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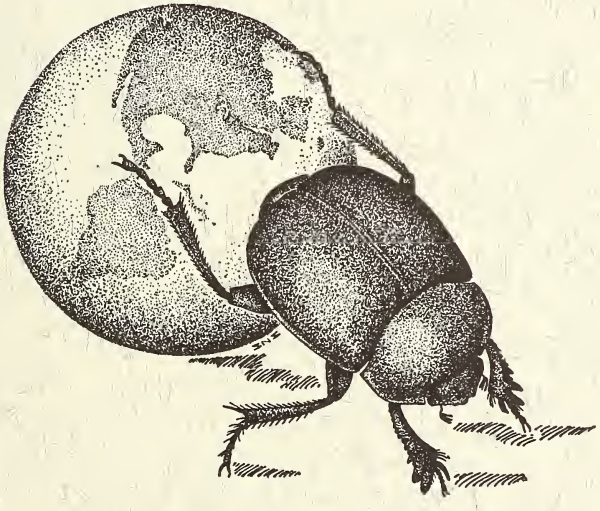

Devoted to Entomology in General

Digger Wasps as Colonizers of New Habitat (Hymenoptera: Aculeata)

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Abstract: Twenty-nine species of solitary wasps occupied a newly bulldozed area of sandy soil at Bedford, Mass., during the summers of 1972 and 1973. Of these, 5 species built up large populations in only two years, having moved into the area from adjacent study plots. Another 17 species occupied the newly bulldozed area in smaller numbers, while the remaining 7 species, present in adjacent plots, failed to occupy the new substrate or did so with no increase in numbers.

INTRODUCTION

Students of solitary wasps often seek out the nests of these insects in plots of soil made bare by man, either in excavations or fresh fills. In the more wooded parts of the country these wasps presumably once inhabited eroded slopes and banks along watercourses, but man's propensity for moving soil about has created many new areas of suitable substrate. On the whole these areas are probably no more or less permanent than the original nesting sites, for an eroded slope, no less than a man-made gravel pit, undergoes its own cycle of development. At first the soil is loose and bare; gradually mosses, grasses, and small herbs take root, reducing the bare spaces and bringing about consolidation of the soil; gradually a new topsoil is built up, and larger plants fill or shade the remaining bare spots. Thus ground-nesting insects must be able to colonize new exposures rapidly, to build up large populations, and to send out new colonizers. These statements are less true of beaches and dunes, but even such areas have their patterns of change to which ground-nesters must adjust.

Set against these facts is the common observation that aggregations of ground-nesting Hymenoptera sometimes persist in the same site for many years. Females tend to nest near the place they emerged, perhaps by some form of locality imprinting, or perhaps simply because the soil near their emergence site is the most suitable in the area. There is evidence that females of some species make a series of nests in the site where they emerged, but later make one or more nests some distance away (Evans, 1966). It is also evident that individual species vary in their tendency to adhere to one site year after year and in their ability to colonize new areas. Evidence on these points is, however, fragmentary.

Acknowledgments: This research was conducted at the Concord Field Station of the Museum of Comparative Zoology, Harvard University. For much assistance in the field work, I am indebted to Victoria Rowntree and to Fred Atwood. The flies were identified by Lloyd Knutson, the weevils by Janice White, the spiders by Herbert Levi.

DESCRIPTION OF STUDIES

An opportunity to study the relative motility of ground nesters was presented to me in the spring of 1972, when an area was bulldozed at the Concord Field Station of the Museum of Comparative Zoology at Harvard (Bedford, Mass., site). I had been studying an area immediately adjacent for several years. The major occupant of this area was *Philanthus gibbosus* (Fabricius) (as reported by Evans, 1973), but I also recorded all nests of other species within the plot. The plot measured 5 × 9 m and had evidently been bulldozed many years earlier; it had since become much overgrown with moss and herbs. It is here referred to as plot X.

The area newly bulldozed in May, 1972, was much larger and the freshly exposed, sandy soil was at first wholly devoid of vegetation, although parts had been filled in by grasses and herbs by late summer of 1973. This area had previously been occupied by a grass-covered bank about 3 m high by 8 m wide, the soil from the bank having been moved elsewhere. Hence the newly exposed soil was at first wholly devoid of ground-nesting insects. The most suitable nesting substrate, to which my studies were confined, was in a strip 8 m wide by 50 m long. For convenience this strip was arbitrarily divided into 3 plots, A, B, and C, A and B being separated by a narrow strip of less suitable substrate (Fig. 1). Plot A was studied intensively, B only slightly less so; C was visited for brief periods several times each day. Observations were recessed during inclement weather, but at other times (mid-June to mid-Aug.) at least one and usually two observers were on duty nearly full time during daylight hours.

Nests were marked with numbered stakes and followed from day to day. It was impossible to record all the activity at even a few nests, since so many were involved. However, there was little difficulty in identifying active nests by the appearance of the burrow and the soil at the entrance. A few females of each of several species were marked with paint of various colors to determine whether they made more than one nest, and if so where the additional nests were dug. Observations were also made on parasites, and a few selected nests were excavated to determine the number of cells and the incidence of successful parasitism.

During the summers of 1972 and 1973, 25 species of Sphecidae and 4 species of Pompilidae were found nesting in these plots. Of these 29 species, only 13 had been found nesting on plot X during the preceding several years. Of the 13, the majority merely moved into plot A without increasing notably in numbers, although 2 species increased greatly and extended over all three plots. The remaining 16 species presumably migrated in from other sandy areas nearby, although I am not aware of any major nesting sites within 1.5 km. Some of these wasps appeared in small numbers, while others became common in only two seasons.

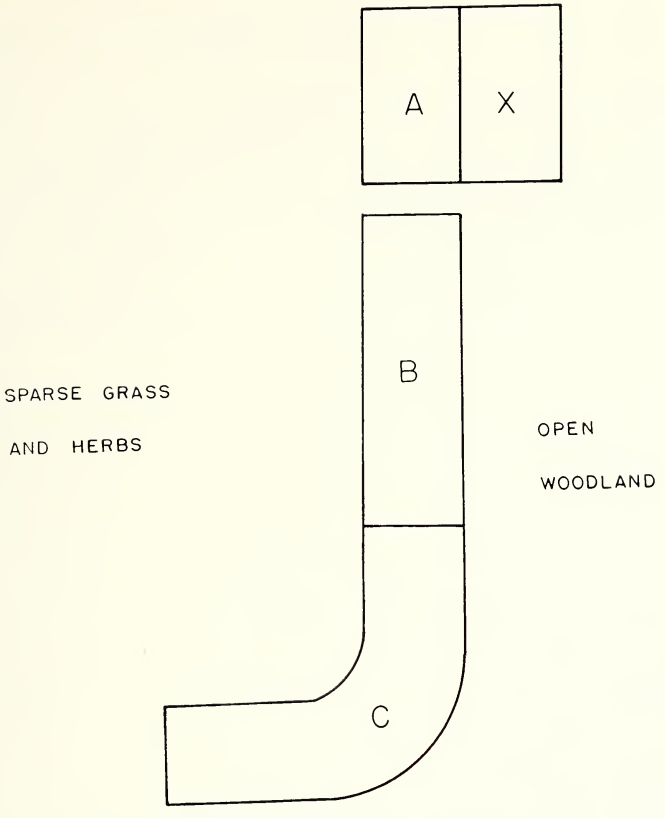

Fig. 1. Relative position of study plots, Bedford, Massachusetts.

In the following list, the species are grouped as rapid colonizers, slow colonizers, and noncolonizers. In each case a few notes are presented on the nature and abundance of the nests. Only a few biological notes are presented, since most of these are well-studied species and biological references can be found in the Synoptic Catalog of Hymenoptera North of Mexico and its supplements. The genera *Ageniella* and *Anoplius* are Pompilidae, all others Sphecidae.

RAPID COLONIZERS

Crabro monticola (Packard). From 1968 to 1971, the number of nests in plot X varied from 0 to 2, although others were noted in paths in nearby woods. In 1972, 28 nests were counted in plots A and B (none in C). In 1973, the number had increased to 123, of which a maximum of 88 were active at one time (22 June) (females commonly make a second nest after closing the first). Since the nests of this species are surmounted by a prominent ring of soil, they could be

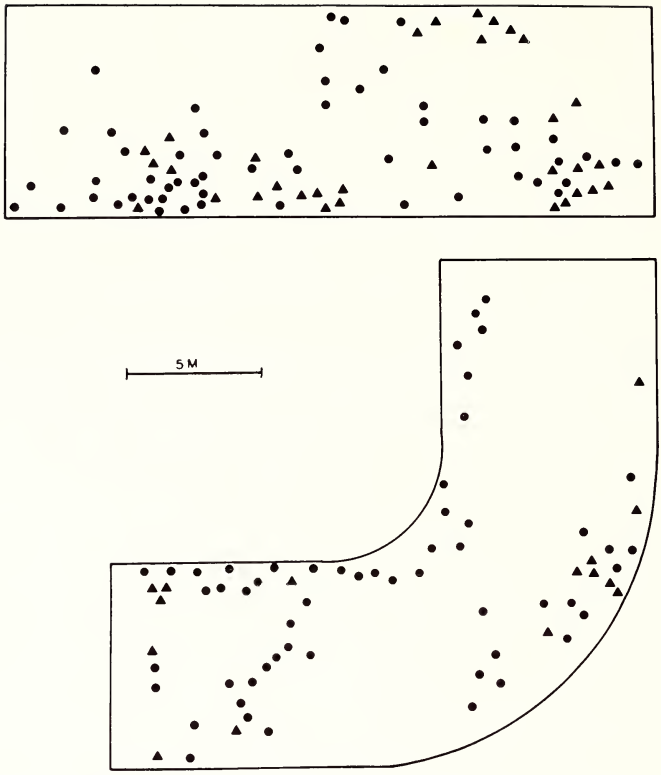

FIG. 2. Nests of *Crabro monticola* (circles) and *Aphilanthops frigidus* (triangles) in plots B and C during summer of 1973 (for correct relative position of plots, see Fig. 1).

easily marked and followed. Prey consisted of flies, mainly *Thereva frontalis* Say (Therevidae), which the *Crabro* found in abundance in the adjacent woods.

Aphilanthops frigidus (Smith). This species nested in plot X each year, 1968–71, the number of nests varying from 1 to 3. Only 4 were noted in the newly bulldozed plots in 1972, but in 1973 the number increased to 58. All of these were dug between 14 July and 2 August, the nesting cycle of the wasp being closely synchronized with mating flights of the prey, queen *Formica* ants. Numerous colonies of *Formica* became established in the newly bulldozed area during 1972 and 1973, and abundance of *Aphilanthops* was undoubtedly partly a consequence of the abundance of prey.

Bicyrtes quadrifasciata (Say). This is a common wasp in Massachusetts, but none had been seen at the Bedford site until 1973. On 23–25 July a number of males were seen flying over the ground in plot C, and over the next two weeks an estimated 12 females nested in plots A–C. It was not possible to keep an

accurate count of nests, since there is no distinctive pattern of soil at the entrance as in the preceding two species.

Oxybelus bipunctatus Olivier and *O. subulatus* Robertson. These two species made their first appearance in 1972, in plot A, but only a few were noted. In 1973, there were at least about 30 nests of each species in plots A and B. It was again impossible to make an accurate count, since these are very small wasps and the nests of short duration. *O. subulatus* preyed exclusively upon therevid flies, but used consistently a smaller species than *Crabro* (*Psilocephala frontalis* Cole), and only males, as reported by Peckham, Kurczewski, and Peckham (1973) in their excellent paper on members of this genus.

SLOW COLONIZERS

Anoplius marginatus (Say) and *A. semirufus* (Cresson). Females of the first species were observed 10 times and females of the second 3 times, in each case carrying spiders from the woodland into areas A and B during 1973. *A. marginatus* sometimes nested from the walls of inactive *Crabro* burrows. Both species had been seen in the area only rarely during previous seasons.

Astata unicolor Say. One nest was found in plot X and 1 in plot A during 1973. The species had not been observed during previous years.

Tachysphex similis Rohwer and *T. tarsatus* (Say). Both of these grasshopper-predators appeared in small numbers in plot A in 1972 and showed no increase in 1973.

Chlorion aerarium Patton. During 1973, 2 females constructed multicellular nests from pre-existing holes, provisioning them with *Gryllus* crickets. The species had not previously been observed in the area.

Sphex ichneumoneus (Linnaeus). This large wasp has nested in a gravel strip at the Bedford site each year, the number of nests varying from 2–10 each year. *Nysson plagiatus* Cresson was seen entering nests on several occasions, and in 1970 we reared a female *N. plagiatus* from cells of *S. ichneumoneus*. This species had been reported as a possible parasite by Ristich (1953), but the relationship had not been confirmed.

This nesting site was about 40 m from plots X and A. None were found nesting in these plots, but 2 females nested in plot B in 1973.

Prionyx parkeri Bohart and Menke. One nest of this wasp was noted in 1972, 2 in 1973; the species had not been seen during previous years. The nests are of short duration, and there were undoubtedly others that were not discovered.

Gorytes canaliculatus Packard and *Hoplisoides nebulosus* (Packard). These two related species, both predators on Homoptera, were seen in small numbers in 1972, but not previously. During 1973 we noted several nests of both species, but it is doubtful if there were more than 3–5 active females of each.

Bembix americana spinolae (Lepeletier). Two nests were noted in plot B in 1972, 8 in plots A and B in 1973. During 4 previous years, the species was sighted each summer, but no nests were ever found.

Lindenius columbianus errans (Fox). This is a minute wasp, but the nests are distinctive and are maintained for several days. We noted none until July, 1973, when 4 appeared within 2 m^2 in plot A.

Ammophila procera Dahlbom and *A. urnaria* Dahlbom. These wasps were seen only occasionally prior to 1973. During that season, we estimated 3–5 females of each species. They were often seen proceeding from the woodland into the newly bulldozed area carrying caterpillars. Most nests were in or near plot A.

Philanthus politus Say. One nest was found in plot B in 1972. None were found in 1973, although males were seen on several occasions on the flowers of *Achillea millefolium* and *Chrysanthemum leucanthemum*.

Philanthus gibbosus (Fabricius). This species maintained a nearly steady population of 32–40 nests in plot X over a period of 4 years (one female usually maintains one nest for the season) (Evans, 1973). In 1972, there were only 12 nests in plot X (now well overgrown with vegetation), but 11 females had established themselves in adjacent parts of plot A. In 1973, only one nest was dug in plot X, 20 in plot A (Fig. 3). Thus the number of females declined slightly over a three-year period, during which time there was a gradual shift into newly available bare soil, although over only a few meters.

Cerceris prominens Banks. This species was not recorded until 1973, when 3 nests appeared 8–14 July in area B, all within 1 m^2. One of these nests was excavated on 14 July, at which time it contained 7 cells at depths of from 12 to 17 cm. Freshly provisioned cells each contained 18–19 weevils, and there were also 8 weevils at the bottom of the burrow, 8 cm deep, in compact soil. All weevils were Baridinae, the 38 specimens preserved belonging to 4 species: *Baris* sp. (17 ♂♂, 1 ♀, 10 of unknown sex), *Limnobaris* sp. (3 ♂♂, 3 ♀♀), *Pachygeraeus* sp. (2 ♂♂), and *Odontocorynus* sp. (1 ♂, 1 ♀).

It should be noted that this is quite a different complex of weevils than those employed by any of the three following species. The four species of weevil-hunting *Cerceris* occurring at this site showed no overlap in prey whatever, providing an excellent example of competitive exclusion.

NONCOLONIZERS

Cerceris atramontensis Banks, *C. halone* Banks, and *C. nigrescens* Smith. These three species all nested in small numbers in plot X during the summers of 1969–71 (Evans, 1971). However, they appeared to be absent during 1972 and 1973

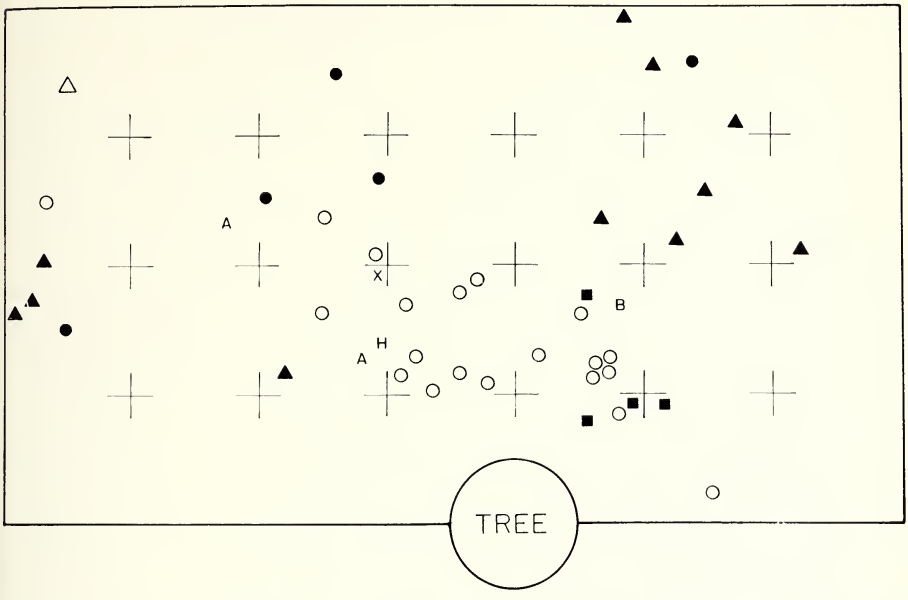

Fig. 3. Nests recorded in plot A during summer of 1973. Plot is marked off into squares 2 m each side. Solid circles: *Crabro monticola*; solid triangles: *Aphilanthops frigidus*; squares: *Lindenius columbianus errans*; hollow circles: *Philanthus gibbosus*; hollow triangle: *Bembix americana spinolae*; A: *Astata unicolor*; B: *Bicyrtes quadrifasciata*; H: *Hoplisoides nebulosus*; X: *Anacrabro ocellatus*.

except for one nest of *C. halone* each year, again in plot X. The original nesting sites were well covered by moss in 1973, but all 3 species failed to establish themselves in plots A–C.

Lyroda subita (Say). This wasp constructed its cells from the walls of the burrows of both *Philanthus gibbosus* and *Sphex ichneumoneus*. Only one female was noted during the summer of 1973, although the species had been fairly plentiful during previous summers.

Ageniella conflicta Banks. During the summers of 1968–71, this species was seen in some numbers within the *Philanthus gibbosus* nesting area. Females were seen carrying spiders into inactive *Philanthus* burrows on several occasions. These burrows were later closed by picking up small pebbles, bits of leaves, and grass blades and placing them in the burrow and in a small pile over the top. One cell was located at a depth of only 7 cm. Two prey spiders taken from wasps both proved to be female *Schizocosa bilineata* (Emerton) (Lycosidae). Both had all the legs amputated. This species was not observed in 1972, and only one female was seen in 1973.

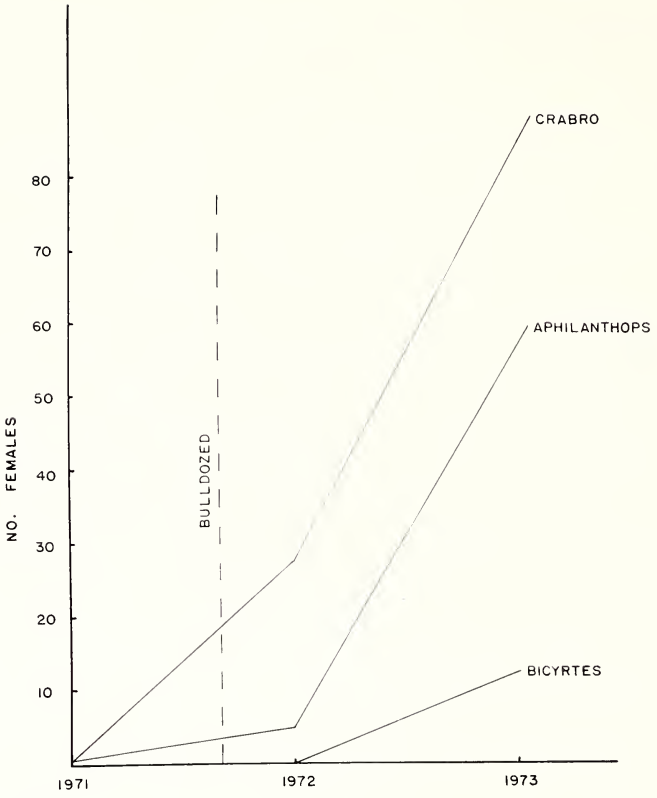

FIG. 4. Number of active females of three species over a 3 year period.

Ageniella partita Banks. This species was observed only in 1969, and like the preceding was closely associated with inactive nests of *P. gibbosus*. One spider taken as prey proved to be *Zelotes* sp., juvenile female (Gnaphosidae). The wasp ran over the ground with her prey and made several short, hopping flights, straddling the prey and holding it by the spinnerets. Only one leg had been amputated. This is evidently the first record of this species from Massachusetts.

Anacrabro ocellatus Packard. One or two females nested in plot X each year, 1968–71. In 1972 one female nested in plot X, one in plot A, only 3 m away. In 1973 one female nested in plot A. Thus the population remained essentially stable despite the large amount of new substrate available.

DISCUSSION

It is evident that in this limited area and over a limited time period, some wasps spread rapidly over newly available bare, sandy soil and increased their numbers greatly. Others increased in numbers only slightly or even showed a

decline. It is unlikely that exactly this same pattern would have been followed under different circumstances. The proximity of the study area to a woodland having a plentiful supply of therevid flies undoubtedly permitted *Crabro monticola* and *Oxybelus subulatus* to flourish. The sudden abundance of *Aphilanthops frigidus* was also very probably related to the fact that its host, *Formica fusca*, had also rapidly occupied the newly available substrate.

On the other hand, there were many blowflies and muscids around the nearby animal pens, and solitary bees abounded in and around plots A–C. Thus there appeared to be ample prey for species of *Bembix* and *Philanthus*. Members of these genera are, in fact, known to remain attached to their nesting sites for many years, and in this instance they showed little tendency to avail themselves promptly of new potential nesting sites.

The differential effect of parasites also undoubtedly plays a role in controlling the numbers of these insects. By colonizing new sites rapidly, species such as *Crabro monticola* and *Aphilanthops frigidus* may in some measure evade the attacks of miltogrammine flies. The latter species is known to be especially susceptible to attacks by these flies (Ristich, 1956). We did not excavate any *Aphilanthops* nests, but of the 7 *Crabro* nests excavated, all but 1 had at least one cell containing maggots of miltogrammine flies. In all, 15 of 37 cells were parasitized (40%). *Metopia argyrocephala* Meigen was reared from 3 nests, *Senotainia trilineata* Wulp from one. Neither species of wasp is known to be attacked by mutillid wasps, the behavior patterns of which seem especially adapted for more gregarious species which persist in one site from year to year. I believe the decline of *Philanthus gibbosus* to be related to the abundance of its parasite, *Dasymutilla nigripes* (Fabricius).

Literature Cited

Evans, H. E. 1966. "The Comparative Ethology and Evolution of the Sand Wasps." Cambridge, Mass.: Harvard Univ. Press.

———. 1971. Observations on the nesting behavior of wasps of the tribe Cercerini. Jour. Kansas Ent. Soc., **44**: 500–523.

———. 1973. Burrow sharing and nest transfer in the digger wasp *Philanthus gibbosus* (Fabricius). Anim. Behav., **21**: 302–308.

Peckham, D. J., Kurczewski, F. E., and Peckham, D. B. 1973. Nesting behavior of nearctic species of *Oxybelus* (Hymenoptera: Sphecidae). Ann. Ent. Soc. Amer., **66**: 647–661.

Ristich, S. S. 1953. A study of the prey, enemies, and habits of the great golden digger wasp *Chlorion ichneumoneum* (L.). Canad. Ent., **85**: 374–386.

Ristich, S. S. 1956. The host relationship of a miltogrammid fly, *Senotainia trilineata* (VDW). Ohio Jour. Sci., **56**: 271–274.