

**Parasite Pressure and Repeated Burrow Use by
Different Individuals of *Crabro*
(Hymenoptera: Sphecidae; Diptera: Sarcophagidae)¹**

by

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ABSTRACT

Females of *Crabro cribrellifer*, nesting in a large aggregation in northern Michigan, were studied over three summers, 1981-1983. The majority of female wasps occupied and provisioned cells in single nests. Based on observations of individually marked females, a significant minority of the wasps (ca. 25%) provisioned in 2 or several nests. Hostilities between females interacting at nests were never observed.

There is a significant diel correspondence between wasp provisioning activity and nest-entering activities of cleptoparasitic miltogrammine flies, *Metopia campestris*. These parasites exact a heavy toll on the wasp population, with parasitism rates exceeding 25% in all years of this study.

The discussion concerns ways by which parasite-host interactions may influence the nesting behavior of the wasps.

INTRODUCTION

At nesting aggregations of solitary bees or wasps, a low percentage of the observed nests may sometimes be simultaneously or sequentially occupied by 2 or more females (Fabre, 1914; Crèvecoeur, 1931; Evans, 1964; Discussion). Such replacement may generate social interactions among typically solitary individuals. Replacement is especially interesting as it could give rise to both cooperative (communal) and parasitic (usurpation) behavior, with each phenotype maintained at some low frequency in the mostly solitary population. The direction in which such a population might evolve, in the context of Wright's (1969) selective surface, depends on complex interactions among numerous factors (e.g.,

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the intensity of selection pressures from natural enemies; population structure; number of generations per season; seasonal size variation; stochastic events).

Replacement is apparently common in the digger wasp subfamily Crabroninae (Sphecidae) (Evans, 1964; Brockmann & Dawkins, 1979), although in the large genus *Crabro* it is known only for *C. monticola* (Alcock, 1982) and suggested for *C. rufibasis* (Miller & Kurczewski, 1976). Our data describe such behavior in a population of *C. cribrellifer*. In an analysis of these data the biology of cleptoparasitic flies, *Metopia campestris* (Diptera: Sarcophagidae: Miltogramminae), is considered. Reviews of the biology of some species of *Crabro* suggest two generalities with respect to nesting behavior: females usually nest gregariously in aggregations having various degrees of viscosity; and they tend to dig multi-celled nests with rather long winding burrows (Evans et al., 1980; Kurczewski & Acciavatti, 1968; Hamm & Richards, 1926). *C. cribrellifer* follows these patterns.

MATERIALS AND METHODS

This study was made during three summers (mid-June to mid-August), 1981-1983, at the University of Michigan Biological Station, Cheboygan Co., Michigan. Females nested in a 2 x 65 m section of a seldom-used sandy two-track road running through forest consisting mainly of big-tooth aspen (*Populus grandidentata*), red maple (*Acer rubrum*), and red pine (*Pinus resinosa*). Bracken fern (*Pteridium aquilinum*) and blueberry (*Vaccinium angustifolium*) are common in the understory. Approximately 75 m west of the nesting site is a large lake.

Female wasps were individually marked using two-dot color combinations of enamel paints on the thorax. The majority of wasps were marked soon after each had established a nest [some females were captured in emergence traps (30 x 30 cm), marked and then released]. Female size (head to tip of extended abdomen length) was measured in the field when females were marked; in 1983 the length of the forewing was also measured.

Each nest was marked using numbered tags pinned into the soil. Weather permitting (provisioning ceased on rainy or cool heavily overcast days), nesting females were observed 5 days/week in 1981 by WTW and BSL (102 hours of wasp activity), and also 5 days/week in 1982 (WTW, 82 hrs of activity), and 7 days/week in 1983 (WTW and CJK, 51 hrs—few wasps were active). The following data on nesting females were recorded: color mark; nest number; times of entry into and exit from a nest; and whether the wasp entered with or without prey [*Machimus (Asilus) sadyates* (Walker) or *Neoitamus flavofemoratus* (Hine) (Diptera:Asilidae)]. Occasionally a female would momentarily leave her prey just inside the

nest entrance and, in these instances, the prey lengths were measured. When a miltogrammine fly, *Metopia campestris*, was seen entering a nest, the time it remained inside was recorded, as was the nest number. Upon leaving the nest the fly was briefly detained in a small net so that its specific identity could be confirmed. Most of the data are based on observations of 54, 59, and 9 nests in 1981, 1982, and 1983 respectively (these nests were in an area about 2 x 10 m).

The contents of cells in nests were determined by excavating 6, 20, and 7 nests in 1981, 1982, and 1983 respectively. For data on parasite density and parasitism rates see Wcislo (1984).

Unless indicated otherwise, all statistical tests are Mann-Whitney U tests (Conover, 1971). Mean values are given with their standard errors.

RESULTS

Female wasps began emerging in late June or early July. Figure 1 shows the phenology of emergence throughout each of 3 summers. This population is univoltine. Females range in length from 10 to 17 mm ($\bar{x}=14.3\pm 0.07$, $N=259$) and there was no correlation between female size and date of emergence ($r=0.04$, $p>0.1$, $N=59$, using only females trapped upon emergence).

Provisioning females were not larger ($\bar{x}=14.3\pm 0.09$, $N=141$) than females entering nests without prey ($\bar{x}=14.1\pm 0.14$, $N=68$, $0.1>p>0.05$). Larger females did not capture larger prey ($r=0.15$, $p>0.1$, $N=14$). Females with prey typically entered the nest in a swooping dive and remained inside longer ($\bar{x}=32.7\pm 1.84$ min, $N=188$) than did nonprovisioning females which entered nests after slower, more serpentine flights ($\bar{x}=7.7\pm 1.05$ min, $N=99$; those remaining in the nest for less than one minute were excluded) ($p<0.0005$). Incidental benefits may accrue from having the nest occupied at such times because of fortuitous guarding against various enemies (see below).

Figure 2 shows diel wasp provisioning activity and miltogrammine nest-entering activity. These two distributions are not significantly different ($p>0.05$, Smirnov test; Conover, 1971). Miltogrammine flies tend to be most active when wasps are most actively provisioning, which is when nests are most likely to contain unsealed cells with a cache of fresh prey. It is not known whether this temporal correspondence reflects an evolutionary response by the parasites, or is a result of two behaviors independently correlated with some environmental factor.

Hole searching miltogrammine flies were abundant at the site and were commonly seen on or near nest tumuli, or flying in a characteristic pattern over a section of the aggregation (Wcislo, in press; Endo, 1980). Flies entered nests, presumably to larviposit, and remained inside from 2 to 79 seconds ($\bar{x}=12.8\pm 1.46$, $N=96$). Occasionally a fly would enter a nest and

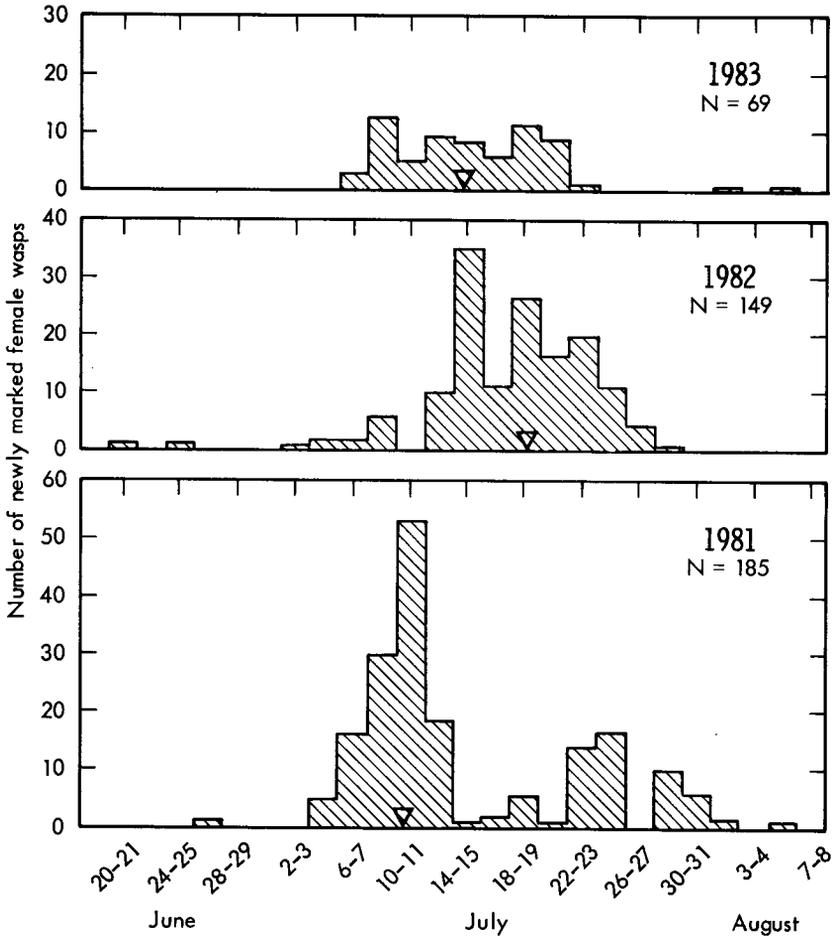


Fig. 1. Histograms of newly marked female wasps, 1981-1983. These distributions are estimates of dates of emergence (see Results). Triangles indicate medians.

Table 1. Summary of contents and structures of nests of *Crabro cribrellifer*. Data from Barrows et al. (1978) were from our Michigan site; **those from Evans et al. (1980) were from Oswego Co., New York.

YEAR	NUMBER OF CELLS				CELL PARASITISM (%)				BURROW LENGTH (cm)			
	\bar{X}	SD	RANGE	NESTS	\bar{X}	SD	RANGE	NESTS	\bar{X}	SD	RANGE	NESTS
1978*	6.5	---	0-19	8	---	---	---	---	---	---	6-44	?
1981	7.8	5.6	1-16	6	38	30.5	0-75	6	20.2	10.6	5-37	5
1982	3.3	0.9	1-5	20	25.1	27.1	0-100	20	21.7	7.5	6-30	14
1983	6.1	3.7	2-10	7	29.4	21.3	25-60	7	24.0	---	16-32	2
1980**	6.3	6.1	0-19	10	42	---	---	---	---	---	8-64	14

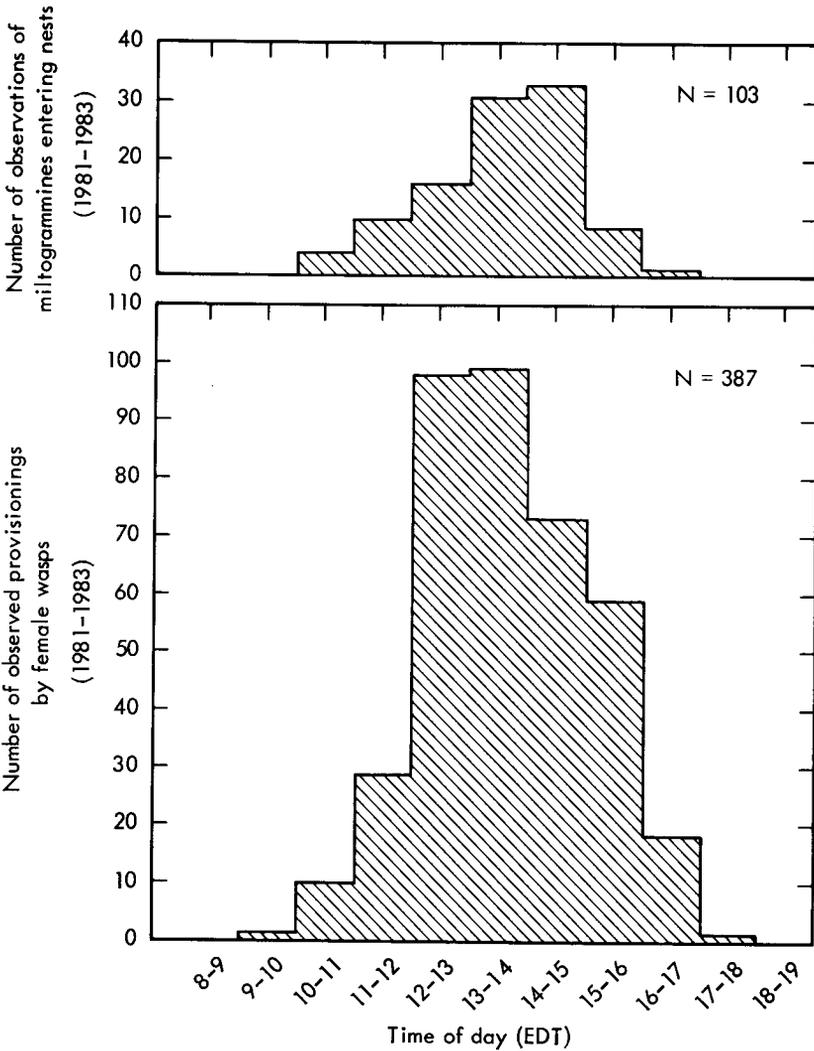


Figure 2. Frequency distributions for the number of observed provisionings by female wasps, and the number of observations of parasitic flies entering nests; both with respect to time of day.

exit almost immediately. Inspection of the nest in 6 such cases revealed that the burrow was blocked by the female wasp, facing outward, 2-3 cm below the surface. It is unknown whether this behavior is for guarding or simply has that effect. The entrances to *C. cribrellifer* nests are surrounded by conspicuous tumuli (2-3 cm in height and 5-11 cm in diameter). When a wasp is away from the nest the entrance is not closed with a soil plug, but is left open.

Table 1 summarizes data on the nest structure and contents of 33 excavated nests, as well as data from two published reports on *C. cribrellifer*. Mean burrow length remained approximately constant for all reports except 1982 of this study when the value was lower. This decrease is probably a consequence of a shortened nesting season for most females in 1982. The median date of emergence for females in 1982 (18 July) was 4 days later relative to 1983 (14 July) and 8 days later relative to 1981 (10 July) (see Fig. 1).

Of the 54 principal observation nests in 1981, 10 nests (18.5%) received provisions by more than one female, although usually on different days (8 nests with 2 wasps; 2 nests with 3 wasps). Similar replacement may have occurred in 7 other nests in this area, but the identity of one of the wasps in each case was uncertain. Two nests were simultaneously provisioned by 2 wasps each, although presumably they were sharing only common burrows. A comparable percentage (25.4%) was obtained in 1982: of the 59 observation nests, 12 were provisioned by 2 females, 2 nests by 3 females, and 1 nest by 4 females (data on 4 other nests were equivocal as above). In 1982 at least 3 nests were provisioned by different females on the same days. Sample sizes from 1983 were too small to obtain such data. Figure 3 presents a sample of nesting data for 10 nests involving 12 marked wasps from 1982. The apparently confusing patterns did not correlate well with the sizes of individuals ($p > 0.1$), and were not more common at a particular time of the nesting season. Females encountered one another infrequently and, based on observations of 11 interactions at nests, no obvious hostilities were evident. It is unlikely that females become "confused" or "forget" where their nests were located (although this does happen), as most females returned repeatedly to their nests. Two females that provisioned in the same nest (in 1982) had emerged as adults into the same emergence trap.

The life span of a nest correlates well with the number of wasps using that nest. Nests provisioned by 3 females were in use longer ($\bar{x} = 19 \pm 0.94$ days, $N = 5$) than nests provisioned by 2 females ($\bar{x} = 10.6 \pm 0.41$, $N = 24$) or by one female ($\bar{x} = 6.5 \pm 0.51$, $N = 26$) ($p < 0.0001$, Medians test). A nest provisioned by 4 females was active for 15 days.

DISCUSSION

With the exception of wasp replacement the provisioning behaviors described here for *C. cribrellifer* do not differ qualitatively from the observations of Evans et al. (1980) and Barrows et al. (1978). The replacement data raise several questions relevant to an understanding of the evolutionary origins of insect sociality and social parasitism (clepto-parasitism). This discussion is focused on these questions.

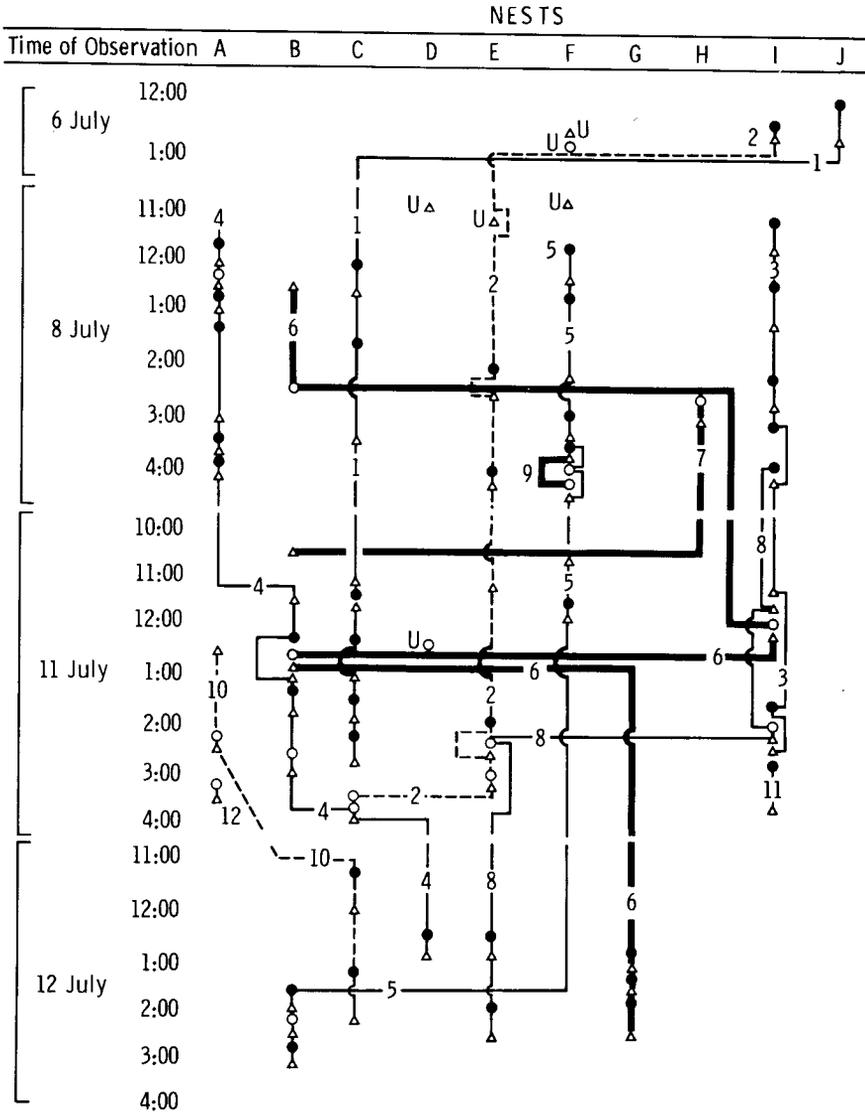


Figure 3. A sample of nesting data for 10 nests involving 12 wasps from 1982. Numbered lines (1-12) represent individually marked females that provisioned in different nests (A-J), during the period July 6-12. Differences in thickness or pattern of the lines are of no significance other than for visual distinction. Closed circles indicate females entering nests with prey. Open circles indicate females entering nests without prey. Triangles indicate females leaving nests. U represents unmarked wasps.

Burrows of *C. cribrellifer* are generally quite lengthy (Table 1) and, acknowledging an investment of time and energy associated with digging a burrow, one predicts a wasp will zealously defend the product of her labors. Yet, based on 11 observations, female-female interactions at nests were pacific and best characterized by disinterest. Alcock (1982) too was unable to account for why females of *C. monticola* did not defend their nests with greater vigor. Other examples of mutual tolerance are readily found among solitary sphecids. (e.g., Evans, 1964, 1973; Miller & Kurczewski, 1973; Alcock, 1975). Furthermore, for *C. cribrellifer*, there were no apparent patterns to replacement which might indicate that the interactions were in fact antagonistic: larger or smaller females were equally likely to replace others. Brockmann, studying *Sphex ichneumoneus* (Sphecidae), also found no significant correlation between female size and patterns of nest use, although these wasps sometimes engaged in violent fights (Brockmann & Dawkins, 1979).

The absence of antagonism among females is interesting given that mutual tolerance is necessary for social evolution. Of 12 marked females whose emergence holes were known, 5 subsequently nested within 1 m of their natal site, the others having died or dispersed. These data suggest this aggregation is at least moderately viscous [see Gadgil et al. (1983) for a model relating population viscosity to the evolution of cooperation]. No estimates are available for the various population parameters (migration rate, mating system, etc.) necessary to evaluate the relevance of various models for the maintenance of such tolerance (Haldane, 1932; Hamilton, 1964, 1971; Wright, 1945, 1969; Wilson, 1980). In this context, however, observations by Genise (1979) are curious. He observed nesting female *Rubrica nasuta* (Sphecidae) fly out of their nests to assault parasitic bombyliid flies hovering over the nest of neighbors.

A daily temporal correspondence between wasp provisioning and fly-entering was shown (Fig. 2), and these flies are highly fecund (Wcislo, in press). Wasp progeny mortality due to parasitism was considerable, exceeding 25% in all years of this study (Table 1). Of 20 nests excavated in 1982, 12 nests (60%) had a mean of 42% of cells parasitized, while 8 nests (40%) had no cells parasitized (Wcislo, 1984). This overdispersion of parasites (*sensu* Price, 1980) throughout the host population is common in parasite-host systems (Price, 1975, 1980), and suggests a possible benefit to females which lay eggs in more than one nest. In other words, a female may benefit by not placing all her eggs in one basket (Alcock, 1975).

At this aggregation there is a potential selective advantage to nesting in areas in high nest density: as density increases the probability of miltogrammine parasitism of cells in individual nests decreases (Wcislo, 1984). It is known for other species, however, that usurpation (intraspecific parasitism) increases in frequency with increasing nest density (Fabre,

1914; Crèvecoeur, 1931, Eickwort, 1975; Myers and Loveless, 1976). In areas of high nest density there are probably at least two countervailing selective forces operating simultaneously.

Given sufficiently intense levels of parasitism, it is possible that sequential nest use might individually benefit all the participating wasps. The nest maker (first occupant) benefits from having the burrow occupied and "guarded" against enemies for a longer period of time. Subsequent occupants are saved whatever energetic expenses are involved in excavating a burrow. This interpretation provides a mechanism for the maintenance of a polymorphism with some individuals being tolerant (and some being parasitic?) but with most remaining solitary. When levels of interspecific parasitism are high, it seems that interactions resulting from replacement will tend toward increasing tolerance and sociality because of benefits associated with nest-guarding (Lin, 1964; Lin & Michener, 1972). Michener (1985) discusses the significance of behavioral polymorphisms for social evolution within species of typically solitary allodapine and ceratinine bees. Alternatively, when parasitism rates are low, there are no obvious mutualistic benefits resulting from replacement, and such interactions may give rise to cleptoparasitic (socially parasitic) forms.

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