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BURROW SHARING AND NEST TRANSFER IN THE DIGGER WASP *PHILANTHUS GIBBOSUS* (FABRICIUS)

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Abstract. *Philanthus gibbosus* is a solitary, ground-nesting wasp in which several individuals have been observed to occupy a single burrow. Evidence is presented which indicates that several emerging males and females often occupy the parental nest for several days, the males sometimes for life. The females, however, soon disperse to found new nests, although one may continue to occupy and expand the parental nest. It appears that the larger female often maintains possession of the nest, although the interactions have not been observed. On rare occasions two females may provision a single nest for a brief period. *P. gibbosus* may represent a unique stage in presociality in which temporary communal nesting occurs at certain phases of the nesting cycle.

One of the most interesting sections of the Peckhams' classic 'Instinct and habits of the solitary wasps' (1898) is concerned with *Philanthus gibbosus* (Fabricius) (=*punctatus* Say), a ground-nesting species in which newly emerged wasps live together for a time in the parental burrow 'before starting out independently to seek their own fortunes.' They found one such nest containing 'three brothers and four sisters' . . . 'on most amicable terms with one another.' A week later one of these females began to enlarge the nest, and a day later she began to provision the nest. In the meantime another of the females left and began a new nest a short distance away, which she soon began to provision. A third female remained in the original burrow, and the Peckhams speak of her as acting as a 'guard' at the entrance. On the next day the second female was also joined by another female (perhaps from the parental nest), but this fourth female left 3 days later and began a new nest 1·2 m away. The males continued to spend their nights in the original burrow with the two females, although on another occasion the Peckhams observed males digging their own 'sleeping burrows.'

Considering the current interest in the initial stages of insect sociality, stimulated particularly by Michener's work on halictid bees (Michener 1969), it is curious that there has been no further work on burrow sharing in *Philanthus gibbosus*, one of the commonest and most widely distributed North American digger wasps. It is true that both Reinhard (1924) and Lin (1968) confirmed the fact that males and females may spend the night together in the same burrow, but others who have worked on this species made no note of burrow-sharing and treated *gibbosus* as a strictly solitary species, one female occupying each burrow (Rau & Rau 1918; Evans & Lin 1959). If siblings do share the parental burrow for a time, what determines which female (if any) will eventually take it over? Are there dominance interactions, and do subordinate females sometimes serve as guards at nest entrances? When more than one female shares a common burrow, does more than one ever provision the nest? Why have some workers failed to observe more than one wasp to a burrow? These and several other problems would seem to be worth investigating, not because *Philanthus* may be the progenitor of the bees or the social wasps (as it certainly is not), but because the genus may exhibit a level of presociality suggestive of that through which the social Hymenoptera may have passed. Some of the most critical problems in understanding the origin of insect sociality relate to the adaptive significance of aggregate nesting and of nest-sharing prior to the evolution of caste differences. A reconsideration of the Peckhams' observations of more than 70 years ago would therefore seem to be worthwhile.

Methods

For four summers (1968 to 1971) we have been making observations on a nesting aggregation of *P. gibbosus* at the Concord Field Station of the Museum of Comparative Zoology (Bedford site). This aggregation occupied an area measuring 5 × 9 m on flat, stony, sandy loam, largely devoid of vegetation. The number of nesting females (between thirty-two and forty) remained relatively constant over the 4 years of study. For three summers (1969 to 1971) we marked and numbered all nests with nails inserted 4 cm

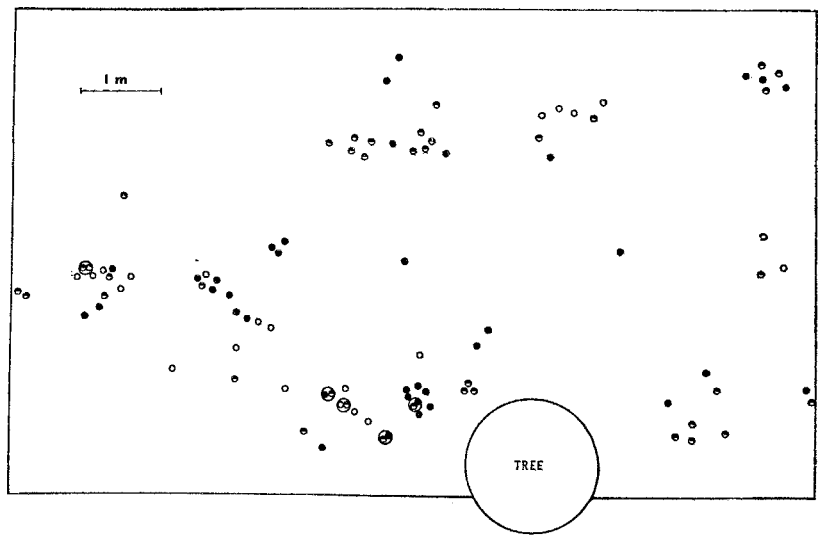

Fig. 1. Map of nesting area of *Philanthus gibbosus*, Bedford, Massachusetts. Nest entrances in 1969 are shown by hollow circles; in 1970 by half-darkened circles; and in 1971 by black circles. Nest entrances apparently used for two successive summers are enclosed by a larger circle. It should be borne in mind that each entrance leads to a burrow sometimes 1 m or more in length, running only 10 to 25 cm beneath the surface.

from each nest entrance; these markers were kept in place permanently, so that the pattern of nests could be followed from year to year. The distribution of nests over the 3-year period is shown in Fig. 1.

The wasps themselves were marked on the back of the thorax (sometimes also on the abdomen) with various colours of Testor's butyrate dope. These spots persisted through the season on the males, but females tended to abrade them away as they expanded their nests through this coarse soil. Hence it was necessary to remark each female approximately every 2 weeks. In order to determine what wasps were present in each nest during the night, we placed a beaker over the entrance early in the morning; as the wasps emerged they were delayed in the beaker until we could identify and record them, then released. Our records are not complete, as it is not possible to record all activity at numerous nests; also there were short periods when no one could be present at the nesting site. However, most gaps in our records represent actual periods of inactivity on the part of the wasps: that is, partial or complete rainy or darkly cloudy days.

We excavated very few nests at this site, since we did not wish to disturb the substrate, also because accurate dissection of the complex nests of this wasp proved very difficult in this stony soil. However, a full understanding of nest structure seemed essential, so we made several careful excavations at another site: 3-km south of Rensselaerville, Albany Co., New York. Observations at this site gave us no reason to believe that there were significant differences in behaviour from the Bedford site. However, at Rensselaerville there are two distinct generations per summer, while at Bedford there is only one, the wasps appearing each year in mid-July and remaining active until the first few days of September.

The difficulties of working under natural conditions are many, particularly with a small aggregation of a species making complex nests and spending much time underground. I am aware of many points that might be clarified by experimental manipulation, and efforts are now being made to develop an artificial nesting situation such as that recently described by Michener & Brothers (1971) for ground-nesting bees. However, as of now no one has succeeded in handling solitary wasps under artificial conditions except in the case of a few species making very simple, unicellular nests (Baerends 1941; Steiner 1962).

Results

Behaviour of Males

Males appear at the beginning of the nesting period and at least a few of them live almost until the females cease nesting. In 1969, a male marked on 15 July remained active until 2 September (49 days), returning each night to the same burrow, a burrow that was inhabited in the course of the season by four different females. During 1970, several males were followed for several weeks, one of them (nest 7, Fig. 2) for 47 days, returning each night to the same burrow, a burrow at times shared with other individuals of both sexes. On the other hand, males did occasionally move from one burrow to another (see nests 1 and 2, Fig. 2).

The maximum number of males found to emerge from any one nest in the morning was three. However, during one nest excavation, on a cool and cloudy day, a tight clump of four males was found 15-cm deep, apparently in an old, unoccupied cell. There is no evidence that males do any appreciable amount of digging; they merely inhabit emergence holes or burrows excavated by females.

On sunny days, males emerge from the burrows in the morning (09.00 to 11.00 hours) and remain outside the nest until middle or late afternoon, returning earlier if it becomes cloudy or windy. Much of their time is evidently spent on flowers, particularly *Solidago*. We assume that mating ocurs on flowers or inside the nest, as we have never observed mating in the vicinity of the nest entrances, and we are not aware that others have observed mating in this species.

Nest Initiation and Transfer by Females

Within a few days of their first emergence from the soil, females begin to dig an oblique burrow, scraping the soil into a small pile at the entrance. At the very beginning of the season, such burrows are started at or very near the entrance to a nest of the previous generation. For example, nest 1 of 1970 (Fig. 2) appeared at the same point as nest 6 of 1969, nest 7 of 1970 at the same point as nest 1 of 1969 (see also Fig. 1). In some cases nests were started not at precisely the same point as a nest of the previous year, but within a very few centimetres. For example, nest 2 of 1970 was started 2 cm from nest 17 of 1969, suggesting that the wasps emerging from old nest 17 did not emerge at precisely the same point, probably as a result of surface erosion. Various excavations confirmed the fact that cells and the lower parts of burrows tend to keep their form for several years, whereas the upper parts of burrows often cave in or are filled by soil from rain or melting snow.

There is reason to believe that nests 1 to 8 of 1970 (Fig. 2) were re-activated nests of 1969, while nests 9 to 30 were new nests initiated by individual females at various times during the early part of the season. It will be noted that nests 1 to 8 all contained more than one wasp at least at some time. For example, nest 1 contained as many as three males and two females at one time, but after 28 July was abandoned. On the other hand, nest 4 was inhabited by a male and a female for several weeks, and the female actively provisioned the nest until 15 August. Nest 11, on the other hand, was founded on 24 July by a female from parental nest 8 (who came originally from 1); this female abandoned nest 11 after 12 August and started nest 29, which she provisioned until 6 September. This is the only record we have of one female being associated with four different nests; much more commonly females simply left the original nest after a few days and founded a new one nearby (e.g. nest 12 in Fig. 2).

This 'sorting out' of females bears some resemblance to the dominance interactions of *Polistes* wasps (Pardi 1948), and leads one to ask whether the female that assumes sole occupancy of a parental nest does in fact 'drive away' the other females. The following case history (from 1969) may provide a clearer picture of the situation.

In this instance two females (A and B) were marked as being active at a reactivated nest of the previous season on 15 July. A was seen provisioning the nest, while B did some digging at the entrance and at times rested in the entrance facing out. On the following day B was seen digging a new nest only 4 cm away, while A remained in the original nest. B provisioned her new nest for several days, but on 22 July a different female (C) appeared at this nest and began to provision it. When C brought in prey, B would often emerge from the nest and wander about outside. Late the same day B was seen starting a new nest 5 cm away; she remained at this nest for the rest of the season (until 16 August). C remained at the nest originally dug by B for the remainder of the season (until 2 September). However, on 15 August she was joined by a second, very small female (D), who had moved there from a neighbouring nest. On one day (20 August) both females were seen

Fig. 2. Records of a selection of seventeen nests, Bedford, Massachusetts, summer of 1970. Males are indicated by triangles, females by circles. Dates omitted were either rainy days when there was no activity or (toward the end of the season, when there was less activity) deliberately omitted in the interests of condensing the chart (e.g. 14 to 24 September). Failure of a wasp to appear on a certain date (e.g. no. 16 on 6 August) may mean a hiatus in observation or failure of the female to emerge from the nest on that date. Only clear-cut cases of nest transfer, involving clearly marked wasps, are indicated; other cases undoubtedly occurred but involved wasps that transferred nest before we had an opportunity to mark them. Note the tendency to spread from reactivated nests of the previous generation, containing several wasps (nests 1 to 8) to new nests containing only one female (nests 9 to 30).

provisioning, but on most days D merely entered and left the nest periodically, or rested in the entrance or on a blade of grass nearby. On 23 August D was seen visiting other nest entrances, and on the 26 August she was seen digging a new nest.

It is noteworthy that in at least two cases the larger of the two wasps prevailed at that particular nest (C was slightly larger than B and considerably larger than D; A and B appeared to be of approximately the same size). In no case did we observe any actual aggression be-

tween females; if such occurred it may have taken place inside the nest. Following these observations, we made a special effort to observe interactions between females occupying a single nest. Although we occasionally saw females working at neighbouring nests fly at one another briefly, with a buzzing sound, in no case did we observe aggressive interactions between females at the same nest. If dominance interactions do occur they may, of course, be exceedingly subtle to our view, and we hope in the future to record on motion picture film as many instances as possible of multiple use of nests, in the hope of detecting the manner in which dominance is achieved.

Communal Nesting

In the example cited above, it will be noted that females C and D provisioned the same nest for 1 day. This is one of only two cases, over a 3-year period, in which we saw two females provisioning a single nest. The second example was somewhat more complex, involving three females, two of which provisioned the nest over a 2-day period. During early August 1969, a marked female (E) occupied nest 15 alone. On 26 August two additional females appeared, a small one (F) and another (G) about the same size as the original occupant. All three were sometimes seen very close together; F often rested in the entrance, facing out, then withdrew when E returned with prey; at other times F rested on a blade of grass nearby. G often dug at the entrance, and on 27 August all three were seen digging at one time or another, but only G was seen to provision. Late on 27 August F was again seen 'guarding' the entrance, but she was not seen again. However, on the following 2 days E and G both provisioned this nest; after that date the nest became abruptly inactive. The following are our records for the 28 and 29 August:

		E	G
28 August	12.39		In with prey
	13.12	Digging	
	13.13		Closed and left
	13.26		Back with prey
	13.45	Digging	
	14.35	Closed and left	
	14.56		Back with prey
	15.16	Back with prey	
29 August	10.53		Digging
	10.54		Closed and left
	11.20	Digging	
	13.43	Closed and left	
	13.48		Back with prey
	14.04		Back with prey
	14.06		Closed and left
	14.50	Back with prey	
	15.08	Closed and left	
	15.36	Back with prey	
	16.02	Back with prey	

It must be emphasized that these represent the only instances in which we saw two females provisioning a single nest at the same time. Both occurred in 1969, and careful observations in 1970 and 1971 failed to reveal further examples. We suspect that the females were provisioning separate cells, but we have no evidence on this point. The long burrows of this wasp would seem to provide opportunity for several females to nest together; yet this rarely seems to occur.

Nest Structure

The nest of *P. gibbosus* consists of a burrow that is at first oblique, at about a 30 to 50° angle with the surface, then, at a depth of 20 to 35 cm, nearly horizontal. The cells are constructed at the ends of short side-burrows from the main tunnel. The first cells are closest to the entrance, additional cells are progressively distant from the entrance as the burrow is extended. The burrow may ultimately be extended to a length of 40 to 70 cm, with twenty or more cells. A burrow that has been occupied by more than one generation may reach a length of 1·5 m. Two nests occupied by wasps of two generations, excavated near Rensselaerville, New York, are shown in Fig. 3.

Nest structure is of considerable relevance in discussions of burrow sharing and nest transfer, as it is obvious that numerous individuals may emerge from a single burrow and that burrows are capable of being extended and re-utilized by wasps of more than one generation. There seems no obvious reason why burrows may not contain several major branches, each with numerous cells, but we have found no such nests.

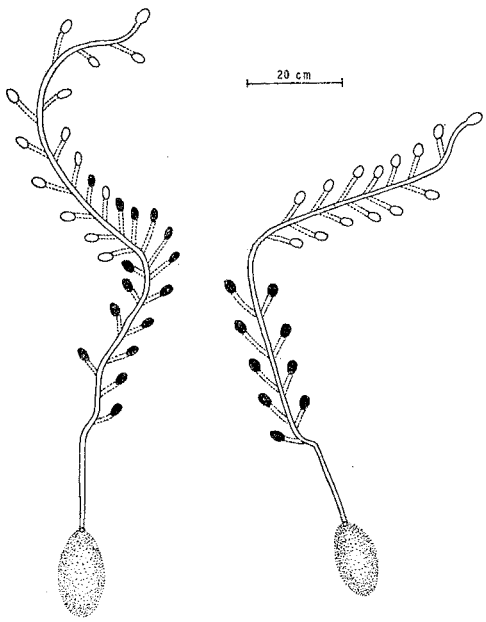

Fig. 3. Plan view of two nests of *P. gibbosus*, Rensselaerville, New York, 1970. The entrances and accompanying pile of sand are at the bottom. The short burrows leading to the individual cells are filled solidly, and could only be approximated (dashed lines). Cells of the previous generation, containing empty cocoons, are shaded.

Discussion

It seems evident that the Peckhams were correct in stating that newly emerged *Philanthus gibbosus* often live together in the parental burrow for several days before the females disperse to found new nests. Until such time as it proves possible to rear these wasps in the laboratory, it will be difficult to prove that the original nest occupants are siblings, but there seems every reason to believe that this is the case. Males may continue to occupy the original burrow for life, or they may move to another burrow which may or may not be occupied by other males or females.

The nature of the interactions which result in females dispersing to form new nests remain unknown. There is some evidence that the larger of two females is more likely to maintain occupancy of a nest. It is possible that larger females are able to rebuff smaller ones during encounters inside the burrow, such that subordinate females restrict themselves to resting in or around the nest entrance and eventually moving to a new site. The presence of males or non-provisioning females in a nest may well have positive selective value, as such individuals often rest in the entrance, forming fortuitous 'guards' against the entry of mutillid wasps or miltogrammine flies. We have little evidence as to the effectiveness of such 'guards'. Wasps resting in the entrance commonly withdraw when approached closely by humans, and on a few occasions we have observed withdrawal in the presence of mutillids.

Whether or not a given parental nest is re-utilized is probably dependent upon its condition. That is, a nest that has been occupied by a single generation and is still in good physical condition may well be re-utilized (as in Fig. 3). On the other hand, some nests probably suffer cave-ins or other physical damage, and nests that have already been occupied by wasps of two or three generations may have burrows of such length that it is no longer practicable to utilize them. Such factors may explain why some nests (e.g. no. 1, Fig. 2) do not persist while others do (nos. 4 and 8).

The provisioning of one nest by two females appears to be a rare phenomenon, and our many observations over a 3-year period have revealed only two instances. In one case dual provisioning lasted 1 day, in the other case 2. The significance of these brief intervals of communal nesting is unknown, and it is not known whether the females provision the same or different cells (probably the latter).

The fact that several observers have treated this species as a strictly solitary wasp is easily explained: after the first few weeks of the season, nearly all nests are, in fact, occupied by a single female. On the other hand, observations at the beginning of the season may create the impression of sociality. Yet *P. gibbosus* is far from being a social wasp; neither is it subsocial or quasisocial (in the sense of Michener 1969). It is, however, an unusual solitary wasp in that communal use of burrows is a temporary phenomenon, occurring at the beginning of the season and during rare intervals of dual provisioning later in the season.

Clearly *P. gibbosus* is worthy of a fuller study than it has yet received. The species has an exceedingly wide range, and in the southern states may well have several overlapping generations. In this case there may be greater opportunity for contact between generations. The species inhabits a variety of substrates, and it would be interesting to learn if the amount of burrow-sharing is greater in heavier soil, such that females expend less energy than would otherwise be required to dig through hard soil.

Also, one wonders if in some parts of the range the abundance of mutillids and other parasites may be sufficient to exert strong selection pressure for the presence of additional individuals that may serve as 'guards' at the entrance. These and several other problems await elucidation.

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