

SIMULTANEOUS CARE OF MORE THAN ONE NEST
BY *AMMOPHILA AZTECA* CAMERON
(HYMENOPTERA, SPHECIDAE)¹

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In attempting to trace the origin of social behavior among wasps, in his *Social Life Among the Insects* (1923), William Morton Wheeler selected *Ammophila* as "a paradigm of the whole group of Sphecoids and solitary Vespoids". Were he alive today, and able to utilize all the considerable knowledge of this genus gained in the last three decades, it seems likely that he would embrace *Ammophila* even more enthusiastically as a paradigm not only of the solitary wasps but of several preliminary stages in the origin of sociality.

It has been shown by Evans (1958, 1959) and by Powell (1964) that the North American species of this genus which have been studied can be arranged in series as follows: (1) strictly solitary species which utilize a single large caterpillar per nest, (2) species which mass-provision with two to several small caterpillars, (3) species in which provisioning is commonly "delayed" such that the last prey is brought in after the egg has hatched, and (4) species employing progressive provisioning regularly. Several other aspects of behavior are roughly correlated with this progression: for example, species using smaller caterpillars usually carry the prey in flight, and these same species generally carry the soil of excavation away from the nest in flight. Also, most records of gregarious nesting pertain to species employing progressive provisioning.

It is apparent that the European species can be arranged in a very similar series (Adriaanse, 1947; Teschner, 1959). One European species, *A. pubescens* Curtis, illustrates still a fifth stage in this ethocline: the female maintains two or three nests at one time, remembering the location of each of them accurately and behaving in accordance with the status of the egg or larva in each nest as determined during frequent inspections (Baerends, 1941). Simultaneous care of more than one nest is otherwise virtually unknown among digger wasps, although a few species of Bembicini which make more than one cell per nest are reputed to begin provisioning a second cell

¹Supported by a grant from the National Science Foundation, no. G17497. Most of the studies reported here were conducted at the Jackson Hole Biological Research Station, Moran, Wyoming.

Manuscript received by the editor January 5, 1965

before the previous cell is fully stocked (Janvier, 1928; Tsuneki, 1956).

Powell (1964) suggested that studies with marked wasps might well reveal that some of our North American *Ammophila* maintain more than one nest simultaneously. By coincidence, during the same week that Powell's paper appeared, I was able to establish that this is, in fact, the case. Working along the Snake River in Jackson Hole, Wyoming, I found that *Ammophila azteca* Cameron behaves in a manner strikingly like *pubescens* in almost every detail relating to provisioning. My studies were relatively brief and leave a number of questions unanswered, but they seem worth putting on record at this time with the thought that others may be able to extend our knowledge of this widely distributed species before I am able to do so.

Ammophila azteca has been the subject of three published notes, all of them brief. Hicks (1935) observed several wasps digging and closing nests near Boulder, Colorado (identified as *aculeatus* Fernald, a synonym). Evans (1963) reported on a single nest found in Yellowstone Park, Wyoming, and Powell (1964) presented prey records from California and Baja California. The last two authors both identified the species as *pilosa* Fernald, a name now regarded as a junior synonym of *azteca* Cameron.² I also found one female of this species nesting at Great Sand Dunes National Monument, Colorado (elevation 7800 feet), in August 1964, and have included this record below. This is chiefly a montane species; Powell's records are from 6000 feet elevation in Baja California and over 10000 feet in California; the Jackson Hole and Yellowstone localities where I have worked are both at about 6800 feet. However, Menke (*in litt.*) reports the species from near sea level in California and various places in Canada.

General aspects of ecology and behavior.—Most of my studies were conducted in a small area of flat, bare soil along the Snake River at the Cattlemen's Bridge, about one kilometer east of the Jackson Hole Biological Research Station, Moran, Wyoming. The first observations were made on July 18, 1964, the last observations on August 14. My impression is that this species became active only a few days before my initial observations and that it had nearly completed its nesting season by August 14. In this area, where the active season for most wasps is no more than 4-6 weeks, progressive

²This is a new synonymy, and should be credited to Arnold Menke, who is currently revising the genus *Ammophila* and who has studied Cameron's type. I am indebted to Dr. Menke for identifying the specimens collected in the course of these studies and for critical reading of the manuscript.

provisioning would seem uneconomical unless the wasp is able to maintain two or more nests simultaneously. However, two progressive provisioners which maintain only one nest at a time nested in some abundance in the same area; these were *Bembix spinolae* and *Steniolia obliqua*. The only other species of *Ammophila* found here was a single female *A. macra* Cresson which nested on the edge of the bare soil on August 14; I have presented a few notes on this wasp below, as it presented a striking contrast to *azteca*.

In Jackson Hole, *A. azteca* appeared to be strictly confined to patches of bare, moderately firm, sandy loam along the river; none were seen or taken in general collecting in other habitats. The major nesting area was about 20 meters long and varied from 5 to 8 meters in width, paralleling the river and separated from it only by a narrow, oblique bank which was not used for nesting. Parts of this area were covered with grass and herbs, chiefly around several trees, but these places were not utilized by the *Ammophila*. Also, the *Ammophila* did not nest in a small plot of very loose sand which was occupied by a colony of *Bembix spinolae*. The area was surrounded on the three sides away from the river by open woodland in which the dominant tree was lodgepole pine (*Pinus contorta latifolia*); near the river there were also narrow-leaved cottonwoods (*Populus angustifolia*) and willows (*Salix* spp.). I estimated that there were about 50 females scattered about the nesting area. My notes cover 20 females, but only a few of these were marked, and only four of the marked individuals were followed over a period of days. The most complete observations pertain to no. 2030, which was marked with a red spot on the second day of study (July 19) and followed until August first, including one complete day of observation (July 31) and observations for several hours on five other days.

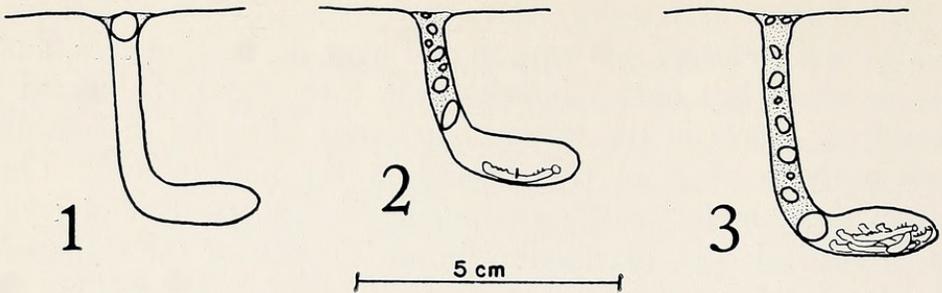
That it was impossible to make continuous records of more than a very few females was a consequence of the fact that females spaced themselves widely, each maintaining a small nesting arena, no more than 30 cm. in diameter, where all her nests were prepared (Figs. 6, 7). These arenas were separated, for the most part, by half a meter or more. On one occasion an unmarked female shared a circumscribed area with a marked female (no. 2028C), the nests of the two being more or less intermingled, but this was exceptional. I observed no aggression among females provisioning their nests, but females digging in proximity would sometimes attack one another. It seems possible that there is a measure of territoriality among females of this species, but since the wasps spend only a small portion of their time in the nesting arenas, contacts between neighboring females are few.

Both males and females were seen frequently on the flowers of *Solidago* and *Erigeron* growing in and near the nesting area, and it is probable that they obtain nourishment throughout the season from this source. Early in the season males were observed in considerable numbers flying close to the ground in the nesting area. On one occasion three males were seen digging intermittently and trying to enter a vertical hole, presumably in anticipation of the emergence of a female. I did not observe mating, chiefly because most of my studies were made a week or more after nesting had begun, when most mating had probably ceased and the males were declining in numbers. Mating in several species of *Ammophila* has been well described (e.g., Baerends, 1941; Olberg, 1959).

As compared to other wasps in this area, *Ammophila azteca* made its appearance rather early each morning (0830-0900) and was active until late in the afternoon (1630). Active wasps were often noted in partial shade or during periods of partial cloudiness, but they invariably disappeared when the sun was heavily obscured for more than a few minutes. I did not discover where they went during these inactive periods or at night. Hicks (1935) found a female of this species "sleeping" on a stem in late afternoon, presumably solitarily. The wasp held her body at nearly a right angle to the stem, grasping the support with her mandibles and some of her legs. A number of species of *Ammophila* are known to sleep in somewhat this manner, often more or less gregariously (e.g., Evans and Linsley, 1960).

Digging the nest. — Nests appear to be started at any time of day, but more especially in the mid-morning hours or late in the afternoon. Digging females periodically produce a "chirping" sound as they break through the soil with their mandibles. One female starting a new nest dug 1 cm in 13 minutes, the second cm in another 7 minutes; she completed the burrow and cell in a total of 58 minutes. This female had previously been digging at another point 10 cm away, but she abandoned this nest after apparently striking a stone; the abandoned burrow was left open.

When the wasp has loosened a small lump of earth, she holds it between her mouthparts and front legs, backs from the burrow, rises into the air a short distance, and with a slight jerk flings it onto the ground. She may fly in any direction from the entrance, but most wasps make the majority of flights on the same side, such that the earth comes to form a diffuse but discernible mound in the form of a small arc. The mound is rarely more than 0.5 cm deep, and varies from 2 to 4 cm wide by at least twice that long, although its borders are ill-defined. In some nests no mound can be seen, as the female



Figs. 1-3. Typical nests of *Ammophila azteca* (all from Jackson Hole, Wyo.) showing the three types of closures. Fig. 1. No. 2018, an empty nest closed with a single pebble and a small amount of sand. Fig. 2. No. 1993, a nest with a single caterpillar bearing the egg, showing a typical temporary closure. Fig. 3. No. 1996, a fully provisioned nest which had received the final closure.

scatters the soil rather widely. In any case it weathers away in a few days, and some of the soil may be used in closures.

There appears to be considerable variation in the distance the female flies with the soil, and consequently the distance from the nest entrance the mound accumulates. In Jackson Hole, most mounds were only a few cm from the entrance (2-6, rarely up to 20). Hicks (1935) observed very similar digging behavior in Colorado, but he found that the soil was carried a considerable distance from the nest, in one case four feet (1.2 m). Hicks timed several females and found that they carried from five to seven loads per minute. "One load", he reports, "was so large and heavy that the wasp was not able to fly with it after a typical and normal fashion and only reached the refuse spot by short flights and hops." Great variation in the distance the soil is carried was noted by Hicks (1932) in another species, *A. aberti*.

Burrow diameter in *A. azteca* is about 5 mm; the terminal cell is horizontal and has a diameter of about 10 mm, a length of 20-25 mm. All burrows at Jackson Hole were vertical or very nearly so; they varied in length from 3 to 6 cm, nearly all of them measuring between 4 and 5 cm (Figs. 1-4). The single nest excavated at the Great Sand Dunes, Colorado, was very similar, having a vertical burrow 3.2 cm long reaching a horizontal cell 2.2 cm long. The nest from Yellowstone was very similar in size but was dug into the sloping of a foot-path and had an oblique burrow (Fig. 5 in Evans, 1963).

Closure of the nest. — As in many species of this genus, three types of closure can be distinguished: initial closure of the empty nest, temporary closures during provisioning, and final closure of the fully provisioned nest. The initial closure consists of a single pebble or hard lump of earth which is placed in the burrow entrance with the

mandibles, often after "trying for size" several such lumps and rejecting each of them until one is found which fits the mouth of the burrow (Fig. 1). A small amount of sand is often scraped over this closure, but no pounding occurs. The wasp normally returns to this nest within a few hours or early the next day with the first prey, on which the egg is laid. The single nest studied at the Great Sand Dunes, Colorado, was like the many observed at Jackson Hole: the female removed a single small stone from the entrance before introducing the first caterpillar and laying an egg upon it.

Following oviposition, and after supplying each additional caterpillar, a very different type of closure is made (Fig. 2). Again, various lumps and pebbles are "tried for size", but this time the initial lump is placed well down in the burrow, at least half way down and often near the bottom; the object selected must lodge perfectly in the burrow so that material may be packed above it (this is the *hauptverschlussklümpchen* of Baerends and other European workers). When the initial lump is in place, the wasp scrapes sand into the nest with her front legs, facing of course away from the hole. She may utilize some of the soil of the mound if this is close by; or if loose soil is not available she may loosen some by biting the ground around the entrance. Periodically small pebbles or bits of earth are picked up and placed in the burrow with the mandibles. From time to time the wasp remains with her head down in the burrow and moves her body up and down, packing the soil in place with blows of the antero-ventral surface of the head in the usual manner of wasps of this genus. When the burrow is full, additional packing occurs, the wasp sometimes retaining her grasp on a small pebble while so doing ("using a tool") and then leaving the pebble in place in the fill (Fig. 8). Finally, sand is scraped in various directions over the top, resulting in thorough concealment of the entrance. The closure is prepared very rapidly and requires only a minute or two; one wasp completed a typical temporary closure in only thirty seconds. It is probable that the same pebbles and lumps of earth serve in successive closures, so one would expect a reduction in the length of time required after the first temporary closure.

Final closure may be indistinguishable from temporary closure unless one follows the provisioning of the nest to determine that this is, in fact, the final closure. My limited data suggest that in the final closure (1) the initial lump is always placed at or near the bottom of the burrow (Fig. 3), and (2) packing with the head is relatively prolonged and some packing while holding a pebble in the mandibles always occurs toward the end of the closure (Fig. 8).

Further studies will be needed to quantify these factors and to determine if there is a real difference between temporary and final closure. The closure observed by Hicks (1935) in Colorado was presumably temporary, since no "tool using" was noted. The wasp studied by Hicks used "an old hackberry seed to close the upper end of the shaft. Sand was scraped in over this, and some score or more of objects were brought to further cover and conceal the nest site".

Provisioning the nest.— Females were observed on several occasions flying closely about low branches of willows and cottonwoods, apparently searching for prey. On one occasion a wasp seized a caterpillar on a willow branch, but the latter thrashed violently and the wasp left without stinging it; this was a considerably larger caterpillar than was ever found in the nests of the wasp. The 44 prey taken from various nests were all of roughly the same size (slender, 12-18 mm in length); all were "naked" larvae, and all were green in color except for a few gray or reddish geometers. Specific identification of the prey was not possible, but many (perhaps all) belonged to groups which feed upon broadleaved trees rather than upon conifers. The following were recovered from the various nests dug out:

HYMENOPTERA [det. B.D. Burks]

TENTHREDINIDAE: NEMATINAE: *Nematus* (*Pteronidia*)
sp. and *Amauronematus* sp. 28

LEPIDOPTERA [det. D.M. Weisman]

GEOMETRIDAE (four spp.) 7

GELECHIIDAE (apparently all one sp.) 8

SPHINGIDAE: *Smerinthus* sp. (early instar) 1

The use of sawfly larvae in considerable numbers is of interest, since Adriaanse (1947) found that *A. pubescens* restricts itself to caterpillars, the closely related *A. campestris* to sawflies. In the population of *A. azteca* studied, several nests contained nothing but sawfly larvae, a few nothing but moth larvae, and a very few (e.g., no. 2012) both sawfly and moth larvae. Individual wasps tended to stock successive nests wholly with sawfly larvae (rarely wholly with caterpillars), but there were numerous exceptions. I noted no shift in type of prey concordant with the progress of the season.

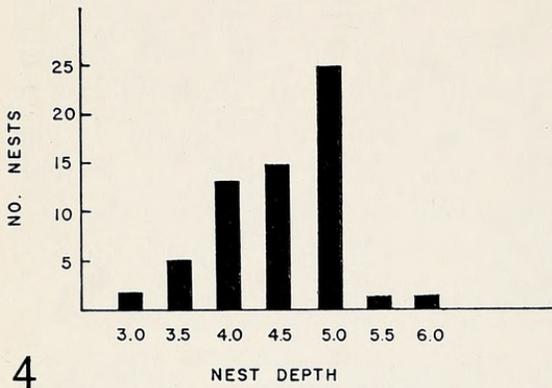
Prey records from other parts of the range of this species indicate use of lepidopterous larvae of several different groups, including relatively hairy forms, but there are no further records of use of sawfly larvae. The single female studied at the Great Sand Dunes brought in a gelechiid larva very similar to those used in Jackson Hole. The nest studied at Yellowstone contained one noctuid, one geometer, and five larvae of lycaenid butterflies (Evans, 1963).

Powell (1964) found a lycaenid larva to be used in Baja California, while in Mono County, California, a larva of the moth family Pterophoridae was employed. As Powell points out, lycaenid larvae are covered with short, secondary setae, while pterophorid larvae have tufts of elongate setae. The caterpillars taken by Powell measured 14 and 15.5 mm in length, while those taken from the nest in Yellowstone measured from 8 to 15 mm in length. Thus it appears that size of the prey is of critical importance, but not its vestiture or taxonomic affinities.

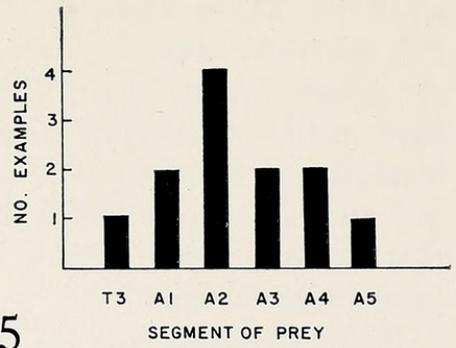
Powell reported that the lycaenid larva was carried in flight, about a meter above the ground. I observed prey carriage in flight once in Colorado and many times at Jackson Hole; in no case did I observe prey carriage over the ground. The female straddles the caterpillar, grasping it with her mandibles a short distance behind the head and during flight embracing the body of the caterpillar with her legs, the prey being venter-up. She lands a short distance from the nest and walks to the entrance, usually without circling or hesitation, then drops the caterpillar at the threshold while she removes the closure. At Jackson Hole, I experienced much difficulty approaching females closely for photography at this time; they would very readily take flight with their prey, often disappearing for several minutes.

Removal of the closure occurs very rapidly, taking only a few seconds if it is an initial closure, generally less than 30 seconds in any case. Soil particles and objects removed from the burrow are deposited within a few cm of the entrance and may be reused when the closure is restored. When the burrow is clear, the wasp grasps the anterior end of the prey with her mandibles and backs into the nest with it. The entire process (arriving with prey — clearing entrance — drawing in prey — reclosing entrance) occurs with remarkable speed, some individuals requiring less than a minute. When it is considered that only from one to four prey are introduced per day, it will be appreciated that even prolonged periods of observation afford one only fleeting opportunities to study this behavior.

In addition to entry with prey, each nest is entered periodically when the wasp is without prey. There are presumably "inspections" which function to impress upon the wasp the size and food requirements of the larva, as Baerends (1941) found to be true in *A. pubescens*. Inspections may occur at any time of day, but most characteristically occur early in the morning (0830-1030). In fact, the first act of each *Ammophila* arriving in the morning consists in entering the nest and closing it again. I did not observe any one female inspect more than one nest at this time; apparently when there



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Fig. 4. Number of nests of *Ammophila azteca* (all Jackson Hole, Wyo.) exhibiting various depths (in centimeters). In each case the measurement was rounded off to the nearest half cm in the field. Fig. 5. Number of examples of oviposition on various segments of the prey (all Jackson Hole, Wyo.). T3 = third thoracic segment; A1 . . . = various abdominal segments.

is more than one active nest, she inspects the one containing a larger larva (see detailed data on no. 2030, below). However, other inspections may occur later in the day (see also below). The entry and reclosure resemble closely the behavior occurring when the wasp is bringing prey.

The maximum number of prey found in any nest at Jackson Hole was six (2030D), but the nest studied in Yellowstone contained seven (Evans, 1963). It appears that about two days are required for hatching of the egg, about five days for larval feeding. Apparently females bring in the last prey and make the final closure when the larva is in the last instar and at two-thirds its full size; thus final closure usually occurs six or seven days after the nest is dug.

Oviposition. — The egg is laid on the first prey placed in the cell. It is glued firmly by the anterior end to the side of the caterpillar, in a more or less vertical position (Fig. 9, lower figure). As in many species of *Ammophila*, there is much variation in the placement of the egg. At Jackson Hole, one egg was found on the third thoracic segment, others on each of the first five abdominal segments, but more on the second abdominal segment than elsewhere (Fig. 5). The single nest studied in Colorado contained a caterpillar bearing an egg on the fourth abdominal segment.

Successive nests of individual females. — As mentioned earlier, it became apparent in the course of studies at Jackson Hole that each female prepares all of her nests in a small nesting arena. It also became apparent that each female prepares an unusual number of nests. For example, when I dug out the nest of no. 2013, an un-

marked female studied early in the season, I found not one nest but six, all in an area measuring 8×14 cm. This was on July 27, and I could not believe that females had been nesting for more than two weeks (I began collecting in this area July 4, and took the first *A. azteca*, a male, on July 7). But if it takes six or seven days to rear a larva, this female should have started nesting at least 30 days earlier (one nest was still unprovisioned). This example and several similar ones made it apparent that some overlapping of successive nests must occur. I therefore marked several individuals and attempted to follow them over several days. Since my observations were not absolutely continuous, and since during the one complete day of observation I could keep only two wasps under full surveillance, because of the wide spacing mentioned earlier, my notes are not entirely convincing except in two cases. The arrangement of successive nests of these two individuals is shown in Figs. 6 and 7, and I here present, in abbreviated form, my field notes concerning one of them, no. 2030, which I painted with a red spot on July 19.

- July 19. Brought prey at 1100 hrs to site A (Fig. 6).
July 20. Working on a nest at B.
July 23. Prey to B at 1530.
July 25. Prey to nest C at 1630.
July 29. Inspection followed by final closure at C.
July 31. Complete day of observation. Arrived in area at 0815.
0845: Wasp appeared at site D and made inspection, followed by temporary closure.
1022: Prey to D, followed by what appeared to be a final enclosure, including "use of tool" and scraping of sand over top for several minutes. Left at 1036.
1037: Reappeared at same site, walked about, flew off.
1047: Reappeared at same site, walked over old nest and around area until 1050.
1053: Back again, walking over nesting arena with her abdomen held high; off at 1055.
1113: Reappeared and began to remove closure at E. This appeared to be a rather thorough temporary closure. After a brief "inspection" she made a hasty temporary closure and left at 1120.
1237: Back to E with a sawfly larva; opened nest and drew it in within one minute of arrival. At closure three pebbles were "tried for size" before finding one which fit the bore of the burrow properly. Left at 1240.
1355: Back to E with another sawfly larva. After introducing

the prey made a fairly prolonged closure which I took to be a final closure but which proved not to be (see Aug. 1). During this she drove away two chrysidids (see below, under "parasites").

- 1400, 1409, 1414, 1445: Each time she reappeared in the nesting arena, walked about for a few seconds to a minute, then flew off.
- 1450: Started digging at G.
- 1457: Stopped digging, leaving hole open, and is now walking about the nesting arena.
- 1502: Digging at G¹.
- 1600: Closed burrow with a single pebble, scraped a small amount of sand over top, and flew off.
- 1632: Landed at nest, then flew to a *Solidago* in blossom two meters away, remained for a few minutes, then was not seen again today.
- August 1. 1020: Landed at G¹, remained two minutes and flew off. This is a cool, partly cloudy morning.
- 1040: Now cloudy and windy (began to rain at 1100). I dug out the nesting arena, eventually finding 12 nests and one incompleated burrow (G) (see Fig. 6). Eight of these had cocoons, one was an empty nest (G¹), one had a single caterpillar with an egg (F), and two had wasp larvae (D and E, closed yesterday, E apparently temporarily, since the wasp larva was small and there were only 3 sawfly larvae in the cell).

Apparently nest F had been initiated on July 30 and was not visited on July 31 (the wasp presumably remembering that it contained an egg and did not require additional prey). Thus we can say that this wasp very definitely maintained two nests simultaneously (D and E), very probably three (if we include F), and that she was associated with three nests in the course of one day (D, E, G¹) while presumably retaining a fourth in her memory. Clearly this calls for a much more detailed study, but it would appear that the models provided by Baerends (1941) for *A. pubescens* apply very well to this species.

Some unexplained features of behavior.— On two different occasions I dug out a series of nests in a single nesting arena and found that all or most of the nests contained eggs. In one case there were six nests, five of them containing a single prey with an egg, the remaining one being empty. In another case there were four nests, all of them containing only one prey; in three cases the prey bore an egg, in the

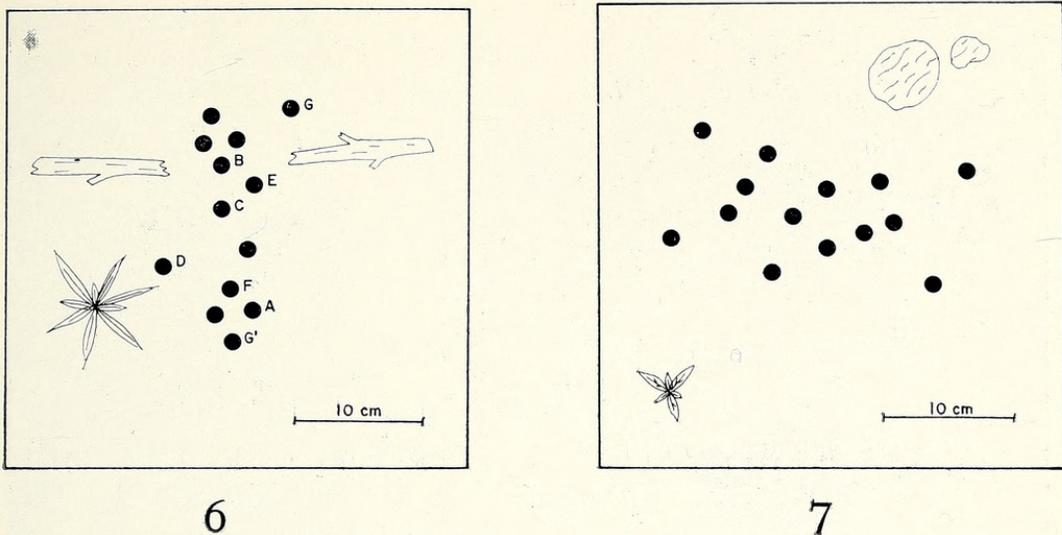


Fig. 6. Arrangement of successive nests of no. 2030. Nests A-G¹ were prepared in that order (see text); unlettered nests were not seen to be dug or provisioned and were presumably completed before the beginning of intensive observations (at least in part). Fig. 7. Arrangement of nests of no. 2031, which nested about 2 meters from the preceding at Jackson Hole.

fourth case a small larva. Unfortunately in both instances the wasp associated with the nesting arena was unmarked, and I did not observe the site for a long enough time to be certain that only one female was responsible for each set of nests. As mentioned earlier, I did find one case in which an unmarked female shared a nesting arena with a marked female. If the above two cases did involve a single female each, then that female must have prepared several nests on the same day, or over no more than two or three days, and laid several eggs in rather rapid succession. When the larvae in these nests approached maturity, the female would have to obtain many prey in order to provision all of these nests. Whether truly synchronous nesting (as opposed to the overlapping of successive nests) occurs in this species remains to be determined.

On one occasion (2007D) I dug out a nesting arena and found three nests, one of which contained one caterpillar, the other two two sawflies each: but none of the nests contained an egg. This suggests that these might have been storage burrows, the prey to be exhumed later and used for oviposition or for feeding a larva. If in fact this species does at times maintain several nests synchronously, then the maintenance of storage nests would seem of great adaptive value, since it would spread out the requisite hunting over a greater number of days. It is possible that the maintenance of storage burrows is not a rare phenomenon in *Ammophila*. Hartman (1905) found two

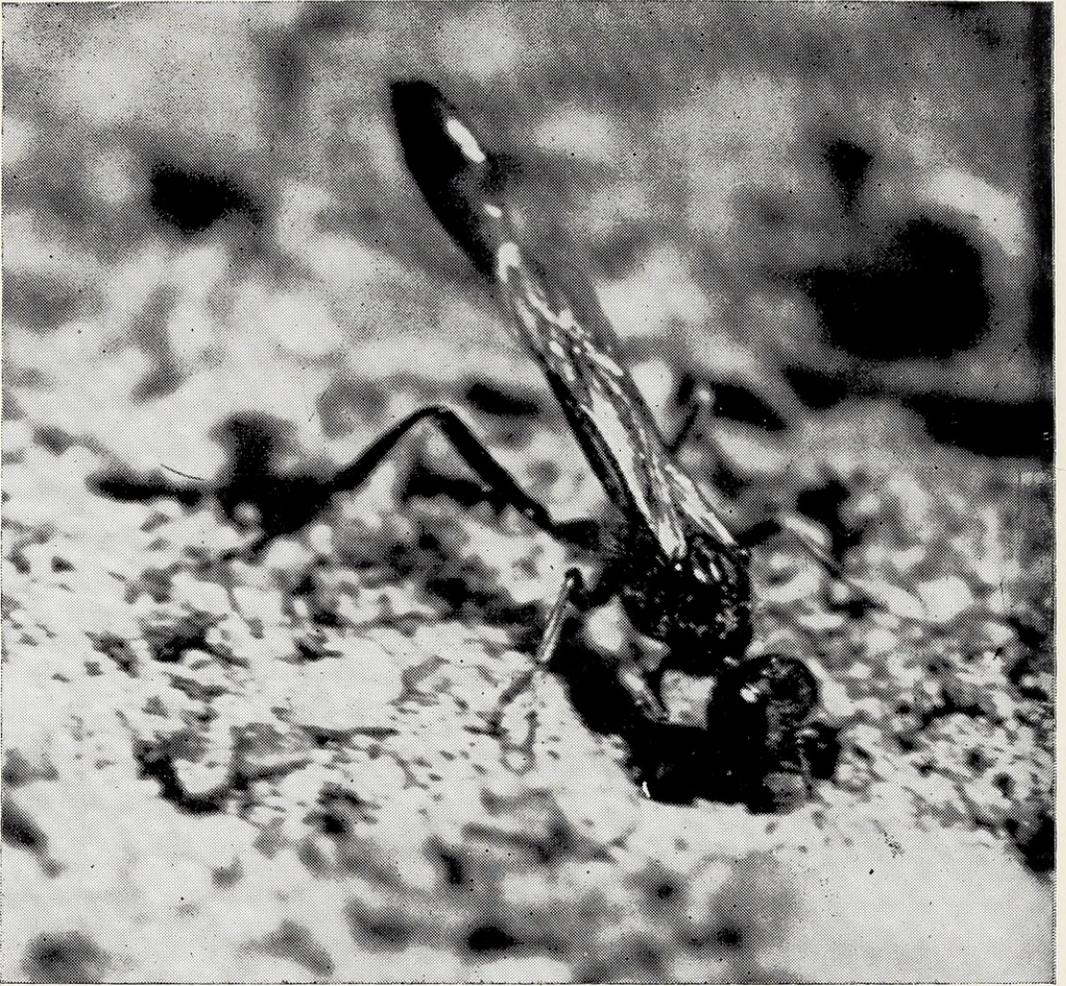


Fig. 8. Female *Ammophila azteca* at final closure of her nest. A small pebble is being held in the mandibles and used for packing soil in the filled burrow.

nests of *A. procera* in Texas which did not contain eggs, Tilden (1953) had the same experience with this species in California, and Criddle (1924) observed a female of this same species in Manitoba place a caterpillar in a nest one day and then dig it out the next day, return it to the nest, and lay an egg upon it. This is an aspect of behavior requiring much further study.

Parasites. — Chrysidid wasps (*Ceratochrysis perpulchra* Cresson) were observed commonly in the nesting area of *A. azteca* at Jackson Hole, but I am unable to state definitely that they were parasitizing the *Ammophila*. The chrysidids would often land on the soil near *Ammophila* nests, and on several occasions they were seen to enter nests either partially dug or partially closed, in which case they were normally driven away by the *Ammophila*. On one occasion a chrysidid returned after the *Ammophila* had completed her closure and spent several minutes around the nest, but I did not see her dig into it.

Notes on Ammophila macra. — As noted earlier, a single female of the large species *A. macra* Cresson was found nesting on the periphery of the *azteca* nesting area at Jackson Hole. She was seen digging her nest at 1100 on August 14. The soil was taken from the burrow in lumps much as in *azteca*, but it was carried over the ground and deposited in a diffuse pile 6-14 cm from the hole. At 1115 the wasp selected a large stone and placed it in the burrow (which was fully 1 cm in diameter). She then dropped in several small pebbles and proceeded to scrape in sand, from time to time turning around and packing the sand in place with her head while making a loud buzzing sound. When the burrow was nearly full, she added several more stones, pressing each into place. Finally, she dug soil from a small, semicircular hole 3 cm from the entrance, making a shallow quarry or "false burrow", and scraping this soil into the nest entrance. This was packed into place by holding a stone in her mandibles and pounding, finally leaving the stone in place. The wasp then picked up a stick 4 cm long and dragged it over the top of the covered nest entrance, then added a second stick 7 cm long. She completed the closure at 1135 and was not seen again. The nest was dug out two days later and found to contain a single large sphingid larva (*Smerinthus geminatus* Say) bearing an egg on the side of the fourth abdominal segment (Fig. 9, upper figure). The burrow was vertical, 6 cm long, the cell horizontal and 5 cm long.

Thus this species differs from *azteca* in several important features: the soil is carried from the nest on the ground (and the prey doubtless carried on the ground); some of the soil for closure is obtained from a quarry and various objects are placed on top of the closed nest; and the nest is stocked with a single large caterpillar, thus eliminating the possibility of progressive provisioning or of the overlapping of provisioning of successive nests. *A. macra* bears a close resemblance to the well-studied species *procera* Dahlbom, and the behavior is similar to that species, although *procera* more commonly flies with the soil when digging.

Summary. — *Ammophila azteca* differs from other known North American species of its genus in that several nests are maintained simultaneously; in this respect it bears a close resemblance to the European species *pubescens*. Data indicate that at least two and at times probably three or more nests in various stages are maintained at one time, the female remembering the precise location of each and inspecting each nest, or at least most nests, each day before provisioning. The total duration of each nest is six or seven days.

The prey consists of caterpillars and sawfly larva of many diverse

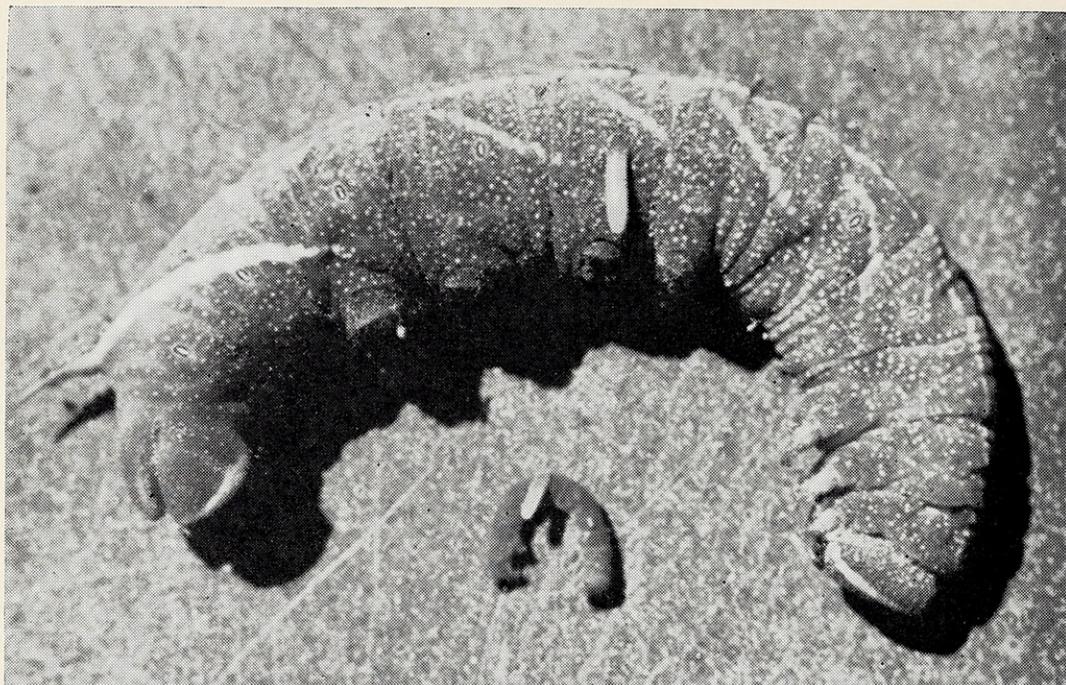


Fig. 9. Above, larva of sphingid bearing the egg of *Ammophila macra*. Below, larva of a geometrid bearing the egg of *A. azteca*. These were extracted from nests in close proximity at Jackson Hole.

groups, all of them diurnal leaf-feeders of about the same size (8 to 18 mm, usually 12 to 16 mm). The egg is laid on the first prey in each nest and shows much variation with respect to the segment on which it is laid. Up to seven prey are provided per nest.

Soil is carried from the burrow in flight, and the prey is carried to the nest in flight.

Initial closure of the nest consists of a single object placed at the top of the burrow. Temporary closures after oviposition consist of a large object blocking the lumen of the burrow on top of which loose soil and smaller objects are packed, with or without "use of a tool". At final closure, a "tool" is apparently always employed.

Fragmentary data suggest the possibility that some females maintain storage burrows, this perhaps being correlated with maintenance of synchronous nests, all at about the same stage, by some females. More data on these and many other points are needed.

Brief observations on one female *A. macra* nesting in the same area revealed several important differences between this species and *azteca*.

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