extremities seizing the scapes of the antennae of the female" (p. 214). Some other eumenids (e.g., *Eumenes*) have sharply-hooked antennae probably used in a similar way.

Antennal movements appear to play an important role in the courtship of various wasps. Barrass (1960) found that the female *Mormoniella vitripennis* (Walker) (Pteromalidae) must depress her antennae (a motion accompanied by abdomen erection) for copulation to occur, and that antenna-less females do not copulate. Antennal tapping by males on the head or antennae of females occurs in the eumenine wasp *Ancistrocerus antilope* (Panzer) (Cooper, 1955) and in the sphecids *Ammophila campestris* Jur. (= *A. pubescens* Curtis) (Baerends, 1941), *Oxybelus sericeus* Robertson (Bohart and Marsh, 1960) and *Mellinus arvensis* Linnaeus (Huber, 1961). Baerends (1941) believes that the antennations of the *Ammophila* male stimulate the female either to make movements facilitating genital attach-

ment or to stop resisting attachment, since the antennations are most intense shortly before genital contact and cease thereafter. Antennal grasping and/or lifting occurs in *Ammophila* (Baerends, 1941) and *Mellinus* (Huber, 1961).

In laboratory observations of semi-immobile females and tethered males, males frequently stood immobile but alert (head tilted, antennae raised) for up to ten minutes when they encountered an immobile female, then attempted copulation when the female strongly moved head, legs and abdomen. Furthermore males would mount immobilized females only if their abdomens were propped up as shown in Fig. 17; females with drooping abdomens were ignored by sexually responsive males. These observations suggest that aggressive movements or posture (abdomen raised as preceding a stinging attack) by the females are important in inducing males to mount.

The mounted male of Fig. 17 sometimes bit at the female's thorax and wings until she moved. Since the extruded sting is visible during both copulation (Fig. 17) and oviposition, sting extrusion may serve to move the sting apparatus clear of the genital opening, permitting insertion of the male genitalia, or, in the case of oviposition, expulsion of an egg. Gary (1963) reports that the sting chamber must be open for successful attachment in honeybees, and the same has been observed in ants (Paul Kownowski, personal communication). Female aggressiveness (stinging) may thus facilitate copulation.

Except for the presence of males, the behavior of clustering wasps in autumn is like that already described in spring females. Clusters tighten and disperse with falling and rising temperatures; and females enter and leave hibernacula and fly about sluggishly on warm days, lending to the annual cycle of *P. fuscatus* an aspect of seasonal symmetry.

SOCIAL BIOLOGY OF POLISTES CANADENSIS

NEST INITIATION

There is little (if any) seasonal synchrony in the foundation and termination of *P. canadensis* colonies near the equator. Censuses of a large population at locality U during early dry season (4 December), late dry season (7 February) and mid rainy season (10 April) revealed large numbers of colonies in all stages of development, as did a census at locality Z on 17 January (Table 11). Rau (1933) found *P. canadensis* colonies of all stages during August and September on Barro Colorado Island (9° N. latitude).

Nest founding sometimes occurs when the nest or brood of an established colony has been destroyed. Seven days after ants invaded colony VI the queen and a group of females from her former nest occupied a new nest

about ten feet away. Colony foundation by a "swarm" of nestmates from a colony whose brood rearing was disrupted by some catastrophe has been noted in tropical *P. canadensis* by Rau (1933).

Colony multiplication is commonly associated with the decline of a parent colony. At each of localities T, W and V there was a single large declining colony and a number of new nests whose foundresses had been marked on the waning nest (locality V), visited it repeatedly (localities V and T), or were presumed to have originated there because no other mature colonies were found nearby (localities V and W).

As in *P. fuscatus*, *P. canadensis* nests are usually initiated by a lone female, and foundress groups form gradually afterwards. Each of eight nests which I saw initiated at locality V was started by a single female. Small (presumably young) nests were usually occupied by only one or two females: Of 121 pre-emergence colonies censused at locality U on 7 February 1965, 20 were newly founded, having nests composed of fewer than ten shallow cells, and containing only eggs or very young larvae. Fifteen of those 20 nests were attended by a single foundress and 5 by 2 foundresses.

FOUNDRESS ASSOCIATIONS

FREQUENCY OF MULTIPLE-FOUNDRESS ASSOCIATIONS.—Nest initiators were almost invariably joined by additional females soon after beginning to build. Among 46 colonies censused in the late pre-emergence stage—containing pupae but no cells from which adults had emerged—only one was attended by a single female. The mode number of foundresses was five, and the mean 4.9 foundresses per nest (locality U, 4 December 1964 and 7 February 1965). The maximum number of foundresses per nest was ten. Some of these estimates are probably low, since colonies were censused in the daytime, when some inhabitants may have been away from the nest.

CHANGE AND STABILITY IN FOUNDRESS ASSOCIATIONS.—During the pre-emergence period there is sometimes a group of idle females sitting dispersed off the nest, while the queen and occasionally a few other females occupy the nest. The "on-off" configuration disappears at night when the "off" wasps cluster near and on the nest.

These groups sitting off the nest are characteristic of colonies early in the pre-emergence period: all of eleven cases observed at locality U on 4 December 1964 were associated with pre-emergence nests containing no pupae. On the other hand, none of 17 pupa-containing pre-emergence nests had idle females sitting nearby. The difference in the behavior of females of late pre-emergence colonies is not entirely due to older nests being larger and therefore accommodating more sitting wasps. On nests W2

and W3 the on-off pattern disappeared gradually as some idle females left the colony and others began to forage or sat passively on the nest, from which they had previously been chased by aggressive contenders during queen determination (described below). At about the time the groups sitting off these nests disappeared, dominance conflict stopped and the size and composition of the foundress associations ceased to change. Therefore it appears that groups sitting beside newly founded nests are at least sometimes an indication that dominance conflict exists among the associated foundresses.

Older pre-emergence colonies have unchanging foundress groups even when near a waning colony from which females are dispersing to join associated newly-founded colonies. A relatively mature (pupa-containing) pre-emergence colony (V3) was located only about twelve inches from a waning colony (V2)—closer than any of the more recently founded nests in a small cave. But none of the four marked residents of colony V3 ever attended another nest; and none of the wandering females in the cave were ever seen on or near nest V3.

The size and composition of early foundress groups sometimes change from day to day. This is illustrated by the history of colony V10, founded on 14 March 1965 by a female (No. 10) marked on waning colony V2 in the cave containing all of the 12 locality V observation colonies. On 23 March at 6:45 a.m.—before the wasps became active—there were three females at the nest: No. 10, No. 33 and No. 35, also marked on V2. At noon, No. 10 was on the nest and six wasps (including No. 33 and No. 35) were sitting nearby. When activity had ceased that night (4:30 p.m.) there were five females on the nest and two off, including all of those present before plus two more marked on V2 and two (No. 22 and No. 36) marked three feet from V10 on V6 (16 March). Thus during 9.5 hours of activity, seven females had joined the association. Twelve days later (4 April) three of these (queen No. 10, No. 22, and No. 36) remained, plus seven additional females.

An experiment performed by ants demonstrated the lack of coherence of early foundress associations compared to the stability of groups on longer-established nests. Nest V6 was abandoned between 16 and 23 March after being invaded by ants. Four marked females which had been associated with the nest appeared near other nests, including V5, V7, and V10. This was in contrast to the behavior of females from a nest (V1) in the emergence-enlargement stage of development after it was invaded by ants on 6 March: On 9 March, while the ants stripped her nest of brood and stored sugar, the queen (No. 1) appeared on the ceiling of the cave accompanied by

several females, which I marked with green paint. She occasionally changed position, and the green-marked females came and went from the cave, always coming back to rest in a loose aggregation near the queen, never elsewhere in the cave. On 13 March the queen and her group occupied an eight-cell nest (V8) initiated on 9 March by female No. 8 (marked on 6 March on waning nest V2). Although unmarked individuals and females marked on other nests sometimes sat near V8, none of the nine or ten green-marked wasps ever joined another colony; and when the queen disappeared after 23 March only the green-marked females remained associated with the nest. The nest was not enlarged after the queen disappeared, and when last observed (4 April) only three green-marked females remained. This indicates that there is an integrity of established colonies which is independent of residence on a particular nest and does not exist in newly-established associations.

The attainment of foundress group stability sometime during the pre-emergence period (above) enhances the likelihood that foundress associations are composed of siblings by restricting the time during which joining is possible. Foundress groups composed of females from more than one parental nest would require either the simultaneous decline of nests in close proximity or migration of foundresses from a waning nest to a distant newly founded one.

As shown in Table 11, there is little or no seasonal synchrony in the decline and foundation of nests by *P. canadensis* at the localities studied; and the likelihood of coincidental synchrony among colonies is reduced by all the differences in individual history and heredity which might cause variations in the timing of queen disappearance or dysfunction on adjacent nests (see "Conclusions: The Colony Cycle and Queen Determination," p. 76).

TABLE 11
PERIODIC CENSUS OF COLONY STAGES PRESENT IN LARGE POPULATIONS
OF *P. canadensis* (1964-65)

Locality	Date	Inhabited	Pre-emergence		Post-emergence:			
		Nests	Colonies		Brood Present	Empty		
		N	#	%	#	%	#	%
U	4 Dec. 1964	205	122	59.3	53	25.8	19	9.2
U	7 Feb. 1965	227	121	48.4	88	38.7	18	7.9
U	10 Apr. 1965	270	97	35.9	130	48.2	43	15.9
Z	17 Jan. 1965	68	30	45.0	30	45.0	8	10.0

There appears to be little dispersal from the parental nest site by *P. canadensis* foundresses. The decline of a mature nest and associated founding of new colonies nearby was followed for nearly a month (6 March–4 April)² at locality V. During that time eight new colonies were founded, each within six feet of declining nest V2; the adult female population of declining colony V2 fell from 21 to zero; and the number of females present on newly founded nests rose from five to 38. Some of the foundresses probably emerged from V2 pupal cells during the observation period (number of V2 pupae went from 72 to two, many of the adults produced during that period being males). Eleven foundresses present on new nests on 4 April had been marked on nest V2 on 6 or 13 March; more frequent marking and observation would be required to determine (1) what proportion of the female progeny remain near the parental nest site, and (2) what proportion of the foundresses on nests near a given waning nest actually originated on that nest. However, these data suggest that there is high “population viscosity” in *P. canadensis*—a large proportion of foundresses remain near the parental nest site. Even if there were some synchrony of colony cycles, in such a population foundress groups formed by non-siblings would be likely to contain relatives.

This high degree of population viscosity may be promoted by (1) the asynchrony of nest dissolution and founding observed in the Colombian populations, making it expedient for females to mate near the parental nest where sexually mature males are likely to be available, and (2) the possible advantage to males of mating on or near newly-founded nests (see p. 76). The combination of these factors may make it more likely for females founding nests near the parental nest to find mates.

QUEEN DETERMINATION

The interactions leading to the presence of only one ovipositing female per colony in *Polistes canadensis* differ from those in *P. fuscatus*. Subordinate foundresses neither initiate new cells nor oviposit; and since only one egg-laying female was ever present on a nest at any one time, differential egg-eating was not observed. Dominant females attacked closely-ranked subordinates until they either left the colony or became idle residents.

The history of colony W2 (summarized in Figure 18) illustrates the nature and consequence of interactions among foundresses in *P. canadensis*. When first observed on 1 December 1964, nest W2 contained 22 cells and five females. Female No. 1 was dominant to the others and seldom left

² Nests were observed for a total of 48 hours on eight different days: 6, 9, 13, 14, 16 and 23 March, and 1 and 4 April.

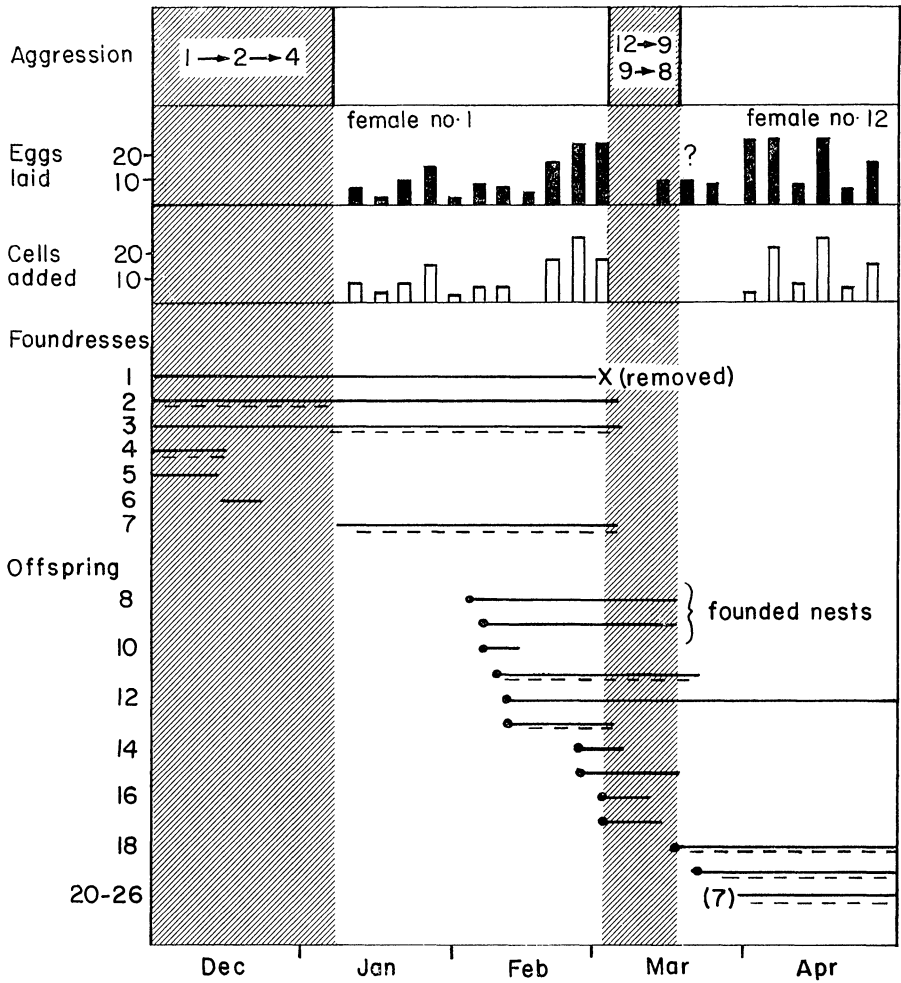


FIG. 18. History of colony W2 (*P. canadensis*). Shaded areas indicate duration of dominance conflict among females identified at top (arrows point from attacker to attacked female). Solid horizontal lines indicate duration of a marked female's presence on the nest, a dashed line the period when she was a forager. Offspring are numbered in order of emergence. Individuals 20-26 were marked the same color; some (an undetermined number) foraged.

the nest face, while Nos. 2 and 4 foraged. Aggression occurred among these three females on every day activity was observed on the nest during the five-week period of 1 December-7 January. No. 1 attacked No. 2 whenever the latter approached the nest, and No. 2 attacked No. 4. However, No. 1

did not always attack No. 4, and once moved aside when No. 4 arrived with a load of pulp and applied it to a central cell. The three active foundresses thus formed a dominance hierarchy No. 1/No. 2/No. 4 in which, as pointed out by Pardi (1948a), aggression between closely-ranked females was more frequent than between individuals further apart in the hierarchy.

During the five-week period of conflict among the contending foundresses there was no new cell building and no observed oviposition (Figure 18). Eggs and larvae present in the cells continued to develop but at a reduced rate: one of six larvae present on 1 December pupated on 8 January, which means that it was a larva for more than forty days—more than 11 days longer than the mean length of the larval period on that nest, which was 28.4 days ($N = 28$). An extended larval period one consequence of low larval nutrition (see p. 00), which probably resulted in this case because the only two foragers present were the subordinate contenders, which were usually attacked upon return to the nest after foraging.

Female No. 4 was not seen after 16 December. Attacks by No. 1 on No. 2 continued through 5 January, which was also the date of the last recorded foraging by No. 2. When the nest was next observed (8 January) a new cell and egg were present, the first new additions to the nest in more than five weeks. Thus there was temporal concurrence of the beginning of idleness on the part of the one remaining contender female, the cessation of dominance conflict, and the resumption of nest growth and oviposition (Figure 18).

Dominance conflict among foundresses on nest W2 thus had the following consequences: Subordinates were chased from the nest. Therefore low-ranking subordinates (non-contenders No. 3, No. 5 and No. 6) usually sat off the nest, and did not forage, perhaps because females having relatively undeveloped ovaries (indicated by the subordination of these females) require contact with the brood for much of their stimulation to work ("comportement d'origine 'externe'," Deleurance, 1957). On the other hand aggressive females No. 2 and No. 4 continued to forage, probably because their more developed reproductive systems (associated with aggressive behavior) stimulated foraging and building behavior comparable to that of subordinate foundresses in *P. fuscatus* (Table 4). However the attacks of dominant contenders on subordinate foragers were apparently sufficient to keep them from enlarging the nest.

There was evidently sufficient difference in dominance between No. 3 and No. 1 to preclude conflict between them, so that when No. 2 became passive (no longer foraging or fighting), No. 3 was able to come on the nest unattacked and function as a worker subordinate to No. 1,

During the ensuing weeks of nest growth, all of four observed new cell additions and ovipositions on nest W2 were by female No. 1. Two other foundresses foraged throughout this period. Eight offspring females emerged: two foraged regularly, and six foraged little or not at all (Figure 18).

I removed the queen (No. 1) on 3 March, with the following results: new cell additions ceased and daily fighting occurred among three offspring females which had foraged little during their recorded histories on the nest. They formed a hierarchy: No. 12/No. 9/No. 8.

Fighting continued until 22 March, when the two subordinate contenders were gone from the nest. No. 8 was found on a nearby new nest containing one cell and egg on 22 March. On 24 March, No. 9 was on a nine cell egg-containing nest about six feet from parental nest W2, and No. 8 was sitting nearby off the nest, along with a male from W3. Both new nests were abandoned after 7 April.

In the absence of contenders, nest growth and oviposition were again resumed on nest W2 (Figure 18).

Growth arrest due to dominance conflict occurred on three of nine pre-emergence observation colonies: colonies W2 (at least 48 days),³ V4 (4 days), and W3 (at least 21 days). On nests W2 and W3 the size of the foundress group declined gradually until growth was resumed, at which time the size and composition of the groups became stable (Figure 18).

In some cases dominance conflict among foundresses led to usurpation of a queen's position by a contender. Two usurpations at locality V involved female No. 4, which resided and oviposited alone on nest V4 when first seen on 6 March. On 9 March another female (No. 4') occupied that nest while No. 4 sat nearby. Whenever the former queen approached, No. 4' attacked and several fights occurred. Although No. 4 sometimes left the nest region, neither female foraged during four hours of observation. This situation persisted on 13 March. On 14 March, No. 4 founded a new nest (V11) and thereafter was not seen near V4, which No. 4' occupied when the nest was last observed on 4 April.

PRE-EMERGENCE GROWTH OF COLONIES

As in *P. fuscatus*, *P. canadensis* nests attended by relatively large foundress associations were generally larger at the end of the pre-emergence period than were nests attended by a relatively small number of foundresses (Table 12).

³ Growth arrests on nests W2 and W3 were in progress when the nests were first observed on 20 November 1964.

TABLE 12
NUMBER OF FOUNDRESSES AND NEST SIZE AT THE END OF THE PRE-EMERGENCE PERIOD
(*P. canadensis*—locality U—7 February 1965)

Number of Foundresses	Number of Nests (N)	Mean Number of Cells in Nests Containing Pupae ¹	Range (No. of cells)
1	1	10	0
2	2	18	16–20
3	4	26	24–29
4	6	37	19–56
5	6	36	25–50
6	8	35	15–56
7	4	50	25–84
8	0	0	0
9	2	42	38–45
10	1	40	0

¹ Shortest recorded time to pupation on locality W mapped nests = 21 days (N = 112), mean time to pupation = 44 days (N = 112), mean total development time (egg to adult) = 64.7 days (N = 39). Therefore all nests containing pupae are at least 21 days old, and probably 44–65 days old.

BROOD PRODUCTION

DURATION OF IMMATURE STAGES.—The mean total development time (egg to adult) of 39 individuals on colonies W2, W3, and W5 was 64.7 days—longer than the longest time (59 days) recorded for *P. fuscatus* nest B38, and more than two weeks longer than the *P. fuscatus* mean (47.8 days).

The duration of immature stages varied among the three colonies: the values for colonies W2 and W5 were nearly identical and differed from those of colony W3 (Table 13). The differences were almost certainly not

TABLE 13
DURATION OF IMMATURE STAGES IN *P. canadensis*
(Based on nest map data accurate to ± 2 days, for the period 1 December 1964–26 April 1965)

Colony	N	Egg Stage		N	Larval Stage		N	Pupal Stage	
		Mean Duration (days)	Range (days)		Mean Duration (days)	Range (days)		Mean Duration (days)	Range (days)
W2	52	17.3	9–28	28	28.4	14–53	35	23.1	21–32
W3	44	16.0	9–26	36	22.8	14–30	29	25.1	7–31
W5	63	17.8	7–30	48	28.5	16–40	24	23.2	13–28
W2 + W3 + W5	159	17.1	7–30	112	26.6	14–53	88	23.8	7–32

due to temperature differences on the three colonies, all of which were beneath the same roof.

Nests W2 and W3 were about two feet apart, were nearly identical in size during most of their histories (Figure 19), and produced their first adults at nearly the same time (1 February and 5 February, respectively). However, in colony W2 there were 12 larvae per worker at the end of the pre-emer-

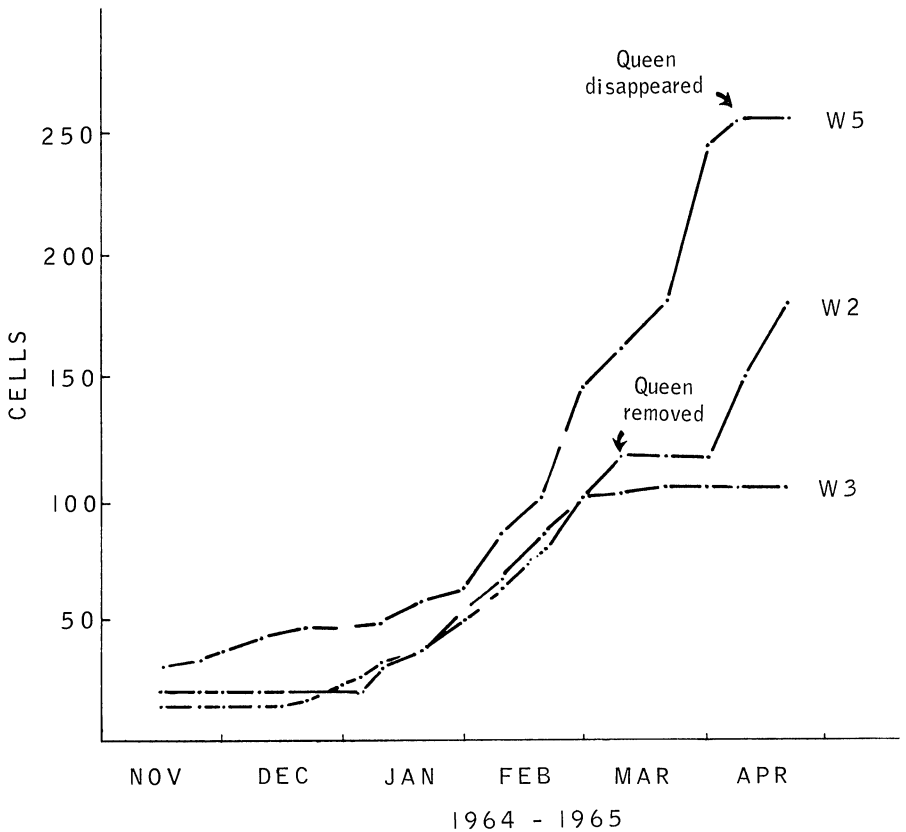


FIG. 19. Nest growth in *P. canadensis*.

gence period (1 February), whereas just prior to adult emergence on nest W3 (4 February) there were only two larvae per worker. Therefore better nutrition probably caused the markedly shorter development times of W3 larvae compared to those of W2 (see "The effect of larval nutrition on development time," above). The number of workers present on nest W5 was not recorded.

Since length of pupal period correlated inversely with length of larval period in *P. fuscatus* (see above), the nutritional differences indicated by the different larva/worker ratios probably also account for the shorter pupal period on W2 compared to W3.

PRODUCTION OF WORKERS, MALES, AND NON-WORKER FEMALES.—In spite of the proximity of nests W2 and W3, none of the 64 adults marked on the two nests was ever seen on a post pre-emergence nest other than that on which it had been marked. Therefore I have assumed that wasps marked on a particular nest at locality W emerged there.

Male production in colonies of *P. canadensis* followed a period of female emergence as in *P. fuscatus*. Males appeared on observation colonies W2, W3, and W5 after the emergence of 8, 11, and 25 females from the respective nests, and 11, 11, and 70 days (respectively) after the first adult emergences.

The three colonies differed considerably in the number of males present among individuals marked on the nests during the five months of observation. Only seven of 33 adults marked on W2 were males, whereas 22 of 31 marked on W3 were males. Although few W5 adults were marked, no males appeared there after 5 March, only one week after the first male was produced on that nest.

On *P. fuscatus* colony B38, male production was directly proportional to oviposition (nest growth) rate (Figure 13). However, this relationship did not seem to hold in *P. canadensis*: calculations of total development time using nest map data show that the first male-producing eggs were laid on nests W2 and W3 either during or before the prolonged growth arrests in progress when observations began on 20 November. On nest W5 male eggs were deposited in mid-December, when nest growth was relatively slow (Figure 19).

Both workers and non-workers emerged on colony W2, but they did not appear in two temporally discrete groups as in *P. fuscatus*. Only two of the first six females which emerged on W2 foraged regularly during their recorded histories on the nest (Figure 18). The first-emerged female never foraged and the second-emerged female foraged only once in over a month of residence on the nest during a period of rapid growth and foraging by associates No. 3, No. 7 and No. 11.

Four females (Nos. 14–17) which emerged just before or during the period of conflict and growth arrest following queen removal did not forage and eventually left the nest (Figure 18). Some females emerging after the establishment of the substitute queen and resumption of nest growth foraged (females 18–28, Figure 18). This suggests that interactions among adults

at the time of emergence or shortly thereafter affect the behavior (caste) of emerging females.

Of the three females which became queens after queen removal, all had been idle during their recorded histories prior to queen removal. This indicates that, as in *P. fuscatus*, females which are non-workers on the parental nest are more likely to become queens than are foragers.

TERMINATION OF THE COLONY CYCLE

EFFECTS OF TERMINATION OF REPRODUCTION BY THE QUEEN.—In *P. canadensis* there is complete cessation of nest growth by new cell addition when the queen disappears or stops ovipositing. Natural disappearance of the queen from colony W5, artificial queen removal on W2 and cessation of oviposition by the queen of colony W3 all were associated with termination of cell addition on those nests (Figure 19).

In all three cases brood decline followed the cessation of nest growth. Large numbers of eggs and larvae disappeared from cells, which then remained empty. In three weeks between the date of addition of the last call on nest W5 (5 April 1965) and collection of the nest (26 April) all of the 101 eggs and 47 of 106 larvae originally present had disappeared. Thirty-nine other larvae pupated and 20 were still present at the time of collection. I saw no evidence of fighting among the 27 females still present when the colony was collected, although four had developed ovaries containing mature oocytes.

After the last new cell addition to nest W3 on 15 March 1965, all 13 eggs and 24 of 44 larvae present on 15 March eventually disappeared. Some larvae pupated, and adults continued to emerge. Two pupae were the only brood remaining when the nest was collected on 26 April. This brood decline occurred even though the queen was present on the nest until she was removed on 7 April.

This indicates that the presence of a reproductively active (ovipositing and cell-initiating) female is required for normal nest expansion and brood care. Presence of an inactive former queen is not sufficient.

Dissection revealed live sperm in the spermatheca of the inactive W3 queen. The basal portion of the ovary was irregular and yellow but the upper portion was full and regular and contained ten mature eggs. Ovary degeneration may have caused cessation of reproduction, or the reverse may have been true. Thus although yolk deposition had continued in the upper portion of the ovaries, the basal irregularities may have prevented not only normal oviposition but also cell initiation. This would support the deduction that construction activity by queens is associated with the presence of a mature egg ready to be laid (at the base of the ovary).

Brood decline occurred even during the temporary (12 days) absence of reproduction following queen removal from colony W2. Thirty eggs disappeared and others became dark and shrivelled. This suggests that the absence of the queen led to the neglect of eggs, and hence that egg care may be a function of the queen or stimulated by her presence.

QUEEN SUBSTITUTION.—Regeneration of nest growth by a substitute queen like No. 12 of colony W2 may be a common occurrence in *P. canadensis*. Such an event is recorded in the nest structure because cell enlargement continues in the absence of cell addition following queen removal or dysfunction. The construction activity of a substitute queen forms a shelf of shallow cells below the deep older ones initiated by the former queen. Such a shelf of shallow cells was formed on nest W2 by the 77 cells initiated by substitute queen No. 12. This feature was common in abandoned nests—so common that for a time I wondered if it might have some “function.” Unfortunately I did not tabulate the proportion of abandoned nests having this evidence of queen substitution because I did not realize the significance of the “shelf” until the Colombian fieldwork had been completed.

Since colony perpetuation by queen substitution occurs and there is no seasonal limit to restriction of nesting activity, prolonged occupation and expansion of nests might be expected in tropical *P. canadensis*. However a count of cells in all abandoned nests at locality U on 10 April 1965 suggests that colony perpetuation by queen replacement is not usual. The average size of 69 abandoned nests was 94.7 cells, and few nests surpassed 300 cells in size (Figure 20). The largest inhabited *P. canadensis* nest I saw in Colombia contained about 750 cells. Since the fastest growth rate observed in mapped colonies was five cells per day, a nest could attain this size in 150 days (about five months) or at the mean growth rate of 1.6 cells per day, 469 days.

BEHAVIORAL CHARACTERISTICS OF WANING COLONIES.—The behavior of wasps on declining nests of *P. canadensis* is in some respects like that in *P. fuscatus*. There is intense solicitation and mobbing of foragers, and drop-making behavior by adults sitting on the nest. Drop-making was less conspicuous on the waning nests observed in Colombia than on those seen in Michigan: I observed three males making drops on only one nest (W2) and on only one day (16 March) of the eight on which that colony was observed during the period 6 March—4 April. This activity may be a means of food concentration by evaporation, as suggested above. In a tropical species it might facilitate food storage and enable individuals to function better during the period between residence on parental and newly-founded colonies, a period of reduced food availability on the nest.

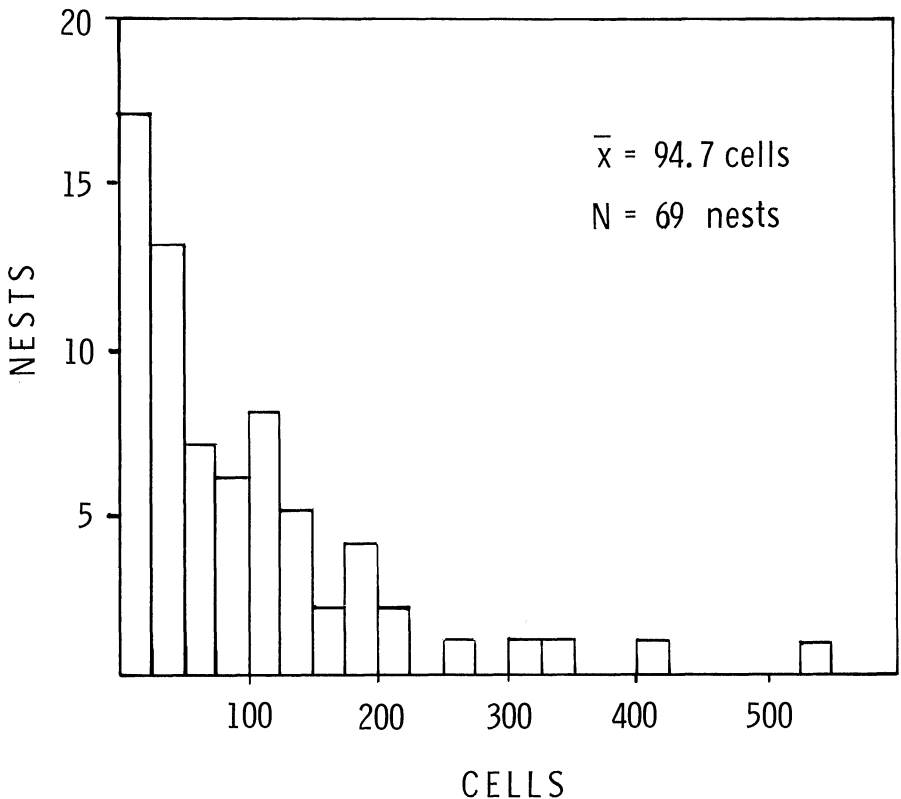


FIG. 20. Size of abandoned nests (*P. canadensis*). Locality U, 10 April 1965. Each bar indicates number of nests in the 25-cell range spanned by the width of the bar.

Waning colony V2 was repeatedly visited by the queens of the more recently founded nests present in the locality V cave. The queen of colony V3 visited V2 ten times in 4.5 hours of observation on 6 March, and the queen of colony V7 visited V2 nine times during 9.5 hours of observation on 14 March. All of the other queens in the cave visited V2 at least once. They solicited vigorously from the females present, then returned after less than a minute to their own nests. Queens were the only foundresses which regularly solicited on the waning nest. This behavior may sometimes serve to augment the number of foragers available to a queen having few or none functioning at her own nest.

Although males were often present on waning nests in *P. canadensis*, they were not chased by resident females as are males in *P. fuscatus*. I never saw evidence of a difference in the behavior of females toward males versus

toward females on any nest in *P. canadensis*. Furthermore, there is an almost complete lack of sexual dimorphism among the adults of a *P. canadensis* colony: males have brown coloration, rounded clypei, and straight antennae as do females, and are difficult to distinguish on the nest. In contrast, male and female *P. fuscatus* are strikingly dimorphic: males have bright yellow coloration on the face, underside and front of the appendages, curled antennae, and indistinct planar clypei, whereas females are brown and have round, conspicuous clypei and straight antennae (see Figure 17). The different reactions of females toward males of the two species may be associated with this difference in degree of sexual dimorphism, although I have been unable to obtain conclusive evidence that the yellow color of male *P. fuscatus* is involved in the recognition of males by females.

MATING

On 7 February 1965, I captured a *P. canadensis* male and female in copulo on a waning nest with only one other adult wasp present. The female was walking slowly with the male hanging from her, attached only by the genitalia. They separated when captured less than a minute later, and the male made copulatory attempts while the pair was in the collecting net. This was the only certain copulation I observed in *P. canadensis*, and the most prolonged attachment of a mating pair I have observed in any *Polistes* species in nature. I suspect for this reason that the copulation may have been abnormal in some way.

On 23 March a male sat in a bush near the entrance to the locality V cave. He pursued females flying past the bush en route to nests in the cave, sometimes following several feet past the entrance, and sometimes falling to the ground with a struggling female. After such flights this male always returned to the same branch of the bush, where he remained from 10:00 a.m. until last noted at 2:00 p.m. Other males pursued passing females from the bushes near the cave during the same period.

These flights undoubtedly represented mating behavior. In one instance after a male chased a female he returned to the bush and sat with his abdomen angled sharply upward and genitalia exposed. The flights at passing individuals and subsequent return to a particular sitting place resemble the behavior of *P. fuscatus* males at mating sites. In this case, however, the males were stationed near the flight path of females attending newly founded nests rather than near hibernation sites as in the temperate wasp.

There is evidence that some females mate after joining new nests. Thirteen of 51 dissected foundresses (25.5 per cent) were unfertilized. Three

of these unfertilized foundresses were probably nest initiators and queens: they were found alone on newly-founded nests consisting of less than 20 cells each, and had ovaries containing mature eggs and 36–45 oocytes each. Queens dissected on more mature nests were invariably fertilized: every queen (female having the most developed ovaries of those present on a given nest) of 27 post-emergence colonies was fertilized. Either the unfertilized females do not persist as queens until nests reach the post-emergence stage, or some foundresses mate after becoming queens. Field observations indicate that the latter alternative is possible: in addition to the mating activity observed in bushes near the newly founded colonies at locality V, I have seen males on five different pre-emergence nests, one of them a marked male from colony W3 which sat for several days off the nest founded by W2 female No. 9 after queen removal and dominance conflict on her parental nest (p. 67).

CONCLUSIONS: THE COLONY CYCLE AND QUEEN DETERMINATION

These observations suggest the following picture of the colony cycle and queen determination in *P. canadensis*: as in *P. fuscatus*, the colony cycle reflects the reproductive cycle of the queen. When the queen becomes dysfunctional or disappears, nest growth either ceases or is regenerated by a substitute queen. In either case female offspring may leave the parental nest and found new colonies, often following dominance conflict with aggressive siblings.

As in *P. fuscatus*, the likelihood of a given female founding a nest and persisting there as the dominant female probably depends on the size of her ovaries relative to those of other foundresses, in this case, of siblings at the time of parental nest decline. Ovary condition might be affected by age and foraging history—whether the ovaries are in the ascending or descending phase of development (Pardi, 1948a), and the extent to which resorption has occurred due to energy expenditure during activity. In this connection it is significant that the W2 progeny which became contenders and, eventually, queens following removal of the parental queen had been non-workers on the parental nest. Thus, as in *P. fuscatus*, non-workers are probably more likely than are workers to become queens. Some unfertilized females found nests, and some queens probably mate after nest founding.

FOUNDRESS ASSOCIATIONS AND THE SIGNIFICANCE OF DOMINANCE HIERARCHIES IN ANIMAL SOCIETIES

Multiple-foundress nests are common in both *P. fuscatus* and *P. canadensis* in spite of the consequent sterility of large numbers of fertilized females.

Following the reasoning of Haldane (1955) and Hamilton (1964a,b), joining would be advantageous to a consequently sterilized female if more replicates of genes like hers were produced as a result of her association with another female than she could produce on her own. Specifically, association is beneficial to a subordinate if it meets the condition $k > 1/r$ in which k is the ratio of gain to loss in fitness and r is an expression of the degree of genetic relationship between the associated females (Hamilton, 1964a). Hamilton (1964b) considered the sterility of daughter workers on a parental nest understandable in these terms since (assuming that the maternal queen mated only once) in insects (such as *Polistes*) with male haploidy females have more genes "identical by descent" with those of their sisters ($r = 3/4$) than they do with their own daughters ($r = 1/2$).

Hamilton's theory suggests an explanation of the observed dependence of the colony cycle on the reproductive longevity of the queen. With the cessation of egg-laying by a queen and the subsequent oviposition by her daughters there is a sudden reduction in the degree of relationship between colony workers and the progeny being reared—from $r = 3/4$ (for sisters) to $r = 3/8$ (for nieces, the offspring of sisters). Therefore the absence of the original queen initiates a time of decision for the colony females: they must weigh the merits of reproducing on their own against the desirability of being a worker on the parental nest (or a newly founded one). Accordingly, in *P. fuscatus* there is a tendency for workers to begin producing their own eggs; and in *P. canadensis* (e.g., in colony W2) there is dominance conflict resulting in the establishment of a new queen in what amounts to a new colony on the parental nest, with some females leaving to begin their own colonies.

Hamilton found it "difficult" to explain "the ready acceptance of non-reproductive roles by the auxiliaries" in *Polistes* foundress associations (Hamilton, 1964b, p. 37) even among siblings since subordinate females are engaged in rearing the offspring of sisters (nieces), which are less closely related ($r = 3/8$) to them than their own offspring would be ($r = 1/2$). However the likelihood of association depends not only on the closeness of relationship among co-foundresses but also on the difference in independent reproductive capacity between associates and the degree to which the presence of the joiner augments the reproduction of the joined queen—the k in Hamilton's expression $k > 1/r$. This condition can be rephrased as follows:

$$\frac{P_{e+j} - P_c}{P_j} > \frac{1}{r}$$

in which P_{e+j} is the productivity of the colony (queen plus worker, including joiner), P_c is the productivity of the colony without the joiner, P_j is the

reproductive capacity of the joiner on her own, and r is the degree of relationship (fraction of genes in common) of the joiner and the joined queen.⁴ When this is true a female (j) produces more replicates of genes like hers by joining the colony (c) as a worker than she could by raising her own offspring.

The reciprocal condition should also hold: when

$$\frac{P_j}{P_{c+j} - P_c} > \frac{1}{r}$$

it would be to the queen's advantage in terms of replication of her genes to expel the potential subordinate worker.

Observations of nest-founding in *Polistes* show that (1) foundresses often initially move from nest to nest, and (2) association requires differential dominance among the individuals of the group. Inasmuch as females are unequally dominant when they associate and relative dominance reflects relative ovary size (Pardi 1946, 1948a), it is likely that associates have correspondingly different reproductive capacities at the time of association. The formation of foundress associations thus may be a process by which siblings sort themselves into groups according to relative reproductive capacity, with inferior reproductives (as measured by relative dominance) becoming sterile helpmates of reproductively superior siblings, and able reproductives (e.g., those in dominance conflict with egg-laying females) likely to found nests on their own. The dominance hierarchy in wasps, and perhaps in other social animals, may thus play an important role in the assignment of different functions (roles) to closely related individuals having different reproductive capacities in a way that both dominant and subordinate individuals derive reproductive benefit (West, 1967b).

Numerous variables in addition to degree of relationship and relative reproductive capacity might affect the desirability of joining a foundress group. The augmentation of productivity ($P_{c+j} - P_c$) would depend on the subordinate's ability as a worker and the capacity of the joined queen to produce more eggs—a capacity which might change as more auxiliaries join the colony. Multiple foundress nests are more likely to survive to produce offspring than are single foundress nests (Owen, 1962). A subordinate on a small nest would be more likely to become a queen in the event of the dominant queen's disappearance or death than would a subordinate on a

⁴ A similar expression, $P_c > P_q + (1/r_1)P_1 + (1/r_2)P_2 \dots (1/r_n)P_n$ (in which P_q, P_1, \dots, P_n are the independent reproductive capacities of the queen and successive joiners), was given in West, 1967b, to describe advantageously formed foundress groups. However, as pointed out by Hamilton in correspondence, the inequality must hold for each successive joiner individually. Hence the above revision, to which the field test given in West, 1967b, also applies.

larger nest; and, as already pointed out, the advantage of joining rather than solitary nest founding would change with time, especially in the temperate zone (where there is a premium on producing mature brood before winter). The frequency of joining (and, hence, of social nest founding) would be expected to vary with availability of suitable nest sites and hence population density, since a poor nest site would reduce a subordinate's chances of independent success. Dispersal might reduce the likelihood of discovery by a predator or parasite (Eickwort, in press).

SIZE OF FOUNDRESS ASSOCIATIONS

One of the oldest surviving generalizations about the behavior of social wasps states that multiple-foundress associations predominate among tropical wasps, whereas the single-foundress mode of colony formation is characteristic of temperate species (H. von Ihering, 1896; see also the review of literature on this subject by Pardi, 1942). This generalization was much discussed and somewhat exaggerated in the writing of early students of social wasps (e.g., H. von Ihering, 1896; Roubaud, 1916) who thought that all temperate species had single-foundress colonies. It is based upon the observations that many tropical social wasps found nests by swarms (see Richards and Richards, 1951) whereas characteristically temperate groups (e.g., the Vespinae) live in colonies founded by single females. *Polistes* is often used as an example of a group showing this kind of variation among species living at different latitudes (Rau, 1933; Hamilton, 1964b; Richards and Richards, 1951; Wheeler, 1922).

Hamilton (1964b), again looking for an explanation in terms of degree of relationship among associates, hypothesized that the greater tendency to associate in tropical wasps is a consequence of a comparatively high degree of relationship among associates in the tropics due to increased inbreeding associated with greater population viscosity and lack of breeding synchrony among colonies. My observations suggest that one contributor to a greater tendency for association among tropical foundresses may be a greater diversity in the dominance behavior (reproductive condition) among females at the time of nest founding, leading to a greater number of females which can associate without conflict. In the tropics, as shown above for *P. canadensis*, siblings disband and reassociate on new nests after the disappearance of the queen. Great diversity of nutritional condition and reproductive development, and hence dominance behavior, might be expected due to diversity in larval nutrition, age, and foraging history at the time of colony disruption. In temperate *Polistes*, on the other hand, there are likely to be (1) fewer wasps in proximity during nest founding due to

winter mortality, and (2) greater uniformity in age, nutrition, and history of foundresses due to selection during winter. Foundresses are likely to be late-emerged, relatively well-fed and formerly non-workers. Furthermore, the degree of ovary development of females emerging from hibernation is similar (Pardi, 1946, 1948a); and most would be in the ascending (rather than descending) phase of ovarian development, a factor which also affects dominance rank (Pardi, 1948a), all having begun development in spring. These factors might be expected to produce more dominance equality, hence less tendency to associate among temperate zone foundresses.

A trend toward dominance uniformity might be expected to go toward completion in temperate-zone species having a bimodal feeding program, with a consequently large proportion of the spring survivors being well fed, and capable of reproduction on their own, resulting in strong and frequent dominance conflict. This may explain the association in the Vespinae of (1) "queen-cell" construction at the end of the season which according to Spradbery (1965) may stimulate the workers to give more food to the larvae and would divide the brood into two more or less distinct nutritional classes, (2) distinct size differences between castes (Blackith, 1958), and (3) virtual absence of foundress associations (Duncan, 1939; Spradbery, 1965).

By similar reasoning, dominance relations may sometimes limit the size of foundress associations possible in a given species. A stable group contains no wasps of "equal dominance" since they would be in conflict until one became subordinate or was expelled. Since wasps can be neither infinitely dominant nor infinitely subordinate there must be a time in the formation of every group when there are no unassociated wasps in the vicinity of the nest which are either more dominant than the queen or more subordinate than the lowest ranking female. Furthermore, there is undoubtedly a range of degrees of dominance reacted to as "equal" by a given wasp. The number of females possible in the group would thus be limited by the number of non-overlapping dominance categories possible among females in the behavioral spectrum from maximum to minimum dominance. Of the 51 foundress associations observed by Owen (1962) and me in *P. fuscatus* (Table 5), none contained more than seven females; and none of 46 *P. canadensis* foundress associations contained more than 10 females at the end of the pre-emergence period. Perhaps a group of seven *P. fuscatus* (or ten *P. canadensis*) females is large enough to span the entire range of degrees of dominance possible among encountering wasps.

Dominance interaction is just one factor possibly affecting foundress group size in *Polistes*. All of the factors mentioned in the preceding section as possibly influencing a female's decision to join or not join a given

foundress association would affect the group size predominant in a given area. These include the egg producing capacity of queens, the ability of given workers to augment the queens' productivity, the availability of suitable nesting sites, the probability of a subordinate eventually taking over as queen, the time of year (relative advantage in joining a somewhat developed colony rather than starting a late one), and the possible desirability of dispersal in escaping parasites or predators. The importance of such factors might vary from one region to another within the range of a species, causing intraspecific variation in predominant foundress number (West, 1968).

SOCIAL ADAPTATIONS TO CLIMATE

MODES OF QUEEN CONTROL

The mode of queen control in *P. canadensis*—attack and expulsion of subordinate contenders—possibly increases the proportion of sexually mature females which become queens: expulsion of a sibling with developed ovaries increases the probability that she will initiate an additional colony. The degree to which this is an advantageous mode of colony multiplication depends on the relative reproductive value of that female as a queen versus as a worker on the nest of a sibling (West, 1967b).

The different mode of queen control in *P. fuscatus*—differential egg-eating accompanied by conflict avoidance (standing aside)—may be favored in the temperate zone wasps *P. fuscatus* and *P. gallicus*, in which the success of a colony depends on the number progeny that can be reared before the onset of winter.

A late-maturing female might further the replication of her own genotype more by foraging and building on the nest of a dominant (reproductively superior and already established) sibling than by initiating a late nest. As shown above, subordinate females begin nesting relatively late, and the late-started nests lag in size behind earlier started nests attended by the same number of females.

The temperate-zone time limit would render growth arrest due to dominance conflict like that which occurs in *P. canadensis* disadvantageous; and it would confer an advantage on queens which tolerate queen-like behavior (cell initiation) in subordinates, since the building and foraging activity of such females accelerates nest growth. As shown above, differential egg-eating is a means of queen control which permits queen-like behavior of subordinates.

In *P. canadensis* prevention of oviposition by subordinates plays a comparatively important role in queen control. This being the case, the fact that the queen is the primary initiator and enlarger of new (eggless) cells

and hence is most likely to encounter them as soon as they are large enough to stimulate oviposition takes on significance in the suppression of reproduction by subordinates, as does the close temporal relationship between building and oviposition. The only previous references to the cell-initiation function of the queen were by Roubaud (1916) in a tropical wasp (*Belonogaster*) and by Michener and Michener (1951) in *Polistes hunteri* Bequaert, a temperate species characterized by the single-foundress mode of colony initiation. This specialization probably escaped the notice of other observers because it is less important in queen control among species which suppress reproduction of subordinates by differential egg-eating, and is therefore less conspicuous in their behavior throughout the colony cycle. Differential egg-eating may be absent in not only tropical species such as *P. canadensis*, which chase potential egg layers from the nest, but also species having single-foundress nest initiation, in which no subordinate egg layers are present during the pre-emergence period.

BEHAVIOR TOWARD MALES ON THE NEST

The fact that *P. fuscatus* males are frequently and forcefully attacked on the nest may be associated with the advantage of mating elsewhere, particularly near hibernacula. Males mating near hibernacula might out-produce those mating on nests since they would less often inbreed; and by mating with females entering hibernation they would be more likely to inseminate future queens, rather than females (such as workers and senile foundresses) unlikely to over-winter. Following the reasoning of Hamilton (1964a, b), chasing male siblings from the nest would thus be advantageous for females since it would result in more replicates of genes like theirs in the following generation.

This hypothesis concerning the function of chasing males from the nest gains credence from the observations that in the non-hibernating (tropical) species *P. canadensis* males (1) are not attacked on the nest and (2) probably mate on or near newly founded nests rather than away from the nest sites. Mating on or near newly founded nests might be favored in *P. canadensis* for the same reason that mating at hibernation sites is favored in *P. fuscatus*: it increases the likelihood of inseminating a female which will become a queen.

If the striking sexual dimorphism found in *P. fuscatus* (and lacking in *P. canadensis*) is indeed associated with the recognition and chasing of males, as suggested above, then a correlary of the present hypothesis is that sexual dimorphism may be more common in temperate zone (hibernating) species than in tropical species; and dimorphic tropical species would be expected to mate away from nests,

TEMPORAL SEPARATION IN THE PRODUCTION OF WORKERS AND NON-WORKERS

In *P. fuscatus* there is exclusive production of workers early in the colony cycle and exclusive production of non-workers later, whereas in *P. canadensis* non-workers may be produced among the earliest brood. This difference is probably also climate-related. In *P. canadensis* it might be advantageous to have non-workers (potential queens) present at all times among the residents of a nest, since queen disappearance and the ensuing queen substitution and/or colony foundation could occur at any time during colony growth. In *P. fuscatus*, on the other hand, premature queen removal or natural disappearance does not ordinarily lead to nest founding by colony offspring. Colony success in terms of colony multiplication rests primarily on the number of females which are able to found nests after overwintering.

Exclusive worker production early in the season might contribute to this success by using first-emerged progeny—those which would be relatively aged the next spring—to rapidly increase the worker/larva ratio (nutritional condition) of the later-emerging brood; and exclusive non-worker production late in the season would mean that fewer progeny reduce their overwintering and nest-founding capacity by attending brood originating too late to mature before the onset of winter.

Caste-correlated (seasonal) size variation may thus be at least in part a consequence of the seasonal separation of worker and non-worker female production.

Caste-correlated seasonal variation in both size and behavior are part of the caste-determination process in *Polistes fuscatus* in that both probably affect the likelihood of a given female becoming a queen. A similar correlation of caste, size and behavior appears to exist among bumblebees and vespine wasps—also primarily temperate-zone social insects in which colonies are founded by overwintered females. Most studies of “caste determination” in these insects (Free, 1955; Cumber, 1949; Spradbery, 1965) are concerned exclusively with causes of variation in adult size, and not surprisingly conclude that “caste” (size) is determined by the amount of food given larvae. Such studies overlook the problem of the determination of the behavioral dimorphism noted in these insects, which, as in *Polistes fuscatus*, may be at least as important in caste determination as differences in size.

CONCLUSION

The major differences noted between *P. fuscatus* and *P. canadensis*—differences in mode of queen determination, behavior toward males, and degree to which worker and non-worker production is separate in time—

appear to be climate-related. Since comparative nest structure indicates that *P. canadensis* is probably more similar to the common ancestor of *Polistes* species than is *P. fuscatus* and that the genus *Polistes* is tropical in origin (see p. 94), it is more likely that the biological characteristics of *P. fuscatus* were derived from characteristics resembling those of *P. canadensis* than that the reverse is true.

NEST CONSTRUCTION AND EVOLUTION

COMPOSITION OF THE NEST MATERIAL

Polistes wasps make their nests from a variety of dry woody substances masticated by the mouth with fluid. I have seen them rasping fibers from fence posts, unpainted boards, dry weed and grass stems, and an old wicker chair. Rau and Rau (1918) report the use of paper bags and Duncan (1928) saw *P. aurifer* (= *P. fuscatus* var. *aurifer* Saussure) gathering hairs from the pubescent leaflets of a plant (*Lupinus albifrons*). I have never seen wasps reuse the paper of old *Polistes* nests in making additions to new nests. However, one *canadensis* queen used material from the battered remains of a nest of an unidentified wasp (probably a polybiine) to which her nest was attached.

The fluid used in paper-making contains water apparently regurgitated from the gut. Pulp and water foraging are associated activities: in the sequence of loads brought to the nest by a given forager pulp is more often followed by water, and water by pulp, than either is by solid food (Table 14). One *P. fuscatus* worker consistently stopped at a dripping faucet to imbibe water before each of her frequent pulp-collecting trips. Table 14

TABLE 14
COMPOSITION OF SUCCESSIVE FORAGED LOADS. (Based on 155 pairs of sequential loads brought to *P. fuscatus* nest B38 by 29 workers.)

Load	Followed by (frequency in % of total observations):		
	pulp	food	water
pulp	58	4	38
food	7	90	2
water	16	3	81

also shows the tendency for workers to persist in a given foraging activity: a given load is usually of the same kind as that preceding it.

In addition to vegetable fibers and water, the nest material ("carton") apparently contains a secretion of the building wasp: microscopic examina-

tion of the carton made by several *Polistes* species (*fuscatus*, *canadensis*, *annularis*, *flavus*, *exclamans*, *major*) reveals that all contain specks of transparent material which gleam in bright light. There is also a hard glossy coating on the top of the nest, most conspicuous near the pedicel. Females "lick" the nest top surface a great deal, and probably apply a fluid as they do so. The substance incorporated in the carton may be the same as that applied to the nest top; the difference in appearance is perhaps due to a difference in amount present. Heselhaus (1922) considered the mandibular glands of *Polistes* to be "glands of construction". They may be the source of the fluid used in construction.

Evidently similar secretions are produced by some bees (Nielsen, 1936), and are widespread among paper-making wasps. Rau noticed shiny inclusions in a nest of the tropical polybiine wasp *Metapolybia pediculata* Saussure (corrected to *M. cingulata* (Fabricius) by Richards and Richards, 1951). The nest envelope contained wood pulp mixed with "small, transparent specks, from one to three millimeters in diameter, which seem to be tiny windows of mica" (Rau, 1933, p. 52). I have seen the nest collected by Rau in Panama, and found one like it in Colombia (locality U). Comparison of these "windows" with the shiny specks of *Polistes* carton shows them to be of similar thin, brittle transparent material. Richards and Richards, 1951) describe the carton of *Mischocyttarus* species (Vespidæ: Polybiinae) as being "joined with a great deal of salivary secretion, sometimes leaving transparent 'windows' or even holes in the walls" (p. 11).

BUILDING BEHAVIOR

When gathering pulp, a wasp walks slowly backward, loosening a strip of pulp with its mandibles, often making a tick-tick sound which can be heard several feet away. From time to time she uses her mouth and forelegs to gather the loosened pulp into a ball which rests on the substrate beneath her. The females I have observed moved in a straight line and removed an unbroken strip of fiber which was always continuous with the growing ball. The forelegs bracket the ball and keep it from sliding sideways. I have looked closely several times to see whether fluid is applied either to the surface being worked or to the fiber as it is loosened and compressed into a ball, and have seen none. However, Rau (unpubl. ms.) saw a female spit a drop of fluid onto a surface from which she was gathering pulp. After two or three minutes spent removing fiber, the female abruptly flies away with the ball of fiber in her mandibles.

At the nest the fiber-laden female inspects cells and nest surface in a characteristic manner, moving quickly about, poking her head briefly

into some cells and antennating the nest surface. Sometimes during this inspection she moves her head along a cell perimeter as if hastily applying pulp but without doing so. Finally she applies the pulp to the perimeter of a cell, usually at a place where the wall is slightly lower than those adjacent to it. As a result the faces of the nests built by *canadensis* and *fuscatus* remain quite planar throughout the nest cycle.

Several minutes are required for a wasp to use up one load of building material in construction. During this time the mandibles "chew" over and over the part being worked. I first assumed that the wasp was applying masticated pulp a little at a time, building the ridge (on a pedicel or cell wall) a bit higher with each pass over it. However, there is no visible ball of unapplied pulp during most of the building process, and the new ridge is initially thick and lumpy. Therefore I have concluded that the entire load is usually deposited on the first pass along the new ridge, and during successive passes the mandibles tamp it into an increasingly thin and uniform wall. There is little or no prior chewing of the pulp, either at the gathering site or upon arrival at the nest. Evidently the pulp is simultaneously masticated and shaped after being placed on the nest.

The mouth of the first cell of a nest is round (Marchal, 1896, and other authors). After the addition of more cells, pulp is applied in straight lines to walls between cells, and in arcs to walls on the nest edge. The mouth of the first cell becomes hexagonal when it is surrounded on all sides by other cells; pulp is then added to its entire circumference in straight lines. The first bit of pulp for a new cell is placed in the groove between adjacent cells, and applied in a short line in both directions from that point. Successive loads of pulp expand the line to a ridge, then to a shelf which eventually cups downward and is lengthened into a tube with sides nearly parallel to those of adjacent cells.

The antennae are in continual and rapid movement against the sides of adjacent cells during pulp application. Darchen (1964) also noticed this in *Vespa orientalis* Linnaeus: "Les antennes semblent jouer un grand rôle dans la construction puisqu'elles sont sans cesse en mouvement de haut en bas de chaque côté des cellules" (p. 148).

Frame-by-frame analysis of motion pictures of building movements indicates that when a worker applies pulp to a wall shared by two cells the ends of the antennae move along the opposite walls, one in each of both adjacent cells, sweeping from in front of the wasp backward, then returning in a short stroke through the cell center (Figure 21). Sometimes one antenna is more active than the other, but usually both move at the same rate (about 6 antennal sweeps per second in *P. fuscatus*).

When the builder's mouthparts reach the intersection of two walls, one antenna moves over into an adjacent cell (Figure 21B), and the wasp turns and moves along the next wall (Figure 21C) with no break in the pulp strip at the corner. Sometimes, e.g., if the following wall is already higher than the one adjoining it, the wasp moves to a non-adjoining wall.

During construction at the edge of the nest the antenna inside a cell continues to move as described while the other whips about in the air (Figure 21D), and the wasp usually builds an arc, making the outer sides of peripheral cells circular in outline. When the adjacent "guide cell" is a

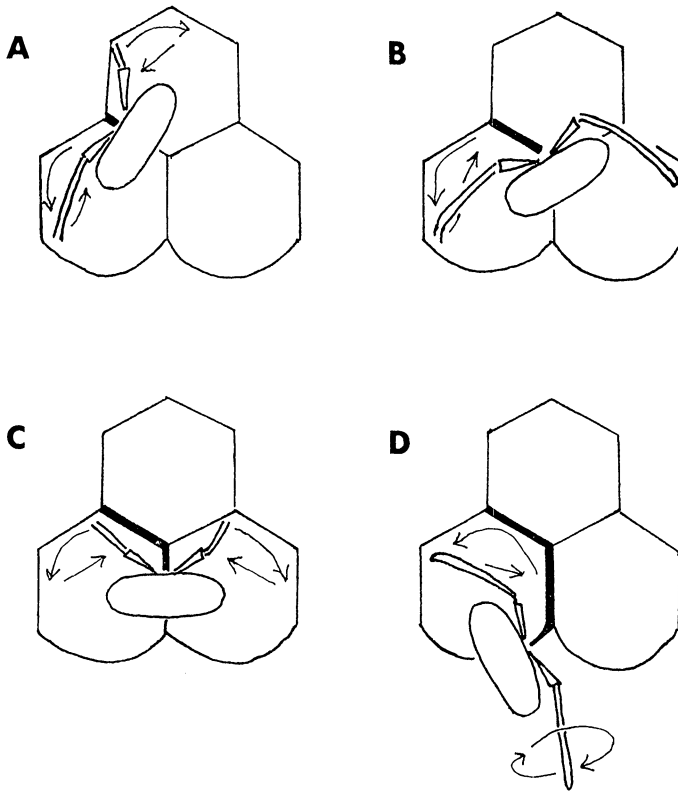


FIG. 21. Antennal movements in *P. fuscatus* during pulp application. *a*—Tips of antennae move along sides of adjacent cells, beginning in front of female, then returning through cell center as shown by arrows. *b*—At a corner, one antenna moves into another cell, and pulp application continues without a break. *c*—Pulp application, continued. *d*—At the outer edge of a peripheral cell, antenna inside cell continues to move as in *a*. Antenna outside cell moves about in the air.

well-defined hexagon, even the outer sides of peripheral cells are sometimes straight.

Thus it appears that in *Polistes* building of cell walls could be guided as follows: Input to one antenna from a contacted surface directs application of pulp at a constant distance from the surface. If that surface is cylindrical an arc results; if it is planar a ridge is built parallel to it. Input from both antennae produces a straight wall midway between the guiding surfaces.

In *P. fuscatus* and *P. canadensis erythrocephalus*, the older the cell the larger the diameter of its opening. As a result, new (peripheral) cells are smaller than older (more central) cells on the same nest, and, as Réaumur (1740) noted in nests of *Vespa* species, mature cells are truncated pyramids rather than regular prisms as they would be if the diameter were kept constant throughout enlargement. Gradual divergence of cell sides indicates that as the cells are extended the antennae are used to determine position relative to pre-existing surfaces, rather than for measuring absolute distances.

Further observation is needed to determine what sets the dimensions of the original cell at its base. If the antennae are the sole building guides, an obvious suspicion is that cell diameter is equal to antennal length or some constant proportion thereof. Table 15 contains antennal lengths of a foundress female and the average diameter of four central cells of her nest for eight *Polistes* species. All of these values are for single foundress colonies before pupation had occurred; therefore all of the cells were constructed by the female whose antennae were measured, and all of the nests were approximately the same age (4–6 weeks). In general, the longer the antennae, the larger the cells; but cell diameter does not equal antenna length. This shows

TABLE 15
CELL SIZE AND ANTENNA LENGTH IN EIGHT SPECIES OF *Polistes*¹

<i>Polistes</i> species	Antenna	Cell diameter (mm)	
	length (mm)	mean	range
<i>exclamans</i>	5.5	4.2	4.0–4.3
<i>fuscatus</i>	6.2	6.1	5.9–6.5
<i>metricus</i>	7.2	6.2	6.1–6.3
<i>apachus</i>	7.3	6.5	6.4–6.7
<i>canadensis</i>	7.5	6.6	6.0–6.9
<i>flavus</i>	7.6	6.5	6.2–7.0
<i>annularis</i>	7.8	6.7	6.1–7.0
<i>rubiginosus</i>	8.0	7.3	7.2–7.5

¹ Based on the antenna length for a foundress female and on the average diameter of four central cells of her pre-emergence nest.

that the antennae could be used to determine cell diameter. However, Rau (1946) pointed out a relationship between cell size and body size among five species, so any part of the body whose length correlates with body size is a potential determinant of cell diameter. The behavioral observations lend support to the suggestion that antennal length is the important factor.

The means of achieving a hexagonal cell form by honeybees evidently differs from that of wasps. A bee's cell begins as an irregular thick-walled cup of wax. While adjacent cells are worked simultaneously as in wasps, the worker bee does not straddle the common wall, but planes the wax with her mandibles from within a cell, tapping with both antennae on the surface of the wall being worked. Martin and Lindauer (1966) report that the tips of the antennae of honeybees have sense organs which check the thickness and smoothness of the cell wall, and that the antennae are superfluous for building cells of normal diameter and angle with respect to gravity. The means by which bees determine the regular diameter of comb cells is still unknown (Martin and Lindauer, 1966).

EVOLUTION OF POLISTINE NEST FORMS

All *Polistes* nests consist of a paper comb attached by one or more stem-like pedicels to a supporting surface, and lack a nest envelope (Figs. 22 and 23).

The pedicel between cells and attachment surface might have been selected for in a progressively provisioning wasp which left larva-containing cells open for long periods of time. A pedicel (*vs.* extensive contact with the substrate) would lessen the probability of a wandering predator discovering the exposed brood. This might be particularly important in the tropics, where there is a notable abundance of ants. I saw a dramatic demonstration of pedicel function in this context when *canadensis* colony V2 was invaded by ants on 6 March 1965. The nest hung from a shelf of rock at the cave-like mouth of an abandoned coal mine. Ants regularly traversed this "ceiling" of the mine entrance, and sometimes crawled onto the pedicel of nest VI and others near the sides of the cave. The wasps reacted to approaching ants as described in a preceding section—by attacking them at the base of the nest pedicel. Several ants persistently approached but left the site after several minutes of repeated attacks by the wasps. When I observed the nest three days later it had been taken over by hundreds of ants which still streamed back and forth over the bridge-like pedicel, until the last particles of brood and stored sugar were gone from the cells. However there is no doubt that the pedicel guards retarded the invasion, and might have been able to halt

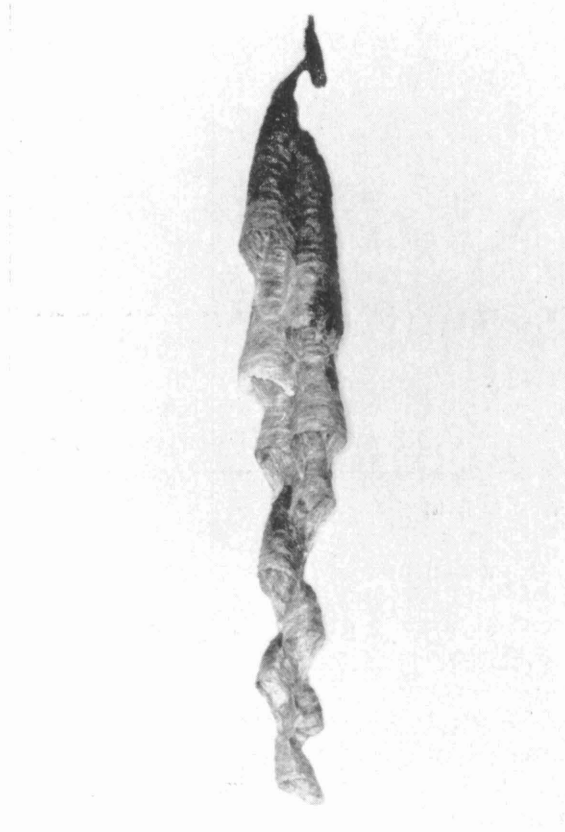


FIG. 22. Nest of *Polistes goeldii*.

one involving small numbers of ants. The efficacy of this mode of defense is obviously enhanced by the fact that the invaders have only one narrow access to the nest *via* the single pedicel.

To my knowledge all primarily tropical *Polistes* build nests having only one thin pedicel. Nests having multiple pedicels or pulp-thickened main pedicels are built by species (e.g., *P. gallicus*, *P. fuscatus*, *P. flavus*) found primarily in the relatively ant-free temperate zone. Most tropical social wasps which are not pedicel builders surround the comb with an envelope having a single small entrance hole (see Richards and Richards, 1951, Figs. 1-10), another method of restricting access to the brood. Richards and

Richards (1951) discuss other ways in which the tropical abundance of ants may have affected the evolution of social wasps.

The paper-making habit may have evolved in association with the placement of a pedicel between cells and substrate: light paper cells would permit use of a thin pedicel. An association of light building material and thin attachment to a supporting surface is found in the nests of some solitary and sub-social *Stenogaster* species, which consist of one cell constructed of particles of decayed wood attached to a hair-like pendant fungus or fern



FIG. 23. Abandoned nest of *P. canadensis erythrocephalus*.

(Williams, 1919). Another species of the same genus which constructs cylinders on the bark of trees (*S. varipictus* Rohwer) uses a greater proportion of sandy mud in construction (Williams, 1919).

The striking regularity of the hexagonal cells of bees and wasps has provoked discussion among philosophers, geometers and naturalists (including Pliny, Aristotle, Kepler, Réaumur, Buffon, and Darwin) for centuries. The history of this discussion is a classic illustration of the absurdity to which highly refined armchair reasoning can lead in the absence of simple observation. Much of it is summarized and epitomized by Thompson (1943). The above observations of building behavior and a comparative consideration of cells built by various solitary and social wasps suggest the following possible evolutionary history of the hexagonal cell in wasps' nests.

Numerous solitary wasps (e.g., *Trypoxylon* and *Sceliphron* species) build cylindrical mud cells of uniform diameter; and the above observations indicate that arc construction is the fundamental behavior pattern of a building *Polistes* female. Therefore it is perhaps justifiable to presume that the solitary ancestors of *Polistes* built cylinders, and that the hexagonal cell form was derived from the cylindrical form. This is not a new idea: Marchal (1896) considered the cylindrical cell to be the "mother of the hexagonal cell". DeSaussure had earlier called the hypothetical cylindrical ancestor the "*cellule primitive*", noting that in *Polistes* marginal cells remain simple arcs on their free (outer) sides, thus being reminiscent of the primordial form (Marchal, 1896, p. 15).

The practice of placing one cylinder upon another in a string rather than making a separate pedicel for each cell ("economy" of pedicel construction) would produce a nest like that of *Polistes goeldii* Ducke (Fig. 22). A colony of that species was collected in the rain forest near Buenaventura, Colombia (locality T). The nest had been enlarged by cell addition to the terminal edge of the end cell. If the end cell was added to the right of the cell above it, the new cell was added to the left. As the cells were lengthened, they eventually came to overlap pre-existing cells. Then the *P. goeldii* female no longer constructed a full cylinder but used the outer surface of the older cell or cells as part of the newer one. Thus there is an economy of materials; but shared cell sides are not planar, since the building female can contact only one cell when a given portion of a wall is constructed.

I think it likely that the nests of *P. goeldii* represent a comparatively primitive polistine nest form, having a small number of primarily cylindrical cells and a thin pedicel. Among polistine nest types (see below) they are most easily derived, as hypothesized above, from the cylindrical cell form common among solitary vespids. *P. goeldii*-like nests are found

in various other social wasp genera, including *Ropalidia* (Vecht, 1962), *Mischocyttarus* (Zikán, 1951), and *Parapolybia* (Vecht, 1966). These nests are remarkably similar to those of subsocial vespids of the genus *Stenogaster* pictured by Williams (1919), further indicating that this is a primitive form.

The planar cell sides found in the nests of most social wasps require not only shared sides (as suggested by Thompson, 1943) but also simultaneous lengthening of adjacent cells. Mud-daubing wasps, e.g., *Trypoxylon rugifrons* Cameron and *Sceliphron caementarium* (Drury), which build clusters of cylindrical cells, usually (perhaps always) arrange the cells in staggered rows with the cells of one row lying in the grooves between the cells of an older row (the "Kreiszyylinder in hexagonaler Anordnung" of Huber, 1965). Yet their cells never share sides or appear hexagonal as do the similarly arranged cells of most paper wasps because the mud wasps generally construct one cell at a time, each cell being completed before another is begun (Rau, 1933; Shafer, 1949).

Addition of pulp at the groove between older cells rather than only to the terminal edge of the newest one would produce a comb of hexagonal cells like that of *P. canadensis* (Figure 23). This practice might be favored by natural selection since it would result in maximum side-sharing, hence maximum economy of pulp (Thompson, 1943).

Thus the hexagonal shape of the wasps' cell is apparently derived from the cylindrical form found in many solitary wasps, and requires a cell surrounded on all sides by others, addition of new cells at the groove between pre-existing ones, and simultaneous lengthening of adjacent cells.

The horizontal nest form of many *Polistes* species (e.g. *P. fuscatus*) may have evolved with northward range extension and the habit of nesting in cavities. Nesting in cavities is commonly associated with life in the temperate zone among vespid wasps: the northernmost American *Polistes* species, *P. fuscatus*, often nests in cavities and near the ground; the northern European wasp *P. gallicus* nests mainly in low enclosures (Pardi, 1948a); in the northernmost part of its range (Arizona) *P. canadensis* (var. *navajoe*) nests exclusively in cavities having very small openings; and the most northern of all social wasps, the ground nesting Vespinae (*Vespula* spp.) excavate a nest cavity in the soil. Perhaps as species ranges extended northward wasps on nests in enclosures (which resemble the hibernacula of *P. fuscatus* and other temperate species) were able to survive the winter, whereas those nesting in the open, as *canadensis* does in the tropics, succumbed or had their activity so curtailed by extreme or fluctuating temperatures that they were at a disadvantage. The horizontal nests of *P. fuscatus* and *P. gallicus* would permit use of cavities too shallow to accommodate a vertical structure.

The center of gravity of a vertical or oblique nest is always approximately directly beneath the pedicel. However a horizontal comb often grows asymmetrically because one or more sides are near an obstruction, displacing the center of gravity so that it is no longer directly beneath the pedicel, which must therefore be stronger to prevent the nest from tipping. This might have favored the evolution of thickened and auxiliary pedicels of horizontal nests (which conform to the contours of the attachment surface and are therefore sometimes very irregularly shaped).

Zikán (1951) arranged nests of *Mischocyttarus* species in a hypothetical evolutionary series resembling that just outlined for *Polistes*, from the cylindrical nests of *M. insolitus* Zikán to the horizontal nests of *M. labiatus* (Fabricius). He also noted an association between multiple pedicel construction and nesting in cavities in *M. crypticus* Zikán and *M. cryptobius* Zikán.

TROPICAL ORIGIN OF POLISTES

Wheeler (1922) and subsequent authors (e.g., Rau, 1933; Richards and Richards, 1951) consider the Polistinae tropical in origin because "the great majority of these insects are tropical" (Wheeler, 1922, p. 88). The likelihood of a tropical origin for *Polistes* is further evidenced by the fact that the vast majority of present-day social wasp genera are exclusively tropical (Richards and Richards, 1951).

Consideration of nest structure also suggests a tropical origin of *Polistes*. All of the species mentioned above as having a primitive nest form live in the tropics. Furthermore, the characteristic tropical *Polistes* nest form resembles that of *P. goeldii* in having a single, thin eccentric pedicel and more or less vertical comb (see descriptions of Bertoni, 1912); and divergence from that form (thick central pedicel and horizontal comb) seems to be associated with life in the temperate zone, as shown above.

SUMMARY

This report describes the natural history and social behavior of *Polistes* wasps, primarily by comparing a temperate zone species, *Polistes fuscatus* (observed in southeastern Michigan) with a tropical species, *P. canadensis* (observed in Colombia, South America). The functions and interactions of marked wasps were followed throughout their lives; and undisturbed colonies were observed at their natural sites for long periods of time in order to determine the sequence of changes in colony composition and behavior.

Colonies of both species are usually initiated by a single female, which is usually joined by others prior to emergence of adult offspring. Foundress

associations contain siblings which return to the parental nest site evidently using orientation cues learned the previous year.

Dominance-subordination behavior like that described by Pardi (1948) is especially conspicuous on newly founded nests. Dominant females perform an abdomen-wagging motion which may be involved in queen recognition. The posture of an individual wasp with respect to others indicates its dominance rank, and may (along with the manner of approach to the nest) be involved in nestmate recognition. Joining a foundress group or a cluster away from a nest requires that the joiner be unequal in dominance to females already in the group. Dominance interactions among foundresses may act as a "measuring stick" of their relative reproductive capacity and thus function to assign reproductive roles to siblings in a way advantageous to both dominants and subordinates. Possible reasons for the relatively large foundress groups of tropical *Polistes* and the predominance of solitary nest-founding in the Vespinae are discussed.

The queen is the primary initiator of new cells, a function which, like dominance, is associated with developed ovaries. In *P. fuscatus* and other temperate zone species queen determination involves differential egg-eating, whereas in *P. canadensis* high-ranking subordinates are attacked until they leave the nest or become inactive non-ovipositing residents. Queen control by differential egg-eating permits queen-like behavior (oviposition and cell initiation) by subordinates, thus accelerating nest growth in colonies having a short nesting season. Dominance conflict in *P. canadensis*, on the other hand, sometimes leads to prolonged arrest of nest growth, but promotes nest founding by subordinates with developed ovaries by enhancing the probability that they will leave and start nests on their own. An oophagic female may avoid eating her own eggs by eating only newly laid eggs, and by doing so only when she has not herself recently oviposited.

In *P. fuscatus* workers and non-workers emerged in two temporally discrete groups: early-emerging offspring of a given colony were usually worker females. Behavioral differences between workers and non-workers are probably not due to the observed quantitative seasonal change in larval nutrition, which, however, may account for an observed seasonal increase in the size of emerging females. Thus caste-correlated behavioral and morphological variations appear to be independently determined. Marked non-workers overwintered and became colony foundresses.

The mean total developmental time (egg to adult) was shorter in *P. canadensis* than in *P. fuscatus*. Developmental rate is affected by temperature and larval nutrition; and the length of the pupal period is inversely related to the length of the larval period for a given individual. The

quantity of food given larvae increases as the season progresses, and may be affected by the position of the larval cell on the nest. In *P. fuscatus* (but not in *P. canadensis*) the proportion of males produced correlated with oviposition rate as predicted by Flanders (1942), and the emergence of males coincided with that of non-worker females, suggesting that aspects of Flanders' (1946) hypothesis of caste determination in social insects bear reconsideration.

The reproductive longevity of the queen determines the length of the colony cycle in both *P. fuscatus* and *P. canadensis*. Waning colonies are characterized by mobbing of returned foragers, occasional cannibalization of the brood, and drop-making behavior (probably a means of concentrating dissolved sugars by evaporation).

In *P. fuscatus* males differ strikingly in appearance from females and are chased from the nest; mating takes place in or near hibernation sites. In *P. canadensis* there is little sexual dimorphism and males are not attacked on the nest; mating takes place on or near newly founded nests. In both species mating occurs at sites frequented by females likely to become queens. Vibrations and grasping by the male antennae during mating resemble movements observed in other Hymenoptera.

Alarm signals in *Polistes* involve aggressive darting movements producing vibrations of the nest. Intense alarm behavior occurs upon discovery of brood parasites such as the ichneumonid *Pachysomoides*, whose biology and behavior as a parasite of *Polistes* pupae are described.

The antennae guide the construction of hexagonal cells, which probably evolved from cylindrical cells like those of some solitary wasps. The evolution of single and multiple pedicels, paper cells, and vertical and horizontal combs in *Polistes* nests is discussed. Comparative study of nest forms suggest that the genus *Polistes* is tropical in origin.

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