The

American Midland Naturalist

Founded by J. A. Nieuwland, C.S.C.

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Vol. 62 October, 1959 No. 2

Observations on the Nesting Behavior of Digger Wasps of the Genus Ammophila

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In the course of studies on the behavior of various digger wasps, I have from time to time made a few notes on various species of *Ammophila* (tribe Ammophilini of the subfamily Sphecinae, family Sphecidae). My reasons for publishing these rather fragmentary notes at this time are two. First, I have been much impressed by the variation in nesting behavior which occurs in this genus, both interspecifically and intraspecifically, suggesting that an intensive comparative study of these wasps might yield important results in the field of the evolution of behavior. Second, I would like to re-examine the idea that wasps of this genus sometimes "use a tool" to assist them in closing their nests. The Peckhams (1898) first reported this behavior in *Ammophila urnaria* and considered it an act of intelligence. Many subsequent writers have not hesitated to cite this behavior as evidence of true intelligence in wasps (e.g., Bouvier, 1918; McDougall, 1923; Hingston, 1929). Recent authors have tended to reject the idea of intelligence and to attach much less significance to the Peckhams' observations (e.g., Frisch, 1940; Baerends, 1941; Thorpe, 1956). Nevertheless the subject still fascinates, and the Peckhams' account still makes its appearance, in one form or another, in many popular books (e.g., Cheesman, 1952; Ley, 1955; Hutchins, 1957). Some writers are apparently unaware that there is now a considerable literature on the subject. My own ideas are summarized at the end of this paper.

Most of the specimens of *Ammophila* which I have studied were identified by myself, but wherever there was any question at all on the identity, specimens were submitted either to K. V. Krombein or to W. D. Murray. The lepidopterous larvae taken as prey were identified by J. G. Franclemont (Noctuoidea), W. C. McGuffin (Geometridae), and H. W. Capps (other groups). The dipterous parasites were identified by C. W. Sabrosky and W. L. Downes, Jr. Some of the observations reported for *procera, harti,* and *urnaria* were made by C. S. Lin and C. M. Yoshimoto. I wish to express my thanks to all of these persons for the assistance rendered.

General Remarks on Ammophila

Probably more has been written on the hunting and nesting behavior of *Ammophila* than has been written about any other genus of digger wasps. Fabre (1879-91) devoted parts of three volumes of his

"Souvenirs Entomologique" to these wasps, and many other European workers have published on them since. The work of Baerends on *"Ammophila campestris"* (1941) has become a classic in the field. Adriaanse (1943) demonstrated that *"campestris"* was, ethologically, two species, and that Baerends' observations were actually made on his "B-form," subsequently described as *adriaansei* Wilcke but later shown to be identical with Curtis' *pubescens* (Richards, 1946). Unfortunately most references to Baerends' work still call the species *campestris,* although this name properly belongs to a species more common farther south, the subject of studies by Grandi and others. Be that as it may Baerends' work is without rival in the field, and there has been no better demonstration of the value of ethological studies in taxonomy than the work of Adriaanse.

Studies of the American species have lagged far behind those on the Palaearctic species. Although the literature is fairly extensive, most of it consists of short notes or of lengthy speculations made from a few observations. I believe the time has come to cut away the shrubbery of speculation and to try to lay the groundwork for a serious comparative study of the American members of this genus. Over 30 species occur in America north of Mexico, and many of the species are common enough to provide excellent material for detailed field studies. I have found the species of *Ammophila* unusually easy to work with; they are large, mild-tempered, and almost impossible to disturb permanently once they are in the process of digging, stocking, or closing a nest.

Ammophila is one of two genera of the tribe Ammophilini. The other genus, *Podalonia,* is in some ways more primitive structurally, and is strikingly more primitive ethologically in that the nest is constructed only after a caterpillar has been paralyzed (in the manner of most Pompilidae). The species of *Ammophila* dig the nest first, close it temporarily, then obtain one or more caterpillars with which to stock it. The majority of species practice mass provisioning, that is, they place the full complement of caterpillars in the cell within a short period, then close the nest permanently and prepare a new one. Others provision progressively, making the final closure only after the larva is quite large; some of these species (*pubescens,* at least) maintain more than one nest at a time. In a sense the Ammophilini are a microcosm of much of the behavioral evolution of family Sphecidae; however, none of the species make multicellular nests or nest elsewhere than in the soil.

The egg is laid on the side of the abdomen of (usually) the first caterpillar placed in the nest. Its upper end is closely fastened to the integument, and the larva begins to feed through the integument at this point of attachment. With its long "neck" the wasp larva reaches around inside the body of the caterpillar and completely hollows it out, leaving the head capsule and the more or less intact body integument. The egg stage usually takes about two days, the larval stage about five days. The larvae of several North American species

have been described by Evans and Lin (1956) and by Evans (1959). The cocoon of *procera* has been described by Krombein (1955).

ACCOUNTS OF INDIVIDUAL SPECIES

In the accounts which follow, I have occasionally made direct reference to my field notes, citing the notes by number. These notes, and accompanying specimens of wasps, prey, and parasites, have been placed on permanent file at Cornell University. A brief review of published observations on each species follows the account of my own observations. I do not pretend that these reviews are complete or that I have done full justice to the work of previous authors. The time is not yet at hand for a comprehensive review of the ethology of all the American species.

Ammophila procera Dahlbom

I have observed one aspect or another of the nesting behavior of this widely distributed species 30 times; 29 of these observations were made in two localities in Pottawatomie Co., Kansas, the remaining one at Ithaca, N. Y. In my experience, *procera* prefers small, flat sandy areas not far removed from trees. The nests are dug in sand which is fairly compact but not overly coarse or hard-packed. Hunting is done in trees well above the ground, and the caterpillars taken are tree inhabiting forms.

My first acquaintance with *procera* was on June 13, 1952, at Blackjack Creek, near Manhattan, Kansas (note no. 51). A female walked into a bare strip of sand along the edge of a cornfield. She was carrying a large caterpillar (*Nadata gibbosa* Smith), holding it with her mandibles on the ventral side behind the hind legs; the caterpillar was venter-up, head-forward, and for the most part did not drag on the ground. The abdomen of the wasp moved up and down rhythmically as she walked along rapidly. The wasp was later found to weigh .18 grams, the caterpillar 1.08 grams, six times as much as the wasp. Once the wasp left the caterpillar briefly as she explored ahead; then she returned and carried it the last 5 meters directly to her nest. She deposited it on the ground, opened her nest by removing several small clods of earth with her mandibles, then entered the nest backward and dragged the caterpillar in behind her. In only a few seconds she reappeared and began to search about for lumps of earth, which she would pick up with her mandibles and either reject or carry into the burrow, depending, I suppose, on their size and consistency. The lumps were placed near the bottom of the burrow and she scraped sand over them. When the burrow was nearly full she took a small lump of earth and ground it down into the burrow with her mandibles. She also packed the earth in the burrow with the ventral part of her head, with her mandibles spread widely. Then she scuffed a little sand over the top and departed.

The nest was dug out and found to be oblique, reaching a depth

of 8 cm and terminating in a horizontal cell 3 cm long and 1.5 cm high. The egg of the wasp, about 3.5 mm long, was laid on the side of the second abdominal segment of the caterpillar, which was well paralyzed. The egg hatched in a rearing tin in two days, and the larva grew steadily for five days, when it began to spin its cocoon. An adult male emerged from this cocoon July 15, 26 days after the spinning of the cocoon.

Digging of the nest was observed in the same area a few days later (June 17; note no. 67). The wasp bit off chunks of soil with her mandibles, forming a small ball of earth between her mouthparts and her front legs. She then flew off about 30 cm, about 10 cm high, and dropped the pellet on the ground. This was repeated many times, rather rapidly, much of the soil being deposited in the same small area. When the nest was completed, she selected several small chunks of earth to close off the entrance, then scraped a little sand over the top.

Subsequent observations confirmed various points and added many details on individual variation. One wasp (no. HE72), in the same area, carried the sand from her nest rather than flying with it, leaving the sand all in a small pile about 15 cm from the nest. All others observed flew with the soil. The temporary closure of the nest usually consisted of several clods of earth, but some used bits of leaves or sand burs; one individual (no. CL24) used a single acorn and another (no. 471) a single rabbit dropping. In making the final closure, one individual used two sand burs and a piece of dried leaf (no. 122), another several pebbles (no. 1474). In some cases some of the same objects had been used for the temporary closure. In searching for objects with which to close the nest, wasps would sometimes go several meters away from the nest. If an object was placed in the burrow and found to be unsuitable, it would be removed and often carried away from the burrow a distance of several centimeters and discarded.

Details of the final closure varied from individual to individual, but always followed the same pattern: solid objects to close lumen of burrow, sand to fill burrow, sand or lumps of earth packed into the top of the filled burrow, sand scraped over the top. When packing, the mandibles are parted and the head moves up and down vigorously; at the same time a loud buzzing noise is emitted. In no instance did I see a wasp actually hold a pebble in her mandibles while packing, although one wasp appeared to lift each pebble up and place it down again several times before finally leaving it in the burrow (no. 1474).

Nineteen nests were dug out. The burrow was found to be usually oblique but sometimes vertical; in a few cases the burrow entered the soil obliquely and then became nearly horizontal. Cell depth varied from 1.5 to 10 cm, with most cells between 7 and 10 cm (avg. 7.2 cm). One unusual nest (no. 320) is not included in these figures. This wasp spent considerable time circling about with her caterpillar before finally dragging it into what appeared to be a

burrow of *Bembix belfragei* Cresson. After a moment the wasp emerged and selected several bits of earth and horse dung to close the burrow; she then proceeded to make a final closure in the usual manner, but did not level off the pile of sand at the entrance which the *Bembix* had left. This burrow was found to reach a depth of 23 cm, but the closure occupied less than half of the burrow, the lower part being left open. Almost certainly, this *Ammophila* had mistaken the *Bembix* burrow for her own.

Every nest dug out contained only a single caterpillar. The egg was found to be laid on the second abdominal segment in four instances, on the third in ten instances, and on the fourth in three instances. All caterpillars belonged to the family Notodontidae with the exception of one noctuid which could not be identified further (no. L57). Fifteen of the notodontids were identified by J. G. Franclemont as follows: *Nadata gibbosa* Smith—12; *Heterocampa manteo* Doubleday—1; *Schizura ipomoeae* Doubleday—1; *Symmerista* sp.—1. *Nadata gibbosa* was used as prey both in Kansas and at Ithaca, N. Y.; it is an oak feeder.

None of the nests in the Kansas localities were parasitized, although in one instance (no. HE72) a small fly was observed near a wasp which was digging a new nest; this fly was attacked by the wasp and driven away. At Ithaca, N. Y., a fly was seen lurking about a nest during the final closure (no. 1474). When this nest was dug out two days later the egg of the wasp had disappeared and six small maggots were feeding on the caterpillar. These maggots reached a large size in two more days and shortly thereafter formed their puparia in the soil beneath the cell (Aug. 2). The following April a single *Senotainia vigilans* Allen emerged from one of these puparia.

The several published observations on this species can be reviewed only briefly. Pergande (1892) observed a female piling pebbles over the top of a filled nest; this nest was dug out and found to contain a single *Heterocampa subalbicans* Grote (=*manteo* Doubleday) (Notodontidae) bearing the wasp egg. The more detailed observations of Hartman (1905) are provided with excellent photographs. Hartman reports that the earth is carried from the burrow over the ground and deposited a short distance away. Larger individuals, he states, use a single caterpillar per nest, in this case a tomato hornworm (Sphingidae), while smaller individuals use several caterpillars per nest.[1] The egg is laid at any point from the third to the seventh abdominal segment. The final closure is made by placing bits of debris in the burrow and "scratching in . . . sand . . . and tamping it down with her head. When the nest is full enough for the wasp to reach down comfortably she presses the pieces firmly down before

[1] This remark leads me to believe that Hartman may have been confusing more than one species under the name *procera*. The size variation in *procera* is not unusual, and no one else has ever observed the species employing more than one caterpillar per nest. Misidentifications are not uncommon in Hartman's paper.

she lets go. . . . It sometimes happens . . . that a piece of wood is pressed down tightly, then pulled out and pressed down again and this repeated several times, so that one might suspect that the wasp were here improvising a tool with which to tamp down the sand."

The "use of a tool" by this species has also been reported by G. C. and E. H. Wheeler (1924), who saw a wasp in northeastern Texas "tamping down filling with a pebble," the body held vertically, "like a pile-driver." I am not aware that any other workers have noted this behavior in *procera*.

Criddle (1924) found this species preying upon Sph[illegible]lae in Manitoba. Of four individuals he watched, three flew with the soil during digging and one ran with it. He noted that during closure the soil is packed with the head and stones are pressed into place in the burrow. Rau (1918, 1922, 1926) on two different occasions saw this species flying with soil from the nest; he reported *Nadata gibbosa* (Notodontidae) as prey and also a noctuid caterpillar. Bohart and Knowlton (1953) also report that this species flies with the soil, "flinging it away with a quick turn of their entire body"; they report Notodontidae as prey, nest depth as 8 inches.

The most extensive recent studies are those of Krombein (1953, 1955, 1958). Krombein reports several species of Notodontidae as prey, only one caterpillar being used per nest. The egg is laid on the side of either the third or fourth abdominal segment. [illegible]reports that the soil removed from the burrow is carried on the wing a distance of 6 to 9 inches from the entrance. Filling consists of sand interspersed with debris. He found the nest depth to vary from 3 to 6 cm. In general, Krombein's observations agree very closely with my own.

Ammophila aberti Haldeman

This species is widely distributed in the western half of the United States. I have observed it nesting once in Grant Co., Kansas, Aug. 18, 1952, and five times on the beach of Laguna Madre, near Port Isabel, Texas, May 8-11, 1958. The species appears to be characteristic of open, semi-arid country, nesting chiefly in firm sand not far from water.

The one individual observed in western Kansas was making a final closure of a nest in flat soil not far from the banks of the Cimarron River (note No. HE106). The wasp picked up a small pebble about five meters from the nest, flew to the nest with it, and pounded the earth in the nest entrance, holding the pebble in the mandibles. Whether the pebble was discarded or used for fill was not noted. She then scraped some sand over the top of the nest entrance. This nest was dug out and found to be oblique, terminating in a cell at a depth of 8 cm. The cell contained 10 caterpillars, all apparently a single species of Geometridae of the subfamily Sterrhinae. Three of the caterpillars appeared to be fresh, but the other seven showed signs of deterioration. The egg was in poor condition and the cell contained

several small maggots, not successfully reared but presumably those of a miltogrammine. Thus provisioning of the nest had apparently taken place over several days, and the female continued to provision even though her egg had been destroyed.

In the Texas locality, several individuals were observed during various stages of nesting, and notes were made on five of these. All nests were in bare places on the upper part of the beach, where the soil was very firm. When digging the nest, the female bites off bits of earth (with a loud buzz) and gathers them into lumps which are held between the mandibles and front legs; she then flies off a distance of from 1 to 1.5 meters (about half a meter high) and drops them on the ground. Most of the soil is deposited in the same general area. After the nest is complete, a temporary closure is made by placing one or more solid objects in the lumen of the burrow and scraping sand over them. In this area pieces of shell or bits of the hard surface crust were used for closing off the burrow.

Several individuals were observed carrying caterpillars, and without exception they carried them in flight, although employing the same grasp as in *procera*. The caterpillar is dropped on the threshold of the burrow; the wasp then removes the closure, enters the nest, turns around, and draws in the caterpillar head first. The egg is laid on the first caterpillar placed in the cell. After each caterpillar but the last, the temporary closure is replaced; after the last one a more elaborate final closure is made. The egg is laid laterally between the second and third abdominal segment (2 records) or between the third and fourth segment (1 record). Only one nest was dug after it was fully provisioned (no. 1542); this nest contained 9 caterpillars, all one species of the genus *Euchlaena* (Geometridae). Most of the other nests contained this same geometrid, but two nests each contained one skipper larva of an unknown genus (Hesperiidae). The burrow was found to be either vertical or slightly oblique, reaching a depth of from 5 to 9 cm (avg. 7.1 cm).

Final closure was observed in detail only once (no. 1542). This individual first placed a small piece of leaf near the bottom of the burrow. She then scraped in some sand, went in and pressed it down with her head, reappeared and scraped in more sand, went in and pressed again, and so on until the burrow was full. Finally she picked up a small seed and pounded the earth over the entrance with it; she then scraped a little more sand and pounded again with another seed. Each time the seed was held firmly in the mandibles and later discarded. She next carried several bits of surface crust and placed them over the entrance. Then she picked up a small stick and used it to pound up the crust; finally she discarded the stick and flew off.

When this nest was dug out, it was found to contain nine rather fresh caterpillars, but the egg had been destroyed by maggots, which were already of fair size. This nest is known to have been provisioned over a period of at least two days, and judging from the size of the maggots, oviposition had probably occured three or four days previ-

ously. Thus some measure of progressive provisioning seems to have occurred. All the other nests dug out contained eggs and up to four caterpillars, but none of these had received the final closure.

The maggots were successfully reared and found to be an undescribed species of the genus *Opsidia* (Sarcophagidae, Miltogramminae). This same species was seen flying about the nest entrances of various digger wasps (chiefly *Bembix*), but it was not observed trailing wasps with prey. Presumably it enters the nest for larviposition.

Ammophila aberti was first studied by Williston (1892, under the name *yarrowi*) in western Kansas. Numerous females were found nesting in hard soil and provisioning their nests with four or five small, green larvae. Closure of the nest, even the temporary closure, was reported to include pressing the soil in the burrow with a pebble which was later discarded. Hicks (1932) later studied this species in much greater detail near Boulder, Colorado, where many individuals were nesting in flat, dry, open areas where the soil was relatively hard. He found that the soil taken from the nest is carried in flight a distance of from a few inches to five feet, a given individual depositing most of the soil in one spot. The nest is provisioned with from 5 to 8 geometrid larvae. These may be brought in over a period of up to 7 days, in which case the larva is quite large during the later stages of provisioning; on the other hand, some individuals complete provisioning rapidly, before the egg has hatched. Hicks believed that more than one nest might be maintained at one time. The nest is about 4 cm deep, the cell 3.5 cm long. The egg is, of course, laid on the first caterpillar placed in the cell. Hicks found *aberti* to be attacked by the miltogrammine fly *Hilarella hilarella* (Zett.) and the chrysidid wasp *Chrysis perpulchra* Cresson.

Most of Hicks' paper has to do with the "use of a tool" by this species. He found that females sometimes leave a nest temporarily before finishing it, and even then they make a temporary closure, sometimes pounding the soil in the burrow briefly with a pebble. The closure made between trips for prey is more thorough than this, the final closure still more thorough. Invariably pebbles of a certain size are selected and "used as a hammer." "Sometimes the wasp vibrated it in place between hammer-like strokes." The pebble is sometimes left in the burrow, sometimes discarded. In his many observations, Hicks noted relatively little variation in the manner of closing the nest.

Amnophila placida Smith

I found this species nesting in great numbers May 8-11, 1958, on the beach of Laguna Madre, near Port Isabel, Texas, in exactly the same area as in the preceding species, thus affording an excellent opportunity to compare the two species. Many individuals were observed in various phases of nesting; in fact, one could walk but a short distance along the beach without hearing the characteristic buzz of a

female digging or filling her burrow. Detailed notes were made on 14 individuals.

Most nests were dug in bare places on the beach, well above the high water mark, but a few were dug close to or beneath halophytes growing on the beach. The earth is scooped out with the mandibles and front legs and is ordinarily carried in flight a distance of 30-50 cm, only a few centimeters high, and dropped on the ground. However, one individual (no. 1531), nesting beneath a large clump of vegetation, where flight may have been difficult, walked from her nest with the earth. In either case the trips from the nest are in various directions, so that the earth is well scattered. A temporary closure is made by placing one or more solid objects — in this area usually bits of shell — in the lumen of the burrow near the top, and scraping a little sand over them.

Many individuals were seen carrying prey, and in every case the prey was carried over the ground in the same manner as in *procera*, although *placida* uses much smaller caterpillars and lifts them well off the ground. The caterpillars were often carried great distances along the beach. In this area only one species of caterpillar was used, a small green skipper (Hesperiidae) of unknown genus and species (50 caterpillars, taken from 14 nests). The number of caterpillars per completed nest varied from 3 to 5. The egg is laid on the first caterpillar placed in the nest. It was found to be laid on the side between the first and second abdominal segment (5 records), between the second and third segment (1 record), on the side of the third segment (1 record), or between the third and fourth segment (1 record).

The nest is a simple burrow, vertical or nearly so, terminating in a horizontal cell about 2.5 cm long. Cell depth varied, in this area, from 4 to 10 cm (avg. 6.7 cm). Burrow diameter approximated 6 mm. Some individuals, at least, tend to make several successive nests in the same small area. Wasp no. 1531 had apparently prepared three successive nests only about 5 cm apart. Most nests are dug in the morning, provisioned during the day, and given a final closure in the late afternoon. However, some nests were not completely provisioned and closed until the second day.

The final closure of the nest of this species is a most unusual performance and was observed many times. The closure requires about 30 minutes, and during much of this time the wasp buzzes so loudly that she can be heard some distance away. The burrow is first closed off near the bottom with a piece of shell or plant material which is selected from the objects lying about the nest entrance. The wasp then begins to dig a new burrow 1-2 cm away, using the soil from this burrow to fill the original one. The soil is carried in lumps from the new burrow to the old, then packed into place with the head, which is moved up and down rapidly while the wasp emits a loud buzzing sound. When the burrow is completely filled, soil is scuffed in various directions over the top, and in most cases lumps of earth

and bits of twigs and other vegetation are placed over the filled burrow. The new or "false" burrow is left open and abandoned. There was considerable variation in the depth of the false burrow, and, as might be expected, the deeper false burrows invariably were associated with the deeper true burrows. In nests in which the true burrow varied in depth from 4 to 6 cm, the false burrow varied in depth from 1.5 to 3 cm; in nests in which the true burrow was 8 to 10 cm deep, the false burrow was from 4 to 4.5 cm deep. The average depth of the false burrow for all nests in which measurements were taken was 3 cm.

The egg of this species hatches in two days and the larva reaches maturity after about five days of feeding. The caterpillars remain fresh and relatively lively until consumed by the wasp larva. Nearly every nest dug out was found to contain fecal pellets of the caterpillars. One larva which spun its cocoon on May 17 produced an adult on August 16.

Two nests (nos. 1513, 1536), when dug out, were found to contain several maggots which had destroyed the egg of the wasp and begun to feed upon the caterpillars. These maggots were removed to rearing tins and in both cases formed their puparia six days after the nest was provisioned. Puparia from both nests later produced adult miltogrammine flies determined by W. L. Downes as a new species of the genus *Opsidia*. This same species was also reared from nests of *A. aberti* in this area. These flies were not observed following wasps laden with prey; presumably they enter the nests for larviposition.

The published observations on this species were all made in localities farther north, and differ considerably from those made by the present author in southern Texas (although agreeing fairly well among themselves). Walsh and Riley (1869) reported on some observations made in southern Illinois, Rau and Rau (1918) on observations made in Missouri,[2] and Standtmann (1945) on observations made in Ohio. All three reports state that a single caterpillar is used per nest; all three state that cutworms (Noctuidae) are used as prey, although the Raus state that hesperiid and geometrid larvae are occasionally used as well as noctuids. Walsh and Riley and the Raus report that the cutworm is carried over the ground as I have described; Strandtmann did not observe this aspect of the behavior. The Raus and Strandtmann both state that the soil removed from the burrow is carried away from the nest on foot; the Raus state that it is piled in one place, Strandtmann that it is scattered in different places. These authors do not describe a distinct "false burrow," but Walsh and Riley say that their wasp (observations quoted from T. A. E. Holcomb) "commenced digging a second hole. . . about an inch away from the first;

[2] Walsh and Riley and the Raus use the name *pictipennis* Walsh for this species. In the former case there is little doubt that the species referred to is the one now called *placida* Smith, but in the case of the Raus there is a possibility that the species concerned was actually *fernaldi* Murray.

and with the dirt that came out of this she filled up the first hole. . . ." The Raus remark that if the wasp "uses all the loose dirt lying nearby, she. . . simply bites some more loose. . . from the surface of the ground and uses that."

Strandtmann mentions that the wasp picks up small pebbles near the nest and presses them in the burrow. "When the hole was nearly full," he states, "she scratched loose sand into the opening and pressed it down with a small pebble held in her mandibles." He reports that the pebble is sometimes left in place, sometimes removed and used again for further pounding. The Raus discuss at considerable length the "use of a tool" by this species. They observed numerous individuals and found relatively little variation in this behavior. At first the burrow is packed with loose dirt only. When the burrow is still about one-fourth inch deep, the wasp placed a series of clods of earth in the burrow, grinding each into dust. When the burrow is full, a firmer clod or piece of wood is selected, with this "she rubs, pounds and hammers down the dirt on the top of the hole until all traces of the fill are obliterated. When she has finished. . . she throws her tool aside a few inches. . ."

Allen (1926) reports that both J. B. Parker, at Washington, D. C., and M. R. Smith, in Mississippi, found the miltogrammine fly *Hilarella hilarella* (Zett.) attacking "*Sphex extrematata* var. *pictipennis* Walsh," presumably *Ammophila placida.* Both these observers found only one caterpillar to a nest; in the latter case the corn earworm, *Heliothis zeae* (Boddie) (Noctuidae) was used.

Ammophila harti (Fernald)

This species is widely distributed in the eastern two-thirds of North America but appears to be restricted to open sandy areas. Within its range *harti* is the only species of the genus which normally occurs in large sand dunes, where it is found in association with such digger wasps as *Bembix pruinosa* and *Microbembex monodonta.* I have observed the species nesting ten times; all observations were made during the summers of 1952-53 in four localities in central Kansas.

The nest is dug in sand which is flat or sloping. The sand is picked up in small lumps which are carried a distance of 10-15 cm in flight and dropped on the ground, the wasp returning very quickly to the burrow and scooping up another lump of sand. When the burrow is complete, the wasp walks about seeking a lump of sand or a small stone to close off the burrow. In the search for this, she may walk several meters from the nest, her abdomen held high, forming about a 30° angle with the ground. Various small objects are embraced with the mandibles; when one is found of the right size and consistency it is grasped with the mandibles and front legs and carried on foot back to the nest. One individual (no. 120) failed to find her nest on two different occasions, and had to abandon the pebble and fly to her

nest, then find another pebble. After closing off the lumen with one or more pebbles, the wasp scuffs loose sand into the outer part of the burrow to complete the temporary closure.

The nine nests dug out were all oblique, with a burrow 7.5-12 cm long (avg. 9.6 cm) leading to a cell 3.5-10 cm beneath the surface (avg. 7.0 cm). The cell measures about 1 cm in diameter and 2-2.5 cm long. The egg is laid on the first caterpillar placed in the cell. In three instances it was found to be laid on the side of the second abdominal segment, in one instance on the third, and in one instance between the third and the fourth.

The caterpillars used as prey by this species are all small, looper-type caterpillars, often green in color. Of twenty caterpillars taken from various nests or wasps, three were Noctuidae, probably of the subfamily Acontiinae, and the remaining 17 Geometridae, some of the subfamily Ennominae and some of the subfamily Sterrhinae. The caterpillars are carried to the nest in a characteristic manner: they are grasped just behind the head and carried in short flights of from .5 to 2.5 meters, the caterpillar dangling freely from the wasp's mandibles. The pause between each flight is brief, so that the wasp seems to be proceeding by a series of long hops over the sand. The prey is, as usual, left at the threshold of the burrow while the wasp opens the burrow; it is then drawn in headfirst from the inside. The largest number of caterpillars found in any nest was four, but the full complement may sometimes be more than this. Since this species provisions progressively, the first caterpillars have been mostly consumed by the time the last ones are added.

Provisioning apparently extends over several days, and the wasp larva is fairly large by the time the last caterpillar is added. Whether this species provisions more than one nest simultaneously remains to be determined. In several nests (nos. CY92, 390, 484, 502) the female provided one or more fresh caterpillars for a fairly large larva, and in each case the only other caterpillars in the cell were partially or wholly consumed. In each case there had apparently been a gap of at least two or three days since the first provisioning and the final period of provisioning. Surely it would seem possible that the wasps may have started another nest in the meantime.

The final closure of the nest does not appear to differ significantly from a temporary closure; a few pebbles are used to close the lumen of the burrow, and the remainder of the burrow is filled by scuffing in sand. No pounding of the sand in the burrow was observed. No parasites were found in association with any of the nests studied.

The observations of the Peckhams (1900, under the name *polita*) agree closely with mine. They found the species nesting in open sand and preying upon four species of small caterpillars; the caterpillars were carried to the nest in short flights as I have described. They found the burrow to be five inches long, the cell two inches beneath the surface. The nest was provisioned progressively with 5 or 6 caterpillars. Rau (1922) observed this species (under the name *argentata*)

nesting in a sandy area and carrying the sand from the nest on the wing; the prey was found to consist of Geometridae. My report (Evans, 1958) that this species employs mass provisioning is in error.

Ammophila juncea Cresson

Nothing has previously been recorded on the nesting behavior of this widely distributed but relatively uncommon species. I have observed it nesting four times, during the summers of 1952 and 1953, in three different localities in Pottawatomie Co., Kansas. In each instance it nested in a somewhat restricted area of sand in the vicinity of trees. The caterpillars used as prey were tree-dwelling species of the families Notodontidae and Noctuidae. Only one of the caterpillars was actually determined, the others used for rearing larvae; this was identified as *Macrurocampa marthesia* (Cramer), a notodontid which feeds on oak.

The nest is dug in flat sand, often near or beneath herbaceous plants. The sand is carried from the burrow in flight and dropped on the ground about a meter away, most of the sand being dropped in the same general area. A temporary closure is made by placing several small solid objects near the top of the burrow and filling the rest with sand. One wasp (no. HE79), nesting near a railroad track, used four black cinders to close off the burrow; another (no. HE81) used one large lump of earth and two smaller ones.

All four burrows were L-shaped; that is, the burrow was straight or nearly so, leading to a horizontal cell. Cell depth varied from 4 to 6 cm (avg. 4.8 cm); cell length varied from 25 to 35 mm. Three of the four nests had received the final closure when dug out; two of these contained one caterpillar and one contained two. In all four instances the egg was laid on the side of the third abdominal segment; in the nest containing two caterpillars (no. 332) the egg had been laid on the second caterpillar placed in the cell rather than the first. The caterpillar is carried to the nest over the ground in the manner described for *procera*.

Final closure of the nest showed some variation from one individual to another. No. HE79, which had used black cinders in the temporary closure, also used such cinders to block off the burrow in the final closure. She then scraped sand into the burrow until it was nearly full, then added more cinders, putting each in place with a certain amount of pressing, but no pounding. No. HE81, after filling the burrow nearly to the top, picked up a small lump of earth and pounded the sand in the burrow while holding the lump in her mandibles. No. 332 placed a number of lumps of earth in the burrow and ground each of them up by pounding and chopping with her mandibles. In each case the burrow was eventually concealed well by kicking sand over the top in various directions.

One wasp (no. 537) was followed by a small fly which hovered about 5-10 cm behind her as she carried her prey to the burrow. The fly apparently did not larviposit on the prey, as no maggots were found

in the cell when it was dug out. The fly was captured and identified as *Senotainia litoralis* Allen.

Ammophila urnaria urnaria (Dahlbom)

This is the commonest *Ammophila* at Ithaca, New York, where I have observed it nesting eight times. The species is characteristic of open country and nests in gravel pits, waste places, and gardens, often where the soil is fairly firm. The small caterpillars which serve as prey include species which feed in trees as well as species which feed on herbaceous plants, so apparently *urnaria* hunts rather widely. Digging of the nest was observed only once, on June 28, 1954 (note no. 687). This individual began a nest about 3 p.m. and completed it 30 minutes later. The earth was removed from the burrow in small lumps which were carried between the mandibles and front legs, over the ground, and deposited 10-20 cm from the hole, mostly in one small area. The temporary closure of this nest consisted of 5 small pebbles plus a small amount of sand. Other nests appeared to have been closed by only one or two pebbles or lumps of earth.

The caterpillars are carried to the nest in the same manner as in *procera,* although because of the small size of the caterpillars they are usually lifted well off the ground. In one instance (no. 1500) a female was seen to fly a considerable distance with her caterpillar, landing not far from the nest and carrying it over the ground the remaining distance. Most characteristically, the wasp would proceed over the group in nearly a straight line until she arrived in the vicinity of the nest, whereupon she would circle about until finding the nest. No. 1551, which I found after she had just stung a caterpillar in my garden on July 13, 1958, proceeded to the edge of the garden between two rows of peas, then made a right angle turn and followed a furrow for about 4 meters. At this point she made another right angle turn away from the garden and proceeded for one meter through a dense tangle of weeds, where she located her nest without any circling whatever. This was the first return of the wasp to her nest in three days (it had rained continuously the preceding two days, and the nest had obviously not been reopened since the rain). Once at the nest, the wasp deposits the caterpillar a short distance from the entrance, removes the closure, and draws the caterpillar in from the inside.

The number of caterpillars used per nest seems to vary considerably. Two nests which had received the final closure contained only one caterpillar (nos. 1013, 1202); in both cases the caterpillar was a large geometrid of the subfamily Ennominae. Three other nests contained two caterpillars each; no. 671 contained two *Scoliopteryx libatrix* L. (Noctuidae), no. 1551 two *Autographa* sp. (Noctuidae), and no 1119 one *Panopoda* sp. (Noctuidae) and one geometrid larva of the subfamily Ennominae. Another nest (no. 918) contained six small geometrid larvae.

The burrow of this species may be vertical or oblique. Cell depth,

in the nests examined, varied from 2 to 5 cm (avg., 3.7 cm). Cell length varied from 1 to 1.25 cm. The egg is laid on the first caterpillar placed in the nest. In four cases it was found to be laid on the side of the fourth abdominal segment, in two cases on the third, in one case between the third and fourth, and in one case between the second and third.

Although this species mass-provisions its nests, on some occasions provisioning may not be completed until after the egg has hatched. No. 918 placed a caterpillar in the nest and made a final closure on Sept. 9, 1954; this nest was dug out immediately and found to contain two fresh caterpillars and four older ones which had been partially consumed by the half-grown larva. No. 1551, mentioned above as having returned to her nest following two days of rain, placed her second caterpillar in the nest after the egg had already hatched.

Final closure of the nest was observed several times. No. 1013 closed off the lumen of the burrow with a single large lump of earth which she selected from several lying near the nest; she then alternately scraped in soil with the legs and packed it in place with the head, her mandibles open wide. When the burrow was filled she scraped more sand over the top, concealing the nest well. She did very little buzzing, and at no time did she pick up pebbles or lumps of earth other than the first one. No. 1551 behaved somewhat similarly, but on three or four occasions picked up small pebbles, pounded with them, then rejected them. Most of the pounding, however, was done with the head itself, with the mandibles open wide as usual.

The work of the Peckhams (1898) on this species is well known. They found numerous individuals nesting in their garden, taking their caterpillars mostly from among weeds and bean plants. Usually two caterpillars were used per nest, but one nest contained only one large caterpillar. The egg was found to be laid on the side of the third or fourth abdominal segment. They found that mass provisioning is ordinarily employed, but one individual brought in her second caterpillar after the larva was at least a day old. Closure of the nest varied greatly from one individual to another, and one particular wasp picked up "a small pebble in her mandibles and used it as a hammer in pounding"; they claim that this wasp "improvised a tool and made intelligent use of it." These remarks of the Peckhams have been widely quoted, and their sketch has been reproduced in many books.

Parker (1915) also studied this species briefly. He states that the soil dug from the nest is usually carried a short distance on the ground and deposited, but one individual was seen to fly with the soil. The caterpillars are carried over the ground to the nest, but occasional flights of a foot or more may be made. He dug one nest which contained five caterpillars, four small Geometridae and one larger specimen which appears from his photograph to be *Polia adjuncta* Boisduval (Noctuidae). The egg was laid longitudinally on the side of a very slender geometer. The paper of Frisch (1940) is primarily a criticism of the Peckhams' claims regarding this species, but he ap-

parently had made some observations on *urnaria*. He says, for example, that he found a nest with two cells. So far as I know, this is the only report of any species of *Ammophila* making more than one cell per nest.

Ammophila aureonotata Cameron

I have observed this species nesting only once, on the campus of Kansas State College, Manhattan, on July 10, 1942 (note no. HE4). At 1 p.m. I noticed a wasp and its caterpillar struggling on a sidewalk; the caterpillar, a notodontid of the *Heterocampa*-group, may have fallen or been flushed by the wasp from a tree directly overhead. When first seen, the caterpillar was twisting back and forth violently and the wasp was buzzing its wings and applying the tip of its abdomen to various points on the body, presumably stinging it in various places. As the caterpillar became somewhat subdued, the wasp grasped it dorsally and posteriorly with her mandibles and stung it once, much more slowly, between the abdominal prolegs. She then turned around and grasped the caterpillar just behind the head and stung it again between the thoracic legs and again on the venter just behind the head. The caterpillar was by this time completely quiet, and the wasp began to squeeze the thorax with her mandibles and lap up the blood which exuded from the wounds. She did this off and on for 30 minutes, carrying the caterpillar about a meter in the meantime. The caterpillar was carried over the ground in the same manner as in *procera;* the abdomen of the wasp was held high and moved up and down rhythmically. Finally she carried the caterpillar directly to her nest, which was beneath a currant bush about 6 meters away. She placed the prey just outside the burrow while she removed the closure, which consisted of a single dried, wrinkled leaf, then pulled it into the nest from the inside. She then placed several pellets of earth and bits of leaves in the burrow with her mandibles and scraped a little soil into the burrow with her forelegs. The nesting process took only five minutes, and the top of the nest was not smoothed off or covered in any way. The burrow was L-shaped, only 5 cm deep. It was dug out with some difficulty, since the soil was a hard-packed loam and full of roots. The egg was dislodged from the caterpillar during digging.

The Peckhams (1898) reported briefly on two specimens of this species (under the name *gracilis*). One of them carried a large green caterpillar out of a woods and through a garden, covering 261 feet in about two hours, before finally abandoning the prey. The second one dug a nest in a garden, made a temporary closure with bits of cornstalk and pellets of earth, but failed to provision the nest. Rau (1922) reported the species (under the name *abbreviata*) preying upon skipper larvae (Hesperiidae). Krombein (1958) observed an individual carrying a notodontid caterpillar, *Heterocampa guttivitta* (Walker). The caterpillar was deposited at the edge of the burrow while the

wasp removed the temporary closure by flying backwards with the litter and dropping it on the ground. The burrow was filled by scratching in sand and packing it in place with the under side of the head, with the mandibles open. The egg was found to have been laid on the side of the fourth abdominal segment.

Ammophila nigricans Dahlbom

I have on three occasions seen this species at Ithaca with its caterpillar, but in no case did I follow the wasp to its nest. In all three instances the wasp was seen in small sandy areas in the proximity of woodland. The caterpillars used as prey are very large, and as a result the wasp and prey are very conspicuous as they proceed over the ground. No. 713 carried a full-grown larva of *Euparthenos nubilis* Hubner (Noctuidae). The caterpillar was dragged along the ground in the manner of *procera,* but was so large the wasp could barely straddle it. The wasp was 23 mm long and weighed .1 gm; the caterpillar was 43 mm long and weighed 1.3 gm, or 13 times as much as the wasp. No. 1136 also carried a larva of *Euparthenos nubilis.* No. 1560 carried a larva of *Zale* sp. which was nearly 60 mm long; this caterpillar was carried sideways rather than venter-up, probably because the curvature of its long body made the usual manner of carriage very difficult. In all three cases progress was very slow; in no case did the wasp use its wings for propulsion and in no case did the abdomen work up and down rhythmically as sometimes occurs in *procera* and *aureonotata.* Both caterpillars feed on the foliage of trees, the *Euparthenos* on *Robinia,* which grows commonly in sandy soil in the Ithaca area.

Rau (1934) reports that this species constructs an L-shaped burrow only 4 cm deep, each nest containing only one caterpillar. The egg in two instances was found to be laid on the side of the second abdominal segment, in one instance on the third. He states that "two of the caterpillars were encrusted with earth; this indicated that they were subterranean. . ."; apparently they were not actually identified. Strandtmann (1945) found the species preying upon *Catocala* sp. in Ohio and using only one caterpillar per nest. The one nest he dug out had an oblique burrow reaching a depth of only 4 cm. The wasp egg was attached to the second abdominal segment.

Ammophila xanthoptera Cameron

This species has been the subject of an excellent study by Hicks (1932), who found it nesting in the moist, sandy soil of a river bed near Los Angeles, California. The prey consisted mostly of the noctuid *Zale lunata* (Drury), and only one caterpillar was used per nest. The soil is dug from the nest in the usual manner and carried on the ground a short distance from the nest entrance, where it comes to lie

mostly in one small area. The temporary closure consists of a lump of sand plus some loose sand which is scraped over the top. The nest varies from 28 to 65 mm deep, the average about 55 mm. The caterpillar is carried to the nest over the ground and placed in the nest in the usual manner. The egg is laid on the first to the fourth abdominal segment, usually on the second.

A considerable section of Hicks' paper is devoted to a description of the final closure of the nest. Much of the sand for filling the burrow is obtained by digging in one spot, so that a small tunnel is dug much as I have described for *placida*. The sand is spread out in the burrow by the head, with the mandibles opened widely. Toward the end of filling, the wasp selects a small pebble and uses it to pound the sand in the burrow, sometimes discarding the pebble and sometimes leaving it in place. Although much variation was observed in the details of final closure, all wasps made use of one or more pebbles for pounding. In fact, they also did this even when filling up the burrow which had been dug to obtain soil for the true burrow.

Ammophila pruinosa Cresson

Hicks' (1933) observations on *Sphex breviceps* (Smith) probably apply to *pruinosa* Cresson. The latter name is cited as a synonym of *breviceps,* although the two species are now regarded as distinct. He reports that this wasp uses several small moth larvae per nest, "often apparently including many species"; the specimens of prey of *pruinosa* I have seen in collections consist of very small microlepidopterous larvae.

Hicks found that the soil is usually carried from the nest on the wing, although one wasp nesting in midst of grass and debris carried the soil over the ground. The nest is very shallow, only 25 mm to about 60 mm deep. The temporary closure consists of a pebble to close the lumen of the burrow plus some sand scraped over the top. The caterpillars are carried to the nest in flight. Apparently mass provisioning is the rule, although in some nests the egg hatches before provisioning is complete. This species was not observed to pound the soil in the nest entrance either with its head or with a pebble held in its mandibles.

DISCUSSION

The reader will have noted that all species of *Ammophila* appear to exhibit a certain amount of variation in their nesting behavior. In a number of instances (but especially in the case of *placida*), all published observations are not in close agreement with my own. What is needed in this genus is a detailed study of one or more species in different parts of their range in order to determine exactly how much variation does occur among the individuals of a single species and what the nature and significance of this variation is. Until this is done, one must be cautious in his treatment of what appear to be interspecific differences in this genus (see Table I).

TABLE I.—A comparison of ten species of *Ammophila* with respect to some aspects of the nesting behavior[3]

Species	Type of prey	No. of prey per cell	Nest depth in cm	Manner of carrying earth	Manner of carrying prey	Type of provisioning	Use of "tool"
procera	Notodontidae (r. Noctuidae)	One [? several]	7.2 (1.5-10)	Flies (r. walks)	Walks	Mass	No [Yes]

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TABLE I.—A comparison of ten species of *Ammophila* with respect to some aspects of the nesting behavior[3]

Species	Type of prey	No. of prey per cell	Nest depth in cm	Manner of carrying earth	Manner of carrying prey	Type of provisioning	Use of "tool"
procera	Notodontidae (r. Noctuidae) [Sphingidae]	One [? several]	7.2 (1.5-10)	Flies (r. walks)	Walks	Mass	No [Yes]
aberti	Geometridae (r. Hesperiidae)	Up to 10	7.1 (5-9)	Flies	Flies	Delayed [r. mass]	Yes
placida	Hesperiidae [Noctuidae, Geometridae]	3-5 [One]	6.7 (4-10)	Flies (r. walks)	Walks	Mass	No [Yes]
harti	Geometridae & looper-type Noctuidae	Up to 6	7.0 (3.5-10)	Flies	Flies	Progressive	No
juncea	Notodontidae & Noctuidae	1 or 2	4.8 (4-6)	Flies	Walks	Mass	Sometimes
urnaria	Noctuidae & Geometridae	1 or 2 (r. up to 6)	3.7 (2-5)	Walks (r. flies)	Walks (r. flies)	Mass (r. delayed)	Sometimes
aureonotata	Notodontidae [Hesperiidae]	One	5.0	?	Walks	Mass	No
nigricans	Noctuidae	One	[4.0]	?	Walks	Mass	?
xanthoptera	[Noctuidae]	[One]	[5.5 (2.8-6.5)]	[Walks]	[Walks]	[Mass]	[Yes]
pruinosa	[Micro-lepidoptera]	[Several]	[2.5-6.0]	[Flies]	[Flies]	[Mass, r. delayed]	[No]

[3] Based mostly on my own observations. Data enclosed in brackets represent information taken from the literature; such information is cited only when it disagrees with my observations or pertains to species or aspects of behavior which I have not observed. The abbreviation r = rarely.

The most primitive wasps capture and sting a single host specimen, then usually conceal it in some manner, such as in a simple, unicellular nest in the ground, then lay their egg upon it and close up the nest. This sequence of behavior is exhibited by the genus *Podalonia,* which is closely related to *Ammophila,* and by other sphecine genera such as *Prionony*x. All species of *Ammophila* prepare the nest first, then close it temporarily while they undertake their hunting behavior. The stocking of the nest with a single caterpillar is unquestionably primitive; apparently *Ammophila aureonotata, A. nigricans,* and *A. xanthoptera* employ but a single caterpillar, and probably also *A. procera.* Hartman's report of more than one in the latter species in my opinion is questionable. This one caterpillar must, of course, approximate the wasp in size, and can scarcely be carried to the nest in any other way than over the ground. After the caterpillar is placed in the nest and the egg laid upon it, the nest is given its final closure.

It was an important evolutionary step when certain species acquired the ability to seek out a second caterpillar to add to the first. Some species (notably *urnaria* and *juncea*) appear to employ either one or two caterpillars, depending, one supposes, on the size of the caterpillars encountered in their hunting. Perceiving that the nest cell is not full, the female of these species (after oviposition) makes a temporary closure instead of a permanent one and then resumes her hunting activities. The amount of reorganization in the nervous system needed for this would, it seems to me, need to be rather slight. Yet this represents an important break-through in behavior. Once it had been accomplished, species could evolve which could exploit exclusively the smaller caterpillars in the environment. These small caterpillars could more efficiently be carried to the nest in flight. Such species as *aberti* and *placida* appear to represent this stage in behavioral evolution.

But such wasps, depending as they do upon the capture of up to ten caterpillars for a single nest, are sometimes faced with the possibility of being interrupted by darkness or inclement weather before provisioning is completed. I have observed, in *urnaria,* an actual case in which a female was interrupted by two full days of steady rain before she brought in her second and final caterpillar. In such cases, the egg may have hatched and the larva even be fairly large by the time the last caterpillar is brought in. "Delayed provisioning" of this type occurs not only in *urnaria,* but also in *aberti,* which uses up to ten caterpillars and exhibits it much more commonly. There may be some advantages (i.e., a certain amount of selective value) in such behavior; at least, the larva receives fresher caterpillars. True "progressive provisioning," in which the caterpillars are always brought in progressively as the larva grows, is apparently exhibited only by *harti* among the ten species considered. Such a species has a certain amount of "time on its hands" while awaiting the hatching of the egg and the growing of the larva; one species, at least, the European *pubescens,*

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Thus there is a close relationship between the size and number of caterpillars used per nest, the way in which they are carried to the nest, and the type of provisioning employed. It will be noted from Table I that species which fly with their caterpillars also invariably fly with the earth which they dig from the nest; certain species, however, walk with their caterpillar and fly with the earth. To a human observer, the practice of flying from the nest with the earth from the burrow seems to be quicker and to result in a better scattering of the earth. Doubtless this behavior is advanced, since it occurs in relatively few other digger wasps and these rather specialized ones (e.g. *Anacrabro ocellatus*).

In general, the species of *Ammophila* do not appear to be very good lepidopterists, that is, they are not very selective of their caterpillars except as to size. Some species, such as *procera,* seem to hunt mostly in trees, where they take a preponderance of tree-dwelling forms, especially Notodontidae. Species such as *urnaria* and *harti* seem to hunt mostly in herbaceous vegetation, the latter species taking mostly if not entirely "loopers." Differences such as these, as well as the differences which can be noted in choice of nesting sites, doubtless function to lessen competition among the species.

The nests of all species of *Ammophila* are of simple structure and quite shallow. Differences in nest depth reflect, in part, differences in the size of the wasp. For example, *procera* and *urnaria* often nest in proximity, but *procera,* a much larger species, makes nests approximately twice as deep as *urnaria.* However, *harti,* a species no larger than *urnaria,* makes nests approximately as deep as *procera* and deeper than in the large species *aureonotata.* But *harti* nests in sand dunes, where there is danger of the cells becoming uncovered by wind action, and doubtless deeper nests are selected for. *Aureonotata* nests in hard soil and the nests are unusually shallow for so large a species.

Differences in position of the egg on the caterpillar, if any, are largely obscured by individual variation. This is a point worthy of further study, as other genera of wasps do exhibit differences in this aspect of the behavior.

There remains to be discussed the manner of nest closure. There appear to be four major components in this aspect of the behavior. (1) *Blocking* the burrow by placing one or more solid objects in the lumen, these objects being picked up from the ground around the nest and accepted or rejected, apparently, according to their size and consistency. (2) *Filling* the burrow by soil scraped in with the tarsal rake on the forelegs, augmented by lumps of earth or other solid objects added with the mandibles. (3) *Packing* the earth in the burrow (discussed further below). (4) *Concealing* the burrow by scraping earth in various directions over the top and often picking up various objects and placing them over the top. All species exhibit all four steps in

some form or other. They are best developed in the final closure of the nest, but the same elements appear during the temporary closure. Here, however, the blocking objects are placed near the top of the burrow and the other elements are correspondingly reduced. It should be mentioned that two species, *placida* and *xanthoptera,* which nest in rather firm soil, obtain most of the soil for filling by digging in one spot, making in fact a short "false burrow" near the true burrow. This behavior also occurs in the European species *campestris* and has been figured by Adriaanse (1947, Fig. 1).

The packing of the burrow (step 3) requires further discussion. Most of the packing is done with the oral surface of the head, with the mandibles spread widely; the body is held nearly vertically and moves up and down rapidly while the wasp emits a loud buzz. Packing with the head occurs in almost all members of the subfamily Sphecinae, but other digger wasps use the tip of the abdomen for this purpose. The term "pounding" is often used to describe these movements, but seems a bit too strong. The soil is actually pushed downward by the labrum, mandibles, and other mouthparts; a slight rotating of the head assists the up and down movements. As noted above, the filling is often augmented by lumps of earth or other objects picked up from the ground; these objects are selected after a much less elaborate behavior than that involved in blocking the burrow. Generally they are soft lumps of earth which are placed on top of the fill and then subjected to the same packing movements described above, which result in the lump being pulverized and spread out. Occasionally such lumps of earth actually remain in the mandibles during a few up-and-down movements before they are actually pulverized. Should the lump be hard, the wasp may merely force it down into the fill without breaking it. In some instances the hard object, often a small stone, may be held in the mandibles at some length during the packing process. At such times it doubtless functions to pack the soil further. Such objects are not always left in the burrow; after some pounding (the word is more applicable here) the pebble may be taken from the burrow and discarded. Presumably it is to the wasp's advantage that the burrow be packed as tightly as possible with fine-grained earth, and the leaving of pebbles in the burrow might provide undesirable air spaces.

It will be seen that there is a gradual progression from simple packing movements to the actual use of a pebble which is later discarded. At no point do we find evidence of the sudden flash of insight which the Peckhams thought they observed. Even the discarding of the pebble is not remarkable, for in other aspects of closure it is not uncommon for a wasp to remove from the burrow some object which it has just put there. This occurs during blocking, packing, and concealing, in each case the stimulus presumably being such as to indicate to the wasp that the object is somehow "undesirable." A progression such as this from simpler to more complex behavior may be termed an ethocline (Evans, 1957). Each step in this ethocline doubtless serves, in itself, some function of survival value to the wasp.

Some workers have been inclined to give the wasp credit for "using a tool" even if the "tool" is left in the burrow. In this case, however, it is difficult to be sure how much effective packing has occurred; all one can be sure of is that the object concerned has become part of the fill. If the pebble is actually discarded after use, then it has obviously functioned as a pounding instrument only. I suppose such a pebble will fit the dictionary definition of a "tool." Yet I hesitate to use the word in this instance, since to most persons the user of a tool is considered to have some perception of the result to be achieved, that is, to exhibit some measure of intelligence. It seems far more probable that the pounding behavior of *Ammophila* is nothing more than a particular combination of instinctive behavioral elements.

Why is it that some species apparently never "use a tool" (e.g., *harti*), others sometimes do and sometimes do not (e.g., *juncea, urnaria*), and others apparently always do (e.g., *aberti, xanthoptera*)? At this stage in our knowledge of the behavior of *Ammophila* it is impossible to answer this question. The necessary movements are probably available in all species, but it may be that a species such as *harti* lacks, in the innate mechanisms controlling the behavior of closure, the necessary nervous associations which would enable it to use a pebble for pounding. But it must be remembered that *harti* nests in sand dunes, where the soil consists of sand grains of more or less uniform size. It is difficult if not impossible to pack sand into a firm plug. *Ammophila harti* is a specialized species and may well have evolved from a form which nested in other situations where pounding with a pebble would have served a useful purpose; if one could force it to nest in firm soil, he might still be able to elicit this behavior. It is noteworthy that the species which "use a tool" regularly, such as *aberti* and *xanthoptera,* nest in rather firm soil. Species such as *urnaria* nest in rather diverse situations; in some cases the soil texture may be such as to elicit the full gamut of packing activities, while in other situations this may not be so.

Clearly this is a subject worthy of a great deal more study. Three lines of study suggest themselves as worthwhile. (1) More field data must be gathered on more species of the genus and on more individuals of the ten species considered here; these observations must be detailed and especially carefully made with respect to closing behavior. (2) An effort must be made to study one species in the field throughout its range and in all ecological situations in which it occurs. (3) An effort should be made to study one or more species under controlled conditions where he can manipulate such factors as soil texture, availability of various types of objects for filling, and the behavioral thresholds of the wasp.

In spite of shortcomings in our knowledge, two points seem clear. First, some species of *Ammophila* do pick up a pebble or some other solid object and pound the soil in the burrow with it, and some species do it with great regularity. At least 16 observers have seen this be-

havior in at least 9 different species (6 North American and 3 European).[4] Second, interesting though this behavior is, there is nothing about it to justify the publicity it has received. *Ammophila* is very far from being "comparable to the man or ape who first took a stone in his hand to crack a nut" (McDougall, 1923). It has merely found a functional value in combining two or three very simple innate acts in a new way.

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[4] The European species are *heydeni, sabulosa,* and *campestris.* For references and discussion, see Baerends (1941, p. 94) and Thorpe (1956, pp. 248-249). Both these authors, incidentally, come to conclusions very similar to mine. Thorpe says: "those species and individuals which use a pebble as a hammer . . . appear merely to be combining two features of the instinctive hole-filling process in a rather unusual way." But he adds: "since the animal is constantly manipulating clods and stones, it has every opportunity to learn by trial and error, from the chances of its normal experience, the results of handling hard objects of various kinds."

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