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PARASITOIDS, PREDATORS, AND GROUP SIZE IN THE PAPER WASP, *POLISTES EXCLAMANS*[1]

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Abstract. The paper wasp *Polistes exclamans* loses part of its brood to the parasitoids *Chalcoela iphitalis* (Lepidoptera:Pyralidae) and *Elasmus polistis* (Hymenoptera:Chalcidoidea:Eulophidae) and loses entire nests to bird predation, *Crematogaster laeviuscula* (Hymenoptera:Formicidae) predation, and orphanage (loss of all adult wasps). More nests fail because of bird predation than from all other causes combined. Larger nests are neither better protected nor more vulnerable to nest predators, though larger nests are less likely to fail because of orphanage than are smaller nests. Larger nests are more heavily attacked by *Elasmus polistis*, which reinfests its natal nest. *Polistes exclamans* may subdivide larger groups of females by forming satellite nests because of the lack of an overall advantage to large nests. Satellite nests increase the probability that the brood in either the original nest or satellite nest will avoid bird predation.

Key words: bird predation; Chalcoela iphitalis; Crematogaster laeviuscula; Elasmus polistis; *group living; life tables;* Pachysomoides; *parasite coexistence;* Polistes exclamans; *population cycles.*

INTRODUCTION

In social organisms, group living itself may have a major impact on individual and group vulnerability to predators and parasites. The group represents a concentrated resource for a predator or parasite, but the grouped individuals together may be better able to defend themselves than isolated individuals. In a study of the impact of predators and parasites on a group-living organism it is important to determine how the group helps or hurts individuals in avoiding predators and parasites and thus to determine what the ecological advantages and disadvantages of group living are. In a general model for social organisms Alexander (1974) states that group living always has the disadvantages of increased disease and parasite transmission since individuals are close together and group-living individuals compete more intensely for resources such as food and mates. To overcome these disadvantages he states that there has to be a specific advantage to group living. He suggests increased protection from predators, dependence on a resource that is highly clumped in the environment, or more efficient group hunting as possible advantages to group living. The specific advantage must be determined for each species while the disadvantages are common to all social organisms.

Polistes wasps are vulnerable to a large number of predators and parasitoids that attack the brood or adults (Rau 1941*a*, 1943, Nelson 1968, Burks 1971, Gillaspy 1973, Reed and Vinson 1979). The parasitoids common in *Polistes* nests are reviewed in Nelson (1968), and the newly described parasitoid *Elasmus polistis* has been studied by Burks (1971) and Reed and Vinson (1979). Ants and birds are most common among whole-nest predators (Rau 1941*b*, Spieth 1947, Jeanne 1970, 1980, Gibo 1978). Adults typically die away from the nest as victims of spiders, birds, robberflies, or stylopid parasitoids (Rau 1946, West Eberhard 1969, Litte 1977, 1979). *Polistes* wasps build open-combed paper nests in which brood is raised. The brood is defenseless but it is guarded by pugnacious adults who maintain a constant vigil against predators and parasites on the nest. Once a parasite or predator discovers a nest it must avoid the adults to attack the brood.

Polistes wasps group only to raise brood. They neither forage nor mate in nesting groups. Thus, according to Alexander (1974), the disadvantage *Polistes* groups are most likely to face is increased parasitism of brood and adults who associate closely on the nest. The most likely advantage to *Polistes* wasps is protection of the brood from predators. In *Polistes*, reproductive castes, kin selection, and increased efficiencies due to a division of labor may also contribute to the advantages and disadvantages of sociality. These factors will not be covered here. In this study numbers of predators and parasitoids attacking nests of *Polistes exclamans* are quantified over 4 yr. The impact of group living on nest vulnerability is measured by comparing smaller nests to larger nests to see if larger nests and the larger groups of wasps associated with them are more or less vulnerable to each predator and parasitoid. Females from a *Polistes exclamans* nest split into two separate colonies ≈30% of the time (Strassman 1981*a*, *b*). The new or satellite nest is started ≈2.5–3 mo after the first nest and may be initiated by either the queen or a former worker, and is then joined by additional workers. Satellite nest formation is a means of reducing group size, because

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the workers are divided between two nests. According to Alexander's model, satellite nests are expected to reduce nest parasitism and increase predation on nests. In this paper these predictions will be tested.

METHODS

A population of naturally occurring *Polistes exclamans* nests was observed during 1976–1979 at Brackenridge Field Laboratory (BFL) of the University of Texas at Austin. All nests discovered were included in the study to avoid any biases. In 1976 and 1977 some nests were not discovered until June or July. They were included in the study for subsequent months because so many of the early nests had failed by that time. In all, 67 nests were followed in 1976, 71 in 1977, 74 in 1978, and 55 in 1979. These numbers do not include satellites or the reconstructed nests built after the original nest was destroyed. Specifics of the location and the study have been described elsewhere (Strassmann 1981*a*, *b*). In addition to this population, three collections of nests and their associated wasps were made in San Antonio on 20–22 June, 26–28 July, and 10 September 1977. Collecting techniques are described elsewhere (Strassmann 1979; Strassmann and Thomas 1980).

Extent of parasitism in all nests was determined by counting (1) total number of cells containing eggs, larvae, and pupae, (2) number of cells where adults had emerged, and (3) number of cells containing evidence that brood had been killed by a parasitoid. All five parasitoids leave evidence of their pupae in the nest. *Chalcoela iphitalis* (Lepidoptera:Pyralidae) leaves characteristic webbing in the cells (Rau 1941*a*). A cell that has been infested with *Elasmus polistis* (Hymenoptera:Chalcidoidea:Eulophidae) has a characteristic flat brown bottom a few millimetres above the cell floor. *E. polistis* larvae pupate under the flat brown bottom (Reed and Vinson 1979). *Pachysomoides stupidus* (Hymenoptera:Ichneumonidae) leaves a pale yellow, longitudinally divided, papery material in which its larvae pupate (Nelson 1968). *Pachysomoides fulvus* leaves an orange, longitudinally divided, papery material in the cells (Nelson 1968). The puparia of sarcophagid flies are also left in the nest. Voucher specimens of all wasps and parasitoids were deposited in the Academy of Natural Sciences, Philadelphia, Pennsylvania, USA. Wasps and parasitoids were identified by James E. Gillaspy. The ants were identified by Donald H. Feener; Timothy Friedlander identified the robberfly. Nests were checked daily to see if they had been attacked by a nest predator. Exact counts of cell contents were made biweekly. Roll calls of wasps on the nests were usually made every 3 d.

Since many of the data are not distributed normally, nonparametric tests are used (see Siegel 1956, Sokal and Rohlf 1969, Nie et al. 1975). The Kruskal-Wallis test is used to compare central tendencies among samples (Siegel 1956, Nie et al. 1975). Kendall's τ correlations are used because of a large number of zero values for number of parasitoids in the data which are therefore highly skewed, making a Pearson (parametric) correlation inappropriate. It should be remembered that the value of a Kendall's τ correlation in a given data set is typically lower than that of a Spearman or Pearson correlation, and the Kendall is superior to the Spearman because it has a more stable distribution.

The probability of a nest present at the beginning of the year not becoming parasitized or destroyed at some time during the year can be calculated by counting number of nests attacked during each month and the total nests present during each month. The probability (S) of a nest avoiding attack is then:

$$S = \prod_{N=1}^{8} \left(1 - \frac{D_N}{T_N}\right) \tag{1}$$

N = 1 is March, N = 2 is April, etc.,
D_N = number nests attacked during month N,
T_N = number of nests present during month N.

This formula has been applied separately to each cause of nest parasitism and nest destruction, and to all destructive factors operating at once.

RESULTS

Brood parasitoids

Four parasitoids were found in *Polistes exclamans* nests: the common *Chalcoela iphitalis* and *Elasmus polistis* and the rare *Pachysomoides stupidus* and *Pachysomoides fulvus*. In addition, pupae of an unidentified *C. iphitalis* hyperparasite were found in a few nests. At BFL a sarcophagid fly was once seen buzzing around a nest in 1976. Empty fly puparia were found in one nest at BFL in 1979.

Chalcoela iphitalis.—*C. iphitalis* females lay eggs in wasp nests at night, though they are often seen during the day resting on a twig near a wasp nest. When a *C. iphitalis* female walks near the nest and a wasp intersects her trail, the wasp responds violently, repeatedly stinging and biting the location where the moth has been. Other wasps become alarmed, probably due to the nest vibrations, and begin to move about the nest jerkily performing a characteristic "parasite dance" (West Eberhard 1969). The wasps leave their nest and walk all over the substrate. If the moth is found (a rare occurrence) it is chewed up immediately. The wasps continue in their parasite dance behavior for at least 10 h after a *C. iphitalis* female is detected on or near the nest.

Along with the parasite dance, wasp pupae are often aborted, eviscerated and chewed up, or just dropped to the ground. This is especially common in late summer when *C. iphitalis* infestations are highest (Table 1). The pupae appear to have been healthy before they were aborted, but might only recently have been parasitized by *C. iphitalis*. Some pupal caps have small

TABLE 1. Numbers of cells and percent of total cells infested with parasites in nests at Brackenridge Field Laboratory (BFL) and San Antonio, Texas.

	Date	Number of nests	Percent of nests infested by:		Number of cells per nest infested by:		Percent of cells per nest infested by:	
			C. iphitalis	*E. polistis*	*C. iphitalis*	*E. polistis*	*C. iphitalis*	*E. polistis*
					($\bar{X}$ ± SD)		($\bar{X}$ ± SD)	
A) All nests								
BFL	1977	27	46	61	13 ± 26	7 ± 10	19 ± 29	8 ± 10
	1978	41 (39)†	73	62	21 ± 34	25 ± 37	23 ± 28	18 ± 21
	1979	28	64	36	36 ± 39	4 ± 8	34 ± 36	5 ± 8
					6.3*	9.5**	3.2	8.5*
San Antonio								
	20 June	75	25		5 ± 10	0.3 ± 1.2	9 ± 18	0.5 ± 1.9
	26 July	41	59		17 ± 29	2.0 ± 6.1	16 ± 18	2.1 ± 5.4
	10 September	32	50		14 ± 25	3.3 ± 8.7	16 ± 24	2.0 ± 4.3
					14.1***	12.7**	10.9**	11.1**
B) Includes only nests with parasites								
BFL	1977				27 ± 33	10 ± 11	40 ± 31	14 ± 10
	1978				28 ± 36	40 ± 41	32 ± 28	29 ± 19
	1979				56 ± 35	11 ± 11	52 ± 33	21 ± 18
					13.2***	14.9***	5.7	9.8***
San Antonio	1977							
	20 June				18 ± 12	3 ± 2	34 ± 22	6 ± 3
	26 July				29 ± 33	7 ± 10	27 ± 16	8 ± 8
	10 September				29 ± 30	9 ± 13	32 ± 26	5 ± 6
					0.2	1.3	1.5	0.8

* $P < .05$; ** $P < .01$; *** $P < .001$, chi-square comparisons among years; df = 2.

† Sample size for *E. polistis* calculations in 1978.

windows chewed in them by wasps who may be checking for parasitoids in these cells. Abortion of pupae may also be a response to visits of other parasitoids. *Polistes exclamans* females cannot chew through the webbing which encases *C. iphitalis* pupae, though they often try. One *C. iphitalis* larva usually kills one wasp pupa or prepupa that has spun its cocoon. However, I have noted holes from one cell to another which may mean some *C. iphitalis* larvae leave one pupa to feed on another. *C. iphitalis* pupae overwinter in abandoned wasp nests and emerge as adults capable of attacking the first generation of wasp pupae which appears in mid-April. Since the evidence of infestation is webbing which is visible only after *C. iphitalis* larvae pupate, parasitism is not detected at first. Several generations of *C. iphitalis* are produced each year with new infestations usually reaching a peak in July and August (Tables 1 and 3). In the three San Antonio collections, nests were more parasitized in late July and September, significantly more so than in June (Table 1). The probability that a nest present at the beginning of the year would avoid *C. iphitalis* at BFL each month in years 1976–1979 is given in the fifth column of Table 3. The biggest decrease in probability of avoiding parasitoids comes in August in 1976, and in July in 1977–1979. In 1976–1978 the probability of avoiding *C. iphitalis* parasitism altogether is between 0.52 and 0.61 but in 1979 it is only 0.26 (Table 3).

C. iphitalis infestations vary not only according to how many nests are infested but also according to how heavily nests are parasitized. Looking only at the end of the year calculations (Table 1A, Fig. 1), in 1977, 46% of all nests still present at BFL contained evidence of *C. iphitalis*. In 1978 and 1979, 73% and 64% of all nests, respectively, contained *C. iphitalis* webbing. The nests at BFL contained a mean of 13–36 cells whose pupae had been killed by *C. iphitalis*, representing 19–34% of all the mature cells in the nest. Mature cells (also called complete cells) are used because *C. iphitalis* attacks pupae; cells so young they have never contained a pupa are not vulnerable. Considering all nests (with and without *C. iphitalis*), number of cells infested in all nests varies significantly among years 1977–1979 (Table 1A). The percent of cells destroyed by *C. iphitalis* does not vary significantly from 1977 to 1979 (Table 1A, Fig. 1). Considering only nests with *C. iphitalis* present (Table 1B), number of parasitized cells varies significantly from year to year, but not over the season, and percent parasitized cells does not vary significantly.

In 1977 and 1978 the number of cells infested with *C. iphitalis* was not significantly correlated with number of mature cells in the nest, but in 1979, the year of highest overall infestation, the correlation was highly significant (Kendall's $\tau = .48$, Table 2, Fig. 1). So only in 1979 are larger nests more infested with *C. iphitalis* than are smaller nests. Percent of all mature

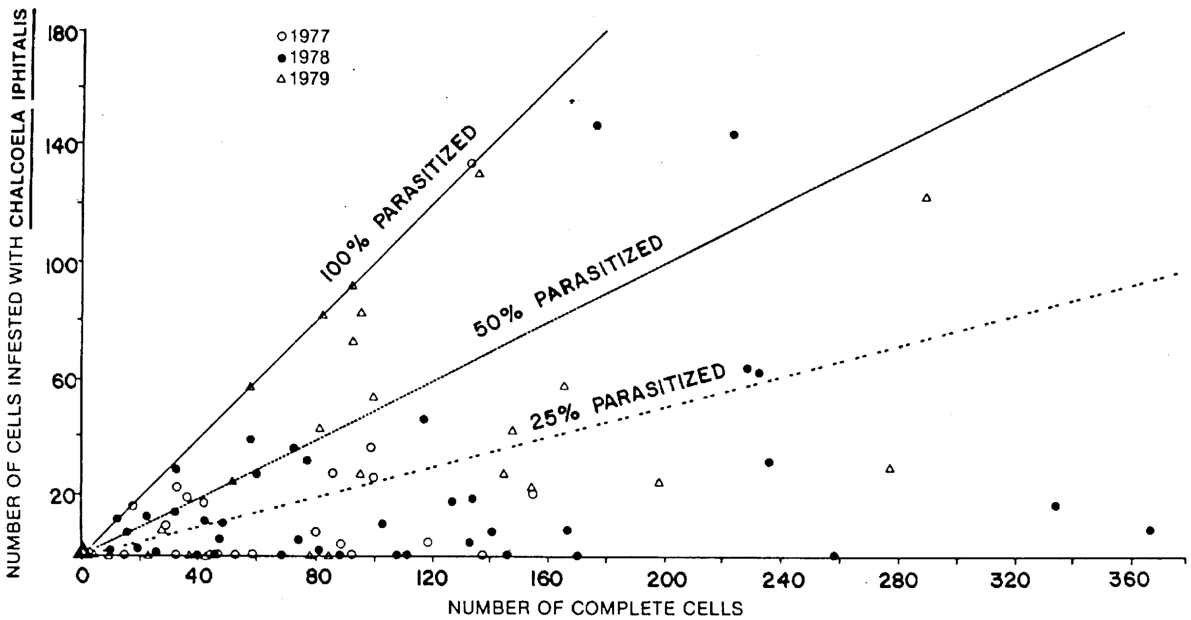

FIG. 1. Numbers of cells containing *Chalcoela iphitalis* webbing as a function of number of complete (or mature) cells in the nest for nests collected at the end of years 1977, 1978, and 1979. Lines indicate where 25, 50, and 100% of the cells in the nest are parasitized. Correlations are given in Table 2.

cells infested with *C. iphitalis* was weakly negatively correlated with total mature cells in 1977 and 1978 but in 1979 it was significantly positively correlated (Table 2). So in 1977 and 1978 large nests lost proportionally fewer of their pupae to *C. iphitalis*, but in 1979 they lost proportionally more pupae to *C. iphitalis*. Thus, neither large nor small nests have a consistent advantage in avoiding *C. iphitalis* parasitism.

In all three San Antonio collections, number of *C. iphitalis*-infested cells was positively correlated with number of mature cells (Table 2). Percent cells with *C. iphitalis* was also positively correlated with number of mature cells, though more weakly so (Table 2). So in the San Antonio population, large nests suffer more, and proportionally more, *C. iphitalis* damage than do smaller nests.

In this study it was not possible to determine whether or not more than one *C. iphitalis* female lays eggs in a nest at the same time. But it was possible to determine how often a nest was parasitized by *C. iphitalis* at two different times simply by noting if additional *C. iphitalis*-damaged cells appeared in a nest over the season. If nests already parasitized by *C. iphitalis* are not avoided by subsequent *C. iphitalis* females, then the probability of being parasitized twice is the square of the probability of being parasitized once. These probabilities are calculated from the biweekly data so the seasonal effect is included. Ex-

TABLE 2. Kendall's τ correlations of number and percent of cells in nests parasitized by indicated species vs. total number of mature cells. Percent is calculated as (number parasitized cells × 100)/number mature cells.

	Correlation coefficients for parasitized vs. mature cells				
	Correlation (τ) of number parasitized		Correlation (τ) of percent parasitized		Number of nests
	C. iphitalis	*E. polistis*	*C. iphitalis*	*E. polistis*	
BFL					
1977	.08	.19	−.07	.03	27
1978	.15	.43***	−.15	.27**	41 (39)†
1979	.48***	.23*	.28*	.14	28
San Antonio 1977					
20 June	.29***	.21**	.25***	.20**	75
26 July	.53***	.21*	.33**	.20*	41
10 September	.42***	.55***	.26*	.47***	32

* $P < .05$, ** $P < .01$, *** $P < .001$.

† Sample size for *E. polistis* correlations in 1978.

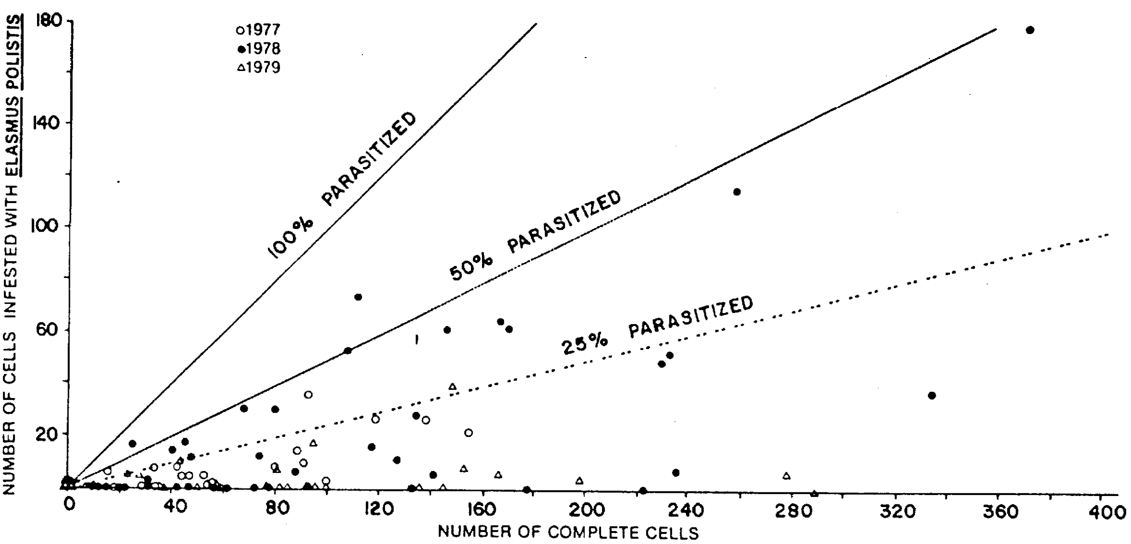

FIG. 2. Numbers of cells containing evidence of *Elasmus polistis* as a function of number of complete (or mature) cells in the nest for nests collected at the end of years 1977, 1978, and 1979. Lines indicate where 25, 50, and 100% of the cells in the nest are parasitized. Correlations are given in Table 2.

pected values are calculated as follows: If P = number of nests parasitized and T = average number of nests present during months when *C. iphitalis* is present, $(P/T)^2$ = probability of being parasitized twice. $(P/T)^2(T)$ = expected number of nests parasitized twice. The expected number of nests parasitized twice is calculated to be 19 in 1976, 8 in 1977, 7 in 1978, and 11 in 1979. The number of nests observed to be parasitized twice in a season is much lower (4 in 1976, and 1 each in years 1977 to 1979; $\chi^2 = 33.2$, $P < .001$). *C. iphitalis* females thus appear to avoid nests previously parasitized by this species, as is also demonstrated by the absence of an increase in number of parasitized cells in infested nests over the season in San Antonio (Table 1B).

Elasmus polistis parasitism.—*Elasmus polistis,* the tiny chalcid parasite, kills many *Polistes exclamans* pupae. As many as 80 *E. polistis* hatch out of a single cell in a nest. Males emerge before females, then wait for females to emerge from the nest. I have seen many male *E. polistis* sitting on leaves and other substrates near the nest. When the females emerge, they mate with the waiting males, who are likely to be their brothers, and return to the same nest to lay their eggs. Since the nest is reparasitized by the adults that emerge from it, infestation in a nest increases over the summer. Parasitism levels are hard to quantify during the summer because the brown bottom characterizing cells infested by *E. polistis* is most visible at the end of the year when the nest is deserted, and earlier counts tend to be inaccurate. *E. polistis* overwinters in the pupal stage in wasp nests.

Over 60% of all nests were infested with *E. polistis* at BFL in 1977 and 1978, as determined by counts of infested cells at the end of the year (Table 1A). But in 1979 only 36% of all nests were infested. The number of cells infested with *E. polistis* varied significantly among years at BFL, reaching a peak in 1978 of 25 parasitized cells per nest on average (Table 1A). Percent cells infested with *E. polistis* also varied significantly among years at BFL, reaching a peak in 1978 of 18% parasitized cells (Table 1A). Thus, *E. polistis* population levels vary from year to year. Considering infested nests only, mean number of infested cells varies from year to year, but not over the season (Table 1B).

The number of cells infested by *E. polistis* was correlated with the number of mature cells in all years at BFL; the value of the Kendall's τ correlation varied from .19 to .43 at BFL (Table 2, Fig. 2). Percent cells parasitized by *E. polistis* was significantly correlated with number of mature cells only in 1978 at BFL, the year of greatest infestation, when the correlation was .27. Larger nests therefore have higher levels of infestation than do smaller nests and are proportionately more severely attacked, as would be expected from a parasite that reinfests its natal nest if larger nests are assumed to be older. This contrasts to the case of *C. iphitalis* where nests are not reinfested by additional *C. iphitalis* females.

Since both *C. iphitalis* and *E. polistis* infest large numbers of *P. exclamans* nests, I decided to investigate any possible effects they might have on each other. Of the 94 nests collected at the ends of the years 1977–1979, at BFL, 30 (32%) contained both parasitoids (Fig. 3). Sixty (63%) contained *C. iphitalis* and 50 (53%) were parasitized by *E. polistis*. If the probability that a nest infested by one parasitoid is independent of prior discovery by the other parasitoid, then the number of nests infested by both parasitoids

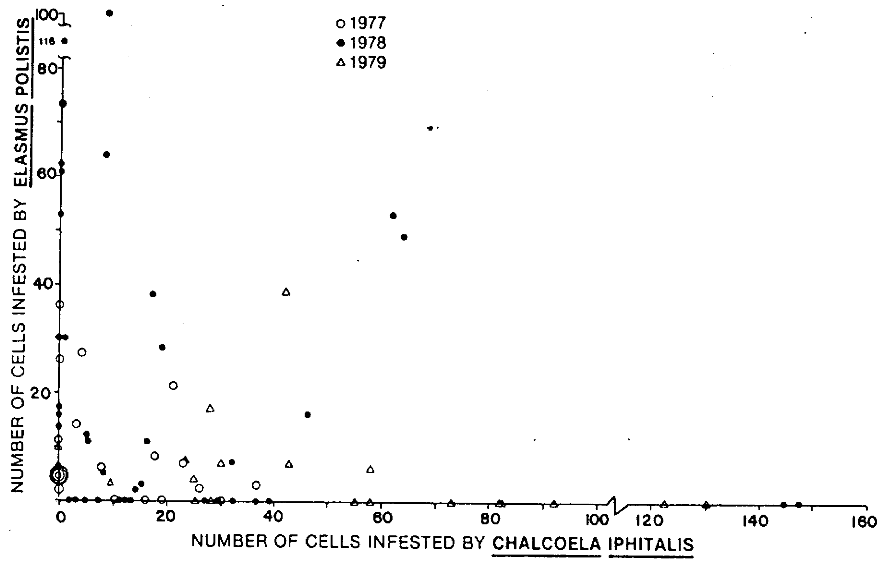

FIG. 3. Number of cells infested by *Elasmus polistis* as a function of number of cells infested by *Chalcoela iphitalis*. Kendall's τ correlations are $-.05$ in 1977, $-.26$ ($P < .05$) in 1978, and $-.03$ in 1979.

will be equal to the product of the probability of being infested by each parasitoid independently, or $.63 \times .53$ which equals .33. Clearly .32, the proportion actually infested by both, is not very different from the predicted proportion assuming independence, so interaction between the parasitoids is not a factor in determining whether or not both will infest a given nest (Fig. 3). Of the 3 yr the greatest infestation by *E. polistis* was in 1978 while *C. iphitalis* was most abundant in 1979.

Pachysomoides spp.—Both *Pachysomoides stupidus* and *Pachysomoides fulvus* are uncommon at BFL. *P. stupidus* females were observed near BFL nests in 1976. Roughly one-fifth of all nests lost three to four cells each to *P. stupidus* that year. Several *P. stupidus* larvae feed on each *Polistes exclamans* pupa. *Pachysomoides stupidus* was absent from Austin nests in 1977, 1978, and 1979, and never appeared in the San Antonio nest collections. *P. fulvus* appeared once at BFL, infesting a *Polistes exclamans* nest heavily in 1977 and destroying over 30 cells.

Nest predators

There are two predators which remove brood from an entire wasp nest at once, destroying the nest in the process: birds, and the ant *Crematogaster laeviuscula*. Their impact is much greater than that of parasitoids, because they kill all brood in a nest at once.

Birds usually knock down nests at dawn or dusk, killing few adult wasps in the process. Bird predation on nests is easily detected because the entire nest disappears at once. Its remains can often be found underneath a nearby perch where the bird presumably sat and ate the brood. In most years more nests are lost to birds than to any other brood predator or parasitoid (Table 3). Bird predation on nests peaks in May or June, though it is present from March through October (Table 3; Strassmann 1981*b*). Table 3 presents the probability that a given nest will survive attack by birds through each month. In most years a nest is more likely to fail due to bird predation alone than it is to survive.

After a nest is knocked down, the remaining adults attempt to rebuild the nest. The attempt usually fails because the adults are likely to die before new ones can be produced in a new nest. In years 1976–1979, 87 nests without satellites were knocked down. Only five were rebuilt and subsequently succeeded in producing reproductives. During the same years 12 nests had satellites when they were knocked down. Females from eight of these produced reproductives by joining the remaining nest. Clearly a satellite nest reduces the chance the females will be unable to produce any reproductives ($\chi^2 = 34.3$, $P < .001$; Strassmann 1981*b*). While increased numbers of wasps on a nest provide no extra protection, both nest concealment and satellite nesting reduce losses to birds (Strassmann 1981*b*).

Crematogaster laeviuscula destroys relatively few wasp nests. When they attack a nest these ants swarm all over the nest, and remove all brood, killing no adults in the process. Once any ants are on a nest, the wasps are ineffectual in deterring them. Wasp guards at the pedicel often turn away lone *C. laeviuscula* individuals. *C. laeviuscula* attacks occur erratically from April through September (Table 3). The probability that a nest will survive the year without succumbing to ant attack was always $>.79$ (Table 3). No

TABLE 3. Probabilities that a nest escapes each cause of brood death, Austin 1976–1979. Chance of survival to a given month is the product of surviving through all previous months (see text for explanation).

Month and year	Probability of surviving each cause of brood death					Total nests present each month	
	Nest knocked down	Nest orphaned and failed	*Crematogaster laeviuscula*	Sum of all nest destruction factors	*Chalcoela iphitalis*		
1976							
Mar	1.00	.81	1.00	.81	1.00	26	
Apr	.88	.78	.97	.67	1.00	34	
May	.43	.73	.97	.28	1.00	29	
Jun	.29	.73	.87	.16	.89	19	
Jul	.26	.70	.87	.14	.83	52	
Aug	.25	.51	.85	.09	.61	45	
Sep	.25	.40	.79	.06	.58	27	
Oct	.23	.35	.79	.05	.56	22	
1977							
Mar	.93	.93	1.00	.86	1.00	14	
Apr	.93	.93	1.00	.86	1.00	13	
May	.83	.68	1.00	.54	.89	19	
Jun	.54	.64	1.00	.32	.89	17	
Jul	.48	.59	1.00	.26	.68	38	
Aug	.44	.46	.98	.18	.68	40	
Sep	.33	.42	.98	.11	.64	31	
Oct	.33	.24	.98	.07	.61	19	
1978							
Mar	1.00	1.00	1.00	1.00	1.00	74	
Apr	1.00	1.00	1.00	1.00	1.00	74	
May	1.00	1.00	1.00	1.00	.97	74	
Jun	.98	1.00	.98	.95	.88	44	
Jul	.88	.95	.91	.75	.67	42	
Aug	.82	.95	.84	.64	.57	27	
Sep	.77	.92	.84	.58	.52	34	
Oct	.77	.87	.84	.58	.52	34	
1979							
Mar	.88*	1.00	1.00	.88	1.00	13	8*
Apr	.58	.92	1.00	.50	1.00	49	35
May	.30	.92	.97	.25	1.00	38	25
Jun	.17	.86	.97	.13	.75	32	21
Jul	.15	.83	.97	.10	.38	24	14
Aug	.12	.83	.97	.09	.27	22	13
Sep	.09	.74	.92	.05	.26	20	12
Oct	.09	.74	.92	.05	.26	14	7

* In 1979 some nests were caged, so probability of being knocked down is computed only from the nests not so protected. The last column gives numbers of unprotected nests present each month.

other ants have been observed attacking *P. exclamans* nests, though I observed that *Monomorium minimum* sometimes cleans out orphaned nests.

Predation on adults

Since predation on adults occurs off the nest it is hard to quantify how many wasps are killed by each species of predator. Life lengths of marked wasps from nests of various sizes can be quantified and will be presented elsewhere.

Adults are most commonly killed by several species of robberflies (Asilidae), orb-weaving spiders, and other spiders. Stylopids are not a major factor in adult death in *P. exclamans*. Of all the tens of thousands of wasps I have observed or collected, only eight were stylopized and only three of these were from the BFL population.

The robberfly *Diogmites angustipennis* Loew may specialize on *P. exclamans*. They are often seen perching near wasp nests where they attack females arriving at the nest loaded down with caterpillar meat. In 1977 a *D. angustipennis* that frequented a nest under observation was marked on 18 July 1977 and subsequently resighted regularly near the nest through 6 August. This robberfly sometimes caught marked wasps from the nest.

When adult mortality is so high that all adults on a nest die, the orphaned nest invariably fails because the larvae starve. The adults that emerge from an orphaned nest usually disappear before their numbers build back up. Large numbers of parasitoids in a nest can also contribute to the orphanage of a nest, because the parasitoids kill pupae that as adults would have replaced adults dying while foraging. In 1976, 40 nests with at least one worker were compared to see if the orphaned nests reached a lower maximum number of wasps. Twenty-seven orphaned nests reached 9 ± 10 wasps at their maximum while 13 successful nests attained an average 37 ± 18 wasps at maximum numbers. Clearly, the more wasps a nest has, the less likely it is to be orphaned. Nests may be orphaned from March through September (Table 3). There was no month when nests are most likely to be orphaned, and the probability of being orphaned varied greatly from year to year (Table 3).

Overall nest survival

The probability of surviving the three causes of total nest failure (bird predation, *C. laeviuscula* predation, and orphanage, was calculated as given in Eq. 1, but including the total nests destroyed by all causes each month as D_x (Table 3). Since parasitoids only partially destroy the nest, they are not included. This is the l_x schedule of the life table for *P. exclamans* nests. Clearly, the odds are usually against survival. In 1978 the probabilities of surviving orphanage and bird predation were higher than in other years.

DISCUSSION

The parasite fauna and its abundance in the BFL population of *P. exclamans* is not unusual for North American *Polistes* populations. In a review of parasites and symbionts of *Polistes*, Nelson (1968) lists *Chalcoela iphitalis* as the most common parasite found in collections of *Polistes* nests in Illinois and Missouri. It infests 40–48% of all nests (Nelson 1968). A hyperparasite of *C. iphitalis*, *Dibrachys* sp. was second in abundance followed by *Pachysomoides* spp. which are third most common. *Elasmus polistis* may be a recent arrival in Texas, or may have recently become a *Polistes* parasite. In spite of extensive studies of *Polistes* nests and parasites in Mexico and the United States (Rau 1941, 1943), including one at Austin, Texas, in which parasites were reared by placing nests in cellophane bags so that minute parasites should not have escaped, the species was not recorded until Burks (1971) described it. It is now widespread across the southern United States and the main host appears to be *Polistes exclamans* (Reed and Vinson 1979). Thus the Texas populations of *Polistes* may not be well adjusted to this parasite.

Each *C. iphitalis* parasitoid kills a wasp pupa, so a female laying several eggs in the nest is killing a number of wasp pupae at once. *C. iphitalis* females not only do not seem to reinfest the same nest, but also other *C. iphitalis* females actually appear to avoid nests that were previously infested, so *C. iphitalis* does all its damage at once. By contrast *E. polistis* kills fewer pupae gradually over the year. By killing pupae gradually over the season *E. polistis* never removes many pupae from the potential labor force at one time. Not only does *C. iphitalis* kill more pupae than *E. polistis* and kill a higher percentage of the total pupae, but it also does it all at once. This is most likely to reduce the wasp's ability to replace dying workers.

The calculations of percent cells parasitized by *C. iphitalis* and *E. polistis* tend to overemphasize the variable with the greatest variance, which in this case is parasitized cells in the numerator of this proportion (Strassmann and Thomas 1980). Therefore, when total number of parasitized cells varies significantly, percent probably will also.

None of the predators or parasitoids which have a major impact on the success of *Polistes exclamans* nests are consistently more effectively avoided by large groups of wasps on large nests than by small numbers of wasps on smaller nests. Bird and *Crematogaster laeviuscula* predation on nests is independent of nest size. However, nests with more wasps on them are less likely to be orphaned. Larger nests actually lost a lower percentage of their brood to *Chalcoela iphitalis* in 1977 and 1978 than did smaller nests, though the situation was reversed in 1979 at BFL and in San Antonio in 1977 (Table 2). Larger nests lost a higher percentage of their brood to *E. polistis* though the correlation was significant only in 1978 at BFL and in San Antonio in 1977 (Table 2).

Larger groups of wasps routinely split up by initiating satellite nests, and subsequently raising brood in both the original nest and the satellite, thus reducing the impact of bird predation because birds usually do not find both original and satellite nest at once. Satellite nests also reduce the impact of *E. polistis* since this parasitoid reinfests its natal nest. However, satellite nesting may increase the infestation by *C. iphitalis* since this parasitoid actively avoids nests that were previously parasitized. Although satellite nest formation does not decrease overall orphanage rates, neither does it increase them since the females from a failed nest can regroup and all join a related satellite nest if their numbers become too low. The inability of larger groups of wasps to avoid predators more effectively may ultimately explain the preponderance of singly founded nests in this species (Strassmann 1981*b*). If there is usually no advantage to a larger group of females on a nest and the concomitant larger nest, then there is no advantage to multiple females founding one nest, though the nest would be less likely to be orphaned.

The predictions generated from Alexander's (1974) model are not wholly upheld in this population. His model predicts that larger groups of wasps are less likely to suffer predation, yet are more likely to suffer parasitism. While larger nests do suffer higher *E. polistis* damage, upholding part of the prediction, they do not consistently experience greater damage from *C.*

iphitalis. Instead of concluding that brood predators have no role in the evolution of sociality in these wasps, I propose that solitary wasps may be victims of additional nest predators that do not attack *Polistes* nests of any size, so no differences between large and small *Polistes* nests are apparent.

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