

## The behaviour of *Philanthus crabroniformis* (Hymenoptera: Sphecidae)

JOHN ALCOCK

Department of Zoology, Arizona State University, Tempe, Az 85281, U.S.A.

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(With 3 plates and 2 figures in the text)

Observations were made over a two year period on the nesting and hunting behaviour of a population of *Philanthus crabroniformis* Smith. Data are presented on the time and speed of provisioning, the capture of prey and the species taken, the design and location of nests, the approach to the nest with prey, and aggressive interactions between females. *P. gibbosus* Fabr., also nested in the same area and took much the same prey. Unlike other sympatric pairs of *Philanthus* which have been studied, the two species in question were not totally segregated by separate nesting seasons nor by mutually exclusive habitat preferences. One aspect of the behaviour of the two *Philanthus* which was highly distinctive was the manner in which prey-laden females approached their nests. Selection for divergence in approach patterns may have been exerted by miltogrammine flies, a major parasite of many digger wasps.

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### Introduction

The behaviour of wasps of the genus *Philanthus* has been the subject of a number of papers. Tinbergen and his associates have examined landmark learning at the nest site and prey capture by *P. triangulum* Fabr. (Tinbergen, 1932, 1935; Tinbergen & Kruyt, 1938; Tinbergen & van der Linde, 1938). In addition, the ethology of 14 North American members of the genus has been described by Evans (1964, 1966*a*, 1970; Evans & Lin,

1959) supplementing pioneer investigations of *P. gibbosus* Fabr. by the Peckhams (1905), the Raus (1918) and Reinhard (1924, 1929). This paper presents behavioural information on the little studied *P. crabroniformis* Smith (although see Evans, 1970) and will discuss the possible ecological significance of its behaviour with respect to competition and parasites.

### Methods

I observed a nesting aggregation of digger wasps in a vacant lot in Seattle, Washington almost every sunny day from 20 July to 20 August 1971, and from 17 June to 5 August 1972, usually in the period from 09.00 to 14.00 hrs. Eleven species of wasps nested in a small grassy field bordering an extensive blackberry patch that had invaded most of the area. The vast majority of nests, including 40–50 *P. crabroniformis* and 15–20 *P. gibbosus* burrows, were located in and along a hard packed sand and gravel path that ran through the centre of the field.

### Behaviour

#### *Reproductive behaviour*

At 10.35 on 2 August 1971, a female and male were seen united end-to-end in flight over the path for a few seconds. It seems likely that the two were disturbed by my approach for they quickly separated. At 14.15 on 1 July 1972, a rather small male flew behind a female carrying a prey to her nest. When she alighted in a bare spot in the middle of the path before going on to the nest entrance the male dropped down onto her back while facing in the same direction as the female. His abdomen curved downward and genital coupling occurred quickly. The female promptly took flight with the male trailing behind *in copulo* facing the opposite direction. As they passed a weed head at the edge of the path about 50 cm from the point of initial contact the male caught hold. The female tried to continue flying but, after perhaps 5 seconds, dropped her prey and alighted (Plate I). The two remained *in copulo* on the weed head for 10 minutes before separating.

On several occasions, most notably 28 and 30 June 1972, a male was seen "patrolling" a small area (about 50 cm<sup>2</sup>) for a period of about 30 minutes in what may have been territorial behaviour. The insect flew slowly about close to the ground alighting frequently on prominent pebbles or weed stems. It remained still on pebbles but walked rapidly up and down the weeds sometimes pausing in a head-down position. Passing insects, including males and females of *P. crabroniformis*, were pursued and twice a male was seen to land on a female in the manner just described (however, copulation did not occur in these cases).

#### *The pattern of daily activity*

Females emerged from their burrows over a period of several hours in the morning. For example, on 25 July 1971 eight wasps under close observation (their burrows had been marked with toothpicks) appeared at 08.30, 08.54, 09.21, 09.45, 09.48, 09.50, and 10.20. Having removed the closure, females then began to dig, kicking sand backwards and dragging small pebbles from the nest, for 15–30 minutes. Afterwards, females regularly flew a short distance from the burrow and alighted for a brief period of grooming before flying off. Some females were seen on flowers (*Cirsium arvense*, *Solidago canadensis*) early in the morning but others were known to begin provisioning the nest at once. Provisioning occurred between 09.00 and 18.30 with peak activity occurring in the early afternoon

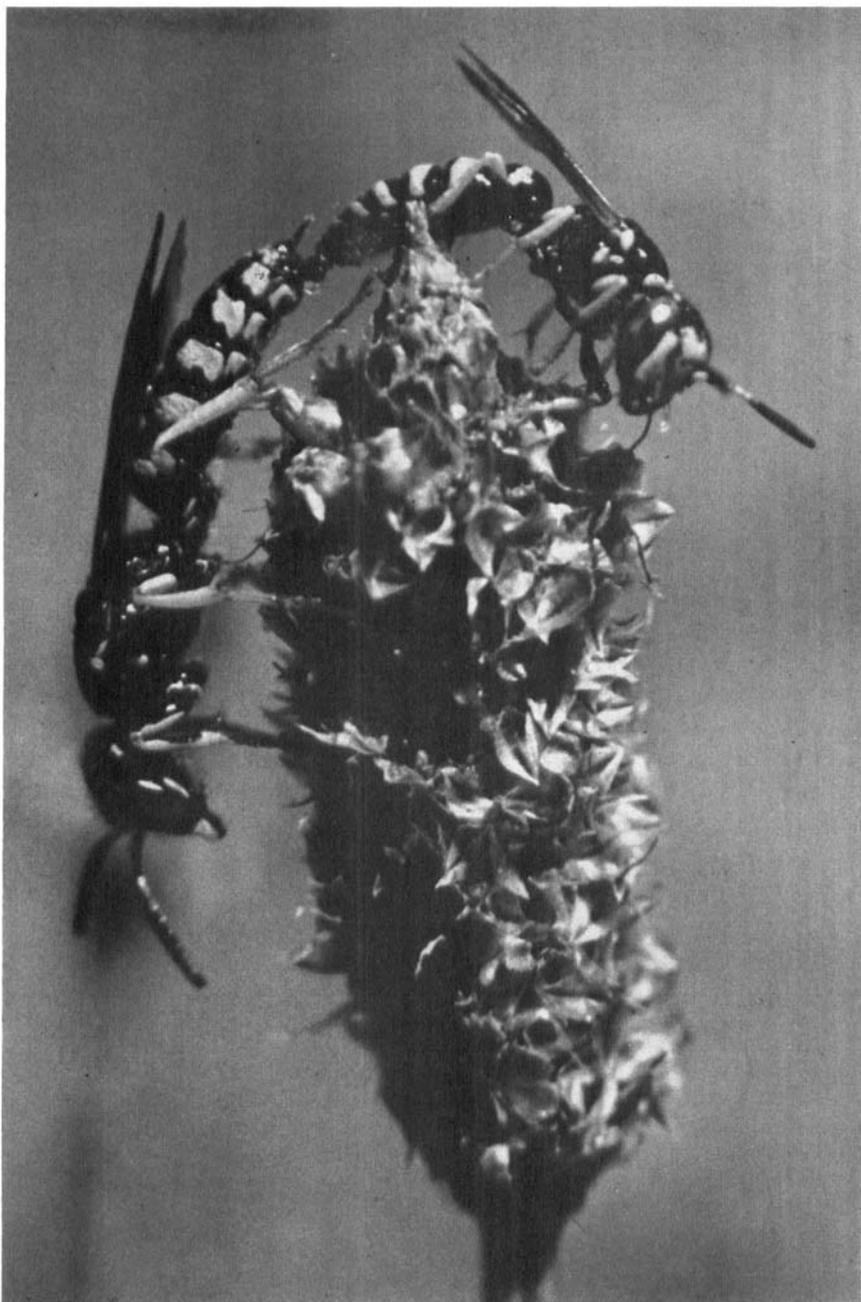


PLATE I. A copulating pair of *Philanthus crabroniformis* (male on the right).

(Table I). In the late afternoon and early evening both sexes began entering burrows, closing off the entrance from inside, to remain there for the night.

TABLE I  
*The number of provisioning trips by eight female P. crabroniformis to eight marked nests*

| Time of day | Observation length (min) | Provisioning trips | Average number of provisioning trips per min |
|-------------|--------------------------|--------------------|--|
| 08.00-09.00 | 45                       | 0                  | 0.00   |
| 09.00-10.00 | 150                      | 6                  | 0.04   |
| 10.00-11.00 | 180                      | 10                 | 0.06   |
| 11.00-12.00 | 40                       | 4                  | 0.10   |
| 12.00-13.00 | 175                      | 25                 | 0.14   |
| 13.00-14.00 | 165                      | 32                 | 0.20   |
| 14.00-15.00 | 50                       | 11                 | 0.22   |
| 15.00-16.00 | 0                        | —                  | —  |
| 16.00-17.00 | 120                      | 12                 | 0.10   |
| 17.00-18.00 | 65                       | 9                  | 0.14   |
| 18.00-19.00 | 40                       | 2                  | 0.05   |
|             | 1030                     | 111                |  |

#### *Prey capture*

Previously only Bohart (1954) has published an observation of *P. crabroniformis* capturing prey (under the name—*P. flavifrons*). He observed a female attack and capture a number of honeybees at a hive entrance. However, honeybees are atypical prey for this species (Evans, 1970; Table II) and most species of *Philanthus* take prey at flowers (Evans, 1970). Although I observed females going from flower to flower (especially *C. arvensis* and *Hypochaeris glabra*) and occasionally darting at halictid bees, no captures were seen at flowers.

TABLE II  
*The response of hunting P. crabroniformis to a variety of stimuli presented to them*

| Object   | Presentations | Attacks | Captures* |
|--|---------------|---------|-----------|
| Freshly paralyzed halictids                          | 39            | 28      | 11        |
| Dead, fresh cuckoo wasp (5 mm)                       | 8             | 8       | 0         |
| Dead, dried halictid                                 | 8             | 6       | 0         |
| Model (splinter wrapped with black thread—6 mm long) | 10            | 7       | 0         |
| Same+fresh halictid rubbed over model                | 10            | 7       | 0         |
| Model (balsa dipped in India ink—13 × 3 × 3 mm)      | 20            | 16      | 0         |
| Same, but not dipped in ink, natural balsa color     | 10            | 0       | 0         |

\* Wasp grapples with object and stings it as opposed to striking the stimulus and then retreating (an attack).

A totally different foraging technique employed by the wasp, and one that is in accord with Bohart's report, involved searching in open areas with dried mosses, the nesting sites of halictid bees, especially *Dialictus laevissimus*. Wasps cruised slowly a few cm above the ground frequently making right angle turns. Foraging flights (lasting 5–20 seconds in the late afternoon or on overcast days and several minutes in the middle of sunny days) were interspersed with stops during which time the wasp perched on a stone, twig, or leaf on the ground. After a brief pause, the female would fly up again. Usually, flights from a perch coincided with the appearance of other flying insects. As is probably typical of *Philanthus* (Tinbergen, 1935; Armitage, 1965), *P. crabroniformis* females pursued many species of insects including yellow jackets, bumblebees and even damselflies. Most chases ended quickly and extended over a distance of no more than 20 cm even when the insect approached was a prey species. *Dialictus* nearing their nests appeared sensitive to the presence of a female *P. crabroniformis* and often flew rapidly off in a highly erratic manner. Although the wasp, by virtue of its aerial agility, was able to orient to a bee darting back and forth, I never saw one capture a halictid that flew away from its burrow. However, if the bee did not leave but continued its final descent to the nest with a wasp slightly above and behind it, the predator would suddenly accelerate diving at its prey with great speed. Usually the female would collide with the bee and the two would fall to the ground. There the victim was manipulated so that the wasp's jaws clamped around the "neck" of the bee; the prey was then stung in the thorax judging from one close observation of a wasp's response to a tethered bee.

Of 81 prey captures observed in the *Dialictus* nesting area, 73 followed the pattern presented above. (However, whether the bee was slammed into the ground and then firmly grasped or whether the bee was caught in mid-air and simply manipulated on the ground was not easily determined. At least seven of the group of typical captures were clearly the latter type.) There were eight unusual captures: in five the wasp captured a bee that was resting or walking on a stem or leaf, in two a bee was taken while it was walking on the ground, and in one case the wasp plucked a bee out of the air and flew off without falling to the ground.

#### *The stimuli releasing attack*

*P. crabroniformis* shares many of the elements of prey capture with *P. triangulum* (Tinbergen, 1935) and presumably other members of the genus. Like the bee-wolf it orients to and often pursues almost any flying insect. Like the bee-wolf it does not attack all the insects it pursues. Tinbergen (1935) found that the species he studied would only grasp honeybees or models that smelled like honeybees. In watching *P. crabroniformis* it was apparent that highly specific olfactory cues do not necessarily provide the signal for attack by this species. Although females never made contact with damselflies or syrphids, they did strike bumblebees three to four times their size, ants, and even small (halictid-sized) round flower buds of a weed found in the halictid nesting area. Confirmation of the hypothesis that olfactory cues were not essential to trigger an attack was provided by some simple experiments. A variety of objects were tied to a strand of sewing thread and then dangled and twisted (by spinning the thread between thumb and forefinger) about 2 cm off the ground and 5–10 cm in front of a perched or slowly cruising wasp (Table II).

Thus, the wasps could be induced to strike a wide variety of stimuli provided they were moving, close to the ground, and dark in colour. However they never grappled with and

stung anything other than suitable prey (fresh bees). The preference for dark as opposed to light coloured stimuli was tested somewhat more systematically by offering the same hunting female two small  $8 \times 2$  mm balsa models in sequence. One was black, having been dipped in India ink, and the other a very pale brown, the natural colour of balsa. Half the wasps tested were presented with the black model first and half were first offered the pale model before receiving the other type. Thirteen of 14 black models were attacked; only one pale model was struck. The preference for dark visual stimuli makes biological sense given the relative abundance of black prey species to white or pale ones. Whether the preference is innate or learned is not known.

#### *Learning in foraging by P. crabroniformis*

Because wasps were present so reliably during the main hunting hours in the *Dialictus* nesting areas, it seemed probable that individuals were returning regularly to these spots to forage. Although it seems certain that digger wasps of many species can learn the location of a productive site and return to it often (Evans, 1966b: 445), there is little direct evidence of this.

On 4 July 1972 eight wasps were captured while they hunted in one halictid nesting area about  $4 \text{ m}^2$  located about 10 m from the northern end of the main wasp nesting site. Each received a dot of red acrylic paint on the thorax. Over the next two days, marked individuals were seen occasionally in the area. Then, after a week of rains with little or no wasp activity, a female with a distinctive mark appeared at the hunting grounds on 15, 17, 19, 20, 21, 22, and 25 July making 15 prey captures there on 15 July. (No observations were made on 16, 23, 24 July; heavy clouds reduced wasp activity on 18 July.) Thus individual wasps may return to the same limited area repeatedly over a period of up to three weeks.

#### *The approach to the nest*

*P. crabroniformis* has a distinctive manner of approaching the nest when returning with prey (Evans, 1970). Its body is tilted slightly so that the head is higher than the abdomen as the female flies slowly toward her nest. Prey-laden wasps often pass their burrow entrance before alighting with extreme abruptness. One moment the wasp is flying and the next it is immobile, clinging to a stem, weed head, leaf or standing on the ground (Fig. 1). Wasps remain frozen for a few seconds or as long as 30 seconds before flying to another spot and stopping or going to the nest entrance. Twenty of 38 provisioning trips recorded on 24 July 1971 were preceded by a single abrupt stop, six by none, six by two stops, and six females froze three or more times before opening the burrow.

This behaviour appears to be an anti-parasite adaptation directed against satellite flies, especially *Senotainia trilineata* Wulp, which larviposit on prey being taken into a burrow (Evans, 1970). Freezing removes the moving stimuli so attractive to these flies. I observed flies that had been closely following a prey-laden female take off in pursuit of another wasp after their first potential host had stopped.

Females appeared to notice when they were being followed and would turn to face their pursuers in flight; they sometimes then flew rapidly away from the nesting area not to return for several minutes. Another strategy seen four times was employed when the female carried a large prey. The wasp would fly slowly away from the nesting site making

no effort to elude *S. trilineata* but gradually gaining altitude until wasp and parasite were 7–10 m in the air. Suddenly the female would turn and literally dive downwards back to the path leaving the fly behind. Once a female closely followed by a fly achieved considerable altitude and then dropped her catch; the parasite may have made contact with the prey.

At other times wasps proceeded to open their burrow despite the presence of a fly a few cm behind them. A number of these individuals entered and then quickly turned to

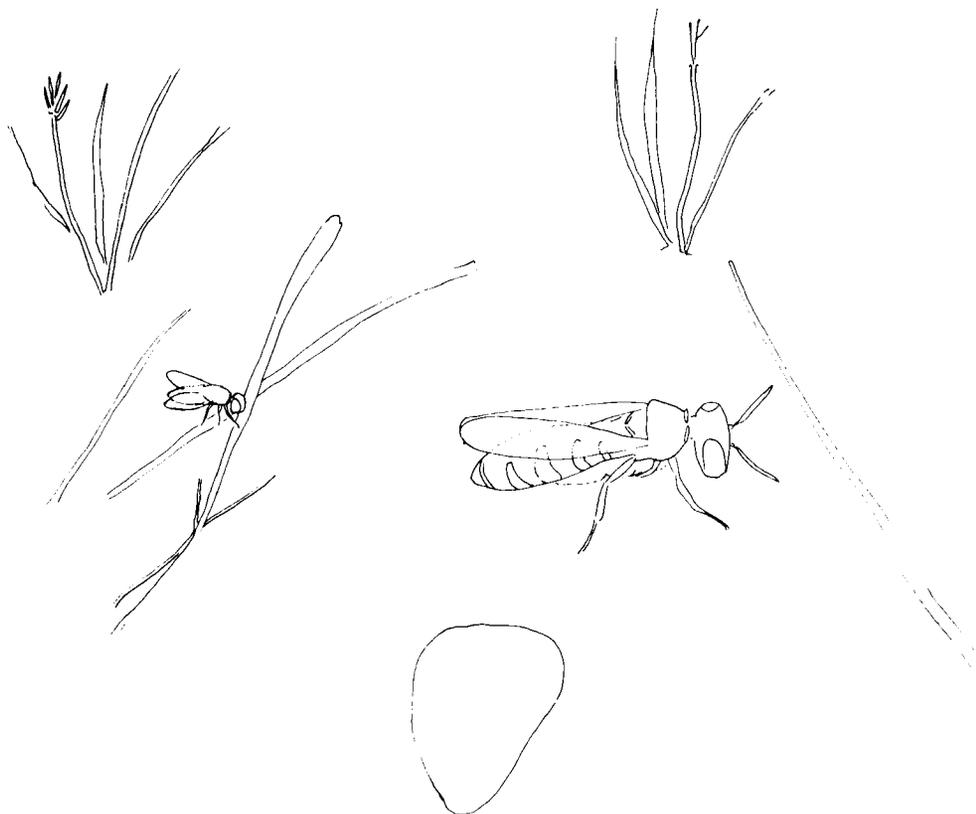


FIG. 1. A sketch of a prey-laden female *Philanthus crabroniformis* standing immobile on the ground with a satellite fly waiting approximately 5 cm behind the wasp. (Drawn from a photograph.)

face out of the nest blocking the entrance with their head. Once a fly that attempted to enter the nest was approached by the wasp; the parasite flew away. In all cases, after entering the burrow, the female closed the entrance from inside before descending to deposit her prey in a storage area in the main burrow.

#### *The rapidity of provisioning*

The average interval between consecutive trips to the nest with prey was about 18 minutes for a group of eight wasps watched over a period of days (Table III). This figure probably only represents the capability of active provisioners; often wasps appeared only

once during an entire observation period. However, if each cell contains 12 to 24 prey (pers. obs.; Evans, 1970) and one assumes a working day of seven hours between 11.00 and 18.00 hrs (Table 1), it should not be difficult for a female to collect enough prey in one day of foraging to fill one cell.

TABLE III  
*The rapidity of provisioning by eight *P. crabroniformis* at eight marked nests*

| Wasp | Number of intervals between provisioning trips | Average interval (min) | Most rapid period of provisioning |
|------|--|------------------------|-----------------------------------|
| Y-0  | 11   | 21.8                   | 5 bees/73 min                     |
| Y-1  | 4  | 19.8                   |                                   |
| Y-2  | 12   | 11.6                   | 5 bees/31 min                     |
| Y-3  | 12   | 14.7                   | 6 bees/31 min                     |
| Y-5  | 4  | 26.3                   |                                   |
| R-1  | 5  | 23.0                   | 4 bees/35 min                     |
| R-3  | 5  | 16.8                   |                                   |
| 854  | 6  | 22.2                   |                                   |
|      | 59   | $\bar{x}$ —18.2        |                                   |

#### *The design of nests*

The nests excavated during this study followed the basic plan illustrated by Evans (1970) for this species. However, three nests possessed a striking feature not shown by Evans. The nest burrow descended downwards for 18–28 cm and then abruptly proceeded

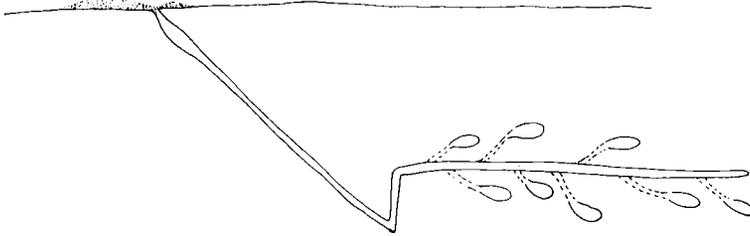


FIG. 2. A diagrammatic side view of a nest of *Philanthus crabroniformis*. Note the chamber by the burrow entrance and the vertical shaft in the main burrow.

up a vertical or nearly vertical shaft for 4–6 cm before running horizontally for some distance with cells off to either side (Fig. 2). Not all *P. crabroniformis* nests were so designed. One nest sloped downward the usual distance but contained only a short 1–2 cm incline upwards before becoming horizontal.

One other feature of some interest was a characteristic increase in the width and height of the burrow shortly after the narrow entrance way. Subsequently the tunnel narrowed again. The broad 2–3 cm long chamber appears designed to permit the wasp to manoeuvre quickly if followed by a parasite.

All 24 cells whose depth was recorded lay 12–16 cm beneath the surface. Cells were added and burrows lengthened in the manner described by Evans (1970); one nest reached a length of 65 cm.

#### *Interactions between females*

Such interactions as did occur between females appeared aggressive in nature. They occurred in two locations—by nest sites and on the mossy hunting grounds. In both areas females darted at one another, sometimes colliding with such force that one or both were driven to the ground. This was especially true in the hunting area where a large percentage of encounters between two individuals involved contact. Whether such behaviour was truly aggressive or whether the wasps were treating each other as potential prey is difficult to determine. However, no female attempted to grapple with and sting a conspecific.

In the nesting area females charged one another on the ground especially if one individual had entered or was trying to enter the burrow of another. The following notes illustrate this point:

23 July 1971. 13.07 hrs. Two females enter Y5 burrow; soon one emerges with the other right behind it. The first to exit sits 4 cm from the entrance while the other wasp remains in the entrance. The outside wasp leaves.

26 July 1971. 09.42 hrs. One female digs at R-2 nest. The occupant of the nest exits and grasps the digger. The two roll about on the ground, separate and then both enter the nest. Less than one minute later both return to the entrance and one female leaves the nest, walks about, and flies off while the other remains inside.

26 July 1971. 10.07 hrs. Wasp approaches Y3 nest. Owner attacks this wasp and both roll about on the ground. The intruder leaves, flies to Y1 nest and enters the open burrow briefly. It then flies to R-3 and enters only to retreat as R-3 owner comes to the entrance. It flies to R-1 nest and begins digging there at which time I collected it.

The function of hostile behaviour of this sort appeared to be to drive other females away from a nest. (Aggressive interactions involving attempts to steal prey were never seen.) The adaptiveness of protecting a nest may stem from (1) the substantial amount of time and energy invested in its construction and (2) a tendency of some females to appropriate nests. It will be necessary to mark a substantial number of individuals to confirm the second possibility.

#### **Discussion**

##### *A comparison of the behaviour of P. crabroniformis and P. gibbosus*

As noted before two species of *Philanthus* nested in the Seattle site. In other areas, as many as five species of this genus have been found in the same general area (Evans, 1970). However, in these cases there are usually large differences in the size of the wasps and in the prey species they exploit. When there is overlap in prey taken there is essentially complete seasonal isolation in nesting or complete separation of nesting sites (Evans, 1970). The differences between *P. crabroniformis* and *P. gibbosus* in my study area were much more subtle and less complete. The discussion will centre on the role competition and parasitism may have played in the evolution of such differences between the species as do exist.

*Prey taken*

These two species of similar size (about 12 mm) were capturing much the same prey (Table IV). Both relied heavily on the same species of *Dialictus*, a small 6 mm bee, although *P. crabroniformis* also took a number of other prey that were only slightly smaller than itself (*H. favinosus*, *Adrena* sp.). In other localities both *Philanthus* exploit halictids almost exclusively (Reinhard, 1924; Cazier & Mortenson, 1965; Evans, 1970). About 60% of the prey taken by *P. gibbosus* studied by Reinhard were species of *Dialictus* and *Halictus* while 85% of the prey records collected by Evans for his group of *P. crabroniformis* belonged to these two genera.

TABLE IV  
*Prey taken by two species of Philanthus at the Seattle site (summer 1971)*

| Prey of <i>P. crabroniformis</i>             |    |    |
|--|----|----|
| Halictidae                                   | ♀♀ | ♂♂ |
| <i>Dialictus laevissimus</i> (Smith)         | 23 | 4  |
| <i>Dialictus incompletus</i> (Crawford)      |    | 1  |
| <i>Dialictus</i> sp. 1                       | 4  |    |
| <i>Dialictus</i> spp.                        |    | 2  |
| <i>Halictus (Sedalonia) confusus</i> (Smith) | 3  | 1  |
| <i>Halictus favinosus</i> (Smith)            | 2  |    |
| <i>Agapostemon texanus</i> (Cresson)         | 1  |    |
| <i>Sphecodes</i> spp.                        | 1  | 1  |
| Colletidae                                   |    |    |
| <i>Hylaeus affinis</i> (F. Smith)            | 1  |    |
| Adrenidae                                    |    |    |
| <i>Adrena</i> sp.                            | 1  |    |
| Sphecidae                                    |    |    |
| <i>Ectemnius</i> sp.                         | 1  |    |
| Prey of <i>P. gibbosus</i>                   |    |    |
| Halictidae                                   |    |    |
| <i>Dialictus laevissimus</i> (Smith)         | 39 | 2  |
| <i>Dialictus incompletus</i> (Crawford)      | 1  |    |
| <i>Dialictus</i> sp.                         |    | 1  |
| <i>Sphecodes</i> spp.                        |    | 2  |
| <i>Halictus (Sedalonia) confusus</i> (Smith) |    | 4  |

*Nest location and nesting season*

Despite taking the same prey the two species of *Philanthus* nested side-by-side at much the same time. Although *P. gibbosus* appeared to prefer the more sandy and weedier banks of the path and *P. crabroniformis* nested primarily in the open hardpacked path, members of each species constructed burrows in both areas.

*P. crabroniformis* does begin nesting before *P. gibbosus* at the site. Females of the former species were provisioning by 28 June with large numbers active by 4 July. The first prey-laden *P. gibbosus* was not seen until 14 July and it was not until 22 July that more than

five nests of this species were active. *P. gibbosus* became more abundant in early and mid-August as *P. crabroniformis* declined in numbers. However, members of both species were found together until the end of the nesting season in the first week of September.

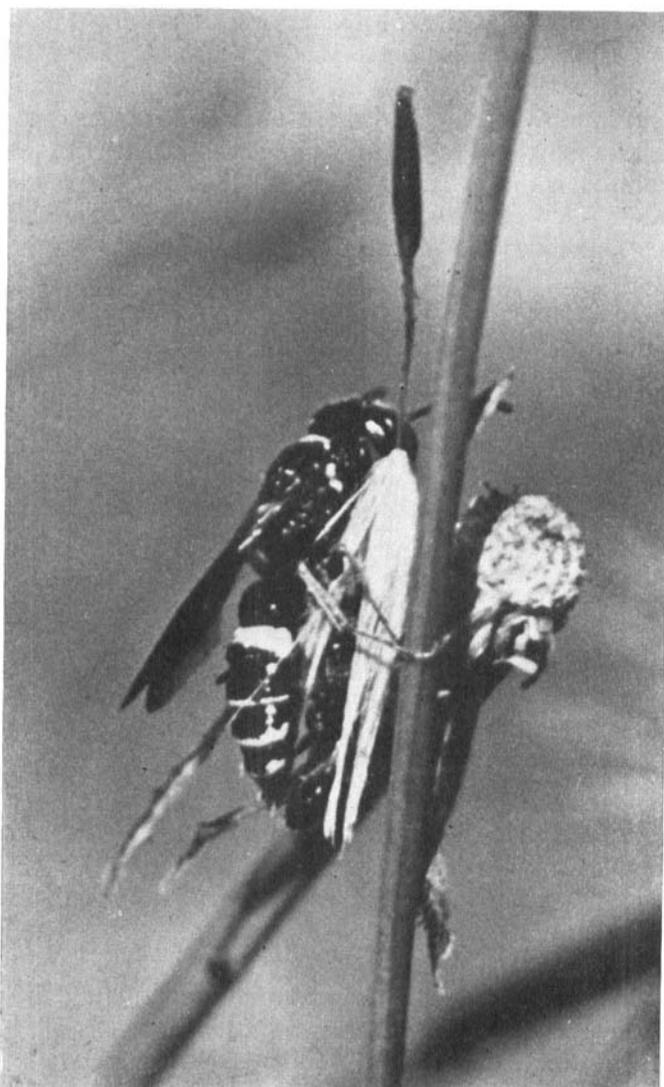


PLATE II. A female *Philanthus gibbosus* grasping a small bee and a plumed seed.

#### *Hunting behaviour*

*P. gibbosus* is known to take prey at flowers (Reinhard, 1924). Although I observed no prey captures by this species I did observe several females flying from flower to flower without stopping. Others visited many weed heads in quick succession (halictids often perched on these weeds). One individual returned to the colony area with a prey but instead of going directly to its nest it alighted on a stem. Inspection of the wasp revealed

that it was carrying a small halictid and a tufted dandelion seed which it had presumably "captured" at the same time it took the bee (Plate II).

In other areas *P. gibbosus* has been seen taking bees at a large halictid colony and reports that the wasps took guard bees indicates that it will capture bees near or from the ground (Peckham & Peckham, 1905). Moreover, Evans & Lin (1959) saw females of this species entering the nest of an halictid bee. Thus *P. gibbosus*, like *P. crabroniformis*, has more than one hunting strategy. But there are no reports in the literature nor observations of my own of its striking bees in flight as they return to a nest entrance in the manner of *P. crabroniformis*. This may be a significant difference between the two species.

In conclusion, although the two wasps do take much the same prey, overlap is not complete in such things as nest location, nesting season, and foraging behaviour and this may serve to reduce competition between the two permitting their coexistence. An alternate hypothesis is that the two species coexist because their populations are so limited by parasite pressure and other factors that they really do not compete for resources, especially the abundant halictid bees. However, the substantial amount of time and energy required for each capture (about 20 minutes of energetically expensive flight for *P. crabroniformis*) suggests that although prey may be abundant they are not exceptionally vulnerable. If the two species avoid foraging in the same manner, they may effectively increase the total number of vulnerable bees and so reduce the costs of searching for individuals. This coupled with other differences in ecological requirements, may facilitate coexistence between these two very similar species.

#### *Approach behaviour*

The two *Philanthus* approached their nests when carrying prey so differently that the behaviour provided a reliable means of identifying individuals as to species at a great distance. Unlike the slow cruising approach of *P. crabroniformis* prey-laden *P. gibbosus* returned to their nests by flying to a spot over the entrance and then descending straight down some 50–150 cm. As the female dropped down slowly it began at some point to move its abdomen rapidly back and forth over a narrow angle in a most pronounced way so that the wasp appeared to vibrate (see also Reinhard, 1924; Cazier & Mortenson, 1965, report a somewhat different pattern for an Arizonan population of this species). Upon landing the female immediately opened its nest. It seems unlikely that these differences are the result of selection pressures associated with competition but may instead stem from selection exerted by parasites, especially miltogrammine flies.

Why has there not been convergence in the approach patterns of these two species of *Philanthus* and, for that matter, other wasps as well? In fact, most of the wasps nesting along the path brought prey to their nests in a species-specific way. It is possible that each technique has evolved independently of any other and simply represents one of many equally effective strategies for thwarting parasites. However, it is likely that there has been direct selection for divergence in the approach behaviour of different species.

Satellite flies are common widespread parasites of many digger wasp species. Plate III shows a *Senotainia trilineata* on a typical raised perch in the path where the wasps were nesting. These flies may be more effective parasites if they scan a portion of the total environment rather than attempting to inspect their entire surroundings. If all wasps employed the same approach pattern, the generalized following parasites could all adopt

the same effective limited scanning strategy. This would increase the possibility that an individual would be detected as it approached the nest. However, by coming to the burrow in different ways, females run the risk of detection by only that fraction of the parasite populations that is searching in a specific approach zone. For example, it seems likely that a fly scanning areas utilized by *P. crabroniformis* would often fail to see a *P. gibbosus* female descending straight down from a point high over its nest. Moreover, the latter, as it drops down wagging, presents a visual image totally different from that of the low flying *P. crabroniformis* cruising in with its body held rigidly in one plane. If these speculations about fly searching behaviour are correct, then it is probable that divergent approach patterns would be adaptive.



PLATE III. A satellite fly (probably *Senotainia trilineata*) perched on a rock in the nesting aggregation.

The effectiveness of species-specific approach strategies depends in part on there being other individuals about, preferably of other species, to distract and occupy portions of the total parasite population. One key pressure favouring nesting in groups and the formation of mixed species aggregations by wasps may then be provided by generalized parasites despite certain disadvantages associated with concentrated nesting groups (the attraction of parasites and increased competition for nest sites and food).

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