

## Evolutionary Implications of Early Male and Satellite Nest Production in *Polistes exclamans* Colony Cycles

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**Summary.** 1. *Polistes exclamans* populations in central Texas have a unique colony cycle. Of all *P. exclamans* nests 20%–38% produce males with the first brood of workers. Nests producing early males have significantly more females, cells, pupae, and emergences at the time of early male production than nests not producing early males.

2. Early male production may have originated as an adaptation caused by the large number of queens that die before autumn reproductive males and females are produced. It allows egg laying by workers with whom early males mate.

3. Queens or workers sometimes leave their original nest and start new nests nearby that must be joined by workers from the original nest if they are to succeed. Such 'satellite nests' were initiated from May to July by 16%–39% of all nests, depending on the population. Although nests initiating satellites have significantly more females and pupae than nests not initiating satellites, satellite nest production by a given nest is not dependent on prior early male production, and is independent of the number of foundresses.

4. More *P. exclamans* nests 1976–1979 were lost to birds than to any other cause. In the period 1976–1979, 66.7% of the 12 nests with satellites succeeded in producing reproductives after being knocked down while only 5.7% of the 87 nests without satellites that were knocked down were subsequently successful. Concealed nests are less vulnerable to bird predation.

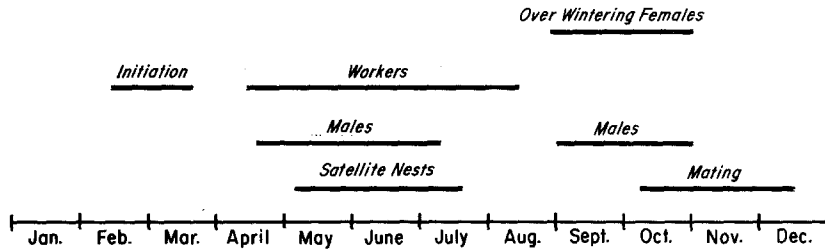
5. The brood parasitoid, *C. iphitalis*, a pyralid moth, avoids previously infested nests, therefore satellite nesting does not reduce the impact of this parasitoid. However, the brood parasitoid *E. polistis*, a chalcid wasp, lays eggs in the nest it emerges from, hence a satellite nest provides an escape when this parasitoid is already in the main nest.

### Introduction

*Polistes* is one of the best-studied genera of social wasps because it is common and widespread, and the nests with open combs allow easy marking and observation of individuals. Since females on a nest are all morphologically similar, and subordinates are often capable of taking over egg laying in the nest, recent studies of kin selection and the evolution of sociality have focused on *Polistes*, principally by comparing behaviors of different females within a population of a given species, but also by comparing behavior among species, often on a latitudinal transect (Alexander 1974; Gamboa 1978; Hamilton 1972; Ihering 1896; Klahn 1979; Metcalf and Whitt 1977; Noonan 1981; Pardi 1940, 1942, 1948; Rau 1933; Richards and Richards 1951; Strassmann 1981a; West Eberhard 1969, 1975). This paper describes the colony cycle of *Polistes exclamans*, a paper wasp abundant in the southern United States and in northern Mexico. This mid-latitudinal species has a nesting season longer than that further north, yet the relative asynchrony of the tropics is lacking. Not surprisingly its colony cycle is in some respects intermediate between those described for northern species, such as *P. fuscatus*, and that of tropical species like *P. canadensis* (West Eberhard 1969). Knowledge of the colony cycle of a given species is critical in testing predictions generated by genetical theories on the evolution of social behavior such as kin selection, because only with this information can the following be determined: (1) the number and tenures of egg layers; (2) the relation of less fertile females (workers) to the brood they raise and defend; (3) the alternatives workers have, if any, to raising this brood. Colony cycles in *P. exclamans* are complex and involve successive egg layers, presenting workers with a choice of raising brood in different nests, and allowing them alternatives to functioning as workers. These and

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**Fig. 1.** Timing of nest initiation, satellite nest initiation, mating, and emergence periods of workers, early males, males, and overwintering females on 181 nests 1976–1979 at BFL. Maximum ranges are given, so the period of any variable for any given year is usually shorter

other characteristics of the *P. exclamans* colony cycle are detailed in this paper.

## Methods

This study was carried out at Brackenridge Field Laboratory (BFL), of the University of Texas in Austin, Texas (USA). Naturally occurring nests of *P. exclamans* were followed through the entire nesting cycle in each of four years (1976–1979). Each nest was assigned a number, its precise location and position were noted, and wasps were marked with Testor's PLA enamel for individual recognition on the thorax and wings at night while on their nests. After marking, each colony was observed for several hours to identify the queen. Queens lay eggs, build new cells, shake their abdomens (tailwag), chew on other females, and seldom leave the nest (Strassmann 1981b).

In the period 1976–1979 roll calls were usually taken every third day when newly emerged wasps were marked and presence of males was noted. Numbers of brood at each stage of development were counted biweekly in all nests and every other day in three nests in 1978 and one nest in 1979. Eggs, larvae, pupae, cells where an adult had emerged and subsequent cell contents, and parasitized cells were distinguished. Nests were checked daily to see if they had been knocked down by a nest predator. Satellite nests were discovered by several methods (Strassmann 1981a).

A part of the analysis that follows investigated a nest's susceptibility to predators. To do this, six nest measurements were made at BFL in 1977. (1) Nest height, (2) distance between a main nest and its satellite, nest visibility (3) from above and (4) from all sides (termed horizontal visibility and estimated as the degrees of a circle from which the nest was visible at a level with the nest), (5) farthest distance from which a nest could be seen on its most open side, and (6) obstruction near the nest, which was assigned a value from 0 (no obstruction) to 5 (access to nest impossible for a bird).

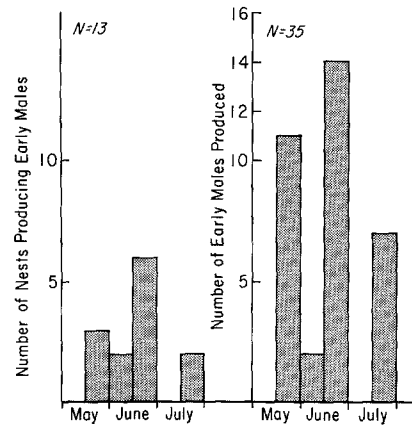
Collections could obviously not be made in the study population (BFL), so three collections of nests and associated wasps were made in 1977. Between 20 and 30 May, 67 nests were collected from house eaves and bushes in a neighborhood about a mile from BFL. These nests were examined for number of cells, number of females, cell contents, and presence of males. Two more collections were made in San Antonio in June and July (for details see Strassmann 1979, and Strassmann and Thomas 1980).

Data were analyzed using the statistical methods of Siegel (1956), Sokal and Rohlf (1969), and Nie et al. (1975). Mean and standard deviation are given for data distributions, unless otherwise indicated.

## Results

### Early Males

The earliest colony cycle variation in *P. exclamans* is that a few males emerge along with the first brood



**Fig. 2.** Numbers of nests producing early males and total numbers of early males produced during each 15-day period, May–July, at BFL, Austin, in 1978 on 44 nests

of workers. Males emerging from May through early July are called early males and distinguished from the greater numbers of males that emerge from late September through early November (Figs. 1 and 2). All males appearing on nests in the BFL population first had black eyes, which indicates they emerged from the nests they were found on and did not join later from other nests. Newly emerged males and females have very black eyes for 2 days, dark brown eyes on days 3–6, brown eyes on days 7–8, and subsequently tan eyes characteristic of mature adults. At BFL in 1978 when nests were censused every third day, most early males were only seen on the nest at one census date. Of 12 nests producing early males, three had males present on two consecutive census dates. Nests producing early males produce  $2.6 \pm \text{SD } 1.3$  ( $n=13$ ) males during any given 2-week period in Austin, 1978 (three nests produced early males in more than one period). Mean number of males emerging per nest in June 1977, San Antonio, is  $2.85 \pm \text{SD } 3.3$  ( $n=26$ ) for any given 2-week period; seven nests produced early males during more than one period.

Of 67 nests collected in Austin in May 1977, 15 nests (22%) produced at least one male during the first 2 weeks of worker emergence in May, establishing beyond all doubt that these males come from

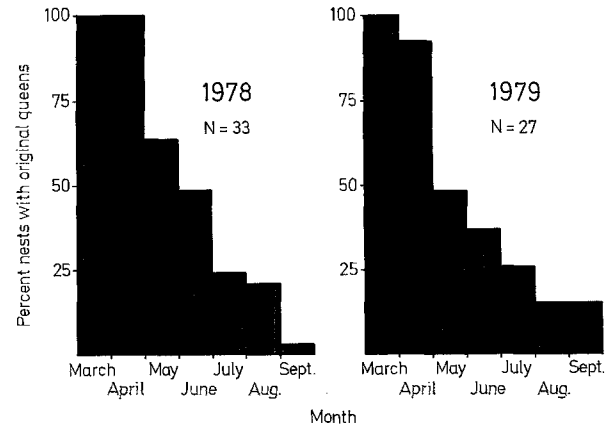
**Table 1.** Number of workers, foundresses, cells, pupae, and emergences (cells vacated by newly hatched adults) on nests with and without early males May 1977, Austin. Means for the two categories are compared using the *t*-test

Variable	Number of nests	Mean	Standard error
May 1977, Austin			
Workers			
No males	52	2.0	0.28
Males	15	4.9	0.77**
Foundresses			
No males	52	1.0	0.20
Males	15	1.2	0.38 n.s.
Cells			
No males	52	39.0	2.75
Males	14	63.9	10.64*
Pupae			
No males	52	4.8	0.65
Males	14	13.4	2.92*
Emergences			
No males	44	5.2	0.94
Males	14	12.5	3.00*
June 1977, San Antonio			
Females			
No males	59	8.5	0.94
Males	16	14.4	2.17**
Egg-layers			
No males	59	1.2	0.15
Males	16	1.8	0.46 n.s.
Cells			
No males	59	69.3	6.08
Males	16	118.8	18.52*
Pupae			
No males	59	11.1	1.53
Males	16	32.9	7.11**
Emergences			
No males	59	15.5	2.12
Males	16	36.0	6.21**

\* $P < 0.05$ ; \*\* $P < 0.01$ ; n.s. = not significant

eggs laid by the queen, since at this time it takes an egg 6–8 weeks to develop into an adult (Strassmann, unpublished data). All nests with early males also had workers, so some fertilized eggs that produce workers are laid before unfertilized male-producing eggs are laid. The nests with early males possessed from 5 to 41 ( $\bar{x} = 12.5 \pm \text{SD } 1.1$ ) emergences and from 1 to 12 ( $\bar{x} = 4.9 \pm \text{SD } 5.0$ ) workers. Since early males are produced after 4 to 40 fertile eggs are laid by the queen, early male production is probably a facultative behavior and does not automatically follow the laying of a certain number of fertile eggs.

Nests which produced early males had significantly more workers, cells, pupae, and emergences, but



**Fig. 3.** Percentage of original queens surviving through each month at BFL, Austin, 1978 and 1979

not foundresses or egg layers than nests without early males in Austin, May 1977, and in San Antonio, June 1977 (Table 1). The difference between number of emergences and number of workers reflects worker mortality as care was taken to collect all returning foragers. The Austin wasps were not dissected, but foundresses could be distinguished from workers by their larger size and worn wings. Queens are substantially and significantly larger than workers as indicated by winglength [queen's:  $\bar{x} = 14.18 \pm \text{SD } 1.19$  mm ( $n = 34$ ); workers:  $\bar{x} = 11.72 \pm \text{SD } 0.62$  mm ( $n = 81$ ); *t*-test  $t = 14.57$ ,  $P < 0.001$ ]. Workers and males were the same size (males:  $\bar{x} = 12.12 \pm \text{SD } 0.84$  mm ( $n = 5$ );  $t = -1.38$   $P > 0.1$ ). The San Antonio wasps were all dissected, so egg layers were known (Table 1).

Thirty nests with known numbers of foundresses produced early males at BFL during 1976–1979. Of those, 26 (86.7%) were nests with single foundresses and the remaining 4 (13.3%) were two-foundress nests (see Table 3). Thus, production of early males is by queens and not by subordinates.

### Queen Death

In 1978 at BFL 51.6% (in 1979, 62.9%) of all nests lost their original queens before July, well before eggs that became autumn reproductives were laid (Fig. 3). Egg-to-adult time in *P. exclamans* varies with nest size from June through September. On a large nest (over 50 workers) at this time, egg-to-adult time averages  $37 \pm \text{SD } 5$  days ( $n = 126$ ). On a smaller nest (15–25 workers), egg-to-adult time was  $45 \pm \text{SD } 3$  days ( $n = 19$ ). So, queens must live past June to lay eggs that become future reproductives that emerge from late August through September or October. After the original queen is lost, a former worker who has mated lays eggs on the nest.

**Table 2.** Numbers of nests producing satellites at Brackenridge Field Laboratory 1976–1979, and in San Antonio in 1977. Only nests surviving at least until June are included

Location and date	Number of nests without satellites	Number of nests with queen-initiated satellites	Total number of satellites (queen and worker) per nest					Total number of systems	Total number of nests	Percent nests with satellites
			1	2	3	4	5			
BFL, Austin										
1976	20	?	6	2	2	1	0	31	53	35
1977	48	0	8	1	0	0	0	57	67	16
1978	27	16	10	4	2	0	1	44	73	39
1979	18	5	10	0	0	0	0	28	38	36
San Antonio										
1977	14	?	3	0	1	1	2	21	41	33

### Satellite Nests

Workers or queens sometimes leave their original nest and start new satellite nests nearby. The original nest is then called a main nest to distinguish it from an independent nest without satellites. Satellites are initiated at a distance of from 0.15 m to 11 m from main nests. Satellites initiated by queens are significantly farther from the main nest ( $4.2 \pm \text{SD } 3.1$  m) than are satellites initiated by workers [ $1.8 \pm \text{SD } 1.3$  (Mann-Whitney *U*-Test,  $n_1 = 16$ ,  $n_2 = 17$ ,  $P < 0.05$ , two-tailed)]. Workers who initiate satellites are older than their nestmates, have more developed ovaries, are more likely to have previously foraged for caterpillars, and were more dominant on their natal nest (Strassmann 1981a). Workers who join satellites are younger than their nestmates and have slightly less developed ovaries (Strassmann 1981a). At BFL 160 nests were observed for satellite initiation 1976–1979. This number includes only nests surviving until the time of year when satellites are usually initiated. Forty-seven (29%) nests produced one or more satellites, though the percentage varies from year to year (Table 2).

Nests with more than one foundress are not more likely to produce satellites than are nests with one foundress [satellite, more than one foundress: 5 nests; satellite, one foundress: 30 nests; no satellite, more than one foundress: 17 nests; no satellite, one foundress: 107 nests ( $\chi^2 = 0.01$ , n.s., Table 3)]. Thirty-five satellites were initiated from nests with known numbers of foundresses at BFL, 1976–1979, and 30 of them (86%) came from the 137 single-foundress nests. Four of the multiply founded nests were associations of sisters marked the previous year.

A comparison of nests with and without queen satellites in Austin 1978, about a week after formation of satellites, revealed that nests forming queen satellites have significantly more workers, pupae, and cells

**Table 3.** Distribution of foundress number among nests at BFL, Austin. For each number of foundresses, the number of those nests producing early males and satellites is given. Only nests with known numbers of foundresses are included

		Number of foundresses			
		1	2	3	4
1976	Number of nests	34	5	4	1
	Number of nests with early males	2	0	0	0
	Number of nests with satellites	5	0	0	0
1977	Number of nests	21	0	0	0
	Number of nests with early males	1	0	0	0
	Number of nests with satellites	1	0	0	0
1978	Number of nests	36	2	0	1
	Number of nests with early males	11	1	0	0
	Number of nests with satellites	17	2	0	1
1979	Number of nests	46	9	0	0
	Number of nests with early males	12	3	0	0
	Number of nests with satellites	7	2	0	0

than nests without queen satellites (Table 4). In 1979, nests with and without queen satellites were compared on 3 June, a couple of days before most satellites were initiated. Nests initiating satellites had significantly more females and pupae than nests not initiating satellites (Table 4). Nests with replacement queens and worker satellites were compared with nests with new queens and no satellites in 1977 (no queen satel-

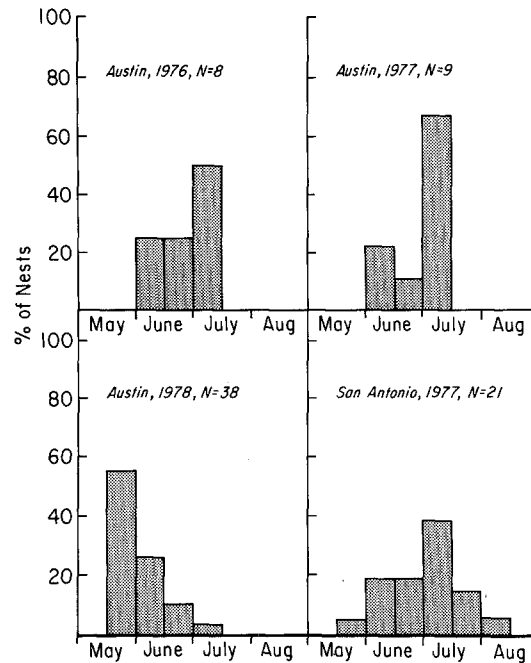
**Table 4.** Numbers of females, cells, and pupae on nests with and without satellites. Central tendencies in the two categories are compared using the Mann-Whitney *U*-Test

Variable	Number of nests	Mean	Standard error
May 1978 BFL, Austin			
Females			
No satellites	11	7.2	1.23
Satellites	8	14.7	2.41**
Cells			
No satellites	11	73.0	6.60
Satellites	8	94.3	16.99 n.s.
Pupae			
No satellites	11	10.7	2.17
Satellites	8	25.8	4.46**
June 1979 BFL, Austin			
Females			
No satellites	20	5.9	0.53
Satellites	8	9.9	1.43**
Cells			
No satellites	17	64.9	5.08
Satellites	8	70.5	9.39 n.s.
Pupae			
No satellites	17	14.9	2.41
Satellites	8	24.3	2.43*

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; n.s. = not significant

lites were formed that year). In this analysis only nests that survived to June, when most worker satellites are formed, were included. Nests producing satellites had more workers on them at their maximum than nests not producing satellites (Mann-Whitney *U*-Test,  $P < 0.025$ , one-tailed,  $n_1 = 7$ ,  $n_2 = 10$ ). In Austin, satellite nests are initiated from mid-May to early July (Figs. 1 and 4). Queens initiate satellites only during May and early June, while workers initiate satellites from late May through early July.

Twelve satellites were initiated by workers and not joined by additional workers at BFL, 1976–1979. All twelve failed, therefore workers are necessary for the success of a satellite. Workers switch freely between a main nest and a queen satellite. By contrast, workers who have joined worker-initiated satellites do not return to the main nest (Strassmann 1981a). After workers emerge from the satellite, worker transfer ends. The queen stays on the satellite and a worker lays eggs in the main nest. Both main nest and satellite usually continue to be used, though after a month or more the main nest is sometimes abandoned, particularly if there are few workers. At BFL in 1976, four of ten (1977: two of eight; 1978: seven of nine) main nests were eventually abandoned and



**Fig. 4.** Percentage of satellite nests produced during each 15-day period May–August, BFL, Austin, 1976–1978 and San Antonio, 1977

all workers joined the satellite. When one nest is destroyed, all females join the remaining nest.

Since queen satellites average 4.2 m from the main nest, the queen must fly this distance during the month she controls both nests. In 1978 and 1979, 6 of 24 queens without satellites (25%) died during June, while 10 queens with satellites (20%) died during the same month. So those queens with satellites do not die more often than do queens without satellites as a result of flights between the nests.

With and without early males, nests with more females produce significantly more satellite nests (Table 5), so early male production is not a precondition for satellite formation.

Late in the summer at BFL (between 20 July and 28 August), two nests in 1978 and four nests in 1979 produced new nests, ‘pseudosatellites’, built within 20 cm of the original nest and joined by all wasps from the original nest 1–3 days after it is initiated and the original nest is then abandoned. Four of six pseudosatellites were from original nests with 40%–73% of the brood destroyed by the pyralid moth *Chalcoela iphitalis*. One nest was deformed by contact with chicken wire; and one nest had nothing apparent wrong with it. Pseudosatellites differ from true satellites in their late summer initiation, greater proximity to original nest and that the original nest is immediately and entirely abandoned, so pseudosatellites do not change the social organization of the nesting females, while true satellites do.

### Satellite Nests and Bird Predation on Nests

Birds knock down wasp nests and eat all brood, usually not harming the adults on the nest. This examination of bird predation focuses on whether or not a satellite nest is a means of avoiding bird predation. Bird predation on nests from March through October is the major cause of brood mortality in *Polistes exclamans*

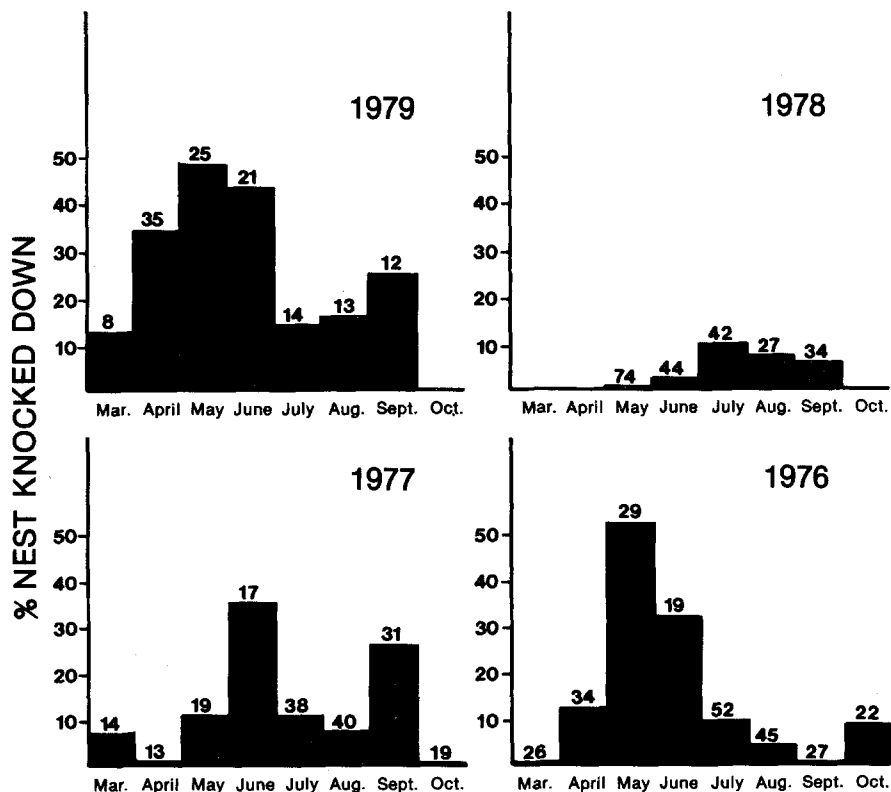
**Table 5.** Number of females on nests with and without satellites, controlling for presence of males. Means for nests with and without satellites are compared using the Mann-Whitney *U*-Test

Variable	<i>n</i>	$\bar{x}$	Standard error
<i>Nests without males</i>			
June			
No satellite	33	7.8	1.30
Satellite	9	12.1	2.42*
July			
No satellite	23	15.4	1.92
Satellite	9	26.6	6.07*
<i>Nests with males</i>			
June			
No satellite	8	9.9	1.86
Satellite	7	20.4	3.42*

\*  $P < 0.05$

(Fig. 5; Strassmann 1981b). After a nest is knocked down, the queen will join and attempt to usurp another female's nest if the queen whose nest was destroyed has no workers. In 1979 at BFL four females successfully joined nests of other females and took over egg laying. If workers had already been produced, the queen and her workers built a new nest at or near the location of the original nest. Because of the high mortality of foraging workers (Strassmann, unpublished data), these nests usually produce no young before all workers have died (Table 6). After all workers die, the queen resumes active foraging for caterpillars, nectar, water, and pulp, and usually disappears, presumably the victim of predation. If a satellite is present when the nest is knocked down, the workers and queen join the satellite. If only the satellite is knocked down, the wasps usually rejoin the main nest. Whether or not the queen is then treated as an intruder by the resident queen varies (see Strassmann 1981a).

Nests that were knocked down were compared to nests not knocked down to see if there were consistent differences between them. First, numbers of females on nests that were knocked down were compared with numbers of females on nests not knocked down in each 2-week period, March through October. The median number of females was determined, and nests were categorized as having more than the medi-



**Fig. 5.** Percentage of the total nests present in each month at BFL, 1976–1979, that were knocked down is given. The number over each column is the total number of nests present that month

**Table 6.** Fate of females whose nest is knocked down, BFL, Austin

Fate after nest is knocked down	Year			
	1976	1977	1978	1979
Fail immediately without renesting	22	14	3	24
Renest, then fail	1	2	3	2
Renest, produce workers, then fail	0	3	1	0
Renest, new nest knocked down, fail	2	3	1	1
Join satellite, satellite knocked down, fail	1	1	0	1
Join satellite, all adults die, fail	1	0	0	0
Succeed with satellite	2	0	2	4
Succeed without satellite	1	1	1	2
Total	30	24	11	34

an number of females, or less or equal to the median number of females. Nests that were knocked down did not differ in number of females from those not knocked down, so increased numbers of females are no defense against birds. (1977: knocked down and above median number of females, 11 nests; knocked down and equal or below median number of females, 14 nests; not knocked down, 98 and 121 nests, respectively;  $\chi^2=0.08$ , n.s.; 1976 number of nests in categories in same order as above: 9, 11, 82, 104;  $\chi^2=0.03$ , n.s.). Second, nests that were knocked down were compared with those not knocked down to see which were more conspicuous. Nests that had been knocked down were visible from more directions, from greater distances, and had less obstruction near the nest (Table 7). After being knocked down, nests with satellites are much more likely to survive to produce autumn reproductives (survive, 8; fail, 4) than are nests without satellites (survive, 5; fail, 82) ( $\chi^2=34.3$ ,  $P<0.001$ , Table 6). Nest concealment reduces the probability that a nest will be knocked down, and a satellite nest reduces the probability of failure after the main nest is knocked down, while increased numbers of females on the nest have no effect.

#### Nest Parasitoids and Satellite Nests

There are two major brood parasitoids present in the BFL and San Antonio populations of *P. exclamans*: (1) the pyralid moth *Chalcoela iphitalis* and (2) the chalcid wasp *Elasmus polistis*. *C. iphitalis* larvae sometimes tunnel from one cell to another, but their larval development period is less than the pupal development period of wasps (Strassmann, unpublished data). Therefore, they are not present in the nest as larvae long enough to kill future brood. *E. pol-*

**Table 7.** Concealment parameters of nests knocked down and nests not knocked down, at BFL, 1977. Kolmogorov-Smirnov test comparisons between the two groups

	Nests knocked down			Nests not knocked down		
	N	$\bar{x}$	S.D.	N	$\bar{x}$	S.D.
Nest height	16	1.2	0.7	16	1.2	0.8 n.s.
Degrees visible horizontally (of 360°)	16	190	100	16	130	110*
Farthest distance visible (m)	16	4.7	2.3	16	3.3	2.2*
Obstruction near nest (1-5)	16	1.6	1.6	16	2.4	1.3*

\*  $P<0.05$ ; n.s. = not significant

*istis* larvae are restricted to the cell they emerge in and therefore kill only the occupant. Neither parasitoid is able to kill brood in cells that were built after the nest was infested with parasitoids, hence a satellite nest is not necessary to protect new brood from parasitoid larvae presently in the nest.

In 1978 an experiment was performed at BFL to determine whether satellites were formed as a response to parasitization attempts by *Chalcoela iphitalis* females. Each nest was approached around 11 p.m. and a live *C. iphitalis* female was rubbed over the surface of five nests. Five control nests were rubbed with a ball of cotton using a different pair of forceps. After this attack, wasps on all five experimental nests acted as if there were a moth present by walking jerkily all about the nest and substrate, and flipping their wings; none of the controls responded in this manner. It was therefore concluded that the experiment had successfully mimicked an actual visit by a *C. iphitalis* female intending to oviposit in the nest. None of the experimental or control nests produced a satellite during the month after the simulated moth attack, so satelliting is probably not an immediate response to the visit of a moth. In June and July 1977 in San Antonio, nests with satellites had no more cells infested by *C. iphitalis* than did nests without (number of cells with *C. iphitalis* July: with satellites,  $\bar{x}=18 \pm \text{SE } 7$  ( $n=7$ ); without satellites,  $\bar{x}=24 \pm \text{SE } 7$  ( $n=23$ );  $P>0.4$ ).

*Elasmus polistis* adults emerge from a nest, mate on substrates within 30 cm of the nest and reinfest the same nest (Strassmann 1981b). A satellite nest, therefore, may offer protection for future brood from reinfestation by *E. polistis* (Strassmann 1981b). When nests with satellites were compared with nests without satellites for numbers of parasitized brood (each para-

site considered separately) in the San Antonio collections, at no time were any significant differences found (July, with satellites, number of cells with *E. polistis*:  $\bar{x}=2 \pm \text{SE } 1$ ; ( $n=7$ ); without satellites:  $\bar{x}=3 \pm \text{SE } 2$ . ( $n=23$ );  $P>0.4$ ).

## Discussion

The production of early males and the ability of workers to take over egg laying in *P. exclamans* may be responses to deal with frequent queen death. Early males provide a clear evolutionary advantage for nests producing them because they are reproductive individuals produced at the beginning of the season before many nests have failed. However, early males are produced at the cost of producing workers. There is probably an essential minimum number of workers necessary to a nest that probably explains why only larger nests produce early males, any one of those nests seldom produces more than three or four early males, and a few workers are always produced prior to early male production.

It is not immediately clear why queen death is so high. I have never seen a predator successfully remove an individual wasp from a nest, so a queen is presumably safe from predation while on the nest. Queen death is high during May when queens are still foraging, but deaths continue after May when queens are not apparently compelled to leave the nest. Queens may die from disease on the nest and fall to the ground where they would not be seen. Winter-time activity during warm days may result in earlier senility as compared with more northern species.

Spring production of males has been reported in a number of other polistine species. Schmitt (1914) mentions a nest of *P. gallicus* that produced males on 19 June. Rau (1946) reported that two males emerged from a *P. variatus* nest in mid-June. He asserts that these males could not possibly have arisen from worker-laid eggs as there were no workers old enough to have laid them. Litte (1977), studying *Mischocyttarus*, a genus that is in many ways similar to *Polistes*, found that a few males were sometimes produced with the first brood in Florida populations of *Mischocyttarus mexicanus*, which nests year-round in Florida. Since queens in *Polistes exclamans* initiate the majority of all satellites, prior production of early males in the population is not necessary for satellite nest production. Substantial queen death and early male production were observed in both *P. annularis* and *P. metricus* in the absence of satellite nesting, therefore it is likely that early males preceded satellite nesting as an adaptation to queen death (Strassmann,

unpublished data). Although other species are variably able to recover after the loss of the queen, *P. fuscatus* nests ordinarily do not grow after the death of the queen (West Eberhard 1969). In *M. drewseni* on the other hand, several queens (daughters or sisters of predecessors) can appear in succession on a colony (Jeanne 1972).

Satellite nests are initiated as early in the spring as possible given that a minimum number of workers is necessary to support two nests. This is consistent with the hypothesis that satellite nests reduce the impact of nest predation by birds, since a satellite should be begun as early as possible to avoid losing all brood to birds. Gibo (1978) attributed the greater success of multiple-foundress nests to their enhanced ability to rebuild the nests after bird attacks. However, the multiply founded nests were just as likely to be attacked by birds as were singly founded nests (Gibo 1977). Nest concealment reduces bird predation, but the long season in Texas makes it possible that a well-concealed nest in March is no longer so concealed later in the spring and summer. The placing of some larvae in a satellite nest (that may be better concealed than the main nest, since it is built later) so that at least some of the brood will escape a bird attack, seems to be the only mid-season way wasps have of reducing the devastating effects of bird predation on nests.

Bird predation on *Polistes* nests is by no means limited to Texas populations of *P. exclamans*. It has been reported for many North American *Polistes* species. Species nesting farther north probably do not have the long season and multiple generations of workers necessary to form and maintain satellite nests. In Texas, *P. metricus* is subject to bird predation on nests, but does not produce satellites as far as I am aware. Most *P. metricus* nests observed in central Texas are small, seldom have more than ten females on them, and may not be able to reach a minimum size necessary for satellite nesting. They are, however, larger in Kansas (Gamboa 1978). *P. annularis* has large sturdy nests that are not attacked by birds (Strassmann 1979), even though all the common bird species found at BFL are also found at the *P. annularis* nesting site (Strassmann, unpublished data).

Satellite nests may function to decrease *Elasmus polistis* damage after infestation in the original nest. The type of parasite a satellite would be good at avoiding is one that destroys many brood when it attacks the nest, one whose offspring reinfest the same nest, and one that does not discover all nests in the area. *E. polistis* may fit this description in years of high infestation, though it usually does not kill many



pupae in a single nest. Satellite nest initiation does not seem to be a response to *E. polistis* infestation in the San Antonio collections. Numbers of cells infested by *E. polistis* were probably under-counted since larvae on top of the remnants of prior infestation sometimes obscure the infestation.

Satellite nests may not be restricted to *P. exclamans*. Rau (1941, 1943) reports swarm-initiated nests in *P. canadensis* in Veracruz, Mexico, in *P. instabilis* at various locations in Mexico, and in one case in *P. exclamans*. These may be satellite nests.

Two other types of renesting have been described for polistine wasps (Jeanne 1979; Litte 1981). *P. canadensis* populations in Brazil are infested with a tineid moth parasite that eats the wasp meconia (a fecal pellet left by the larva on pupation; Jeanne 1979). In an infested nest, adult wasps leave empty the cells from which larvae have emerged and raise new brood in a new nest only a few centimeters from the original nest. The conglomerate main comb and new combs are treated by the wasps as if they were one large nest. This situation is quite different from that found in *P. exclamans* in that the additional combs are adjacent to the original nests whereas in *P. exclamans* they are some distance away, and the queen and workers move freely from one nest to the other, while in *P. exclamans* the satellite eventually has a different queen and a different set of workers.

*Mischocyttarus labiatus*, in Colombia (Litte 1981), have nests that are frequently infested with a phorid fly whose larvae kill all wasp brood present in the nest. Litte (1981) found that wasps entirely abandon their nest after a visit by an adult female phorid fly, often cutting the pedicel and allowing the parasitized nest to fall to the ground. If there are enough females in the group, they reneest near their original nest. This is quite different from *P. exclamans*, because the parasitoid is so devastating. Groups of nesting females in *M. labiatus* never reach great enough numbers to make new nest initiation before a parasitoid attack is a viable possibility.

Ultimately, early male production, queen death, and satellite nest formation are probably adaptations to long Texas summers. Queens may die early after light Texas winters during which they repeatedly leave hibernacula, resulting in an evolutionary advantage to producing early males who have springtime opportunities to mate. Satellite nests are only possible where multiple generations of workers are present, and perhaps most necessary where a long dry summer often results in falling leaves that expose main nests that were previously concealed. Yet the summer is not long enough for two complete colony cycles; the result is the long and unusual *P. exclamans* colony cycle.

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