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Notes on a Nesting Aggregation of Digger Wasps in Seattle, Washington (Hymenoptera)

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In the summers of 1971 and 1972, I observed the nesting behavior of a group of digger wasps in a vacant lot near Union Bay, Lake Washington, in Seattle. The behavior of a majority of the species in this aggregation has not been described in detail before.

The methods employed in this study were simple. I watched the main nesting area, a 10 m. portion of a path running through a grassy field by the edge of a large blackberry patch, for periods ranging from 1–4 hours on most sunny days between July 17 and September 4, 1971, and between June 2 and August 4, 1972. The path was less than 1 m. wide. It was weakly banked on either side and composed of sand patches with earth and pebbles elsewhere. Small grasses and a few weeds were scattered about the path with a dense mat of grasses and weeds on the sloping sides of the trail.

The results are presented in the form of a list of the species observed nesting in the study site with a description of their natural history based on notes taken during and immediately after each observation period.

POMPILIDAE

Pompilus angularis (Banks).

Although this wasp was often seen about the path apparently hunting over the ground, only 1 nest was located. This was dug in an open area of hard-packed earth in the center of the path. The female required about 45 minutes to dig its nest which was 4 cm. long and 3 cm. deep (fig. 1). The prey, a crab spider somewhat larger than the wasp, was left about 25 cm. from the nest entrance.

The wasp visited the spider twice during burrow construction and once it moved the prey about 15 cm. from one resting place on the ground to another spot on a leaf. When the nest was complete, the wasp returned to the spider, grasped it by the base of a leg, and pulled it to the nest entrance. After it had entered the burrow the wasp hauled its prey down the shaft. The egg was placed vertically on the side of the abdomen near the thorax.

Episyron quinquenotatus quinquenotatus (Say); **E. q. hurdi** Evans.

Two nests of this species were found dug in sandy areas at the side of the path. See Evans (1963a) for a description of the nesting behavior of this spider predator.

Priocnemis notha Banks.

This species was seen crossing the path carrying spider prey.

SPHECIDAE

Dryudella montana (Cresson).

The behavior of *D. montana* is the subject of 2 brief accounts (Evans, 1963a; 1970). The species was a common one whose nests were found exclusively in the barren sandy patches in or near the path from mid-June to the end of August. The average burrow length was 10.9 cm. (7–15 cm.) and the average cell depth was 6.0 cm. (4–9 cm.) with data recorded for 8 cells. The burrows were often strongly curved (fig. 2).

One nest when excavated held 8 prey at the end of the burrow. No egg was found and so it would appear that *D. montana* collects a group of prey before placing them in a cell or cells as suggested by Evans (1963a) and by Parker (1969) for the genus as a whole.

The wasp makes multicelled nests on occasion. In 2 nests 2 cells were placed, one after the other, and 1 other nest had 2 burrows, 1 leading to a double cell and 1 running to a single cell (fig. 3).

The species is an active ground forager walking rapidly and erratically through and over grasses and flattened weeds for short periods of time (15–30 seconds) before flying a short distance to a new area where it repeats its searching pattern.

They fly to the nest holding their prey with the jaws and prob-

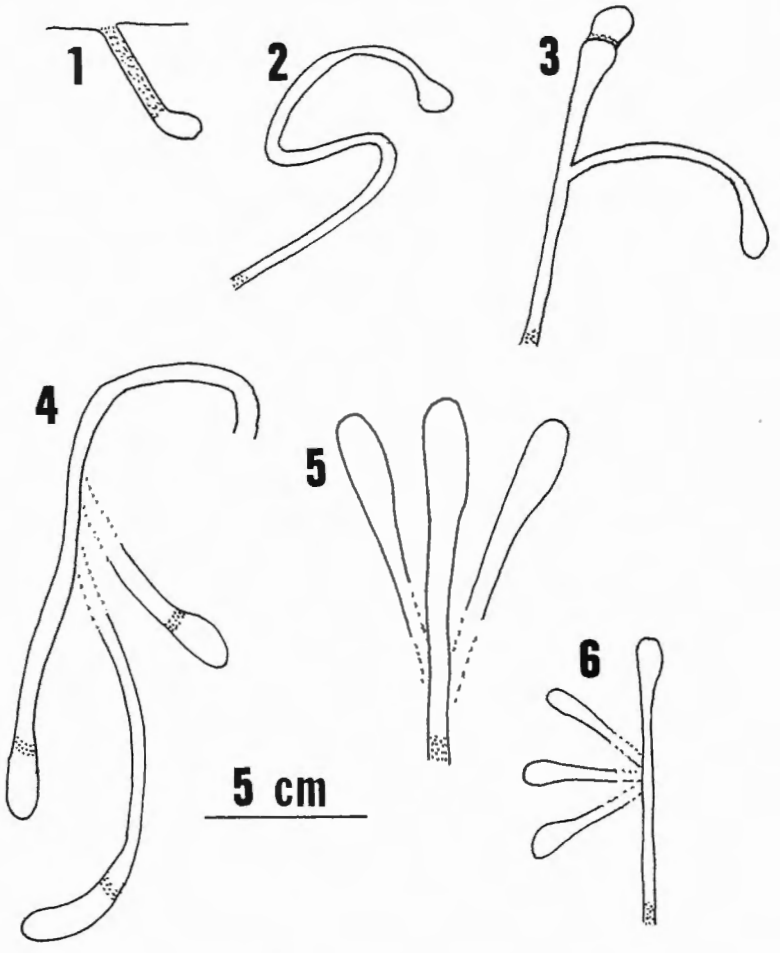

FIGURE 1. A view from the side of the nest of *Pompilus angularis*.
FIGURE 2. A view from above of a single-celled nest of *Dryudella montana*.
FIGURE 3. A view from above of a triple-celled nest of *Dryudella montana*.
FIGURE 4. A view from above of a triple-celled nest of *Dryudella caerulea*. Dotted lines indicate connection not clear.
FIGURE 5. A view from above of a triple-celled nest of *Tachysphex aethiops*.
FIGURE 6. A view from above of a nest of *Gorytes asperatus*.

ably with the legs as well. Once at the entrance the prey is dropped to one side (figs. 7 & 8) and the wasp proceeds to open the nest (also observed by Evans, 1963a). The female then enters, disappears for a few seconds, reappears at the entrance, and pulls the prey in after it. Twice *D. montana* wasps were watched as they were followed by satellite flies, *Senotainia trilineata* (Sarcophagidae). In both cases the flies waited on the ground until the nest had been opened and the female had just gone inside. The parasites then darted in, ignoring the unprotected prey lying a short distance from the entrance. They were driven off by the female as she returned to the opening to retrieve her prey. There is no doubt that the fly's behavior is better suited for those wasp species (the vast majority at the site) that carry their prey directly into the burrow without releasing them. It has been suggested that parasite pressure has been responsible for the evolution of the direct entrance with prey (Evans, 1963b). But this in turn may have exerted selection on satellite flies, favoring those with a tendency to enter the nest immediately after a potential host has entered. It is at this moment that the wasp's prey is most vulnerable to attack (because it trails after the female, which holds it with a hind leg at this stage, as she descends down the burrow). If the fly's behavior has evolved to counter the prevalent antiparasite adaptation of most digger wasps, it may mean that the "primitive" response of dropping the prey at the entrance while the burrow is opened may actually be an effective antiparasite behavior. It is even conceivable that some species (*D. montana*?) may have lost the direct-entrance-with-prey pattern and have returned to something approximating the ancestral pattern.

Dryudella montana captures the early instar nymphs of several families of Heteroptera: Rhopalidae, *Aufeius impressicollis* Stäl (in one nest only), 8 specimens; Scutelleridae, *Eurygaster alternatus* Say, 10 specimens; Pentatomidae, *Euschistus conspersus* Uhler, 8 specimens.

→

Figure 7. A *Dryudella montana* female arriving at the nest carrying a prey (*Aufeius impressicollis*).

Figure 8. The prey is deposited to one side of the entrance to the nest. In the lower right hand corner a satellite fly that had followed the female to the nest is about to dart into the burrow ignoring the exposed prey.


7


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Dryudella caerulea (Cresson).

Nothing at all has been previously reported on the behavior of this species although it is widespread in western North America (Parker, 1969).

Three nests were found in the period from July 29 to August 1, 1972. All were located in the grass-covered weedy slopes on either side of the path. The entrance to the nest was left open but was very inconspicuous because of the dense matted cover over the nest.

Figure 4 illustrates the design of the most complete nest excavated. Prominent features include the strongly curved nature of each tunnel, the sandy inner closure sealing each cell and the 1–2 cm. empty space behind each cache of prey. A total of 6 burrows were excavated. Their average length was 15.0 cm. (13–18) with the average depth of the cell 6.5 cm. (4.5–9.0).

The females were watched on a few occasions walking rapidly up and down grass and weed stems and running quickly over the ground. One female believed to belong to this species foraged along blackberry stems and the undersides of blackberry leaves. One wasp took a stinkbug (*Euschistus conspersus*) and fell a few inches onto the ground by the edge of the path. It sat for a brief moment straddling its prey which was upside down before flying off with surprising speed. Wasps coming to the nest arrived very suddenly at a spot just above the nest entrance. They then dropped down a short distance and entered the open burrow.

The 3-celled nest was provisioned entirely with 15 nymphs of *Hyalmenus tarsatus* (Fabricius) (Alydidae), a striking ant mimic (4, 5, and 6 to a cell). Another nest held 4 late-instar nymphs of *E. conspersus*, while the third contained a single nymph of this species.

The egg was attached to the coxa of a foreleg and was placed across the venter of the thorax under the beak of the alydid. Egg-laying occurred when the cell had been filled judging from the 4 cases in which the egg was found on a prey at the entrance of the cell. In the 3-celled nest, each cell held a complete complement of bugs and 1 unhatched egg. This would seem to indicate that *D. caerulea* builds a nest with multiple cells and either provisions rapidly enough to stock 3 cells before the first egg hatches or the wasp collects a store of prey, distributes them in 3 cells, and lays a series

of eggs at once. The latter mode of operation is characteristic of *Dryudella* (Parker, 1969).

Tachysphex aethiops (Cresson).

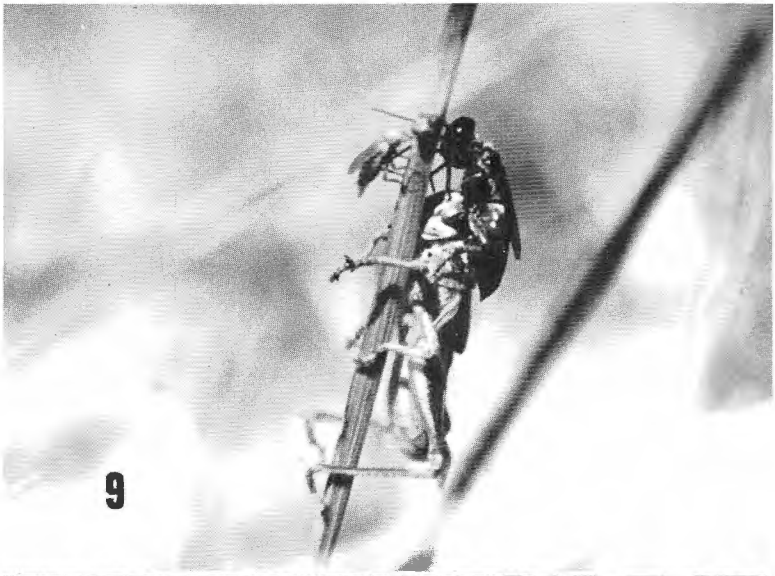
Tachysphex aethiops is the subject of a short report by Evans (1970). This species was seen very infrequently. Twice I observed it entering open *Bembix* burrows in the path. In 1 case a female remained inside a nest for over an hour before it left and was collected. In the other instance, the wasp modified a probable *Bembix* sleeping burrow constructing a complete nest in about 70 minutes of digging. Five hours after making this nest, the cell was empty; the wasp was collected as it returned without prey to its burrow at 17:30. Both this nest and another were placed in the center of the path in open areas with hard packed soil. An active nest had 3 cells (fig. 5) containing (1) a partially decayed grasshopper, (2) a wasp grub with grasshopper debris, and (3) a fresh hopper about 20 mm. long with an egg laid across the venter of the prothorax. In all cases the burrows were 10–12 cm. long with the terminal cell about 4 cm. deep.

Tachysphex parvulus (Cresson).

This was a fairly common species in the area. Three nests were found in late July 1972. All were dug into the bank of the path in fairly dense cover. All were single-celled averaging 7.2 cm. (5.5–10) in length and 3.0 cm. (2.5–3.5) in depth. Two nests contained 2 small (11 mm.) hoppers with the egg or larva found on the second hopper brought to the nest. The egg was placed across the venter of the prothorax. The third nest held a single large (21 mm.) grasshopper; the nest was excavated before the wasp laid an egg on this prey.

When foraging, *T. parvulus* walks rapidly through grasses and weeds close to the ground. A part of a prey capture was observed. A small hopper jumped once. The wasp nearby rushed to the insect and pounced upon it. In the confusion I only definitely saw the wasp insert its stinger by the base of the 2 front legs on 1 side but I feel fairly certain that the hind leg received similar treatment. The abdomen of the wasp vibrated strongly as the stinger was inserted.

In taking prey to a nest the wasp straddled the grasshopper pulling it by its antennae. The legs supported the prey at least while



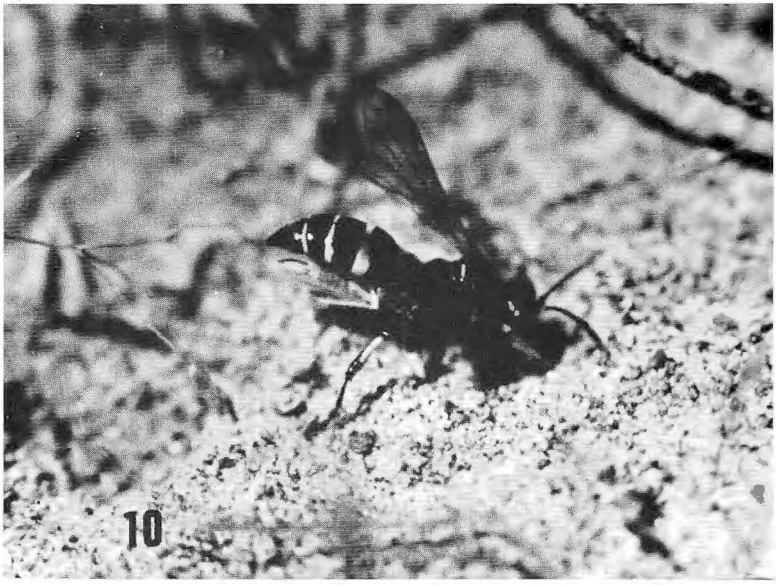


Figure 9. A *Tachysphex parvulus* female resting with prey up a weed stem. The satellite fly that had been perched on the hind leg of the grasshopper moved onto the stem.

Figure 10. A female of *Gorytes asperatus* carrying a leafhopper just as she starts to open her burrow. Notice the elevated wings.

TABLE 1. *The prey of* Bembix americana *(August 1971).*

Muscidae	
Coenosia tigrina (Fabricius)	62
Calliphoridae	
Pollenia rudis (Fabricius)	44
Phaenicia sericata (Meigen)	19
Syrphidae	
Sphaerophoria sulphuripes (Thomson)	4
Metasyrphus subsimus Fluke	1
Eristalis tenax (Linnaeus)	1
Melanostoma sp.	3
Helophilus sp.	1
Syrphus sp.	1
Bombyliidae	
Villa sp.	1
Anthomyiidae	
Spaziphora cincta (Loew)	1
Hylemya sp.	1
Sarcophagidae	
Sarcaophaga sp.	1

the wasp was resting after having climbed a grass or weed stem. Miltogrammine or satellite flies sometimes follow *T. parvulus* or even ride on the hind leg of the grasshopper, perching nearby during rest stops (fig. 9).

Once at the burrow the wasp entered and pulled its prey in after it. The grasshopper was positioned upside down in the cell.

Copulation or attempted copulation was observed on 2 occasions. A pair would remain in flight for a period of about 30 seconds. In 1 case the 2 collided with a bembix and separated. The other pair alighted with the male above the female still attempting to copulate—unsuccessfully as the female walked quickly about. The 2 separated shortly after landing.

Bembix americana Fabricius.

This species has been intensively studied (Evans, 1957; 1966). However, I present some information on the prey taken (table 1) and the provisioning of nests by this population of *B. americana.*

As is evident from table 1, the wasps were primarily exploiting 2 species of flies. *Coenosia tigrina* was abundant in the dense vegetation in swampy parts of the lot and presumably was captured there.

Pollenia rudis was probably taken largely or entirely at the many garbage cans and omnipresent dog droppings scattered about Union Bay Village, a tightly packed cluster of University housing units next to the lot. Wasps were often seen flying directly from the nesting site toward the nearby houses of the Village. Specialization in prey capture was also noted in 1972. One nest contained 26 identifiable flies; 25 belonged to *C. tigrina*. Another held a total of 8 flies all of which were syrphids of an unidentified species of *Melanostoma*.

In the course of the study, 5 cells were found with complete or nearly complete complements of flies. Four of these contained more than 30 flies, a large number for *Bembix* which normally uses about 20–24 prey (Evans, 1957; 1966). The 5 cells held 26, 33, 34, 39, and 44 flies with 3 also containing an active larva that had undoubtedly eaten a number of flies prior to my excavation of the burrow. The rather large number of prey used may reflect the fact that the heavily preyed upon *C. tigrina* is a comparatively small and delicate species. It was also chosen as the support fly for the egg in all 5 cases in which a support fly was found.

Despite the fact that many insects were required to fill a cell, females were capable of completing the task in a few days. A group of 13 females watched for a total of 1067 minutes during periods of active provisioning brought 137 prey to their nests (one fly/8.2 minutes). One individual captured 21 flies in less than 2 hours as well as stealing an additional prey from a neighbor.

Gorytes asperatus Fox.

This rather uncommon wasp nested throughout the summer in open areas of the path both in sandy soil and hard-packed earth. One nest with 4 cells (fig. 6) was excavated and the female collected and identified by R. M. Bohart. Each cell was approximately 6–7 cm. deep and 9–12 cm. from the nest entrance. All contained leafhoppers of the genus *Idiocerus* (*I. cinctus* DeLong & Caldwell, 31 specimens; *I. pallidus* Fitch, 5 representatives; *I. spp.*, 6 examples). These were stacked in cells with the head of the insect slightly raised and the venter facing the entrance to the cell. One cell held 11 prey, 1 of which was carrying an egg in the same position as shown for *G. canaliculatus* (Evans, 1966; fig. 39, p. 63). Another cell contained 9 leafhoppers but no egg indicating that oviposition occurs after complete provisioning of a cell.

In 1972 5 nests presumed to be those of *G. asperatus* were dug out. The 6 cells located averaged about 6 cm. deep and were at the end of burrows averaging about 10 cm. long. All the prey were leafhoppers (15, 15, and 9 in completely provisioned cells). The 1 egg discovered was in the same position as before. However, 2 of the nests contained cells with more than 1 cocoon. One nest had a cell with 2 and the other (which was provisioned for at least 3 days) had a single cell with 4 cocoons when excavated. I believe that these were *G. asperatus* burrows but unfortunately I did not collect the females.

Several individuals presumed to be *G. asperatus* were seen hunting in the dense foliage near Lake Washington. They walked along stems and undersides of leaves flying occasionally to a new site.

Wasps carrying leafhopper prey approached the nest in a distinctive manner. Many alighted some distance (3–6 m.) from the nest before flying toward the entrance at a height of about 50 cm. The approach was highly erratic and looping, with the female turning away from the nest many times before finally touching down by the entrance. As is the case with *G. canaliculatus*, the prey is held with the middle legs and just before scraping open the entrance the female raises her wings upward before replacing them in the normal resting position (fig. 10). Still another behavioral similarity between *G. canaliculatus* and *G. asperatus* is the use of the tip of the abdomen to tamp sand down into the nest entrance upon leaving the burrow, although this was only rarely seen in the case of *G. asperatus*.

Philanthus crabroniformis Smith and **P. gibbosus** Fabricius.

These 2 common species at the site were studied in some detail and are the subject of a separate paper. Suffice it to say, the 2 are very similar behaviorally, digging similar nests and specializing in the capture of halictid bees.

Discussion

The behavior of this group of 11 wasps serves to reinforce the points made so well by Evans (1970). On the basis of his investigations of a much larger complex of species found in Jackson Hole, Wyoming, Evans concluded that the behavioral differences between the wasps at this location were related to (1) the pressure of com-

petition between species and (2) the effects of selection exerted by parasites. This also appears true of the wasps at the Seattle site.

COMPETITION. The 11 species showed great divergence in the prey taken, with different genera exploiting entirely different major groups of arthropods as shown below:

Spiders—Thomisidae—*Pompilus angularis*
" Araneidae—*Episyron quinquenotatus*
" ? —*Priocnemis notha*
Heteroptera—Small nymphs—*Dryudella montana*
" Large nymphs and adults?—*D. caerulea*
Homoptera—*Idiocerus*—*Gorytes asperatus*
Orthoptera—Primarily small hoppers—*Tachysphex parvulus*
" Primarily large hoppers?—*T. aethiops*
Diptera—Many families—*Bembix americana*
Hymenoptera—Halictidae—*Philanthus crabroniformis* and *P. gibbosus*

There was a degree of overlap in prey taken within genera. However in these cases there was usually a substantial size difference correlated with a size difference in prey taken (with *D. montana* smaller than *D. caerulea* and *T. parvulus* smaller than *T. aethiops*). The situation is more complex with *Philanthus* where the 2 species are nearly the same size and both were taking much the same prey. However, incomplete differences in foraging behavior and nesting season may be the key to coexistence of these 2 species in Seattle (Alcock, in preparation). Moreover, within each pair of species of the same genus there were fairly distinct differences in nest location preference. *Dryudella montana*, *T. aethiops*, and *P. crabroniformis* constructed burrows exclusively or primarily in the relatively open center of the path. *Dryudella caerulea*, *T. parvulus*, and *P. gibbosus* nested exclusively or primarily on the sloping banks of the path which were covered with a fairly dense mat of grasses and weeds.

Thus for the group as a whole, and within genera as well, ecological divergence in prey taken and in nest site preferences is evident and probably contributes to the ability of this aggregation of species to coexist in 1 location.

PARASITE PRESSURE. Evans (1963b; 1970, pp. 469–472) has summarized the many behavioral adaptations of digger wasps that appear to counter the actions of their many parasites. Here I shall

focus on 1 antiparasite adaptation whose significance has been rather little discussed. The sphecid wasps in the aggregation, with the exception of *Tachysphex*, flew to their nests carrying prey. Each species had a highly distinctive and characteristic approach flight outlined below:

Dryudella montana—rapid approach, appears abruptly at the nest entrance, drops prey to 1 side, enters, retrieves prey.

Dryudella caerulea—rapid flight to spot directly above nest entrance, brief pause prior to short vertical descent through grasses to open nest entrance.

Bembix americana—fairly rapid flight only a few cm. above the ground accompanied by pronounced abdominal waggle, wasp sometimes alights some distance from nest before proceeding directly to the nest entrance.

Gorytes asperatus—moderately rapid approach, highly erratic looping zig-zag flight 20–40 cm. from ground, wasp often alights some distance from nest before proceeding closer.

Philanthus crabroniformis—quick return to nesting area but once there a very slow flight usually no more than 10 cm. off ground; the wasp interrupts this flight from 1–3+ times with abrupt stops during which time it rests on the ground or clings immobile to a stem or leaf; after these abrupt stops the wasp finally turns and flies to the nest entrance.

Philanthus gibbosus—rapid direct flight to a point usually 50–100 cm. directly over the nest entrance. The wasp then descends very slowly straight down all the while waggling its abdomen from side to side very rapidly.

Elsewhere (Alcock, in preparation) I have argued that the divergence in approach patterns in *Philanthus* may represent antisatellite fly adaptations. These parasites wait near the nesting area and follow prey laden females as they approach their nests. Presumably they scan some part of their environment for potential hosts. It may be that the effectiveness of a satellite fly's scanning and detection abilities is reduced when different wasps coming into a nesting aggregation employ different approach patterns. This might force a parasite to examine its total environment or to specialize to some extent on a more limited area used by only a few of the species nesting there. Either way, an individual wasp in a mixed species aggregation should benefit from reduced parasitism because only a

portion of the total parasite population is likely to be inspecting its approach zone. The fact that each wasp species in the Seattle site has its own stereotyped approach pattern may support this hypothesis.

Summary

The nesting behavior of some members of an aggregation of 11 species of digger wasps at one site in Seattle is described. The interspecific differences in prey taken and nest site location are related to competition between species for limited resources. Interspecific differences in approach patterns of prey-laden females may be adaptive by making it less likely that a satellite fly will detect an individual returning to its nest in a mixed-species aggregation.

Acknowledgments

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