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Predator–prey interactions between the digger wasp *Clypeadon laticinctus* and the harvester ant *Pogonomyrmex occidentalis*

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Females of the digger wasp *Clypeadon laticinctus* prey exclusively on workers of the western harvester ant *Pogonomyrmex occidentalis*. There is considerable variability in the size of ant workers both within and between ant mounds, and wasps tend to select larger workers as prey. Worker ants were most likely to be outside the nest at surface temperatures of 25–35°C. Wasps were seen at ant mounds most frequently when surface temperatures were between 40 and 50°C. Wasps captured ants outside and inside ant nests. Predation attempts were equally likely to result in a successful capture in either location, but entering the ant nests was more time consuming. Approximately 63% of visits by wasps to ant mounds resulted in a successful prey capture. In general, ant mounds that were visually conspicuous or close to wasp nest aggregations were more likely to be visited by wasps. However, frequency of visitation and rates of predation at a given mound varied considerably from week to week. Agonistic interactions between female wasps involving chases and occasional fights were likely to occur whenever two wasps were simultaneously present at an ant mound, especially when the only access to prey was by entering the mound.

Introduction

Although a great deal of attention has been directed at the nesting behaviour of digger wasps, relatively little is known about how and where female wasps capture prey. The best-known study is Tinbergen's (1935) classic work on *Philanthus triangulum*. More recently, Steiner (1968, 1971, 1978, 1979) has conducted detailed laboratory studies of sequences of interactions between the wasps *Liris nigra* and *Oxybelus uniglumis* and their prey. All of these studies were primarily concerned with describing the sequence of stimuli the wasps used in recognizing and capturing prey.

Hunting and nest provisioning by a female wasp are direct forms of parental investment which should influence her reproductive success. It seems reasonable to postulate that individuals vary in hunting ability. With an appropriate distribution and density of prey, females might compete directly for hunting sites. Where wasp nests are densely aggregated, there is also an opportunity for some wasps to take advantage of the hunting success of conspecifics, either by usurping provisioned nests or by stealing prey from other nests.

Several authors have noted that wasps in the genus *Clypeadon* are quite specific and restricted in their selection of prey, taking only worker ants of the genus *Pogonomyrmex* (Ainslee 1909, Hicks 1927, Bohart 1959, Evans 1962, 1977). Established colonies of *P. occidentalis* may vary in size from about 400 to 9000 workers (Lavigne 1969). Nests

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are easily recognized by large gravel mounds (height, 2–4 cm; diameter, 4–17 cm), typically with one or two small-diameter entrances open when workers are foraging for seeds or insects. Because *Pogonomyrmex* nests are conspicuous, wasp hunting-sites were easily found. Ant activity patterns were monitored both in the absence and in the presence of wasp predation. Tallies of the number and/or size of ants taken by different wasps could be used to assess individual differences in hunting success. An aspect of *Clypeadon's* hunting behaviour which greatly facilitated the collection of quantitative data is that these wasps are very rapid provisioners, sometimes capturing ants as rapidly as one per minute (Ainslee 1909, Hicks 1927, Evans 1962).

The principal objectives of this study were: (1) to characterize the activity patterns and size variation of the prey, (2) to describe the methods *Clypeadon laticinctus* females used to locate and capture prey, and to relate these methods to the behaviour of the prey, and (3) to determine whether wasps competed directly, via agonistic interactions, over access to prey or nesting sites.

Adult females of *Clypeadon laticinctus* capture worker ants of the species *Pogonomyrmex occidentalis*, and carry the prey on the tip of their abdomen. Evans (1962) showed that the wasp's pygidium and hypopygium are modified to fit tightly against the ant's coxae, and thus function as an 'ant clamp'.

Multicellular nests are dug in sandy soil. Cells are apparently mass provisioned with several ants per cell, and reported numbers of prey per cell vary. Evans (1962) found 15–26 ants per cell in 13 cells from five nests. Hicks (1927) reported eight to 12 ants per cell, but did not indicate how many cells or nests were sampled. Evans found cells at depths from 10 to 21 cm below the surface, with no more than three cells per nest. Both Evans and Hicks observed wasps entering ant mounds to capture prey, as well as taking ants on the surface. A wasp leaves her nest open while hunting and provisioning, and individual provisioning trips rarely take longer than 10 or 15 min. Prey are temporarily stored in the main burrow before being moved to a cell deeper in the soil.

I found the wasps hunting from the first week of July until the first week of September. There was evidence that two adult generations were active at my study site in the summer of 1982 (Alexander 1983).

Methods

Preliminary observations were made at Great Sand Dunes National Monument, Alamosa Co., Colorado during August 1981; and in Fort Collins, Larimer Co., Colorado during late August and early September 1981. More extensive observations were made in Fort Collins between 21 May and 9 September 1982.

The Fort Collins study site was an area of river floodplain adjacent to the Cache la Poudre River. The soil consisted of sand interbedded with layers of water-worn pebbles and coarse gravel. The ground was mostly level, with a few slight depressions. Vegetation at the study site consisted of common weeds such as *Tribulus terrestris*, *Cirsium arvense*, *Ambrosia* sp., *Amaranthus* sp., *Helianthus* sp., *Chenopodium* sp., and several grasses.

At least 36 active nests of *Pogonomyrmex occidentalis* were located and marked within a 100 × 50 m study area. A few small ant nests away from the main aggregation of wasp nests may have escaped notice.

Fifteen *Pogonomyrmex* nests were selected for close monitoring. Nests were classified according to size category and location within the study area, and randomly selected from within each category. A square plot, 0·5 × 0·5 m, was laid out with buntin wire on each of the selected mounds. Ant activity was monitored by taking hourly counts of the number of ants present within the wire plot. When the ants were actively moving about on the surface, the number of ants within the square at a given instant could vary considerably. Consequently, during each census three separate counts were made at each mound, with a 15-s interval between each count. If more than 50 ants were present within the square, no attempt was made to obtain an accurate count, although a rough estimate of the number of ants was recorded. When exact counts were possible, all three counts were recorded and the median value was used for analyses. When *C. laticinctus* began hunting, counts of wasps seen at each mound were also included.

For scheduling purposes, the day was divided into three 5 h periods. Each week two observation sessions were done for each of these periods of the day, with the sequence of periods determined from a random number table. No hourly censuses were taken on the seventh day. This schedule was followed from 7 June until 7 September. Between 16 July and 12 August, hourly censuses were also taken every day between 10.00–13.00 hours and 15.00–18.00 hours. The main purpose of these counts was to gather data on wasp activity patterns, since this was a period of intensive activity by the wasps and, at least initially, minimal ant activity.

Ground surface temperature was recorded at the start, middle, and end of each hourly census, and the mean of these three readings was used in analyses. Measurements were taken by placing the thermometer on the ground and covering the bulb with a thin layer of soil.

Head width was used as a standard measure of size for both ant and wasp. Measurements were made with a Mitutoyo micrometer caliper calibrated to 0·05 mm.

On 24 and 25 May 1982, samples of approximately 50 ants were obtained from the surfaces of four randomly selected mounds. All ants were collected between 13.00 and 14.00 hours. On 27 July, a second sample of 50 ants was collected from three of the four mounds used in the May sample (the fourth mound was inactive). On four days during July and August, a series of 38 ant workers captured by wasps was collected by netting wasps as they returned to their nests. On 4 September, two wasp nests were excavated and a total of 25 ants were recovered.

A total of 140 female wasps were captured and marked for individual recognition with dots of coloured enamel paint on the thorax.

Data on predation and agonistic interactions were collected by making observations at ant mounds. Seven ant mounds were selected as observation sites, by a procedure similar to that used in selecting mounds for monitoring ant activity patterns. Each mound was observed once a day for 30 min. During the course of a week, each nest was watched once at each of the 7 h during which observations were recorded every day. Data were collected from 13 July to 7 August. Observations were tape recorded and later transcribed on to standard data forms.

Results

Size variation in Pogonomyrmex occidentalis *workers*

There was considerable variation in the head width of worker ants in the *Pogonomyrmex* nests in May (fig. 1). For both sample periods, the distribution of head widths differed significantly for ants from different mounds (Kruskal–Wallis one-way analysis of variance (ANOVA). May: $H = 39{\cdot}1$, d.f. $= 3$, $P < 0{\cdot}0001$; July: $H = 17{\cdot}27$, d.f. $= 2$, $P < 0{\cdot}005$).

For any given mound, the frequency distributions were different for the May and July samples. In every case, the head width of ants collected in July was significantly

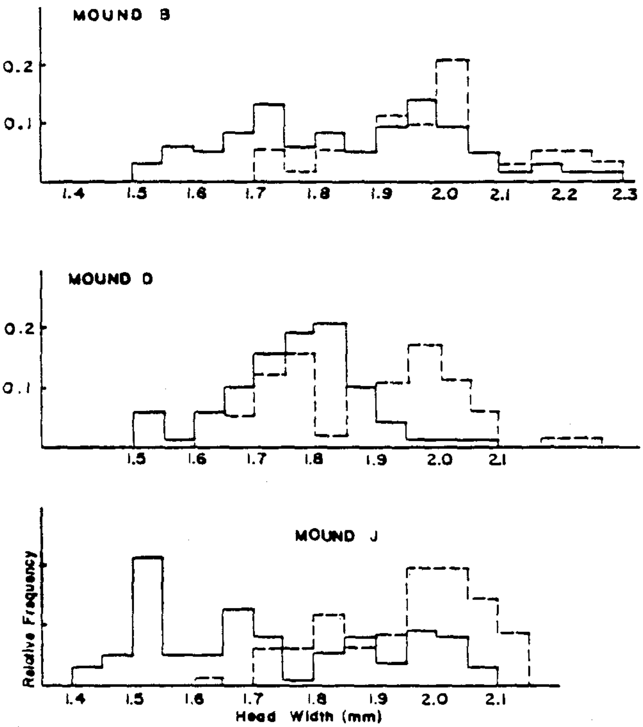

FIG. 1. Head widths of *Pogonomyrmex occidentalis* workers collected from three mounds on 24 and 25 May and 27 July 1982. ---, May; —— July.

smaller than for ants collected in May (Mann–Whitney U-test: mound B, $Z = 9{\cdot}1$, mound D, $Z = 9{\cdot}87$; mound J, $Z = 9{\cdot}56$; $P < 0{\cdot}001$ in each test).

Harvester ant activity patterns

For any hour of the day between roughly 09.00 and 19.00 hours, levels of activity were much higher in June than in July or August (fig. 2). Both the overall level and the general pattern of activity were similar for July and August.

Throughout the summer, the ants did not emerge until several hours after sunrise, and they re-entered the mound before dark (fig. 2). I found no evidence that workers were active outside their nests at night during this study. The twice-weekly censuses at 21.00 hours inevitably showed little or no activity, and on 26 July I checked the mounds at midnight and found no ants on the surface.

To investigate the relationship between temperature and the presence of ants on the surface, I calculated the mean number of ants counted at mounds over temperature intervals of 5°C (fig. 3). Ants were unlikely to be outside the mound when surface temperatures were less than 20°C or greater than 55°C, which agrees with other studies (Lavigne 1969, Rogers 1974). The greatest number of ants were out when surface temperatures were between 25 and 35°C. However, there was much variation in the number of ants active on the surface at a given temperature. In July, the variance was so great that there was no statistically significant temperature effect (Kruskal–Wallis one-way ANOVA, $H = 14{\cdot}5$, $0{\cdot}20 > P > 0{\cdot}10$). The differences in numbers of ants counted in

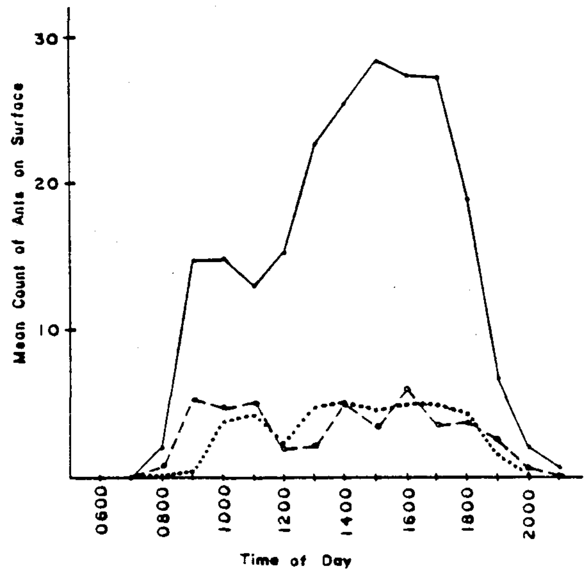

FIG. 2. Mean number of harvester ants counted at ant mounds at different times of day during the summer of 1982. Means are based on counts at 15 ant mounds. ——, 7–30 June; – – –, 2–31 July; ····, 1 August–7 September.

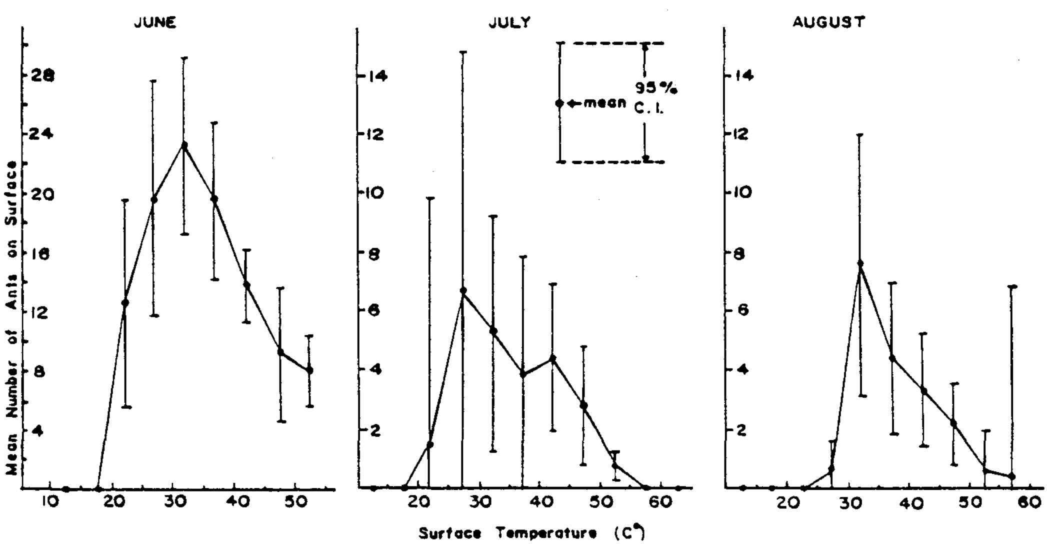

FIG. 3. Relationship between surface temperature and the mean number of harvester ants counted on the surface during hourly censuses at ant mounds.

different temperature intervals during June and August were statistically significant (Kruskal–Wallis one-way ANOVA: June, $H=67{\cdot}02$, $P<0{\cdot}001$; August, $H=23{\cdot}03$, $P<0{\cdot}001$).

The activity measure used in fig. 2 is useful for an initial inspection of general activity patterns, but it does not indicate the range of variation among different mounds. A clearer picture is obtained by showing the percentage of mounds that were active at a given time of day (fig. 4). Measured this way, activity levels through most of

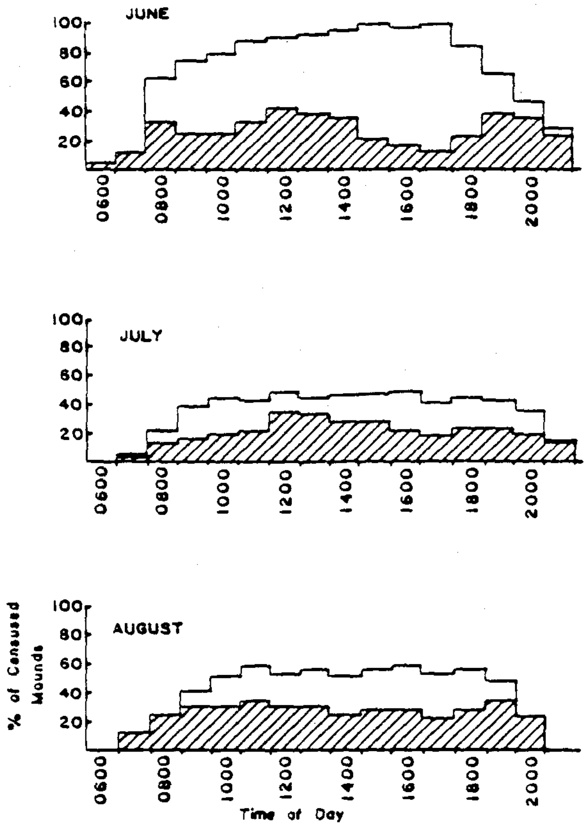

FIG. 4. Mean percentage of active harvester ant mounds at different times of day. □, > 10 ants; ▨, 1–10 ants.

the day were roughly twice as high in June as in July and August. From mid-morning until late afternoon in June, almost all of the ant mounds were usually active. Most had more than 10 ants within the counting grid, especially in mid-afternoon. During July and August, only half the mounds surveyed were active even during times of peak activity. At least half of these mounds had fewer than 10 ants on the surface, often only two or three.

Individual mounds exhibited considerable day-to-day variability in activity. The most complete information on this short-term variation comes from the daily censuses taken between 16 July and 12 August. Between 16 and 26 July, activity was minimal at all mounds, with no apparent pattern to pulses of activity. After 26 July, a dramatic change occurred. All mounds showed a marked increase in activity, at least for a few days. This was correlated with a change in weather: it rained intermittently throughout the period 27 to 29 July. The average daily maximum surface temperature for 23–26 July was 61°C (range 59–64·5°C). The average maximum between 27 and 31 July (no data for 29 July) was 37°C (range 33–44°C). I repeatedly observed throughout the summer that the number of ants active on the surface of mounds increased dramatically following a period of rain.

Wasp activity patterns

Figure 5 shows late morning and afternoon peaks in hunting activity, with a lull at mid-day, suggesting that there might have been a certain temperature range over which

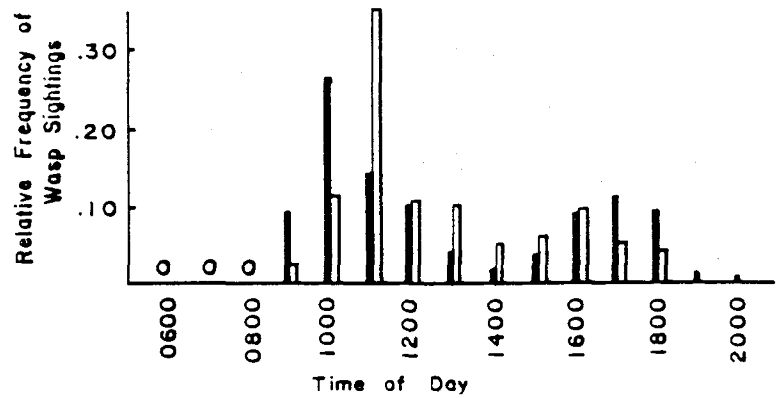

FIG. 5. Relative frequencies of sightings of *Clypeadon laticinctus* at different times of day. Data are based on hourly censuses at ant mounds during July and August. ■, July; □, August.

the wasps were most likely to be hunting. During both July and August, wasps were most frequently sighted at ant mounds when the surface temperature was between 40 and 50°C (fig. 6). The differences in numbers of wasps sighted in the different temperature intervals are statistically significant (Kruskal–Wallis one-way ANOVA: July, $H = 51{\cdot}064$, $P < 0{\cdot}001$; August, $H = 32{\cdot}74$, $P < 0{\cdot}001$).

Selection of hunting sites

Frequency of wasp visits to ant mounds: hourly census data. The hourly census data suggest that female *C. laticinctus* were more likely to visit some ant mounds than others (table 1). A χ^2 goodness-of-fit test for the data summed over both months indicates that sightings were not evenly distributed across all mounds ($\chi^2 = 77{\cdot}20$, d.f. = 14, $P < 0{\cdot}005$). Mounds B, C and CC were among the five most frequently visited mounds during both months, and FF and Q were consistently among the four least frequently visited mounds.

If these observations reflect general patterns of preference by the wasps, what do they suggest about the types of ant mounds that were being chosen? Size and conspicuousness of the mound may have been important. Mounds B, C and CC were

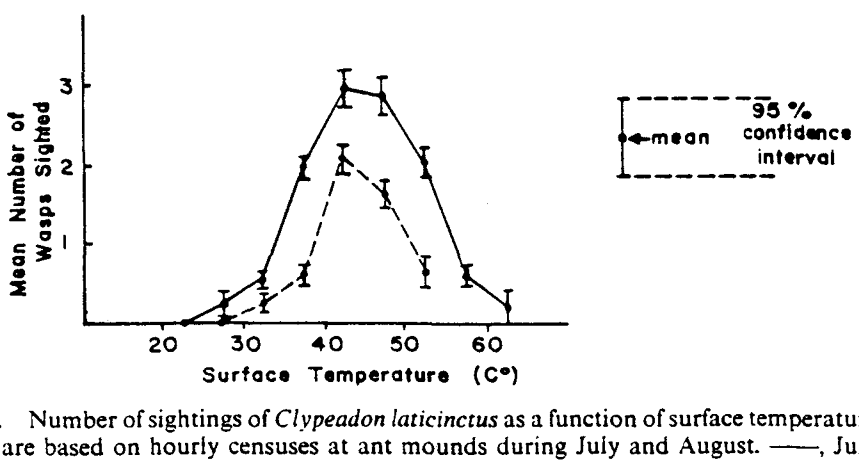

FIG. 6. Number of sightings of *Clypeadon laticinctus* as a function of surface temperature. Data are based on hourly censuses at ant mounds during July and August. ——, July; – – –, August.

Table 1. Numbers of *Clypeadon laticinctus* females sighted at different ant mounds during hourly censuses between 3 July and 2 September 1982

Mound	Total no. of wasps	July subtotal	August subtotal
Q	5	0	5
FF	5	2	3
W	16	13	3
P	16	9	7
O	17	10	7
X	23	18	5
Y	23	16	7
BB	24	17	7
N	25	15	10
F	25	13	12
GG	33	25	8
K	33	25	8
CC	38	28	10
C	39	29	10*
B	44	27	17
Total	366	247	119

all large and surrounded by an extensive denuded zone. Mounds FF and Q were small and inconspicuous (to a human observer). However, size of the mound cannot account for all the apparent preferences shown by the wasps. Mound W was one of the least frequently visited mounds throughout the study period, yet it was also one of the largest. It was surrounded by a thick screen of weeds which made it difficult to see from a distance, yet so was the very 'popular' Mound CC. There was no apparent difference in the level of ant activity at the two mounds.

Frequency of visitation: data from 30-min observations. Information on the relative frequency of visits to different ant mounds is also available from the 30-min observations at individual mounds (table 2). A Friedman two-way ANOVA showed that the mounds were not all visited with equal frequency ($\chi^2 = 14{\cdot}375$, d.f. $= 6$, $P < 0{\cdot}05$). Some mounds were consistently visited or avoided, but others changed dramatically in frequency of wasp sightings from one week to the next. These data make it difficult to define any particular attributes of ant mounds which make them more likely to be visited by wasps. The most visited mound (H) and the two least visited mounds (C and W) were all large and conspicuous. Mound H was very close to the main wasp nesting

Table 2. Numbers of visits by *Clypeadon laticinctus* to harvester ant mounds during 30-min observation periods

	Mound							
	B	C	GG	H	N	P	W	Total
Week I	22	14	27	51	33	0	15	162
Week II	5	3	13	18	3	19	0	61
Week III	19	1	2	10	6	6	1	45
Total	46	18	42	79	42	25	16	268

Ranking: H > B > (GG = N) > P > C > W.

area, whereas W and C were both far from any aggregation of wasp nests. This suggests that proximity to wasp nests was an important factor. However, the hourly census data indicated that Mound C was frequently visited by wasps. For the other five mounds included in both types of data collection, there was general agreement in the estimated frequencies of mound visitation by wasps. The contradictions in the data for Mound C make it impossible to determine how frequently this mound was visited.

Frequency of predation at different mounds. The presence of a wasp at an ant mound does not necessarily mean that she is capturing prey there. Estimated frequencies of predation were obtained from the 30-min watches at ant mounds (table 3). Although there were significant differences in the total number of predations observed at different mounds (χ^2 goodness-of-fit test, $\chi^2 = 29{\cdot}498$, d.f. $= 6$, $P < 0{\cdot}01$), a Friedman two-way ANOVA indicated no consistent difference among mounds when the week-to-week variation at each mound was taken into account ($\chi^2 = 5{\cdot}086$, d.f. $= 6$, $P > 0{\cdot}05$). There was no clear relationship between size of the mound, or its proximity to wasp nests, and the number of predations recorded at the mound.

Mound visitation and parasitic flies. Miltogrammine flies *Senotainia trilineata*, which are cleptoparasites of ground-nesting wasps, were sometimes seen perched on or near large ant mounds. They would frequently approach wasps at the mound; or if a wasp disappeared into the mound entrance, a fly might approach the hole and wait there. Flies approached wasps regardless of whether they had prey. During the 30-min watches at ant mounds, there were 100 observations of miltogrammine flies approaching *Clypeadon* females. On 40 occasions, a wasp left a mound within 5 s after a fly had approached it. The wasp did not have prey on 29 (73%) of these occasions.

A wasp was much more likely to encounter miltogrammine flies at large ant mounds surrounded by a denuded area. Only three of the 100 encounters recorded between wasps and flies occurred at a *Pogonomyrmex* nest which lacked a conspicuous mound and was overgrown with vegetation. Consequently, a wasp visiting large, conspicuous mounds might encounter a risk factor that would not be present at less conspicuous mounds.

Agonistic interactions among wasps

Another factor that caused wasps to leave ant mounds was the presence of other wasps. Agonistic interactions such as chasing or grappling were fairly common. There were approximately 70 separate occasions when at least two wasps were simultaneously present at an ant mound. Agonistic interactions were recorded on 47 of these occasions. There were eight occasions when more than two wasps were simultaneously present, and agonistic interactions were recorded on seven of these. These observations

Table 3. Number of predations by *Clypeadon laticinctus* observed at different harvester ant mounds. Data from 30-min observations at ant mounds

	Mound							
	B	C	GG	H	N	P	W	Total
Week I	11	7	8	3	11	0	0	40
Week II	2	1	5	0	0	16	0	24
Week III	9	0	0	4	3	4	0	20
Total	22	8	13	7	14	20	0	84

Ranking: B > P > N > GG > C > H > W.

suggest that agonistic interactions were likely to occur whenever females encountered one another at an ant mound, especially if more than two were simultaneously present.

Agonistic interactions were also observed at Great Sand Dunes National Monument during August, 1981. In seven different observation periods during which wasps were seen hunting at ant mounds, agonistic interactions were recorded on three occasions. These interactions involved wasps vying for access to the entrances of ant mounds.

If both wasps were on the surface of an ant mound when they met, they would usually turn to face one another. This action alone might lead one wasp to fly away a short distance, or even leave the mound. More frequently, one wasp would run toward the other, who would then fly away. Many interactions consisted of no more than a single brief chase of this kind.

Agonistic interactions were most likely to occur when the only way wasps could obtain ants was by entering their mounds. Approximately 50 instances of chases or fights involving physical contact were recorded during the study. Ants were present outside the mound during only five of these. The other 45 agonistic interactions were more or less centred around the entrances to ant mounds. Often one wasp would try to enter a mound while another was inside. This would inevitably result in a chase, with the occupant usually driving the intruder away. Sometimes an intruder would persist in trying to enter the mound, but usually she would simply wait for the other wasp to leave. There were four occasions when three to five wasps were simultaneously trying to get into an ant mound, and the wasps outside began chasing one another. Within 2 to 10 min the chases were over and only one wasp remained.

Actual fights, with physical grappling and biting, were less common than chases. I never saw any direct evidence that a wasp was injured as a consequence of fighting. A total of nine fights were recorded during the study, seven of them at the entrance to an ant mound.

Capturing of prey

Workers of *P. occidentalis* would seem to be formidable prey. These ants have powerful jaws and a well-developed sting capable of injecting a venom whose effect on vertebrates is quite potent. It is not known whether the venom has a comparable effect on *C. laticinctus*. I never saw a wasp obviously injured by an ant during this study, but I did see ants successfully resist predation attempts.

Of 84 predations observed during scheduled morning watches at ant mounds, 31 occurred on the surface or at the entrance to the mound, and 53 occurred inside. A Wilcoxon test indicated that there was no statistically significant difference in the distribution of predations between the two locations ($T = 4$, $N = 6$, N.S.). Mounds were observed with unequal frequency in the afternoon, due to thunderstorms, or after 7 August, when the major focus of observations was shifted to wasp nests. If observations made in the afternoon and after 7 August are included, the total number of predations recorded is 175, with 96 inside ant mounds and 79 outside.

Predation inside ant mounds. Hunting wasps would usually enter a mound only if there were no ants on the surface. There were only four instances when wasps attempted to dig into an ant mound while there were ants on the surface in the vicinity of the mound. In two cases, the ants were using an entrance which was hidden at the base of weeds on the edge of the denuded area, away from the main mound where the wasps were hunting. In the other two cases, there had not been any ants on the surface during previous visits, and the wasps had been going directly to the mound entrance without any pause to survey the surface of the mound.

There were 177 occasions when wasps visiting a mound went inside or dug at an entrance to the mound. In 96 cases (54%), the wasp definitely emerged with an ant, or stung an ant as it came to the entrance. In 66 cases (37%) the wasp definitely did not capture prey. The outcome of the remaining 15 visits (9%) could not be determined with certainty.

A wasp sometimes remained inside a mound for a long time. One emerged with an ant after being inside for 6 min 9 s. Another stayed inside for 9 min 17 s before emerging without an ant. However, such lengthy forays were exceptional. The mean duration of 107 visits was 116·5 s (S.E. = 149·55 s). This is a measure of the total amount of time the wasp spent at the mound, and not the amount of time she spent inside the mound. The latter measure would be very tedious to calculate, since a wasp usually did not just walk into a mound and come out with an ant. Often she spent much time digging at the entrance; or she repeatedly stepped inside, poked her head out at the entrance a few seconds later, went back inside for a few seconds, and reappeared at the entrance. This continued until she captured an ant, flew away without prey, or was driven away by another wasp.

There were 23 visits when a wasp dug at the entrance to a mound without ever going inside. Every one of these resulted in a successful predation. Presumably this was because the wasp stopped digging when ants inside the mound came to the entrance, and she was able to capture one. If no ants appeared, she continued digging until she disappeared from view inside the mound. There were 38 occasions when ants came to the entrance from inside the mound, either in apparent response to a wasp's digging, or after the wasp had gone inside the mound. In every case the wasp captured and paralyzed an ant at the mound entrance.

Predation outside ant mounds. There were 125 times when wasps visiting a mound approached *Pogonomyrmex* workers on the surface, and were therefore assumed to be hunting. On 79 of these visits (63%), the wasp departed with an ant; in the remainder, she left without prey. There were nine occasions when an ant was stung and paralyzed, but then abandoned by the wasp. On five of these occasions the wasp then captured another ant and departed with it. The average duration of visits in which ants were captured outside was 67 s (S.E. = 53 s). Table 4 presents a summary comparison of predations inside and outside ant mounds.

Observations of wasps hunting on the surface of a mound suggested that they were selective in their prey choice. The criteria used to choose prey were not obvious, but a wasp did not always try to seize the first ant she approached. The wasps almost always ran up to an ant and grabbed it, rather than waiting in ambush for prey to wander by. A

Table 4. Outcomes of predation attempts by *Clypeadon laticinctus* inside and outside mounds (nests) of *Pogonomyrmex occidentalis*. Data from 30-min observations at ant mounds

	Location of predation attempt	
Outcome	Inside mound	Outside mound
Success	96 (54%)	79 (63%)
Unknown	15 (9%)	0
Failure	66 (37%)	46 (37%)
Total	177	125

wasp might approach more than one ant, or the same ant more than one time, before trying to seize and sting her prey. During the visits which ended in successful predations, the mean number of times the wasp approached an ant, regardless of whether it was the ant she captured, was 2·8 (S.E. = 2·4, range: 0–11). For visits which ended without a successful predation, the mean number of approaches was 2·9 (S.E. = 2·4, range: 0–11). For visits which ended without a successful predation, the mean number of approaches was 2·9 (S.E. = 2·9, range: 1–14). There was no apparent relationship between the number of times prey were approached and the probability of a successful predation.

Ant responses to wasp predation attempts. It seems likely that an ant's response to a wasp's predation attempt would affect the wasp's chance of success. Somewhat surprisingly, most ants made no obvious response to a wasp's approach. Wasps were recorded approaching ants 256 times. Ant responses are summarized in table 5. These observations suggest that any attempts to either resist or evade a wasp's predation attempts would increase an ant's probability of escaping (χ^2 contingency test, $\chi^2 = 8{\cdot}465$, d.f. = 3, $P < 0{\cdot}05$). If the easily observed responses really do substantially reduce an ant's risk of falling prey to a wasp, it is surprising that such responses were not seen more often. One possible explanation is that the wasps depend on swift attacks which catch ants by surprise before they are able to respond. Often a wasp would walk at some distance from an ant before quickly rushing up to grab it, but on other occasions the wasp simply ran up to the ant without any preliminary 'stalking'.

Although an ant outside the mound seemed to benefit from any kind of active response to a wasp attack, ants which rushed to the entrance of a mound from inside were at serious risk. Wasps never failed to capture ants under these circumstances, although the reasons for such high success were not obvious.

Prey selection

Two different samples of ants that had been captured by wasps were obtained. One sample consisted of 38 ants taken from wasps returning to their nests. The mean head width of ants in this sample was 1·86 mm (S.E. = 0·169 mm, range: 1·50–2·15 mm). The other sample was 25 ants found in two wasp nests excavated on 4 September 1982. The mean head width of ants in this sample was 1·88 mm (S.E. = 0·122 mm, range: 1·70–2·15 mm). The difference in mean head width from these two samples is not statistically significant (t-test, $t = 0{\cdot}333$, $P = 0{\cdot}74$), so both samples were lumped for analyses.

If all the ants collected alive from the surface of Mounds B, D, and J on 27 July are lumped together, the mean head width is 1·75 mm (S.E. = 0·18 mm, range: 1·40–2·25 mm). This is significantly smaller than the mean head width of ants which were taken as prey (Mann–Whitney U-test, $Z = 4{\cdot}58$, $P < 0{\cdot}00001$, see fig. 7). Thus it

Table 5. Consequences of different responses shown by harvester ant workers to predation attempts by *Clypeadon laticinctus*

Ant's response to wasp	Ant captured	Ant not captured
No apparent response	66 (33%)	135 (67%)
Turn and face wasp	6 (19%)	26 (81%)
Run or lunge at wasp	2 (17%)	10 (83%)
Run away from wasp	0 (0%)	11 (100%)

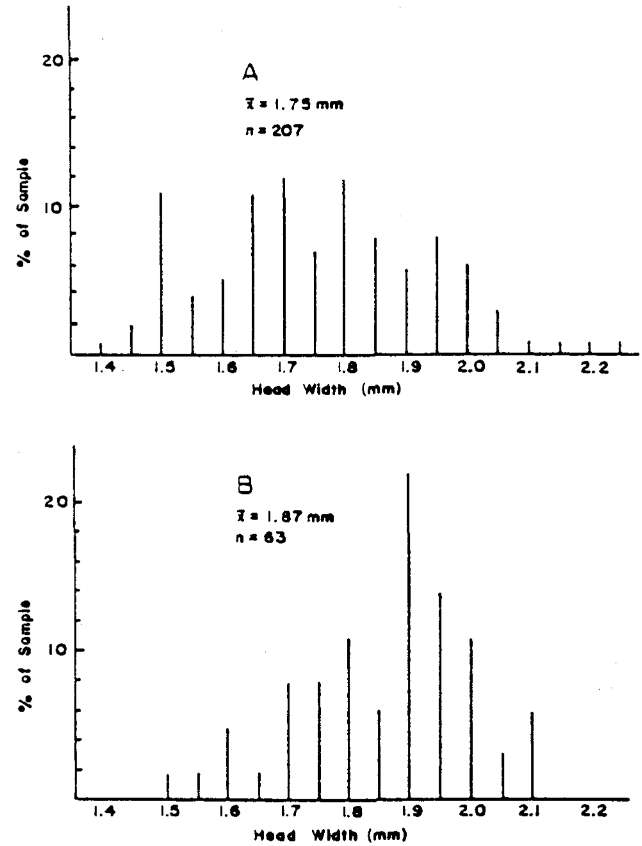

FIG. 7. A, Head width of harvester ant workers collected at three ant mounds on 27 July 1982; B, head width of harvester ant workers captured by *Clypeadon laticinctus*.

would appear that wasps were taking larger-than-average ants, although the method of collecting ants on 27 July was not directly analogous to hunting done by wasps, and therefore may not accurately reflect the size distribution of ants encountered by hunting wasps. I could not distinguish whether the wasps were deliberately selecting large ants or were just more likely to encounter them.

A wasp would sometimes sting an ant and then discard it. One of these ants immediately walked away, after the wasp had spent 2 min repeatedly stinging it and walking around with it attached to her abdomen. The other eight ants I saw being discarded appeared to have been immobilized. It was not unusual to find immobilized ants at mounds during hourly censuses after the second week of July, although such sightings were extremely rare earlier in the summer.

It was not clear why these ants had been discarded. I collected a sample of 44 ants which I found immobilized on the surface of nine different mounds between 18 and 22 August. Although the ants in this sample all had relaxed and flexible appendages, suggesting that they were either paralyzed or had recently died, there was no direct proof that they had fallen prey to *C. laticinctus*. The mean head width of these immobilized ants was 1·71 mm (S.E. = 0·17 mm, range: 1·45–2·05 mm), which is significantly smaller than the mean head width of ants taken as prey (t-test, $t = 5{\cdot}09$, $P < 0{\cdot}000001$). This suggests that wasps may discard ants on the basis of their size.

No *C. laticinctus* ever used any species other than *P. occidentalis* as prey. Other ants, especially a species of *Formica* which was very abundant in the study area, were frequently approached but never grabbed or stung. Although wasps took *P. occidentalis* workers when both workers and alates were milling about the nest entrance during nuptial swarms, they never tried to capture winged reproductives.

Discussion

Nature of the prey resource

Harvester ant mounds are visually conspicuous and reliable sources of prey, and in this respect they are a patchy but predictable resource. Although the probability of a successful predation does not seem to depend on whether the ants are captured inside or outside the mound, the effort required to obtain prey is less predictable and probably does depend on where the prey is taken. It is more time-consuming for a wasp to make entries into a mound than to capture ants outside, and it seems likely that digging into a mound requires more energy.

It was not possible to predict when ants would come out on the surface of a given mound. There was a rough correlation between surface temperature and the number of ants on the surface of a mound, but my observations indicate that at a given favourable surface temperature not all colonies will have ants on the surface. Whitford and his colleagues (Whitford and Ettershank 1975, Whitford *et al.* 1976) made similar observations on three species of *Pogonomyrmex* in New Mexico and Arizona. Temperature unquestionably influences ant activity, but it is only one of several factors which determine when ants will be present on the surface.

Environmental conditions associated with rainfall reliably triggered high levels of ant activity outside the nest. The exact nature of the triggering stimuli is unclear, but Whitford and Ettershank (1975) have demonstrated that artificial wetting of the soil stimulated intense activity in *P. rugosus* and *P. desertorum* while control colonies were inactive. However, rainfall was associated with a decrease in hunting activity by *C. laticinctus*. It may have been a reliable cue indicating that ants could be found on the surface, but it was not a useful cue for the wasps.

In summary, it may be more efficient for a wasp to hunt at mounds where ants are out on the surface, but there are no obvious ways for a wasp to know where such mounds are without visiting them. The cost in time and energy spent searching for an active mound would have to be balanced against the cost of digging into a mound with no ants on the surface. These considerations may account for the observation that wasps showed no clear tendency to visit active mounds more frequently than inactive mounds, and that predations were equally frequent inside and outside mounds.

Methods of utilizing the prey resource

The worker ants used as prey by *C. laticinctus* were quite variable in size, both within and between mounds. Ants taken as prey were significantly larger than the mean size of workers present on the surface. This could be either because wasps encountered larger ants more frequently, or because they selected larger ants as prey. There is some indirect evidence, based on the size distribution of ants apparently discarded by hunting wasps, that wasps chose larger-than-average ants as prey. Inferences about selectivity in choice of prey were based on comparisons of prey captured by wasps with samples of the prey species collected in the field by the researcher. A difficulty in interpreting such data is knowing whether the field samples collected by the researcher really reflect the prey that are 'available' to the predator, since the latter may perceive the environment differently from a human investigator. However, when a wasp is observed to discard captured prey, this indicates some kind of selectivity, although it says nothing about the mechanism by which the selection is made.

Possible sources of variability in reproductive success

Direct measurements of reproductive success were not obtained in this study, so it is only possible to infer probable differences in reproductive success. Such inferences are based primarily on differences in time spent provisioning by different females, and on observations of factors which interfered with hunting and provisioning.

Rates of capture, provisioning and hunting behaviour indicate that the wasps capture ants efficiently. Factors other than differences in the ability to capture ants may have had a more important impact on female reproductive success, and direct intraspecific competition was observed in two major contexts:

(1) Access to hunting sites. Agonistic interactions were commonly seen when two or more wasps were present at an ant mound. Such competition was especially common when access to prey was restricted, i.e. when wasps had to enter the mounds to find prey. Since the agonistic interactions usually involved unmarked females, it was not possible to tell whether certain individuals consistently won such encounters and drove other wasps away from hunting sites. Defence of a resource is most likely to occur when that resource can be economically defended and when there is competition for access to the resource (Brown 1975). It seems plausible that as hunting efforts are narrowed to a smaller area, the number of predators converging on the area and the feasibility of defending the contested area may both increase.

(2) Competition for nesting sites. Some wasps lost their nests to other individuals and did not provision a nest afterwards (Alexander 1983, in press). Several nests changed occupants at least once. Being unable to provision a nest obviously results in a loss of reproductive output, unless the wasp can lay her aggs in the nests of other wasps without having them destroyed. Being forced to spend time searching for a new nest takes away from time which could be spent provisioning.

Competition in these contexts should have a direct effect on a female's ability to provision a nest and produce offspring. The magnitude of this effect is difficult to measure, but the high frequency of agonistic interactions whenever two or more wasps were present at a mound, and the high rate of turnover in nest occupancy, suggest that intraspecific competition may have a substantial influence on female reproductive success in this population of *Clypeadon laticinctus*.

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